Partitioning of soil water among tree species in a Brazilian Cerrado ecosystem

PAULA C. JACKSON,[1] FREDERICK C. MEINZER,[2,7] MERCEDES BUSTAMANTE,[3] GUILLERMO GOLDSTEIN,[4] AUGUSTO FRANCO,[5] PHILIP W. RUNDEL,[1] LINDA CALDAS,[5] ERICA IGLER[6] and FABIO CAUSIN[6]

[1] *Department of Biology, University of California, Los Angeles, CA 90024, USA*

[2] *Hawaii Agriculture Research Center, 99-193 Aiea Heights Drive, Suite 300, Aiea, HI 96701, USA*

[3] *Departamento de Ecologia, Universidad de Brasilia, CEP 70919-970, Brasilia, DF, Brazil*

[4] *Department of Botany, University of Hawaii, Honolulu, HI 96822, USA*

[5] *Departamento de Botanica, Universidad de Brasilia, caixa postal 04457, Brasilia, DF, Brazil*

[6] *Departamento de Ciencias Biológicas, FCEN, Universidad de Buenos Aires, Buenos Aires, Argentina*

[7] *Author to whom correspondence should be addressed*

Summary Source water used by woody perennials in a Brazilian savanna (Cerrado) was determined by comparing the stable hydrogen isotope composition (δD) of xylem sap and soil water at different depths during two consecutive dry seasons (1995 and 1996). Plant water status and rates of water use were also determined and compared with xylem water δD values. Overall, soil water δD decreased with increasing depth in the soil profile. Mean δD values were −35‰ for the upper 170 cm of soil and −55‰ between 230 and 400 cm depth at the end of the 1995 dry season. Soil water content increased with depth, from 18% near the surface to about 28% at 400 cm. A similar pattern of decreasing soil water δD with increasing depth was observed at the end of the 1996 dry season. Patterns consistent with hydraulic lift were observed in soil profiles sampled in 1995 and 1997. Concurrent analyses of xylem and soil water δD values indicated a distinct partitioning of water resources among 10 representative woody species (five deciduous and five evergreen). Among these species, four evergreen and one deciduous species acquired water primarily in the upper soil layers (above 200 cm), whereas three deciduous and one evergreen species tapped deep sources of soil water (below 200 cm). One deciduous species exhibited intermediate behavior. Total daily sap flow was negatively correlated with xylem sap δD values indicating that species with higher rates of water use during the dry season tended to rely on deeper soil water sources. Among evergreen species, minimum leaf water potentials were also negatively correlated with xylem water δD values, suggesting that access to more readily available water at greater depth permitted maintenance of a more favorable plant water status. No significant relationship between xylem water δD and plant size was observed in two evergreen species, suggesting a strong selective pressure for small plants to rapidly develop a deep root system. The degree of variation in soil water partitioning, leaf phenology and leaf longevity was consistent with the high diversity of woody species in the Cerrado.

Keywords: deciduous, deuterium, evergreen, hydraulic lift, neotropical savanna, resource partitioning, roots, stable hydrogen isotope composition.

Introduction

Neotropical savannas are the second most extensive vegetation type in South America, and among them, the Cerrados of central Brazil form the largest regional system (Goodland 1971, Texeira de Oliveira-Filho et al. 1989). The more than 1.5 million km² area is characterized by seasonal rainfall with a five-month dry season, oligotrophic soils, and frequent fires. Whereas tropical savannas in northern South America possess a relatively limited diversity of woody plant species, Cerrado communities are remarkably complex, and are characterized by a tree species diversity far higher than in any other Neotropical savanna region (Sarmiento 1984). The principal factors influencing the structure of Cerrado vegetation, including fire, soil fertility, high temperature and evaporative demand, and pronounced seasonality of precipitation (Hills 1969, Furley and Ratter 1988, Cochrane 1989, Texeira de Oliveira-Filho et al. 1989, Medina 1992, Pivello and Coutinho 1992), have been debated extensively.

Models explaining the structure of savanna ecosystems typically involve water and nutrients as limiting resources, and a two-layered (grasses versus woody species) soil–water system (Walker and Noy-Meir 1982, Knoop and Walker 1985). According to this model, the shallow roots of grasses make them superior competitors for water in the upper part of the soil profile, whereas deeply rooted woody plants have exclusive access to a deeper, more predictable water source. This two-

layered model implies that tree recruitment is dependent on the capacity of seedlings to withstand grass root competition during early growth stages, until their roots reach deeper and more reliable soil water sources to sustain them during dry periods (Medina and Silva 1990). However, results of recent studies are in apparent conflict with this model. For example, a study in West African humid savannas found that both grasses and shrub species used water from the upper layers of the soil profile during the dry and wet seasons (Le Roux et al. 1995). Furthermore, a study of seedling establishment in several woody species in a Brazilian Cerrado found seedling mortality was similar in both the wet and dry seasons (Franco et al. 1996). Early studies of root distribution in Brazilian savannas suggest that soil water exploitation is much more complex than predicted by the two-layered model originally proposed by Walker and Noy-Meir in 1982 (Ferri 1944, Rawitscher 1948, Ferri and Coutinho 1958).

