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Tree roots: conduits for deep recharge of soil water

Abstract In previous work, we provided evidence from sap flow measurements that when root systems span soil layers of different moisture content, water is redistributed by roots in the direction of the difference in water potential. In addition to the phenomenon termed "hydraulic lift", where water is redistributed from depth to dry topsoil, the process of "hydraulic redistribution" includes downward transfer of water when the surface layers of soils with low permeability become wet after rainfall. In this paper, we support our previous findings with evidence from measurements of soil water and estimate the quantities of water transferred to depth following rain. Amounts of water stored at depth are not likely to be significant for drought avoidance by plants. However, downward transfer of water may be important to plant establishment and the reduction of waterlogging in certain soil types.

Keywords Plant roots · Hydraulic lift · Water use · Sap flow · Soil moisture

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Introduction

The movement of water through the soil-plant-atmosphere continuum is greatly influenced by plant function. Plants capture, redirect, store and release water in response to environmental and physiological stimuli and in doing so affect soil hydrology and ecology. Roots, partly as a consequence of their intimate contact with soil, and perhaps also as a benefit to growth and survival, exude as well as absorb water in response to gradients in water potential between themselves and the soil. Hence, root systems that span soil layers of different water potential can act as conduits that transfer soil water from wet soil layers to dry soil (Burgess et al. 1998; Smith et al. 1999). Further knowledge regarding the quantities of water involved and the conditions required for hydraulic redistribution is needed to determine the importance of this process to individual fine roots, individual plants, plant communities and the hydrological balance of catchments.

Whilst substantial information is available concerning the process of hydraulic lift (e.g. Caldwell et al. 1998; Horton and Hart 1998), little is known about the downward transfer of water to deep soil layers. Three recent studies have contributed details concerning this latter process, which other authors have termed either "inverse hydraulic lift" (Schulze et al. 1998) or "downward siphoning" (Smith et al. 1999). Burgess et al. (2000b) suggested that downward transfer of water is unlikely in sandy soils with fast rates of hydraulic conductivity (e.g. 30 m per day; Sharma and Hughes 1985), since an "inverted" gradient in water potential would not be established for more than a few hours following rainfall. Schulze et al. (1998) did demonstrate "inverse hydraulic lift" in very dry sand over a short measurement period (~3 days) and interpreted the importance of this phenomenon as mainly allowing the roots of plants growing in water-limited environments to penetrate dry soil layers and reach deep sources of moisture. Smith et al. (1999) estimated the proportion of daily water uptake by lateral roots transferred to deeper soil layers at 26% and suggested that this might comprise a substantial component of the soil water balance.

Recent developments in the "heat ratio method" (HRM) of measuring sap flow in woody roots (Burgess et al., in press) allow quantities of water redistributed by tree roots to be measured. We used the HRM to estimate the amounts of water transferred to deep soil layers by the roots of two eucalypt trees of contrasting growth form, following the break of season rains. By measuring changes in soil water content in conjunction with sap flow, we sought to test whether quantities of water redistributed by tree roots increased water contents of deep soil layers by amounts significant to plant ecology and soil hydrology.

Materials and methods

Site description

The research site was located west of Katanning in the agricultural zone of south-west Western Australia (33°45′ S, 117°27′ E). The site has a typical Mediterranean-type climate of cool wet winters and hot dry summers, with an annual rainfall of 485 mm (116 days with rain) and a class A pan evaporation of 1,826 mm. The soil profile is duplex (Typic Palexerult, USDA Soil Taxonomy) with an A horizon of loamy medium sand to clayey coarse sand to between 35–50 cm, underlain by a B horizon of medium to light clay with 10–20% smooth-faced lateritic gravel at depth (Burgess et al. 2000c). The soils at the site are prone to episodic waterlogging, which is largely due to the hydraulic discontinuity created by a sharp textural contrast between the A and B horizons. Water tends to pond at the base of the sandy A horizon, since the extremely low permeability of the clay B horizon restricts water entry (Tennant et al. 1992; Cox and McFarlane 1995). Historically, the conversion of vegetation in this region from functionally complex and largely perennial native plant communities to monocultures of shallow-rooted annual crops (principally wheat) has led to a hydrological imbalance. In an attempt to reduce groundwater recharge and episodic waterlogging (Eastham et al. 1994), 8-m-wide belts of a mixture of *Eucalyptus* trees (*Eucalyptus camaldulensis* Dehnh. var. obtusa Blakely 21%, *E. platypus* Hook. var. heterophylla Blakely 13%, *E. saligna* Smith 32% and *E. leucoxylon* F. Muell 34%) were planted in 1986. Tree belts were planted along contour lines spaced 100–200 m apart, with an average of 47 trees per 100 m of tree belt (yielding a within-belt density of ~600 stems ha^{-1}). The trees had an average height of 5.5 m in September 1997 (White et al., in press).

