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Hydraulic lift in a neotropical savanna

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Summary

1. We report hydraulic lift in the savanna vegetation of central Brazil (*Cerrado*). Both heat-pulse measurements and isotopic (deuterium) labelling were used to determine whether hydraulic lift occurred in two common species, and whether neighbouring small shrubs and trees were utilizing this water.
2. Both techniques showed water uptake by tap-roots and reverse flow of water in lateral roots. Roots transferred hydraulically lifted water to the soil, and small shrubs and trees neighbouring the labelled individuals were labelled by deuterated water.
3. Isotopic mass-balance equations and sap-flow measurements showed that water taken up by the central tap-root in each individual constituted only a small percentage of total flux of water through the treated plants. Mass-balance equations also indicated that small shrubs and trees neighbouring the treated plants utilized only a few thousandths of a per cent of the label.
4. The small proportion of water uptake by the tap-root of these two species may be limiting hydraulic lift in this system, unless sinker roots descending from lateral roots contribute to hydraulic lift.

Key-words: Deuterium labelling, heat pulse, hydraulic lift, neotropical savanna, soil water redistribution

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Introduction

Tropical savannas are characterized by two growth forms: a herbaceous component and a woody shrub and/or tree component. Unlike the herbaceous layer, the woody component may have roots deeper than 1 m (Rawitscher 1948; Abdala *et al.* 1998). Savannas experience a pronounced dry season in which the herbaceous plants either die back or enter dormancy, whereas shrubs and trees can continue photosynthesis (Walter 1971; Walker & Noy-Meir 1982; Sarmiento 1984). Earlier studies proposed a two-compartment model to explain the coexistence of the two growth forms (Walter 1971; Walker & Noy-Meir 1982; Sarmiento 1984; Sarmiento, Goldstein & Meinzer 1985). This model suggests that herbaceous and smaller shallow-rooted plants rely mostly on water in the upper layers of the soil (top 1 m), while shrubs and trees depend on deep-water sources. A variation of this model proposes that trees and shrubs in arid regions have a dimorphic root system and depend on shallow water during the wet season and on deeper water during the dry season (Pate, Jeschke & Aylward 1995).

Several investigators, using stable isotope techniques, have tested the two-compartment savanna model with different results depending on the habitat type (LeRoux, Bariac & Mariotti 1995; Weltzin & McPherson 1997; Midwood *et al.* 1998; Moreira, Sternberg & Nepstad 2000). Season did not appear to be a major factor in determining whether or not partitioning of soil water sources occurred, as these studies usually took place throughout the year, encompassing all seasons. Studies of a temperate savanna in Arizona (USA) support the compartment model: Weltzin & McPherson (1997) observed that mature oaks (*Quercus emoryi*) utilize deeper soil water compared to grasses and tree seedlings. On the other hand, there is evidence that in humid tropical or semitropical savannas no such source partitioning occurs. LeRoux *et al.* (1995) observed that shrubs and grasses were both competing for shallow water in a West African tropical savanna. The water-uptake pattern was consistent with shallow rooting by both grasses and shrubs. Similarly, Midwood *et al.* (1998) observed shallow water competition in a semitropical savanna in Texas (USA). Competition for shallow water by grasses and

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shrubs also occurred in a savanna-like abandoned pasture in Brazil (Moreira *et al.* 2000). In the latter case, grasses absorbed more water from deeper layers of the soil profile than did shrubs. The observation that soil water partitioning does not occur in tropical and semitropical savannas is consistent with an extensive review by Schenk & Jackson (2002) showing that soil water partitioning is likely to occur only in drier habitats (<500 mm mean annual precipitation) that receive substantial winter precipitation.

A possible factor preventing water-source partitioning in tropical savannas is the modification of the water-potential gradient along the soil profile by hydraulic lift. Hydraulic lift is the passive movement of water from the lower wetter layers to the upper drier layers of the soil profile via plant root systems. Since hydraulic lift was first reported (Corak *et al.* 1987; Richards & Caldwell 1987), several investigators have confirmed this phenomenon (see review by Jackson, Sperry & Dawson 2000). The hydraulic redistribution of water downward (from wetter upper layers to drier lower layers of the soil profile) has also been reported and is known as inverse hydraulic lift (Schulze *et al.* 1998; Smith *et al.* 1999; Burgess *et al.* 2001).

The impact of hydraulic lift on ecosystem processes is of critical interest. It has been estimated that hydraulic lift nearly doubles the loss of water by evapotranspiration in a sugar maple stand (Jackson *et al.* 2000). On the other hand, a simulation model for an *Artemisia tridentata* stand showed that hydraulic lift increased total transpiration during a period of 100 days by only 3·5% on average, although it could reach 20% on some days (Ryel *et al.* 2002).