The low relative humidity and relatively high daytime temperatures in the Cerrado impose a consistently high evaporative demand during the prolonged dry season. During this period, water in the upper soil layers is severely depleted as evidenced by the dieback of grasses and by the extremely low water potentials in the first few centimeters of soil (Franco 1998). In this study, we investigated the extent of spatial partitioning of soil water among 10 ecologically dominant Cerrado woody species during the dry season. Our objectives were to determine whether patterns of soil water partitioning were associated with seasonal patterns of leaf production, and with physiological features such as plant water status and rates of water use. Source water used by different species was assessed by comparing the stable hydrogen isotope composition (δD) of xylem sap with that of water obtained from different depths in the soil profile.

Materials and methods

Study site

The study was carried out during the dry seasons of 1995 (August to September), 1996 (August) and 1997 (August) at the ecological reserve of the Instituto Brasileiro de Geografía e Estatistica (IBGE), an experimental field station located approximately 33 km south of Brasilia (15°56′ S, 47°53′ W, altitude 1100 m). Mean annual rainfall is 1500–1600 mm, with a distinct rainy season from October to March or April, and a single long dry season from early May to September. During the dry season, mean daily relative humidity is around 55% and can reach low values of about 15% at midday. Mean annual temperature is about 22 °C, with small seasonal variation. Rainfall from May to August was 32 mm in 1995, 74 mm in 1996 and 136 mm in 1997. The periods during which soil and plant measurements were made were without rain.

The Cerrado vegetation of the area is classified into four structural types differing mainly in tree density: (a) *cerradão*, medium to tall woodlands with closed or semi-closed canopies; (b) *cerrado sensu stricto*, savanna woodland with low trees or shrubs, and open canopy cover of about 20%; (c) *campo sujo* (or *campo cerrado*), open savanna with scattered trees or shrubs; and (d) *campo limpo*, grassland with woody plants essentially absent. The study site was located in *cerrado sensu stricto*, with a mean tree and shrub density of ~1400 individuals ha^{-1}. The woody species mostly occur in a mixture of deciduous and evergreen trees with a low, almost shrubby growth form; most trees and shrubs have thick bark and twisted limbs and trunks. Leaves are usually large and scleromorphic. The herbaceous vegetation is seasonal in that most of its aerial portion dies back during the dry season, with regrowth usually beginning just after the rains resume (Eiten 1972). The soils are distrophic, deep and well drained.

Soil water

Soil samples were collected with a Dutch auger from two profiles at a *cerrado sensu stricto* site in August 1995 and one profile in August 1996. In August 1997, soil samples were collected at a *cerradão* site and at a nearby *campo sujo* site with similar soil characteristics. Two replicate samples were collected every 5 cm through the first 20 cm of the soil profile, then at 10 cm intervals down to 50 cm, and then every 20 cm down to 400–500 cm depth, depending on the site. To eliminate evaporation before extraction of water for δD, soil samples were collected in glass containers sealed with a rubber stopper (vacutainers), wrapped with Parafilm, and placed in a cooler with ice for transportation to the laboratory. In the laboratory, samples were stored frozen (−20 °C) for later processing by vacuum distillation (see below). For determination of gravimetric water content, separate soil samples were collected in metal cans and sealed with electrical tape. Gravimetric soil water content was determined by comparing fresh and dry weights of the samples. Dry weights were obtained after placing samples in an oven at 110 °C for 48 h.

Xylem water

Ten woody species were sampled for isotopic composition of xylem water during August 1995 (Table 1). Five deciduous and five evergreen species were selected based on their phenology and abundance among the dominant families of Cerrado vegetation. Deciduous species fell into two categories: (1) species that were leafless for a significant period in the late dry season (*Qualea grandiflora* Mart., *Q. parviflora* Mart., and *Kielmeyera coriacea* (Spr.) Mart.); and (2) species that were leafless for only a few weeks (brevi-deciduous) (*Pterodon pubescens* Benth. and *Dalbergia myscolobium* Benth.).

Xylem tissue samples were obtained either by extracting small cylinders of wood with an increment borer, or by cutting suberized, mature, stem segments. At least two individuals were sampled per species, and at least two samples were taken per plant. The outer bark and phloem were removed from all samples, and the remaining xylem tissue was immediately placed in stoppered vacutainers, sealed with Parafilm, and stored on ice. All samples were collected in the afternoon (1330 to 1600 h).

To evaluate potential relationships between plant size and source water, 10 individuals of different sizes growing in the same stand were selected from each of two species, *Miconia ferruginata* DC. and *Didymopanax macrocarpum* (Cham. &

Table 1. Characteristics of woody species used for xylem water δD analyses.

Species	Family	Leaf phenology	Leaf flush	Height (m)	Stem diameter (cm)	n
Didymopanax macrocarpum	Araliaceae	Evergreen	Throughout year	4.6 ± 1.9	6 ± 2	10
Dalbergia myscolobium	Caesalpinoidae	Briefly deciduous	End of dry season	4.5 ± 0.4	7 ± 1	10
Sclerolobium paniculatum	Caesalpinoidae	Evergreen	Wet season	3.8 ± 0.9	5 ± 1	4
Pterodon pubescens	Faboideae	Briefly deciduous	End of dry season	8.2 ± 0.5	18 ± 2	3
Kielmeyera coriacea	Guttiferae	Deciduous	End of dry season	4.0 ± 1.0	6 ± 1	3
Miconia ferruginata	Melastomataceae	Evergreen	Wet season	1.9 ± 0.4	6 ± 2	10
Roupala montana	Proteaceae	Evergreen	End of dry season	2.4 ± 0.7	6 ± 2	3
Qualea grandiflora	Vochysiaceae	Deciduous	End of dry season	3.9 ± 0.3	9 ± 4	3
Qualea parviflora	Vochysiaceae	Deciduous	End of dry season	2.2 ± 0.6	5 ± 1	3
Vochysia elliptica	Vochysiaceae	Evergreen	End of dry season	2.9 ± 0.3	6 ± 1	4

Schl.) Seem. during August 1996. Height, mean stem diameter and total number of leaves were determined for all plants.