Study trees

The proximal regions of the roots of specimens from two contrasting species, a 5-m-tall river red gum (*E. camaldulensis*) and a 4-m-tall coastal moort (*E. platypus*) were carefully excavated. *E. camaldulensis* had a dimorphic root system with lateral roots confined mainly to the sand horizon and only one large taproot penetrating the clay subsoil to significant depth. *E. platypus* had a pronounced lignotuber and a relatively small taproot. During summer, predawn leaf water potentials of *E. platypus* were –4.1 MPa compared to –0.9 MPa for *E. camaldulensis*, suggesting that roots of *E. camaldulensis* accessed deep sources of water, but those of *E. platypus* did not (White et al., in press). Depth to groundwater beneath the belt of trees was approximately 7 m.

Sap flow

This study employed the HRM to measure xylem sap flow (Burgess et al. 1998; Burgess et al. 2000a). For *E. camaldulensis*, two sets of sensors were placed in the stem and taproot and single sets of sensors were placed in four major lateral roots. These lateral roots comprised 104 cm^2 of the 115 cm^2 total cross-sectional area (CSA) of all lateral roots. The taproot had a CSA of 152 cm^2. Each sensor contained two thermocouple pairs to measure sap flow at different radial depths within the root, hence there were seven measurements of sap velocity in lateral roots (one thermocouple pair was faulty) and four in the taproot. For *E. platypus*, one set of sensors was installed in the taproot (CSA=76 cm^2, n=2) and three lateral roots (CSA=122 cm^2, n=5). There were further lateral roots comprising 23 cm^2, which were too small to accommodate sensors. For each species, mean and SE values of sap velocity were calculated for all lateral root measurements and all tap root measurements and these values were then multiplied by the total CSA of roots in each class of root.

Since transfer of water between different parts of the root system (hydraulic redistribution) occurs in the absence of demand for water by above-ground parts of the plant, all measurements of sap flow reported in this paper are night-time averages calculated from half-hourly measurements made between 2130 and 0530 hours. This avoided measuring flow that was a result of transpiration. Sap flow caused by hydraulic redistribution tends to be fairly constant during the night (see Fig. 3), reflecting the standing gradient in water potential between soil layers. Measurements commenced during April 1997 and terminated in August 1998. Additional details of the experimental set-up are recorded in Burgess et al. (1998).

The long-term nature of the sap flow study created some difficulties when correcting for probe misalignment (Burgess et al., in press). Accurate discrimination between reverse and positive rates of flow using the HRM relies on measurement of final probe position at the end of the experiment when roots are severed (Burgess et al. 1998). Disturbance to probes (e.g. by animals) has the potential to alter probe positions slightly during the course of the experiment. If this happens, earlier data will be difficult to correct for probe bias. In the single instance where acute probe disturbance was identified (a sudden baseline shift in the data), corrections were made after normalising the data with reference to a corresponding and undisturbed set of measurements.

Soil moisture

Soil moisture was measured by installing Enviroscan (Sentek Australia) capacitance probes within the tree belt, approximately ~10 m distal to the study trees due to access requirements. Hourly measurements of soil moisture were made every 10 cm to a depth of 50 cm, and every 20 cm from thereon to a depth of 270 cm. Where data for adjacent depths were similar, these were averaged for clarity. As part of a separate investigation at the research site, measurements of soil moisture were also made using a neutron moisture meter and time-domain reflectometry (unpublished data). These measurements served as a reference to verify the accuracy of measurements made with the capacitance probe. Daily rainfall was also recorded.

