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Partitioning of soil water among canopy trees in a seasonally dry tropical forest

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Abstract Little is known about partitioning of soil water resources in species-rich, seasonally dry tropical forests. We assessed spatial and temporal patterns of soil water utilization in several canopy tree species on Barro Colorado Island, Panama, during the 1997 dry season. Stable hydrogen isotope composition (δD) of xylem and soil water, soil volumetric water content (θ_v), and sap flow were measured concurrently. Evaporative fractionation near the soil surface caused soil water δD to decrease from about –15‰ at 0.1 m to –50 to –55‰ at 1.2 m depth. Groundwater sampled at the sources of nearby springs during this period yielded an average δD value of –60‰. θ_v increased sharply and nearly linearly with depth to 0.7 m, then increased more slowly between 0.7 and 1.05 m. Based on xylem δD values, water uptake in some individual plants appeared to be restricted largely to the upper 20 cm of the soil profile where θ_v dropped below 20% during the dry season. In contrast, other individuals appeared to have access to water at depths greater than 1 m where θ_v remained above 45% throughout the dry season. The depths of water sources for trees with intermediate xylem δD values were less certain because variation in soil water δD between 20 and 70 cm was relatively small. Xylem water δD was also strongly dependent on tree size (diameter at breast height), with smaller trees appearing to preferentially tap deeper sources of soil water than larger trees. This relationship appeared to be species independent. Trees able to exploit progressively deeper sources of soil water during the dry season, as indicated by increasingly negative xylem δD values, were also able to maintain constant or even increase rates of water use. Seasonal courses of water use and soil water partitioning were associated with leaf phenology. Species with the smallest seasonal variability in leaf fall were also able to tap increasingly deep sources of soil water as the dry season progressed. Comparison of xylem, soil, and groundwater δD values thus pointed to spatial and temporal partitioning of water resources among several tropical forest canopy tree species during the dry season.

Key words Roots · Sap flow · Leaf phenology · Stable hydrogen isotope ratio · Panama

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Introduction

Many species-rich tropical forests experience a prolonged dry season during which little or no rain falls and the upper soil layers undergo severe drying (Wright 1996). It has been suggested that competition for limited resources such as water may be minimized, and therefore species diversity maximized, by intensive spatial and temporal partitioning of resource utilization (Tilman 1982; Cody 1986). In seasonally dry tropical forests, the principal mechanisms of soil water partitioning are likely to consist of differences in rooting patterns, root activity, and leaf phenology. It is difficult to draw inferences about spatial partitioning of soil water in tropical forests based on direct observation of rooting patterns because of the large and intricate root biomass, high species diversity, and the uncertain relationship between the presence of roots in a particular soil layer and the magnitude of their contribution to the water budget of a plant. Infor-

mation on spatial partitioning of soil water in tropical forests is scant, but suggests that during the dry season, partitioning among trees, and among trees and understory shrubs, may be intense (Jackson et al. 1995).

The relationship between leaf phenology and temporal partitioning of soil water utilization in seasonally dry tropical forests is difficult to characterize, in part because diverse phenological patterns defy classification into simple categories such as evergreen and deciduous. Data on seasonal patterns of leaf fall collected over the past 10 years on Barro Colorado Island, Panama (S.J. Wright, unpublished observations) exemplify this broad range of behavior and the difficulty in devising simple phenological categories. For example, some dry-season-deciduous species such as *Pseudobombax septenatum* seem to be rigidly programmed to lose their leaves at the end of the wet season regardless of whether the transition from wet to dry conditions is abrupt or gradual in a given year. Meanwhile, the degree of leaf retention in other dry-season-deciduous species (e.g., *Spondias* spp.) varies facultatively with the severity of the dry season. Other species rapidly lose all of their leaves during the wet/dry season transition, rapidly expanding a new flush of leaves during the dry season, and thus could be considered functionally evergreen or brevideciduous (e.g., *Anacardium excelsum*). Still other species exhibit progressively increasing leaf fall through the end of the dry season, decreasing leaf fall throughout the dry season, a peak in leaf fall after the wet season has begun, or more than one peak in leaf fall during the year. Even evergreen species exhibit pronounced seasonal variation in total crown leaf area. Because other mechanisms such as stomatal control may influence seasonal patterns of water use, the impact of a given pattern of leaf phenology on temporal partitioning of soil water cannot be established without direct measurements of whole-tree water use.

The recent development of stable isotope techniques has greatly facilitated the characterization of seasonal patterns of water uptake from different depths in the soil profile. Analysis of the stable hydrogen (D, H) or oxygen (^{18}O, ^{16}O) isotope composition of soil and xylem water allows differential access to soil water pools to be inferred without excavation of root systems (Ehleringer and Dawson 1992). The isotopic composition of the soil water varies with depth because each successive precipitation event has a distinct isotopic signature and because water near the soil surface becomes enriched in the heavier isotopes as a result of evaporative fractionation (Allison 1982; Allison and Hughes 1983). In tropical lowland regions where the isotopic composition of precipitation may exhibit little seasonal variation (Yurtsever and Gat 1981), evaporative fractionation is the major determinant of variation in the isotopic composition of soil water with depth in sites subjected to a pronounced dry season (Jackson et al. 1995).

