In situ measurement of water absorption by fine roots of three temperate trees: species differences and differential activity of superficial and deep roots†

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Summary  The spatial heterogeneity of water uptake by fine roots under field conditions was analyzed in situ with miniature sap flow gauges in a mature beech–oak–spruce mixed stand. Sap flow rate (\(J_s\)), sap flow density (\(J_{sd}\)), and root surface-area-specific flow rate (uptake rate, \(J_u\)) were measured for eight to 10 small-diameter roots (3–4 mm) per species in the organic layer (superficial roots) and in the mineral soil (30–80 cm, deep roots) during four months in summer 1999. We calculated \(J_u\) by relating \(J_s\) to the surface area of the section of the fine root system distal to the position of the gauge on the root. When measured synchronously, roots of the three species did not differ significantly in mean \(J_u\), although oak roots tended to have lower rates. However, \(J_{sd}\) decreased in the sequence spruce > beech > oak in most measurement periods. Microscopic investigation revealed differences in fine root anatomy that may partly explain the species differences in \(J_u\) and \(J_s\). Oak fine roots had a thicker periderm than beech and spruce roots of similar diameter and spruce roots had fewer fine branch rootlets than the other species. Synchronously recorded \(J_u\) and \(J_s\) of nearby roots of the same tree species showed large differences in flow with coefficients of variation from 25 to 150% that could not be explained by patchy distribution of soil water. We hypothesize that the main cause of the large spatial heterogeneity in root water uptake is associated with differences between individual roots in morphology and ultrastructure of the root cortex that affect root radial and root–soil interface conductivities. The high intraspecific variation in \(J_s\) may mask species differences in root water uptake.

Superficial roots of all species typically had about five times higher \(J_u\) than deep roots of the same species. However, \(J_u\) values were similar for superficial and deep roots in beech and spruce because small diameter roots of both species were more branched in the organic layer than in mineral soil. In oak, deep roots had lower \(J_u\) (maximum of 100 g m\(^{-2}\) day\(^{-1}\)) than superficial roots (about 1000 g m\(^{-2}\) day\(^{-1}\)). We conclude that temperate tree species in mixed stands have different water uptake capacities. Water flow in the rhizosphere of forests appears to be a highly heterogeneous process that is influenced by both tree species and differences in uptake rates of individual roots within a species.

Keywords: Fagus sylvatica, Picea abies, Quercus petraea, root surface area, water transport, water uptake.

Introduction

Root water uptake is probably the least studied process in the soil–tree–atmosphere continuum of water transport. In contrast to leaf transpiration and water flow in trunks and twigs, water uptake by fine roots has not been studied under field conditions with respect to surface-area-specific flow and the key control factors. Information on the process of root water uptake obtained from laboratory experiments is difficult to relate to water uptake in the field because the experimental conditions alter the rhizosphere and the water potential gradients in the root–soil system, and the measurements are usually made on decapitated root systems (Steudle 2000).

Field studies of root water uptake by trees have depended on tracers (isotopically marked water or dyes, e.g., Plamboeck et al. 1999) or used the soil water depletion approach. Neither technique can provide real time data on mass flow of water in single roots or branch root systems. Thermoelectrical root sap flow measurements in agroforestry systems and orchard trees have yielded interesting details on water transport in tree root systems, but have focused on coarse roots, not the fine roots through which soil water uptake occurs (Green and Clothier 1995, Lott et al. 1996, Burgess et al. 1998, Smith et al. 1999). Senock and Leuschner (1999) and Coners and Leuschner (2002) measured water uptake of tree fine roots in real time in undisturbed forest soils. They applied the miniature sap flow technique first developed by Sakuratani (1981) to small-diameter roots (2–5 mm) and calibrated the system against volumetrically derived flow data. After extracting the terminal branch fine roots distal to the gauge mounting point and determining their total surface area, Coners and Leuschner (2002) calculated mean uptake rates by relating measured flow to fine root surface area.