Water sample analyses

Soil and xylem samples were sent to Mountain Mass Spectrometry (Evergreen, CO) where water was extracted by cryogenic vacuum distillation. Hydrogen gas for isotopic analysis was generated from 4-μl subsamples by the zinc reduction method. Stable hydrogen isotopic composition (δD) determined with an isotope ratio mass spectrometer was expressed as the D/H ratio relative to Vienna Standard Mean Ocean Water (V-SMOW) with a precision of 1.5‰ as:

$$\delta‰ = (R_{sample}/R_{standard} - 1)1000, \qquad (1)$$

where R_{sample} and $R_{standard}$ are the molar ratios of D/H of the sample and the standard, respectively.

Plant water status and sap flow

Predawn and midday water potentials were determined with a pressure chamber in 3–4 leaves from two individuals of each evergreen species during August and September 1995. In addition, maximum sap flow rates were estimated for eight of the 10 species over periods of three to four days by the constant heating method described by Granier (1985; see below). Sap flow is not reported for two of the deciduous species, *Kielmeyera coriacea* and *Qualea grandiflora*, which were completely leafless at the time.

For the determination of sap flow, each tree was equipped with a pair of thermal probes (UPGmbH, Munich, Germany) inserted in the main stem below the lowest branching point. The upper probe of each pair was continually heated, whereas the lower unheated probe (located ~10 cm upstream) gave the reference temperature of the sapwood. The area of the stem where the probes were installed was thermally insulated by covering the stem with rubber foam, an outer layer of reflective material, and clear plastic. Probe temperatures were recorded continuously with a data logger (CR21X, Campbell Scientific Inc., Logan, UT) equipped with a 32-channel multiplexer (AM416, Campbell Scientific) and 10-min means were stored in a solid state storage module (SM196, Campbell Scientific). Sap flow density was calculated from the temperature differ-

ence between the probes using a standard empirical relationship (Granier 1985, 1987). Mass flow of sap was obtained by multiplying flow density by the sapwood cross-sectional areas. Sapwood areas were estimated from stem diameter–sapwood area relationships obtained for each species by injecting dye near the base of the stem of several individuals of differing diameters. After several minutes, plants were decapitated a few centimeters above the point of injection, and sapwood area was determined from the pattern of staining. Sapwood depth was always greater than the 20-mm length of the probes (Clearwater et al. 1999).

Results

At the end of the 1995 dry season, soil water δD values decreased sharply from about −21‰ near the surface to −45‰ at 40 cm, then increased to about −33‰ at 50 cm (Figure 1A). Soil water δD remained relatively constant between 50 and 170 cm, then decreased rather abruptly to −58‰ at 270 cm, followed by nearly constant values down to the maximum sampling depth of 400 cm. Mean δD values were −35 ± 2‰ for the upper 170 cm of the soil profile and −55 ± 4‰ between 230 and 400 cm. Variation in soil gravimetric water content with depth (Figure 1B) mirrored that of δD. The relationships shown in Figure 1 allowed xylem water δD values to be used as an indicator of both the relative depth of water extraction by
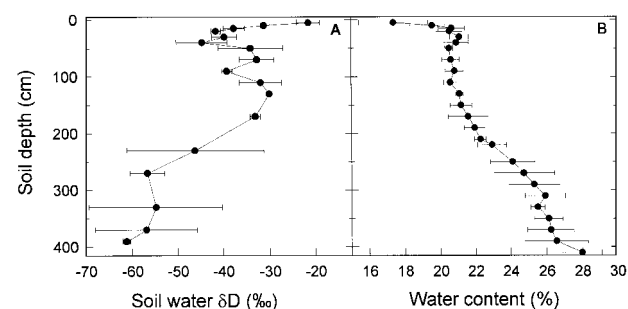

Figure 1. (A) Mean soil water δD and (B) soil gravimetric water content in relation to soil depth from two profiles in a *cerrado sensu stricto* site at the IBGE reserve during August, near the end of the 1995 dry season. Values are means ± 1 SE of two replicate samples from each profile.

roots and the relative availability of the water obtained, given the nearly uniform soil texture and water holding capacity over the range of depth sampled.

The vertical profile of soil water δD at the end of the 1996 dry season (Figure 2) was similar to that observed in the dry season of 1995 in that δD decreased substantially between the surface and 400 cm. In 1996, mean δD values were −27‰ between the surface and 110 cm where δD decreased sharply, to −44‰ between 130 and 350 cm where δD remained relatively constant, and to −62‰ between 370 and 410 cm. Soil water δD values at around 400 cm were nearly identical during August 1995 and August 1996 (cf. Figures 1 and 2). Soil water δD profiles determined in a *cerradão* and a *campo sujo* site near the end of the 1997 dry season (Figure 3) were partially anomalous with respect to profiles determined in 1995 and 1996. As in previous years, δD values decreased sharply between the surface and 50 cm depth, but then increased gradually to a depth of about 300 cm where δD values comparable to those observed near the soil surface were again attained. Thus, in contrast with 1995 and 1996, mean δD values in the upper 170 cm of the soil profile at the *cerradão* site (−55 ± 6‰) were more negative than those for the 230 to 400 cm depth range (−38 ± 2‰). Soil water δD values were consistently more negative in the *campo sujo* site than in the *cerradão* site at all depths.

