

Chapter 2

Hydrological Effects on Below Ground Processes in Temperate and Mediterranean Forests

**Boris Rewald, Panagiotis Michopoulos, Lise Dalsgaard,
David L. Jones, and Douglas L. Godbold**

Introduction

Water is a critical factor limiting forest growth, either by absence (Stephenson 1990; Pigott and Pigott 1993) or excess (Kreuzwieser et al. 2004). In most parts of Central Europe, moderate water 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-Hughes and Saunders 2002). In the Mediterranean Basin water strongly limits plant growth and survival (Lloret et al. 2004). This is especially true for some Mediterranean tree genera, which are thought to have evolved before the onset of the present summer-dry climate (Petit et al. 2005). Floods, temporary cover of land by water, occur in most parts of Europe on a regular basis and originate among other things from rivers, mountain torrents and Mediterranean ephemeral water courses (EXCIMAP 2007).

B. Rewald (✉)

Plant Ecology, University of Göttingen, Untere Karspüle 2, 37073 Göttingen, Germany
and

Blaustein Institutes for Desert Research, Ben-Gurion University of the Negev, 84990
Midreshet Ben Gurion, Israel
e-mail: brewald@rootecology.de

P. Michopoulos

Forest Research Institute of Athens, Terma Alkmanos, Athens, 115 28, Greece
e-mail: mipa@fria.gr

L. Dalsgaard

Norwegian Forest and Landscape Institute, Høgskoleveien 8, box 1151431 Ås, Norway
e-mail: Lise.Dalsgaard@skogoglandskap.no

D.L. Jones and D.L. Godbold

Environment Centre Wales, Bangor University, Gwynedd, LL57 2UW, UK
e-mail: d.jones@bangor.ac.uk; d.l.godbold@bangor.ac.uk

There is now convincing evidence that the global climate is changing at an unprecedented rate, putting forest health in jeopardy (Chapter 3, this volume). While total annual precipitation is predicted to be stable in most Northern and Central European regions, model calculations of the future climate predict an increasing frequency and severity of exceptional summer droughts and heatwaves, and floods during winter and spring, thus increasing the risks of both water-logging (Bárdossy and Caspary 1990; Nisbet 2002; Hundsdoerfer and Bárdossy 2005) and drought (Hulme et al. 2002; Kunstmann et al. 2004; Rowell 2005; Frei et al. 2006). In the Mediterranean Basin, a disproportionately strong increase of summer temperature and aridity is predicted under future climates (Iglesias et al. 2000; IPCC 2007). While existing meteorological models still embody considerable uncertainty in predicting future precipitation pattern in detail, especially for mountain regions, changes in the seasonal pattern of precipitation, severer summer droughts and winter flooding will lead to changes in a range of below ground processes. These changes include effects on gas exchange, nutrient mineralization, interactions between trees and mycorrhizal fungi, as well as effects on root growth and physiology. Such changes may potentially alter the distribution and composition of European forest by affecting the water- and nutrient-uptake directly, and indirectly by changing the competitive abilities of tree species to obtain these resources (Kozłowski 1997; Geßler et al. 2007; Rewald and Leuschner 2009b).

In this chapter we discuss the effects of soil water on below ground processes, first briefly describing the spatial heterogeneity of tree roots and soil water, and then discuss the effects of soil water deficit and soil water excess.

Biogenic Causes of Soil Moisture Heterogeneity

In predictions of the effects of changing water availability on below ground processes, soil water availability within a stand is often assumed to be relatively homogeneous. However, it has become increasingly apparent that soil moisture varies greatly within a stand (Göttlein and Manderscheid 1998). These authors could show that variability in the hydraulic properties of soil and tree root distribution causes substantial heterogeneity of soil water tension. Furthermore, the degree of heterogeneity increased at high water tension compared to low water tension. Much of the heterogeneity was due to preferential water flow. Preferential water flow has been shown to be due to factors such as macropore flow (Beven and Germann 1982), fingering (Hillel and Baker 1988) and funnelled flow (Kung 1990). In addition stand structural factors such as tree rooting density (Pärtel and Helm 2007; Lange et al. 2009) and tree canopy effects on throughfall and stemflow will influence the spatial and temporal variability of soil moisture (Staelens et al. 2006; Dalsgaard 2007). This may be due to individual crown interception efficiency in relation to crown structure (Staelens et al. 2006) and to the formation of canopy gaps (Dalsgaard 2007). An example of the influence of canopy gaps on soil moisture is shown in Fig. 2.1. While soil water content was relatively homogenous in January to April, it decreased

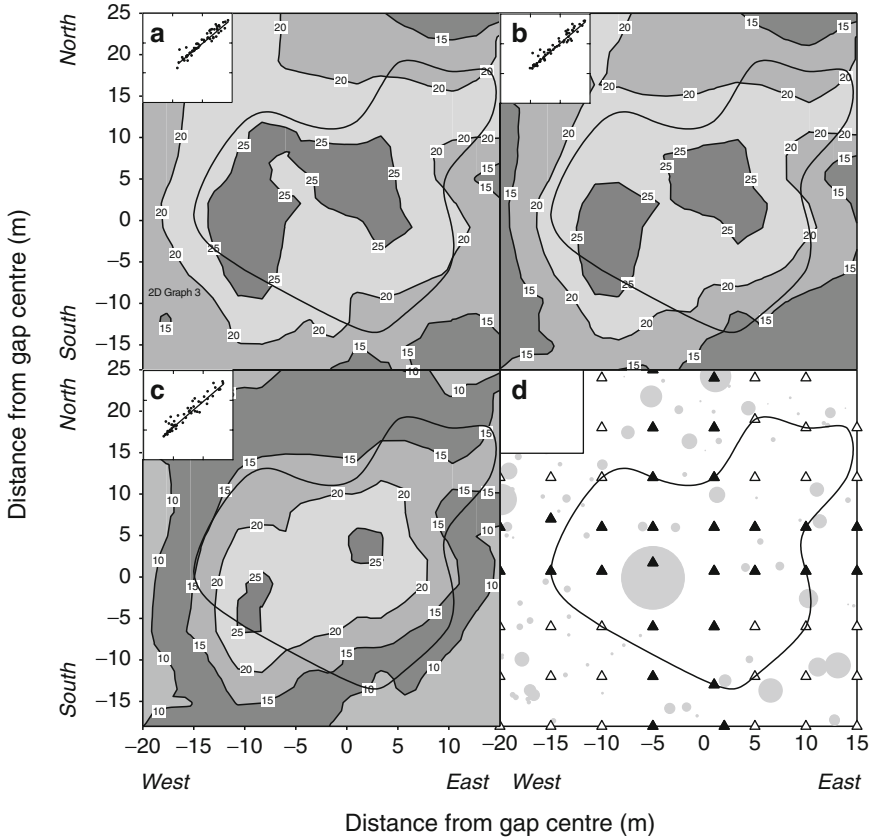


Fig. 2.1 Smoothed values of volumetric soil water content (Θ) at 0–0.5 m depth in and around a canopy gap during the summer of 2000 in a *Fagus sylvatica* forest at Suserup Skov, Denmark. The maps show values for July (**a**), August (**b**) and September (**c**). The Θ values are placed at the boundaries between the different zones of Θ (see Dalsgaard 2007 for details). Field capacity (FC) varied across positions, but there was no significant difference in FC between zones. Panel (**d**) shows the location of trees in and around the gap (gray circles). The size of the circles is scaled from tree diameter. The gap centre is at (0.0) m, a black line indicates the edge of the gap

steadily during spring and summer in two growing seasons to 64% and 68% of field capacity in the closed forest (June–September; $n = 10$, 0–0.9 m depth) but remained high, 90% and 93% of field capacity in gap positions ($n = 10$). Differences were significant (Tukey–Kramer adjusted t-test; $P < 0.05$; Dalsgaard 2007). Throughfall was significantly higher in gaps than in closed forest positions in spring (20%, April–May), summer (30%, June–September) and annually (17%).

Root architecture of structural roots and distribution of fine roots in the soil are of great importance as they determine plant access to water. Fine root density generally shows an exponential decrease with soil depth (Gale and Grigal 1987; Leuschner et al. 2004b), however many species of trees have a structural coarse root

system which penetrates into deeper soil layers, thus enabling access to subsoil resources of water (Köstler et al. 1968; Kozłowski et al. 1991; Jackson et al. 1999; Chapters 7 and 10, this volume). For example, *Quercus* spp. have been found to successfully reduce water 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) and *Fagus* might thus be more susceptible to drought.

The capability of root systems to explore the soil for heterogeneously distributed moisture is crucial for successful water uptake (Cole and Mahall 2006). Although it is known that water uptake of individual 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 (Rewald and Leuschner 2009a), where competitors could potentially pre-empt moist soil patches. In Loblolly pine (*Pinus taeda*), Parker and Van Lear (1996) investigated the effect of soil moisture and heterogeneity on root distribution. Fine root density was higher on xeric and sub-xeric soils than soil with intermediate water contents. However, on all soil types fine root density was ca. 17 times higher in old root channels and ca. four times higher on rock surfaces compared to the bulk soil matrix. Root channels provide not only easier root penetration paths through the soil but were also preferential flow paths for water, as were rock surfaces. Rooting in soil patches with different moisture contents as shown in a study by Parker and Van Lear (1996), can allow 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, possibly facilitate nutrient uptake and buffer plants against water deficits (Richards and Caldwell 1987; Ryel 2004; Pereira et al. 2006; Chapter 4, this volume).