Results

Patterns of sap flow

Night-time patterns of sap flow in the taproot and lateral roots of *E. camaldulensis* and *E. platypus* in the period immediately before and after break of season (20 February–16 April 1998) are shown in Fig. 1. Missing data are the result of intermittent electrical problems associated with high humidity. Outliers, as defined by sudden (e.g. a single, isolated data point) and unexplained (e.g. not supported by data from corresponding measurements) changes to sap flow by a magnitude beyond the normal

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Fig. 1 A Patterns of sap flow during the night in the taproot and lateral roots of *Eucalyptus camaldulensis* growing on a duplex (Typic Palexerult) soil at Katanning, Western Australia, during 1998. Values are mean rates of flow calculated from half-hourly measurements made between 2130–0530 hours. Sap velocity data for each class of root (taproot and lateral roots) were first combined by calculating average and SE values and then multiplying these values by total cross-sectional areas in each class of root. Negative values indicate reverse (acropetal) flow. **B** Patterns of sap flow during the night in the taproot and lateral roots of *E. platypus*. **C** Progression of the wetting front through the sand and upper clay horizons of a duplex soil at Katanning, following break of season rains, 1998. **D** Daily rainfall at break of season and absolute increases in the moisture content (%) of clay soils at depth beneath *Eucalyptus* trees. Equipment failure occurred on days 26–39 (19–31 March)
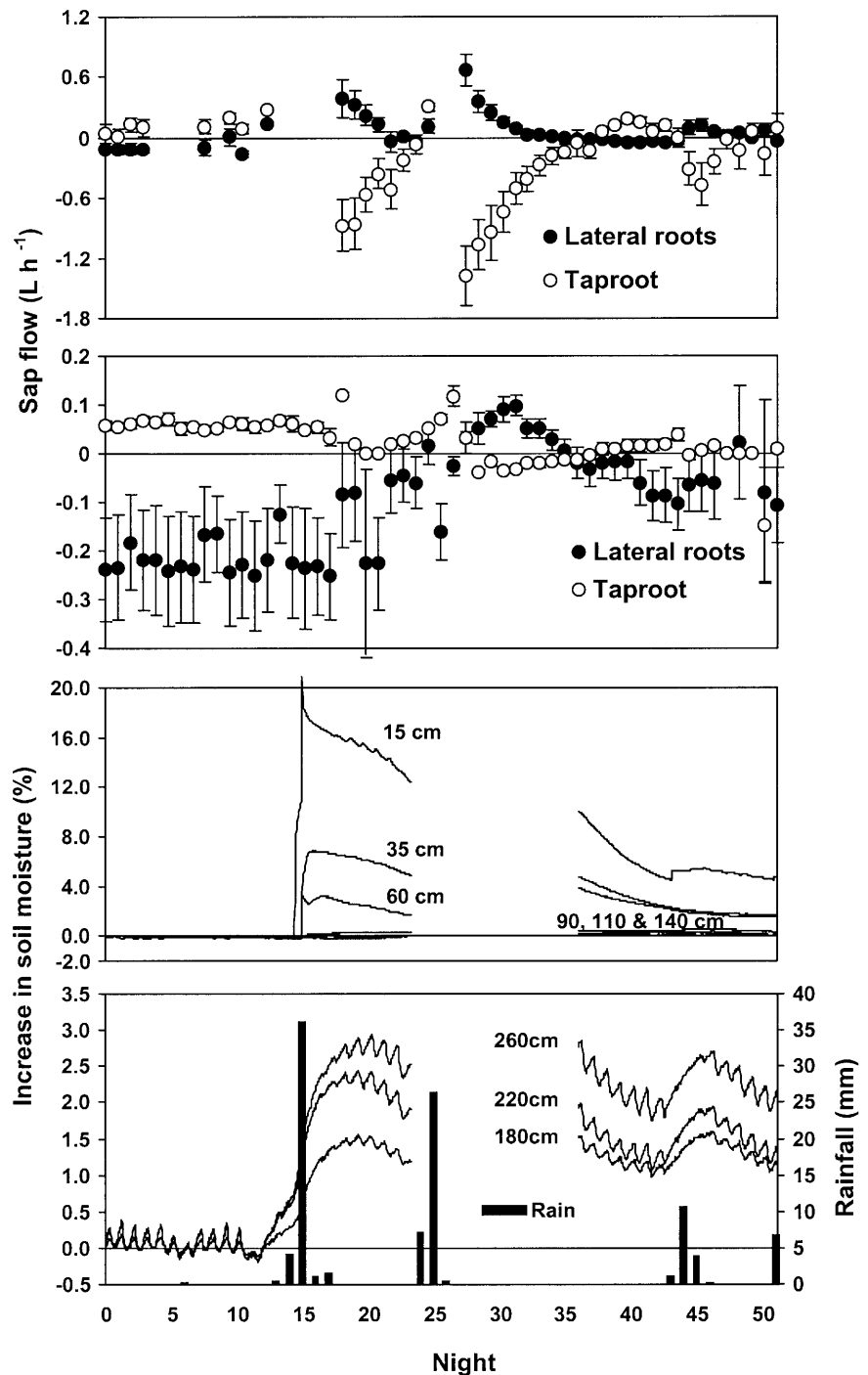
measurement range were disregarded from calculations of night-time means.

