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## The redistribution of soil water by tree root systems

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**Abstract** Plant roots transfer water between soil layers of different water potential thereby significantly affecting the distribution and availability of water in the soil profile. We used a modification of the heat pulse method to measure sap flow in roots of *Grevillea robusta* and *Eucalyptus camaldulensis* and demonstrated a redistribution of soil water from deeper in the profile to dry surface horizons by the root system. This phenomenon, termed “hydraulic lift” has been reported previously. However, we also demonstrated that after the surface soils were rewetted at the break of season, water was transported by roots from the surface to deeper soil horizons – the reverse of the “hydraulic lift” behaviour described for other woody species. We suggest that “hydraulic redistribution” of water in tree roots is significant in maintaining root viability, facilitating root growth in dry soils and modifying resource availability.

**Key words** Plant roots · Hydraulic lift · Water use · Sap flow

### Introduction

Use of soil water resources by vegetation largely determines the agronomic, ecological and hydrological outcomes of plant growth. Changes to the hydrological balance that accompany the clearing of native vegetation and forested catchments can lead to salinisation and land degradation (Eastham et al. 1994; Nepstad et al.

1994) and emphasise the need to understand how different plant species use soil water. Increasing evidence of the transfer of water from deep soil layers to dry soil by plant root systems (termed “hydraulic lift” by Richards and Caldwell 1987), strongly suggests that existing hydrological and physiological models of water uptake and loss to the atmosphere by plants require further knowledge of the significance and extent of such transfers.

Earlier this decade, evidence for hydraulic lift was considered inconclusive (Vetterlein and Marschner 1993). There are now data for nearly 30 species which show that root systems can facilitate transfer of water from deep layers to surface soil layers (Caldwell et al. 1998). This process may significantly improve plant water and nutrient status, as well as provide benefits to neighbouring plants (Caldwell and Richards 1989; Caldwell 1990; Dawson 1993) and even soil biota (Duncan and Elmorshedy 1996). While the number of reports of hydraulic lift has increased, its ecological importance is yet to be fully determined.

Most evidence for hydraulic lift has come from measurements of soil water potential or content near plant roots and often has been accompanied by the use of stable isotopes to trace water sources (Caldwell and Richards 1989; Dawson 1993, 1996; Emerman and Dawson 1996). As most studies to date have described hydraulic lift with reference to changes in soil water potential, little is known about the movement of water within the root. Measurement of sap flow within root systems is one way to study this phenomenon more closely.

A number of different types of sap flow gauge have been applied to roots of woody perennials in order to determine their patterns of water use (Cabibel and Do 1991; Green and Clothier 1995; Lott et al. 1996; Green et al. 1997). The “constant heat balance technique” measures the mass flow of sap on the basis of heat dissipation by convection (Lott et al. 1996; Smith and Allen 1996), but is easily disrupted by fluctuations in ambient temperature (Khan and Ong 1995; Lott et al. 1996). The bulky insulation required to prevent interference from

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changes in soil temperature makes this technique difficult to install on roots. A second type of device utilises a pulse of heat as a marker to measure sap velocity and has been used successfully on stems of a wide variety of species in recent years (Barrett et al. 1995; Hatton et al. 1995; Dawson 1996; Smith and Allen 1996). The most common method of this type is known as the "compensation method/technique" (Edwards et al. 1996). It has been used to study water flow in roots as well as stems (Green and Clothier 1995; Moreno et al. 1996), but the method is inaccurate at the low rates of flow (Swanson and Whitfield 1981; Cohen et al. 1993; Hatton et al. 1995) (e.g.  $V_h < 3.6\text{--}7.2\text{ cm h}^{-1}$ ; Becker 1998) common in individual roots. Under these conditions, diffusion of the heat pulse by conduction is more rapid than the movement of the heat pulse by convection (the component of heat transport related to sap flow). This results in an overestimation of sap flow (Becker 1998). A recent development that represents a compromise between the above methods (Granier et al. 1994) has also been used on roots (Cabibel and Do 1991), but is unable to determine direction of flow.

In view of the difficulties associated with currently available techniques, we developed a modified heat pulse technique to measure sap flow in roots of woody plants. The objectives of this study were to compare the modified technique with the compensation method and to use it to determine the pattern and direction of water uptake/transfer by the roots of two tree species.