Effects of Soil Water Deficit

Soil

Water deficit causes major changes in the biological, chemical and physical nature of the soil. For example, extreme drought conditions typically induce a dramatic reduction in the amount, structure and activity of the soil microbial community. In general, however, soil microorganisms can survive and persist at much lower soil water potentials than plant roots, particularly as they have the ability to enter a dormant state and survive in very thin water films. Unlike roots, the soil microbial community can also rapidly recover from this inactive state within minutes of rewetting (Jones and Murphy 2007). The impact of drought on soil processes and ecosystem functioning and resilience remains somewhat controversial (Borken and Matzner 2009). Drought tends to reduce mineralization of soil organic matter while

subsequent rewetting can significantly enhance the turnover of carbon (C) and nitrogen (N) in soils (Sardans et al. 2008; Chapter 3, this volume). However, the net balance of greenhouse gas exchange remains unclear as it depends greatly on forest type, soil type and the duration and severity of the drought (Almagro et al. 2009). It is well documented that drought induces lysis of root and microbial cells and that rewetting-induces a flush of nutrients and a stimulation of soil respiration (Inglisma et al. 2009). Originally, it was thought that this enhanced CO₂ evolution and associated loss of soil organic matter would cause a decline in soil quality. Recent evidence, however, suggests that the loss of CO₂ from soil is much less than if the soil had been maintained at an optimal water content for microbial activity (i.e. -0.05 to -0.5 MPa; Borken et al. 2006). The benefit of drought in reducing greenhouse gas emissions has also been seen for N₂O where water deficit turned a Norway spruce forest from a N₂O source to a sink (Goldberg and Gebauer 2009). A similar response has also been observed for CH₄ (Muhr et al. 2008). In a comprehensive review, Borken and Matzner (2009) concluded that organic matter stocks are progressively preserved with increasing duration and intensity of drought periods; however, increased fire risk may ultimately enhance the risk of organic matter losses under dry conditions. Another major issue associated with drought periods is that water deficit induces organic surfaces in soil to become hydrophobic and water repellent (Cerdà et al. 1998). Consequently, upon rewetting, water tends to travel down macropores resulting in hydrological bypass of the soil's upper horizons, resulting e.g., in losses of nitrate contained in rain and snow-melt water (Schleppi et al. 2004). Alternatively, the hydrophobic organic horizons can prevent infiltration inducing surface runoff and erosion (Doerr et al. 2009). This hydrophobicity also tends to reduce soil organic matter cycling and can reduce potential leaching losses due to bypass flow (Hentschel et al. 2007).

Mycorrhizal Fungi

Mycorrhizas are among the most widespread associations between microorganisms and higher plants, and provide a range of benefits to forest trees of which the best demonstrated is an increased nutrient acquisition, but they also may be beneficial for water uptake and protection against pathogens. The extensive extramatrical or extraradical mycelium formed by ectomycorrhiza and arbuscular mycorrhiza, respectively, is thought to play a primary role in promoting nutrient acquisition (especially P; Smith and Read 2008). Both arbuscular- and ectomycorrhizas form associations with forest tree species, and both are more pronounced in infertile soils. Ectomycorrhizas are more common on moist soils with a high organic matter content, whereas trees infected with arbuscular mycorrhizas tend to be growing on more mineral soils (Smith and Read 2008). The degree of colonisation by mycorrhizas is often influenced by the availability of N and P in the soil. Paul and Clark (1996) argue that the total nutrient pool in soils is of no importance and it is the low concentration of a nutrient such as P in the aqueous phase that promotes the infection.

Mycorrhizas have the potential to affect tree water relations both through direct uptake of water and via nutritional factors. Considerable uncertainty exists about the influence of mycorrhizas on host hydraulics and water uptake (Hampp and Schaeffer 1999; Nardini et al. 2000), but also on the response 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 to the host plants (Duddridge et al. 1980; MacFall et al. 1991; Augé 2001), and to support acclimation to drought stress (Davies et al. 1996; George and Marschner 1996). However the benefits to the host tree may be species-specific. Steudle and Heydt (1997) found only a marginal influence of mycorrhization on water uptake of *Fagus sylvatica* saplings, however *Quercus* spp. showed a strong decline in transpired water after the extramatrical hyphae net of the mycorrhiza had been severed (Egerton-Warburton et al. 2003). Furthermore, the extramatrical 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. These benefits could include enhanced water and nutrient uptake and/or redistribution (Leake et al. 2004), a rapid recovery from desiccation, or refilling of embolized vessels. However, it remains an open question if similar mechanisms exist in other tree species, and if the quantities of redistributed water account for significant reduction of water stress.

Drought reduces both nutrient uptake by roots and transport from the roots to shoots, due to decreased transpiration rates and impaired active transport and membrane permeability (Alam 1999). The decline in soil moisture also results in a decrease in the diffusion rate of nutrients in the soil to the absorbing root surface (Raynaud and Leadley 2004). P is a nutrient the uptake of which is mostly affected by low soil moisture (Marschner 1997). Under conditions of reduced P mobility, the extensive hyphal network and increased P mobilisation through exudates from the hyphae and plant roots help to maintain P acquisition (Liebersbach et al. 2004). Another beneficial effect of the mycorrhizal association in dry conditions is the increased uptake of potassium (K) by trees especially in the seedling stage. K increases the drought resistance of plants through its function in stomatal regulation and osmoregulation (Marschner 1997). Maintenance of water balance at low soil water potentials is critical for maintenance of a positive carbon balance. In Mediterranean countries, where summers are dry, mycorrhizas help seedling survival among plants considered resistant to drought. Domínguez Núñez et al. (2006) used seedlings of *Quercus ilex* and *Quercus faginea* inoculated with the mycorrhizal fungus *Tuber melanosporum* to establish a stand in south-eastern Spain. These authors could show that mycorrhizal inoculation improved seedling growth and increased water and P uptake during summer drought.

Despite the beneficial effect of the mycorrhizal association on forest plants during drought periods, the development of the mycorrhizal association is affected by low soil moisture content. Valdéz et al. (2006) observed that drought years reduced biomass of both fine and ectomycorrhizal roots of *Pinus oaxacana* by almost 60%. In the field, Bell and Adams (2004) found that the number of root tips of *Pinus pinaster* and *Pinus radiata* associated with the fungus *Rhizopogon* was

reduced in areas of low rainfall amounts (<380 mm). It seems that extreme moisture deficit affects mycorrhizas to such extent that below a certain moisture percentage mycorrhizal plants are equally affected as nonmycorrhizal ones. Similarly, in *Pinus pinaster*, Bakker et al. (2006) demonstrated an increase in long-distance exploration types of ectomycorrhizas (*Rhizopogon* and *Scleroderma* spp.) on drier sites and an increase in contact exploration types on wetter sites. In both the work of Bell and Adams (2004), and Bakker et al. (2006) soil organic matter was a co-variant, with the wetter sites having higher organic matter contents. In a growth chamber experiment, Kennedy and Peay (2007) found that *Pinus muricata* plants infected by the ectomycorrhizal fungus *Rhizopogon* had similar biomass, photosynthesis, conductance and total leaf biomass as non-mycorrhizal plants. However, all these parameters increased significantly in the mycorrhizal plants when soil moisture increased and reached a percentage of 13. This work emphasises that mycorrhizas may not be beneficial to plants at very low soil water contents.

Although mechanisms of improved drought tolerance by mycorrhization have been postulated, the effect of water stress on mycorrhizal community diversity is only poorly understood. Kernaghan (2005) reviewed the environmental factors influencing the mycorrhizal fungal communities. He argued that the most important factor is the structure of the associated plant communities through the variety of root exudates. It is probable that drought indirectly affects mycorrhizal diversity by selection of the most drought resistant plants.

Fine Roots

The root:shoot ratio is an important means of adjustment to altered soil moisture levels (Osunubi and Davies 1981; Chapter 4, this volume). Alteration of this ratio can be achieved by long term developmental changes in allocation, or through short term responses to changes in a specific environmental variable. It has been well documented that tree species adapted to more xeric conditions have higher root:shoot ratios (Joslin et al. 2000), thus increasing the ratio between water absorbing and transpiring surface. However, results for both seedlings and mature trees grown under different soil moisture regimes are contradictory (e.g. Thomas 2000; Pronk et al. 2002; Meier and Leuschner 2008a, b). Changes in root:shoot ratio are often achieved by alteration of fine root biomass. The direction of change, i.e. increase or decrease, and magnitude of root biomass response to drought largely depends on tree species or variety, but also on study duration and/or study design (e.g., light regime; Climent et al. 2006; Manes et al. 2006). However, two general trends can be noticed: (i) an increase of root biomass in response to drought have mostly been found in conifer species (e.g., Gower et al. 1992; Parker and Van Lear 1996), which are known to differ in their root growth strategies from deciduous broad-leaved trees (Bauhus and Messier 1999), and (ii) a decrease of root biomass in European deciduous tree species (e.g., Fort et al. 1998; Chiatante et al. 2006).

Table 2.1 Case study within two unmanaged forest patches stocked with 200 years-old *Quercus petraea* trees (see Rewald 2008 for details). Root density (RD_{org.}) and proline concentration of fine roots in the organic layer after 3-month (June–August 2004) of two different soil moisture treatments (Control and Reduced soil moisture). Specific conductivity (k_s) and degree of embolism of fine roots (diameter $d = 0.7\text{--}2\text{ mm}$) and coarse roots ($d = 2\text{--}6\text{ mm}$) after three subsequent summers differing in water availability (June–August, 2004–2006). Significant differences are indicated by different letters (RD_{org.} and proline: Scheffé test, $P < 0.05$; k_s and embolism: Kruskal–Wallis H test, $P < 0.05$; mean \pm SE; n = sample size; n.d. = no data)

	n	RD _{org.} [g d.wt l ⁻¹]	n	Proline [mmol g d.wt ⁻¹]	n	k_s [10 ⁻³ m ² MPa ⁻¹ s ⁻¹]	Degree of embolism [%]
<i>Control</i>							
Fine roots	20	6.5 \pm 0.1 a	10	10.4 \pm 3.3 a	9	1.2 \pm 0.3 a	20.8 \pm 6.7 ab
Coarse roots	–	n.d.	–	n.d.	15	3.0 \pm 1.7 ac	10.5 \pm 5.3 b
<i>Reduced soil moisture^a</i>							
Fine roots	20	2.3 \pm 0.1 b	10	93.0 \pm 29.4 b	11	2.5 \pm 0.8 b	36.7 \pm 9.3 ac
Coarse roots	–	n.d.	–	n.d.	10	10.0 \pm 3.1 c	46.3 \pm 10.9 c

^a A sub-canopy roof (11 m \times 11 m \times 2 m) was used to reduce soil moisture during summer months (June–August), resulting in a soil moisture reduction of 5–15 vol% compared to ambient-watered control.