Studies of soil water partitioning carried out using stable isotope techniques often yield results that are somewhat counterintuitive at first sight. For example, Valentini et al. (1992) found that evergreen Mediterranean macchia species tended to rely on rainwater while deciduous species relied almost exclusively on groundwater; Dawson and Ehleringer (1991) concluded that streamside trees in central Utah used little stream water; and Le Roux et al. (1995) concluded that both shrubs and grasses in an African savanna obtained most of their water from the upper soil layer implying potentially strong competition for soil water and raising questions concerning the general applicability of the two-layer model for water partitioning in savannas (Walter 1971). Other stable-isotope-based studies have shown that trees of different size classes belonging to the same species can preferentially tap different sources of soil water (Dawson 1996) and that source water utilization can change seasonally in species with dimorphic root morphology (Dawson and Pate 1996).

Here we present data on spatial and temporal partitioning of soil water among several diverse canopy tree species in a lowland tropical forest on Barro Colorado Island, Panama, during a 4-month dry season. The species selected represent a broad range of leaf phenology categories and phylogeny. Concurrent measurements of xylem and source water hydrogen isotope ratios (δD values) were used to characterize seasonal patterns of source water utilization, and the relative magnitude of whole-tree water use was estimated from seasonal courses of sap flow. Our objectives were to assess the intensity of soil water partitioning, to determine the extent to which patterns of source water utilization are related to leaf phenology and tree size, and to examine relationships between seasonal courses of whole-tree water use and seasonal variation in source water utilization.

Materials and methods

Field site and plant material

The study was carried out from January to May 1997 in a tropical moist forest on Barro Colorado Island (BCI), Panama (9°09' N, 79°51' W). The site was located on the plateau area of BCI near a 50-ha permanent plot established in 1980 (Hubbell and Foster 1983). Mean annual rainfall is 2600 mm with a pronounced dry season from mid-December through April during which only about 8% of the total annual rainfall is received (Windsor 1990). During this period, the water potential in the upper 20 cm of the soil profile can fall to –2.0 MPa (Becker et al. 1988). Fifteen circular plots were established during 1996 in which all trees >20 cm diameter at breast height (DBH) were marked, identified and their DBH recorded. A subset of these trees was used for the measurements of xylem sap δD and sap flow reported here. A list of the 17 species studied and their salient characteristics, including leaf phenology, are presented in Table 1. Sap flow was measured in 10 of the species from which xylem water was extracted for stable hydrogen isotope analysis (see below).

In four of the study plots, soil volumetric water content (θ_v) at 0–15, 15–30, 30–60, 60–90, and 90–120 cm depth was monitored throughout the dry season with 1.2-m multi-segment profiling TDR probes (Type A, Environmental Sensors, Victoria, Canada) installed in the soil during the latter part of 1996. The probes were interrogated and read with an MP-917 TDR unit (Environmental Sensors) at approximately 1-week intervals.

Monthly leaf fall data over a 10-year period (1987–1996) were utilized for *A. excelsum*, *Alseis blackiana*, *Cordia alliodora*,

Table 1 Characteristics of the tree species selected for study. Leaf phenology categories are tentative and comprise a continuum with considerable overlap between categories. The timing of leaf expansion and leaf fall may vary widely within a category

Species	Family	Individuals	Diameter at breast height (cm)	Sap flow	Leaf phenology	Peak leaf fall
Alseis blackiana	Rubiaceae	3	22–34	Yes	Partially deciduous	March–April
Anacardium excelsum	Anacardiaceae	1	32	Yes	Brevideciduous	January
Cordia alliodora	Boraginaceae	3	40–48	Yes	Deciduous	April–June
Ficus insipida	Moraceae	1	122	Yes	Evergreen	–
Guapira standleyanum	Nyctaginaceae	3	46–69	Yes	Evergreen	November–December
Hura crepitans	Euphorbiaceae	3	60–74	No	Brevideciduous	–
Jacaranda copaia	Bignoniaceae	3	73–86	Yes	Brevideciduous	–
Lonchocarpus latifolius	Leguminosae	4	25–43	Yes	Brevideciduous	December–January
Luehea seemannii	Tiliaceae	3	24–41	Yes	Facultatively deciduous	–
Platymiscium pinnatum	Leguminosae	3	33–68	No	Facultatively deciduous	–
Platypodium elegans	Leguminosae	3	25–82	No	Facultatively deciduous	–
Pseudobombax septenatum	Bombacaceae	2	130–159	No	Deciduous	December–January
Quararibea asterolepis	Bombacaceae	3	23–37	Yes	Evergreen	May, November–December
Spondias radlkoferi	Anacardiaceae	4	44–64	No	Deciduous	–
Tabebuia rosea	Bignoniaceae	2	41–48	No	Deciduous	–
Trichilia tuberculata	Meliaceae	3	24–25	Yes	Evergreen	–
Zuelania guidonia	Flacourtiaceae	2	22–46	No	Deciduous	–

Jacaranda copaia, *Luehea seemannii*, *Quararibea asterolepis*, and *Trichilia tuberculata*. Fifteen litter traps were located randomly in each of four 2.25-ha plots. Traps were emptied monthly. Leaves were identified to species, dried to a constant mass at 60°C and weighed. To facilitate comparisons among species, monthly leaf fall was normalized with respect to its annual maximum value within each species.