The objectives in this study were to: (1) analyze differences among tree species in root surface area-specific water uptake rates; and (2) compare uptake of superficial and deep roots in the soil profile. We studied mature trees of three species in a mixed stand with a complete overlap of the fine root systems.
and, thus, similar access by all species to soil water reserves. Species differences in root water uptake were expected because whole-tree water turnover and leaf transpiration rates of co-occurring tree species differ greatly in mixed forests (e.g., Kaufmann 1985, Pataki et al. 2000, Hölscher et al. 2004), which implies that water uptake must also be species specific. Another paper (H. Coners and C. Leuschner, in preparation) will describe the temporal variability in water uptake by fine roots of the same species and its dependence on soil and atmospheric factors.

Methods

Study sites

The study was conducted in a mature mixed stand of beech, oak and spruce (Fagus sylvatica L., Quercus petraea Matt. Liebl. and Picea abies Karst.) located 2 km west of Unterlüß (52°45’N, 10°30’E) in the Lünburger Heide area (German northwestern diluvial lowlands, 115 m a.s.l.). The climate is humid sub-oceanic with mean annual temperature and rainfall of 8 °C and 800 mm, respectively. The 28–32 m high beech, oak and spruce trees are 90–100, 180–200 and 80–100 years old, respectively. Stem density is similar for the three species, at about 250 trees per hectare. There is no herbaceous layer in the shade of the stand.

The soil profiles are spodo–dystric cambisols with thick organic layers (mean depth of 72 mm) that are highly acidic (pH_0.01: 2.6 to 3.0 in the organic Of and Oh layers). The mineral soil consists of medium-grained sand with a clay content of less than 5% that results in rapid soil drying during periods of low rainfall. The thick organic layer atop the profile plays an important role in stand nutrient turnover and water storage. In the studied stand, about 83% of the annual net nitrogen mineralization was found to occur in the organic layer (F. Hellwig, Universität Göttingen, and C. Leuschner, unpublished results). The organic layer is an important site of water storage, supplying about 28 to 37% of the water used in annual stand transpiration (Leuschner 1998). These distribution patterns of nutrients and water in the soil are reflected by the abundance of tree fine roots in the profile. Fine root density decreased exponentially with depth from >2.50 kg m^-3 in the organic layer to <0.05 kg m^-3 in the subsoil. More than 40% of the fine root biomass and >91% of the root tips in the soil profile to 60 cm depth are located in the organic layer (Hertel and Leuschner, unpublished data.). Similar distribution patterns were found for spruce fine roots in this stand. A detailed account of abundance and distribution of beech and oak fine roots in this stand is given by Leuschner et al. (2001).

Miniature sap flow gauges

Sap flow rates in fine roots (3–4 mm in diameter) were measured with miniature heat balance sap flow gauges. The branch fine root system distal to the sensor was subsequently excavated to enable calculation of flow rates per unit root surface area. We used gauges embedded in a flexible cork–neoprene jacket as described by Senock and Ham (1993) to ensure good contact between the gauge and the small and often irregularly shaped roots. For a detailed technical description see Senock and Leuschner (1999) and Coners and Leuschner (2002).

Briefly, constant heating of 0.4 to 0.7 W is applied to the root segment by a Kapton film resistance heater (Heater Designs, Bloomington, CA). Two pairs of thermocouples and a thermopile record the heat dissipation from the heater segment in the axial and radial directions. Based on these data, the heat balance of the system is solved for the mass flow term. Sap flow rate is then calculated based on the heat capacity of water (4187 J kg^-1 K^-1) to convert heat flow (in W) to mass flow of water (in g h^-1).

A key parameter in the calculation is the gauge heat conductance, K_g, which is determined at zero flow by cutting the root after measurement. To avoid errors due to small drifts in K_g during extended measuring periods, gauge conductance was recalculated every day at 0300 h before dawn assuming that flow ceased late in the night. A graphical interactive software tool (H. Coners, unpublished) allows correction of K_g on days with significant night flow, for example, when nights are dry and windy, by extrapolating from preceding and subsequent days.

Because flow rates in 3–4 mm diameter roots of temperate trees are small, sap flow measurements are based on very small heat fluxes. Peak flows at noon were usually <10 g h^-1. Preliminary laboratory and field calibration experiments revealed that measurement errors increased with decreasing flow rate. At flows < 2 g h^-1, gauge readings were highly unreliable (Coners and Leuschner 2002). Although these low flows contribute only about 10% to the total daily flow of the 3–4 mm diameter roots, they cannot be ignored because they occur every morning and evening. To minimize errors in the integration of daily totals, a modified calculation method was applied to flows < 2 g h^-1, based on an empirically derived relationship between axial temperature difference across the root T_{so} - T_{si} and sap flow (Coners and Leuschner 2002).