Results for *E. camaldulensis* (Fig. 1A) were similar to those obtained in our previous study of this species (Burgess et al. 1998). Rates of sap flow in the lateral roots and the taproot were inversely correlated (r^2=–0.71) during the night.

After rain (Fig. 1D), fast rates of positive (basipetal) flow in the lateral root corresponded to significant reverse (acropetal) flow in the taproot. This indicates a downward transfer of water from lateral roots to the tap-

root, the reverse of hydraulic lift. Downward flow slowed quickly between rain events and increased quickly with further rain.

Results for *E. platypus* (Fig. 1B) were similar to those of *E. camaldulensis*. Rates of sap flow in the lateral roots and the taproot were inversely correlated (r^2=–0.70) during the night. Reverse flow was strongly evident in the lateral roots prior to rain, indicating significant hydraulic lift. Following rain, the direction of sap flow in the taproot was reversed. However, the roots of *E. platypus* appeared to respond more slowly than those

Fig. 2 A Progression of a wetting front through the sandy A horizon (0–50 cm) and the upper B horizon (kaolinite clay) of a duplex (Typic Palexerult) soil associated with break of season rains in 1997 at Katanning, Western Australia. **B** Absolute increase in the moisture content (%) of clay subsoils (lower B horizon) associated with downward transfer of water through tree roots systems by hydraulic redistribution. **C** Pattern of sap flow during the night in the taproot of *E. camaldulensis* following break of season rains
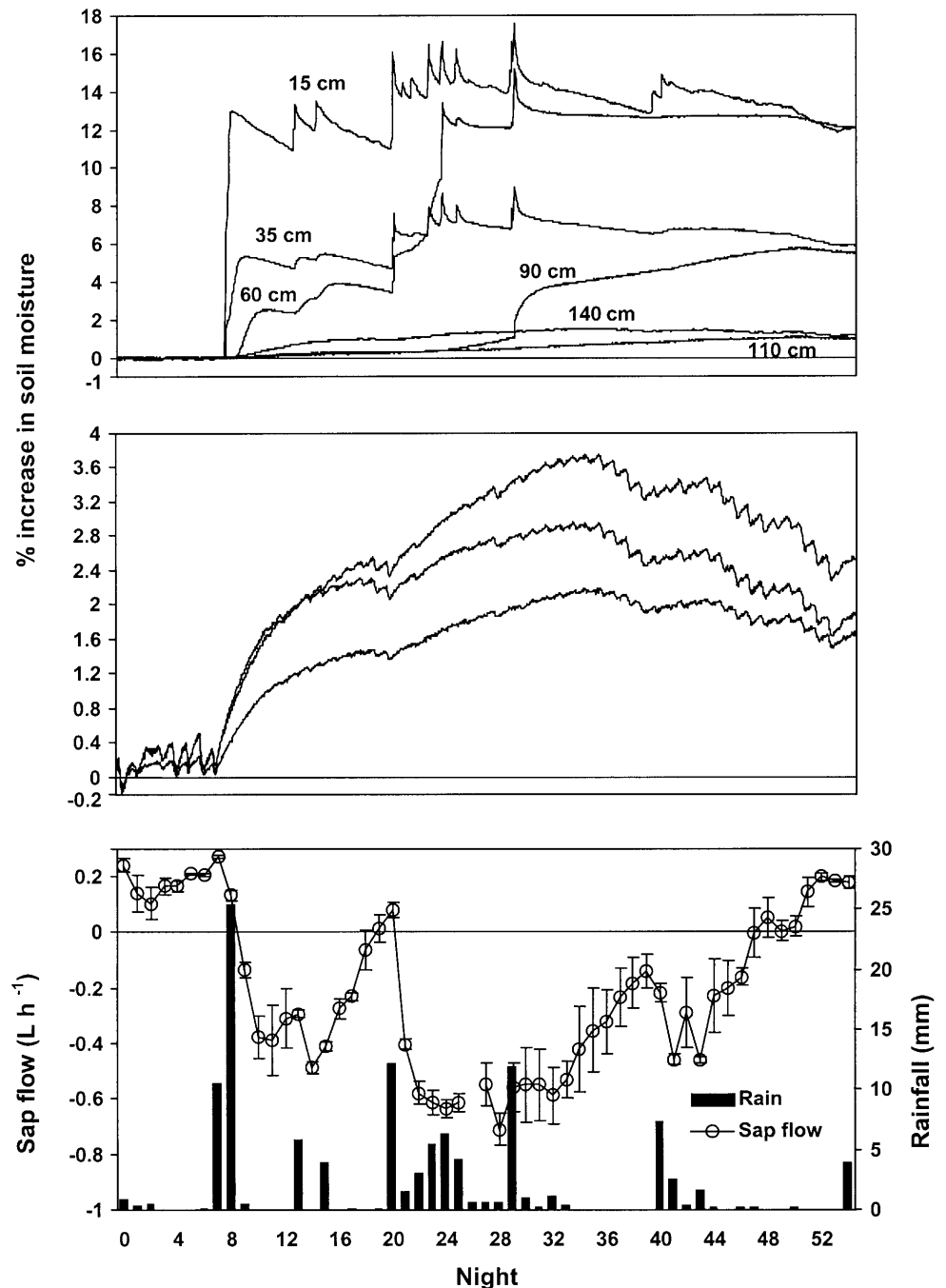
of *E. camaldulensis* in terms of the onset and reduction of hydraulic redistribution to the taproot. Furthermore, measured quantities of sap flowing down the taproot of *E. platypus* were comparatively small (Fig. 1B).

