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# Root water uptake of field-growing plants indicated by measurements of natural-abundance deuterium

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## Abstract

Measurements of stable-isotope ratios of water extracted from stems and, in some studies, soils are increasingly being used to study the integrated root function of field-growing plants. This study explored if additional measurements on water extracted from roots could indicate the activity of roots in different areas of the soil profile and their influence on canopy water sources, so providing advantages over more common sampling strategies. Studies were conducted on trees and shrubs located in diverse habitats: a saline, semi-arid floodplain, a subhumid mountain-range front and a cold desert. At each site, roots, soil immediately surrounding the roots, and plant stems were sampled. Roots were taken from different depths in the soil, to approximately 2 m at one site. Overall, 80% of roots sampled had H isotope ratios different from the surrounding soil. The differences up to $37^0/_{00}$, were significant ($p<0.05$) at two of the sites. Thus water in most of the roots sampled did not come entirely, if at all, from the surrounding soil, illustrating movement and possible mixing of water within the root system. This condition was not simply related to the availability of water surrounding the soil, which was also measured. There were also differences in root and stem H isotope ratios (up to $17^0/_{00}$) in 67% of samples, although the difference was only significant in shallow samples from the floodplain. The general similarity in stem and root $\delta^2H$ values indicates that most roots sampled were involved in the main supply of water to the canopy. Patterns of root function varied between the individual sites. Trees were primarily using groundwater at the floodplain and mountain front sites, as the surface soils had mean matric potentials of -1800 kPa. At the mountain front site, the surface roots were transporting groundwater to the canopy in isolation form the surrounding soil. In contrast, surface roots at the floodplain were taking up water from the surrounding soil, although this water was not a significant source in the trees' overall water supply. This activity of surface roots would not have been evident from the $\delta^2H$ data without the root samples. At the cold desert the roots in moist surface soil provided the main source of water for the shrubs. There too the root data indicated different water uptake patterns than otherwise would have been assumed. The root data showed that groundwater could not have been a water source, a conclusion which had been reached in a previous study. Thus measurements of stable isotope ratios in root water may be a valuable tool in assessing water uptake patterns and root function.

## Introduction

Information on the activity of roots in situ is usually inferred from indirect measurements, such as changes in soil water contents with time or uptake of chemically labelled compounds, because direct observations are costly (Caldwell and Virginia, 1989). However, problems can arise with these indirect methods, particularly in arid and/or saline areas where plants commonly suffer water stress. When transpiration rates are low, the rate of change in soil water contents with time may be less than the precision of soil moisture measurements. With labelled compounds, especially water-borne tracers, the act of applying the compound may alter the root zone conditions causing the root behaviour observed

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to be different from that under natural conditions. In an effort to overcome these problems, measurements of natural abundance H or O stable isotope ratios in plant stems are increasingly being used to infer plant water uptake.

Water in different parts of the root zone may have different isotopic signatures due to either seasonal or geographic effects on rainfall (as summarised by Dawson, 1993) or, more importantly, enrichment of water during evaporation from the soil (Thorburn and Walker, 1993). Since (1) water moves from the soil into roots, and then to stems of terrestrial plants without fractionation, and (2) water can be sampled from soils and plant tissues without fractionation or isotopic contamination (Dawson and Elheringer, 1993; Thorburn et al., 1993b; Thorburn and Mensforth, 1993), the isotopic composition of water extracted from woody stems can be compared to the possible water sources in the root zone to indicate the origin of the water in the plant.

Applications of this technique have provided unexpected results. For example, perennial groundwater sources are more important to trees and shrubs than anticipated in many situations (e.g. Dawson and Ehleringer, 1991; Dawson, 1993; Mensforth et al., 1994; Thorburn et al., 1993a; Thorburn and Walker, 1994). These unexpected results indicate that our understanding of root system function in field soils is incomplete. Similar claims have recently been made by Gardner (1991) after analysing data on water extraction by crops and trees.