Gauge operation in the field

We selected two or three sample trees per species with representative stem diameters. In a 5-m radius around these individuals, four to five superficial and five to six deep roots (3–4 mm in diameter) were carefully uncovered with a jet of compressed air (0.3 MPa) (Coners and Leuschner 2002). Microscopic analysis indicated that this technique led to negligible loss of root biomass. To access roots, segments about 15 cm in length were exposed in small pits measuring 15–30 cm wide and 15–70 cm deep. Superficial roots could be located easily at any given distance from the tree because fine roots in this mixed stand reach high densities in the topsoil and overlap with roots of neighboring trees (Hertel 1999, Leuschner et al. 2001).

To locate deep roots, differences in root system morphology for the three species were taken into account. Beech and oak form heart-shaped root systems with coarse roots spreading downward at various angles from the tree base, whereas spruce has a superficial root system with long horizontal roots that form vertical sinker roots. Thus, deep beech and oak roots that were uncovered in soil pits near the stem base ran mainly in a horizontal direction, whereas almost all spruce sinkers had a
vertical orientation.

Because the fine root systems of the three species overlapped in the study plot, the species had to be identified based on fine root branching patterns, periderm morphology and color of the root surface. Hertel (1999 and unpublished observations) has compiled a basic root identification key for several central European broad-leaved and coniferous tree species that allows species identification of more than 95% of the fine root biomass. This key was extended and applied in our study. The sap flow gauges were mounted on the uncovered root segments and continuous measurements (readings every 10 s, 15-min averages) made for periods of 3 to 6 weeks. Gauge signals were read with solar-powered Campbell CR10X data loggers (Campbell Scientific, Cambridge, U.K.). To avoid errors caused by root growth, the measurements were terminated after 3 to 6 weeks and the sensors were re-installed on other roots nearby. Superficial roots of beech and oak were studied in three consecutive measuring periods between June and October 1999 (i.e., two re-installation cycles), deep roots of these species and all spruce roots were studied during two measuring periods (i.e., one re-installation cycle).

After measurement, the section of the fine root system distal to the gauge mounting point on the root was excavated with compressed air. Superficial roots of the three species (3–4 mm-diameter) typically had appending fine root systems 0.5 to 1.0 m in length. Spruce sinker roots 3–4 mm in diameter were usually quite short (about 0.3 m), whereas many deep roots of beech and oak explored the mineral soil to a depth of 1 to 3 m requiring several days of excavation for complete extraction. We carefully screened the soil for root fragments detached during excavation. Based on microscopic investigation of superficial and deeper roots, we confirmed that mass losses attributable to damage during excavation were no more than about 5–10%.

In the laboratory, the excavated roots were rinsed and, with the aid of a stereomicroscope, separated according to whether they were dead and or alive based on color and mechanical strength (Hertel 1999). Root surface area was determined with an image processing unit (WinRhizo, Régent, Quebec, Canada) in order to calculate mean surface area-specific flow rates (Jd; g m⁻² h⁻¹, i.e., uptake rates). Sap flow density (Jd; g mm⁻² h⁻¹) was calculated by relating flow rate to the sapwood area at the measuring point.

Soil water and atmospheric measurements

Soil water content was monitored synchronously with sap flow. To avoid disturbance to the measured roots, we installed the sensors about 2 m from the plot where the gauges were mounted. Solar-powered time domain reflectometry (TDR) probes (P2Z, IMKO, Ettingen, Germany) and pressure transducer tensiometers were used to measure soil water content (θ) and soil matric potential (Ψm), respectively, at soil depths of 5, 30 and 60 cm. Three TDR and tensiometer sensors per depth were installed. We recorded θ every 2 h and Ψm every 15 min. During the study (May–October 1999), θ fluctuated between 7 and 30% (by volume) with lower θ prevailing throughout the year in the lower, but not the upper horizons, because of increasing soil bulk density with profile depth. Values of Ψm varied between 0 and –800 hPa, which is the lower limit of tensiometer operation. From May to July, Ψm of the sandy soil was close to field capacity (–100 hPa), but it decreased to low values during dry periods in August and September when midday leaf water potential may have been close to the wilting point (–1.5 MPa).