Xylem and soil water hydrogen isotope composition

Xylem tissue samples were obtained from trees by extracting small cylinders of wood from the main trunk with an increment borer at a height of approximately 1.3 m. Immediately upon extraction of a core, all tissue external to the xylem was removed and the first 5 cm of xylem tissue was rapidly placed inside a glass vial sealed with a rubber stopper and Parafilm to prevent evaporative fractionation prior to vacuum distillation. Each tree was sampled from one to three times between January and April. Soil samples were collected with an auger at 5 cm, 10 cm, and then at 10-cm intervals to 100 cm during January, March, and April. Soil bore holes were made in plots with the highest density of trees destined for isotopic analysis of their xylem water. Soil samples were sealed in stoppered glass vials following the same procedure as used for xylem samples. In addition, samples of groundwater were obtained from two nearby springs at the point where they emerged from the ground. Xylem, soil, and groundwater samples were kept frozen until vacuum distillation.

All samples were sent to Mountain Mass Spectrometry (Evergreen, Colorado) for preparation and analysis. Water was extracted from xylem and soil samples by cryogenic vacuum distillation. Hydrogen gas for isotopic analysis was generated from 4-µl subsamples by the zinc reduction method (Coleman et al. 1982). The stable hydrogen isotope composition of the water samples was expressed in conventional delta (δ) notation as the D/H ratio relative to the V-SMOW and -SLAP standards as:

$$\delta=[(D/H_{sample}-D/H_{standard})-1]\times 1000‰$$

The average daily change in xylem sap δD during the dry season was calculated for individual trees that were sampled on two or more dates between January and the end of April.

Sap flow measurements

Sap flow was measured using the constant-heating method described by Granier (1985, 1987). Pairs of 20-mm-long, 2-mm-diameter temperature probes (UP GmbH, Munich, Germany) were installed at about 1.5 m height. The upper (downstream) probe was continuously heated with a constant-current power supply (UP) while the lower unheated probe measured the reference temperature of the wood. The protruding portions of both probes were insulated with a layer of foam rubber surrounded by an outer shield of reflective material and transparent plastic. Probe temperatures were recorded continuously with a datalogger (CR21X, Campbell Scientific, Logan, Utah) equipped with a 32-channel multiplexer (AM416, Campbell Scientific) and 10-min averages were stored in a solid-state storage module (SM192, Campbell Scientific). Sap flow velocity was calculated from the temperature difference between the probes using an empirical relationship developed by Granier (1985). This relationship was revalidated by comparing known and calculated flow rates through detached 5- to 7-cm-diameter branch segments of *A. excelsum* and *L. seemannii* in the laboratory. Measurements were made from January through May in a subset of the trees from which xylem water samples were obtained (Table 1). Sensors and instrumentation were continuously rotated among groups of trees so that sap flow in a given tree was measured during a 3- to 5-day period on approximately five occasions between January and May. The average daily change in sap flow during the dry season was calculated for individual trees in which sap flow was measured on at least five occasions between January and May. Total daily sap flow was normalized by total daily solar radiation to minimize the effect of variation in solar radiation among measurement days. Constraints on availability of instrumentation precluded sap flow measurements in all 46 individuals designated for xylem water sampling.

Results

Total rainfall on BCI from January through April 1997 was 100 mm, about 46% of the 68-year average value for the period. The only significant precipitation for the period during which soil and xylem water δD were measured was about 20 mm of rainfall on both February 5 and 6,

and 31 mm on April 22 (Fig. 1A). Soil θ_v in the upper 30 cm increased from about 19% prior to the rainfall on February 5 to 30% after which it declined steadily to a minimum value of 13% before the rain on April 22 (Fig. 1B). Soil θ_v at 60 to 120 cm depth was unaffected by the rain in early February and declined from about 50% at the beginning of the dry season to 40% at the end of April.