Here the relative magnitude of hydraulic lift in the savanna vegetation of central Brazil, known as *Cerrado*, was evaluated. The *Cerrado* occupies 2 million km^2 in the central part of the Brazilian shield, extending from south of Amazonian basin approximately 5° down to 20° S. It occurs from sea level to 1800 m a.s.l. on mostly very deep acidic and nutrient-poor soils. Reverse flow of water in lateral roots, a prerequisite for hydraulic lift, has previously been observed at the site studied here (Scholz *et al.* 2002). Hydraulic lift in the *Cerrado* could therefore be potentially important for plant water relations during the dry season. In the study presented here, deuterated water labelling was used in conjunction with a heat-pulse technique to test whether (1) two species of trees found abundantly at the study site hydraulically lift water; and (2) whether this hydraulically lifted water is utilized by neighbouring plants. In addition to confirming previous heat-pulse measurements showing hydraulic lift in this system (Scholz *et al.* 2002), deuterium (D) labelling allows us to determine the relative proportion of label in the various compartments involved during hydraulic lift. To answer the first question, hydraulic lift was partitioned into the following subprocesses which were tested individually: the uptake of water by tap-roots; the reverse sap flow in the lateral roots; and the release of hydraulically lifted water to surrounding soil. To answer the second question, the D content of the stem water of plants neighbouring the treated plants was measured.

Materials and methods

SITE

Measurements were taken at the end of the 2001 dry season from 4–14 August. The end of the dry season was chosen because the water potential gradient between shallow and deep soil layers would be maximal, and therefore hydraulic lift would be more likely to occur. Measurements of water potential from 7–13 August in a nearby site with the same vegetation showed midnight water potentials averaging −1·78 ± 0·02 MPa (± SEM) at 0·1 m depth and −0·80 ± 0·01 MPa (± SEM) at 1 m depth. The study site is a *cerrado denso* and was located at RECOR (Reserva Ecologica do Roncador – IBGE, 15°56′ S, 47°53′ W) located 35 km south of Brazilia, Brazil. The *cerrado denso* is a dense savanna where the woody cover ranges from 50–70% and has a height of <8 m (Moreira 2000). Soils at this site, which is 1100 m a.s.l., are classified as well drained, deep oxisols with 72% clay content (Scholz *et al.* 2002). The water table varies depending on the locale, and may be as deep as 35 m (Eiten 1993) or as shallow as 4–5 m, even during the dry season (Jackson *et al.* 1999). The average annual precipitation is 1500 mm; during the dry season <100 mm of precipitation occurs. In 2001 rainfall was well distributed until 30 May, when the last precipitation before the initiation of these experiments amounted to 6·6 mm. During this dry period until 4 August, relative humidity averaged normal values between 20 and 60% at midday.

TESTING FOR HYDRAULIC LIFT

Three trees of each of *Byrsonima crassa* Nied. (Malpighiaceae) and *Blepharocalyx salicifolius* (H.B. & K.) Berg. (Myrtaceae) were selected for sap-flow measurements and D labelling. *Byrsonima crassa* is a brevideciduous shrub or tree with large (≈10 cm long), scleromorphic leaves. *Blepharocalyx salicifolius* is a brevideciduous small tree up to 10 m high with small leaves (≈3 cm long). Both are characterized by a tap-root system (>0·5 m deep) with five to eight lateral roots (≈5 cm diameter).

To determine background abundances of D, stem samples were collected >20 m from three individuals each of *B. crassa* and *B. salicifolius*; this was also done for one individual each of *Caryocar brasiliensis* Camb., *Miconia albicans* (Sw.) Triana, *Ouratea hexasperma* (St. Hil.) Baill., *Periandra mediterranea* (Vell.) Tamb., and *Protium ovatum* Engl.

WATER UPTAKE BY TAP-ROOTS

Tap-roots were exposed by excavating a pit of radius ≈0·75 m, centred on the main trunk. Care was taken to

avoid damaging lateral roots. Heat-pulse probes were installed on tap-roots approximately 10–30 cm from the main trunk between 17:00 and 20:00 h. The root region where the probes were installed was covered with aluminium foil to decrease temperature fluctuations and light damage to the exposed roots. For two trees (*Blepharocalyx* 3 and *Byrsonima* 3), sap-flow rates in the central tap-root were measured for 1 day before the central tap-root was cut and the deuterated water treatment started. Heat-pulse measurements were taken every 0·5 h in each tree for 3 days coinciding with the deuterated water treatment, and analysed as in Scholz *et al.* (2002).

Tap-roots were cut on the same evening or on the day after heat-pulse systems were implanted. The first cut was ≈0·75 m from the root crown. Tap-roots were re-cut under water about 0·25 m above the first cut to reduce cavitation. Solutions containing 75% D_2O were fed to tap-roots using a volumetrically calibrated container. Uptake of D_2O was monitored by noting the volume change in the container over the 3 days. Stem samples of D-labelled plants were obtained in the morning at 8:00 h and at nightfall (≈19:00 h) over the 3 days of monitoring, and sealed in Vacutainer tubes (7 ml, Becton Dickinson, NJ, USA) for isotopic analysis of stem water. A mass-balance equation to determine the proportion of deuterated water (x) taken by the stems of labelled plants was used. δD values were converted to mole fractions and the proportion of label taken up was calculated according to:

$$x = (M_S - M_C)/(M_L - M_C) \qquad \text{eqn 1}$$

where M_S, M_L and M_C are mole fractions of D in the stem sample, of the labelling solution, and the mean of the control stems, respectively.

