Water use by woody plants on contrasting soils in a savanna parkland: assessment with δ^2H and δ^{18}O

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Abstract

In savanna parklands of southern Texas, patches of grassland and 'discrete clusters' of small trees and shrubs occur on sandy loam surface soils underlain by an argillic horizon (claypan) at 40 cm. Large trees and shrubs in 'groves' occur on deep (2 m) sandy loam soils without an argillic horizon. δ^2H and δ^{18}O of rainfall, groundwater, and soil and plant water were measured to: (1) determine if coexistence in woody patches occurs via vertical stratification of soil water uptake; (2) document differences in plant water acquisition on contrasting soil types; and (3) evaluate recharge and evaporative losses of soil moisture from grassland vs. wooded landscape elements. Groundwater was isotopically similar to weighted rainfall, suggesting local recharge at this site. Linear regressions of soil water δ^2H on δ^{18}O yielded slopes less than the meteoric water line, indicating significant evaporative losses of soil moisture in all landscape elements. Interspecific differences in root density distribution were significant; some woody species had roots well below 1.6 m, while others had few roots below 0.8 m. δ^2H and δ^{18}O values of stem water from all plants in groves were lower than those of soil water in the upper 1.5 m of the profile, suggesting all species obtained their water from depths >1.5 m. Deep roots of trees and shrubs at this savanna parkland site thus appeared to have a functional significance that was not revealed by biomass or density determinations. Root densities of species in discrete clusters (claypan present) were typically greater than those of the same species in groves (claypan absent), especially in the upper 80 cm of the soil profile. Consistent with rooting profiles, δ^2H and δ^{18}O values of plant water indicated that trees and shrubs in discrete clusters with fine-textured subsoils obtained most of their water at depths <1.5 m. As with groves, there was no indication of water resource partitioning between species. In summary, we saw no isotopic evidence that co-occurring woody plants at this savanna parkland site were partitioning soil moisture vertically during late summer/early fall, despite marked differences in their root density distributions. This supports other lines of evidence which indicate that species interactions in tree/shrub clumps are competitive, and that species composition is therefore unstable in those landscape elements.

Introduction

The availability of light, water and nutrients are major determinants of plant community structure and function. In arid and semiarid ecosystems, availability of soil moisture drives primary production and influences nutrient dynamics. Plant communities are thus comprised of species with various adaptations for acquiring and conserving soil moisture. When water requirements, phenology and rooting patterns are similar, competitive exclusion may occur; when they differ, species may coexist. In tree and shrub savannas, woody plants and grasses are often presumed to coexist by partitioning the soil water resource vertically (Eagleson and Segarra, 1985; Walker and Noy-Meir,

1982; Walter, 1971). Although some field studies support this hypothesis (Pelaez et al., 1994; Sala et al., 1989), others do not (LeRoux et al., 1995; Scholes and Archer, 1997). Such inconsistencies reflect the fact that a variety of factors, including rainfall amount and seasonality, soil texture and depth, and disturbance (fire, grazing, browsing) can affect species interactions.

Though seldom documented experimentally, competition and self-thinning of woody plants in savannas has been inferred from field studies of the spacing and size of plants. However, in some savannas (often termed 'savanna parklands'), tree and shrub distributions are highly aggregated. Woody plant interactions in these multispecies, clumped assemblages remain largely unknown. If resource partitioning is prevalent, species aggregates may be dynamically stable; if competition occurs, one species or functional group may be in the process of displacing another. Previous work in savanna parklands of southern Texas suggests that tree/shrub clumps develop when the tree legume, *Prosopis glandulosa* var. *glandulosa* Torr., invades and establishes in grassland patches (Archer et al., 1988). Over time, *Prosopis* modifies soils and microenvironment to facilitate the ingress and establishment of subordinate, bird-dispersed shrub species. This process occurs both on soils which are coarse-textured throughout, and on soils underlain by a shallow argillic or claypan horizon at approximately 40 cm below the soil surface. However, plants are larger and rates of cluster development and plant growth are more rapid on sites with deep, coarse-textured, non-argillic soils (Archer, 1995).

The compositional stability of tree-shrub patches in this savanna parkland may depend upon the intensity and symmetry of species interactions. Coexistence of species in tree/shrub clusters may be achieved through horizontal and/or vertical stratification of roots which reduces belowground competition for water and nutrients (Caldwell and Richards, 1986; Manning and Barbour, 1988; Yeaton et al., 1977). Pre-dawn leaf water potentials of overstory *Prosopis* plants on fine-textured soils are relatively constant during the growing season, and range from approximately -0.5 to -1.5 MPa. In contrast, those of an associated understory shrub, *Zanthoxylum fagara* (L.) Sarg., ranged from -0.5 MPa during moist periods to -6.5 MPa during hot, dry periods (Archer, 1995). These data suggest that *Zanthoxylum* is shallow-rooted and its physiological activity is coupled closely to soil water availability in the upper profile. In con-

trast, *Prosopis* plants are deeply rooted with access to more stable stores of soil water. Their physiological activity is, therefore, independent of moisture conditions in the upper soil profile. If these inferences are correct, *Prosopis* and *Zanthoxylum* may be effectively partitioning soil moisture and their association may be relatively stable. Evaluation of the validity of these inferences requires direct determination of vertical stratification of plant water use.