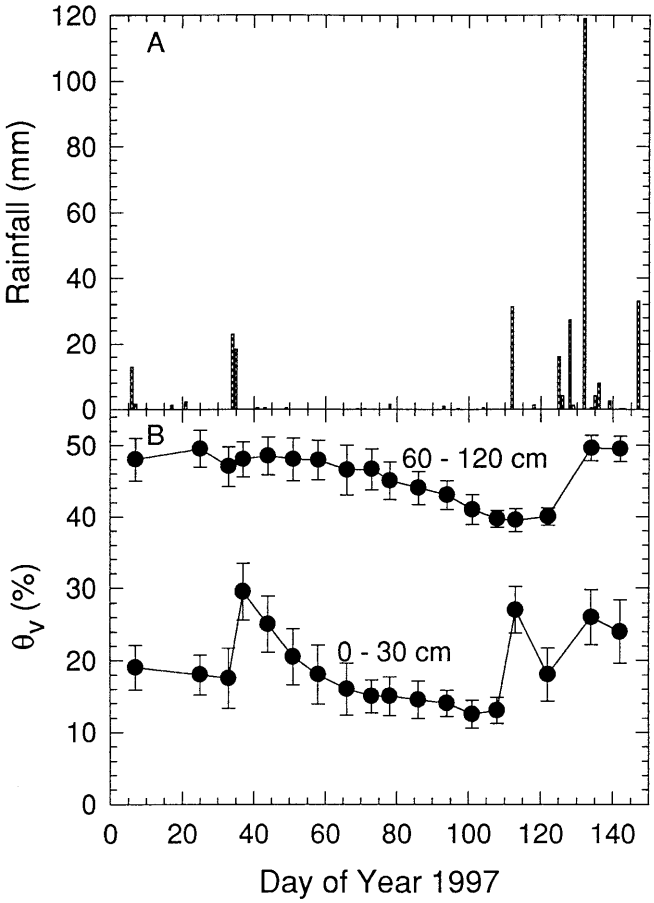

Fig. 1 Rainfall (**A**) and soil volumetric water content (θ_v) at 0–30 cm and 60–120 cm depth (**B**) during the 1997 dry season on Barro Colorado Island, Panama

During March and April, soil water δD values decreased sharply from about –16.5‰ at 5 cm to –34.0‰ at 20 cm, then remained within 7.5‰ of the value at 20 cm to a depth of 70 cm, followed by a steady decline to about –50‰ at 100 cm (Fig. 2A). Groundwater sampled at the sources of springs on BCI during this period yielded an average δD value of –60‰. A 50-cm portion of the soil profile between about 20 and 70 cm thus constituted a zone of relative uncertainty with regard to the relationship between δD and depth. Soil θ_v increased continuously with depth from about 12% in the 0–15 cm layer to 47% in the 90–120 cm layer (Fig. 2B). However, the increase in θ_v over the 30 cm between the 60–90 and 90–120 cm layers was relatively small compared to the increase in θ_v between 30–60 and 60–90 cm. The patterns shown in Fig. 2 resulted in a relationship between soil water δD and soil θ_v (Fig. 3) that permitted soil and therefore xylem water δD values >about –30‰ and <about –40‰ to be used as an indicator of the relative availability of the water obtained by roots. Intermediate δD values (–35±5‰) were associated with greater uncertainty with respect to soil water availability.

The range of xylem sap δD exceeded that of soil water δD between 5 and 100 cm depth in 12 tree species for which adequate sample replication was obtained during the same time period (Fig. 4). In *Guapira standleyanum*, the species with the least negative xylem sap δD value (–28.9‰), soil water uptake appeared to be largely restricted to the layer between the surface and 20 cm based on the data presented in Fig. 2. In *L. seemannii*, on the other hand, the average xylem sap δD value of –56.9‰ was between that of soil water at 100 cm (–51‰) and groundwater (–60‰), suggesting that most of the water in its xylem was taken up from depths greater than 100 cm. Three other species, *T. tuberculata*, *Platypodium elegans*, and *Platymiscium pinnatum*, had xylem water δD values consistent with access to soil water at depths >100 cm. Xylem sap δD values in *C. alliodora* and *A. blackiana* (about –47‰) were consistent with access to water at least 80 cm deep (cf. Fig. 2) or with uptake of a mixture of groundwater and water above 80 cm depth. The locations of soil water sources for the remaining five

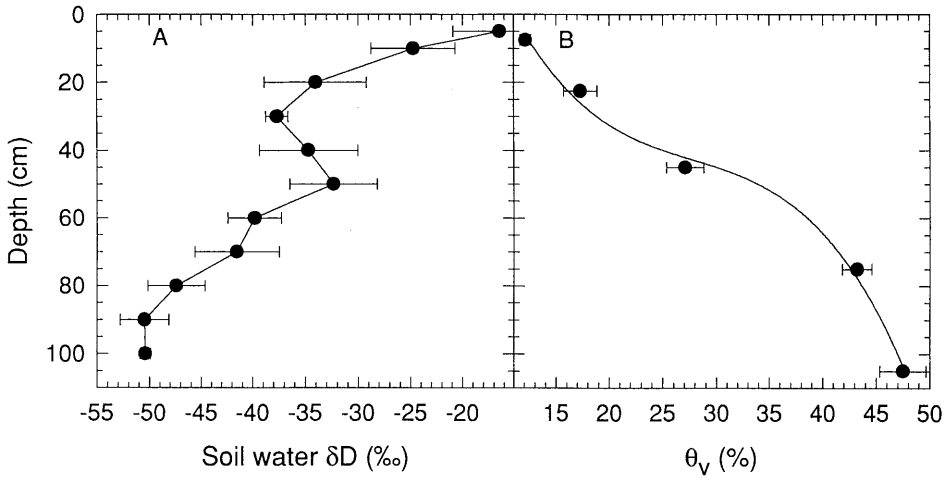

Fig. 2 Soil water δD (**A**) and soil volumetric water content (**B**) in relation to soil depth on Barro Colorado Island, Panama during March and April 1997

species were less certain because their xylem δD values fell within the range over which the relationship between soil depth and soil water δD was variable (cf. Figs. 2, 4).