Change in root biomass is highly species-specific and connected to altered root turnover rates. Although data on changes in root turnover rates under soil drought are scarce, both unaltered (Joslin et al. 2000) and increased (Pietikäinen et al. 1999; Chiatante et al. 2006) turnover rates have been found in Mediterranean and temperate forests. For example, the fine root biomass in the organic layer (0.5–6 cm thick) of an unmanaged mature *Quercus petraea* stand (Unterlüß, Lower Saxony, Germany; 52°83'N, 10°26'E; stem density: 44 ha⁻¹, tree height: 28 m, stem basal area: 12.3 m² ha⁻¹) was significantly reduced after three months of experimentally-induced summer drought (Table 2.1). In contrast, more drought sensitive tree species like *Fagus sylvatica* and *Quercus robur* were found to retain their root biomass in the upper soil horizons even under severe drought, resulting in high turnover rates (Konôpka et al. 2005; Mainiero and Kazda 2006). It is possible that a less flexible carbon-investment strategy during drought and the subsequently increased fine root turnover are partly involved in a higher drought sensitivity of tree species.

Change in fine root morphology is another potential adaptation to altered soil moisture. However, the detection of adaptation 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). The finest (first order) roots are most important parts of the root system for water uptake (Rieger and Litvin 1999; Lindenmair et al. 2004; Rewald et al. 2010). Thus, specific root area (SRA) and length (SRL) could be expected to increase during drought. In contrast to this assumption, both the SRA and the SRL of *Betula pendula*, *Fagus sylvatica* and other tree species decreased under reduced water availability (Aspelmeier and Leuschner 2006; Ostonen et al. 2007; Meier and Leuschner 2008b).

The underlying mechanisms must remain speculative, but may include increased mortality/shedding of root tips and finest roots, stimulated ethylene production resulting in larger root diameter, (re-) growth of less ramified roots by increased turnover rates and higher soil mechanical impedance, and increased root tissue densities (Clark et al. 2003; Manes et al. 2006; Trubat et al. 2006).

Root elongation rate, which is positively correlated with root diameter, could be a more important attribute for maximizing uptake rates of low-diffusive nutrients such as P than root surface area (Silberbush and Barber 1983; Raven and Edwards 2001). In order to exploit 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. Furthermore, roots of larger diameter, and consequently a lower SRA:SRL ratio have lower construction and maintenance costs per unit biomass than thinner 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. However, rates of water uptake per root surface area have been found to vary significantly between individual root branches and species (Korn 2004; Burk 2006). For example, *Fagus sylvatica* has been found to possess higher root-surface-area related sap-flow rates than *Quercus petraea* (Coners and Leuschner 2002). Furthermore, even under well-watered conditions, *Fagus sylvatica* roots showed higher root surface-specific flows on a site with a more continental climate than on a more oceanic site (Burk 2006), indicating a yet unknown, but highly plastic uptake pattern on drier sites. Unfortunately, no information is available about such plasticity in uptake kinetics for other tree species.

Physiological Adaptation of Roots

The capacity of roots for water uptake is determined not only by root surface area and foraging, but by the resistance of tissues to water transport as well. Drought is 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 drought stress (Yamada et al. 1997). Although data for woody plants is scarce, studies on herbaceous plants suggest that aquaporins are present in virtually all root types (Kirch et al. 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 water-stressed olive trees, explaining in part the above-average

drought-tolerance of this species (Lovisolo et al. 2007; Secchi et al. 2007). However, knowledge of drought-induced adaptations in root physiology, resulting in altered water uptake rates, is still rare for most European tree species.

Osmotic adjustment is another mechanism, allowing plants to tolerate periods of drought (Chaves et al. 2003; Aranda et al. 2004; Chapter 3, this volume). 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 of this osmoregulation; its concentrations have been found to increase strongly in response to drought stress in roots of mature *Fagus sylvatica* and *Quercus petraea* trees (Table 2.1; Rewald 2008) and has been suggested to explain differences in drought-tolerance (Hare et al. 1998; Ennajeh et al. 2006; Garcia-Sánchez et al. 2007). Drought 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 stress might therefore correlate better with general stress-tolerance (Schreiber et al. 2005), instead of explaining different water uptake rates (Leuschner et al. 2003).

Changes in Root Axial Conductivity and Hydraulic Safety Under Drought

Different species or even genotypes of woody plants may differ substantially with respect to root axial conductivity (e.g., Huber 1956; Larcher 2001). A majority of previous studies has reported reduced root conductivities in response to stress (e.g., Machado and Tyree 1994; Nardini and Pitt 1999; Trubat et al. 2006), thereby improving plant water status by reducing water loss to the atmosphere and the soil (Meinzer et al. 1996; Trillo and Fernández 2005). In contrast, the rarely observed increase of root axial conductivity (Table 2.1) is suggested to facilitate water uptake by reducing the flow resistance (Nardini and Pitt 1999). Although axial conductivity has previously been considered a minor limiting factor of whole-root conductivity as compared to radial conductivity (e.g., Steudle 1994), Hacke et al. (2000) demonstrated that whole-plant water use and axial conductivity of woody plants during water stress were in accordance. Especially the large root systems of mature trees with greater path lengths (West et al. 1999; 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. Increased root conductivities could be a particularly effective adaptation in plants that respond to drought with a reduction of fine root biomass.

Another plastic 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 soils (Göttlein and Manderscheid 1998). 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; Chapter 4, this volume). 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.

While some embolism may occur even in roots of well-watered plants (Alder et al. 1996; Domec et al. 2004; Table 2.1), fine roots have been suggested to be weak, replaceable segments of the soil-plant-atmosphere continuum (SPAC; Sperry and Saliendra 1994; Domec et al. 2004; Chapter 3, this volume), 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 (Sperry and Ikeda 1997; Hacke et al. 2000). ‘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 (Vera-Estrella et al. 2004; Schreiber et al. 2005). Because there is now convincing evidence that embolism is reversible in many cases (Pickard 1989; Zwieniecki and Holbrook 1998; Lovisolo and Schubert 2006), cavitation is suggested to be another, possibly reversible, ‘hydraulic fuse’ mechanism in roots (Rewald 2008). Thus, the recently found increased vulnerability to cavitation in drought-stressed *Quercus petraea* roots (Rewald 2008) seems to be a straightforward adaption to drought rather than impairment by drought.

Effects of Excess Soil Water

Soil

In comparison to water deficit, the effects of excess soil water on below ground soil processes are relatively well understood (Richardson and Vepraskas 2000). Briefly, saturation of soil with water (waterlogging) for prolonged periods of time generates a negative impact on nearly all forests that are not adapted to hydromorphic or riparian soil conditions (White 2007). The incidence of periodic waterlogging is predicted to increase in European forests due to increases in the frequency and intensity of winter rainfall events (Fuhrer et al. 2006). The resultant changes in nutrient cycling induced by waterlogging may have profound consequences on forest development with some species more resilient to flooding (e.g., oak) than others (e.g., beech; Gebler et al. 2007). In Mediterranean woodlands, precipitation can be very abundant during the wet season, inducing temporary waterlogging. When the soil becomes saturated the rate of O₂ diffusion into the soil is greatly reduced leading to rapid depletion of soil O₂ and an inducement of hypoxic and anoxic conditions. These conditions reduce seed germination, root growth, soil microbial activity and may promote the attack of trees by pathogenic soil organisms (Burgess et al. 1999;

Gómez-Aparicio et al. 2008; Pérez-Ramos and Marañón 2009). Prolonged waterlogging tends to lead to a reduction in microbial activity, an increase in soil organic matter and greater emissions of N_2O and CH_4 (Pinay et al. 2000; Eglin et al. 2008). Flooding may also stimulate the input and redistribution of soil particles which can strongly influence C storage and greenhouse gas emissions (Pinay et al. 2000). To some extent this is driven by a reduced microbial biomass and changes in its community structure (i.e. reduction of aerobic bacteria, Gram-negative and Gram-positive bacteria, mycorrhizal fungi and mesofauna) and an inhibition of O_2 -requiring enzymes which are central to the breakdown of forest litter (e.g., phenol oxidase; Langer and Rinklebe 2009; Unger et al. 2009). One study indicates that while CO_2 emissions from soil decline in flooded conditions, this is more than offset by the concomitant increase in N_2O and CH_4 making some wetland forests greater net emitters of greenhouse gases (GHG) than non-flooded ones (Yu et al. 2008). However, the overall response of soil flooding on GHG emission is likely to be highly dependent on a range of factors (e.g., geographical location, topography, climatic regime, catchment size, land use and management) making generalisations across landscapes difficult. In some regions of Europe deliberate flooding of organic soils is now occurring in an attempt to try and preserve soil organic matter stocks whose loss has been stimulated by historical drainage and oxygenation. Whilst this management approach appears to reduce CO_2 emissions and losses of dissolved organic carbon, it may stimulate emissions of N_2O and CH_4 and may reduce forest growth and therefore above and below ground C storage (Silvan et al. 2002).

Mycorrhizal Fungi

In *Pterocarpus officinalis*, Fougnyes et al. (2007) found that arbuscular mycorrhizas contributed to flood tolerance and P acquisition. In contrast, Ray and Inouye (2006) found that the development of arbuscular fungus associated with *Typha latifolia* was adversely affected by flooding. Stenström (1991) could show that species of ectomycorrhizas vary greatly in tolerance to waterlogging. Based on the formation of ectomycorrhizas with *Pinus sylvestris*, the fungi *Thelephora terrestris*, *Laccaria laccata*, and *Hebeloma crustuliniforme* were not sensitive to flooding, whereas *Suillus flavidus* and *S. bovinus* were highly sensitive. It is highly probable that fungal species and periodicity of flooding play a crucial role in the final mycorrhizal distribution in forest soils.

