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Seasonal water uptake and movement in root systems of Australian phraeatophytic plants of dimorphic root morphology: a stable isotope investigation

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Abstract A natural abundance hydrogen stable isotope technique was used to study seasonal changes in source water utilization and water movement in the xylem of dimorphic root systems and stem bases of several woody shrubs or trees in mediterranean-type ecosystems of south Western Australia. Samples collected from the native tree *Banksia prionotes* over 18 months indicated that shallow lateral roots and deeply penetrating tap (sinker) roots obtained water of different origins over the course of a winter-wet/summer-dry annual cycle. During the wet season lateral roots acquired water mostly by uptake of recent precipitation (rain water) contained within the upper soil layers, and tap roots derived water from the underlying water table. The shoot obtained a mixture of these two water sources. As the dry season approached dependence on recent rain water decreased while that on ground water increased. In high summer, shallow lateral roots remained well-hydrated and shoots well supplied with ground water taken up by the tap root. This enabled plants to continue transpiration and carbon assimilation and thus complete their seasonal extension growth during the long (4–6 month) dry season. Parallel studies of other native species and two plantation-grown species of *Eucalyptus* all demonstrated behavior similar to that of *B. prionotes*. For *B. prionotes,* there was a strong negative correlation between the percentage of water in the stem base of a plant which was derived from the tap root (ground water) and the amount of precipitation which fell at the site. These data suggested that during the dry season plants derive the majority of the water they use from deeper sources while in the wet season most of the water they use is derived from shallower sources supplied by lateral roots in the upper soil layers. The data collected in this study support the notion that the dimorphic rooting habit can be advantageous for large woody species of floristically-rich, open, woodlands and heathlands where the acquisition of seasonally limited water is at a premium.

Key words Dimorphic roots · Hydrogen stable isotope ratio· Water uptake patterns · Phreatophyte · Australia

Introduction

For nearly a century plant ecologists have studied the rooting depths and patterns of plants living in water-limited environments (Cannon 1911, 1948; Weaver 1919; Oppenheimer 1960; Barbour 1973; Kummerow et al. 1977; Dodd et al. 1984). The marked differences in the rooting patterns among species have been suggested to serve as adaptations minimizing competition for water during prolonged periods when no precipitation occurs and upper soil layers become extremely dry (Barbour 1973; Mooney et al. 1980). Interestingly, with the exception of work on cacti and other succulents which experience marked drought (Nobel and Sanderson 1984; North and Nobel 1992, 1994; North et al. 1992), few studies have explored how rooting morphology relates to water uptake patterns amongst co-occurring taxa within the same arid habitats. Thus, although it is well established that deeply rooted (phraeatophytic) plants are capable of exploiting deep water sources during drought periods (Ehleringer et al. 1991), the dynamics of water uptake and movement throughout an entire wet-dry cycle remain largely unexplored.

Recently, stable hydrogen isotope analyses of source waters and plant tissue water have provided new insights into the patterns of water uptake and use in different plant species (reviewed in Ehleringer and Dawson 1992; Dawson 1993a) and the possible relationships of such information to rooting depth (Ehleringer et al. 1991; Dawson and Ehleringer 1991; Jackson et al. 1995), water-use efficiency (Flanagan et al. 1992), and seasonal interspe-

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cific competition for water (Dawson 1993b). Globally, the isotopic ratio of deuterium to hydrogen (relative to a standard) in meteoric waters varies by over 400‰ (see Ehleringer and Rundel 1989). This leads to large differences in the hydrogen isotope ratio (or δD) of water sources available to plants and an attendant potential, therefore, to trace where, when and how different co-occurring, and potentially competing, species access the water resources currently available in a particular habitat (Dawson 1993a). For example, Ehleringer et al. (1991) have compared the δD of stem xylem tissue water with the δD of near surface soil water and with deeper soil water and have demonstrated that certain desert species within the same community use shallow soil water, others soil moisture from deep soil layers and yet others some combination of these two sources. In the seasonally wet tropics, Jackson et al. (1995) have recently recorded that evergreen and deciduous tree species use deeper and more shallow water sources, respectively. Likewise, in a temperate deciduous forest in the northeastern United States, Dawson (1996) has shown that large and small sugar maple trees preferentially use ground water and soil water respectively. These later two investigations also demonstrated that the water source used by a species can influence their water use patterns.

