

Chapter 24

Ecohydrology and Biogeochemistry of the Rhizosphere in Forested Ecosystems

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24.1 Introduction

The rhizosphere, defined as the narrow zone within the soil centered on the root–soil interface, has long been recognized as a hotspot for biogeochemical cycling within the soil (Richter et al. 2007). Life on earth is directly dependent upon processes occurring within the small volume of soil surrounding roots (Hinsinger et al. 2009), making the rhizosphere the “epicenter” of the critical zone, where soil weathering, biogeochemical cycling, and root uptake of water and nutrients take place. The physical dimensions of the rhizosphere should be considered in mechanistic rather than in absolute terms, as its width (measured as the distance outward from the center of the root) varies in scale from sub-micron to supra-centimeter depending on the process considered (Hinsinger et al. 2009). For most considerations related to ecohydrology and soil water dynamics, the width of concern for the rhizosphere is on the order of several (<5) centimeters.

The first use of the term “rhizosphere” appeared in the literature over 100 years ago (Hiltner 1904), an occurrence which was commemorated in 2004 with an international conference organized to mark the first century of research explicitly focused on the rhizosphere (Hinsinger and Marschner 2006). The uniqueness of properties and functions of the rhizosphere relative to bulk soil¹ has motivated much of the rhizospheric research to date, which has focused primarily on soil biology and ecology of the rhizosphere (Gregory 2006). Despite the centrality of rhizospheric processes for soil hydrology, hydrologic aspects have received relatively little attention to date in studies of the rhizosphere. For instance, in recent years (e.g., since 2000) there have been an average of 827 papers per year indexed by Web of Science that address some aspect of the rhizosphere. Of these rhizosphere studies, only 2% have appeared in water resources journals. Nevertheless, rhizospheric considerations are central to the study of ecohydrology, particularly within forested ecosystems.

¹In this paper, the term “bulk soil” is used to describe soil in the area outside of the rhizosphere but still within the rooting depth.

Several comprehensive reviews have demonstrated the importance of the rhizosphere to understanding soil biophysical and ecological processes (Gregory 2006; Richter et al. 2007; Hinsinger et al. 2009). In this chapter, we focus on three rhizosphere mechanisms that differentiate the ecohydrological and biogeochemical processes characteristic of the rhizosphere from those of bulk soil. These are (1) double-funneling of stemflow into root-induced preferential flow pathways; (2) hydraulic redistribution (HR) of soil water by roots from wetter to drier soil zones; and (3) CO₂ dynamics of the rhizosphere. We follow with several examples of external influences on the ecohydrology of the rhizosphere. Finally, we present suggestions for future research directions for advancing our understanding of ecohydrology and biogeochemistry of the rhizosphere, and discuss global change issues as they relate to the rhizosphere of forested ecosystems.

24.2 Ecohydrological and Biogeochemical Differences Between Rhizosphere and Bulk Soil

One of the organizing aspects for ecohydrology and biogeochemistry in the rhizosphere is that the transpiration-driven flow of water due to plant water uptake occurs at the interface of roots and soil in the midst of a “central commodities exchange, where organic carbon flux from roots fuels decomposers that, in turn, can make nutrients available to roots” (Cardon and Gage 2006). This makes the rhizosphere a hotspot (*sensu* McClain et al. (2003)) for biogeochemical cycling.

Biogeochemical cycling in the rhizosphere is central to plant nutrient uptake, weathering reactions, and soil respiration of CO₂. Soil microbial populations are concentrated in the rhizosphere (Richter et al. 2007), in part because root exudates provide a principle energetic resource for microbes. Even deep in the soil profile, the few roots present at depth generate a rhizospheric oasis within the oligotrophic bulk soil, where the rhizosphere hosts microbial populations that are almost undetectable in bulk soil (Richter et al. 2007). The rhizosphere is responsible for a large fraction of weathering (Richter et al. 2007), soil carbon fluxes (Cheng and Gershenson 2007), and plant nutrient availability and uptake through associations with soil mycorrhizas (Hughes et al. 2008). The latter is an underappreciated aspect of the rhizosphere, in that 90% of plant species form symbiotic relationships with mycorrhizal fungi, making the “mycorrhizosphere” the rule rather than the exception (Linderman 1988). The coupled role of the rhizosphere in weathering processes and the global carbon cycle is discussed further in subsequent sections of this chapter.

Ecohydrology of the rhizosphere exhibits large differences in mechanisms and fluxes as compared to bulk soil. For instance, soil water uptake by trees follows an increasingly negative water potential leading from the rhizosphere to the stomata in the leaf. As this uptake follows a diurnal cycle, rhizospheric soil experiences a periodicity in soil water potential dynamics that is not experienced in the bulk soil.

Further, the rhizosphere is an autogenic environment, where the physical space is gained from bulk soil through compressive forces exerted radially by root expansion during plant water uptake as well as axially at the root apex during root elongation (Hinsinger et al. 2009). These rhizopathways are then lined by root exudates and microbial rhizodeposits that are frequently hydrophobic (Jarvis 2007), thus ensuring that water percolation occurs through soil zones most advantageous to the plant.

A significant portion of the water routed through the rhizosphere originates as stemflow and throughfall centered on the trunks of trees. This canopy redistribution of rainfall into heterogeneous distribution of precipitation occurs for most species (Levia and Frost 2003), with the highest relative precipitation rates centered on the trunks of trees. The hydrological continuity between stemflow and root-derived preferential flowpaths belowground has been termed “double-funneling” (Johnson and Lehmann 2006). Stemflow has been found to contribute up to nearly 19% of groundwater recharge (Taniguchi et al. 1996), despite occurring on only a very small fraction of the total forest area. For example, Chang and Matzner (2000) found 13.5% of infiltration to occur over just 3% of the forest floor. Liang et al. (2009) explicitly accounted for double-funneling in a soil moisture model by representing stemflow as a separate soil water input from net precipitation, and were able to obtain much better model representation of soil moisture measurements as a result.