Direct assessment of root function and water uptake with respect to depth in the soil is problematic. Root biomass and density distribution do not necessarily quantify root viability, level of physiological activity, or resource availability. Consequently, root distributions do not necessarily correlate with zones of water uptake (Knoop and Walker, 1985; Walker and Richardson, 1991). Inferences regarding vertical stratification of plant water use based on plant ecophysiological performance or soil water budgets are also equivocal (Walker and Richardson, 1991). Natural ^{2}H/^{1}H (δ^2H) and ^{18}O/^{16}O (δ^{18}O) ratios can be used to quantify spatial utilization of soil moisture by matching the isotopic signature of plant xylem water with that of soil water from different depths within the soil profile (Brunel et al., 1991, 1995; Dawson, 1993a; Ehleringer and Dawson, 1992; Schulze et al., 1996; Walker and Brunel, 1990; Walker and Richardson, 1991; White et al., 1985). In savanna systems, comparisons of the δ^2H and δ^{18}O of potential source waters with plant xylem sap have indicated that deeply rooted trees in low rainfall zones (600 mm annual rainfall) effectively partition soil moisture with grasses (Weltzin and McPherson, 1997), whereas shallow-rooted trees in humid savannas (1000 mm annual rainfall) do not (Le Roux et al., 1995).

In this study we used the δ^2H and δ^{18}O of plant and soil water, precipitation, and groundwater in conjunction with root distribution patterns to test the hypotheses that: (1) trees and shrubs in woody patches utilize soil water from different depths in the profile; (2) this vertical partitioning of soil water differs between tree/shrub patches occurring on deep, coarse-textured sites and shallow sites underlain by an argillic (clay) horizon; and (3) evaporation is greater in grass-dominated patches than woody patches.

Materials and methods

Site description

Research was conducted at the Texas Agricultural Experimental Station, La Copita Research Area, a 1093 ha site near Alice, Texas (27°40′ N; 98°12′ W) in the eastern Rio Grande Plains of the Tamaulipan Biotic Province. The site has been grazed heavily to moderately by cattle since the late 1800s. The climate is subtropical with a mean annual temperature of 22.4 °C. Mean annual precipitation is 720 mm yr^{-1}, 70% of which occurs between April and September. Mean annual potential evaporation is 1540 mm. Maritime tropical air masses from the Gulf of Mexico control the weather in this region from May to September and contribute most of the annual precipitation. Winter and early spring precipitation is often derived from cool continental air masses originating in northern North America.

Upland surface soils are sandy loams (Typic and Pachic Argiustolls). A subsurface argillic, clay horizon is laterally continuous throughout much of the uplands which are dominated by C_4 grasslands interspersed with small, widely spaced, discrete clusters of woody plants (2–15 woody species per cluster). Non-argillic inclusions (e.g. soils coarse-textured throughout) occur within the uplands, and typically support large groves of woody vegetation. Both groves and discrete clusters are dominated by a honey mesquite (*P. glandulosa* var. *glandulosa* Torr.) overstory with numerous shrubs in their understory (Archer, 1995; Archer et al., 1988). See Boutton et al. (1998) and Scifres and Koerth (1987) for additional details on climate, vegetation, and soils. Plant names are based on Correll and Johnston (1979).

Collection of groundwater, precipitation, soil and plant samples

Samples from each rainfall event from January through October 1991 were quantified and then frozen. Rainwater was removed from the collector immediately following each precipitation event to prevent isotopic fractionation due to evaporation. Groundwater (>60 m below the surface) was sampled from four wells on the La Copita Research Area in January and October, 1991, and frozen until isotopic analyses were performed.

Stem samples (>2 cm dia. × 15 cm length) were collected in October 1991 from woody species in a grove, a cluster, and from 2 juvenile, solitary *P. glandulosa* saplings growing in grassland patches. A soil core (5 cm × 150 cm) from each of these sites and grass-dominated patches was collected on the same day and divided into 16 depth intervals (0–5, 5–10, and then 10 cm increments to 150 cm). To minimize evaporative isotopic fractionation, soil increments and individual stem samples were sealed in 250 mL bottles containing 200 mL of dry toluene (<0.03% H_2O) immediately after collection.

Root density and biomass distribution

Root biomass was estimated from soil cores (5 cm × 150 cm) obtained from individual groves ($n = 6$) and adjacent grassland patches ($n = 6$). Each core was divided into 6 depth intervals (0–15, 15–30, and at 30 cm increments thereafter). Roots were removed by flotation in saturated NaCl solution (density = 1.2 g cm^{-3}). Floated material consisted primarily of live and dead roots. The 0–15 cm increment also contained fragments of aboveground litter, but no attempt was made to separate these materials.

Root density was determined along trenches (1 m wide × 2 m deep) in two grove and two cluster patches. The trenches extended completely through the clusters, while at the larger grove sites the trenches extended only from the outer edge to the center. Trench walls were smoothed and roots exposed by removing 3–5 mm of soil. Roots within spatially registered 20 cm × 20 cm grid cells along trench faces were counted and keyed to species (Watts, 1993). We report here on select species common to groves and discrete clusters.

Plant and soil water extraction and isotopic analyses

Water was extracted from soil and stem samples by azeotropic distillation in dry toluene (Revesz and Woods, 1990). This method has been shown to extract hydrologically active water, but not heat-labile or crystallization water which is isotopically fractionated and not intimately associated with active soil water (Ingraham and Shadel, 1992; Revesz and Woods, 1990). A comparison of the mean (± SD) δ^2H value before (-25.8 ± 1.7‰) and after (-26.0 ± 1.1‰) distillation of six 3 mL aliquots of tap water confirmed that this procedure did not alter isotopic composition.