Here, we present information on the seasonal changes in the δD of xylem water within different parts of the root systems and lower shoots of several phraeatophytic woody plants in mediterranean type ecosystems of south Western Australia. As shown elsewhere, dimorphic root morphology, where a species possesses both superficial nutrient-acquiring lateral roots and deeply penetrating tap (sinker) roots, is a common feature within such ecosystems (Lamont and Bergl 1991; Jeschke and Pate 1995; Pate and Dixon 1996) and, in certain cases, species so endowed outnumber and grossly exceed in terms of size and biomass those of shallow-rooted habit (Pate et al. 1984; Pate and Dixon 1996). In this study we used the δD values of source waters and xylem water within the dimorphic root system and trunks of several woody shrub or tree species to trace how uptake and then movement of water within shallow lateral roots and deep tap (sinker) roots change over the course of a winter-wet/summer-dry cycle. We set out to determine (1) how roots in different parts of the soil profile behave as water availability from different sources also changes over a season, and (2) how shallow lateral roots survive during the dry season after the surrounding soil has completely dried out and they have lost their fine nutrient-acquiring roots (see Jeschke and Pate 1995; Pate and Jeschke 1993). By answering these questions we hoped to understand better how the seasonal water economies of species of different rooting behavior influence their respective performances in terms of water-use efficiency, carbon acquisition, and nutrient relations.

Materials and methods

Study sites, water sources, and plant material

Two study sites were utilized in south Western Australia. The first was located in a natural open *Banksia* woodland on deep Bassendean sand near Yanchep, 50 km north of Perth (31° 33′ S, 115° 41′ E; see Pate and Beard 1984). Recruitment from seed following a fire in January 1986 provided a uniformly-aged population of young trees of *B. prionotes* (Proteaceae) which were sampled at monthly intervals for xylem water of roots and trunks (Fig. 1) from July 1992 to December 1993. During this period, water moving within the xylem was also collected from three other proteaceous species possessing root morphology similar to that of *B. prionotes* (Figs. 1A and 2) on three occasions at the study site in winter of 1992 and the summer of 1993. These species comprised a fire sensitive seeder shrub *Dryandra sessilis*, a root crown resprouting, fire-tolerant shrub species of *Grevillea* (species unknown) and the fire-tolerant, clonally reproducing tree *Banksia ilicifolia*. The non-saline water table at the site varied from 2.6 m deep in summer to 1.8 m deep following rains in autumn and winter. The soil profile at the site was wet to the surface (at field capacity) only during late winter (July and August) whereas the upper 1.5 m of sand was extremely dry (no measurable soil moisture) from early summer (November) until the onset of autumn rains in (March or April) (see Dodd et al. 1984). Other details of the site are provided by Jeschke and Pate (1995) and Pate et al. (1995).

The second study site was located on the property of Mr. and Mrs. J. Bush at Mt. Barker (31° 33′ S, 117° 40′ E; approximately 310 km south of Perth) in a region of deep sand overlying gravel on partly cleared farmland. Plantation crops of *Eucalyptus globulus* and *E. camaldulensis* had been established by the owners at the site in 1990 and an additional plantation of *E. globulus* was established in 1992. The plantations had been established in an effort to lower water tables and thereby possibly combat encroaching salinization of lower-lying soils on the property as well as for wood chipping in the future. All three plantations were visited in September 1993, January 1994, and June 1994 and xylem water of lateral and tap roots (1990 plantings) and lower trunks (all plantings) collected together with samples of highly saline underground water (at ~4.5 m) and rain water (as available) at the respective sites. Two native tree species (*E. calophylla* and *E. marginata*) fringing the plantations were also sampled for trunk xylem water on each visit to the site. The tree species, *B. grandis*, flanking a permanently wet fresh-water swamp on the Mt. Barker property, was also studied. The site at Mt. Barker experiences annual precipitation closely similar to that at Yanchep (see Fig. 2) but with usually earlier onset of autumn rains and prolongation of rains later into early summer than at Yanchep.

Collection and isotopic analysis of xylem and source waters

Water in the xylem was obtained by mild vacuum extraction of 20–40 cm segments of freshly harvested roots or shoots. The relatively broad and long vessels in the diffuse porous wood of the study species enabled virtually complete recovery of mobile xylem fluids within vessel lumens using a mild vacuum (0.5–0.75 MPa). Details of this technique are described by Jeschke and Pate (1995) and Pate et al. (1995). Wherever possible three or more separate laterals were excavated and sampled at locations exceeding 30 cm outwards from the root crown (Fig. 1). Each tap root was sampled at 60–120 cm depth, and in all cases following excavation of sand around the root systems to a level well below the point of attachment of the deepest lateral roots. Samples (0.5–20 ml volume) were immediately placed in air tight vials to prevent changes in the isotopic value through evaporation (see Dawson and Ehleringer 1993). Precipitation (all rain water) samples were also collected (when available) during the actual rain events. Samples of ground water were also collected from a well (bore hole) installed previously at the site. The precipitation and ground water samples were treated as previously stated and all