Xylem sap δD values of the 10 study species during the 1995 dry season ranged from −34‰ for *Sclerolobium paniculatum* Vogel to −55‰ for *Dalbergia myscolobium* (Figure 4), suggesting different zones of active root function and therefore substantial differentiation among species in the zone of water extraction from the soil profile (cf. Figure 1). Generally, deciduous species had more negative xylem sap δD values than evergreen species, implying that deciduous species preferentially tapped deeper sources of soil water than evergreen species. Notable exceptions to this trend were *Vochysia elliptica* (C.K. Spreng) Mart., an evergreen with a mean xylem δD value of −53‰ and *Pterodon pubescens*, a briefly deciduous species with a mean xylem δD of −37‰.

Total daily sap flow was negatively correlated with xylem sap δD values ($r^2 = 0.78$ and $P < 0.01$; Figure 5A) indicating

Figure 3. Soil water δD in relation to soil depth for a *cerradão* and a *campo sujo* site at the IBGE reserve during August 1997, 100 days after 70 mm of rain originating from an unusually cold frontal system.

that species with higher rates of water use tended to access deeper soil water sources. Among evergreen species, minimum leaf water potentials were also negatively correlated with xylem water δD values ($r^2 = 0.8$ and $P < 0.01$; Figure 5B) suggesting that access to more readily available water at greater depth permitted maintenance of a more favorable plant water status (higher leaf water potentials). In contrast to the preceding relationships between physiological characteristics and xylem sap δD values, no significant relationship between xylem δD and plant size was observed in two species (Figure 6), which implies that both small and large individuals of the same species tapped water from similar depths in the soil.

Discussion

Xylem water δD values can provide an integrated estimate of water uptake by roots. By comparing these values to δD values
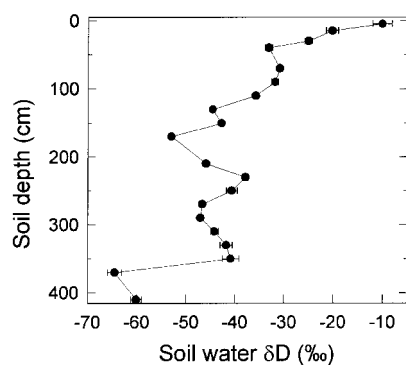

Figure 2. Soil water δD in relation to soil depth from one profile at a *cerrado sensu stricto* site at the IBGE reserve during August, near the end of the 1996 dry season. Values are means ± 1 SD of two replicate samples.
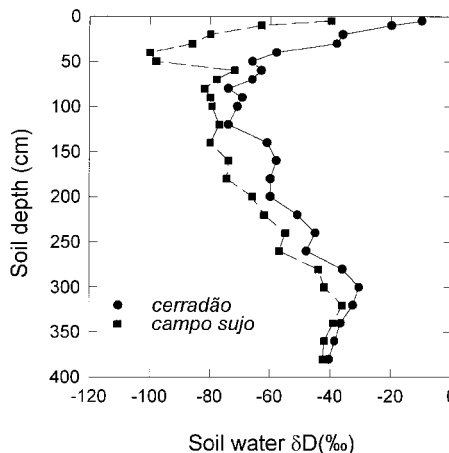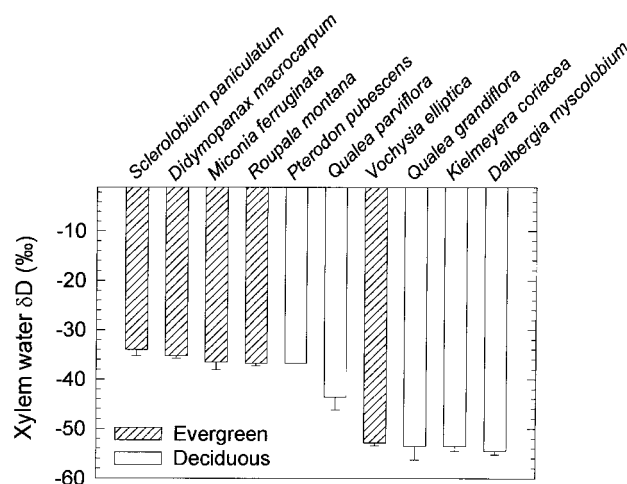