Xylem water δD was strongly dependent on tree size. Plots of xylem water δD against DBH for individual trees showed that δD increased asymptotically with tree size within plots (Fig. 5A) and among adjacent plots with similar slopes and soil water profiles (Fig. 5B), implying that smaller trees were preferentially tapping deeper sources of soil water than larger trees. The steepest increase in xylem δD with DBH was observed over the range from about 20–50 cm. The slope of the relationship was substantially more gradual for individuals with DBH greater than 50 cm. The relationship between xylem δD and DBH appeared to be species independent.

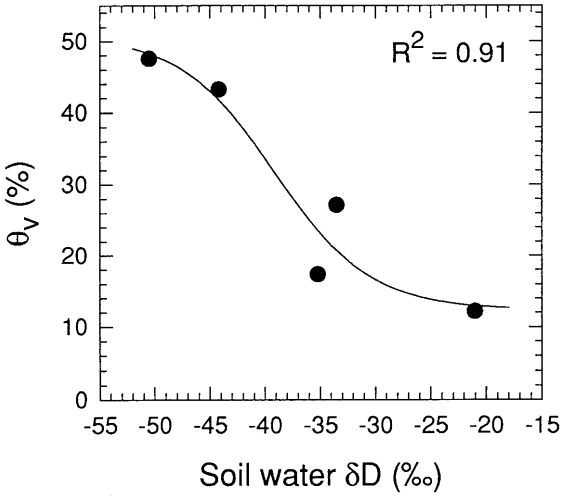

Fig. 3 Relationship between soil volumetric water content and soil water δD for the data shown in Fig. 2

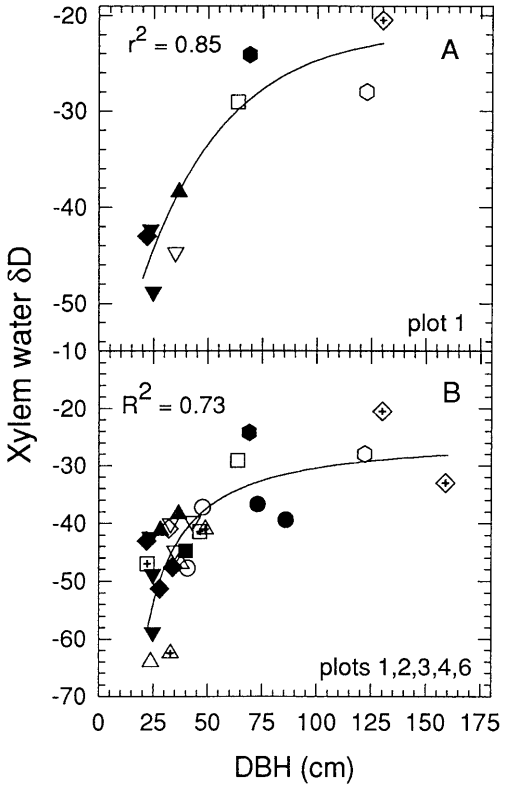

Fig. 5 Xylem sap δD during March 1997 in relation to diameter at breast height (*DBH*) for trees in plot 1 (**A**)and plots 1, 2, 3, 4, and 6 (**B**) on Barro Colorado Island, Panama. (*closed diamond, Alseis blackiana*; *closed down triangle, Trichilia tuberculata*; *open up triangle, Luehea seemannii*; *closed up triangle, Quararibea asterolepis*; *open diamond, Anacardium excelsum*; *closed square, Cordia alliodora*; *open down triangle, Lonchocarpus latifolius*; *open circle, Tabebuia rosea*; *open square, Spondias radlkoferi*; *closed hexagon, Guapira standleyanum*; *closed circle, Jacaranda copaia*; *open hexagon, Ficus insipida*; *square with plus, Zuelania guidonia*; *triangle with plus, Platymiscium pinnatum*; *diamond with plus, Pseudobombax septenatum*

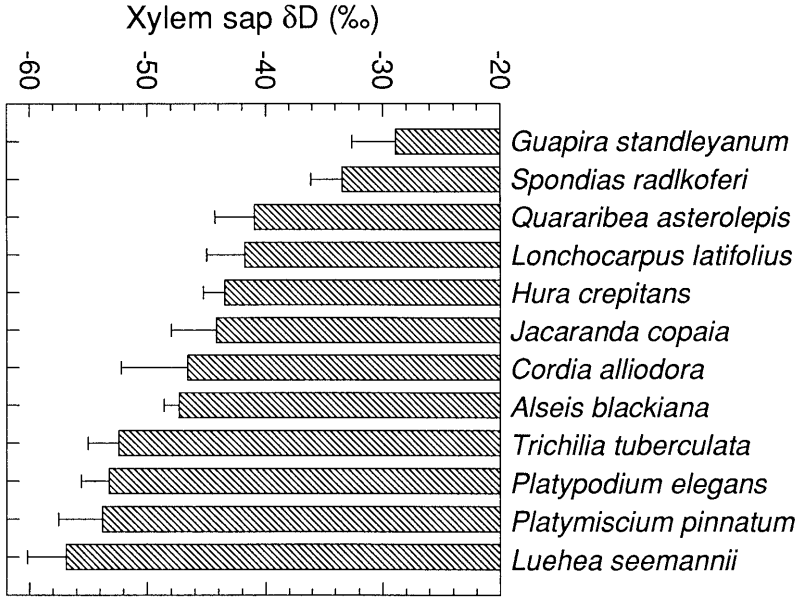

Fig. 4 Average xylem sap δD (±SE) sampled during March and April 1997 for 12 tree species on Barro Colorado Island, Panama. Only species for which both March and April sampling data were available for three or more individuals are shown