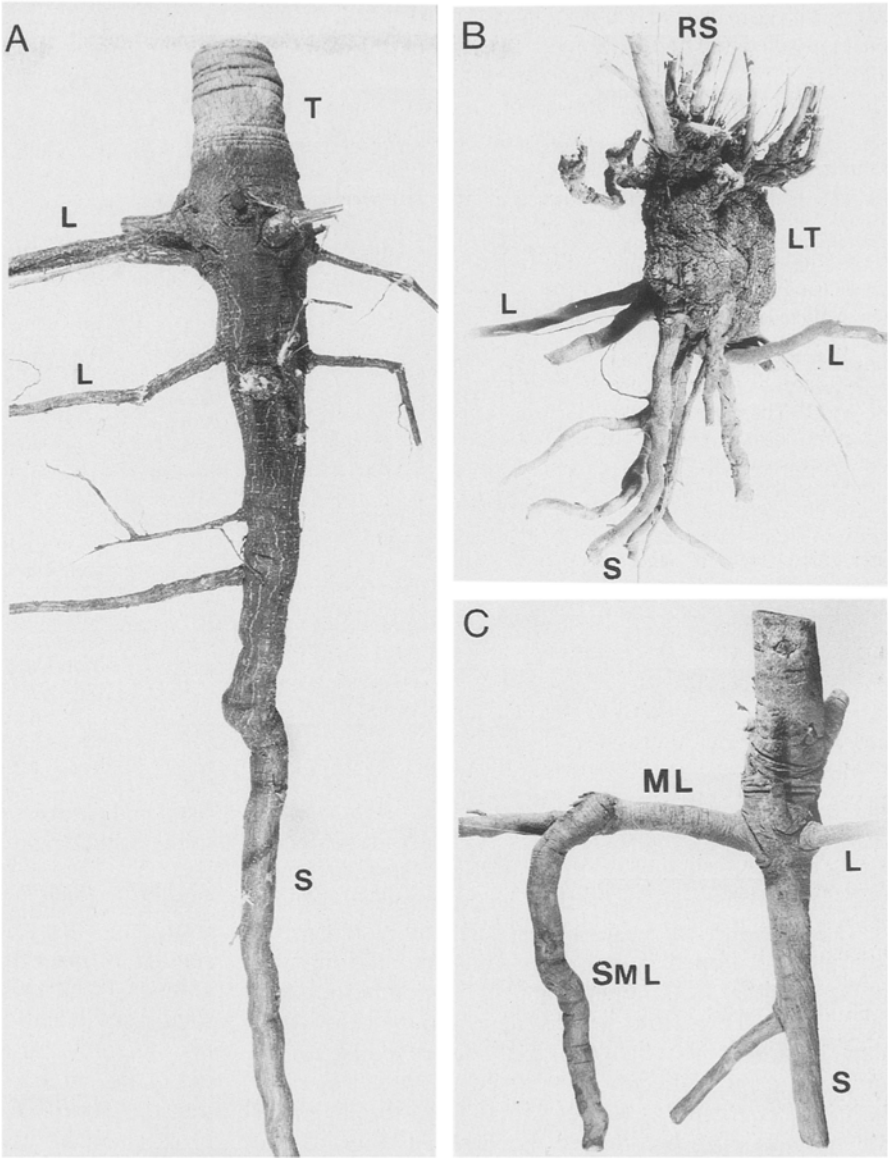


Fig. 1A–C Examples of the dimorphic type of root system exhibited by all species studied in the investigation. **A** The fire sensitive tree, *Banksia prionotes,* with single tap (sinker) root(s) and a number of shallow lateral roots (*L*). Note relatively unswollen upper root junction to which sinker, laterals and trunk (*T*) are attached. **B** A fire-resistant lignotuberous shrubby species of *Grevillea.* Note swollen lignotuber (*LT*), and multiple laterals (*L*) and sinkers (*S*) arising from the tuber. The specimen had been burnt 5 years previously and a number of resprout shoots (*RS*) had formed from epicormic buds on the lignotuber. **C** Part of the root system of the clonally-reproducing, fire-tolerant tree *B. ilicifolia.* The ramet illustrated has its own lateral root (*L*) and sinker (*S*) and formed as a sucker on one of the main laterals (*ML*) of the parent tree. This lateral has developed a sinker (*SML*). Xylem-mobile water was collected by vacuum extraction of segments of lateral root, sinker and trunk as described in the text

samples were stored frozen until their analysis. Some samples were slightly discolored by tannins and other compounds; these substances were removed by treatment with activated charcoal prior to their analysis. The stable hydrogen isotope ratio (δD) of the xylem or source water were determined by reacting 5 µl of water in a capillary for 60 min at 550°C with a zinc foil catalyst obtained from the isotope laboratory of J. Hayes, Indiana University, United States (modified from Coleman et al. 1982) in an evacuated 7-mm Vycor glass tube (after Ehleringer and Osmond 1989). The hydrogen gas resulting from the combustion-reaction was analysed with an isotope ratio mass spectrometer (Finnigan MAT 252 or model delta S, San Jose, Calif.) at SIRFER (University of Utah). The δD values were expressed in conventional delta notation ‰ as:

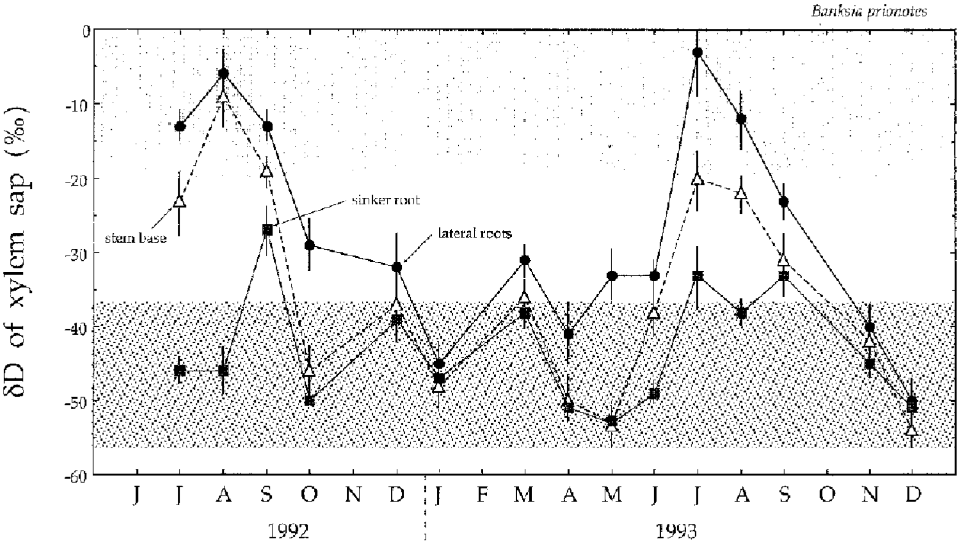
$$\delta D = (D/H_{sample}/D/H_{standard}) - 1) \times 1000‰ \qquad \text{(Eq. 1)}$$

The standard was SMOW (standard mean ocean water).

Results

Root morphology of the study species

Earlier investigations (see Pate and Dixon 1996 for references), or those of the present study, confirmed that all study species exhibited a typical dimorphic root morphology (Fig. 1), consisting of a set of lateral roots radiating out from the main root crown and one or more deeply penetrating tap (sinker) roots. Laterals were always restricted to the top 40 cm of the soil profile. An occasional major lateral root bore sinker roots but in most cases these attained depths of less than 1 m and were accordingly rated as being out of range of the water table at the sites under study (see also Pate et al. 1995). Tap roots, by contrast were shown by excavation or soil coring to reach the water table at 2–5 m. Within the species which had a dimorphic root system, some interest-



rainfall per month (mm)

215	119	184	63	33	58	12	2	46	5	16	120	97	95	160	86	46	2	4

rain days per month

14	13	16	12	5	9	2	2	2	4	1	7	8	10	7	9	10	4	4

Fig. 2 The mean (*bar* SD) δD values of xylem sap (water) from lateral roots (●), the stem base (△) and the sinker roots (■) from a 6-year-old population of trees of *B. prionotes*. Samples were obtained for 15 months during an 18-month period at Yanchep, western Australia. Rainfall and the number of days per month with rain were also recorded. The δD values of rainfall varied from near zero to –20‰ throughout the study and is shown as the *light gray bar* across the top of the figure. The δD of ground water varied from –38 to –56‰ and is shown as the *stippled bar* across the bottom of the figure. Note greater dependence of stems on water from laterals in winter (July and August) of each year. Stems and laterals appear to be obtaining ground water in summer (December/January)

ing variation did exist. For example, *B. prionotes* (Fig. 1A) and *Dryandra sessilis* typically developed a single tap root, between three and ten surface lateral roots, and a relatively unswollen junction region between laterals and the tap root. The species of *Grevillea*, by contrast, developed several tap roots and a somewhat larger number of laterals from its lignotuberous root stock (Fig. 1B), from which new shoots arose after plants had their above-ground parts destroyed by fire. *B. ilicifolia* at the Yanchep site proved to spread clonally, with ramets arising as sucker shoots from the major lateral roots of each parent tree. Each ramet (Fig. 1C) developed its own set of laterals in addition to the parent lateral on which it had developed, and sinker roots formed at intervals along the parent laterals as well as from the lignotubrous base of each ramet. Excavations of the two introduced plantation eucalypts at Mt. Barker showed relatively stronger development of lateral than tap roots in the faster-growing *E. globulus*, and evidence of decay was observed in the tap roots if they penetrated the saline ground water at ~5 m. The slower-growing *E. camaldulensis* was strongly tap-rooted, developed relatively few laterals and carried healthy tap and sinker roots down to the saline ground water at 5 m. The two dominant native trees (*E. calophylla* and *E. marginata*) studied in relic vegetation close to the plantations, were not excavated, but previous examination had shown both to be deep-rooted and to access ground water (Pate et al. 1984).