## Materials and methods

### Theory

Much of the work involving sap flow measurement relies heavily on the early work of Marshall (1958). We have adopted one of his suggestions, namely that temperature probes placed at equal distances down- and upstream from a heater, rather than at unequal distances as with the compensation method, allow sensitive measurement of low rates of sap flow. Swanson (1983) conducted extensive theoretical and experimental analysis of the method of Marshall (1958) and Hogg and Hurdle (1997) have recently applied a similar technique to tree stems. However, such an approach has not been previously tested for its ability to measure extremely low rates of sap flow in roots. The modified technique does not require a heat pulse to move a specific distance within a limited time, but instead compares the heat transported to points down- and upstream from a heat source. Slow velocities and direction of flow can be accurately measured using this technique, which we call the "heat ratio method".

### The heat ratio method

When a heater is implanted into the xylem tissue of a woody plant at a central point between two temperature sensors such that they form a line parallel with the sap flow, heat pulse velocity ( $V_h$ ) is derived (Marshall 1958) as follows:

$$V_h = \frac{k}{x} \ln \left( \frac{v_1}{v_2} \right) \text{ cm s}^{-1} \quad (\text{Eq. 1})$$

where  $k$  is the thermal diffusivity of wet wood,  $x$  the distance between the heat source (heater) and temperature sensors, and  $v_1$  and

$v_2$  are the increases in temperature (from ambient) at equidistant points downstream and upstream, respectively,  $x$  cm from the heater.

### Application

The instrumentation required for this method is similar to that of the compensation method (Swanson and Whitfield 1981). In the present study, we placed copper-constantan thermocouple temperature probes 0.6 cm down- and upstream from a 38- $\Omega$  line heater in order to measure the increase in temperature produced by a 6-second pulse of heat. Probes were greased before inserting them into holes drilled radially into a root or trunk (stem), correctly spaced and aligned along the root/trunk axis. A steel drill guide was used to ensure accurate placement of the holes. Proximal root collars were carefully exposed around the stem base of each tree to avoid damage and care was taken to install probes on smooth, straight sections of roots and trunk, away from branch nodes. Temperatures were logged whilst their ratios were most constant (between 60 and 100 s after the release of the heat pulse) and calculations were averaged.

The initial measurements were made at the International Centre for Research in Agroforestry (ICRAF), Machakos Station, Kenya (1°33' S, 37°14' E, altitude 1660 m), which has a bimodal rainfall distribution with two clearly defined wet and dry seasons annually. Soils are a shallow (120 cm or less) well-drained sandy clay-loam overlying petroplinthite (murrum). Here, a comparison of the sensitivity and accuracy of the heat ratio method and the compensation method (as described by Swanson and Whitfield 1981) was made on the trunk of a 5-m-tall, 5-year-old silky oak (*Grevillea robusta* Cunn.). Measurements began in June 1996. The heat ratio method was then applied to two lateral roots on the same tree, and a further two lateral roots were instrumented for the compensation method. As results for both roots measured by each method were qualitatively similar, data for only one root representing each method is presented. Measurements on roots commenced in October 1996 at the end of a 4-month dry season and continued through the wet season until early December 1996.

A second set of experiments was conducted west of Katanning in the agricultural zone of south-west Western Australia (33°45' S, 117°27' E), which has a typical Mediterranean-type climate of cool wet winters and hot dry summers. Soils are "duplex", made up of sand (generally 50 cm) over heavy clay. Here, all five major lateral roots, taproot, secondary sinker (of approximately the same size as the taproot) and the trunk of a 5-m-tall, 6-year-old river red gum (*Eucalyptus camaldulensis* Dehnh. var. *obtusa* Blakely.) were instrumented with both the compensation method and the heat ratio method. *E. camaldulensis* at Katanning had a dimorphic root system with lateral roots confined mainly to the sand horizon and only the taproot/sinker penetrating the clay subsoil. Measurements commenced during April 1997, at which point no significant rain had been recorded at the site for the previous 6 months. Sap flow measurements on a 4-m-tall, 6-year-old moort (*E. platypus* Hook. var. *heterophylla* Blakely.) commenced in June 1997 and these, along with measurements on *E. camaldulensis* are ongoing. Unpublished data collected for *E. platypus* confirm the patterns of sap flow reported here for *E. camaldulensis*.