δ^2H determinations were made by reducing the water samples to H_2 gas by zinc reduction in pyrex vessels at 495 °C (Wong et al., 1987). Zinc was obtained from the Biogeochemical Laboratories at

University of Indiana (Bloomington, IN, USA). H_2 was analyzed on a Sigma 6 (CJS Sciences, Winsford, UK) gas isotope ratio mass spectrometer. $\delta^{18}O$ was determined after equilibration of water samples with CO_2 in Vacutainers^{TM} (Midwood et al., 1992). The $\delta^{18}O$ content of the CO_2 was then determined on a VG-903 (VG Isogas, Middlewich, UK) gas isotope ratio mass spectrometer. Precision of duplicate analyses was <2‰ for δ^2H, and <0.4‰ for $\delta^{18}O$. δ^2H and $\delta^{18}O$ values were expressed in conventional δ-notation relative to V-SMOW:

$$\delta^2H_{V-SMOW} \text{ or } \delta^{18}O_{V-SMOW}(‰)$$
$$= \{(R_{SAMPLE}/R_{V-SMOW}) - 1\} \times 10^3 \qquad (1)$$

where R_{SAMPLE} and R_{V-SMOW} are the $^2H/^1H$ or $^{18}O/^{16}O$ ratios of the sample and V-SMOW, respectively. δ^2H_{V-SMOW} and $\delta^{18}O_{V-SMOW}$ values were normalized relative to the VSMOW/SLAP scale (Gonfiantini, 1981).

Weighted mean δ^2H and $\delta^{18}O$ values for rainfall were calculated monthly and for the entire January-through-October period using the equation:

$$\delta_{WT} = \sum_{x=1}^{n} \delta_x f_x \qquad (2)$$

where δ_{WT} is the weighted mean δ^2H or $\delta^{18}O$ value for rainfall, δ_X is the isotopic composition of an individual rainfall event, f_x is the fractional contribution of that event to either the monthly or January-October rainfall total, and n is the number of rainfall events.

Results

δ^2H and $\delta^{18}O$ of precipitation and groundwater

Monthly rainfall amount was inversely related to weighted monthly mean δ^2H ($R^2 = 0.54$; $p < 0.015$) and $\delta^{18}O$ ($R^2 = 0.45$; $p < 0.032$) of the precipitation, with enriched monthly precipitation values associated with lower rainfall amounts (Figure 1). The weighted mean isotopic composition of rainfall over the 10 month period ($\delta^2H = -22.4‰$, and $\delta^{18}O = -4.3‰$) was similar to that of groundwater from the 4 wells sampled in January ($\delta^2H = -25 \pm 2‰$; $\delta^{18}O = -4.4 \pm 0.6‰$) and October 1991 ($\delta^2H = -24 \pm 1‰$; $\delta^{18}O = -3.8 \pm 0.2‰$). When plotted in δ^2H–$\delta^{18}O$ space (Figure 2), precipitation and groundwater values fell along the Meteoric Water Line (MWL) (Craig, 1961).

δ^2H and $\delta^{18}O$ of plant stem and soil water

Correlations between δ^2H and $\delta^{18}O$ values of soil water were linear and strong ($R^2 = 0.75$–0.96) for each patch type (Figure 2). Slopes (b) of δ^2H–$\delta^{18}O$ correlations for soil water were lower than those of the MWL. Slopes obtained for grove (b = 2.9±0.26) and cluster (b = 2.6 ± 0.19) patches were significantly lower ($p < 0.05$) than the slope for the grassland (b = 4.1 ± 0.49), but clusters and groves were not significantly different from each other ($p > 0.05$).

δ^2H and $\delta^{18}O$ of soil water from groves (coarse-textured soil throughout the profile) and discrete clusters (argillic horizon at approximately 40–100 cm) declined exponentially with depth (Figure 3a, b). Although the isotopic signatures of water in the upper profile (0–30 cm) were consistently higher than those of deeper soil water (30–150 cm), the presence or absence of an argillic horizon had no discernible affect on the isotopic composition of soil water in these woody patch types. For woody plant species in groves, stem water exhibited a narrow range of δ^2H (-27 to $-34‰$; mean = $-32 \pm 2‰$) and $\delta^{18}O$ (-3 to $-6‰$; mean = $-4\pm 1‰$) values which were consistently more depleted than the soil water in the upper 150 cm of the profile (Figure 3a). Woody plants in discrete clusters had stem water δ^2H (range -25 to -36; mean = $-29 \pm 4‰$) and $\delta^{18}O$ (range -2 to $-6‰$; mean = $-4 \pm 1‰$) values comparable to plants in groves. However, the isotopic composition of water from plants in discrete clusters was similar to that of soil water at depths between 50–150 cm (Figure 3b). Species differences in δ^2H and $\delta^{18}O$ were small, inconsistent, and gave no clear indication that trees and shrubs were vertically partitioning the soil water resource in either the grove or cluster patch types during this late summer/early fall sample period.