Global radiation (J) and atmospheric water vapor saturation deficit (D) were measured with a solarimeter (Kipp & Zonen, Delft, The Netherlands) and ventilated wet and dry bulb thermometers above the canopy from a 32-m scaffolding tower.

Statistical analyses

All calculations were conducted with SAS software, Version 8.01 (SAS Institute, Cary, NC). In the case of data with a Gaussian distribution, mean values of sap flow parameters were compared by a one-factorial analysis of variance followed by a Scheffé test. The majority of data sets showed a non-Gaussian distribution according to a Shapiro and Wilk test. In these cases, the data were compared among the three species by one-way Kruskal-Wallis single factor analyses of variance. If H0 (no significant difference among the species) was rejected, a non-parametric multiple comparisons test after Wilcoxon was applied to locate the differences. Significance was determined at P < 0.05 in all analyses.

Results

Species differences in root sap flow

During the 4-month study, Jd ranged from < 1 to 30 g mm⁻² day⁻¹ in beech and oak roots, whereas in spruce roots Jd peaked at 50 g mm⁻² day⁻¹. In the majority of measuring periods in summer 1999, spruce roots showed a tendency for higher Jd compared with beech and oak roots. In most cases, oak roots had lower Jd than beech and spruce roots, but a reversed order of species was observed during certain periods. Because of the large variation in flow among roots of the same species, any differences in Jd among the three species were significant during only part of the study period. An example of marked species differences in Jd occurred between September 4 and 8, when spruce roots in the organic layer had significantly higher Jd than oak roots (P < 0.05), whereas the difference in Jd between spruce and beech was not significant (Table 1).

Values of Jd varied between < 100 and > 2000 g m⁻² day⁻¹ in the three species (Figure 1). Differences in Jd between co-occurring beech, oak and spruce roots were less distinct than for Jc; however, oak roots tended to have lower Jd than beech and spruce roots, although these differences were not significant in most periods.

Roots of the same tree species (or even the same tree) showed great variation in simultaneously measured flow, even though the roots explored the same patch of soil. A high spatial heterogeneity was detected not only for Jc, but also for Jd. At the maximum, two roots of the same species differed in simultaneously measured Jc or Jd by a factor of 10. Coefficients of variation ranged between 25 and 150% for four to six roots of a species in a soil horizon (Table 1).
Table 1. Sap flow rate per root ($J$), sap flow density ($J_d$) and root surface area-specific flow ($J_s$) in 3–4 mm diameter roots of beech, oak and spruce measured with miniature sap flow gauges on five consecutive late-summer days (September 4–8, 1999) at the Lüneburger Heide site. Soil water content at 5, 30 and 60 cm was 0.19, 0.09 and 0.07 m$^3$ m$^{-3}$, respectively. Significant differences (Sig, $P < 0.05$) between means of different horizons (upper case) or between different species (lower case) are indicated by different letters. Abbreviations: CV = coefficient of variation (%); and SE = standard error of mean.