Simultaneous measurement of  $V_h$  by the two methods allowed  $k$  (initially based on published values from Marshall 1958) to be estimated for use with Eq. 1, following Cohen et al. (1993). Data from both methods were collected every 30 min using a datalogger (model CR21X, Campbell Scientific Inc. Logan, Utah, USA). Since results among lateral roots of *E. camaldulensis* were similar, as were the results for the taproot and the secondary sinker, only one representative lateral root and the taproot are presented for clarity.

### Validation

At the end of both experiments,  $V_h$  measured in the roots by the heat ratio method was tested empirically for zero bias arising from

errors in probe spacing by severing the roots to stop all sap flow. When the measured  $V_h$  differed from 0, Eq. 2 was used to determine the probe spacing error.

$$4kt \ln\left(\frac{v_1}{v_2}\right) = (x_2^2) - (x_1^2) + 2V_h t(x_1 - x_2) \quad (\text{Eq. 2})$$

where  $x_1$  and  $x_2$  are distances in centimetres of the up- and downstream probes, respectively, and  $t$  is the time of measurement (in seconds) after the release of a heat pulse (Marshall 1958). At  $V_h = 0$ , Eq. 2 yields:

$$x_2 = \sqrt{\left(4kt \ln\left(\frac{v_1}{v_2}\right) + x_1^2\right)} \quad (\text{Eq. 3})$$

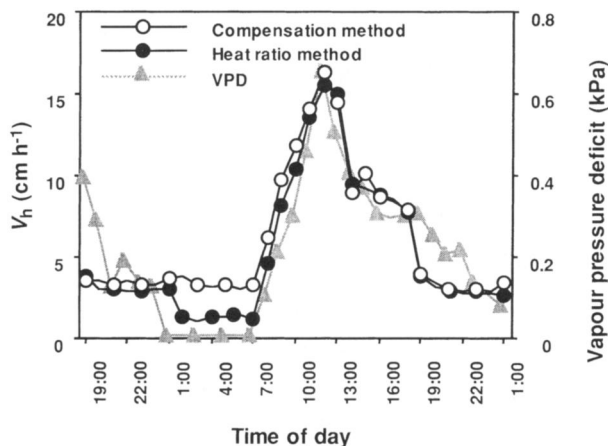
where  $x_2$  is designated the incorrectly spaced probe, and  $x_1$  is assumed to be correctly spaced at 0.6 cm. Since it was not known whether one probe was spaced under the designated 0.6 cm, or whether the other probe was spaced over 0.6 cm, or if both probes partly contributed to the error, the above equation was also solved assuming  $x_1$  was incorrectly spaced. The solutions were then averaged to yield an intermediate solution to the two possible solutions. In practice, all solutions produced similar results. Corrected  $x_1$  and  $x_2$  values and measured values of  $v_1$  and  $v_2$  were then used with Eq. 2 to calculate the corrected  $V_h$ .

In order to compare among methods, species and site, the data are presented as  $V_h$  (the primary measurement of both methods) which is an index of the rate of sap flow independent of the size of the root or trunk. Isolated missing data points (due to transient electrical noise) are interpolated, but where more than one occurs in succession, data are not interpolated.

## Results and discussion

### Comparison of heat ratio method and compensation method

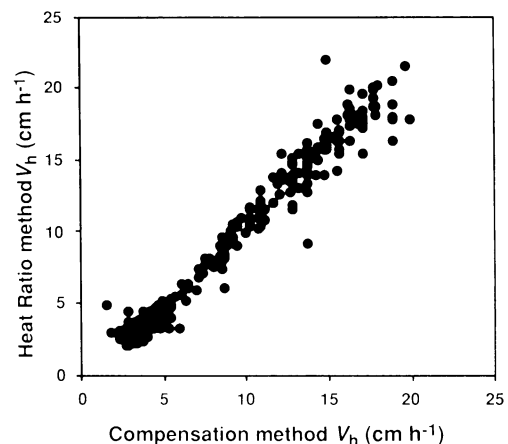
Both the heat ratio and the compensation methods of measurement of  $V_h$  agreed closely in the trunk of *G. robusta* when sap flow was fast (Fig. 1). Over ten sequential diel cycles when sap flow rates were consistently within the measurement range of both methods