The δ^2H and $\delta^{18}O$ values of soil water in grassland patches were markedly different from those of grove and discrete cluster patches (Figure 3c). The δ^2H of soil water at the surface, $-18.3‰$, declined sharply with depth to $-37.0‰$ at 40 cm, increased to $-21.3‰$ at 60 cm, and then decreased gradually over the remainder of the profile to $-34.2‰$ at 150 cm. This pattern was mirrored by the $\delta^{18}O$ values. *P. glandulosa* saplings (basal dia. = 1.5 and 2.0 cm) growing in the grassland patches had mean δ^2H ($-28.9 \pm 2.5‰$) and $\delta^{18}O$ ($-2.7 \pm 0.3‰$) values well within the ranges observed for soil water in that patch type. In contrast to mature *P. glandulosa* plants in groves and clusters, the isotopic composition of water in *P. glandulosa*
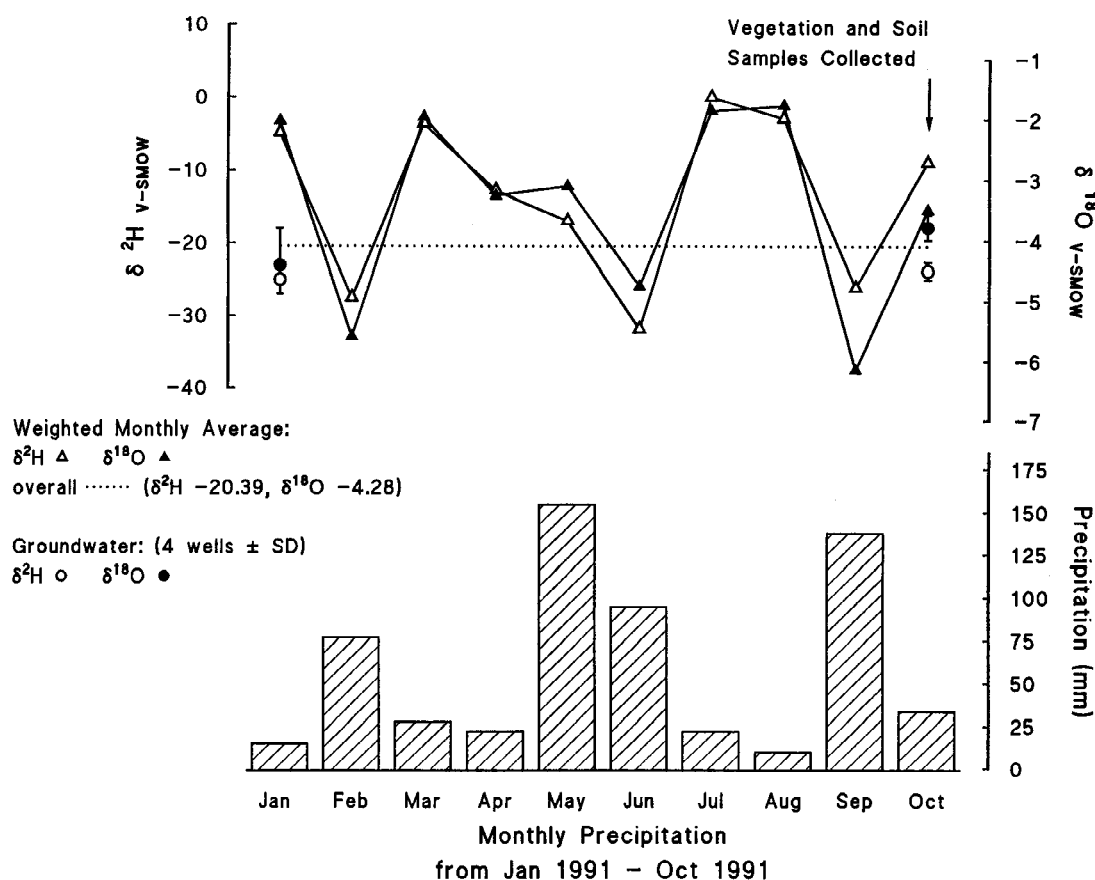
Figure 1. Monthly precipitation amounts and isotopic composition (monthly weighted mean and overall mean) at the La Copita site during the 10 month period preceding plant and soil water sample collection.

saplings in the grassland was similar to that of soil water at depths <50 cm.

Root biomass and density distribution

Total mean (± SD) root biomass in groves (20.2 ± 3.3 kg m^{-2}) was nearly five times that in grassland patches (4.5 ± 0.4 kg m^{-2}). The decrease in root biomass with increasing soil depth was exponential in groves, and nearly linear in grassland patches (Figure 4). *P. glandulosa* and *Z. fagara* dominated root density in grove and cluster patches (Figure 5). However, while *P. glandulosa* roots were abundant throughout the 200 cm sampling depth, those of *Z. fagara* were restricted to depths above 120 cm. Species common to grove and discrete cluster patches were highly plastic with regard to root density-soil texture interactions, and exhibited a marked tendency for root proliferation above the argillic horizon in discrete clusters.