REVERSE FLOW IN LATERAL ROOTS

One to four lateral roots were partially excavated for the insertion of heat-pulse probes ≈30 cm from the main trunk for each individual. The root region where the probes were installed was covered with soil to decrease daily temperature fluctuations and damage by light. As in the tap-root, heat-pulse measurements were taken for 3 days. Following the 3 days of measurement, lateral roots with probes were cut to measure zero flow and thereby to calibrate measurements for the previous days (Scholz *et al.* 2002).

Samples from lateral roots with heat-pulse probes, as well as any other similar roots available from the labelled individuals, were collected after 3 days and sealed in Vacutainers for isotopic analysis of root water. In one plant (*Byrsonima* 3) two lateral roots were sampled at various distances from the root crown.

RELEASE OF HYDRAULICALLY LIFTED WATER IN SURROUNDING SOIL

On termination of sap-flow measurements, four soil samples approximately 0·5 m from the main trunk of each labelled individual were collected from 0·1 m below the soil surface, early in the morning (≈7:00 h). These soil samples were sealed in culture tubes for isotopic analyses of soil water.

Table 1. Individuals of *Byrsonima crassa* and *Blepharocalyx salicifolius* fed deuterated water through their tap-roots, and the species and distance (m) of their neighbours analysed for deuterium abundance

Species and neighbours	Distance of neighbours (m)
Blepharocalyx (1)	
Caryocar brasiliensis	2·06
Myrsine guianensis	0·50
Miconia ferruginata	2·00
Miconia ferruginata	0·40
Periandra mediterranea	1·70
Periandra mediterranea	2·28
Blepharocalyx (2)	
Salacia crassifolia	0·34
Periandra mediterranea	0·78
Qualea parviflora	1·70
Periandra mediterranea	0·79
Byrsonima crassa	1·80
Miconia albicans	1·10
Blepharocalyx (3)	
Rouria induta	1·22
Blepharocalyx salicifolius	1·44
Baristeriopsis sp.	0·64
Byrsonima crassa	0·85
Miconia albicans	0·93
Miconia albicans	1·77
Byrsonima (1)	
Miconia sp.	0·60
Myrcia torta	0·50
Miconia albicans	1·42
Miconia ferruginata	0·91
Protium ovatum	1·60
Mackaerium opacum	2·26
Byrsonima (2)	
Guapira noxia	0·50
Qualea multiflora	0·40
Davilla elliptica	0·33
Davilla elliptica	0·37
Rouria induta	0·94
Ouratea hexasperma	0·44
Byrsonima (3)	
Ouratea hexasperma	0·32
Chomelia ribesioides	0·73
Periandra mediterranea	0·72
Miconia sp.	1·40
Qualea multiflora	1·45
Rouria induta	1·70

UTILIZATION OF HYDRAULICALLY LIFTED WATER BY NEIGHBOURING PLANTS

Six individual small shrubs or trees neighbouring the treated individuals were selected to determine whether they were acquiring hydraulically lifted labelled water

(Table 1). Stem xylem tissue from these individuals was sampled during the 3 days of sap-flow monitoring and D feeding, at 8:00 h and nightfall (≈19:00 h). Samples were sealed in Vacutainers for isotopic analysis of stem water. The highest proportion of label utilized by each neighbouring individual was calculated in three ways: (1) proportion relative to total water taken up by the tap-root; (2) proportion relative to water taken up by the tap-root only during the night; and (3) proportion relative to the water utilized by the labelled plant shoot. The highest proportion of labelled water taken up by a neighbour plant relative to the total water taken up by the tap-root (y) was calculated by substituting the highest D mole fraction during the 3 days of stem water collection from the neighbour in place of M_S in equation 1. To calculate the proportion of labelled water taken up by a neighbour relative to the volume of water taken up by the tap-root during the night, y was divided by the volumetric fraction of deuterated water taken up only at night relative to total volume of deuterated water taken up by the tap-root. The presumption here is that nighttime water uptake is released mostly to the soil, as there is little transpiration during the night. To calculate the proportion of water utilized by neighbouring plants relative to that utilized by the shoots of the labelled plant, y was divided by the proportion of deuterated stem water in the labelled individuals (x in equation 1).

ISOTOPE ANALYSIS

Samples were taken to the laboratory for water extraction and determination of D content according to Moreira *et al.* (2000). Hydrogen isotope ratios are expressed as deviation in parts per thousands (‰) from the international standard V-SMOW (Vienna-Standard Mean Ocean Water), by:

$$\delta D_{sample}(‰) = \left[\frac{D/H_{sample}}{D/H_{VSMOW}} - 1\right] \times 1000 \qquad \text{eqn 2}$$

where D/H is the ratio of D to hydrogen in the extracted and standard water.