Soil moisture 1997

Soil moisture data are presented as change in soil moisture (% water content) from initial values measured immediately prior to break of season rains (Figs. 1C, D, 2A, B). In both 1997 and 1998, the initial moisture contents were approximately 7% in the sand A horizon, 15% in the upper clay B horizon and 20% in the lower clay B horizon. Total rainfall was below average in 1997 at 323 mm. Changes to soil moisture content resulting from break of season rains in 1997 are shown in Fig. 2. A wetting front progressed rapidly through the sand A horizon (upper ~50 cm soil layer) following heavy rain (Fig. 2C) beginning on day 9 (18 April).

The wetting front moved more slowly through the clay, reaching 90 cm in the upper B horizon 21 days later (day 30, 8 June). The front did not progress beyond this depth during the course of 1997 measurements. There

was a sharp, but small increase in the moisture content of clay soils at 180–260 cm depth in the lower B horizon, coinciding with break of season rains (Fig. 2B). Subsequent increases in soil moisture at these depths coincided with further rainfall events. Increases in soil moisture at depth also corresponded closely with reversal of sap flow in the taproot of *E. camaldulensis* (Fig. 2C).

Soil moisture 1998

Rainfall in 1998 was above average and approximately 160 mm greater than in 1997. The response of soil moisture contents to break of season rains was similar to that of the previous year. The wetting front did not penetrate beyond 90 cm (Fig. 1C) in response to break of season rains (a front did penetrate to depth in September due to above-average rainfall late in the season). Despite the shallow penetration of the wetting front for much of the season, soil moisture in the 180–260 cm soil layers once again increased immediately after break of season rains (Fig. 1D). These increases in soil moisture coincided with reversal of sap flow in the taproots of *E. camaldulensis* and *E. platypus* (Fig. 1A, B) in the same manner as seen for *E. camaldulensis* in the 1997 data.

Discussion

Patterns of sap flow

Measurements of sap flow in the roots of *E. camaldulensis* and *E. platypus* confirm a previously reported (Burgess et al. 1998) pattern of hydraulic redistribution within root systems. Water acquired by roots growing in moist soil and excess to the requirements for transpiration was transferred to roots growing in relatively dry soil.