Discussion

$\delta^2 H$ and $\delta^{18} O$ of rainfall and groundwater

Weighted monthly δ^2H and δ^{18}O of rainfall were strongly and positively correlated over the 10 month study period and showed a clear 'amount effect', whereby the isotope ratios were low during months with high rainfall and high during months with low rainfall. This 'amount effect' has been well-documented in other tropical and sub-tropical regions (Hartley, 1981; Mathieu and Bariac, 1996), and is related to both fractionation and exchange processes (Dansgaard, 1964). These processes are particularly important at the beginning of a shower, or during a short shower before the air beneath the rain cloud becomes saturated and achieves isotopic equilibrium with the falling rain (Dansgaard, 1964; Hartley, 1981). This leads to relatively enriched precipitation during periods of light rain and a more depleted signature
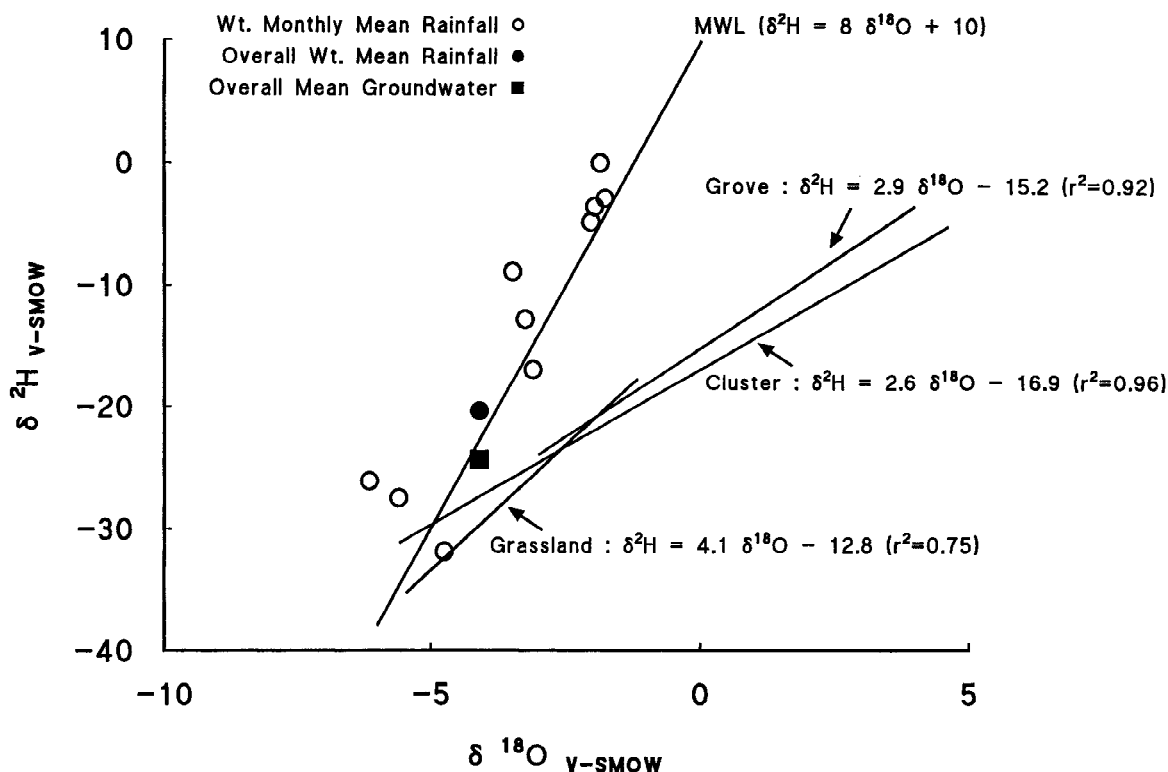
Figure 2. Isotopic composition of precipitation and soil water plotted in δ^2H–$\delta^{18}O$ space. Lines of best fit are drawn through soil water data from each of the three patch types (grassland, woody clusters, groves) sampled in a subtropical savanna parkland. MWL refers to the Meteoric Water Line.

with prolonged rainfall. We observed no seasonality in rainfall isotope content. This contrasts with higher latitudes where seasonal variation is pronounced and related to changes in temperature (Dansgaard, 1964).

Weltz and Blackburn (1995) monitored soil moisture to 2 m depth in discrete cluster and grassland patches for 18 months in 1984–85. They found no evidence of soil moisture recharge below 2 m in cluster patches and only slight (22 mm) deep drainage in grassland patches. Brown and Archer (1990) also monitored soil moisture in grassland patches at La Copita and observed deep (1.5 m) recharge after a series of large rainfall events totalling 230 mm over a 10 day period. Historical records indicate such events have occurred in 23 of the 52 years of weather records, and that for years in which this pattern of rainfall occurs, there was an average of 1.5 such events. For the period of our study, the overall weighted mean isotopic composition of precipitation was comparable to that of groundwater, implying direct, local recharge (Gat, 1971). In addition, groundwater at La Copita had a very consistent isotopic composition both between the

4 wells sampled and across the 10 month study period. This consistency suggests wells were drawing water from a single, well-mixed water mass beneath La Copita Research Area.