<table>
<thead>
<tr>
<th>Soil layer</th>
<th>Species</th>
<th>Mean</th>
<th>SE</th>
<th>Sig</th>
<th>Median</th>
<th>Min</th>
<th>Max</th>
<th>CV</th>
<th>n</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>$J$ (g day$^{-1}$)</strong></td>
<td>Organic</td>
<td>Beech</td>
<td>51.4</td>
<td>9.4</td>
<td>A, a</td>
<td>61.2</td>
<td>15.0</td>
<td>65.0</td>
<td>40.7</td>
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<td>2.2</td>
<td>A, b</td>
<td>21.1</td>
<td>12.3</td>
<td>22.4</td>
<td>26.9</td>
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<tr>
<td></td>
<td></td>
<td>Spruce</td>
<td>24.7</td>
<td>3.9</td>
<td>A, b</td>
<td>22.5</td>
<td>18.2</td>
<td>35.7</td>
<td>31.8</td>
</tr>
<tr>
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<td>3.8</td>
<td>B, a</td>
<td>4.8</td>
<td>0.6</td>
<td>25.2</td>
<td>103.6</td>
<td>6</td>
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<td>2.8</td>
<td>B, a</td>
<td>2.3</td>
<td>0.2</td>
<td>18.2</td>
<td>147.8</td>
<td>6</td>
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<tr>
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<td>Spruce</td>
<td>2.6</td>
<td>0.6</td>
<td>B, a</td>
<td>2.0</td>
<td>1.1</td>
<td>4.2</td>
<td>51.2</td>
<td>5</td>
</tr>
<tr>
<td><strong>$J_d$ (g mm$^{-2}$ day$^{-1}$)</strong></td>
<td>Organic</td>
<td>Beech</td>
<td>9.7</td>
<td>1.8</td>
<td>A, ab</td>
<td>11.6</td>
<td>2.9</td>
<td>12.7</td>
<td>41.6</td>
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<td></td>
<td>Oak</td>
<td>4.8</td>
<td>0.6</td>
<td>A, a</td>
<td>5.6</td>
<td>3.1</td>
<td>6.0</td>
<td>29.7</td>
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<tr>
<td></td>
<td></td>
<td>Spruce</td>
<td>12.5</td>
<td>2.0</td>
<td>A, b</td>
<td>13.2</td>
<td>7.0</td>
<td>16.6</td>
<td>32.3</td>
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<tr>
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<td>B, a</td>
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<td>0.1</td>
<td>4.15</td>
<td>134.7</td>
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<td>0.4</td>
<td>B, a</td>
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<td>&lt; 0.05</td>
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<td>B, a</td>
<td>0.9</td>
<td>0.4</td>
<td>2.27</td>
<td>65.3</td>
<td>5</td>
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<tr>
<td><strong>$J_s$ (g m$^{-2}$ day$^{-1}$)</strong></td>
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<td>191.1</td>
<td>A, a</td>
<td>592.2</td>
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<td>61.2</td>
<td>A, a</td>
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<td>101.0</td>
<td>437.4</td>
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<td></td>
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<td>60.5</td>
<td>A, a</td>
<td>318.9</td>
<td>181.7</td>
<td>451.6</td>
<td>38.1</td>
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<tr>
<td>Mineral</td>
<td>Beech</td>
<td>470.7</td>
<td>640.7</td>
<td>A, a</td>
<td>184.7</td>
<td>29.5</td>
<td>1483.9</td>
<td>144.8</td>
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<tr>
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<td>47.1</td>
<td>14.3</td>
<td>B, a</td>
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<td>17.0</td>
<td>71.6</td>
<td>60.7</td>
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</tr>
<tr>
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<td>38.3</td>
<td>A, a</td>
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<td>58.2</td>
<td>246.5</td>
<td>53.9</td>
<td>5</td>
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</table>

Figure 1. Seasonal course of root surface area-specific flow, $J_s$, in beech, oak and spruce fine roots in the organic layer (left) and the mineral soil (right) as measured with miniature sap flow gauges in the Lüneburger Heide mixed forest in the summer of 1999. Sap flow per root (g day$^{-1}$) was divided by the total surface area of the excavated fine roots distal to the measuring point. Data represent daily flow totals derived from 15-min means. Dotted vertical lines separate different measuring periods in which different roots (4–6 per species) were investigated.
Species differences in fine root morphology and anatomy

Excavation of the terminal branch fine roots adjacent to the 3–4 mm-thick root segment that was used for mounting each gauge revealed a mean total root surface area of about 1000 cm² for beech, oak and spruce roots in the organic layer (Figure 2, left panel). Roots of 3–4 mm diameter in the mineral soil had a four times smaller surface area (about 250 cm²) than in the organic layer as a result of a greatly reduced degree of branching and fewer fine root tips. There were no significant differences between the three tree species in the organic layer or the mineral soil with respect to total root surface area of the 3–4 mm diameter roots.

Seventy-five percent of the total surface area of beech and oak root systems used for measurement were contributed by branches < 1 mm in diameter. The remaining surface area comprised sections of the root system that were either 1–2 mm (18%) or 2–4 mm in diameter. Spruce differed from the two broad-leaved species by having a much smaller proportion of fine root branches < 1 mm contributing to the total surface area of the 3–4 mm diameter roots (Figure 3). Consequently, branches with larger root diameters were more abundant in the 3–4 mm diameter measuring roots of spruce. Finest rootlets (< 1 mm diameter) were much less frequent in the mineral soil than in the organic layer in all three species, contributing only 18 to 34% to the total surface area.