Seasonal changes in dD of xylem water at the Yanchep site

Figure 2 shows the δD of xylem water within the lateral roots, tap root, and the stem base of the principal study species *B. prionotes* for the study period June 1992–December 1993. Information is also provided for monthly total rainfall and number of days per months with rain for the study period. The seasonal patterns of change in δD of the three xylem compartments indicated that during the wet season (June–September) shallow lateral roots obtained most of their water by direct uptake of recent rain water (δD = –1 to –20‰), whereas tap roots derived water from a separate deeper ground water source (δD = –38 to –56‰). The stem base at this time contained xylem water reflecting a mixture of the two water sources. δD values of the three xylem compartments in July and August indicated that the major fraction of the water moving into the trunk came from water absorbed by the laterals. By September almost as much water was being derived from a deep water source by tap roots as that being obtained from the shallow soil water by lateral roots. As rainfall declined further and upper soil layers dried out in spring and early summer (October to December), δD values suggested accentuated dependence on ground water. In addition, during this same period a declining (more negative) δD value in xylem water of laterals suggested that the tap roots was supplying at least some water to these roots. In January (1993), the driest summer month of the study, δD of all three xylem samples were similar (–45 to –48‰) indicating that water for shoot transpiration and continued hydration of the laterals originated from the water table via the tap root.

Table 1 The stable hydrogen isotopic ratio (δD; ‰) of xylem-mobile water in lateral roots (*LRW*) and tap roots (*TRW*) for select native phraeatophytic plant species growing during the early spring (October/November) wet season and summer (March) dry season near Yanchep, south Western Australia. Shallow soil water δD ranged between −13 and −23‰, while ground water δD was −33±1.5‰ (mean and SD) during the wet season and −36±2.1‰ during the dry season respectively at this site

Species	Season	LRW δD	TRW δD
Dryandra sessilis	wet	−13 to −23	−33
	dry	−31 to −33	−34
Banksia ilicifolia	wet	−27 to −30	−32
Grevillea sp.	dry	−30 to −31	−34

A very similar pattern of changes occurred in the second winter of study (1993) (Fig. 2).

Of the other species sampled at the Yanchep site, *D. sessilis*, in early spring (October 1992, when the soil was still moist) showed lateral root xylem water δD values of −13 to −23‰ (Table 1). Lateral root xylem water δD sampled from other species at this site and time averaged −31‰, a value typical for deeper water at that time of year. *D. sessilis* sampled at the end of the summer drought (March 1993) showed a mean δD value for laterals of −31‰, more similar to the isotopic composition of water within the tap roots (−33‰). These data suggested that the lateral roots in the upper part of the root system were being recharged with ground water obtained by the tap root (Table 1) as also observed in *B. prionotes* (Fig. 2). Similar evidence that lateral root systems of a ramet are recharged with water taken up by tap roots was also observed in *B. ilicifolia* during November 1992. δD values for xylem water in this species were −30 and −27‰ for laterals of the ramet and −32‰ for the sinker of the ramet (Table 1; also see Fig. 1B). A single plant of *Grevillea* sp. excavated in March 1993 showed a very similar pattern, with lateral root water δD values of −30 and −31‰ versus a mean value for the multiple sinker roots (Fig. 1C) of −34‰ (Table 1).

Seasonal changes in dD of xylem water at the Mt. Barker Site

Data for the δD of xylem water obtained from the 1990 plantation-grown trees of the two species of *Eucalyptus* are shown in Fig. 3. In both cases, δD values were lower in the mid summer (January) than spring (September) or winter (June), showing that plants had a greater dependence on ground water (δD of −55‰) than on rain water at the site (seasonal variation −7.5 to −21.5‰) during the drought-prone summer period. The δD of sinker root xylem water was also significantly lower than that of lateral root or stem water in both species. There was a tendency for all δD values of *E. globulus* to be appreciably less negative than corresponding values for *E. camaldulensis*, indicating that *E. camaldulensis* had heavier reliance on saline ground water, a result also reported by Mensforth et al. (1994) for trees growing in south-east Australia.