Whilst strict comparisons between species cannot be made using only a single specimen of each species, our data indicated differences between the two trees in their response to break of season rains that may be related to their differing morphologies. Downward transfer of water in response to rainfall began more slowly and was less pronounced in the comparatively shallow-rooted *E. platypus* compared to *E. camaldulensis* (Fig. 1). After rainfall ceased, downward transfer also declined more slowly in *E. platypus*. The lag in the onset of downward transfer of water might arise if the majority of active fine lateral roots of *E. platypus* were distributed deeper in the profile, or in soil less easily wetted than that under *E. camaldulensis*. Alternatively, large hydraulic resistances in the lignotuber of *E. platypus* (Myers 1995) may have hampered transfer of water between the different parts of the root system that meet here. Slower transfer of water by the roots of *E. platypus* would cause the "inverted" gradient in water potential caused by rain to persist longer and reach a later peak – if recharge of the upper layers continued to exceed infiltration/hydraulic

redistribution. We observed persistent waterlogging in soil under *E. platypus* which was not seen under *E. camaldulensis* only 5 m distant. Whilst soil properties and topography might also have contributed, the shallow, lignotuberous root system of *E. platypus* possibly transferred water less effectively than the deeper dimorphic root system of *E. camaldulensis*.

A second difference between the two sample trees is that quantities of water flowing down the taproot of *E. platypus* appeared disproportionately small when compared to flow in lateral roots (Fig. 1B). Our taproot measurements were apparently substantially underestimated. Whilst it was beyond the scope of this study to investigate spatial variation in the speed and direction of sap flow within the lignotuber, vessel arrangement in lignotubers is often complex and not conducive to simple measurement of sap flow. Burgess et al. (2000b) measured sap flow in the taproot of *Banksia prionotes*, which has spiralled vessels, and suggested that the angle of flow and distribution of wounding in relation to probe alignment can cause underestimation of sap flow.

Soil moisture

Prior to the break of season, diurnal variation in soil water content at 180–260 cm indicated that plant roots were active (see days 0–11 in Fig. 1D). The diurnal changes were closely related to the pattern of transpiration/sap flow measured in the trunk (data not shown); daytime transpiration corresponded to a decrease in soil water content. Water content recovered during the night either due to influx from surrounding bulk soil or by release of water from roots. The influence of processes such as direct soil evaporation can be discounted since the variation in water content was absent in shallower soil layers. This, and the negative relationship between moisture content and diurnal variation in soil temperature, also argues that temperature artefacts were not responsible (Paltineanu and Starr 1997). If efflux of water from roots caused the increase in soil moisture during the night, this water must have been acquired by roots with access to water in deeper soil layers (i.e. below 270 cm).

Diurnal variation in soil water content was not observed in the shallow soil layers, despite diurnal variation in patterns of sap flow in the lateral roots of both species consistent with hydraulic lift. Since the overall pattern of sap flow in lateral roots responded quickly to rain and mirrored closely the overall changes to soil moisture in shallow soil layers, to argue that roots were not active in these layers is difficult. Instead, either diurnal changes to soil moisture were too small to be detected by the capacitance probe or were patchy and beyond the small zone of sensitivity (a few centimetres; Paltineanu and Starr 1997; Chanzy et al. 1998) of the capacitance probe in the shallow soil layers.

Following the break of season, the wetting front transmitted rapidly (~2 days) through the sand (0–50 cm) horizon. Further rain, approximately 2 weeks later,

moved the wetting front into the clay B horizon (presumably after the sand horizon was saturated), but it did not progress beyond about 90 cm. We concur with Tennant (1976) that infiltration of rainfall into yellow duplex soils beyond 1 m is rare because of their low permeability.

Despite rainfall wetting the soil profile to a depth of less than 1 m, the moisture content of clay layers between 180–260 cm increased sharply *immediately* following break of season rains. One interpretation might be that hydrological processes such as capillary rise or increased piezometric pressure at depth were the cause of this increase. However, if this were the case, the 280–180 cm layers should have been affected in a sequence reflecting rates of hydraulic conductivity, with the deepest layers wetting first as water was moved upwards from depth. A close examination of data for individual soil depths showed no such sequence; instead, there were almost simultaneous responses at 270, 250, 230 and 210 cm over a matter of hours. The slow hydraulic conductivity of the kaolinite clay at these depths (only a few mm/day; Tennant et al. 1992) precludes the possibility of water infiltrating from any direction at such rates. Instead, the concerted increase in soil moisture over this soil band was most likely the result of hydraulic redistribution of water by plant roots dispersed throughout this horizon (Burgess et al. 1998). This hypothesis is strongly supported by the coincident reversal of sap flow in the taproots of *E. camaldulensis* and *E. platypus*.