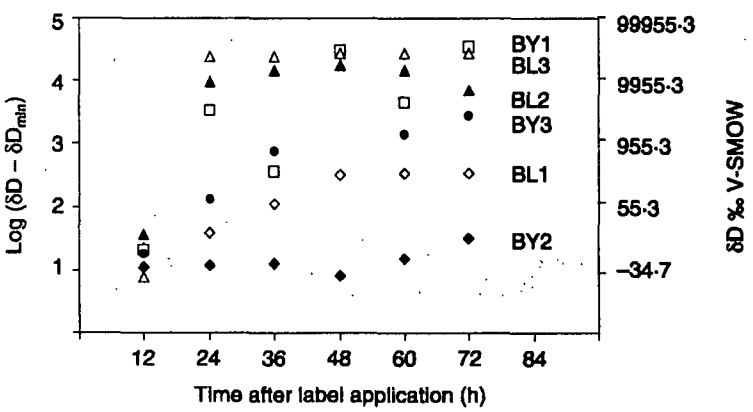

Fig. 1. Log of difference between δD of stem water of treatment plants and control plants (δD_{min}) as a function of time after D_2O introduction (BL = *Blepharocalyx*; BY = *Byrsonima*). Actual δD values equivalent to those reported on the log scale are shown on the right axis. Plants with stem water with δD within the grey area are not significantly different from control plants; those outside the grey area are significantly different at $P < 0{\cdot}05$ according to a single-sample comparison with the control population (Sokal & Rohlf 1995).

Results

HYDRAULIC LIFT

Uptake of water by tap-roots

The total cumulative volume of water conducted by the tap-root for each individual calculated from sap-flow measurements ranged from 0·12 to 1·09 l. Cutting of the central tap-root to feed deuterated water caused a twofold decrease in tap-root flow of *Blepharocalyx* 3 and a threefold decrease of *Byrsonima* 3. This also occurred in the studies for Scholz *et al.* (2002) (F.G.S., personal communication).

Volume of labelled water uptake by the central tap-root ranged from 0·14 to 1·4 l. With the exception of one outlier (*Blepharocalyx* 2) these values were consistent with sap-flow measurements using the heat-pulse technique and having a near one-to-one relationship [heat-pulse sap flow = (1·2 × volumetric sap flow) −0·071, $r^2 = 0{\cdot}92$; $P < 0{\cdot}01$, $n = 5$, regression done without data for *Blepharocalyx* 2]. There was no difference between species with respect to the volume of water absorbed by the tap-root (two tailed t-test, $F = 1{\cdot}14$; $P = 0{\cdot}345$).

With the exception of *Byrsonima* 2, all plants had labelled stem water significantly above background 24 h after label introduction (Fig. 1). Significance above background was tested by comparing a single sample with a population mean (Sokal & Rohlf 1995). The concentration of D reached an asymptotic value between 24 and 36 h after label application for most of the trees. Although treated plants took up as much as 1·4 l labelled water over 3 days, mass balance indicated that this labelled water constituted, at most, 0·72% of the total water flux in treated individuals.

Reverse sap flow in lateral roots

Three different sap flow patterns in shallow lateral roots were observed (Fig. 2). The pattern observed in *Byrsonima* 1 shows no reverse flow (Fig. 2a). The same pattern was seen in *Blepharocalyx* 1 (data not shown). The second pattern, observed in *Blepharocalyx* 2, shows continuous reverse flow throughout nearly the entire experimental period, even during daylight hours (Fig. 2b). The same pattern was observed in *Byrsonima* 2 and 3 (data not shown). The third pattern observed in *Blepharocalyx* 3 shows only nocturnal reverse sap flow (Fig. 2c). The two patterns of reverse sap flow in lateral roots have previously been observed at this site (Scholz *et al.* 2002).