Fine Roots

In soils with permanent or seasonal waterlogging, hypoxic conditions prevent deep rooting (Glenz et al. 2006) by inhibiting root exploration of those soils layers (Chapter 4, this volume). This may be due to both physical factors such as water

preventing gas diffusion in soil pores and chemical factors such as high levels of reduced iron. In *Picea sitchensis*, the thickness of the root plate was lower in stago-orthic gleys than humic stagno-orthic gleys (Ray and Nicoll 1998), and decreased individual tree stability. Bakker et al. (2006) showed that in *Pinus pinaster* growing on a humid and dry site, root distribution was significantly shallower and root diameter increased more with depth at the humid site. This was suggested to be due to more adverse soil conditions such as the presence of a hardpan, higher amounts of aluminium oxides and/or anoxia at depth. Similarly, Xu et al. (1997) showed that seasonal waterlogging of subsoils restricted the growth of fine roots of *Picea abies* and *Abies grandis*, but this influence was greater in *Picea abies* than *Abies grandis*. During the water logging period, in *Abies grandis*, the dead fine root biomass was greater than the live fine root biomass, but the fine root biomass increased by 50% during the non-waterlogged period. Figure 2.2 shows the effect of a high soil water table on the fine root distribution of *Picea abies* growing at three sites in the Krkonoše mountains, Czech Republic. At the mesic Modrý Důl and Alžbětinka

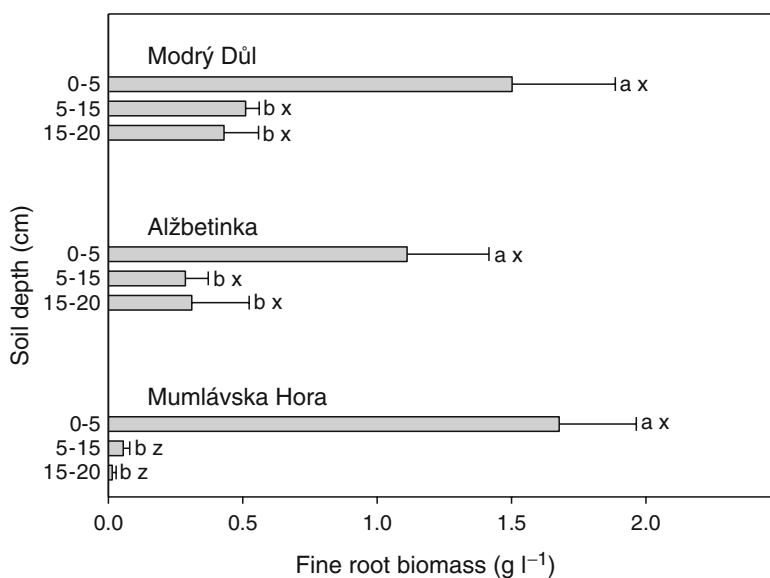


Fig. 2.2 Vertical distribution of fine roots of *Picea abies* at three sites with a different degree of forest decline in the Krkonoše mountains, Czech Republic. The damage to the forest cover in Modrý Důl, Alžbětinka and Mumlávská Hora were classified according to the Czech Forest Authority as second, third and fourth degree respectively. The three sites are relatively homogeneous in soil parent material (granite and gneiss), elevation (1,190–1,220 m a.s.l.), average annual precipitation (1,390–1,500 mm year⁻¹) and temperature (2.5–3.8°C). The original forest cover consist of plantations of Norway spruce approximately 130 years old in Modrý Důl, older (210 and 190 years) in Alžbětinka and Mumlávská Hora. The sites differ in the geomorphic position, Modrý Důl and Alžbětinka are located at mid slope, while Mumlávská Hora is on a summit. Within a site, bars not followed by the same indices (a, b) vary significantly between soil depths. Within a soil depth, bars not followed by the same indices (x, z) vary significantly between sites (Two-way ANOVA on log transformed data, Holms-Sidik corrected, $P < 0.05$; mean + SE)

sites fine roots are found to a depth of 20 cm. In contrast at the Mumlávska Hora site which is subject to regular waterlogging, the fine roots are restricted mostly to the upper 5 cm of soil.

In sensitive tree species (e.g., *Picea sitchensis*), waterlogging results in death and dieback of fine root tips (Nicoll and Coutts 1998). However, the timing of fine root growth and dormancy influences the degree to which the roots are affected. Provenances of *Picea sitchensis* with earlier root dormancy were less sensitive to autumn waterlogging than late-dormant provenances. This has also been shown in floodplain tree species where root growth of *Quercus pagodaefolia*, which has early season root growth, was more sensitive to spring floods than *Quercus lyrata* which had delayed root growth (Burke and Chambers 2003).

On soils with a permanently high water table even deep rooting species develop shallower rooting systems (Burke and Chambers 2003). The effect on rooting varies between species depending upon tolerance to water-logging (Kozłowski 1984), but even tolerant trees tend to have shallower root systems (Lehnardt and Brechtel 1980) in permanently wet soils. In heterogeneously waterlogged soils, root biomass of more flooding tolerant species (e.g., *Fraxinus pennsylvanica*) decreased, but biomass of the less tolerant *Liquidambar styraciflua* was not affected. These species-specific differences illustrate that a response of root biomass is related to a complex interplay of root proliferation, altered uptake kinetic, and nutrient diffusion rate (Neatrour et al. 2007).

However, the rooting pattern can change rapidly due to death of roots after prolonged inundation (Polomski and Kuhn 1998). Further, these authors have suggested in *Salix* spp., *Populus canadensis* and *Alnus glutinosa* that the dieback of the root system due to flooding led to promotion of renewal of the fine root system. However, under non-waterlogged conditions these tree species also tend to have high rates of root turnover (Lukac et al. 2003; Ostonen 2003), which may be a reflection of high plasticity of the fine root system to deal with large fluctuations in environmental conditions. Again similar relationships have been shown in floodplain forests. Burke and Chambers (2003) could show that in *Quercus laurifolia* habitat with a shallow root zone and episodes of flooding and drought greater changes in root structure and physiology occurred than in *Nyssa sylvatica* habitat that had a deeper rooting zone and a more consistently moist to flooded hydroperiod.

The most frequently reported reactions of tree root systems to waterlogging, and hence hypoxia, are increased formation of lenticels (Coutts 1982; Angeles et al. 1986), followed by the differentiation of adventitious and flood-adapted roots (Topa and McLeod 1986; Colin-Belgrand et al. 1991). These adaptations have been described for a broad range of temperate tree species (compare Kozłowski 1997). Adventitious roots are produced on the original root system and on the submerged portions of stems and have been found to have larger SRA and more intercellular space (aerenchyma) than roots growing in well-aerated soils (*Nyssa sylvatica* var. *biflora*; Hook et al. 1971). They are thought to increase water absorption (Hook and Scholtens 1978; Tsukahara and Kozłowski 1985; Herrera et al. 2008), oxidizing the rhizosphere and venting soil-bound

ethylene and CO₂ (Hook and Brown 1973; Drew 1997; Colmer 2003). Under waterlogged conditions, Havens (1997) found a 30% higher soil redox-potential within the rhizosphere of *Fraxinus pennsylvanica* seedlings than in non-rhizosphere soil areas.

Physiological Adaptation of Roots

As stated above, drought is thought to facilitate suberization of the root rhizodermis. Under waterlogging, an increased suberization of the rhizodermis is thought to reduce the radial loss of oxygen in herbaceous species (Enstone et al. 2003). Unfortunately, no studies on suberization of the roots of European tree species under waterlogging are known to these authors. However, it was shown that water logging results in an increased osmotic permeability and a decreased solute reflection coefficient of *Larix laricina* and *Picea glauca* (Reece and Riha 1991). A decrease of membrane permeability and subsequently a decrease of root conductivity (i.e. sum of radial and axial hydraulic conductivity) was measured on waterlogged *Fagus sylvatica* and *Quercus* spp. seedlings (Schmull and Thomas 2000). Decreases in the hydraulic conductance of the root system due to hypoxic conditions, as one would expect to find during flooding, have previously been measured in different *Populus* species (Harrington 1987; Smit and Stachowiak 1988).

In *Fagus sylvatica* and *Quercus petraea* seedlings, nitrate reductase activity of the roots was found to be increased under hypoxic conditions (Schmull and Thomas 2000). Nitrate reduction can act as a sink for protons, thus helping to avoid damaging cytoplasmic acidosis (Fan et al. 1997). Armstrong et al. (1994) summarized that survival of flooding by woody plants depends on more than one of the following metabolic adaptations: (1) control of energy metabolism, (2) availability of energy resources, (3) provision of essential gene products and synthesis of macromolecules, and (4) protection against post-hypoxic injury. See Drew (1997) and Kreuzwieser et al. (2002, 2004) for extensive reviews about metabolic adaptations of roots and whole trees to flooding. Decreased xylem sap osmotic potentials due to waterlogging (e.g., in *Quercus petraea* seedlings, Folzer et al. 2006) are not considered to be adaptive mechanisms but have been attributed to enriched solutes provided by degenerating roots, a reduction in root water absorption (Jackson et al. 1996) or decreased membrane selectivity (Barrett-Lennard 2003; Kolb et al. 2004).

Studies about the influence of flooding on root hydraulics properties of European tree species are virtually lacking. However, in a study on *Picea sitchensis* and *Pinus contorta* seedlings, xylem growth in woody roots was found to be ceased in the centre of the water-logged area and highly reduced in non-flooded parts of root system (Coutts 1982). Thus, when the flood water drains away, the previously flooded plants may be more drought-sensitive as their smaller and less conductive root systems cannot adequately replenish transpirational losses (Kozłowski 1997; Chapter 8, this volume).

Conclusion and Outlook

The climate is changing, which may affect forest health and composition by increasing flood and drought events. Although, below ground traits are likely to play significant roles as adaptation mechanisms of current European forest communities, the current state of knowledge of the reaction of soils, tree roots and their symbiotic fungi to changing soil water status is poor. Where controlled drainage and flooding are undertaken there is also an urgent need to translate research findings into policy and practice to prevent negative impacts of forest management (see Part II). In addition to the traditional research on root biomass and root:shoot ratio, the variability and plasticity of physiological and anatomical root traits in heterogeneous soil environments as well as interactions with mycorrhizas should be considered in future studies. Furthermore, to predict the development of European forest under a future warmer climate there is an urgent need to evaluate the outcome of below and above ground competition and subsequently seedling establishment in forest communities under changed environmental conditions. Under increasing drought conditions heterogeneity of soil moisture is likely to increase, but will be strongly linked to changes in canopy structure (Chapter 3, this volume) and the wetting characteristics of the forest floor, thus introducing both positive and negative ecological feed-back mechanisms. In addition, increased spatial heterogeneity may change the outcome of competition between tree species, benefiting tree species with a greater plasticity and precision of root development rather than physiological adaptation per se. Much of the current knowledge is derived from single species growing in homogeneous environments. This knowledge base is insufficient to make meaningful predictions of the effects of changes of soil water status on forests and forest processes.