Double-funneling is also important toward understanding nutrient fluxes within the rhizosphere. For instance, De Schrijver et al. (2007) reviewed 20 studies that presented data for both (1) nitrogen deposition rates in throughfall plus stemflow, and (2) seepage rates of inorganic N ($\text{NO}_3^- + \text{NH}_4^+$), and found a strong linear relationship ($R_{\text{adj}}^2 = 0.632$, $P < 0.001$) irrespective of forest type (e.g., conifer vs. deciduous forests). While N seepage fluxes were higher under conifer forests, N deposition rates were also higher in throughfall plus stemflow for conifer stands (De Schrijver et al. 2007).

Another key ecohydrological process of the rhizosphere is HR of soil water by roots. During the daytime when leaf stomates are open to allow CO_2 to diffuse into the leaf for photosynthesis, the water potential gradient drives the transpiration stream of water from soil, through the root network, plant stems and leaves and into the atmosphere, which is at a much more negative pressure relative to that of the soil. However, when stomates are closed (e.g., at night or in response to excessive transpirational demands), soil moisture can move through roots from zones of less negative soil water potential (e.g., moister regions of soil) to layers that have more negative soil water potential (e.g., drier regions of soil).

This mechanism, referred to as HR, has been documented for numerous species in ecosystems as diverse as coniferous forests of the Pacific Northwest of North America (Warren et al. 2005), deciduous forests in the Amazon (Oliveira et al. 2005), as well as for trees in arid environments (Hultine et al. 2003). While sometimes referred to as “hydraulic lift,” HR results from redistribution of water from wetter to drier areas, and so can transfer water upward or downward relative to the soil surface in response to soil water potential gradients (Baker et al. 2008).

In order for HR to take place, the individual plant must have a dimorphic root distribution consisting of both shallow lateral roots and deeper tap roots (Jackson et al. 2000). For the Amazon forest, HR has been estimated to increase dry-season transpiration by 40% (Lee et al. 2005).

It remains difficult to upscale water redistribution in the rhizosphere to the whole plant level (Darrah et al. 2006). Although the rhizosphere is clearly one of the most complex ecosystems on the planet (Jones and Hinsinger 2008), part of the difficulty in scaling may be due to mycorrhizal associations, which have been found to be involved in the transfer of water and nutrients from mature trees to seedlings (Warren et al. 2008).

Through ecohydrological processes such as double-funneling and HR, the rhizosphere sees water fluxes of a greater magnitude than the bulk soil, and experiences changes in soil water potentials that are much more dynamic than in bulk soil. These processes and other create conditions by which rhizosphere cycling of carbon and nutrients is more pronounced than in bulk soil. The enhanced production of CO₂ within the rhizosphere is one biogeochemical manifestation of the difference between the rhizosphere and bulk soil.

24.3 CO₂ Dynamics in the Rhizosphere

Production of CO₂ within soils occurs predominantly within the rhizosphere, and is controlled in large part by soil moisture dynamics. With this in mind, we present a discussion of the role of the rhizosphere in the global carbon cycle, and on ecohydrological feedbacks on the biogeochemical cycling of carbon within the rhizosphere.

The belowground contribution toward terrestrial carbon fluxes to the atmosphere (e.g., soil CO₂ efflux or soil respiration) is a principle component of the global carbon budget, and is one of the most challenging carbon cycle components to study in detail (Chapin and Ruess 2001). It is also heavily influenced by rhizosphere processes. Hanson et al. (2000) reviewed published studies of the efflux of CO₂ from soil, including 48 field-based studies of forested ecosystems. For the field-based forest studies, the “root” contribution toward total soil respiration was found to represent approximately 50% on average of the total soil respiration in forest ecosystems, and ranges up to 80% of total soil respiration, despite the minor fraction of total soil represented by the rhizosphere. Many of these studies considered autotrophic and heterotrophic respiration within the rhizosphere as an aggregated “rhizosphere respiration” term (Hanson et al. 2000).

The distinction between autotrophic respiration (e.g., respiration by roots and mycorrhizae) and heterotrophic respiration (e.g., microbial respiration) within the rhizosphere is both nontrivial and methodologically challenging from carbon-cycling and ecohydrological perspectives. Autotrophic respiration directly involves the water film at the root interface, and as a product of autotrophic respiration, CO₂ enters the soil in a dissolved form. Heterotrophic respiration under aerobic conditions

also produces CO_2 that is primarily in the dissolved form, as soil bacteria and other microbes live principally within soil water (Hinsinger et al. 2009). Here, we should note that dissolved CO_2 is composed of both “free” CO_2 (e.g., gaseous molecules of CO_2 within a water matrix) and the hydrated form of CO_2 as H_2CO_3 (carbonic acid). At equilibrium conditions, carbonic acid is only a very minor component of dissolved CO_2 , as the ratio of free CO_2 to H_2CO_3 is 650 at 25°C (Butler 1982).

Once introduced into the soil environment, rhizosphere-derived dissolved CO_2 is subject to transport with mobile water (including being drawn into plants via root water uptake, Jassal et al. 2004), participation in weathering reactions as carbonic acid, or equilibration with CO_2 concentrations in soil gas. The general assumption that gaseous and liquid phases of CO_2 are in equilibrium concentrations within the soil environment overlooks two key processes: (1) differences in rates of diffusion between liquid and gaseous forms of CO_2 , and (2) temperature dependencies on equilibrium conditions between liquid and gaseous forms of CO_2 . Diffusion of CO_2 in the aqueous phase is 10,000 times slower than in the gaseous phase. At equilibrium, the partial pressure of CO_2 dissolved in water (e.g., $\text{pCO}_2(\text{aq})$) by definition will be equal to the partial pressure of CO_2 in the soil atmosphere. However, the $\text{pCO}_2(\text{aq})$ level depends upon Henry’s Law, which includes a temperature-dependent component. If $\text{pCO}_2(\text{aq})$ remains constant as temperature rises, the result is lower molar concentrations of dissolved CO_2 and higher molar concentrations of gaseous CO_2 . Since it is the molecules of dissolved CO_2 that are involved in generating soil acidity and chemical weathering as carbonic acid, this distinction can be significant, particularly in near surface layers where the root length density (km roots m^{-3} soil) is highest, soil microbial populations are highest (Richter and Markewitz 1995), and soil moisture and temperature are most dynamic.