Figure 4. Mean xylem sap δD sampled near the end of the 1995 dry season for five evergreen and five deciduous species growing in a *cerrado sensu stricto* site at the IBGE reserve.
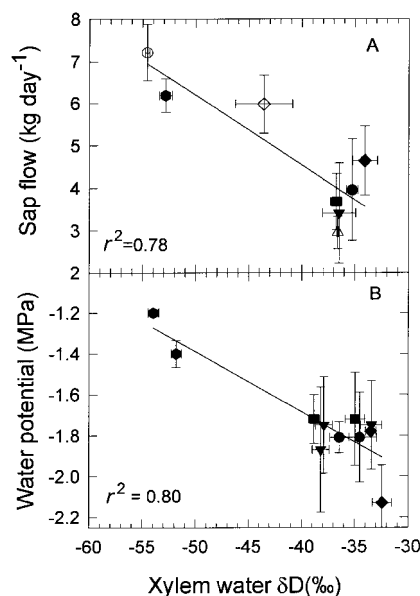
Figure 5. (A) Total daily sap flow in relation to xylem sap δD for five evergreen (closed symbols) and three deciduous (open symbols) species at the end of the 1995 dry season in the IBGE reserve. Symbols: (○) *Dalbergia myscolobium*, (●) *Didymopanax macrocarpum*, (■) *Miconia ferruginata*, (◇) *Qualea parviflora*, (△) *Pterodon pubescens*, (▼) *Roupala montana*, (◆) *Sclerolobium paniculatum*, (□) *Vochysia elliptica*. (B) Minimum leaf water potential in relation to xylem sap δD for the five evergreen species. Each point represents a different individual.
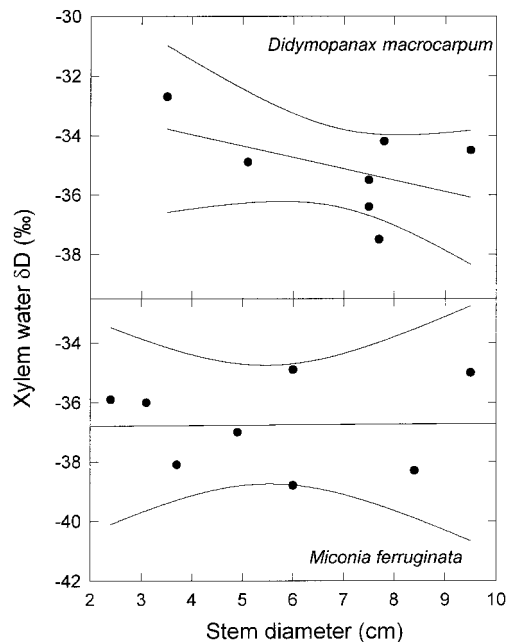

Figure 6. Relationship between xylem sap δD and stem diameter for two evergreen species at the IBGE reserve near the end of the 1996 dry season. Linear regression lines and 95% confidence limits are shown.

of potential water sources, it is possible to determine the main water source used by a plant (White et al. 1985, Sternberg and Swart 1987, White 1989, Ehleringer et al. 1991, Flanagan and Ehleringer 1991, Ehleringer and Dawson 1992). This method has been used extensively in temperate areas where seasonal variation in the isotopic composition of precipitation is pronounced (White et al. 1985, Ehleringer et al. 1991, Flanagan et al. 1992). However, it may also be used in tropical areas, where seasonal variation in the isotopic composition of precipitation is generally less pronounced, if seasonal drought is sufficient to allow the upper portion of the soil profile to become enriched in D through evaporative fractionation (Jackson et al. 1995, Le Roux et al. 1995). Our results indicated that, on average, for soil samples collected in 1995 and 1996, soil water between the surface and 110–170 cm was substantially richer in D than soil water at 200 cm or deeper (Figures 1 and 2). This pattern is consistent with evaporative fractionation of water in the upper soil layers (Zimmermann et al. 1967, Dincer et al. 1974, Thoma et al. 1979, Allison 1982, Allison and Hughes 1983, Jackson et al. 1995).

Soil water samples from the deeper layers of profiles sampled in 1995 and 1996 yielded δD values substantially more negative (less than −60‰) than those expected from temperature-based models developed to predict isotopic composition of precipitation (Gat and Gonfiantini 1981). However, soil water δD values at the study site are likely to be strongly influenced by occasional large pulses of precipitation originating from cold frontal systems arriving from subantarctic lati-

tudes. During the dry season of 1997 (August), for example, soil water δD at a *campo sujo* site attained a minimum value of −100‰ at 50 cm depth and fluctuated around −80‰ between 70 and 150 cm depth (Figure 3). In a nearby *cerradão* site, minimum δD values of about −70‰ were observed between 50 and 120 cm depth (Figure 3). Inspection of weather records revealed a large 70 mm pulse of cold precipitation during May near the end of the previous wet season (Figure 7A). An abrupt 9 °C drop in maximum air temperature was associated with the passage of the cold front bearing the precipitation (Figure 7B). Because this was one of the last major precipitation events of the previous wet season, its isotopic signature probably dominated the upper 150 cm of the soil profile (Figure 3).

Although tropical sites are often assumed to have relatively constant temperatures and therefore relatively constant isotopic composition of precipitation, additional data from a nearby precipitation sampling station at Brasilia (IAEA/WMO 1998) point to pronounced intra- and interannual variation in δD values of precipitation. Analysis of 15 years of monthly data showed a significant negative correlation between monthly δD values and monthly precipitation with δD values ranging between +20 and −80‰ (data not shown). Mean annual precipitation-weighted δD values for the 15-year period ranged between −25 and −64.5‰. This intra- and interannual variation in soil water δD profiles and in δD values of precipitation indicates the importance of obtaining concurrent, site-specific soil water δD profiles whenever xylem water δD values are analyzed. Because mean soil water δD values in the upper and lower portions of the soil profile were inverted in 1997 compared with 1995 and 1996, reliance on xylem water
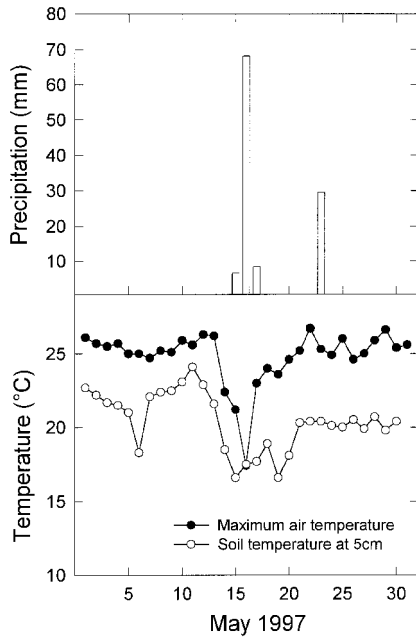
Figure 7. Daily precipitation and maximum air and soil temperatures at the IBGE reserve during May 1997.