In most isotopic studies of plant water sources the canopy is the only part of the plant sampled, so results show the *integrated* response of the root system to below-ground conditions. However, more detail on root activity may be gained if natural-isotope methods are extended to the level of individual roots. Water can be extracted from individual roots (Thorburn et al., 1993b) and its isotopic composition compared with that of water from surrounding soil and above-ground parts of the plant. Similarity between the root and stem water isotopic compositions indicates that the roots were involved in the supply of significant proportions of water to the canopy. Likewise, comparison of root and soil waters can indicate if water in roots was derived from the nearby soil. Such information may provide further insights into soil-root-canopy water pathways and aid in the assessment of plant water sources from stable isotope data.

This paper reports an exploratory study comparing root, soil and stem water isotopic compositions to determine the activity of roots in different areas of the soil profile and their influence on canopy water sources. All samples were taken from sites where previous isotopic studies of plant water sources had shown that groundwaters were important water sources for the native plants. These studies provided a background against which to assess the advantages gained from studying root isotope ratios.

## Experimental details

At each site, root, soil and stem samples were taken for isotopic analyses. Soil matric and plant stem water potentials were also measured. The site descriptions and sampling details are given below.

### *Field sites*

Studies were conducted in three contrasting environments; a semi-arid floodplain with saline soils, a cold desert and a subhumid mountain front, with a consequent range in plant species, root zone and groundwater conditions (Table 1). As stated above, all sites had been the subject of previous natural abundance H isotope studies.

The floodplain site was in a *Eucalyptus* forest in the Chowilla Anabranch region of the River Murray in eastern South Australia. The two dominant tree species were sampled. Four plots were distributed across the floodplain to encompass the variation in soil and groundwater salinity. Rain prior to sampling (Table 1) had unevenly wet the soil up to 0.1 m depth.

The mountain front site was in an oak-maple scrub on an alluvial meadow, in the Red Butte Canyon Research Natural Area east of Salt Lake City, Utah. The two dominant tree species were sampled.

The cold desert site was an ephemeral wash in a shrub land located in the Glen Canyon Recreation Area, southern Utah. Three woody, perennial species were sampled. Rain prior to sampling had wet the soil to approximately 0.4 m depth, and the wetting was more even than occurred at the floodplain.

### *Isotope sampling*

Roots, soil surrounding the roots, and stems were taken from each plant studied. Samples were taken at practically the same time (e.g. within 30 minutes) to minimise the effects of changing environmental conditions. Further details are given below.

*Table 1.* Field site and sampling details

| Site | Floodplain | Mountain front | Cold desert |
|---|---|---|---|
| Previous study | Thorburn et al. (1993a) | Dawson and Ehleringer (1991) | Ehleringer et al. (1991) |
| Latitude, Longitude | 140° 52' E, 33° 59' S | 111° 47' W, 40° 48' N | 111° 36' W, 37° 01' N |
| Elevation (m) | 20 | 1850 | 1200 |
| Average annual rainfall (mm) | 260 | 700 | 150 |
| Groundwater depth (m) | 2–4 | 3 | 5 |
| Groundwater salinity (total dissolved salts, g $L^{-1}$ | 3–10[a] | < 1 | < 1 |
| Groundwater $\delta^2H$ ($^0/_{00}$) | -27 | -131 | -91 |
| Species sampled | *Eucalyptus largiflorens* and *Eucalyptus camaldulensis* | *Acer negundo* and *Acer grandidentatum* | *Atriplex canescens*, *Chrysothamnus nauseosus* and *Vanclevea stylosa* |
| Number of plants sampled | 12 | 6 | 10 |
| Number of area of plots | Four, each 2500 $m^2$ | One, 2400 $m^2$ | One, 1200 $m^2$ |
| Rain prior to sampling (mm) | 25 mm, 10 days earlier | None | 35 mm over the previous two weeks |

[a] Corresponds to an osmotic potential of ~ -400 to -1300 kPa.

*Roots*

On the floodplain, 14 roots were sampled from the wet surface layer (i.e. 0-0.1 m depth), and a further 10 from 0.1-1.9 m depth (note, more than one root sample was taken from many trees). The roots appeared to be live and suberised, and were 10-20 mm in diameter. The shallow roots were lateral roots uncovered in holes up to 0.3 m depth, and generally had finer (~ 2 mm diameter) roots branching from them. The deeper roots were sampled from hand augered holes under the trees on the floodplain.