Evaporation from grassland and wooded patches

By plotting surface soil water isotope values in δ^2H–$\delta^{18}O$ space, the relative importance of evaporative loss can be estimated. Evaporation from surface soils will generally produce slopes between 2 and 5, with lower slopes associated with drier soils (Barnes and Allison, 1988). This evaporative enrichment arises from both an equilibrium fractionation associated with small differences in chemical potentials of the isotopic species, and kinetic fractionation associated with differences in rates of vapor diffusion of isotopic species through the atmospheric boundary layer (Barnes and Allison, 1988). Kinetic fractionation increases as the dominant diffusive resistance changes from being atmospheric (as in the case of evaporation of open water) to being a result of diffusion through a porous medium (Allison
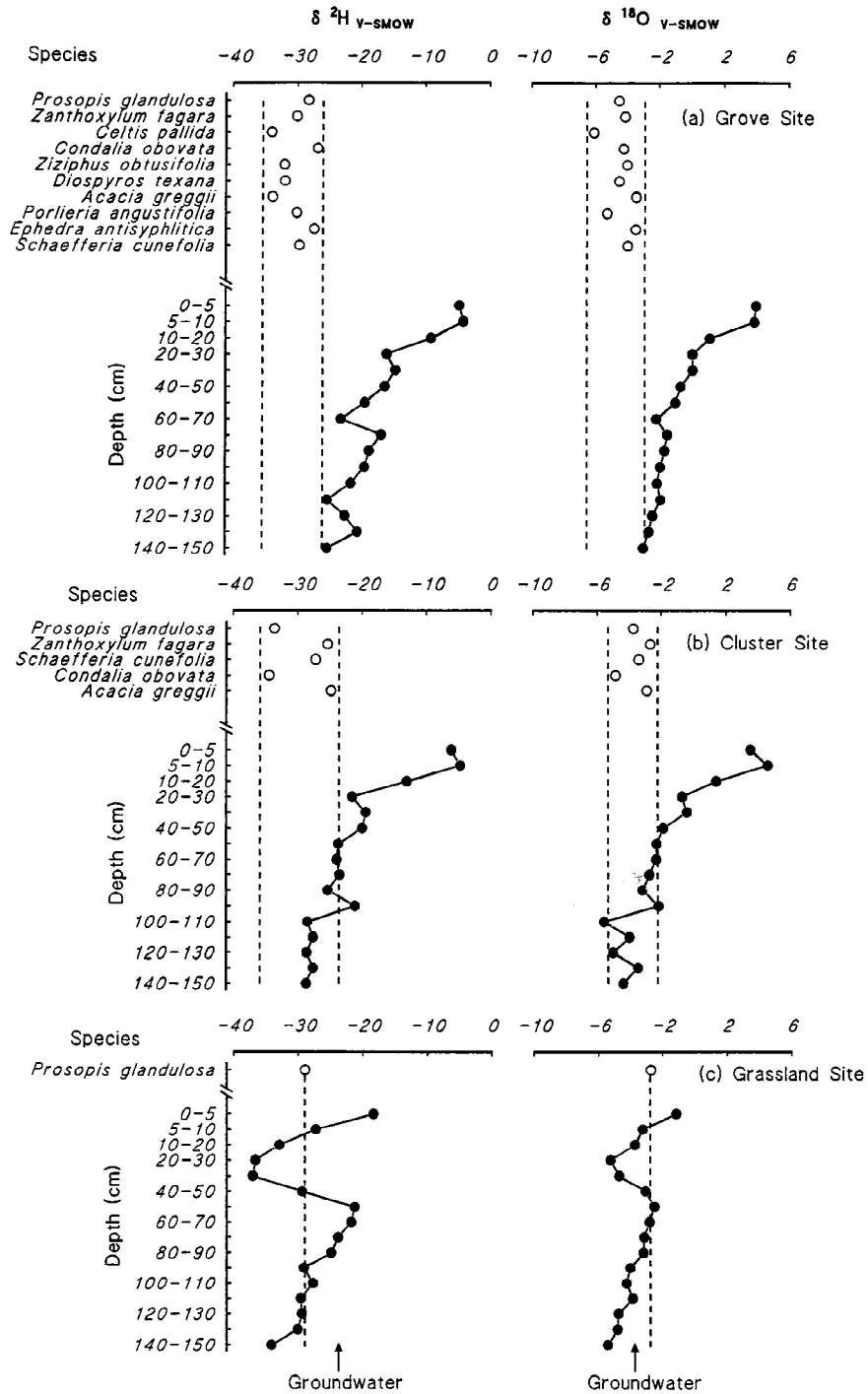
Figure 3. δ^2H and δ^{18}O of soil water and plant stem water from three patch types, (a) grove, (b) cluster and (c) grassland, in the savanna parkland at the La Copita site.
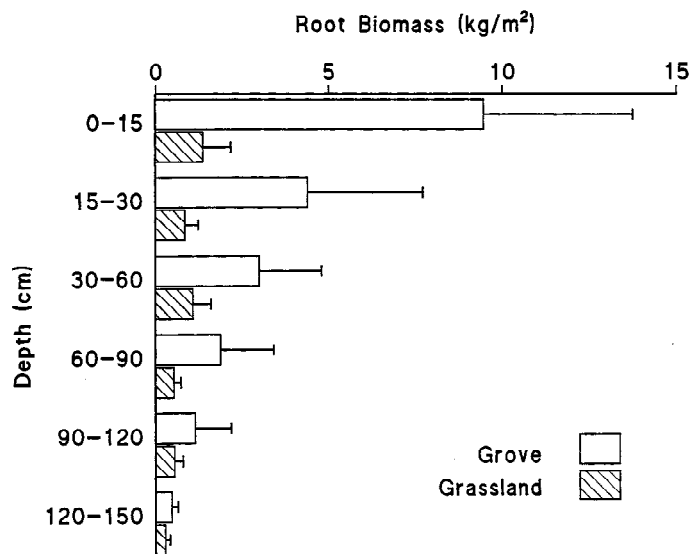
Root Biomass (kg/m²)

Figure 4. Mean (±SD; *n* = 6 cores) root biomass (kg m⁻²) distribution with soil depth in grove and grassland patches.

et al., 1983; Barnes and Allison, 1988). Hence, kinetic fractionation is greater in dry soils, and the thickness of the dry soil layer above the evaporating front is negatively correlated with slopes obtained when residual soil water is plotted in $\delta^2 H$–$\delta^{18}O$ space (Barnes and Allison, 1988).

Soil water from all 3 sites described regression lines with slopes significantly lower than the MWL, indicating that the isotopic composition of soil water from all sites was influenced by evaporation. In addition, slopes for the wooded sites (grove = 2.9; cluster = 2.6) were lower than the slope describing soil water in the grassland (4.1), suggesting that evaporation is greater in the wooded areas than in the grassland. This result is counterintuitive since leaf area in the wooded clusters and groves is much greater than in the grasslands, resulting in lower radiation loads at the soil surface in woodlands. Thus, microclimatic conditions established by the vegetation would favor lower evaporation rates in groves and clusters relative to the grassland. In fact, pan evaporation in wooded landscape elements is 15–40% lower than in the surrounding grasslands (Archer et al., unpublished).