isotopic signatures alone in 1997 would have led to erroneous conclusions concerning partitioning of soil water uptake among evergreen and deciduous species (see below).

Soil and xylem water δD data collected during the 1995 dry season revealed a clear partitioning of soil water uptake among the 10 woody species studied. Two groups were identified based on similarity of their mean xylem water δD values. One group, comprising five species, had a mean xylem water δD value of $-36\permil$ and appeared to be drawing water preferentially from the upper 170 cm of the soil profile where mean water content was about 20% (cf. Figures 1 and 4). The second group, consisting of four species with a mean xylem δD value of $-54\permil$, appeared to be preferentially tapping water from depths greater than 250 cm where soil water content was 25 to 28%. In addition, a single species, *Qualea parvifolora*, had xylem δD values intermediate between those of the other two groups, suggesting that it was either tapping water from a combination of shallow and deep sources, or that its water uptake was confined to a narrow range of depth where soil water δD was near $-45\permil$ (e.g., 50 cm or 230 cm).

Based on their xylem water δD values, evergreen species tended to rely on shallower soil water sources than deciduous species (Figure 4). The pattern shown in Figure 4 was similar to that observed by Valentini et al. (1992) who studied source water partitioning among evergreen and deciduous species in a Mediterranean macchia community in Italy. In both their study and ours, new leaf production in deciduous species coincided with the driest months of the year, implying a requirement for a more constant and reliable water source than in evergreen species, which may be able to modulate the timing of leaf production in accord with variations in soil water availability (Valentini et al. 1992). Consistent with this as-

sumption, our preliminary data on leaf production and loss (Caldas et al., unpublished observations) indicate that although most deciduous species followed a similar pattern of leaf production, with new leaves flushing at the end of the dry season, the timing of leaf production and loss was more variable among evergreen species. For example, whereas *Sclerolobiumpaniculatum* and *Miconiaferruginata* produced new leaves during the rainy season, *Didymopanax macrocarpum* tended to flush throughout the year, and *Roupala montana* Aubl., and *Vochysia elliptica* produced new leaves towards the end of the dry season. Of the two latter species, *V. elliptica*, with a mean xylem water δD of $-53\permil$, showed a pattern of soil water partitioning consistent with that of three of the deciduous species rather than with the other four evergreen species. Predawn water potential was also greater (less negative) in *Vochysia elliptica* than in the other evergreen species (data not shown). On the other hand, xylem water δD values of *Pterodon pubescens*, a brevi-deciduous species, suggested that its pattern of soil water uptake was more similar to that of the evergreen species than to the other deciduous species. However, *P. pubescens* was a typical deciduous species in that it produced new leaves at the end of the dry season.

Two important physiological indices of relative water availability were consistent with patterns of soil water partitioning inferred from xylem and soil water δD values. First, midday leaf water potential was less negative in individuals of evergreen species having more negative xylem water δD values (Figure 5B). This result was consistent with previous observations in a pinyon–juniper woodland (Flanagan et al. 1992) and a lowland tropical forest (Jackson et al. 1995). Secondly, total daily sap flow was greatest in species with the most negative xylem water δD values (Figure 5A). Similar behavior was reported for shrubs growing in gaps in a Panamanian forest (Jackson et al. 1995). However, in contrast with earlier reports that larger individuals can preferentially tap deeper sources of soil water than smaller individuals of the same species (Dawson and Ehleringer 1991, Dawson 1996), our results point to the absence of a pronounced influence of plant size on soil water partitioning among Cerrado woody species. Xylem sap δD values fell between -33 and $-39\permil$ among individuals of *Didymopanax macrocarpum* and *Miconia ferruginata* having stem diameters ranging between 2 and 10 cm (Figure 6). Because mean soil water δD between the surface and 110 cm was $-27\permil$ (Figure 2), both species appeared to rely significantly on water obtained from depths below 110 cm where mean δD was $-47\permil$. The lack of a marked size dependence of xylem δD values in Cerrado woody species is intriguing and suggests that there may be strong selective pressure for small plants to develop a relatively deep root system rapidly. Access to greater depths where substantial soil water depletion does not occur during the dry season may facilitate establishment and survival of small plants by allowing them to maintain relatively constant or even increased rates of water use during the dry season.