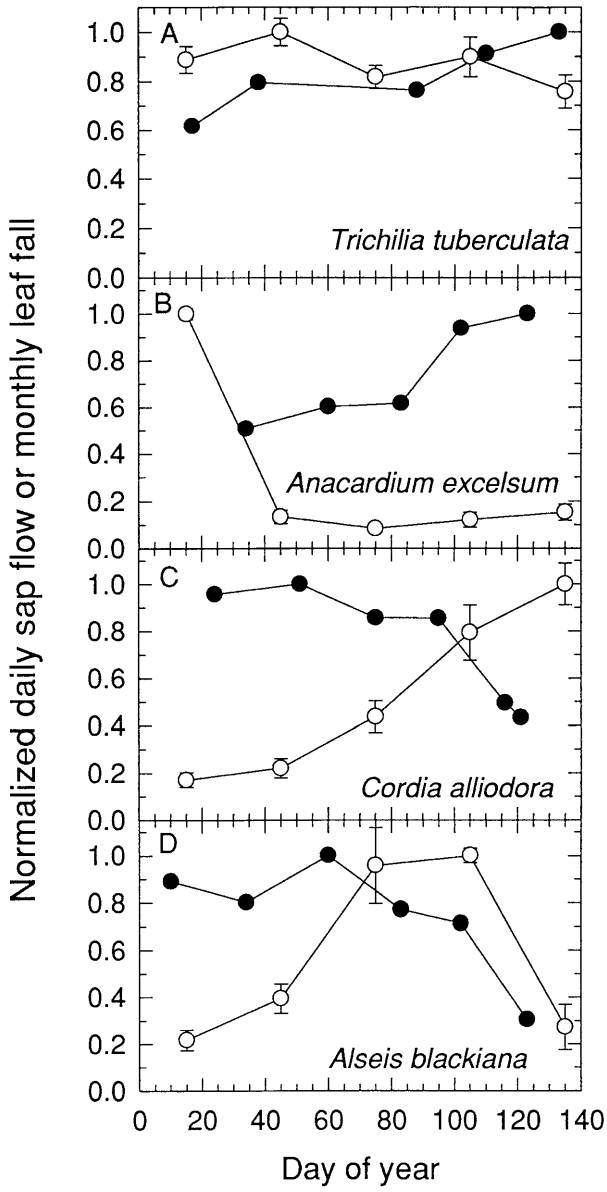

Fig. 6A–D Seasonal courses of total daily sap flow (*closed circles*) normalized with respect to its maximum value and with respect to variation in total irradiance for individual trees in which xylem sap δD data were also available, and seasonal courses of mean monthly leaf fall (*open circles*) normalized with respect to its annual maximum.

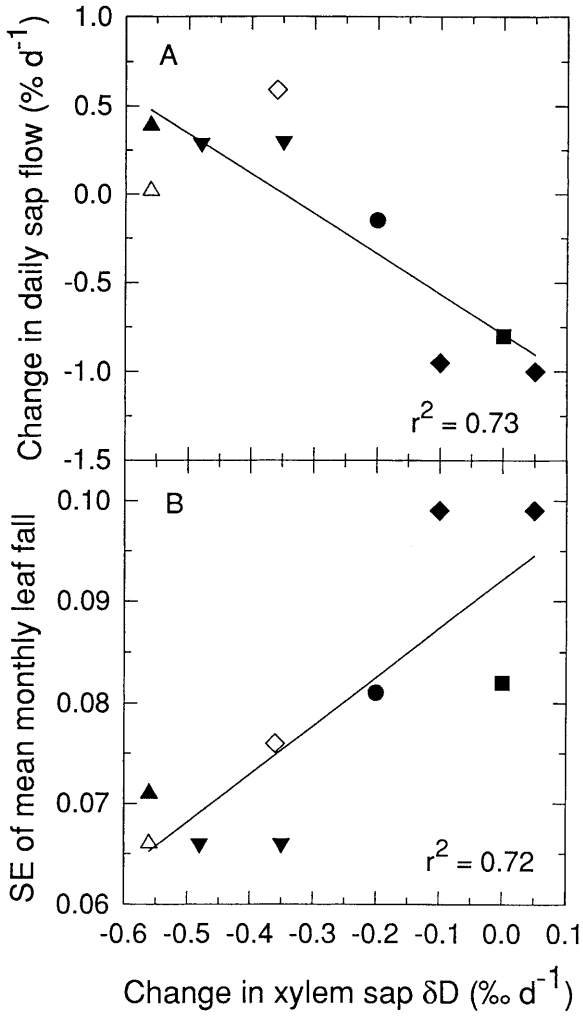

Fig. 7 A Average percent daily change in normalized sap flow (**A**) and the SE of normalized mean monthly leaf fall (**B**) in relation to average daily change in xylem sap δD during the 1997 dry season. Nine individuals representing seven tree species were selected on the basis of availability of seasonal sap flow and xylem sap δD data. See legend to Fig. 5 for symbols