References

- Addington RN, Donovan LA, Mitchell RJ, Vose JM, Pecot SD, Jack SB, Hacke UG, Sperry JS, Oren R (2006) Adjustments in hydraulic architecture of *Pinus palustris* maintain similar stomatal conductance in xeric and mesic habitats. *Plant Cell Environ* 29:535–545
- Alam SM (1999) Nutrient uptake by plants under stress conditions. In: Pessarakis M (ed) *Handbook of plant and crop stress*. Marcel Dekker, New York, pp 285–314
- Alder NN, Sperry JS, Pockman WT (1996) Root and stem xylem embolism, stomatal conductance, and leaf turgor in *Acer grandidentatum* populations along a soil moisture gradient. *Oecologia* 105:293–301
- Almagro M, López J, Querejeta JJ, Martínez-Mena M (2009) Temperature dependence of soil CO₂ efflux is strongly modulated by seasonal patterns of moisture availability in a Mediterranean ecosystem. *Soil Biol Biochem* 41:594–605
- Angeles G, Evert RF, Kozlowski TT (1986) Development of lenticels and adventitious roots in flooded *Ulmus americana* seedlings. *Can J For Res* 16:585–590
- Aranda I, Gil L, Pardos JA (2004) Osmotic adjustment in two temperate oak species [*Quercus pyrenaica* WILLD. and *Quercus petraea* (MATT.) LIEBL.] of the Iberian Peninsula in response to drought. *Invest Agrarior: Sist Recur Forestales* 13:339–245

- Armstrong W, Braendle R, Jackson MB (1994) Mechanisms of flood tolerance in plants. *Acta Bot Neerl* 43:307–358
- Aspelmeier S, Leuschner C (2006) Genotypic variation in drought response of Silver birch (*Betula pendula* Roth.): leaf and root morphology and carbon partitioning. *Trees* 20:42–52
- Augé RM (2001) Water relations, drought and vesicular-arbuscular mycorrhizal symbiosis. *Mycorrhiza* 11:3–42
- Backes K, Leuschner C (2000) Leaf water relations of competitive *Fagus sylvatica* and *Quercus petraea* trees during 4 years differing in soil drought. *Can J For Res* 30:335–346
- Badot PM, Lucot E, Bruckert S (1994) Soil-moisture in deep levels is the main source of mid-day water potential variations in oak (*Quercus sp.*). *C R Acad Sci III-Vie* 317:341–345
- Bakker MR, Augusto L, Achat DL (2006) Fine root distribution of trees and understory in mature stands of maritime pine (*Pinus pinaster*) on dry and humid sites. *Plant Soil* 286:37–51
- Bárdossy A, Caspari HJ (1990) Detection of climate change in Europe by analyzing European atmospheric circulation patterns from 1881 to 1989. *Theor Appl Climatol* 42:155–167
- Barrett-Lennard EG (2003) The interaction between waterlogging and salinity in higher plants: causes, consequences and implications. *Plant Soil* 253:35–54
- Bauhus J, Messier C (1999) Soil exploitation strategies of fine roots in different tree species of the southern boreal forest of eastern Canada. *Can J For Res* 29:260–273
- Bell TL, Adams MA (2004) Ecophysiology of ectomycorrhizal fungi associated with *Pinus* spp. in low rainfall areas of Western Australia. *Plant Ecol* 171:35–52
- Beven KJ, Germann P (1982) Macropores and water-flow in soils. *Water Resour Res* 18:1311–1325
- Borken W, Savage K, Davidson EA, Trumbore SE (2006) Effects of experimental drought on soil respiration and radiocarbon efflux from a temperate forest soil. *Global Change Biol* 12:177–193
- Borken W, Matzner E (2009) Reappraisal of drying and wetting effects on C and N mineralization and fluxes in soils. *Global Change Biol* 15:808–824
- Bréda N, Granier A, Barataud F, Moyne C (1995) Soil-water dynamics in an oak stand. 1. Soil-moisture, water potentials and water-uptake by roots. *Plant Soil* 172:17–27
- Burgess SSO, Adams MA, Turner NC, Ong CK (1998) The redistribution of soil water by tree root systems. *Oecologia* 115:306–311
- Burgess T, McComb JA, Colquhoun I, Hardy GES (1999) Increased susceptibility of *Eucalyptus marginata* to stem infection by *Phytophthora cinnamomi* resulting from root hypoxia. *Plant Pathol* 48:797–806
- Burk D (2006) Physiological, anatomical and chemical aspects of the regulation of water uptake by beech, pine and birch roots in two different water-supplying locations (In German). Ph.D. thesis, University of Göttingen, Germany. (<http://webdoc.sub.gwdg.de/diss/2006/burk>)
- Burke MK, Chambers J (2003) Root dynamics in bottomland hardwood forests of the southeastern United States coastal plain. *Plant Soil* 250:141–153
- Caldwell MM, Dawson TE, Richards JH (1998) Hydraulic lift: consequences of water efflux from the roots of plants. *Oecologia* 113:151–161
- Cerdà A, Schnabel S, Ceballos A, Gomez-Amelia D (1998) Soil hydrological response under simulated rainfall in the Dehesa land system (Extremadura, SW Spain) under drought conditions. *Earth Surf Proc Land* 23:195–209
- Čermák J, Huzulák J, Penka M (1980) Water potential and sap flow-rate in adult trees with moist and dry soil as used for the assessment of root-system depth. *Biol Plantarum* 22:34–41
- Chaves MM, Maroco JP, Pereira JS (2003) Understanding plant responses to drought – from genes to the whole plant. *Funct Plant Biol* 30:239–264
- Chiatante D, Di Iorio A, Sciandra S, Scippa GS, Mazzoleni S (2006) Effect of drought and fire on root development in *Quercus pubescens* Willd. and *Fraxinus ornus* L. seedlings. *Environ Exp Bot* 56:190–197
- Chung HH, Kramer PJ (1975) Absorption of water and ^{32}P through suberized and unsuberized roots of Loblolly pine. *Can J For Res* 5:229–235
- Clark LJ, Whalley WR, Barraclough PB (2003) How do roots penetrate strong soil? *Plant Soil* 255:93–104

- Climment JM, Aranda I, Alonso J, Pardos JA, Gil L (2006) Developmental constraints limit the response of Canary Island pine seedlings to combined shade and drought. *For Ecol Manage* 231:164–168
- Cole ES, Mahall BE (2006) A test for hydrotropic behavior by roots of two coastal dune shrubs. *New Phytol* 172:358–368
- Colmer TD (2003) Long-distance transport of gases in plants: a perspective on internal aeration and radial oxygen loss from roots. *Plant Cell Environ* 26:17–36
- Colin-Belgrand M, Dreyer E, Biron P (1991) Sensitivity of seedlings from different oak species to waterlogging – effects on root-growth and mineral-nutrition. *Ann For Sci* 48:193–204
- Coners H, Leuschner C (2002) *In situ* water absorption by tree fine roots measured in real time using miniature sap-flow gauges. *Funct Ecol* 16:696–703
- Coners H, Leuschner C (2005) *In situ* measurement of fine root water absorption in three temperate tree species - Temporal variability and control by soil and atmospheric factors. *Basic Appl Ecol* 6:395–405
- Coutts MP (1982) The tolerance of tree roots to waterlogging. V. Growth of woody roots of Sitka spruce and Lodgepole pine in waterlogged soil. *New Phytol* 90:467–476
- Czajkowski T, Kuhling M, Bolte A (2005) Impact of the 2003 summer drought on growth of beech sapling natural regeneration (*Fagus sylvatica* L.) in north-eastern Central Europe. *Ger J For Res* 176:133–143
- Dalsgaard L (2007) Above and below ground gaps – the effects of a small canopy opening on throughfall, soil moisture and tree transpiration in Suserup Skov, Denmark. *Ecol Bull* 52:81–102
- Davies Jr. FT, Svensen SE, Cole JC, Phavaphutanon L, Duray SA, Olalde-Portugal V, Meier CE, Bo SH (1996) Non-nutritional stress acclimation of mycorrhizal woody plants exposed to drought. *Tree Physiol* 16:985–993
- Doerr SH, Woods SW, Martin DA, Casimiro M (2009) Natural background' soil water repellency in conifer forests of the north-western USA: its prediction and relationship to wildfire occurrence. *J Hydrol* 371:12–21
- Domec JC, Warren JM, Meinzer FC, Brooks JR, Coulombe R (2004) Native root xylem embolism and stomatal closure in stands of Douglas fir and Ponderosa pine: mitigation by hydraulic redistribution. *Oecologia* 141:7–16
- Domínguez Núñez JA, Salva Serrano J, Rodríguez Barreal JA, Omeñaca González JAS (2006) The influence of mycorrhization with *Tuber melanosporum* in the afforestation of a Mediterranean site with *Quercus ilex* and *Quercus faginea*. *For Ecol Manage* 231:226–233
- Drew MC (1997) Oxygen deficiency and root metabolism: Injury and acclimation under hypoxia and anoxia. *Annu Rev Plant Physiol Plant Mol Biol* 48:223–250
- Duddridge JA, Malibari A, Read DJ (1980) Structure and function of mycorrhizal rhizomorphs with special reference to their role in water transport. *Nature* 287:834–836
- Egerton-Warburton LM, Graham RC, Hubbert KR (2003) Spatial variability in mycorrhizal hyphae and nutrient and water availability in a soil-weathered bedrock profile. *Plant Soil* 249:331–342
- Eglin T, Walter C, Nys C, Follain S, Forgeard F, Legout A, Squidant H (2008) Influence of waterlogging on carbon stock variability at hillslope scale in a beech forest (Fougères forest, West France). *Ann For Sci* 65:202
- Eissenstat DM, Yanai RD (1997) The ecology of root lifespan. *Adv Ecol Res* 27:1–60
- Enstone DE, Peterson A, Ma FS (2003) Root endodermis and exodermis: structure, function, and responses to the environment. *J Plant Growth Regul* 21:335–351
- Ennajeh M, Vadel AM, Khemira H, Ben Mimoun M, Hellali R (2006) Defence mechanisms against water deficit in two olive (*Olea europaea* L.) cultivars 'Meski' and 'Chemlali'. *J Horti Sci Biotech* 81:99–104
- EXCIMAP (2007) Annex 2: Atlas of flood maps - Examples from 19 European countries, USA and Japan. In: Martini F, Loat R (eds) Handbook on good practice for flood mapping in Europe. Netherlands Ministry of Transport, Public Works and Water Management, The Hague, The Netherlands, 197 pp
- Fan TWM, Higashi RM, Frenkiel TA, Lane AN (1997) Anaerobic nitrate and ammonium metabolism in flood-tolerant rice coleoptiles. *J Exp Bot* 48:1655–1666