Interestingly, positive flow in the taproots did not deplete soil moisture in the 180–260 cm soil layers as much as equivalent rates of reverse flow increased soil moisture. Thus, less water was extracted from than deposited to these layers. We cautiously suggest that most water extracted by taproots arises from wetter soil, presumably at depths greater than the 180–260 cm soil band (i.e. at the capillary fringe for *E. camaldulensis*). After the "break of season", water acquired from the wetted topsoil would not primarily be redistributed to roots growing in the wettest deep soil layers but to roots terminating in the driest layers (e.g. the 180–260 cm soil band). Sap flow in the upper regions of the taproot clearly reflects the integrated effect of uptake and efflux in the distal regions of the root and thus quantities of sap flow in the taproot cannot be directly compared with changes in the quantity of water in specific soil layers.

Other soil layers

No significant increase in moisture content was observed in the 90–140 cm soil layers that might be ascribed to hydraulic redistribution. Likewise, there was no evidence of uptake from these layers prior to the break of season. We conclude that roots were not abundant in these layers, presumably because of the dimorphic pattern of root growth possessed by most trees at the study site.

Deferred water use and drought avoidance

The eventual penetration of a wetting front into the 180–260 cm soil layers by spring (September) 1998 and equipment failure during late winter (August) 1997 prevented monitoring of the likely fate (through the drying cycle) of hydraulically redistributed water in the deep soil layers. However, a number of inferences can be made. Within the 170–270 cm depth of soil, the largest rise in water content during 1998 averaged 2.3%, or 23 mm. During a 13-day period without rain, plants extracted water from these layers at a rate of approximately 1 mm (0.94% soil water content) per day. At this rate, the maximum observed amount of water stored at this depth would be depleted within 25 days. Figures for 1997 were almost identical: a peak of 27.8 mm of water was transferred as a result of 96 mm of rain over 28 days. This water was depleted at rates up to 1 mm/day, suggesting that this additional source of water would persist no more than 28 days, and probably less, since rates of depletion would increase as the season progressed.

We conclude from these simple predictions that redistributed water is unlikely to make a significant contribution to drought avoidance over the summer period but may benefit plants during early spring, when growth and transpiration rates increase following winter conditions. Delayed depletion of topsoil water may also prolong and enhance nutrient availability into spring/early summer when flowering and shoot extension are important. For plants such as *E. camaldulensis*, which also have roots reaching the water table, the main benefit may be to reduce the hydraulic resistance of the root system by involving a greater surface area of roots in uptake (Simonneau and Habib 1994).

Does the plant forfeit any redistributed water?

The above comparison of amounts of water exuded into dry soil versus rates of re-extraction suggests that redistributed water is re-acquired by the plant relatively quickly. In soils with slow rates of hydraulic conductivity, the water should remain close to the roots. Furthermore, drainage is not likely to result from hydraulic redistribution, since the motive for water transport would decrease as water potentials in the deeper soils increase. Unlike hydraulic lift, water redistributed to deeper layers is not subject to evaporation and thus the only probable source of depletion is extraction by plant roots.

Quantities of sap flow compared to changes
in soil moisture

Whilst more extensive sampling of both trees and soil would be required to link the hydrological processes observed here for plants and soil, some broad comparisons can be gained by extrapolating the available data to the
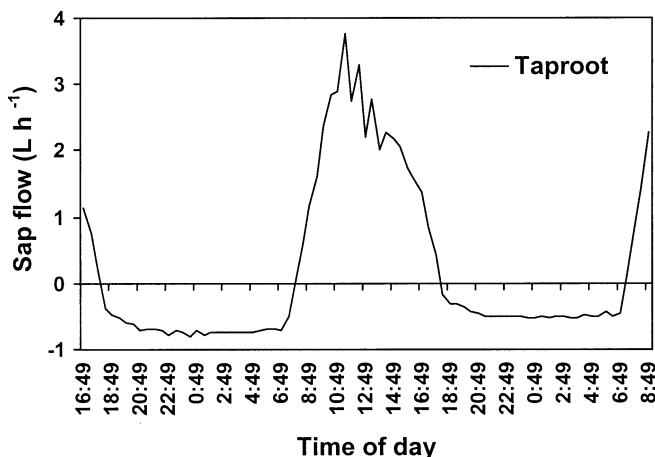
Fig. 3 An example of the diurnal pattern of sap flow in the taproot of *E. camaldulensis*, showing the duration of reverse flows associated with hydraulic redistribution of water by the root system