Once produced in the rhizosphere, the CO_2 can be converted to bicarbonate depending on the pH status of the soil environment. In the case that the pH conditions of the soil favors CO_2 in deprotonated forms as bicarbonate (HCO_3^-) or carbonate (CO_3^{2-}), the biogenic (bi)carbonate ions can be involved in other plant–soil reactions or transported by percolating water within the soil. Much of the HCO_3^- transported by rivers originates in the rhizosphere, and represents a “hidden” respiration product that is “masquerading” as the bicarbonate ion (Cole et al. 2007).

Soil moisture dynamics are strongly related to both CO_2 production within soils and the direction of its subsequent transport, making soil CO_2 a key ecohydrological parameter (cf. Johnson et al. 2007). In general, CO_2 production within the rhizosphere increases with soil moisture until conditions become limiting to further production, either due to substrate exhaustion or due to oxygen depletion. Gaseous transport of CO_2 to the soil surface (e.g., soil CO_2 efflux or soil respiration), however, remains inversely related to soil moisture contents across the full range of soil moisture conditions. This is because increasing water content greatly reduces soil diffusivity by reducing the interconnection of air-filled pores, effectively increasing the distance over which CO_2 must travel to reach the soil surface. This is because travel across water-filled pore spaces (or even water films between

air-filled pores) involves gaseous CO_2 entering into and out of solution where the diffusion rate is four orders of magnitude lower than in air-filled pore spaces.

On the one hand, lateral transport of dissolved CO_2 within the vadose zone and eventually to groundwater and streams (Fiedler et al. 2006; Johnson et al. 2008), on the other hand, is enhanced by increasing soil moisture contents. Johnson et al. (2008) compared the lateral transport of dissolved CO_2 to streams with estimates of soil CO_2 efflux, finding that CO_2 drainage was about 50% of the magnitude of soil CO_2 efflux, suggesting that plot-based studies focusing on soil respiration that only consider soil CO_2 efflux systematically underestimate total CO_2 production.

Looking beyond CO_2 to other trace gases in the rhizosphere, it should be noted that heterotrophic respiration by methanogenic microbes, which results in methane (CH_4) as a respiration product, can occur in soil in both water-filled pore space that have become anoxic, as well as in oxygen-depleted air-filled pore spaces. Decreases of pO_2 in the rhizosphere accompany increases in pCO_2 , but are sparsely documented in the literature (Hinsinger et al. 2006). Low levels of soil pO_2 result in conditions favorable to methanogenesis (production of CH_4). Given that soils contribute 60% of global CH_4 sources (Conrad and Smith 1995), these dynamics are in need of further study.

24.4 Process-Based Examples of Ecohydrology, Biogeochemistry, and the Rhizosphere

24.4.1 Aboveground and Soil Surface Processes that Influence the Rhizosphere

There are a number of mechanisms by which aboveground and surface mechanisms exhibit functional control over processes within the rhizosphere. Perhaps, foremost among these is the spatial redistribution of incident precipitation into throughfall and stemflow. This redistribution results in a heterogeneous distribution of rainfall with highest relative precipitation rates centered on the trunks of trees for most species (Levia and Frost 2003). Snowfall is also redistributed by forest canopies, with snowmelt-derived stemflow providing a significant water flux centered on the rhizosphere (Levia and Underwood 2004). Further discussion on throughfall and stemflow processes are found in a companion chapter of this volume (Levia et al. 2011, Chap. 21).

A relatively understudied mechanism that influences the fluxes of water and nutrients that enter the rhizosphere is soil water repellency (e.g., soil hydrophobicity). Although there has been a large increase in the number of studies of soil water repellency in recent years (Doerr et al. 2007), few have explicitly considered the spatial coordination of surficial water repellency and belowground wetting patterns. Soil water repellency is known to be spatially heterogeneous and ephemeral. Soil hydrophobicity is most strongly exhibited when soils are dry, and decays slowly

with the progression of the rainy season (Doerr et al. 2000; Wessolek et al. 2008). Repellency at the soil surface influences subsequent routing of soil water through the rhizosphere, which has an added impact on the distribution of nutrients within the soil, particularly since wetting events following dry periods are characterized by the mobilization of high concentrations of solutes that build up on soil and litter layers during dry periods in a process known as the “Birch effect” (Jarvis et al. 2007). Here, we present an example of soil water repellency occurring during the dry season in the Amazon forest that demonstrates the role of surficial processes controlling water fluxes within the rhizosphere.

A water repellent layer at the soil surface soil of an undisturbed primary forest in the seasonal southern Amazon was identified in a study that initially assumed soil water repellency would be negligible in the tropical forest environment (Johnson et al. 2005). Nevertheless, soil at the forest floor was found to exhibit extreme hydrophobicity during the dry season (Johnson et al. 2005). In further study, a manipulative experiment was conducted to evaluate the role of surface repellency on patterns of soil water distribution within the soil. In this experiment, soil on the control plot remained unaltered, while the treatment plot was rendered nonrepellent through application of a soil surfactant (Aquagro-L, Aquatrols Inc., Paulsboro, NJ, USA).

Ammonium carbonate was dissolved in water and applied as a tracer to both the surfactant-treated soil and the hydrophobic control soil for 30 min at a rainfall rate of 50 mm h^{-1} using a mini-rainfall simulator (Ogden et al. 1997). This application rate simulated precipitation events typical of the study area. One hour following tracer application, a trench was excavated centering on the location of simulated rainfall, and a pH indicator was sprayed onto the exposed soil surface within the trench to determine the tracer distribution within the soil profile (Wang et al. 2002).