Contrasting seasonal patterns of sap flow were observed, with sap flow increasing from the beginning to the end of the dry season in some species (Fig. 6A,B), decreasing in others (Fig. 6C,D), and remaining essentially constant in yet other species (data not shown). Seasonal courses of sap flow normalized with respect to daily total irradiance were often associated with patterns of leaf phenology. For example, in *C. alliodora* and *A. blackiana*, sap flow at the end of April was only 30–40% of that in January, coinciding with steadily increasing rates of leaf fall between January and April (Fig. 6C,D). In *A. excelsum* (Fig. 6B), sap flow nearly doubled between February and May while new leaves were expanding following peak rates of leaf fall during January (Table 1). In *T. tuberculata*, sap flow in January was 60% of that in May, coinciding with a period of relatively steady but near maximal rates of leaf fall, probably indicative of rapid leaf turnover rather than progressive leaf loss in this evergreen species.

In some trees, notably *T. tuberculata* and *Q. asterolepis*, δD decreased by about 25–30 ‰ from the beginning to the end of the dry season, suggesting an increasing reliance on deeper soil water (Fig. 2A) as the upper soil layers dried (Fig. 1B). In other trees such as *A. blackiana* and *C. alliodora*, seasonal variation in xylem δD was less than 5‰. There was a significant negative correlation ($P<0.01$) between the daily average percentage change in normalized sap flow during the dry season and the daily average change in xylem δD (Fig. 7A). Thus, trees showing the largest average daily declines in xylem δD values were also those that showed the largest average daily in-

creases in sap flow. It should be noted that although the ranges of the ordinate and abscissa in Fig. 7A are relatively small, cumulative differences for the 60-day period over which these variables were evaluated were large. An index of leaf phenological behavior, the SE of mean monthly normalized leaf fall, was also significantly correlated ($P<0.01$) with the daily average change in xylem δD (Fig. 7B). Trees showing the smallest seasonal variability in leaf fall were thus also those that showed the largest seasonal decline in xylem δD values.

Discussion

Comparison of xylem, soil, and groundwater δD values pointed to spatial and temporal partitioning of water resources among several diverse tropical forest canopy tree species during the dry season. Based on xylem δD values, water uptake in some individuals appeared to be restricted largely to the upper 20 cm of the soil profile where θ_v dropped below 20% during the dry season, whereas other individuals appeared to have access to water at depths greater than 1 m where θ_v remained above 45% throughout the dry season. The depths of water sources for individuals with intermediate xylem sap δD values were less certain because variation in soil water δD between 20–70 cm was relatively small and not monotonic.

The extent to which the observed patterns of water resource partitioning were species specific remains to be resolved. For example, average xylem sap δD values ranged from about –29‰ to –57‰ for a subset of individuals of 12 species sampled on the same dates in March and April (Fig. 4), suggesting a large interspecific range in the depth of water extraction from the soil profile. However, other results showing size-related variation in xylem δD within and among species (Fig. 5), and different patterns of temporal variation in xylem δD (Fig. 7) make it difficult to assign a static xylem δD to a given species during the course of the study.

The implication that smaller trees were preferentially tapping deeper sources of soil water than larger trees (Fig. 5) at first seems counterintuitive, especially in the light of results from other stable isotope studies showing that larger trees had access to groundwater, whereas smaller trees did not (Dawson 1996). However, it has been estimated that 70–90 years may be required for a slow-growing subcanopy tree on BCI to reach the canopy (O'Brien et al. 1995). The presence of deep roots in smaller trees in this forest would therefore substantially reduce the probability of mortality during exceptionally severe dry seasons when the soil water potential in the upper portion of the profile on BCI can fall to as low as –2 MPa (Becker et al. 1988). Consistent with this hypothesis, severe wilting and enhanced mortality are observed among shallow-rooted understory shrubs during severe dry seasons on BCI (Wright et al. 1992).

The tendency for larger trees to rely primarily on water taken up from the upper portions of the soil profile also seems counterintuitive and remains unexplained. Although larger trees presumably retained their complement of deep roots that provided access to deeper sources of soil water when they were younger, the role of these roots in their water economy appeared to be diminished. In large trees with their extensive emergent crowns exposed to high atmospheric evaporative demand during the dry season, preferential reliance on the smaller pool of water available in the upper portions of the soil profile would seem to carry the risk of developing severe leaf water deficits leading to pronounced stomatal restriction of transpiration, and therefore CO_2 assimilation, to avoid damaging leaf water deficits.

A number of factors may mitigate the potential negative consequences of the apparent pattern of soil water utilization by large trees. First, the extensive horizontal area explored by root systems of large trees may partially compensate for the reduced water content in the upper portion of the soil profile. Second, we have recently shown that diurnal stem water storage capacity increased exponentially with tree size in tropical forest canopy trees and that although the amount of water consumed from internal storage was relatively small compared to total daily water uptake from the soil, maximum transpiration rates were maintained for a substantially longer fraction of the day in trees with greater storage capacity (Goldstein et al. 1998). Thus diurnal water storage in large trees may reduce peak demands for soil water uptake and delay the onset of diurnal leaf water deficits. Finally, soil water partitioning in larger trees may reflect a necessary trade-off resulting from higher nutrient demand associated with maintenance of an extensive crown leaf area. The soil nutrient content is greatest in the upper portion of the profile where the water content is lowest during the dry season. Although soil water is freely available throughout the dry season at depths of 1 m and below, its nutrient content is expected to be low compared to that of surface water.