tree belt as a whole. Using the example of *E. camaldulensis*, for which the data are most extensive and reliable, the following can be surmised. Within the soil layers measured, ~28 mm of water was exuded by deep roots over 30-day period following the break of season in 1997. This amounts to 28 l per 1 m² of ground surface or 22,400 l over a 100-m length of the 8-m-wide tree belt (800 m²). Each of the 47 trees comprising the 100-m length of tree belt would therefore be required to redistribute 477 l, or 16 l per day. Since hydraulic redistribution generally persisted for a 12-h night-time period (see Fig. 3), the required rate of reverse flow through the taproot would be 1.3 l/h. The corresponding rate of reverse flow measured in the taproot of *E. camaldulensis* peaked at about 0.6 l/h and averaged about 0.3 l/h, i.e. about one-quarter of the amount expected. This comparison suggests that the amounts of water which flowed down the taproot and amounts of water that appeared in the subsoil were not greatly dissimilar; however, other processes may also have brought water to the deep soil layers. Water from the capillary fringe may have also been transported by roots to the 1.7–2.7 m layers, in addition to that transferred from surface layers, without this water flowing through the proximal regions of the taproot where sensors were placed. Similarly, other "sinker" roots (e.g. Burgess et al. 2000b) may span the soil horizons from the surface to this depth and contribute to redistribution. Secondly, the presence of macropores or preferred pathways for water infiltration (Johnston 1987) may have contributed to recharge of subsoil near the capacitance probe. Since such pathways lead to patchy recharge and may be angled, infiltration from this source would not necessarily be detected first in shallow layers by the capacitance probe as would be the case with the progression of a wetting front.

Other implications

Hydraulic redistribution should increase total water uptake by removing excess water from the topsoil and out of the reach of evaporation, shallow-rooted competitors, runoff and lateral flow (on sloping land). Augmented uptake of water from topsoil may also increase capture of mobile nutrients such as nitrogen. Nutrient status may also be improved if mineral uptake from deeper soil layers follows re-extraction of water redistributed to depth (Schulze et al. 1996).

In environments where infiltration is reduced by subsoils with low permeability, by hardpans, or by hydraulic discontinuity between soil layers, we suggest that hydraulic redistribution may be a primary pathway for wetting subsoil. By bridging soil layers, and acting as conduits for water transport, root systems may thus avoid the "twin evils" of waterlogging (Cox and McFarlane 1995) in the topsoil and impenetrably dry subsoils (Stone and Kalisz 1991). The latter may be extremely important to the establishment of young phreatophytic plants whose roots have not reached the water table (Burgess et al. 1998; Schulze et al. 1998).

The net changes to soil moisture arising from downward hydraulic redistribution reported in this paper are larger than those generally recorded for hydraulic lift (Caldwell et al. 1998). This is not surprising, since the hydraulic conductivity of both soils and xylem are often greatest during wet weather, whereas transpiration rates are likely to be low (Williams et al. 1993). Thus, transfers of water should be large and the resulting deposits of water are likely to persist for a substantial period of time. Downward transfer of water may therefore be more significant than hydraulic lift in terms of its magnitude and may be non-trivial where isotopic and hydrological models of water movement within the soil-plant-atmosphere continuum are concerned (Burgess et al. 2000c).

Conclusions

Tree roots transfer significant quantities of water downward to dry soil layers when surface soil layers become wet following rain. The benefits of this modification to the external environment include reduced waterlogging in surface soils and increased moisture content in dry subsoils. The latter are of some significance to the growth of deep roots through otherwise dry soil. Further benefits may include improved nutrient status due to increased uptake of water from surface layers and increased water availability for a number of weeks following rain. In terms of plant establishment, the suggestion of Schulze et al. (1996) that deep root growth follows wetting fronts might be modified to "wetting fronts follow deep root growth", at least in soils where wetting fronts do not penetrate deeply.

The differences in amounts of water redistributed by the two contrasting tree specimens we studied presumably arose because of the differing distributions and hy-

draulic architecture of their root systems. Cataloguing such features of root systems for various species would be useful for predicting the role of vegetation type in governing seasonal and spatial variation in water availability.

The distribution of roots in deep soil layers is poorly described compared to shallow layers. Relating measurements made in the basal regions of taproots (which reflect the water balance of the whole root) to amounts of water acquired/released in specific soil layers is thus difficult. We suggest further quantification of the influence of hydraulic redistribution on the water balance of the rhizosphere and landscape should be based on detailed measurements of soil moisture and perhaps the use of isotopic tracers. Sap flow methods will help in investigating the physiological constraints and functional role of specific plant ecotypes.

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