The experiment demonstrated that the wetting front below the water repellent soil had reached twice the depth of the nonrepellent soil (Fig. 24.1). Further, the wetting front below the water repellent soil exhibited a high degree of preferential

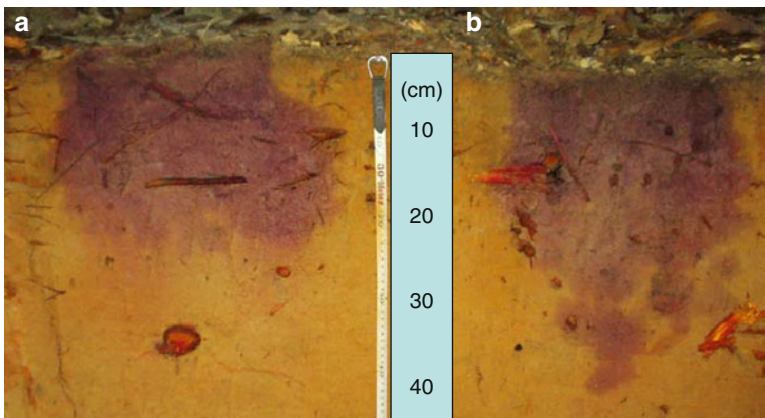


Fig. 24.1 Infiltration patterns for nonrepellent soil (a) and soil exhibiting surficial hydrophobicity (b)

flow, whereas the infiltration pattern under the nonrepellent soil appeared to be more readily drawn into the bulk soil matrix as evidenced by the pH indicator, which clearly demonstrated where the tracer traveled.

This example is illustrative of the importance of surficial processes on subsurface flow dynamics in the rhizosphere. Wessolek et al. (2008) also found soil water repellency to influence percolation patterns. Due to repellency, a smaller portion of the bulk soil was filled than would be expected in the absence of repellency, which decreased the water storage capacity. This decreased soil water storage capacity, in combination with repellency-induced preferential flow, resulted in a 20-fold increase in the soil water percolation rate (Wessolek et al. 2008). As the repellency was found within the soil profile, and not as a result of burning, it is likely the result of rhizodeposition of microbial and root exudates leading to water repellency of aggregate surfaces and macropore linings, which has been shown to reduce water exchange between macropores and bulk soil (Jarvis 2007).

24.4.2 Species Affects on Soil Moisture Dynamics in the Rhizosphere

Vegetation alters precipitation into spatially variable throughfall, which contributes to persistent patterns of soil moisture in the rhizosphere and bulk soil. Although highly variable in space, throughfall patterns show some stability in time as they are caused by relatively static spatial factors such as canopy density, agglomeration of trees, and species distribution (Jost et al. 2005; Keim et al. 2005). In terms of the rhizosphere, these throughfall patterns contribute toward spatial patterns in soil moisture within the rooting zone. Jost et al. (2005) studied spatial patterns of soil moisture dynamics for a mixed stand of Norway spruce (*Picea abies* (L.) Karst.) and European beech (*Fagus sylvatica* L.) in Kreisbach, Lower Austria, finding that both soil water recharge patterns (Fig. 24.2) and soil water discharge patterns (not shown) closely match patterns of tree species distribution.

These spatial patterns are clearly important considerations for biogeochemical and ecohydrologic processes in the rhizosphere. However, due to the intensity of measurement requirements for adequate spatial representation, it remains an area that should receive additional attention in future research. Some advances have been made in model representation of soil moisture dynamics by explicitly considering spatial throughfall patterns. This approach has shown improved performance over lumped soil moisture representations, because the connectivity between wet patterns can be used to conceptualize lateral flow for moderate rainfall events and improve runoff predictions (Keim et al. 2008).

Antecedent soil moisture determines the capacity of an ecosystem to absorb water and thus to buffer runoff. Due to differences in rates of root water uptake and rooting depths and patterns in the rhizosphere, tree species can enhance or diminish the absorption capacity of a given soil. With a large number of spatially distributed time domain reflectometry (TDR) measurements, Schume et al. (2004) showed how

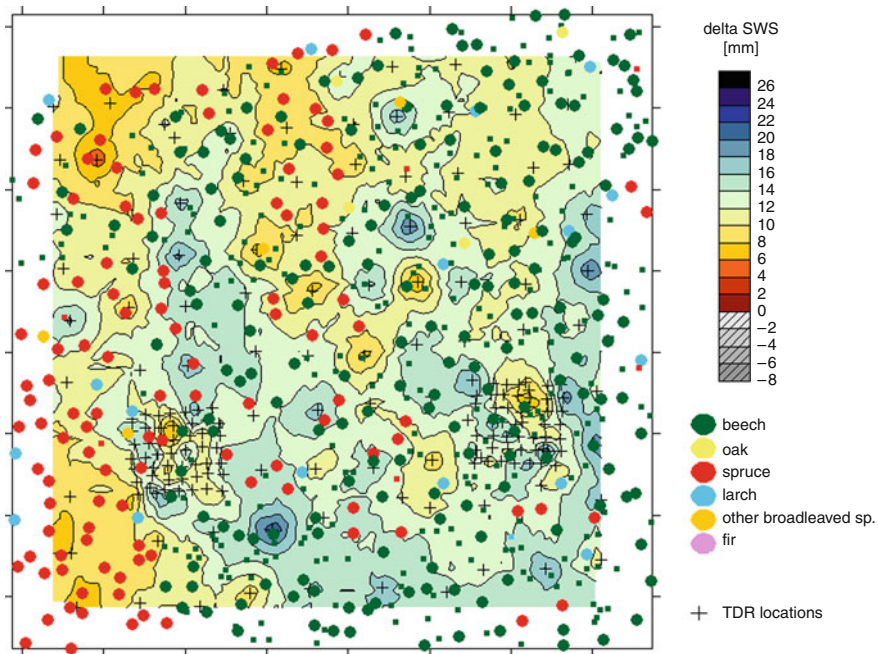


Fig. 24.2 Change in soil water storage (delta SWS) following a 31 mm rainfall in a mixed spruce-beech stand (from Schume et al. 2004)

tree species can alter stand scale hydrology through a combination of processes involving the rhizosphere. In a comparison between spruce and beech forests, the beech stands showed that higher stand precipitation (e.g., throughfall) was compensated by higher transpiration rates and faster soil depletion in both topsoil and subsoil. As a result, there were higher seasonal fluctuations in soil water content under beech compared to spruce (Fig. 24.3). Throughout the growing season, the soil water content under spruce was generally dryer compared to beech. Tree species effects in the study proved to be nonadditive (a mixed spruce-beech stand behaves very much like a pure beech stand), which suggests that mixed species forests need to be investigated using research methodologies that address the role of individual tree species on the rhizosphere within mixed forest stands.