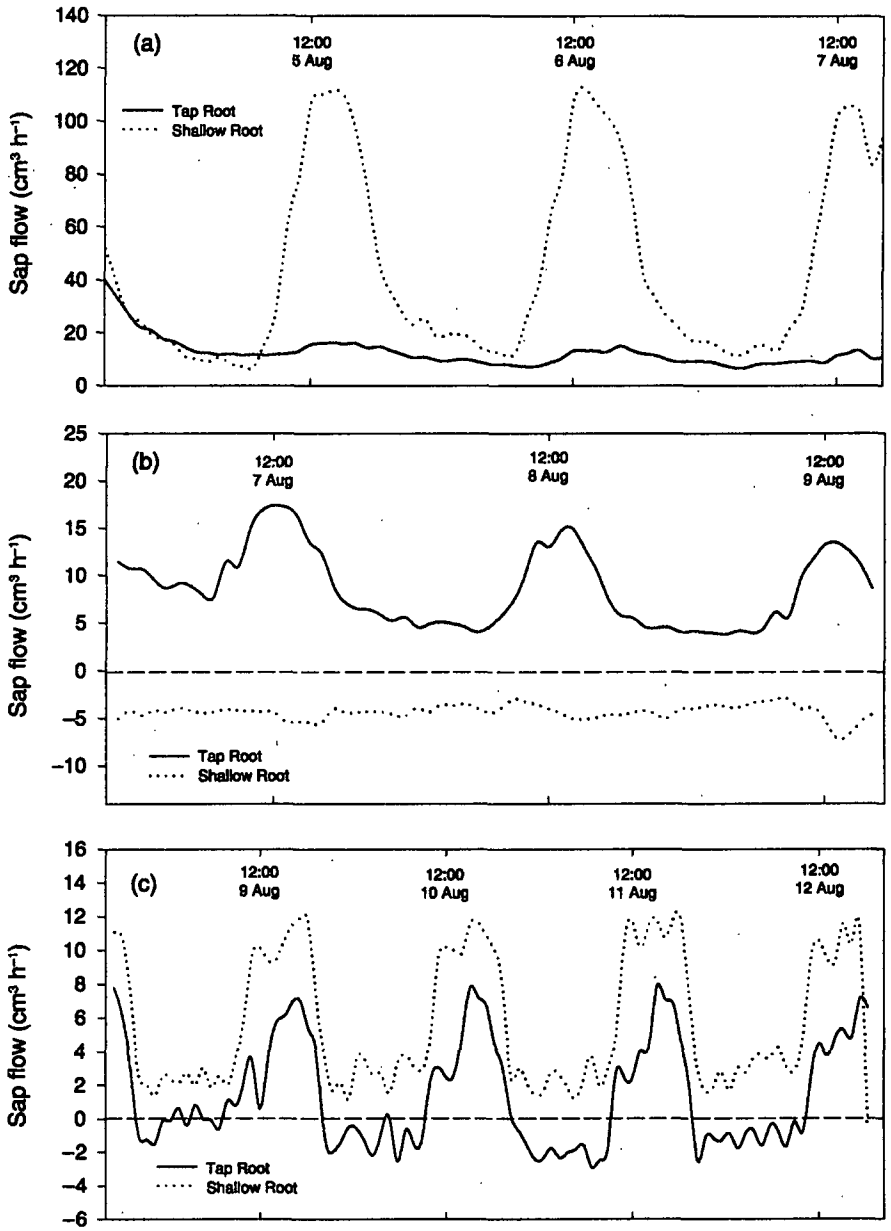

Fig. 2. Three typical sap-flow patterns observed in the field. (a) No reverse sap flow, *Byrsonima* 1; (b) continuous reverse sap flow throughout 24 h. *Blepharocalyx* 2; (c) only nocturnal reverse sap flow, *Blepharocalyx* 3. Only two lateral roots, one showing reverse flow and the other not, are shown in (c).

Deuterium label was observed not only in the main stem but also in lateral roots for most of the treated plants (Fig. 3). In some cases label was at a higher concentration in the lateral roots compared to the main stem (*Blepharocalyx* 1 and *Byrsonima* 2). The opposite was also observed for some trees (*Blepharocalyx* 3 and *Byrsonima* 1). Roots sampled in *Blepharocalyx* 3 and *Byrsonima* 1, as well as three roots of *Byrsonima* 3, showed little labelling, indicating little reverse flow for the roots sampled here (Fig. 3). Decrease in label with distance from the main trunk was observed in one of the lateral roots of *Byrsonima* 3, having δD up to +48‰ and decreasing to background abundances 1·38 m away from the trunk (Fig. 3).

Release of water to the soil

Label moved from lateral roots to soil near *Blepharocalyx* 1–3 and *Byrsonima* 1 and 2 (Fig. 4). Soil water having δD up to +2443‰ was observed. In general, soil water around *Blepharocalyx* had higher D abundance compared to that around *Byrsonima* (Fig. 4, two-tailed t-test, $F = 8{\cdot}66$, $P = 0{\cdot}04$). It is impossible to determine the amount of hydraulically lifted water that is released to the soil using isotopic mass balance as the volume of soil water affected by this release is unknown. However, on average 30–70% of the total water uptake by tap-roots occurred during the night (≈17:00–08:00 h). The bulk of this water is probably released to the soil because nocturnal transpiration demand is low.