Although profiles of soil water δD taken during the 1995 dry season showed the expected evaporative enrichment in D near the surface (Figure 1A), there was a transient shift toward more

negative values at a depth of about 40 cm, followed by a return to less negative values to a depth of about 170 cm. The transient shift in δD values at 40 cm coincided with a temporary shift in soil gravimetric water content toward greater values at 40 cm (Figure 1B). These patterns are consistent with the occurrence of hydraulic lift, the passive movement of water from drier to moister portions of the soil profile via root systems (Dawson 1993, Caldwell et al. 1998). Thus, water with a more negative isotopic signature taken up by roots from greater depths may have been released by shallow roots in drier soil. It has been suggested that hydraulic lift can contribute significantly to the water balance of not only the plant responsible for it, but also to neighboring plants (Caldwell et al. 1998). The partially anomalous soil water δD profiles obtained in a *cerradão* and a *campo sujo* site during the 1997 dry season (Figure 3) were also consistent with the occurrence of hydraulic lift. These two sites were in close proximity to each other, had similar soils and differed largely in the density of woody plant cover. In the *campo sujo* site, which contained mostly grasses and herbaceous vegetation, soil water δD values at 50 cm (−100‰) were more negative than either at the surface or at 400 cm. As suggested above, the extremely negative δD value at 50 cm probably reflected precipitation input from a cold front near the end of the previous wet season (Figure 7). Soil δD values above 50 cm were likely to have been influenced by evaporative fractionation, and below 50 cm, increasingly influenced by the precipitation-weighted mean δD value for the rest of the previous wet season. In the *cerradão* site where the woody plant density was relatively high, soil water δD values at 50 cm were about 40‰ less negative than in the *campo sujo* site, but below 50 cm, δD values in the two sites tracked each other closely and were nearly identical below 300 cm. Thus, when the *campo sujo* site is used as a nearly treeless reference or control, the soil water δD profile in the *cerradão* is consistent with the lifting of water with a less negative isotopic signature from the deeper portions of the soil profile and its redeposition into the upper portion of the profile.

The degree of soil water partitioning and variation in timing of leaf production and loss among Cerrado woody species suggest that mechanisms of resource partitioning may play an important role in maintenance of the high diversity of woody species in the Cerrado. However, these mechanisms may imply a series of trade-offs. For example, although a deep rooting pattern in deciduous plants may allow for new leaf production during the driest months of the year, it may also impose hydraulic limitations on the amount of water that the plants can extract and transpire daily (Meinzer et al. 1999). Traditional models explaining leaf loss and production developed mainly for temperate areas may therefore be inadequate for describing the mechanisms underlying the same processes in tropical ecosystems such as the Cerrado.

Acknowledgments

References

Allison, G.B. 1982. The relationship between ^{18}O and deuterium in water in sand columns undergoing evaporation. J. Hydrol. 55:163–169.

Allison, G.B. and M.H. Hughes. 1983. The use of natural tracers as indicators of soil water movement in a temperate semi-arid region. J. Hydrol. 60:157–173.

Caldwell, M.M., T.E. Dawson and J.H. Richards. 1998. Hydraulic lift: consequences of water efflux from the roots of plants. Oecologia 113:151–161.

Clearwater, M.C., F.C. Meinzer, J.L. Andrade, G. Goldstein and N.M. Holbrook. 1999. Potential errors in measurement of nonuniform sap flow using heat dissipation probes. Tree Physiol. 19:681–687.

Cochrane, T.T. 1989. Chemical properties of native savanna and forest soils in central Brazil. Soil. Sci. Soc. Am. J. 53:139–141.

Dawson, T.E. 1993. Hydraulic lift and water use by plants: implications for water balance, performance and plant-plant interactions. Oecologia 95:565–574.

Dawson, T.E. 1996. Determining water use by trees and forests from isotopic energy balance and transpiration analyses—the roles of tree size and hydraulic lift. Tree Physiol. 6:263–272.

Dawson, T.E. and J.R. Ehleringer. 1991. Streamside trees that do not use stream water. Nature 350:335–337.

Dincer, T., A. Al-Mugrin and U. Zimmermann. 1974. Study of the infiltration and recharge through the sand dunes in arid zones with special reference to the stable isotopes and thermonuclear tritium. J. Hydrol. 23:79–109.

Ehleringer, J.R. and T.E. Dawson. 1992. Water uptake by plants: perspectives from stable isotope composition. Plant Cell Environ. 15:1073–1082.

Ehleringer, J.R., S.L. Philips, W.S.F. Schuster and D.R. Sandquist. 1991. Differential utilization of summer rains by desert plants. Oecologia 88:430–434.

Eiten, G. 1972. The Cerrado vegetation of Brazil. Bot. Rev. 38:201–341.

Ferri, M.G. 1944. Transpiracão de plantas permanentes dos "cerrados." Boletim de Faculdade de Ciencias e Letras. Universidade de São Paulo, Botanica 4:1–161.

Ferri, M.G. and L.M. Coutinho. 1958. Contribucão ao conhecimento da ecologia do cerrado. Estudo comparativo da economia d'agua de sua vegetacão em Emas, Campo Grande e Goiania. Boletim Faculdade de Filosofia Ciencias e Letras, Universidad de São Paulo, Botanica 15:102–150.

Flanagan, L.B. and J.R. Ehleringer. 1991. Stable isotope composition of stem and leaf water: applications to the study of plant water use. Funct. Ecol. 5:270–277.

Flanagan, L.B., J.R. Ehleringer and J.D. Marshall. 1992. Differential uptake of summer precipitation among co-occurring trees and shrubs in a pinyon–juniper woodland. Plant Cell Environ. 15:831–836.