- Fitter AH (1994) Architecture and biomass allocation as components of the plastic response of root systems to soil heterogeneity. In: Caldwell MM, Pearcy RW (eds) Exploitation of environmental heterogeneity by plants: ecophysiological processes above- and belowground. Academic, San Diego, CA, pp 305–323
- Frei C, Scholl R, Fukutome S, Schmidli R, Vidale PL (2006) Future change of precipitation extremes in Europe: Intercomparison of scenarios from regional climate models. *J Geophys Res-Atmo* 111
- Folzer H, Dat JF, Capelli N, Rieffel D, Badot PM (2006) Response of Sessile oak seedlings (*Quercus petraea*) to flooding: an integrated study. *Tree Physiol* 26:759–766
- Fort C, Muller F, Label P, Granier A, Dreyer E (1998) Stomatal conductance, growth and root signaling in *Betula pendula* seedlings subjected to partial soil drying. *Tree Physiol* 18:769–776
- Fougnies L, Renciot S, Muller F, Planchette C, Prin Y, de Faria SM, Bouvet JM, Sylla SN, Dreyfus B, Bâ AM (2007) Arbuscular mycorrhizal colonization and nodulation improve flooding tolerance in *Pterocarpus officinalis* Jacq. seedlings. *Mycorrhiza* 17:159–166
- Fuhrer J, Beniston M, Fischlin A, Frei C, Goyette S, Jasper K, Pfister C (2006) Climate risks and their impact on agriculture and forests in Switzerland. *Clim Change* 79:79–102
- Gale MR, Grigal DF (1987) Vertical root distributions of northern tree species in relation to successional status. *Can J For Res* 17:829–834
- García-Sánchez F, Syvertsen JP, Gimeno V, Botia P, Perez-Perez JG (2007) Responses to flooding and drought stress by two citrus rootstock seedlings with different water-use efficiency. *Physiol Plant* 130:532–542
- George E, Marschner H (1996) Nutrient and water uptake by roots of forest trees. *Z Pflanzenernährung Bodenkunde* 159:11–21
- Geßler A, Keitel C, Kreuzwieser J, Matyssek R, Seiler W, Rennenberg H (2007) Potential risks for European beech (*Fagus sylvatica* L.) in a changing climate. *Trees* 21:1–11
- Glenz C, Schlaepfer R, Iorgulescu I, Kienast F (2006) Flooding tolerance of Central European tree and shrub species. *For Ecol Manage* 235:1–13
- Göttlein A, Manderscheid B (1998) Spatial heterogeneity and temporal dynamics of soil water tension in a mature Norway spruce stand. *Hydrol Proc* 12:417–428
- Goldberg SD, Gebauer G (2009) Drought turns a Central European Norway spruce forest soil from an N₂O source to a transient N₂O sink. *Global Change Biol* 15:850–860
- Gómez-Aparicio L, Pérez-Ramos IM, Mendoza I, Matías L, Quero JL, Castro J, Zamora R, Marañón T (2008) Oak seedling survival and growth along resource gradients in Mediterranean forests: implications for regeneration in current and future environmental scenarios. *Oikos* 117:1683–1699
- Gower ST, Vogt KA, Grier CC (1992) Carbon dynamics of Rocky-Mountain Douglas fir – influence of water and nutrient availability. *Ecol Monogr* 62:43–65
- Grier CC, Vogt KA, Keyes MR, Edmonds RL (1981) Biomass distribution and above-ground and below-ground production in young and mature *Abies amabilis* zone ecosystems of the Washington Cascades. *Can J For Res* 11:155–167
- Hacke UG, Sperry J, Pittermann J (2000) Drought experience and cavitation resistance in six shrubs from the Great Basin, Utah. *Basic Appl Ecol* 1:31–41
- Hampp R, Schaeffer C (1999) Mycorrhiza-carbohydrate and energy metabolism. In: Hock B, Varma A (eds) *Mycorrhiza*, 2nd edn. Springer, Berlin, Germany, pp 273–303
- Hare PD, Cress WA, Van Staden J (1998) Dissecting the roles of osmolyte accumulation during stress. *Plant Cell Environ* 21:535–553
- Harrington CA (1987) Responses of Red alder and Black cottonwood seedlings to flooding. *Physiol Plant* 69:35–48
- Havens KJ (1997) The effect of vegetation on soil redox within a seasonally flooded forested system. *Wetlands* 17:237–242
- Head GC (1973) Shedding of roots. In: Kozlowski TT (ed) *Shedding of plant parts*. Academic, New York, pp 237–293
- Hentschel K, Borken W, Matzner E (2007) Leaching losses of inorganic N and DOC following repeated drying and wetting of a spruce forest soil. *Plant Soil* 300:21–34

- Herrera A, Tezara W, Rengifo E, Flores S (2008) Changes with seasonal flooding in sap flow of the tropical flood-tolerant tree species, *Campsiandra laurifolia*. *Trees* 22:551–558
- Hillel D, Baker RS (1988) A descriptive-theory of fingering during infiltration into layered soils. *Soil Sci* 146:51–56
- Hook DD, Brown CL, Kormanik PP (1971) Inductive flood tolerance in swamp tupelo (*Nyssa sylvatica* var. *biflora* (WALT.) SARG.). *J Exp Bot* 22:78–89
- Hook DD, Brown CL (1973) Root adaptations and relative flood tolerance of five hardwood species. *For Sci* 19:225–229
- Hook DD, Scholtens JR (1978) Adaptation and flood tolerance of tree species. In: Hook DD, Crawford RMM (eds) *Plant life in anaerobic environments*. Ann Arbor Science Publication, Ann Arbor, MI, pp 299–331
- Hsiao TC, Xu LK (2000) Sensitivity of growth of roots versus leaves to water stress: biophysical analysis and relation to water transport. *J Exp Bot* 51:1595–1616
- Huang BR, Nobel PS (1993) Hydraulic conductivity and anatomy along lateral roots of cacti: changes with soil water status. *New Phytol* 123:499–507
- Huber B (1956) Die Gefäßleitung. In: Ruhland W (ed) *Handbuch der Pflanzenphysiologie*, vol 2. Springer, Berlin, Germany, pp 541–582
- Hulme M, Jenkins GJ, Lu X, Turnpenny JR, Mitchell TD, Jones RG, Murphy JM, Hassell D, Boorman P, McDonald R, Hills S (2002) Climate change scenarios for the United Kingdom: The UKCIP02 Scientific Report. Tyndall Centre for Climate Change Research. School of Environmental Sciences, University of East Anglia, Norwich, UK, 112 pp
- Hundecha Y, Bárdossy A (2005) Trends in daily precipitation and temperature extremes across western Germany in the second half of the 20th century. *Int J Climatol* 25:1189–1202
- Iglesias A, Rosenzweig C, Pereira D (2000) Agricultural impacts of climate change in Spain: developing tools for a spatial analysis. *Global Environ Change* 10:69–80
- Inglisma I, Alberti G, Bertolini T, Vaccari FP, Gioli B, Miglietta F, Cotrufo MF, Peressotti A (2009) Precipitation pulses enhance respiration of Mediterranean ecosystems: the balance between organic and inorganic components of increased soil CO₂ efflux. *Global Change Biol* 15:1289–1301
- IPCC (2007) Climate change 2007: the physical science basis – 4AR. The Intergovernmental Panel on Climate Change, Geneva, Switzerland
- Jackson MB, Davies WJ, Else MA (1996) Pressure-flow relationships, xylem solutes and root hydraulic conductance in flooded tomato plants. *Ann Bot* 77:17–24
- Jackson RB, Moore LA, Hoffmann WA, Pockman WT, Linder CR (1999) Ecosystem rooting depth determined with caves and DNA. *PNAS* 96:11387–11392
- Jones DL, Murphy DV (2007) Microbial response time to sugar and amino acid additions to soil. *Soil Biol Biochem* 39:2178–2182
- Joslin JD, Wolfe MH, Hanson PJ (2000) Effects of altered water regimes on forest root systems. *New Phytol* 147:117–129
- Kaldenhoff R, Fischer M (2006) Aquaporins in plants. *Acta Physiol* 187:169–176
- Kennedy PG, Peay KG (2007) Different soil moisture conditions change the outcome of the ectomycorrhizal symbiosis between *Rhizopogon* species and *Pinus muricata*. *Plant Soil* 291:155–165
- Kernaghan G (2005) Mycorrhizal diversity: cause and effect? *Pedobiologia* 49:511–520
- Kirch HH, Vera-Estrella R, Golldack D, Quigley F, Michalowski CB, Barkla BJ, Bohnert HJ (2000) Expression of water channel proteins in *Mesembryanthemum crystallinum*. *Plant Physiol* 123:111–124
- Kolb RM, Dolder H, Cortelazzo AL (2004) Effects of anoxia on root ultrastructure of four neotropical trees. *Protoplasma* 224:99–105
- Konôpka B, Yuste JC, Janssens IA, Ceulemans R (2005) Comparison of fine root dynamics in Scots pine and Pedunculate oak in sandy soil. *Plant Soil* 276:33–45
- Korn S (2004) Experimental investigation of water uptake and hydraulic properties of the root system of six European tree species (In German). Ph.D. thesis, University of Göttingen, Germany (<http://webdoc.sub.gwdg.de/diss/2004/korn>)