We speculate that greater leaf area coupled with greater root mass in groves and clusters results in rapid consumption of soil water in the rooting zone via transpiration, a non-fractionating water flux (Dawson and Ehleringer, 1991; Forstel, 1996, 1982; Wershaw et al., 1966; Zimmerman et al., 1967). Because kinetic fractionation of water vapor increases as the thick-

ness of the dry surface soil layer increases (Barnes and Allison, 1988), it is possible that the higher $\delta^2 H$ and $\delta^{18}O$ values of soil water in the grove and cluster could be a consequence of increased kinetic fractionation occurring after rapid consumption of soil water via transpiration.

Edaphic mediation of $\delta^2 H$ and $\delta^{18}O$ of plant and soil water

The $\delta^2 H$ and $\delta^{18}O$ values of stem water from woody plants in the grove (restrictive argillic horizon absent) were lower than those observed for soil water at every depth increment sampled (Figure 3a). We infer from this that all plant species in groves were obtaining significant amounts of soil water from depths below those sampled (i.e., >1.5 m). This apparent acquisition of deep soil water (below 1.5 m) was unanticipated because 84% of the root biomass in groves was located above 60 cm (Figure 4). In addition, several plant species in groves had few or no roots below a depth of 80 cm (Figure 5). Deep roots of savanna trees and shrubs at this site thus appear to have a functional significance that could not have been recognized from either root biomass or density distributions. Dawson and Pate (1996) also found that water uptake patterns of woody plants in a semiarid woodland in Australia were less related to root density distribution than to the functional characteristics of those roots.

In discrete cluster patches, which occurred on soils with a well-developed claypan (argillic) horizon, plant
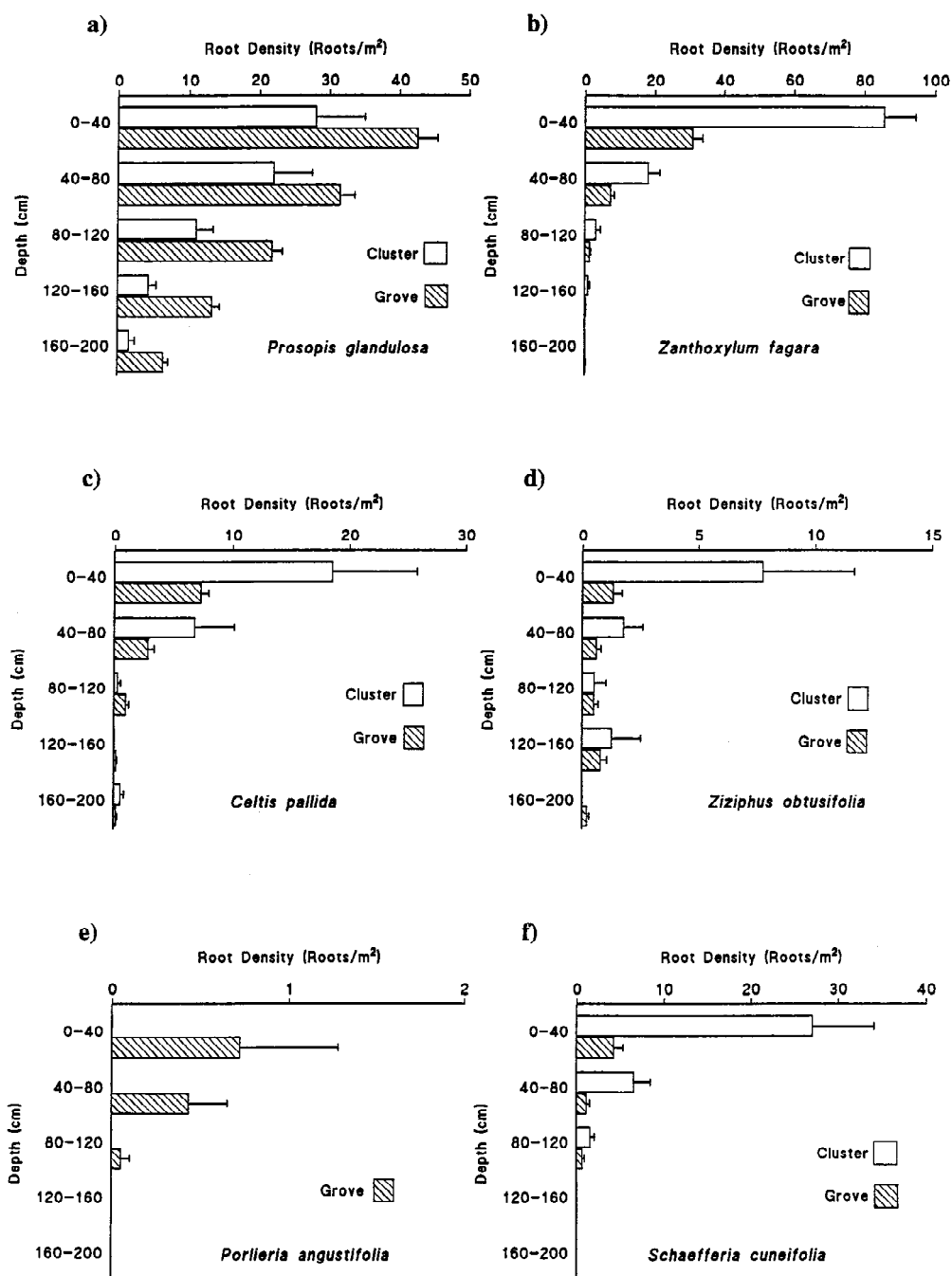
Figure 5. Mean (±SD) root density (number per m²) with depth for woody plant species common to grove and discrete cluster patch types. Note scale differences in the density axes.

root distributions were skewed markedly towards upper regions of the profile. This may reflect the fact that the claypan horizon presents a mechanical barrier to root penetration and water and nutrient movement. As a result, roots proliferated in the upper horizons where resource availability may have been greater. Accordingly, the δ^2H and δ^{18}O signatures of stem water of plants in discrete clusters closely matched those of soil water in the argillic horizon, which extends from approximately 0.4–1.0 m (Archer, 1995; Boutton et al., 1998).