At the mountain front site, shallow lateral roots were taken from holes excavated to 0.2 m depth. The roots were similar in size to those sampled from the eucalypts on the floodplain, and also had fine roots branching from them. No deep roots were sampled at this site.

At the cold desert site, the tap-roots of the shrubs were excavated from the soil and two root segments sampled; one from the upper wet zone (between 0.1 and 0.3 m) and the other from the dry soil below the wetting front (0.4–0.7 m depth). The roots were 10-50 mm thick, the thickest being from the *Atriplex canescens*. There were fine (1-2 mm diameter) lateral roots from the tap roots of most shrubs in the upper wet zone of the soil profile.

All root samples were stored in sealed, air-tight containers until water extraction.

*Stems*

Stems were sampled from the plants to provide stem water for isotopic analysis. In the trees non-green, suberised stems approximately 10 mm in diameter were taken in the manner described by Thorburn et al. (1993b). Three twigs were taken from each tree and combined to provide a single representative sample of the tree. Non-green stems were sampled from shrubs (as described by Ehleringer et al., 1991) at the cold desert and salt lake sites. All twig samples were stored in sealed, air-tight containers until water extraction.

*Soils*

The soil surrounding each root was sampled with the roots. The soil was taken from ~ 30 mm around the roots, then placed into air-tight glass jars and sealed.

*Soil water conditions*

Matric potentials (Greacen et al., 1989) and chloride concentrations (Taras et al., 1975) were determined on all soil samples. These measurements were made to

assess the availability of water in the soil surrounding the roots.

*Sap flow and stem-water potentials*

To establish if the plants were transpiring during the study, sap flow was measured directly in trees on the floodplain and midday and predawn water potentials were measured at the mountain front and cold desert sites. Sap flow was measured in one tree per plot using the heat pulse technique (following Thorburn et al., 1993a). The trees varied in size from 150 to 530 mm in diameter. Midday water potentials were determined with a Scholander-type pressure bomb on the day of the root sampling at both the mountain front and cold desert sites. Measurements were made on the six study trees at the mountain front site and on 10 shrubs within the plot at the cold desert site. Pre-dawn water potentials were also determined on the trees at the mountain front site on the day of the root sampling. At the cold desert site, pre-dawn (and midday) water potentials had been determined on the shrubs species two weeks prior to this experiment.

*Isotopic analyses*

Water was extracted from plant and soil samples collected on the floodplain by azeotropic distillation with kerosene (Revesz and Woods, 1990; Thorburn et al., 1993b). For samples taken at the other two sites, water was extracted by vacuum distillation (Ehleringer and Osmond, 1989). Samples were immersed in boiling water during the vacuum distillations, while the extracted water was collected in a liquid-nitrogen trap.

The $^2H/^1H$ ratios of waters were determined by conventional mass spectrometry after reduction of water to $H_2$, over uranium at 800°C for floodplain samples, and over zinc at 500°C for the samples collected in Utah. Results were expressed in conventional $\delta$ notation:

$$\delta^2H\ (^0/_{00}) = (R_i/R_s - 1)1000,$$

where R is the ratio $^2H/^1H$, $i$ indicates the isotope sample and $s$ the standard (V-SMOW).

*Data analysis*

To provide an overview of the relationship between root, stem and soil $\delta^2H$ values, these data were subjected to analysis of variance. Data from each site was analysed separately. Samples from the floodplain and the cold desert were further separated into two groups on the basis of depth, because of the large difference in mean soil matric potential between shallow and deep soils both sites (Table 2).

More detail on the behaviour of the plants sampled was provided by compaying soil, root and stem samples taken from individual plants. Where more than one root sample was taken from a plant (e.g. at the cold desert), the plant's stem $\delta^2H$ value was grouped with each root and soil sample pair.

## Results

*Soil water conditions*

There was a wide range of matric potentials in the soils sampled, from near saturation to air dry (Table 2). At the floodplain, mean soil matric potential was lower in the shallow samples than in the deep samples. However, there was considerable variability in matric potential (from -50 MPa to -60 kPa) in the shallow sample group due to differential wetting of the soils across the floodplain by rain prior to sampling. Matric potentials at the mountain front site were less variable than at the floodplain, and ranged from -1000 to -3000 kPa. At the cold desert, shallow soils had very high matric potentials ( > -16 kPa) from the rain prior to sampling, with deep samples having considerably lower matric potentials (Table 2). The surface soil wetting was more uniform than at the floodplain.