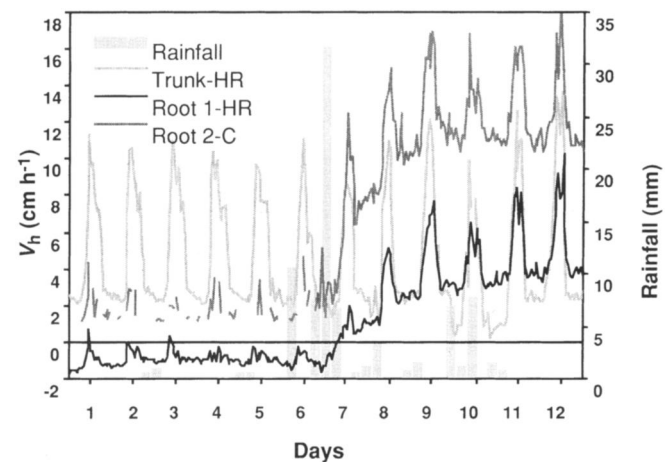
**Fig. 1** An example of diurnal variation in heat pulse velocity ( $V_h$ ) measured by the compensation method (open circles) and the heat ratio method (filled circles) in the trunk of a 5-year-old *Grevillea robusta*. Vapour pressure deficit (VPD) (filled triangles) was estimated from meteorological data collected at ICRAF Machakos Field Station, Kenya

(i.e.  $> \sim 3.6 \text{ cm h}^{-1}$ : Becker 1998),  $V_h$  measured by each method was correlated at  $r^2 = 0.99$  (Fig. 2). However, estimates consistently differed during periods when sap velocity was slow. For example, the heat ratio method measured a sharp reduction in sap flow rate (from  $\sim 4 \text{ cm h}^{-1}$  to  $\sim 1 \text{ cm h}^{-1}$ ) coinciding with low vapour pressure deficits that occurred on foggy nights (McAneney et al. 1992). On the other hand, no changes in rates of flow were detected by the compensation method during these conditions, resulting in overestimation of sap flow.

Measurements on the four lateral roots of *G. robusta* were similarly informative. The compensation method was largely ineffective in measuring sap flow in lateral roots during dry conditions (Fig. 3). Only the highest



**Fig. 2** The relationship between measurements of heat pulse velocity ( $V_h$ ) using the heat ratio method and compensation method on the trunk of a 5-year-old *G. robusta*. During this period (22 November – 2 December 1996), values of  $V_h$  generally remained within the measurement range of both techniques



**Fig. 3** Hourly averages of heat pulse velocity ( $V_h$ ) (6–17 November 1996) measured by the heat ratio (Root 1-HR) and compensation (Root 2-C) method in two lateral roots of *G. robusta* at Machakos Field Station, Kenya. Negative flow in Root 1-HR indicates flow away from the trunk, towards the root tips. Missing data in Root 2-C are due to disruption of the compensation method by reverse, or extremely slow sap flow

rates of flow (i.e.  $> 3\text{--}4\text{ cm h}^{-1}$ ) could be measured reliably. In contrast, the heat ratio method measured flow rates effectively throughout the diurnal cycle. Data collected by the two methods over an 11-month period in the lateral and taproots of *E. camaldulensis* and *E. platypus* confirm the inadequacy of the compensation method at low rates of flow, as well as the similarity between methods at  $V_h > \sim 4\text{ cm h}^{-1}$ .

#### Hydraulic redistribution of water

Before rain (days 1–6, Fig. 3), rates of flow in lateral roots of *G. robusta* were negative (i.e. moving away from the stem base towards the root tips) during the night and at lower rates of transpiration and were only positive during periods of high transpiration demand (i.e. at midday). This pattern of sap flow strongly suggests “hydraulic lift”. After the onset of rain (day 7 onward), sap flow was positive in the lateral roots as water was quickly taken up from the surface layers. Once the shallow soil layers were moist, water continued to be taken up by the lateral roots during the night even when sap flow in the trunk was negligible due to fog (see for example nights 9 and 10, in Fig. 3). An estimate of the volume of sap flowing in the lateral roots and the trunk (based on the area of conductive xylem tissue in the trunk and lateral roots and  $V_h$ ) suggests that the four lateral roots were absorbing twice the amount of water required by the trunk on dry nights and 4 times that required on foggy nights. Water acquired from the rehydrated surface soil layers may have been used for “refilling” the stem reservoir in the xylem parenchyma, or moving to roots in deeper and drier parts of the soil profile. The observation that nocturnal sap flow in roots did not progressively decrease during nights when vapour pressure deficit  $VPD = 0$ , suggests that the water was not simply being acquired for the progressive recovery of turgor in xylem parenchyma, but was moving into the roots in the dry deep soil horizons.