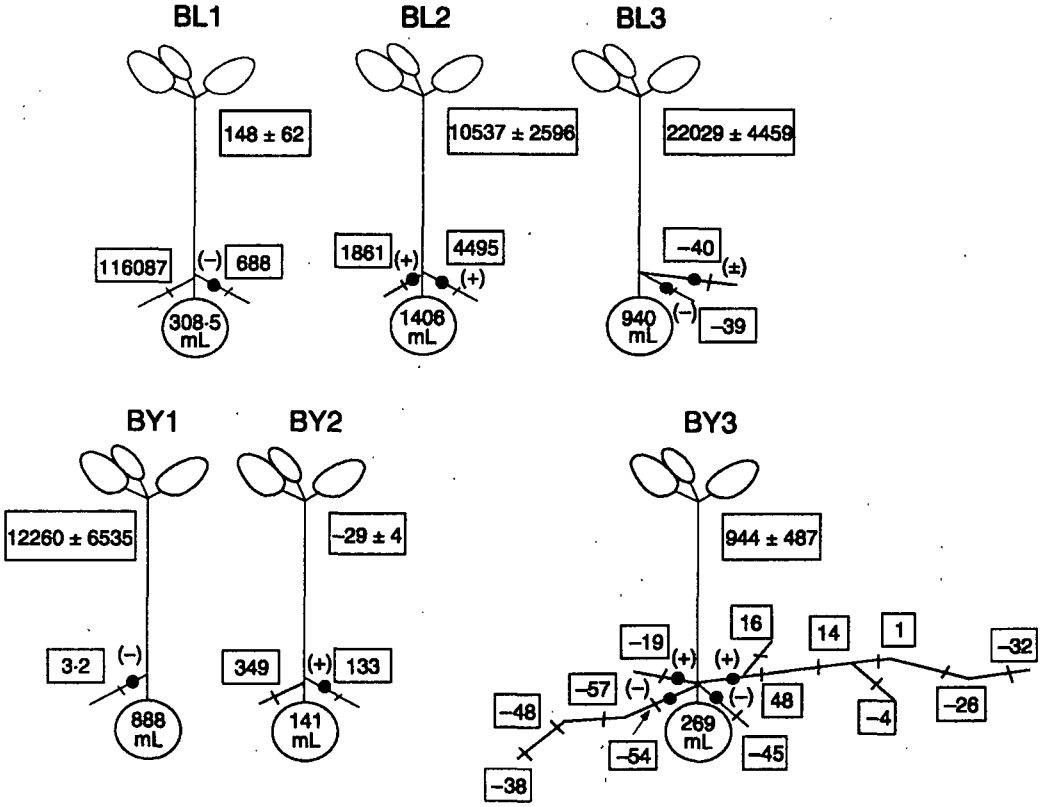

Fig. 3. Three individuals of *Blepharocalyx* (BL) and *Byrsonima* (BY) showing D_2O uptake. Circle at base of plant indicates total volume of water absorbed by tap-root at the end of the experimental period. Heat-pulse measurements were made in roots with a black dot and indicated as (+), reverse flow detected day and night; (–), no reverse flow detected; (+/–), reverse flow only at night. Number in rectangle at base of plant indicates δD (‰) of water from lateral roots; number in rectangle at tip of the plant indicates average δD (‰) of water from stems during the experimental period. See text for further description.

Table 2. Proportion of stem water in treated plants from water uptake by the tap-root, and mean (± SE) maximum proportion of water in stems from neighbouring plants, relative to: total amount of water taken up by tap-root; amount of water taken up by tap-root during the night and released to soil; and amount of water utilized by stems of treated plants

	BL1	BL2	BL3	BY1	BY2	BY3
Treated plant*	0·10	3·57	5·82	7·20	0·01	0·56
Neighbour plants						
Total tap-root*	0·011 ± 0·002	0·015 ± 0·008	0·014 ± 0·004	0·010 ± 0·002	0·010 ± 0·002	0·005 ± 0·001
Released to soil*	NR	0·028 ± 0·014	0·027 ± 0·008	0·034 ± 0·006	0·013 ± 0·002	0·007 ± 0·001
Treated stem	0·104 ± 0·016	0·004 ± 0·002	0·002 ± 0·001	0·001 ± 0·000	1·45 ± 0·279	0·010 ± 0·001

*Values ×1000.
NR, values for nocturnal water uptake were not recorded.

UPTAKE OF HYDRAULICALLY LIFTED WATER BY NEIGHBOURING PLANTS

High D abundance was detected in neighbouring small shrubs and trees. Each treated individual had at least two neighbouring plants with stem water D above background (Fig. 5). The highest D abundance in neighbouring plants was in stems of plants neighbouring *Blepharocalyx* (2 and 3), but there was no significant difference among the two species' neighbours (Fig. 5, two-tailed t-test, $F = 0{\cdot}014$, $P = 0{\cdot}911$). The average maximum proportion of D uptake by small shrubs and trees neighbouring the treated plants, relative to the total water taken up by the tap-root of treated plants, ranged from 0·005 to $0{\cdot}015 \times 10^{-3}$ (Table 2). The average maximum proportion of D uptake by neighbours relative to that released in the soil ranged from 0·007 to $0{\cdot}034 \times 10^{-3}$. The average maximum proportion of D uptake in the neighbouring plants relative to that taken up by the stem of the treated plants ranged from 0·001 to 1·45. The highest value for the latter proportion are for plants neighbouring *Byrsonima* 2, which had neighbouring plants utilizing hydraulically lifted water more readily than the shoots of the treated plant utilized label uptake from its own tap-root.

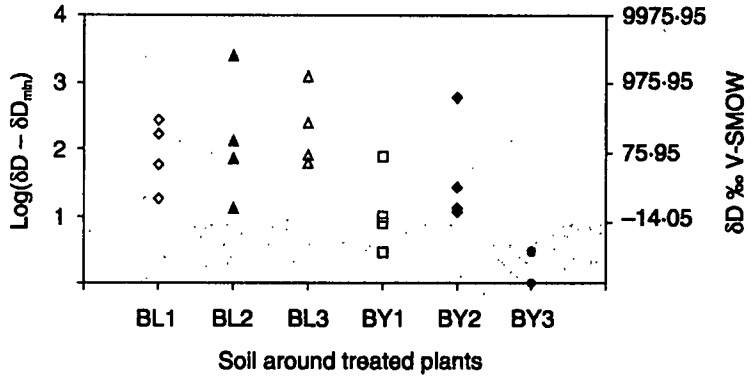

Fig. 4. Log of difference between δD of soil water from samples collected near treated plants (BL = *Blepharocalyx*; BY = *Byrsonima*) and those collected near control plants. Actual δD values equivalent to those reported on the log scale are shown on the right-hand axis. Soil water with δD outside the grey area are significantly different from control soil samples at $P < 0{\cdot}05$ according to a single sample comparison with the control population (Sokal & Rohlf 1995).