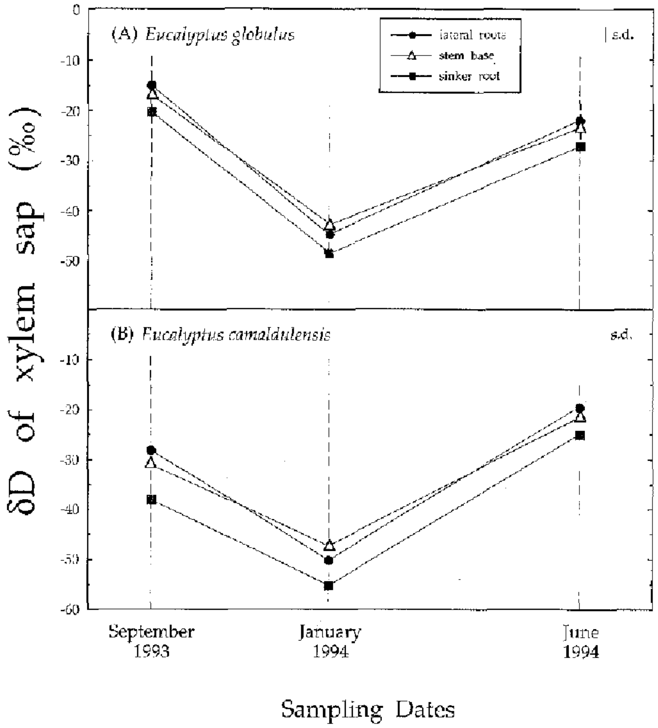


Fig. 3 Seasonal variation in δD of xylem sap of lateral roots (●), the sinker root (■), and the stem base (△) of **A** plantation-grown *Eucalyptus globulus* and **B** *E. camaldulensis* on deep sand overlying a saline water table at Mt. Barker, Western Australia. The *bars* in the upper right-hand corner of the figure are standard deviations (SD) from the mean of all values. Note generally lower δD values for the more strongly tap rooted, slower growing *E. camaldulensis*. The δD of ground water was −55‰, that of rain water −21.5 to −7.5‰ (depending on season)

Corresponding data for the xylem water within the stem bases of the two native eucalypts growing adjacent to the plantation gave values of −44‰ for both *E. calophylla* and *E. marginata* in September, −49 to −54‰ in high summer (January) and −24 to −26‰ in winter. Again, the data suggest a seasonal switch in the predominant water source with greater dependence on water at depth during the summer drought (see mixing model results below). The same pattern was evident in the plantation of *E. globulus* during November (stem xylem water), when upper soil was extremely dry. The δD values of stem water were −38 and −39‰, compared with values that ranges from −11 to −21‰ in June when the soil profile at the site was saturated.

The native population of *B. grandis* fringing the fresh water swamp on the Mt. Barker property provided the data for δD values of xylem water shown in Fig. 4. Unlike the situation in the plantations, a relatively shallow water table (at 1.7 m) and lateral drainage into the swamp permitted soil layers to remain moist well into summer, and this may have explained the closely similar sets of δD values for early summer (November 1993) and the following winter (June 1994). Nevertheless, δD

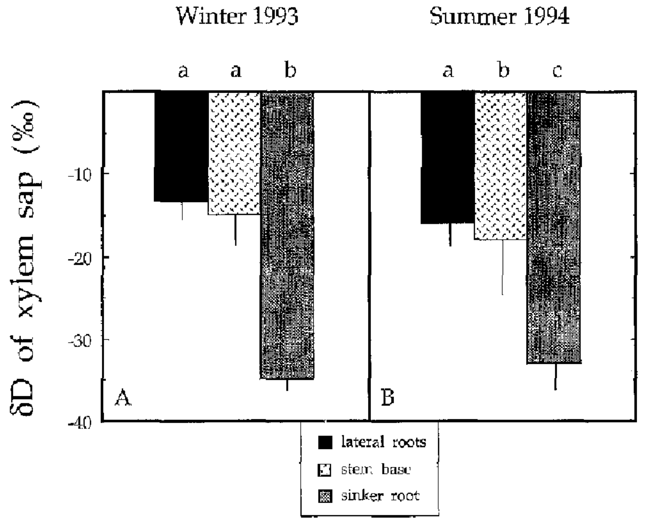


Fig. 4 The mean δD of xylem sap collected from lateral roots (*black bar*), the sinker root (*gray bar*), and the stem base (*stippled bar*) during the **A** winter 1993 and **B** summer 1994 growing seasons for plants of *B. grandis* growing on deep sand fringing a fresh water swamp at Mt. Barker, south western Australia. *Error bars* are given for data from the replicate group of trees sampled on each occasion. The mean (±SD) δD of rain water was –7.5 (2.3)‰ and of ground water was –35.5 (1.9)‰ across both sampling periods. Within a sampling period, significant differences ($P = 0.05$) in the mean δD values of the xylem sap of each tissue type are shown with different *letters above the histogram bars*. Letters above the bars that are the same indicate that these do not differ from one another