In this regard, for the same soil type, tree species with different rooting systems and different water consumption can lead to different soil moisture dynamics and lateral flow processes during rainfall and hence to different runoff responses. Soil moisture patterns and interflow were investigated at different soil depths in a Norway spruce (*P. abies* (L.) Karst) forest and in a European beech (*F. sylvatica* L.) forest during sprinkling experiments on two 6×10 m hillslopes with the same soil type (stagnic Cambisol). The deeper rooting system of beech directs more water toward deeper soil horizons, from where the water table rises into the top soil, while the topsoil remains substantially below saturation. Saturation excess overland flow is therefore highly unlikely under beech due to the structure of its rhizosphere.

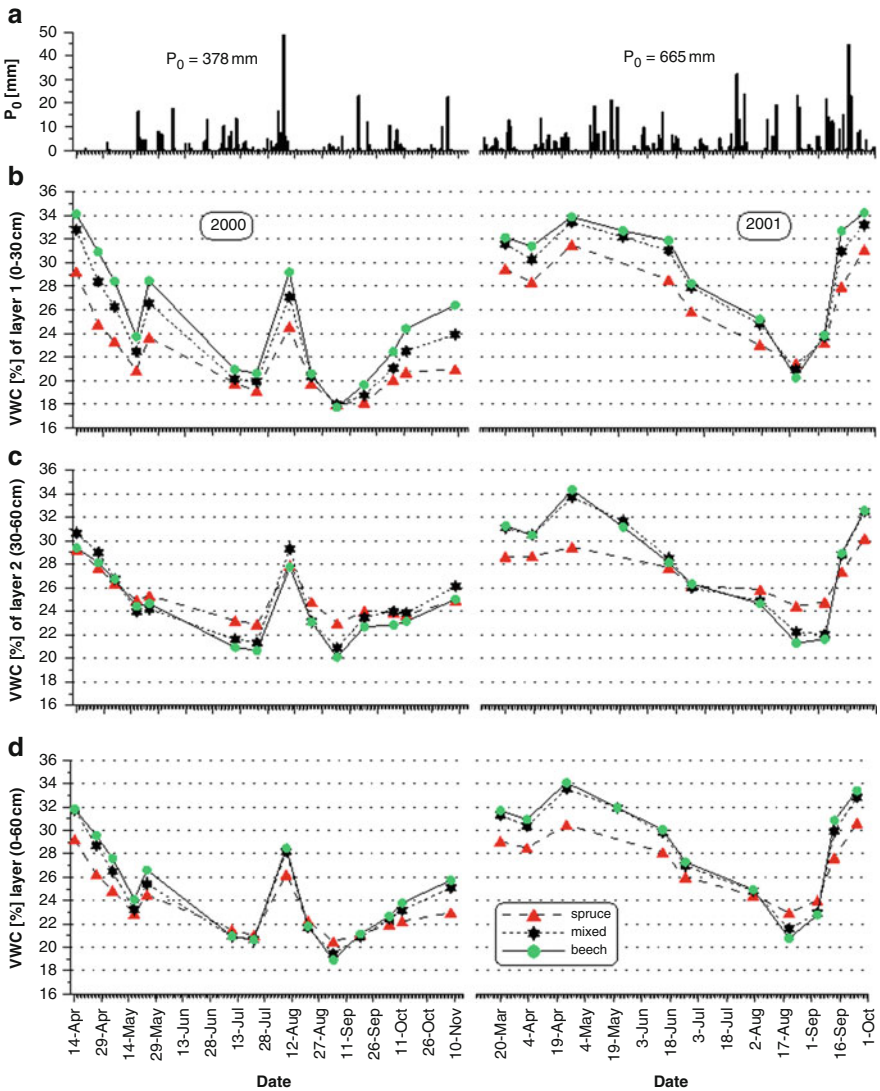


Fig. 24.3 Precipitation (a) and seasonal changes of soil water storage in topsoil (b), subsoil (c), and over soil profile (d) under a spruce, a beech, and a mixed spruce-beech stand (from Schume et al. 2004)

Under spruce, the soil water content in the subsoil shows only little changes over time and remains below saturation. However, a perched water table builds at the base of the maximum rooting depth causing near saturated conditions in the topsoil with a higher risk of saturation overland flow. Beech forests contain more macropores because of the more active soil fauna that they recruit (Scheu et al. 2003) and because of the deeper rooting system, which results in higher subsurface flow rates through the rhizosphere relative to surface runoff rates.

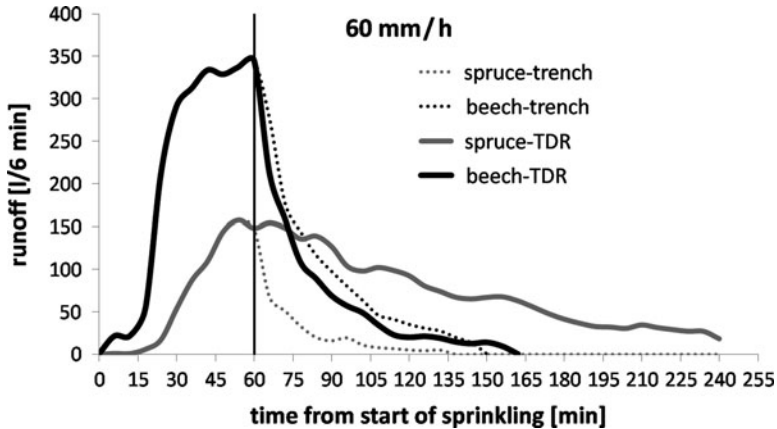


Fig. 24.4 Comparison of runoff responses of spruce and beech in a sprinkling experiment with measured runoff (spruce-trench, beech-trench) and runoff with recession approximated from mean (48 TDRs) decreases of soil water storage (spruce-TDR, beech-TDR) to correct for mass balance errors. The vertical lines denote the end of sprinkling (duration = 1 h). TDR time domain reflectometry

We see that tree species can lead to different runoff responses for the same soil type. Because of the higher subsurface flow rates, small to moderate rainfall events will cause faster fluxes of water through the rhizosphere and correspondingly higher runoff response in beech forests (Fig. 24.4). For high and extreme rainfall events, however, spruce forests will likely result in faster runoff responses compared to beech, because spruce is more prone to saturation excess overland flow.