A study with *E. camaldulensis* confirmed the suggestion of transfer of water from wetter, shallow layers to deeper, drier parts of the soil profile. Prior to significant rainfall, nocturnal sap flow in the taproot of *E. camaldulensis* was positive in agreement with movement of water from deep in the profile (Fig. 4). At the same time, sap flow in the lateral roots was negative demonstrating that water lifted from the deeper subsoil moved into shallow lateral roots which were in dry soil (i.e. hydraulic lift). After rain, however, this pattern was reversed (Fig. 4). Clearly, water moved from the shallow lateral roots to deeper taproots when the surface soil layers were moister than the deeper profile. As the gradient in soil water potential gradient with soil depth fluctuated due to wetting, drying and further wetting, nocturnal flows in tap and lateral roots also fluctuated (Fig. 5) and were strongly and inversely correlated ( $r^2 = -0.99$ ). These data support the hypothesis that there was a reversal of “hydraulic lift” and strongly

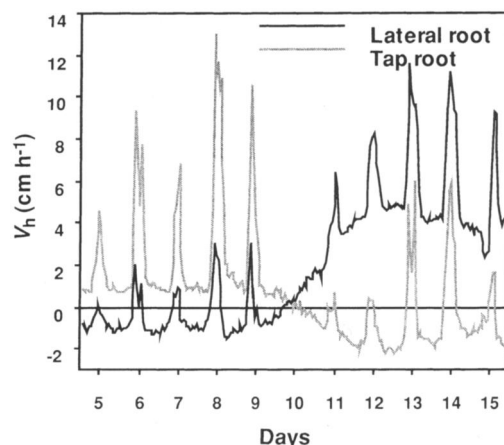


Fig. 4 Diurnal sap flow pattern in the taproot and a single representative lateral root of *Eucalyptus camaldulensis* for 5 days before and after break of season rains (14–24 May 1997) at Katanning, Australia. Day numbers correspond to the night numbers in Fig. 5, and tick marks represent midday. Data shown are hourly averages of  $V_h$ .

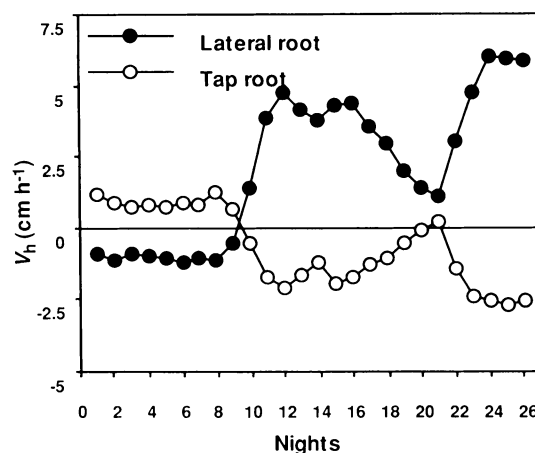


Fig. 5 Nocturnal heat pulse velocity measured by the heat ratio method in the taproot and a single lateral root of *E. camaldulensis*, 10 May–4 June 1997. Measurements of  $V_h$  between 8:30 p.m. and 5:00 a.m. were averaged. The break of season rains occurred on night 9 (19 May) and further significant rain (12 mm) occurred on night 21.

suggest that water is redistributed whenever the water potential of roots is unequal. This makes the term “hydraulic lift” inappropriate for our observations. Instead, “hydraulic redistribution” is a more comprehensive description of the observed phenomenon.

Since measurement of sap flow does not demonstrate per se that water moved out of roots into the soil, the possibility that reverse flow was due to refilling of root tissue capacitance must be considered. However, two features of the data provide evidence that this is not the case and that water did move from the root to the soil in accordance with the gradient in water potential. Firstly, “reverse” flow in the taproot increased progressively during some nights (for example nights 10 and 11, Fig. 4), when positive flow in the lateral root also in-

creased progressively (i.e. uptake by the lateral root). Since maximum tissue water deficits arising from transpiration occur prior to sunset and decrease during the night, it seems unlikely that sap flow to refill the root will *increase* during the dark period. A more probable scenario is that rainfall during nights 10 and 11 (approximately 26 mm) progressively increased the gradient in water potential between soil layers, leading to an increase in hydraulic redistribution by the root system. Secondly, the data contain examples when reverse flow into a root exceeded flow out of the root for a number of days in succession. For example, during Days 5–10 in Fig. 4 (prior to rain), net sap flow *to* the lateral root was more than three times greater than sap flow *from* the lateral root. Similarly, after rain (Days 10–15), more than twice as much sap flowed to the taproot than from it. The data argue strongly that the quantity of sap flowing in reverse through the roots was too great to simply refill the root tissues and that the water was leaving the fine roots and entering the soil.