As expected, the maximum soil water chloride concentrations were highest at the floodplain (Table 2). The osmotic potentials equivalent to the chloride concentrations, estimated assuming all salts were present in the soil as NaCl, were as low as -1300 kPa in all soils at this site. Soil salinity was lower at the other sites, with equivalent osmotic potentials of -50 kPa at the mountain front and higher than -1000 kPa at the cold desert.

*Transpiration*

The trees at the floodplain were actively transpiring, with sap flow rates between 20 and 160 L $day^{-1}$ depending on the tree size.

At the mountain front and cold desert sites, midday stem water potentials were between -2000 and -3300 kPa. These potentials were 1000 to 2100 kPa lower than the pre-dawn water potentials, which shows

*Table 2.* Depth range of samples, mean soil matric potential ($\Psi$), maximum soil chloride ($Cl^-$) concentration and the results from the analysis of variance at each site ($\delta^2H$ values of stems, roots and soils sampled, and the least significant difference (lsd, $p < 0.05$). Similar superscripts indicate that means at a site were not significantly different in the analysis of variance

| Site | Depth (m) | $\Psi$(kPa) | $Cl^-$ (g $L^{-1}$) | $\delta^2H$ ($^0/_{00}$) | | | lsd |
|---|---|---|---|---|---|---|---|
| | | | | Stem | Root | Soil | |
| Floodplain - *shallow* | 0–0.1 | -1740 | 8.0 | -25 | $-19^A$ | $-15^A$ | 4.0 |
| Floodplain - *deep* | 0.1–1.9 | -58 | 9.0 | $-25^A$ | $-28^A$ | $-28^A$ | 3.0 |
| Cold desert - *shallow* | 0–0.3 | -7 | 0.6 | $-73^A$ | $-75^A$ | -64 | 4.9 |
| Cold desert - *deep* | 0.4–0.7 | -5270 | 2.5 | $-73^A$ | $-77^A$ | -82 | 4.6 |
| Mountain front | 0–0.2 | -1870 | 0.3 | $-130^A$ | $-128^A$ | -100 | 8.0 |

that the plants were transpiring at the time of sampling. Although the pre-dawn measurements at the cold desert site were made prior to the root sampling, soil water contents were lower when they were made (J R Ehleringer, unpubl. data). Thus it is reasonable to assume that the pre-dawn water potentials when the root samples were taken were similar to, or higher than, those measured earlier.

### *Overall differences in soil, root and stem $\delta^2H$ values*

Approximately 80% of all samples had root $\delta^2H$ values that were different with respect to analytical precision from the surrounding soil values, (Fig. 1). Differences were up to 37% and significant ($p < 0.05$) at the cold desert (both depth groupings) and mountain front sites (Table 2).

The greatest isotopic differences between root and soil samples would be expected in dry soils, where roots can not take up water from the soil, while differences between root and soil $\delta^2H$ values should be least in soils with high matric potentials. However, the differences between root and soil $\delta^2H$ values, expressed in absolute terms, were not significantly correlated ($p > 0.05$, r = -0.10) with soil matric potential (Fig. 2). Differences between root and soil $\delta^2H$ may also be common in saline soils, due to relatively lower osmotic potentials in these soils. However, root and soil $\delta^2H$ values were closest in the saline soils of the floodplain (Fig. 2, Table 2).