24.5 Advancing Ecohydrology and Biogeochemistry in Study of the Rhizosphere

24.5.1 Future Research Directions

One of the key difficulties in advancing ecohydrology and biogeochemistry in study of the rhizosphere and isolating processes occurring within the rhizosphere from those of the bulk soil is the small spatial scale of the phenomena of interest. Thus, identifying effective methodologies for segregating rhizospheric from bulk soil processes is the most important area at present for better understanding ecohydrology and biogeochemistry of the rhizosphere. Field-based research involving tracer applications provides one way forward for distinguishing rhizospheric processes. The advent of increasingly smaller instruments is facilitating advances for in situ measurements of the soil environment, including miniaturized infiltrometers for the determination of rhizosphere hydraulic properties (Hallett et al. 2003).

Micro-tensiometry and miniaturized TDR sensors have also been developed that are appropriate for measurements of moisture conditions at scales relevant for study of the rhizosphere (0.1–10 mm) (Neumann et al. 2009). These will aid in distinguishing the soil water-release characteristics (e.g., soil water characteristic curves or soil moisture retention curves) for rhizosphere vs. bulk soil, which has been demonstrated for agricultural crops (Gregory 2006; Hinsinger et al. 2009) but is not yet well studied in forest soils.

The use of genetically engineered “microbiosensors” has already been applied to the study of the rhizosphere. For example, engineered strains of *Escherichia coli* bacteria have been developed that vary in expression of a green fluorescent protein (GFP) in response to variations in total water potential (Herron et al. 2010). The response of these “microbiosensors” in the form of fluorescence was consistent with rhizosphere theory, with lower water potentials developing away from plant roots in response to transpiration water demand and root water uptake, demonstrating soil water potential gradients at the millimeter scale under laboratory conditions (Herron et al. 2010).

Approaching the study of water in the rhizosphere from a macro-level is also needed. Advances in the use of industrial (rather than medical) computed tomography (CT) scanners are providing both high-resolution and time-series data on soil microstructures, although to date this is only possible on soil columns extracted from the field (Luo et al. 2008). A range of tracer application and other techniques have also proven useful for elucidating preferential flow processes within soil, and were reviewed by Allaire et al. (2009). Many of these techniques can be adapted to focus on rhizosphere vs. bulk soil processes, since rooting networks provide one of the principle conveyances for vertical as well as lateral preferential flow (Weiler and McDonnell 2007).

Modeling approaches that explicitly consider rhizosphere processes in relation to those of the bulk soil represent another research pathway for understanding the rhizospheric components of ecohydrological and biogeochemical processes, particularly when developed and applied in an iterative manner with field-based observations. For example, empirical study has shown rhizosphere soil to be drier than bulk soil at the same matric potential (Whalley et al. 2005). Characterizing these differences within a model structure that extends the mobile-immobile water concept with explicit treatment of mobile and immobile water within both the rhizosphere and bulk soil could be one way forward.

Recent isotopic studies have emphasized that current mobile-immobile conceptualizations are unlikely to capture seasonal variability in bulk soil vs. rhizosphere regimes in soil water recharge and plant transpiration source water dynamics (Renée Brooks et al. 2010). Modelers have had some success incorporating HR into land-surface models used to represent biophysical processes in climate models, but are continuing to work to resolve potential issues of equifinality when HR and other changes are simultaneously incorporated into models (Baker et al. 2008). Future conceptual frameworks and model structures will need to take rhizosphere complexity into account and explicitly address ecohydrological feedbacks between rhizosphere processes and the bulk soil (cf. Domec et al. 2004).

24.5.2 *Global Change and the Rhizosphere*

Empirical CO₂ enrichment studies have identified potential changes in rhizosphere biogeochemistry, including increases in root exudation under high CO₂ treatments (Phillips et al. 2009) and enhanced root respiration relative to root biomass (Cheng 1999). Effects of elevated CO₂ on ecohydrology are perhaps more significant, as the water fluxes through the rhizosphere may significantly increase as a result of reduced plant transpiration due to CO₂-induced stomatal closure (Gedney et al. 2006). While the magnitude of this mechanism for explaining observed changes in global river discharge relative to other drivers is still the subject of debate in the literature (Piao et al. 2007; Gerten et al. 2008), the impacts on the rhizosphere of a CO₂-derived increase in the water flux are essentially unstudied. Further, as the species compositions of entire forested ecosystems appear to be undergoing change due to differential species and genera-level responses to increased atmospheric CO₂ (Laurance et al. 2004), the importance of processes such as rhizosphere respiration, HR, and double-funneling in the tree-rhizosphere continuum is also likely to change. Given the plasticity of responses in rooting patterns due to changes in climate, where an increasingly wet state for a previously dry climate results in deeper roots, and an increasingly wet state for a previously wet climate results in shallower rooting depths (Guswa 2008), there is certain to be another century of study on the rhizosphere.