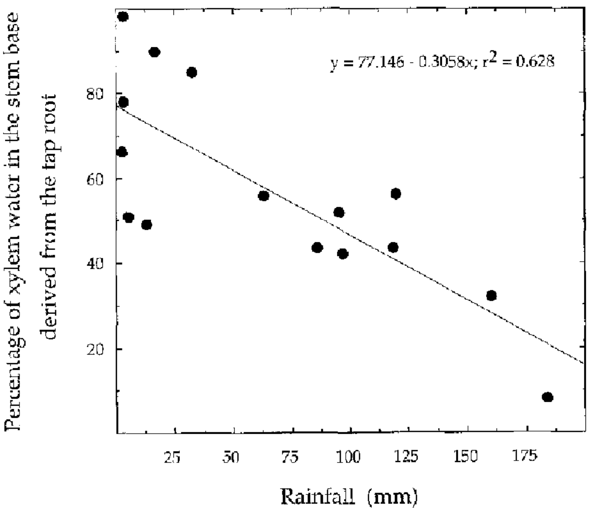


Fig. 5 The percentage of xylem water in the stem base of *B. prionotes* derived (supplied) from the tap root as a function of rainfall which fell at the site during the same period. The data show that in the wet winter season when rainfall is more abundant, plants obtain a greater fraction of their moisture from shallow soil water absorbed and supplied by lateral roots. The data are from Fig. 2

Table 2 The percentage of xylem water in the stem bases of *Eucalyptus globulus*, *E. camaldulensis* and *Banksia grandis* that is supplied by the tap root (ground water) in the winter-wet and summer-dry periods near Mt. Barker, south Western Australia. The values shown are the ranges measured during each season (from Figs. 3 and 4)

Species	Percentage of stem water from tap roots in	
	Summer	Winter
Eucalyptus globulus	9–15	0–7
E. camaldulensis	26–47	1–11
Banksia grandis	13–43	0–3

values of sinker roots were significantly more negative at both sampling times (–33 to –35‰) than those of either lateral roots or stems (–14 to –19‰). This was expected from the substantial difference we observed between the δD of rainfall [–7.5 ± 2.3 (SD)‰] and ground water (–35.1 ± 1.9‰) collected at the site during these sampling periods. The data shown in Fig. 4 suggest that at both sampling periods the bulk of the water within the shoot was derived from the most recent rainfall event that was taken up by the shallow lateral roots.

Application of a mixing model

The data shown in Figs. 2–4 were used to calculate the amount of different water sources, absorbed by different parts of the dimorphic system, which were used by each species at different times. These calculations are based on a modified version of a mixing model developed by Dawson (1993b) but used here for the special case of species with dimorphic root systems. The two end-members used in the model were shallow soil water obtained by lateral roots derived from rain and ground water obtained by tap roots. The δD of water in the xylem of the stem base was an index of the water source currently being used by a plant. The proportion of water at any point in time in the xylem of the stem base which was supplied by the tap root was calculated as the ratio of differences along the mixing line between lateral root water and the stem base water to the difference between tap root water and stem base water. Using this calculation the proportion of water in the stem base of *B. prionotes* which was derived from the tap root (i.e. ground water) at each sampling period was plotted against the rainfall during each period (Fig. 5). The strong negative correlation ($r^2 = 0.628$) suggests that during the dry season when rainfall is low, plants derive the majority of the water they use from deeper sources which is supplied by the tap root. In contrast, during the wet season when rainfall was high plants used a high proportion of shallow soil water taken up by lateral roots. This same type of pattern was also seen in *E. globulus*, *E. camaldulensis*, and *B. grandis* (Table 2).

Discussion

The present study on patterns of water uptake and movement within the dimorphic root systems and stems of a few selected woody Australian species provides new insight into how plants of deep-rooted habit are well-adapted for utilizing very different water sources in a mediterranean-type environment. Moreover, these water uptake patterns fit well with previous research on the nutrient relations of these same species. For example, in *B. prionotes*, the major study species at the Yanchep site, water uptake occurs by both lateral and tap root throughout the winter-wet season. Since concentrations of critically limiting nutrients such as N and P during the winter-wet season are significantly higher in lateral root xylem sap compared with the xylem sap of tap roots (Jeschke and Pate 1995; Pate and Jeschke 1993) and since the major fraction of the water moving into the shoot at this time comes from shallow, not deep, sources of water (Figs. 2 and 5), by far the largest proportion of nutrients obtained in the wet season comes from surface layer sources via the proteoid root clusters which form on the lateral roots of the species (Jeschke and Pate 1995).