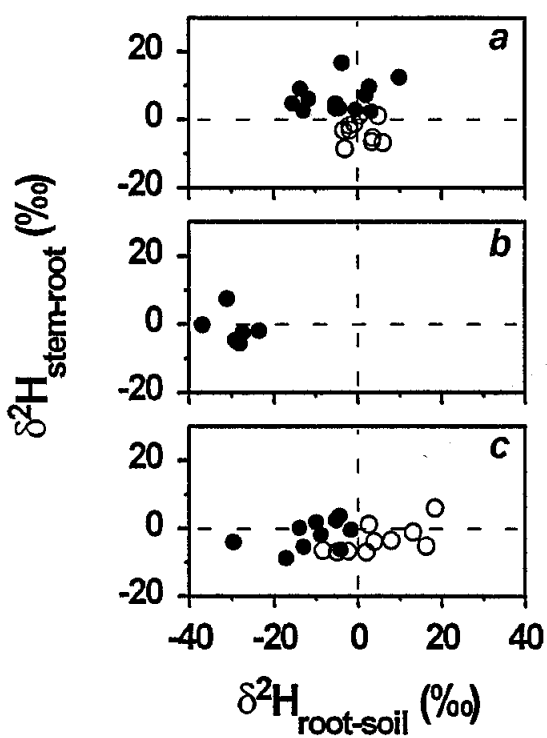


*Fig. 1.* The difference between root and stem $\delta^2H$ values ($\delta^2H_{root-stem}$) versus the difference between root and soil $\delta^2H$ values ($\delta^2H_{root-soil}$) at the three environments studied (a. floodplain, b. mountain front and c. cold desert). The analytical precision of the differences was 2.6 $^0/_{00}$ (i.e. twice that of an individual analysis). Shallow samples (see Table 2) are indicated by ●, with deep samples indicated by ○.

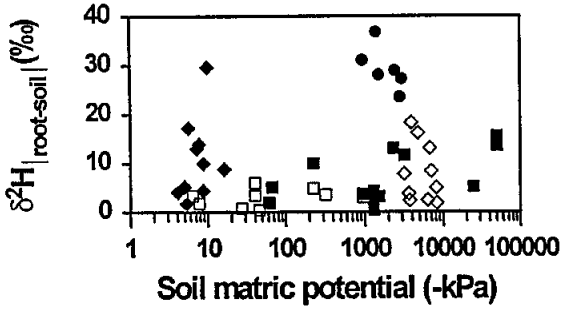


*Fig. 2.* The absolute difference between root and soil $\delta^2H$ values at all sites (floodplain shallow, ■; floodplain deep, □; mountain front, ●; cold desert shallow, ♦; cold desert deep, ◇) as a function of soil matric potential.

Stem and root $\delta^2H$ values were different in 67% of samples (Fig. 1). However, the magnitude of the differences (< $17^0/_{00}$) was lower than when roots and soils were compared, and the difference was only significant in shallow samples at the floodplain (Table 2). The general similarity in stem and root $\delta^2H$ values indicates that most roots sampled were involved in the main supply of water to the canopy.

*Plant water sources*

At the floodplain, stem, deep root and deep soil $\delta^2H$ values were similar to those of the groundwater (Fig. 3), indicating that groundwater was the *dominant* water source used by the plants. The water would have been taken up from the deep soil profile where matric potentials were highest. In the shallow samples, soil and root $\delta^2H$ values were not significantly different (Table 2), indicating that the surface root systems were in hydraulic contact with the soil and were potentially contributing water to the canopy. Given that there were shallow soil samples with $\delta^2H$ values similar to those of the groundwater and stems, and matric potentials of some shallow soils were relatively high (e.g. -60 kPa), it seems likely that some water was taken from the surface soil as well.

Stem and groundwater $\delta^2H$ values were similar at the mountain front site (Fig. 4), indicating that these trees were taking up groundwater. This result is consistent with the soil water availability results. The shallow root $\delta^2H$ values were similar to the groundwater and stem values indicating that these roots were involved in transporting groundwater to the canopy. Unlike the floodplain trees however, the root $\delta^2H$ values were different from the surrounding soil, showing that the roots were hydraulically isolated from the soil.