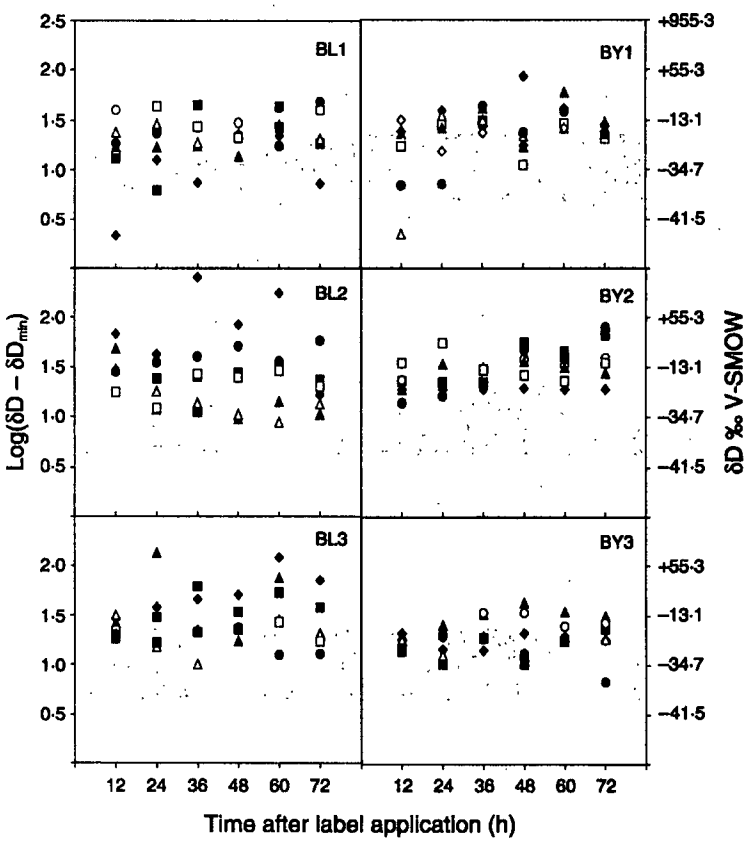

Fig. 5. Log of difference between δD of stem water from plants neighbouring treated plants and those of control plants (Table 1). Actual δD values equivalent to those reported on the log scale are shown on the right axis. Values shown outside the grey area are significantly different from control values at $P < 0{\cdot}05$ according to a single sample comparison with the control population (Sokal & Rohlf 1995).

Discussion

During the dry season, roots of savanna trees and shrubs encounter a soil profile that exposes upper lateral roots to soil with a substantially lower water potential (≈–1·8 MPa, midnight, 0·1 m depth) than that experienced by tap-roots (≈–0·8 MPa, midnight, 1 m depth). Given the large driving force for water movement from deeper to shallower soil layers, hydraulic lift could be an important ecological process in savanna. However, for hydraulic lift to occur and affect neighbouring plants, a minimum set of water transport processes must occur. First, roots penetrating the deeper, wetter soil layers must take up water from this layer. We have demonstrated this process with heat-pulse measurements here and in another study at this site (Scholz *et al.* 2002). Deuterated water uptake by the tap-root was also measured in all cases and, with the exception of *Blepharocalyx* 2, good agreement was observed between volume of label uptake and heat pulse-based measurements. It is possible that the location of heat-pulse probes in *Blepharocalyx* 2 was not representative of the xylem density throughout the circumference of its tap-root, leading to the discrepancy between the two techniques.

Using isotopic mass balance, we calculated that the water absorbed by the central tap-root was, at most, only 0·72% of that absorbed by the treated plant (Table 2). This low proportion is not an artefact of high plant capacitance (Goldstein *et al.* 1998), as the labelling of the plants showed a typical saturation curve, with saturation occurring 24–36 h after label introduction (Fig. 1). This low proportion could, however, have been caused by cavitations in the central tap-root resulting from cutting and immersion in deuterated water. We observed up to a threefold decrease in the tap-root flow rate after treatment. Even when this factor is taken into account, however, the ratio of the tap-root to stem flow is relatively low (2·2%). The ratio of central tap-root to stem sap flow via the heat-pulse method measured previously, without tap-root manipulation, also indicates a low contribution of tap-root water uptake to the total plant uptake (5–6%, F.G.S., unpublished results). Therefore, even during the dry season, roots other than the central tap-root are responsible for most of the plant's total water uptake. We note that lateral roots may have sinker root tips that deeply penetrate the soil profile (Dawson & Pate 1996; Burgess *et al.* 2000). The findings reported here do not preclude the possibility that these species utilize a considerable amount of deep soil water through these sinker roots.

A second prerequisite for hydraulic lift is reverse flow (away from the trunk) in the lateral roots, particularly at night when water potential gradients are favourable for water movement from the plant to the upper soil layers. Heat-pulse and isotopic techniques confirmed that this process occurred. The heat-pulse technique indicated reverse flow in some lateral roots in most of the plants (with the exception of *Blepharocalyx* 1 and *Byrsonima* 1; Figs 2 and 3). Deuterium was also observed in the lateral roots of most plants (with the exception of *Blepharocalyx* 3 and two roots of *Byrsonima* 3; Fig. 3). The agreement between isotopic

labelling of water in lateral roots and flux measurements is complicated by the possibility that, during the day, basipetal flux washes away label acquired by night-time reverse flow in lateral roots. Another complication in the relationship between D labelling of water in lateral roots and heat-pulse measurements is the distance from the trunk where lateral root samples were taken for water extraction and isotope analysis. There is a decrease in δD of lateral root water as the distance from the trunk increases (*Byrsonima* 3; Fig. 3). Therefore if a lateral root shows reverse flow, but root water is sampled for isotopic analysis beyond the distance travelled by the label, there would be a disagreement in the results produced by these two techniques.