Anatomical analyses showed that the periderm of beech and oak fine roots consisted of only 2–3 cell layers close to the root tip, but the number of cell layers increased to 7–8 (beech) or even 12 (oak) at distances > 20 cm from the root tip (Figure 4). Spruce fine roots, in contrast, had less than four peridermal cell layers along the first 40 cm from the terminal tip. Thus, at distances > 10 cm from the tip, oak fine roots possessed a significantly higher number of peridermal cell layers than the other tree species. During summer 1999, we found no fine branch rootlets of beech, oak or spruce at a primary stage of root development with intact endodermis, cortex and rhizodermis. All fine roots examined lacked a cortex and rhizodermis but possessed a well-developed periderm up to the terminal root tip region.

Water uptake by superficial and deep roots

From June to October 1999, superficial roots in the organic layer generally had about 5 times higher \( J_d \) than deep roots in the mineral soil at 30–80 cm depth (Figure 5). These differences were significant in all three species during most of the season. In contrast, \( J_s \) was similar for beech and spruce roots in the upper and lower horizons (Figure 1). Oak roots in the mineral soil reached a maximal \( J_s \) of 100 g m\(^{-2}\) day\(^{-1}\), whereas surface roots in the organic layer had much higher \( J_s \) with peak rates of 1200 g m\(^{-2}\) day\(^{-1}\).

Discussion

Is root water uptake influenced by tree species?

Co-occurring tree species in temperate mixed forests differ significantly in leaf conductance and, hence, transpiration rate, even if they experience the same edaphic and atmospheric environment (e.g., Kaufmann 1985, Pallardy et al. 1995, Leuschner et al. 2001). Similarly, xylem sap flow in the trunk of tree species in mixed stands may differ significantly, indicating species differences in whole-tree water consumption (Čer-
Species differences in canopy water loss may exist as a result of differences in leaf conductance ($g_c$), or contrasting leaf area indices ($L_o$) of the species, or a combination of both. Litter trapping studies in several broad-leaved mixed forests in central Germany showed differences in $L$ of more than 100% among co-occurring tree species in a stand (D. Hölscher, C. Leuschner and B. Rewald, unpublished observations). This indicates considerable spatial heterogeneity in the transpiring leaf surface area in temperate mixed stands. Thus, canopy water loss can be expected to vary among species, which should affect root water uptake in these species because the canopy is a major driver for water uptake.

To our knowledge, data indicating similarity or dissimilarity in root water uptake between co-occurring tree species have not been published. In theory, species differences in canopy water loss could be balanced by differences in root water absorption rates, or in the total size of the absorbing root surface, or a combination of both. Our measurements in fine roots of beech, oak and spruce, which explored the same soil volume, showed that tree species can differ in $J_s$ even when they have access to similar soil water reserves. During most measurement periods, we observed a tendency for oak roots to have a lower $J_s$ than beech and spruce roots. However, the data also revealed a high variability in sap flow among roots of the same species with the consequence that a large number of roots (10 to 20) had to be measured in parallel in order to detect significant differences in root activity among species.

S. Korn (University of Göttingen, Germany, unpublished data) measured 10 replicate roots per species and was able to show significant differences in $J_s$ between roots of Acer, Fraxinus and Quercus in a study on root sap flow in five co-occurring tree species.
occurring broad-leaved tree species in a species-rich stand in Thuringia (central Germany). Mean $J_s$ of the species differed up to threefold in this stand. These results and our own data indicate that co-occurring tree species differ greatly in root water uptake.