It is possible that xylem water isotopic signatures in large trees were influenced by water removed from storage in their voluminous nonhydroactive xylem. However, a large influence of stored water seems unlikely because of its relatively small contribution to total diurnal water use and because the data in Fig. 5 were obtained after more than 60 diurnal cycles of discharge and recharge of internal water stores since the beginning of the dry season. Furthermore, the isotopic composition of stored water would be expected to reflect that of previous wet-season precipitation rather than that of water near the soil surface enriched in D via evaporative fractionation. Although δD values of precipitation falling during the wet season preceding our study period were not available, historical data from a nearby precipitation sampling station in the former Panama Canal Zone (IAEA/WMO 1998) show average precipitation-weighted δD values for the rainiest months of the wet season ranging between about –40 and –60‰ with monthly minimum values as low as –80‰. This range of values is substantially more negative than those observed in the

upper 20 cm of the soil profile (Fig. 2A) and in the xylem sap of the largest trees (Fig. 5).

The apparent ability of some trees to tap increasingly deeper soil water as the upper soil layers dried suggested highly opportunistic exploitation of water sources. This behavior was consistent with that reported for woody species in other types of habitat (Smith et al. 1991; Mensforth et al. 1994; Thorburn and Walker 1994; Dawson and Pate 1996). Based on their xylem δD values, trees able to draw water from greater depths in the soil profile as the dry season intensified also tended to show progressively increasing water use (Figs. 6, 7). On the other hand, trees showing little apparent flexibility in exploitation of soil water sources based on their relatively constant xylem δD values tended to show declining rates of water use from the beginning to the end of the dry season. Seasonal patterns of water use and soil water partitioning were associated with leaf phenology. Although direct phenological observations were not made in the individuals studied, some general inferences can be drawn from 10 years of seasonal leaf fall data collected on BCI. For example, in the brevideciduous *A. excelsum* and evergreen *T. tuberculata*, sap flow increased (Fig. 6) and xylem δD decreased substantially (Fig. 7A) over the course of the dry season. The relationship between leaf phenology, sap flow, and xylem δD in these species suggests that their water use was not limited by the progressive drying that occurs in the upper portion of the soil profile (Fig. 1). In the progressively deciduous *A. blackiana* and *C. alliodora*, on the other hand, sap flow declined sharply near the end of the dry season (Fig. 6C,D) and xylem δD values were nearly constant (Fig. 7). Further evidence of a link between leaf phenology and spatial and temporal partitioning of soil water was seen in the relationship between seasonal variability in leaf fall and xylem sap δD (Fig. 7B). Species able to tap increasingly deep sources of soil water as the dry season progressed also showed the smallest seasonal variability in leaf fall.

Detailed observations of seasonal courses of water use, xylem δD, and leaf phenology in individual trees are required to establish the nature of the mechanistic link between various patterns of leaf phenology, tree size, and spatial and temporal partitioning of soil water among species on BCI. Prior work in a forest near BCI (Jackson et al. 1995) points to a relatively consistent trend of evergreen and brevideciduous species having more negative xylem δD values than deciduous species during the dry season. However, the extent to which previously observed patterns were influenced by tree size, sampling date, and location is not known. In the present study, the largest trees yielded the least negative xylem δD values regardless of their leaf phenology (Fig. 5). For example, a 123-cm-DBH individual of the evergreen *Ficus insipida* and a 130-cm-DBH individual of *P. septenatum*, a species that is completely leafless by January, both had xylem sap δD values >–29‰.

Although profiles of soil water δD showed the expected evaporative enrichment in D near the surface (Fig. 2), there was typically a transient shift toward more negative values at a depth of about 30 cm. This pattern is consistent with the occurrence of hydraulic lift, the passive movement of water from moister to drier 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 not only of the plant responsible for it, but also to neighboring plants (Caldwell et al. 1998). Detailed measurements of daily courses of soil water potential near the surface or isotopic tracer studies using deuterated water would be required to establish the magnitude of hydraulic lift and its consequences for the water budget of the forest on BCI.

It is conceivable that the complex spatial and temporal partitioning of soil water resources observed in the present study minimized competition for water among individual trees as well as species, thereby maximizing exploitation of water reserves throughout the entire soil profile during the dry season. Although results of a number of studies suggest a high degree of water resource partitioning within and among species and life forms (Ehleringer et al. 1991; Flanagan et al. 1992; Valentini et al. 1992), examples of apparent direct competition between different life forms for the same limited pool of soil water have been reported (Le Roux et al. 1995). In the forest on BCI, a mosaic of phenology-driven contrasting seasonal courses of sap flow and flexibility in exploitation of soil water sources may result in stand-level evapotranspiration remaining nearly constant throughout the dry season.

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