- Köstler JN, Brückner E, Bibelriether H (1968) Die Wurzeln der Waldbäume. Parey, Berlin, Germany, 284 pp
- Kozlowski TT (1984) Response of woody plants to flooding. In: Kozlowski TT (ed) Flooding and plant growth. Academic, Orlando, FL, pp 129–193
- Kozlowski TT, Kramer PJ, Pallardy SG (1991) The physiological ecology of woody plants. Academic, San Diego, CA, 657 pp
- Kozlowski TT (1997) Responses of woody plants to flooding and salinity. Tree Physiol Monogr 1:1–29
- Kreuzwieser J, Furniss S, Rennenberg H (2002) Impact of waterlogging on the N-metabolism of flood tolerant and non-tolerant tree species. Plant Cell Environ 25:1039–1049
- Kreuzwieser J, Papadopoulou E, Rennenberg H (2004) Interaction of flooding with carbon metabolism of forest trees. Plant Biol 6:299–306
- Kung KJS (1990) Preferential flow in a sandy vadose zone 2 – mechanisms and implications. Geoderma 46:59–71
- Kunstmann H, Schneider K, Forkel R, Knoche R (2004) Impact analysis of climate change for an Alpine catchment using high resolution dynamic downscaling of ECHAM4 time slices. Hydrol Earth Syst Sci 8:1030–1044
- Lange B, Luescher P, Germann PF (2009) Significance of tree roots for preferential infiltration in stagnant soils. Hydrol Earth Syst Sci 13:1809–1821
- Langer U, Rinklebe J (2009) Lipid biomarkers for assessment of microbial communities in floodplain soils of the Elbe River (Germany). Wetlands 29:353–362
- Larcher W (2001) Ökophysiologie der Pflanzen, 6th edn. Ulmer, Stuttgart, Germany, 408 pp
- Leake JR, Johnson D, Donnelly DP, Muckle GE, Boddy L, Read DJ (2004) Networks of power and influence: the role of mycorrhizal mycelium in controlling plant communities and agroecosystem functioning. Can J Bot 82:1016–1045
- Lehnardt F, Brechtel HM (1980) Durchwurzelungs- und Schöptiefen von Waldbeständen verschiedener Baumarten und Altersklassen bei unterschiedlichen Bodenbedingungen. AFZ 151:120–127
- Leuschner C, Backes K, Hertel D, Schipka F, Schmitt U, Terborg O, Runge M (2001) Drought responses at leaf, stem and fine root levels of competitive *Fagus sylvatica* L. and *Quercus petraea* (MATT.) LIEBL. trees in dry and wet years. For Ecol Manage 149:33–46
- Leuschner C, Coners H, Icke R, Hartmann K, Effinger ND, Schreiber L (2003) Chemical composition of the periderm in relation to in situ water absorption rates of oak, beech and spruce fine roots. Ann For Sci 60:763–772
- Leuschner C, Coners H, Icke R (2004a) In situ measurement of water absorption by fine roots of three temperate trees: species differences and differential activity of superficial and deep roots. Tree Physiol 24:1359–1367
- Leuschner C, Hertel D, Schmid I, Koch O, Muhs A, Hölscher D (2004b) Stand fine root biomass and fine root morphology in old-growth beech forests as a function of precipitation and soil fertility. Plant Soil 258:43–56
- Liebersbach H, Steingrobe B, Claasen N (2004) Roots regulates ion transport in the rhizosphere to counteract reduced mobility in dry soil. Plant Soil 260:79–88
- Lindenmair J, Matzner E, Zimmermann R (2004) The role of woody roots in water uptake of mature spruce, beech and oak trees. In: Matzner E (ed) Biogeochemistry of forest catchments in a changing environment. Springer, Berlin, Germany, pp 279–289
- Lloret F, Peñuelas J, Estiarte M (2004) Experimental evidence of reduced diversity of seedlings due to climate modification in a Mediterranean-type community. Global Change Biol 10:248–258
- Lloyd-Hughes B, Saunders MA (2002) A drought climatology for Europe. Int J Climatol 22:1571–1592
- Lovisolo C, Schubert A (2006) Mercury hinders recovery of shoot hydraulic conductivity during grapevine rehydration: evidence from a whole-plant approach. New Phytol 172:469–478
- Lovisolo C, Secchi F, Nardini A, Salleo S, Buffa R, Schubert A (2007) Expression of PIP1 and PIP2 aquaporins is enhanced in olive dwarf genotypes and is related to root and leaf hydraulic conductance. Physiol Plant 130:543–551

- Lukac M, Calfapietra C, Godbold DL (2003) Production, turnover and mycorrhizal colonisation of root systems of three *Populus* species grown under elevated CO₂ (POPFACE). *Global Change Biol* 9:838–848
- MacFall JS, Johnson GA, Kramer PJ (1990) Observation of a water-depletion region surrounding Loblolly pine roots by magnetic-resonance-imaging. *PNAS* 87:1203–1207
- MacFall JS, Johnson GA, Kramer PJ (1991) Comparative water-uptake by roots of different ages in seedlings of Loblolly pine (*Pinus taeda* L.). *New Phytol* 119:551–560
- Machado JL, Tyree MT (1994) Patterns of hydraulic architecture and water relations of two tropical canopy trees with contrasting leaf phenologies: *Ochroma pyramidale* and *Pseudobombax septenatum*. *Tree Physiol* 14:219–240
- Mainiero R, Kazda M (2006) Depth-related fine root dynamics of *Fagus sylvatica* during exceptional drought. *For Ecol Manage* 237:135–142
- Marschner H (1997) Mineral nutrition of higher plants, 2nd edn. Academic, London, UK, 889 pp
- Manes F, Vitale M, Donato E, Giannini M, Puppi G (2006) Different ability of three Mediterranean oak species to tolerate progressive water stress. *Photosynthetica* 44:387–393
- Meier IC, Leuschner C (2008a) Genotypic variation and phenotypic plasticity in the drought response of fine roots of European beech. *Tree Physiol* 28:297–309
- Meier IC, Leuschner C (2008b) The belowground drought response of European beech: fine root biomass and carbon partitioning in 14 mature stands across a precipitation gradient. *Global Change Biol* 14:2081–2095
- Meinzer FC, Fownes JH, Harrington RA (1996) Growth indices and stomatal control of transpiration in *Acacia koa* stands planted at different densities. *Tree Physiol* 16:607–615
- Muhr J, Goldberg SD, Borken W, Gebauer G (2008) Repeated drying-rewetting cycles and their effects on the emission of CO₂, N₂O, NO, and CH₄ in a forest soil. *J Soil Sci Plant Nutr* 171:719–728
- Nardini A, Pitt F (1999) Drought resistance of *Quercus pubescens* as a function of root hydraulic conductance, xylem embolism and hydraulic architecture. *New Phytol* 143:485–493
- Nardini A, Salleo S, Tyree MT, Vertovec M (2000) Influence of the ectomycorrhizas formed by *Tuber melanosporum* Vitt. on hydraulic conductance and water relations of *Quercus ilex* L. seedlings. *Ann For Sci* 57:305–312
- Neatrou MA, Jones RH, Golladay SW (2007) Response of three floodplain tree species to spatial heterogeneity in soil oxygen and nutrients. *J Ecol* 95:1274–1283
- Nicoll BC, Coutts MP (1998) Timing of root dormancy and tolerance to root waterlogging in clonal Sitka spruce. *Trees* 12:241–245
- Nisbet NR (2002) Implications of climate change: soil and water. In: Broadmeadow M (ed) Climate change: impacts on UK forests. Forestry Commission, Edinburgh, UK, pp 53–67
- Ostonen I (2003) Fine root structure, dynamics and proportion in net primary production of Norway spruce forest ecosystems in relation to site condition. *Dissertationes Biologicae Universitatis Tartuensis* 84, Tartu University Press
- Ostonen I, Püttsepp Ü, Biel C, Alberton O, Bakker MR, Löhmus K, Majdi H, Metcalfe D, Olsthoorn AFM, Pronk A, Vanguelova E, Weih M, Brunner I (2007) Specific root length as an indicator of environmental change. *Plant Biosyst* 141:426–442
- Osunubi O, Davies WJ (1981) Root growth and water relations of oak and birch seedlings. *Oecologia* 51:343–350
- Parker MM, Van Lear DH (1996) Soil heterogeneity and root distribution of mature Loblolly pine stands in Piedmont soils. *SSSAJ* 60:1920–1925
- Pärtel M, Helm A (2007) Invasion of woody species into temperate grasslands: relationship with abiotic and biotic soil resource heterogeneity. *J Veg Sci* 18:63–70
- Pate JS, Jeschke WD, Aylward MJ (1995) Hydraulic architecture and xylem structure of the dimorphic root systems of South-West Australian species of Proteaceae. *J Exp Bot* 46:907–915
- Paul EA, Clark FE (1996) Soil microbiology and biochemistry. Academic, London, UK, 340 pp