Factors that could explain species differences in root water uptake include differences in root radial conductivity ($L_{pr}$) and root xylem water potential ($\Psi_r$). Laboratory measurements with the root pressure probe in which water is forced through the root by use of externally applied pressure or osmotic gradients showed that fine roots of *Fagus sylvatica*, *Quercus petraea* and *Picea abies* saplings differed 5- to 15-fold in $L_{pr}$ (Rüdiger et al. 1994, Steudle and Mischeryatov 1996, Steudle and Heydt 1997). These experiments with excised root systems indicated much higher radial conductivities for spruce roots ($4.9 - 7.8 \times 10^{-8} \text{ m s}^{-1} \text{ MPa}^{-1}$) than for beech and oak roots ($0.35 - 1.6$ and $0.33 - 1.1 \times 10^{-8} \text{ m s}^{-1} \text{ MPa}^{-1}$). Our comparative root sap flow measurements in the three species do not allow the calculation of exact values of $L_{pr}$, but they enable rough species comparisons because uptake occurred at similar soil matrix potentials in all three species.

In general, oak seemed to have lower $J_s$ than spruce and beech, which could reflect the low $L_{pr}$ values measured with the root pressure probe. Anatomical and chemical analyses showed that oak fine roots had more periderm cell layers and higher amounts of suberin per surface area than beech or spruce fine roots of similar diameter (cf. Leuschner et al. 2003). However, our data do not confirm higher $L_{pr}$ for spruce than for beech, because measured $J_s$ was not significantly higher in spruce than in beech.

It is possible that, under field conditions, a major control on water flow into roots is exerted by hydraulic conductivity of the root–soil contact zone and the soil itself, and not by $L_{pr}$. This situation may prevail particularly in drying soils (Veen et al. 1992). A rapid decrease in hydraulic conductivity with increasing soil water depletion is to be expected in substrates with high porosity, such as in the organic layer horizons in our study and in sandy soils. Tree species might differ in their contact with the soil matrix in drying soil because of differences in fine root surface structure, fine root diameters, branching patterns and mycorrhizal infection. Therefore, it is possible that low conductivity in the root–soil interface masked species differences in $L_{pr}$ of the three species under the field conditions of our study. This could explain why we were unable to confirm the high radial conductivity of spruce based on root pressure probe measurements.

Water absorption is also dependent on the water potential in the root xylem. Species differences in root water uptake in the absence of differences in soil water content could, therefore, result from differences in $\Psi_r$. Measurements made with a pressure chamber in branch fine roots of beech, oak and spruce in this stand in summer 1999 showed significant differences in $\Psi_r$ among the species during periods of drought. Beech generally had more negative values than oak and spruce (H. Coners, unpublished results). Thus, differences in the root–to–soil water potential gradient can help to explain our observation that beech roots tended to have higher $J_s$ than oak roots; however, differences in the potential gradient cannot account for the apparent differences in $J_s$ between spruce and oak roots.

**Spatial heterogeneity of water absorption in tree root systems**

We observed that neighboring roots of the same species or even the same tree regularly differed greatly in their simultaneous water uptake rates. We obtained coefficients of variation for root water uptake that were several times larger than those of transpiration rates of nearby sun leaves in the upper canopy of a mature tree (Coners and Leuschner 2004). The high spatial variation in tree root water absorption is not a consequence of measurement errors caused by the miniature sap flow technique and is unrelated to a corresponding spatial heterogeneity in soil water content.

Calibration experiments in the laboratory and the field showed that miniature gauges, as used in this study, typically record root sap flow with a measurement error of not more than 20% if the flux is $> 2$ and $< 5 \text{ g h}^{-1}$, with a much higher bias at low flow rates. Errors associated with low flow rates were reduced by introducing a correction procedure based on an empirically determined positive relationship between flow and axial temperature difference in the root segment (Coners and Leuschner 2002). Large differences between the simultaneous activity of neighboring roots were visible in both $J_s$ and $J_d$, and were not confined to the low flows measured at hourly rates, because they were also evident in the daily flow totals. Moreover, sap flow in four or five roots in close proximity fluctuated synchronously from day to day under variable weather conditions, and the ratio in flow between these roots remained approximately constant over days or weeks. These patterns are not consistent with an explanation based on high variability caused by measuring errors.