As soil water becomes less abundant, *B. prionotes* and the other species we examined appear to draw proportionally more water from deeper in the soil profile via sinker roots. When the upper soil layers become very dry in summer, lateral roots remain recharged by a continuous supply of ground water provided by the sinker root. Data provided by Pate et al. (1995) have demonstrated substantial differences in hydraulic conductivity (K_s; on an organ transectional area basis) between sinker (tap) roots, lateral roots and stems of proteaceous species. In *B. prionotes*, for example, K_s of sinker roots is extremely high ($30–780\times10^3$ m^2 MPa^{-1} s^{-1}) and xylem vessels extremely long (1.5–2.0 m). This compares with much lower K_s values ($2–50\times10^3$ m^2 MPa^{-1} s^{-1}) and much shorter xylem vessels (0.75 m) in lateral roots. The K_s values in the lower trunk were $0.5–9\times10^3$ m^2 MPa^{-1} s^{-1} and xylem vessel lengths were only 0.04 m long by comparison (Pate et al. 1995). It is likely that during dry periods water follows paths of least hydraulic resistance along water potential gradients. If so, the path of water movement would be up through the sinker root with high K_s, distally into lateral roots and, at times when transpiration is occurring, into the xylem of the shoot system with the lowest hydraulic conductivity and water potential.

The dimorphic root system appears to be very beneficial for the species we studied because it permits plants to maintain most of their root system, including the shallow lateral roots, through the long summer, when the surrounding soil has completely dried out. Only the fine 'feeder' roots had senesced and were shed during the drought, despite the fact that the lateral roots from which they originate were kept well hydrated. This is understandable in light of the fact that during drought, soil nutrient (N and P) availability is extremely low and thus the maintenance of feeder root clusters very costly for these plants (Jeschke and Pate 1995; Pate and Jeschke 1993). Continuing to tap and use deep soil water throughout summer, however, permits transpiration and carbon assimilation to continue as well as any vital transport processes between root and shoot that should be maintained. This water-use behaviour permits a species of the dimorphic rooting habit to continue growth and whatever mineral uptake might exist from the ground water during periods when shallow-rooted species are forced to cease gas exchange or else become severely desiccated. By maintaining the integrity of its lateral root system, a species such as *B. prionotes* is also able to respond rapidly to the onset of autumn rains by developing new sets of feeding roots well before the upper soil is fully wetted (J. S. Pate, unpublished work). It may be that initial hydration of these opportunistically produced roots can occur because of the unique water translocation patterns which exist between the sinker root and the laterals.

At our second site at Mt. Barker, it was also evident that both the eucalypts and *B. grandis* used a large proportion of ground water during the summer and very little in winter. However, with rainfall spread more evenly across the season at this extreme south western site, recharge of laterals with sinker water is not always observed. Consistent differences in δD values are also observed for xylem water of sinker, laterals and stems of the two plantation species *E. globulus* and *E. camaldulensis*, and subtle difference in δD between the two species suggests that patterns of water utilization might be modulated by the relative strengths of a developing sinker root as opposed to the lateral root system. Previous water uptake research conducted by Mensforth et al. (1994) and Thorburn and Walker (1994) with *E. camaldulensis* shows that this species is highly opportunistic in which water sources it uses, switching between using shallow and deep water sources depending upon their availability and/or salinity. These findings are consistent with the observations we present here for plantation-grown trees of the same species.

The patterns of water movement we've shown here force us to wonder if any of the species we studied demonstrate hydraulic lift (i.e. night-time water loss from lateral roots) of the kind observed by Richards and Caldwell (1987), Caldwell and Richards (1989), and Williams et al. (1993) for *Artemisia tridentata*, a widespread and deeply rooted shrub inhabiting the Great Basin deserts of the United States. The stable isotope information shown here for *B. prionotes* and our other study species would suggest that the potential for hydraulic lift exists. One might wonder, however, whether obtaining *only* water by hydraulic lift would be of any advantage to a species which inhabits very dry habitats. The possibility does exist that hydraulic lift may provide some advantage for phreatophytic species with dimorphic root systems in acquiring nutrients as discussed by Richards and Caldwell (1987) and Dawson (1993b). For the species studied here the potential benefits of an enhanced nutrient uptake linked to hydraulic lift seems unlikely however, because these taxa have shed their fine feeding roots well before onset of summer drought. Further studies are planned to monitor soil water potential and content in rooting zones of species such as *B. prionotes*, and match the information obtained to δD of soil, ground and plant water, essentially along the lines already conducted on sugar maple (*Acer saccharum*) by Dawson (1993b, 1996). This kind of information could be coupled with that obtained from studies on nutrient uptake (Pate and Jeschke 1993; Jeschke and Pate 1995) and hydraulic architecture (Pate et al. 1995) to provide a more comprehensive view of the spatial and temporal processes occurring above- and below-ground and the ecological implication for these and other tap-rooted plant taxa within both the Western Australian flora and other regions where dimorphically rooted plant taxa are present.

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