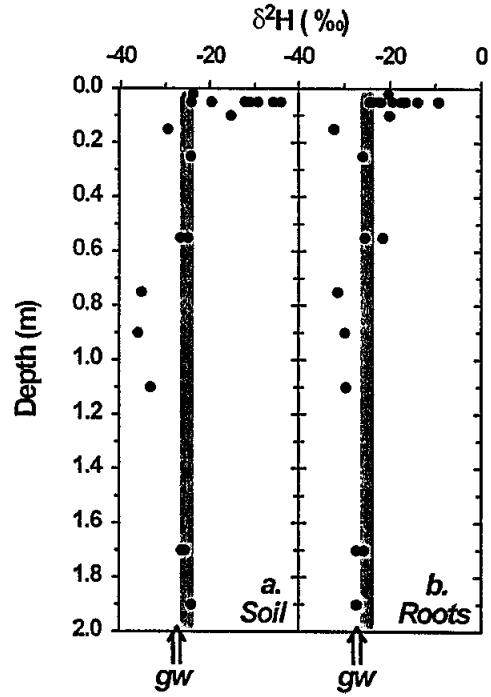


*Fig. 3.* Variation in $\delta^2H$ with depth in (a) soil and (b) root samples from the floodplain. The shaded area indicates the mean stem $\delta^2H$ value while the arrow indicates the groundwater $\delta^2H$ value.

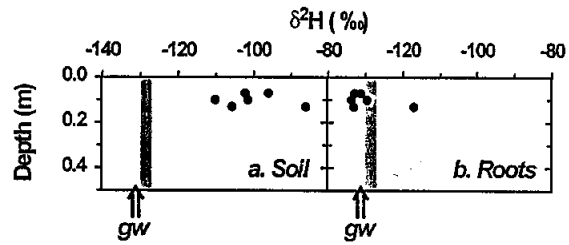


*Fig. 4.* Variation in $\delta^2H$ with depth in (a) soil and (b) root samples from the mountain front site. The shaded area indicates the mean stem $\delta^2H$ value while the arrow indicates the groundwater $\delta^2H$ value.

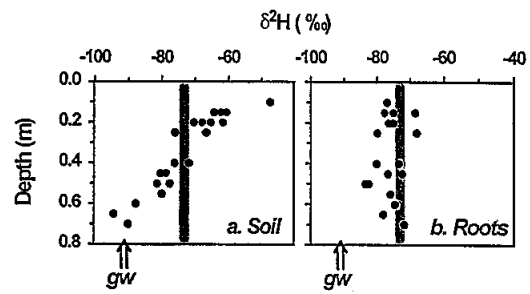


*Fig. 5.* Variation in $\delta^2H$ with depth in (a) soil and (b) root samples from the cold desert site. The shaded area indicates the mean stem $\delta^2H$ value while the arrow indicates the groundwater $\delta^2H$ value.

At the cold desert site, the soil $\delta^2H$ values decreased with increasing soil depth, being similar to the local groundwater $\delta^2H$ values ($-91^0/_{00}$) below approximately 0.6 m depth (Fig. 5). The shallow stem and root values were not significantly different (Table 2), and they were similar to the soil values around 0.3 to 0.4 m depth, indicating that water was being taken from this depth in the soil profile. This depth is the bottom of the wetting front in the soil. The deeper soil sampled below the wetting front could not have contributed water to the plant as the matric potentials were very low (Table 2).

There was no depth trend in root values at the cold desert site (Fig. 5): Shallow and deep root $\delta^2H$ values were not significantly different (t test, $p = 0.26$). Thus water appeared to be moving from the soil both up to the canopy and down the tap root, possibly in the phloem. The uniformity of tap root $\delta^2H$ values also shows that water was not being taken up deeper in the profile or from the water table. If that had been happening, deep tap root $\delta^2H$ values would have been closer to the deep soil water or groundwater values (i.e. $-91^0/_{00}$).

## Discussion

Comparison of $\delta^2H$ values in soil-root-canopy water pathways can be used as a tool to survey the activity of individual roots. The plants studied were *generally* taking water from the most available source. That source was the water table (or capillary fringe) at the mountain front, wet surface soil at the cold desert, and a possible combination of those two sources at the floodplain. However, the behaviour of the root systems appeared to be complex.

When all the $\delta^2H$ data are considered, differences in root and soil values showed that water in most of the roots sampled was not derived entirely, if at all, from the surrounding soil (Fig. 1). While this result may have been expected in some situations, e.g. where soils were dry and/or saline, it also occurred in soils with available water such as at the cold desert (Fig. 2). At that site, shallow root and soil $\delta^2H$ values were different in samples taken around 0.15 m depth (Fig. 5). While there were fine roots branched from the tap roots in this zone the isotopic differences show that these roots were not taking up significant amounts of water. There are two possible reasons why these roots may not have been active. Firstly, soil temperatures may have been too high at shallow depths for optimal root function (Gur et al., 1972; Moore et al., 1972). Secondly, the age of the lateral roots may have been a contributing factor. The hydraulic conductivity of lateral roots of desert plants decreases rapidly with age, e.g. halving between 5 and 15 days (Huang and Nobel, 1992). The lateral roots deeper in the wet soil zone may have been younger, having been initiated in response to a gradual downward redistribution of infiltrated water, and responsible for the majority of water uptake.