The patterns of reverse flow observed here (Fig. 2) can be interpreted on the basis of the relative water potential gradient and the hydraulic conductivity between deep soil, surface soil layers and the leaf. For the case where reverse flow occurs constantly, even during the day, we hypothesize that soil water potential around the lateral root, where reverse flow was measured, is the least of all other components along the water potential gradient, including that of the leaves (Fig. 8 of Scholz *et al.* 2002). The hydraulic conductance between the tap-root and the leaf, however, should be sufficiently higher than that between the tap-root, lateral root and soil, so that leaves can still effectively import water from the tap-root. Nevertheless, in this case water moves preferentially to the lateral roots, rather than to the above-ground main stem and on to the leaf, as observed in *Blepharocalyx* 1 and *Byrsonima* 2 (Fig. 3). The plants that transported most D to lateral roots absorbed only a small quantity of labelled water (0·308 l for *Blepharocalyx* 1; 0·141 l for *Byrsonima* 2), whereas those that absorbed large quantities of labelled water (1·4 l for *Blepharocalyx* 2; 0·94 l for *Blepharocalyx* 3; 0·888 l for *Byrsonima* 1) also contained elevated D abundances in their stem water (Fig. 3). Evidently, the transpiration demand exceeds that imposed by the loss of water from lateral roots.

The third condition necessary for hydraulic lift is the release of water from lateral roots to soil. Water movement from plant to soil was confirmed with the detection of D enrichment of soil water near the treatment plants (Fig. 4). With the exception of *Byrsonima* 3, the ΔD of water extracted from soil around the treated plants was up to 2443‰, far above any natural D abundance. Our observations also indicate that D was present in the soil near *Blepharocalyx* to a greater extent than was observed near *Byrsonima* individuals (two-tailed t-test, $F = 8{\cdot}66$, $P = 0{\cdot}04$). In one case (*Blepharocalyx* 3), soil samples around the treated plants were D-enriched, while no label in lateral roots and/or reverse flow was detected in the sampled roots (Fig. 3). This phenomenon could be accounted for by other roots in the plant, with reverse flow 'leaking' water to the soil (*Blepharocalyx* 3). In another case, no label was observed in the soil even though reverse flow in lateral roots was detected (*Byrsonima* 3); either the lateral roots were not releasing labelled water to the soil, or our sampling was not able to detect the released label.

The second question addressed in this study was whether hydraulically lifted water is utilized by plants neighbouring their respective labelled individuals. This process was confirmed by isotopic measurements of stem water of neighbouring small shrubs and trees (Fig. 5). All treated plants had at least two neighbours with stem water showing D abundances above background. Presence of label in neighbouring plants was correlated with presence of label in the soil around the treated plants, for example, *Blepharocalyx* 2 had the largest concentration of D in surrounding soil and neighbouring plants, whereas *Byrsonima* 3 had the smallest. However, there might be alternative pathways, such as via root grafting or mycorrhizal connections (Querejeta *et al.* 2003) through which water could travel from a treated plant to its respective neighbours. Because some treated plants could shunt tap-root water uptake mostly to lateral roots (*Blepharocalyx* 1 and *Byrsonima* 2; Fig. 3), neighbouring plants utilized hydraulically lifted water to the same or a greater extent than shoots of the respective treated plants utilized water taken up from their own tap-roots (Table 2).

All the processes necessary for hydraulic lift to occur were demonstrated. Water moved up through the central tap-root to lateral roots, to the soil, and into neighbouring small shrubs and trees. As the above processes were quantified, it is possible tentatively to assess which of them may be limiting hydraulic lift in this ecosystem. The fraction of water taken up by the tap-root and released to the soil was 30–70%, yet water uptake by tap-roots, even when corrected for treatment effects, in these two species comprised only a small fraction of the total plant water uptake. This leads us to the conclusion that the low water uptake by the tap-root of these two species may be the factor limiting hydraulic lift in this system. Contrary to our expectations, deep-water uptake by the tap-root of these two species, comprising only about 5% of the total plant water flux, was probably insufficient to modify the dry-season water potential gradient. If, however, sinker roots branch off lateral roots in these two species, and account for a greater uptake of water from deeper soil compared with water acquired by their respective tap-roots, then the potential for hydraulic lift in this system could be much greater. Neighbouring plants were utilizing only a small fraction (a few μl) of the total taken up by the treated plants and of the hydraulically lifted water released to the soil (Table 2). Even when the decrease in tap-root water uptake caused by any cavitation is taken into account, the assimilation of labelled water by neighbouring shrubs and trees still represents a very small proportion of their water flux. Nevertheless, it is important to note that the moisture-release characteristics of many soils are such that when soil water potential is low, relatively small additions of water are required to keep it from falling further. The release of relatively small amounts of hydraulically lifted water

to the soil could still be important to maintain nutrient uptake (Caldwell *et al.* 1998); prevent root cavitation (Brooks *et al.* 2002); and ensure the survival of mycorrhizal hyphae (Querejeta *et al.* 2003).

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