References

- Allaire SE, Roulier S, Cessna AJ (2009) Quantifying preferential flow in soils: a review of different techniques. *J Hydrol* 378:179–204
- Baker IT, Prihodko L, Denning AS et al (2008) Seasonal drought stress in the Amazon: reconciling models and observations. *J Geophys Res Biogeosci* 113:1. doi:[10.1029/2007JG000644](https://doi.org/10.1029/2007JG000644)
- Butler J (1982) Carbon dioxide equilibria and their applications. Addison-Wesley, Reading
- Cardon ZG, Gage DJ (2006) Resource exchange in the rhizosphere: molecular tools and the microbial perspective. *Ann Rev Ecol Evol Syst* 37:459–488
- Chang SC, Matzner E (2000) The effect of beech stemflow on spatial patterns of soil solution chemistry and seepage fluxes in a mixed beech/oak stand. *Hydrol Process* 14:135–144
- Chapin FS, Ruess RW (2001) Carbon cycle: the roots of the matter. *Nature* 411:749–752
- Cheng W (1999) Rhizosphere feedbacks in elevated CO₂. *Tree Physiol* 19:313–320
- Cheng W, Gershenson A (2007) Carbon fluxes in the rhizosphere. In: Cardon ZG, Whitbeck JL (eds) *The rhizosphere: an ecological perspective*. Academic Press, New York, pp 31–56
- Cole JJ, Prairie YT, Caraco NF et al (2007) Plumbing the global carbon cycle: integrating inland waters into the terrestrial carbon budget. *Ecosystems* 10:172–185
- Conrad R, Smith KA (1995) Soil microbial processes and the cycling of atmospheric trace gases [and discussion]. *Philos Trans Phys Sci Eng* 351:219–230
- Darrah PR, Jones DL, Kirk GJD, Roose T (2006) Modelling the rhizosphere: a review of methods for ‘upscaling’ to the whole-plant scale. *Euro J Soil Sci* 57(1):13–25
- De Schrijver A, Geudens G, Augusto L et al (2007) The effect of forest type on throughfall deposition and seepage flux: a review. *Oecologia* 153:663–674

- Doerr SH, Shakesby RA, Walsh RPD (2000) Soil water repellency: its causes, characteristics and hydro-geomorphological significance. *Earth Sci Rev* 51:33–65
- Doerr SH, Ritsema CJ, Dekker LW et al (2007) Water repellence of soils: new insights and emerging research needs. *Hydrol Process* 21:2223–2228
- Domec JC, Warren JM, Meinzer FC et al (2004) Native root xylem embolism and stomatal closure in stands of Douglas-fir and ponderosa pine: mitigation by hydraulic redistribution. *Oecologia* 141:7–16
- Fiedler S, Höll BS, Jungkunst HF (2006) Discovering the importance of the lateral CO₂ transport from a temperate spruce forest. *Sci Total Environ* 368:909–915
- Gedney N, Cox PM, Betts RA et al (2006) Detection of a direct carbon dioxide effect in continental river runoff records. *Nature* 439:835–838
- Gerten D, Rost S, von Bloh W et al (2008) Causes of change in 20th century global river discharge. *Geophys Res Lett* 35:L20405. doi:[10.1029/2008GL035258](https://doi.org/10.1029/2008GL035258)
- Gregory PJ (2006) Roots, rhizosphere and soil: the route to a better understanding of soil science? *Euro J Soil Sci* 57:2–12
- Guswa AJ (2008) The influence of climate on root depth: a carbon cost-benefit analysis. *Water Resour Res* 44:W02427
- Hallett PD, Gordon DC, Bengough AG (2003) Plant influence on rhizosphere hydraulic properties: direct measurements using a miniaturized infiltrometer. *New Phytol* 157:597–603
- Hanson P, Edwards N, Garten CJ et al (2000) Separating root and soil microbial contributions to soil respiration: a review of methods and observations. *Biogeochemistry* 48:115–146
- Herron PM, Gage DJ, Cardon ZG (2010) Micro-scale water potential gradients visualized in soil around plant root tips using microbiosensors. *Plant Cell Environ* 33:199–210
- Hiltner L (1904) Über neuere Erfahrungen und probleme auf dem gebiete der Bodenbakteriologie unter besonderer Berücksichtigung der gründung und Brache. *Arb Deutsch Landwirtsch Ges* 98:59–78
- Hinsinger P, Marschner P (2006) Rhizosphere – perspectives and challenges – a tribute to Lorenz Hiltner 12–17 September 2004 – Munich, Germany. *Plant Soil* 283:vii–viii
- Hinsinger P, Plassard C, Jaillard B (2006) Rhizosphere: a new frontier for soil biogeochemistry. *J Geochem Explor* 88:210–213
- Hinsinger P, Bengough AG, Vetterlein D et al (2009) Rhizosphere: biophysics, biogeochemistry and ecological relevance. *Plant Soil* 321:117–152
- Hughes JK, Hodge A, Fitter AH et al (2008) Mycorrhizal respiration: implications for global scaling relationships. *Trends Plant Sci* 13:583–588
- Hultine KR, Williams DG, Burgess SSO et al (2003) Contrasting patterns of hydraulic redistribution in three desert phreatophytes. *Oecologia* 135:167–175
- Jackson RB, Sperry JS, Dawson TE (2000) Root water uptake and transport: using physiological processes in global predictions. *Trends Plant Sci* 5:482–488
- Jarvis NJ (2007) A review of non-equilibrium water flow and solute transport in soil macropores: principles, controlling factors and consequences for water quality. *Euro J Soil Sci* 58: 523–546
- Jarvis P, Rey A, Petsikos C et al (2007) Drying and wetting of Mediterranean soils stimulates decomposition and carbon dioxide emission: the “Birch effect”. *Tree Physiol* 27:929–940
- Jassal RS, Black TA, Drewitt GB et al (2004) A model of the production and transport of CO₂ in soil: predicting soil CO₂ concentrations and CO₂ efflux from a forest floor. *Ag For Meteorol* 124:219–236
- Johnson MS, Lehmann J (2006) Double-funneling of trees: stemflow and root-induced preferential flow. *EcoScience* 13:324–333
- Johnson MS, Lehmann J, Steenhuis TS et al (2005) Spatial and temporal variability of soil water repellency of Amazonian pastures. *Aust J Soil Res* 43:319–326
- Johnson MS, Weiler M, Couto EG et al (2007) Storm pulses of dissolved CO₂ in a forested headwater Amazonian stream explored using hydrograph separation. *Water Resour Res* 43: W11201