The study also showed contrasting behaviour of tree roots in shallow soils of similar water potential (Table 2). At both the mountain front and floodplain sites shallow roots were not taking significant amounts of water from the soil. The shallow roots at the mountain front site were carrying water to the canopy in isolation from the shallow soil (Fig. 4). However, shallow roots at the floodplain were in hydraulic connection with the surrounding soil (Fig. 3). This hydraulic connection may have been evidence that the roots were starting to respond to wetting of the soil prior to the sampling. However, the trees' stem $\delta^2H$ values, which were monitored over the month following the rain, did not increase through time (P J Thorburn, unpub. data) as they would have if increasing amounts of water were taken up from the isotopically enriched surface soil.

The reasons for the observed behaviour in root water uptake are not clear from this study. It may be that the observations were of transient behaviour in response to varying soil conditions, e.g. wetting and drying (Green and Clothier, 1995; Rundel and Nobel, 1991). However, this study was exploring if natural-isotope methods could indicate the activity of roots and their influence on plant water sources, rather than seeking to provide detailed explanations of root behaviour. Any methods relying on destructive sampling will only provide information at one point in time. Spatial variability in soil conditions and root activity will also have to be considered when designing a sampling strategy. Combination of the isotopic methods used in this study with measurement of root sap flow, as recently demonstrated by Green and Clothier (1995), may provide further detailed insights into function of individual root systems as it has for integrated root system activity (Thorburn et al., 1993a).

The results at the mountain front site were as expected from the earlier study of stem and groundwater $\delta^2H$ values (Dawson and Ehleringer, 1991). At the cold desert and floodplain sites however, inclusion of the root and soil $\delta^2H$ results provided a different interpretation of the plant water sources than that which

would have been indicated from stem and groundwater $\delta^2H$ data alone. At the cold desert site Ehleringer et al. (1991) had previously determined the $\delta^2H$ values of stem waters of shrubs to be $-77^0/_{00}$ and concluded that the stem waters were a varying mixture of groundwater ($\delta^2H = -91^0/_{00}$) and summer rainfall ($\delta 2H > -40^0/_{00}$) stored in the soil. While our stem $\delta^2H$ values are close to those measured by Ehleringer et al. (1991), our root results (Fig. 5) are inconsistent with this simple mixing of soil and groundwaters.

At the floodplain, the similarity of the stem and groundwater $\delta^2H$ values alone would have been interpreted as groundwater uptake by the trees. Inclusion of soil $\delta^2H$ data may still have led to this conclusion as the mean $\delta^2H$ value of the shallow soils was significantly higher than that of the stems (Table 2). However, comparison of the root and soil data suggested that some water could also have been taken up from shallow soils. It should be noted that this conclusion was also reached by Thorburn et al. (1993 a) by comparing *both* $\delta^2H$ and $\delta^{18}H$ values in soils and stems. The simultaneous examination of both H and O data in plant water source studies is not common however (Thorburn and Walker, 1993), usually because of limitations in analytical facilities or the high cost of isotopic analyses. When these circumstances confine studies to examination of only one isotope inclusion of root data may provide additional insights into plant water sources.

All the roots sampled in this study would have been detected using common field-based root length density measurement techniques (Caldwell and Virginia, 1989). Models of root water extraction are commonly based on these measurements, assuming that water potential gradients are the driving force for water uptake from the surrounding soil (Gardner, 1991). Often, however, simulated patterns of water uptake do not agree with observed patterns. Factors such as nonlinearities in the water flux-water potential relationship of roots (Gardner, 1991) and the uneven distribution of roots in the soil (Tardieu et al., 1992) have been given as reasons for this lack of agreement. The results of this study further show that root presence, even in soil with water that is apparently available to plants, does not correspond with root activity.

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