#### Ecophysiological Implications

Hydraulic redistribution of water by plant root systems may facilitate a number of important physiological functions. A number of authors (see for example, Dawson 1993) have suggested maintenance of fine root viability in dry soil is a key function of hydraulic lift. Improvements to plant nutrient and water status are likely results of this. In the present study, the rapidity with which lateral roots acquired water from the newly wetted topsoil argues strongly that fine roots in the topsoil were maintained in a functional state throughout the dry season. In contrast to the roots of certain crop species which took up to four days after rain for water and nutrient uptake to recommence even when deep roots were in moist soil (Brady et al. 1995), the lateral roots of the trees in this study showed a rapid increase in water uptake on the day of the “break of season” rainfall. The maintenance of an active root system also allows a rapid response to small rainfall events. Such opportunistic uptake is likely to increase the plant’s success as a competitor for water.

The transfer of water away from wet topsoil to deeper, dry layers prevents shallow-rooted competitors from utilising the water and also reduces losses by soil evaporation. This allows plants to maximise their resource acquisition during periods of high water availability and to “store” the water for use later in the season when the shallow soil layers are dry. This may be an important mechanism for drought avoidance by plants growing in climates having a short, intense wet-season (e.g. semi-arid, Mediterranean and sub-tropical climates). If shallow soil water is redistributed by trees out of the reach of shallow rooted species, positive plant-plant interactions suggested to result from hydraulic lift (Emerman and Dawson 1996), such as “water parasitism” (Caldwell and Richards 1989), may be counteracted.

In view of the ability of “hydraulic lift” to operate in reverse, we also propose that the growth and viability of deep roots in extremely dry subsoils may be supported by water transferred from wetter topsoils. Such a mechanism may explain how phreatophytic species become established in extremely dry environments, since it would facilitate root growth through dry subsoil allowing the plant to reach deep water tables. At our Katanning site, up to 7 m of extremely dry clay must be penetrated for tree roots to access groundwater.

Transport of water from the topsoil to deep soil layers by tree roots partially bypasses the normal process of infiltration. Soil macropores and cracks which also bypass bulk soil and increase infiltration can reduce the leaching rates of mobile nutrients such as nitrogen (Van Noordwijk et al. 1991). Roots that transfer water to deep soil layers in response to hydraulic gradients may also aid in reducing leaching and maintain a ‘safety net’ role of tree roots (Van-Noordwijk et al. 1996) in agro-forestry systems.

#### Implications for xylem sap transport theory

Reversal of xylem sap movement within the root system in response to changes in soil moisture cannot be explained by recent controversial interpretations of water transport in plants (Pockman et al. 1995; Milburn 1996).

If, as Zimmermann and co-workers suggest, an “osmotic compartmentation of the xylem” is responsible for a step-like transport of sap (Zimmermann et al. 1994, 1995), then osmotic gradients along the whole conductive pathway must be reversed to effect reversal of sap flow. A mechanism capable of such reversal and capable of redistributing solutes in a co-ordinated manner has yet to be demonstrated.

Reversal of sap flow also creates difficulty for Canny’s tissue-pressure model (Canny 1995) which requires the presence of unidirectional valves at the terminal ends of the transport system in order to maintain pressure. In contrast, the cohesion-tension theory of water transport readily accommodates the findings of this study and with Milburn (1996) and Tyree (1997) we agree that the conventional view has yet to be seriously challenged.

#### Conclusions

While suggestions have been made that hydraulic lift may be reversible (Caldwell et al. 1998), this is the first evidence that water can move down the taproot of trees when the surface soil layers are wetter than the deeper soil layers. Clearly, redistribution of water by the root systems of *G. robusta* and *E. camaldulensis* is not restricted to hydraulic lift, but we suggest occurs throughout the root system whenever a water potential gradient exists across soil layers spanned by roots in hydraulic contact with the soil. Ecological interactions are also modified by hydraulic redistribution and the

possibility of both benefits and costs to neighbouring plants requires further investigation. Measurement of sap flow in roots holds much scope for further quantification of the impact of hydraulic redistribution of water on plant communities, hydrology and the rhizosphere.

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