- Pereira JS, David JS, David TS, Caldeira MC, Chaves MM (2004) Carbon and water fluxes in Mediterranean-type ecosystems – constraints and adaptations. In: Esser K, Lüttge U, Beyschlag W, Murata J (eds) Progress in botany 65. Springer, Berlin, Germany, pp 468–495
- Pereira JS, Chaves MM, Caldeira MC, Correia A (2006) Water availability and productivity. In: Morison JIL, Morecroft MD (eds) Plant growth and climate change. Blackwell, Oxford, UK, pp 118–145
- Pérez-Ramos IM, Marañón T (2009) Effects of waterlogging on seed germination of three Mediterranean oak species: ecological implications. *Int J Ecol* 35:422–428
- Petit RJ, Hampe A, Cheddadi R (2005) Climate changes and tree phylogeography in the Mediterranean. *Taxon* 54:877–885
- Pickard WF (1989) How might a tracheary element which is embolized by day be healed by night. *J Theor Biol* 141:259–279
- Pietikäinen J, Vajärvi E, Ilvesniemi H, Fritze H, Westman CJ (1999) Carbon storage of microbes and roots and the flux of CO₂ across a moisture gradient. *Can J For Res* 29:1197–1203
- Pigott CD, Pigott S (1993) Water as a determinant of the distribution of trees at the boundary of the Mediterranean zone. *J Ecol* 81:557–566
- Pinay G, Black VJ, Planty-Tabacchi AM, Gumiero B, Décamps H (2000) Geomorphic control of denitrification in large river floodplain soils. *Biogeochemistry* 50:163–182
- Polonski J, Kuhn N (1998) Wurzelsysteme. Haupt, Bern, Switzerland, 290 pp
- Pronk AA, De Willigen P, Heuvelink E, Challa H (2002) Development of fine and coarse roots of *Thuja occidentalis* ‘Brabant’ in non-irrigated and drip irrigated field plots. *Plant Soil* 243:161–171
- Raven JA, Edwards D (2001) Roots: evolutionary origins and biogeochemical significance. *J Exp Bot* 52:381–401
- Ray AM, Inouye RS (2006) Effects of water-level fluctuations on the arbuscular mycorrhizal colonization of *Typha latifolia* L. *Aquat Bot* 84:210–216
- Ray D, Nicoll BC (1998) The effect of soil water-table depth on root-plate development and stability of Sitka spruce. *Forestry* 71:169–182
- Raynaud X, Leadley PW (2004) Soil characteristics play a key role in modelling nutrient competition in plant communities. *Ecology* 85:2200–2214
- Reece CF, Riha SJ (1991) Role of root systems of Eastern larch and White spruce in response to flooding. *Plant Cell Environ* 14:229–234
- Rewald B (2008) Impact of climate change-induced drought on tree root hydraulic properties and competition belowground. Ph.D. thesis, University of Göttingen, Germany (<http://webdoc.sub.gwdg.de/diss/2008/rewald>)
- Rewald B, Leuschner C (2009a) Belowground competition in a broad-leaved temperate mixed forest – pattern analysis and experiments in a four species stand. *Eur J Forest Res* 128:387–398
- Rewald B, Leuschner C (2009b) Does root competition asymmetry increase with water availability? *Plant Ecol Div* 2:255–264
- Rewald B, Ephrath JE, Rachmilevitch S (2010) A root is a root is a root? – Water uptake rates of *Citrus* root orders. *Plant Cell Environ* DOI: 10.1111/j.1365-3040.2010.02223.x
- Richards JH, Caldwell MM (1987) Hydraulic lift – substantial nocturnal water transport between soil layers by *Artemisia tridentata* roots. *Oecologia* 73:486–489
- Richardson MJ, Vepraskas JL (2000) Wetlands soils: genesis, hydrology, landscapes and classification. CRC Press, Boca Raton, FL
- Rieger M, Litvin P (1999) Root system hydraulic conductivity in species with contrasting root anatomy. *J Exp Bot* 50:201–209
- Rowell DP (2005) A scenario of European climate change for the late twenty-first century: seasonal means and interannual variability. *Clim Dyn* 25:837–849
- Ryel RJ (2004) Hydraulic redistribution. In: Esser K, Lüttge U, Beyschlag W, Murata J (eds) Progress in botany 65. Springer, Berlin, Germany, pp 413–435
- Sardans J, Peñuelas J, Ogaya R (2008) Drought-induced changes in C and N stoichiometry in a *Quercus ilex* Mediterranean forest. *For Sci* 54:513–522

- Schäffner AR (1998) Aquaporin function, structure, and expression: are there more surprises to surface in water relations? *Planta* 204:131–139
- Schleppi P, Hagedorn F, Providoli I (2004) Nitrate leaching from a mountain forest ecosystem with Gleysols subjected to experimentally increased N deposition. *Water Air Soil Pollut Focus* 4:453–467
- Schreiber L, Franke R, Hartmann KD, Ranathunge K, Steudle E (2005) The chemical composition of suberin in apoplastic barriers affects radial hydraulic conductivity differently in the roots of rice (*Oryza sativa* L. cv. IR64) and corn (*Zea mays* L. cv. Helix). *J Exp Bot* 56:1427–1436
- Schmull M, Thomas FM (2000) Morphological and physiological reactions of young deciduous trees (*Quercus robur* L., *Q. petraea* [MATT.] LIEBL., *Fagus sylvatica* L.) to waterlogging. *Plant Soil* 225:227–242
- Schulze ED, Caldwell MM, Canadell J, Mooney HA, Jackson RB, Parson D, Scholes R, Sala OE, Trimbom P (1998) Downward flux of water through roots (i.e. inverse hydraulic lift) in dry Kalahari sands. *Oecologia* 115:460–462
- Secchi F, Lovisolo C, Uehlein N, Kaldenhoff R, Schubert A (2007) Isolation and functional characterization of three aquaporins from olive (*Olea europaea* L.). *Planta* 225:381–392
- Shani U, Waisel Y, Eshel A, Xue S, Ziv G (1993) Responses to salinity of grapevine plants with split root systems. *New Phytol* 124:695–701
- Shi LB, Guttenberger M, Kottke I, Hampp R (2002) The effect of drought on mycorrhizas of beech (*Fagus sylvatica* L.): changes in community structure, and the content of carbohydrates and nitrogen storage bodies of the fungi. *Mycorrhiza* 12:303–311
- Silberbush M, Barber SA (1983) Sensitivity analysis of parameters used in simulating K uptake with a mechanistic mathematical model. *Agron J* 75:851–854
- Silvan N, Regina K, Kitunen V, Vasander H, Laine J (2002) Gaseous nitrogen loss from a restored peatland buffer zone. *Soil Biol Biochem* 34:721–728
- Smit BA, Stachowiak M (1988) Effects of hypoxia and elevated carbon-dioxide concentration on water flux through *Populus* roots. *Tree Physiol* 4:153–165
- Smith SE, Read DJ (2008) Mycorrhizal symbiosis, 3rd edn. Academic, London, UK, 787 pp
- Sperry JS, Saliendra NZ (1994) Intra- and inter-plant variation in xylem cavitation in *Betula occidentalis*. *Plant Cell Environ* 17:1233–1241
- Sperry JS, Ikeda T (1997) Xylem cavitation in roots and stems of Douglas fir and White fir. *Tree Physiol* 17:275–280
- Staelens JA, De Schrijver A, Verheyen K, Verhoest NEC (2006) Spatial variability and temporal stability of throughfall water under a dominant beech (*Fagus sylvatica* L.) tree in relationship to canopy cover. *J Hydrol* 330:651–662
- Stenström E (1991) The effects of flooding on the formation of ectomycorrhizae in *Pinus sylvestris* seedlings. *Plant Soil* 131:247–250
- Stephenson NL (1990) Climatic control of vegetation distribution: the role of the water balance. *Am Nat* 135:649–669
- Steudle E (1994) Water transport across roots. *Plant Soil* 167:79–90
- Steudle E, Heydt H (1997) Water transport across tree roots. In: Rennenberg H, Eschrich W, Ziegler H (eds) *Trees – contributions to modern tree physiology*. Backhuys, Leiden, The Netherlands, pp 239–255
- Steudle E (2000) Water uptake by roots: effects of water deficit. *J Exp Bot* 51:1531–1542
- Thomas FM (2000) Growth and water relations of four deciduous tree species (*Fagus sylvatica* L., *Quercus petraea* [MATT.] LIEBL., *Q. pubescens* WILLD., *Sorbus aria* [L.] CR.) occurring at Central-European tree-line sites on shallow calcareous soils: physiological reactions of seedlings to severe drought. *Flora* 195:104–115
- Topa MA, McLeod KW (1986) Responses of *Pinus clausa*, *Pinus serotina* and *Pinus taeda* seedlings to anaerobic solution culture. I. Changes in growth and root morphology. *Physiol Plant* 68:523–531
- Trillo N, Fernández R (2005) Wheat plant hydraulic properties under prolonged experimental drought: stronger decline in root-system conductance than in leaf area. *Plant Soil* 277:277–284

- Trubat R, Cortina J, Vilagrosa A (2006) Plant morphology and root hydraulics are altered by nutrient deficiency in *Pistacia lentiscus* (L.). *Trees* 20:334–339
- Tsukahara H, Kozlowski TT (1985) Importance of adventitious roots to growth of flooded *Platanus occidentalis* seedlings. *Plant Soil* 88:123–132
- Unger IM, Kennedy AC, Muzika RM (2009) Flooding effects on soil microbial communities. *Appl Soil Ecol* 42:1–8
- Valdéz M, Asbjornsen H, Cárdenas MG, Juárez M, Vogt KA (2006) Drought effects on fine-root and ectomycorrhizal-root biomass in managed *Pinus oaxacana* MIROV. stands in Oaxaca, Mexico. *Mycorrhiza* 16:117–124
- Vanninen P, Ylitalo H, Sievanen R, Mäkelä A (1996) Effects of age and site quality on the distribution of biomass in Scots pine (*Pinus sylvestris* L.). *Trees* 10:231–238
- Vera-Estrella R, Barkla BJ, Bohnert HJ, Pantoja O (2004) Novel regulation of aquaporins during osmotic stress. *Plant Physiol* 135:2318–2329
- West GB, Brown JH, Enquist BJ (1999) A general model for the structure and allometry of plant vascular systems. *Nature* 400:664–667
- White TCR (2007) Flooded forests: death by drowning, not herbivory. *J Veg Sci* 18:147–148
- Xu YJ, Röhrig E, Fölster H (1997) Reaction of root systems of grand fir (*Abies grandis* LINDL.) and Norway spruce (*Picea abies* KARST.) to seasonal waterlogging. *For Ecol Manage* 93:9–19
- Yamada S, Komori T, Myers PN, Kuwata S, Kubo T, Imaseki H (1997) Expression of plasma membrane water channel genes under water stress in *Nicotiana excelsior*. *Plant Cell Physiol* 38:1226–1231
- Yu KW, Faulkner SP, Baldwin MJ (2008) Effect of hydrological conditions on nitrous oxide, methane, and carbon dioxide dynamics in a bottomland hardwood forest and its implication for soil carbon sequestration. *Global Change Biol* 14:798–812
- Zimmermann MH (1983) Xylem structure and the ascent of sap. Springer, Berlin, Germany, 143 pp
- Zimmermann HM, Steudle E (1998) Apoplastic transport across young maize roots: effect of the exodermis. *Planta* 206:7–19
- Zwieniecki MA, Holbrook NM (1998) Diurnal variation in xylem hydraulic conductivity in White ash (*Fraxinus americana* L.), Red maple (*Acer rubrum* L.) and Red spruce (*Picea rubens* SARG.). *Plant Cell Environ* 21:1173–1180

Forest Management and the Water Cycle

An Ecosystem-Based Approach

Bredemeier, M.; Cohen, S.; Godbold, D.L.; Lode, E.;

Pichler, V.; Schleppi, P. (Eds.)

2011, XV, 531 p., Hardcover

ISBN: 978-90-481-9833-7