Franco, A.C. 1998. Seasonal patterns of gas exchange, water relations and growth of *Roupala montana*, an evergreen savanna species. Plant Ecol. 136:69–76.

Franco, A.C., G.B. Nardoto and M.P. de Souza. 1996. Patterns of soil water potential and seedling survival in the cerrados of Central Brazil. Proc. 1st Int. Symp. Tropical savannas: biodiversity and sustainable production of food and fibers in the Tropical savannas. Eds. R.C. Pereira and L.C.B. Nasser. EMBRAPA-CPAC, Planaltina, Brazil, pp 277–280.

Furley, P.A. and J.A. Ratter. 1988. Soil resources and plant communities of the central Brazilian cerrado and their development. J. Biogeogr. 15:97–108.

Gat, J.R. and R. Gonfiantini. 1981. Stable isotope hydrology. Deuterium and oxygen-18 in the water cycle. Int. Atomic Energy Agency, Vienna, 142 p.

Goodland, R. 1971. A physiognomic analysis of the "cerrado" vegetation of central Brasil. J. Ecol. 59:411–419.

Granier, A. 1985. Une nouvelle méthode pour la mesure du flux de sève dans le tronc des arbres. Ann. Sci. For. 42:193–200.

Granier, A. 1987. Evaluation of transpiration in a Douglas-fir stand by means of sap flow measurements. Tree Physiol. 3:309–320.

Hills, T.L. 1969. The savanna landscapes of the Amazon Basin. Savanna Research Series No. 14, Dept. Geography, McGill Univ., Montreal, Canada, 41 p.

IAEA/WMO. 1998. Global network for isotopes in precipitation. The GNIP database. May 2, 1998. URL: http://www.iaea.org/programs/ri/gnip/gnipmain.htm.

Jackson, P.C., J. Cavelier, G. Goldstein, F.C. Meinzer and N.M. Holbrook. 1995. Partitioning of water resources among plants of a lowland tropical forest. Oecologia 101:197–203.

Knoop, W.T. and B.H. Walker. 1985. Interactions of woody and herbaceous vegetation in a Southern African savanna. J. Ecol. 73:235–253.

Le Roux, X., T. Bariac and A. Mariotti. 1995. Spatial partitioning of the soil water resource between grass and shrub components in a West African humid savanna. Oecologia 104:147–155.

Medina, E. 1992. Mineral nutrition in tropical savannas. Prog. Bot. 54:237–253.

Medina, E. and J.F. Silva. 1990. Savannas of northern South America: a steady state regulated by water-fire interaction on a background of low nutrient availability. J. Biogeogr. 17:403–413.

Meinzer, F.C., G. Goldstein, A.C. Franco, M. Bustamante, E. Igler, P. Jackson, L. Caldas and P.W. Rundel. 1999. Atmospheric and hydraulic limitations on transpiration in Brazilian Cerrado woody species. Funct. Ecol. 13:273–282.

Pivello, V.R. and L.M. Coutinho. 1992. Transfer of macro-nutrients to the atmosphere during experimental burnings in an open cerrado (Brazilian savanna). J. Trop. Ecol. 8:487–497.

Rawitscher, F. 1948. The water economy of the vegetation of the campos cerrados in southern Brazil. J. Ecol. 36:237–267.

Sarmiento, G. 1984. The ecology of neotropical savannas. Harvard Univ. Press, Cambridge, MA, 235 p.

Sternberg, L.S.L. and P.K. Swart. 1987. Utilization of fresh water and ocean water by coastal plants of Southern Florida. Ecology 68:1898–1905.

Texeira de Oliveira-Filho, A., G.J. Shepherd, F.R. Martins and W.H. Stubblebine. 1989. Environmental factors affecting physiognomic and floristic variation in an area of cerrado of central Brazil. J. Trop. Ecol. 5:413–431.

Thoma, G., N. Esser, C. Sonnatag, W. Weiss, J. Rudolf and P. Leveque. 1979. New technique of *in situ* soil moisture sampling for environmental isotope analyses applied at Pilat sand dune near Bordeaux. *In* Proc. 1978 Symp. on Isotopes in Hydrology. Int. Atomic Energy Agency, Vienna, pp 753–766.

Valentini, R., G.E. Scarascia Mugnozza and J.R. Ehleringer. 1992. Hydrogen and carbon isotope ratios in selected species of a Mediterranean macchia ecosystem. Funct. Ecol. 6:627–631.

Walker, B.H. and I. Noy-Meir. 1982. Aspects of the stability and resilience of savanna ecosystems. *In* Ecology of Neotropical Savannas. Ecol. Stud. 42. Springer, Berlin, pp 556–590.

White, J.W.C. 1989. Stable hydrogen isotope ratios in plants: a review of current theory and some potential applications. *In* Stable Isotopes in Ecological Research. Eds. P.W. Rundel, J.R. Ehleringer and K.A. Nagy. Springer, Berlin, pp 142–162.

White, J.W.C., E.R. Cook, J.R. Lawrence and W.S. Broecker. 1985. The D/H ratios of sap in trees: implications for water sources and tree rings D/H ratios. Geochim. Cosmochim. Acta 49:237–246.

Zimmermann, U., D. Ehhalt and K.O. Munnich. 1967. Soil water movement and evapotranspiration: changes in the isotopic composition of the water. *In* Proc. 1966 Symp. on Isotopes in Hydrology. Int. Atomic Energy Agency, Vienna, pp 567–584.