- Johnson MS, Lehmann J, Riha SJ et al (2008) CO₂ efflux from Amazonian headwater streams represents a significant fate for deep soil respiration. *Geophys Res Lett* 35:L17401
- Jones DL, Hinsinger P (2008) The rhizosphere: complex by design. *Plant Soil* 312:1–6
- Jost G, Heuvelink GBM, Papritz A (2005) Analysing the space-time distribution of soil water storage of a forest ecosystem using spatio-temporal kriging. *Geoderma* 128:258–273
- Keim RF, Skaugset AE, Weiler M (2005) Temporal persistence of spatial patterns in throughfall. *J Hydrol* 314:263–274
- Keim RF, Weiler M, Jost G et al (2008) Consequences of spatiotemporal redistribution of precipitation by vegetation for hillslope and runoff processes. *Eos transactions AGU* 89: Fall meeting supplement, Abstract H14A-03
- Laurance W, Oliveira A, Laurance S et al (2004) Pervasive alteration of tree communities in undisturbed Amazonian forests. *Nature* 428:171–174
- Lee JE, Oliveira RS, Dawson TE et al (2005) Root functioning modifies seasonal climate. *Proc Natl Acad Sci U S A* 102:17576–17581
- Levia DF, Frost EE (2003) A review and evaluation of stemflow literature in the hydrologic and biogeochemical cycles of forested and agricultural ecosystems. *J Hydrol* 274:1–29
- Levia DF, Underwood SJ (2004) Snowmelt induced stemflow in northern hardwood forests: a theoretical explanation on the causation of a neglected hydrological process. *Adv Water Res* 27:121–128
- Levia D, Keim RF, Carlyle-Moses DE (2011) Throughfall and stemflow in wooded ecosystems. In: Levia D, Carlyle-Moses D, Tanaka T (eds) *Forest hydrology and biogeochemistry: synthesis of research and future directions*. Springer, New York
- Liang W-L, Ki K, Mizuyama T (2009) A three-dimensional model of the effect of stemflow on soil water dynamics around a tree on a hillslope. *J Hydrol* 366:62–75
- Linderman RG (1988) Mycorrhizal interactions with the rhizosphere microflora – the mycorrhizosphere effect. *Phytopathology* 78:366–371
- Luo LF, Lin H, Halleck P (2008) Quantifying soil structure and preferential flow in intact soil using x-ray computed tomography. *Soil Sci Soc Am J* 72:1058–1069
- McClain ME, Boyer EW, Dent CL et al (2003) Biogeochemical hot spots and hot moments at the interface of terrestrial and aquatic ecosystems. *Ecosystems* 6:301–312
- Neumann G, George T, Plassard C (2009) Strategies and methods for studying the rhizosphere – the plant science toolbox. *Plant Soil* 321:431–456
- Ogden CB, vanEs HM, Schindelbeck RR (1997) Miniature rain simulator for field measurement of soil infiltration. *Soil Sci Soc Am J* 61:1041–1043
- Oliveira RS, Dawson TE, Burgess SSO et al (2005) Hydraulic redistribution in three Amazonian trees. *Oecologia* 145:354–363
- Phillips RP, Bernhardt ES, Schlesinger WH (2009) Elevated CO₂ increases root exudation from loblolly pine (*Pinus taeda*) seedlings as an N-mediated response. *Tree Physiol* 29:1513–1523
- Piao S, Friedlingstein P, Ciais P et al (2007) Changes in climate and land use have a larger direct impact than rising CO₂ on global river runoff trends. *Proc Natl Acad Sci U S A* 104:15242–15247
- Renée Brooks J, Barnard HR, Coulombe R et al (2010) Ecohydrologic separation of water between trees and streams in a Mediterranean climate. *Nat Geosci* 3:100–104
- Richter DD, Markewitz D (1995) How deep is soil? *BioScience* 45:600–609
- Richter DD, Oh N-H, Fimmen R et al (2007) The rhizosphere and soil formation. In: Cardon ZG, Whitbeck JL (eds) *The rhizosphere: an ecological perspective*. Academic Press, New York, pp 179–200
- Scheu S, Albers D, Alpei J et al (2003) The soil fauna community in pure and mixed stands of beech and spruce of different age: trophic structure and structuring forces. *Oikos* 101:225–238
- Schume H, Jost G, Hager H (2004) Soil water depletion and recharge patterns in mixed and pure forest stands of European beech and Norway spruce. *J Hydrol* 289:258–274
- Taniguchi M, Tsujimura M, Tanaka T (1996) Significance of stemflow in groundwater recharge. 1. Evaluation of the stemflow contribution to recharge using a mass balance approach. *Hydrological Process* 10:71–80

- Wang Z, Lu J, Wu L et al (2002) Visualizing preferential flow paths using ammonium carbonate and a pH indicator. *Soil Sci Soc Am J* 66:347–351
- Warren JM, Meinzer FC, Brooks JR et al (2005) Vertical stratification of soil water storage and release dynamics in Pacific Northwest coniferous forests. *Ag For Meteorol* 130:39–58
- Warren JM, Brooks JR, Meinzer FC et al (2008) Hydraulic redistribution of water from *Pinus ponderosa* trees to seedlings: evidence for an ectomycorrhizal pathway. *New Phytol* 178:382–394
- Weiler M, McDonnell JJ (2007) Conceptualizing lateral preferential flow and flow networks and simulating the effects on gauged and ungauged hillslopes. *Water Resour Res* 43:W03403. doi:[10.1029/2006WR004867](https://doi.org/10.1029/2006WR004867)
- Wessolek G, Schwarzel K, Greiffenhagen A et al (2008) Percolation characteristics of a water-repellent sandy forest soil. *Euro J Soil Sci* 59:14–23
- Whalley WR, Riseley B, Leeds-Harrison PB et al (2005) Structural differences between bulk and rhizosphere soil. *Euro J Soil Sci* 56:353–360