Therefore, soil depth and texture significantly influenced the vertical distribution of plant roots and the depth from which they acquired soil water. Where soils were deep and coarse-textured throughout, plants were rooted more deeply and utilized deeper (>1.5 m) stores of soil water. Where soils were relatively shallow and underlain by a well-developed claypan horizon, the same plant species were rooted more shallowly and utilized soil moisture primarily from the upper 1.5 m of the soil profile.

The pattern and absolute magnitude of soil water δ^2H and δ^{18}O values in grassland patches differed markedly from those of woody patches (Figure 3). Soils of grassland patches exhibited a pronounced subsurface minima in the isotope profile at approximately 40 cm (δ^2H = −39‰; δ^{18}O = −6‰). Such variation in the isotopic composition of soil water can result from isotopically unique rainfall events (Barnes and Allison, 1988), and this appears to have been the case in our study. Approximately one month before obtaining our soil samples, there were two days of rainfall amounting to 72 mm. The weighted mean isotopic composition of this water (δ^2H = −40.7‰; δ^{18}O = −8.9‰) was similar to the minima observed at 40 cm depth in the grassland soil. These rainfall events were followed by 57 mm of rain spread over the next 4 weeks (weighted mean δ^2H = −11.3‰; δ^{18}O = −3.49‰).

Preservation of the isotopically light event may have been enhanced by the fact it was followed by a period of fairly frequent rainfall which displaced the water from the unusual event into the argillic horizon where it was retained at greater tension in the small pore spaces of the clay soils and less subject to evapotranspirational loss. This explanation is consistent with isotope labelling studies which showed that within 5 days of a simulated 83 mm rainfall event, ^{2}H- and ^{18}O-labeled water had percolated to 0.6 m (Walker and Richardson, 1991).

Why was this isotopically depleted rainfall event not evident in the soil water beneath the wooded landscape elements? Lack of a retentive argillic horizon might explain the contrasting profile in groves, but could not account for the isotopic composition of soil water in discrete clusters where the argillic horizon was well-developed. However, clusters and groves have greater leaf area and root biomass and density, which probably results in more rapid water consumption and transpirational loss in wooded landscape elements relative to the grasslands. Therefore, water from this isotopically unusual rainfall event may have been consumed by transpiration more quickly in woody patches than in grassland patches.

Water resource partitioning among co-occurring woody plants

Despite marked differences in root distribution patterns (Figure 5), we saw no isotopic evidence that co-occurring woody plants in clusters and groves were consistently utilizing moisture from different regions of the soil profile during late summer/early fall. On a given soil type, shallow-rooted species such as *Z. fagara* had stem water δ^2H and δ^{18}O values generally similar to those of deeply rooted *P. glandulosa* plants (Figures 3 and 5). The δ-values of stem water of all species in clusters (δ^2H = −29 ± 4‰; δ^{18}O = −4 ± 1‰) and groves (δ^2H = −32 ± 2‰; δ^{18}O = −4 ± 1‰) showed little variation, implying that all species relied on similar sources of soil water. Seasonal sampling will be required to determine if this pattern persists during other portions of the growing season.

This lack of isotopic evidence for marked resource partitioning implies that competition for soil moisture may be the overriding interaction among plants in woody clusters and groves. Field observations that overstory *Prosopis* plants appeared to be undergoing high levels of mortality suggested that root competition from understory shrubs was a factor contributing to its demise in woody clusters (Archer, 1995). This hypothesis was supported by selective removal experiments which indicated that while loss of *Prosopis* has had no discernible effect on understory plants, the removal of understory shrubs increased *Prosopis* growth and seed production significantly (Barnes and Archer, 1996).

Alternatively, isotopic differences between woody plant species in this ecosystem may have been obscured by hydraulic lift of deep soil water into upper, drier soil layers via the roots of one or more of the

deeply rooted plant species (Caldwell and Richards, 1989; Dawson, 1993b). The water transported from deep to upper soil layers may have been reabsorbed subsequently by surficial roots of the same plant, or by roots of associated species. In groves, δ-values of plant stem water were clearly lower than those of soil water in the upper 1.5 m of the profile (Figure 3a), even in species that had no detectable root mass and density below 0.8 m (Figure 5). Since *Prosopis* had significant root mass and density below 1.5 m (Figure 5), the possibility exists that this species supplied the more shallowly rooted woody species with isotopically depleted, deep soil water (>1.5 m) via hydraulic lift. Thus, rather than competing, *Prosopis* may have been ameliorating the water relations of co-occurring plant species, as shown by Dawson (1993b) for plant species living in the understory of sugar maple. In support of this possibility, predawn xylem water potentials of *Zanthoxylum fagara* and *Berberis trifoliolata* during a dry period at our study site were significantly higher in clusters with a live *Prosopis* than in clusters where *Prosopis* had been removed (Barnes and Archer, 1996). Although Mooney et al. (1980) found evidence for hydraulic lift in *Prosopis tamarugo* in the Atacama Desert, no studies have demonstrated conclusively that *Prosopis glandulosa* is capable of hydraulic lift. Until the existence and functional significance of hydraulic lift is documented in this ecosystem, it will remain difficult to utilize the isotopic composition of plant and soil water to differentiate between competition and facilitation.

Acknowledgements

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24

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Section editor: H Lambers