Local differences in $\Psi_r$ or $\theta$ do not seem large enough to explain the observed variability in uptake rates. Measurements with up to 10 replicate instruments along a 4-m-long horizontal transect in the soil at the study site gave coefficients of variation for $\Psi_r$ of 20 to 50% (C. Leuschner, unpublished results), which is considerably less than the 25 to 150% of variation in $J_s$ and $J_d$. However, considerable variability in fine root length density (i.e., root surface area per soil volume) may exist on a finer scale that could lead to a patchy distribution of soil water even if uptake rates were similar. For example, if two branch roots had the same length, but one was confined to a smaller soil volume, then at the same initial potential gradient, soil water would be depleted more rapidly where the root density was higher. This small-scale variation in volume-specific depletion rate must, in turn, lead to considerable variability in flow rates through small roots, as observed.

Other factors that could account for a high spatial variability in root water uptake include differences in the structure and chemistry of cortical tissue, variable branching patterns and fine root tip frequencies of individual fine roots, and a high spatial variability in the root–soil interface conductivity. It is also possible that differences in mycorrhizal infection influence water uptake rate of tree fine roots, although the majority of experimental data indicate a negligible role of fungal hy-
The miniature sap flow gauge technique does not allow precise localization of water uptake along the horizontal axis of fine roots. Our calculations of surface-area-specific flows are estimates only of mean absorption rates for individual branch fine root systems and do not take differences in uptake activity along the root axis into account. The fine root systems distal to the gauge mounting point had a total surface area of about 850 to 950 cm² with, on average, 80% (oak), 68% (beech) and 35% (spruce) of the surface area being located on root segments < 1 mm in diameter. The specific roles of different root diameter classes in water uptake are a matter of dispute (Escamilla and Comerford 2000). The profile of water uptake along a root is determined by the relative magnitudes of the radial and axial resistances (Zwieniecki et al. 2003). There is evidence that larger root diameters with thicker peridermal or exodermal tissues can be active in water absorption, but rates are much lower than in smaller roots (van Rees and Comerford 1990, Göttlein et al. 2001). Peterson and Enstone (1996) reported that root maturation reduces the extent of the uptake zone of roots. Studies of water uptake in different zones of onion roots, however, indicated that apical root regions have a higher resistance to water inflow than the mature and more suberized root segments (Barrowclough et al. 2000). Based on theoretical considerations, Zwieniecki et al. (2003) concluded that only 30% of the root length in maize roots is needed to deliver 90% of the total root water uptake. Although the precise location of water uptake is unknown for most roots, a large spatial heterogeneity of uptake along the root is likely, implying that individual tree fine root systems, as investigated in this study, have contrasting water uptake rates per unit root surface area if the root systems differ in diameter, branching and the degree of maturation. Measurement approaches that are able to locate the sites of water absorption in tree roots under field conditions are needed to identify the major resistances of water flow in the root–soil system.

Our data and those of a related study (H. Coners, unpublished results) in the Ziegelrodaer Forest in central Germany indicate that \( J_r \) may differ between superficial and deep roots as a consequence of differences in soil water content in the upper and lower profile. In the Lüneburger Heide stand, oak roots at 30 to 80 cm depth had significantly lower \( J_r \) in September 1999 than superficial roots. A likely explanation is that soil water content decreased, instead of increasing, with soil depth in the sandy soil profile of this stand. In contrast, significantly higher uptake rates for deep roots have been observed (H. Coners, unpublished results) compared with superficial roots of beech in the Ziegelrodaer Forest, and these high rates in deep roots were related to topsoil water depletion. In both stands, vertical differences in water uptake rates were apparently caused by differences in soil water content along the profile.

In conclusion, by applying miniature sap flow gauges in situ, we showed that fine roots of different temperate tree species have different water uptake capacities. Tree species that differ in maximum stomatal conductance at the canopy level also seem to differ in surface area-specific flow at the root level. Future research on root water uptake of trees should search for relationships or tradeoffs in leaf and root functioning with respect to water flow, to better understand the functional coupling of water loss and water uptake in large trees and the role of capacitance in the trunk. Water uptake capacities of tree fine roots could be genetically determined and thus vary with species, or could depend on environmental factors such as soil physical properties and water availability. It would be interesting to identify tree species with particularly high uptake rates per root surface and to trace high uptake capacities to morphological, biochemical and molecular characteristics of the root, because such a trait could enhance tree fitness in competition for water. A deeper understanding of genetic and environmental influences on root water uptake capacities is fundamental for modeling water fluxes in the rhizosphere of forest ecosystems and for assessing adaptation potentials of trees to changes in water availability.

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References


