Isotopic evidence for the role of plant development on transpiration in deciduous forests of southern United States

Germán Mora
Department of Geological and Atmospheric Sciences, Iowa State University, Ames, Iowa, USA

A. Hope Jahren
Department of Earth and Planetary Sciences, Johns Hopkins University, Baltimore, Maryland, USA

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[1] We evaluated D/H ratios of soil- and plant-extracted water during the 1997 growing season to assess the influence of temperature, humidity, and rainfall on water distribution in deciduous forests. Three state parks (Chicot in Arkansas; Natchez in Mississippi, and St. Bernard in Louisiana) were identified along a 13.5-cm precipitation gradient established during the studied growing season within the Mississippi River basin. Samples were collected for isotopic determinations from five to six species at each site early (March) and late (June) in the growing season. To capture the isotopic variability in water sources, samples of rainwater, groundwater, and soil water were collected. Isotopic results for rainwater showed an average increase of 4‰ from March to June. This increase did not transfer to soil water: soil water δD values throughout the growing season showed values close to those measured for March rainwater. In contrast, leaf water showed δD values that were 15‰ to 20‰ higher in March compared to June δD values. Elevated March δD values in leaf water were observed in virtually all species at the three sites. Change in leaf water δD value during the growing season was not correlated with precipitation rate, temperature, humidity, or changes in atmospheric water vapor isotopic composition. We propose that this widespread March isotopic enrichment resulted from enhanced evaporative demand induced by accelerated plant growth early in the growing season. This suggestion implies a decoupling of environmental factors and plant response, pointing to the important role of plant developmental timing in ecosystem functioning. *INDEX TERMS:* 1851 Hydrology: Plant ecology; 0315 Atmospheric Composition and Structure: Biosphere/atmosphere interactions; 1655 Global Change: Water cycles (1836); 1818 Hydrology: Evapotranspiration; *KEYWORDS:* hydrogen isotopes, evaporation, hydrological cycle, soil water, deuterium

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1. Introduction

[2] In continental interiors, water transfer to the atmosphere (''evapotranspiration'') occurs through two important mechanisms: evaporation and plant transpiration. Global estimates indicate that these two fluxes are responsible for an annual transfer of about 71,000 km^3 of water [*Schlesinger*, 1997]. The distinction between evaporation and transpiration and an assessment of their fluxes is needed to understand and predict future climate trends as the release of water from soils and plants into the atmosphere is associated with a significant energy transfer (latent heat). Evapotranspiration, for example, could account for up to 75% of the total land energy flux in tropical rain forests [*Shukla et al.*, 1990]. This distinction is even more crucial if it is considered that evaporation and transpiration appear to respond differently to environmental conditions. This is illustrated by micrometeorological measurements in deciduous forests that suggest that soil evaporation responds to changes in litter water [*Wilson et al.*, 2000], whereas plant transpiration responds to humidity deficit and phenology [*Wilson and Baldocchi*, 2000].

[3] A promising approach to differentiate evaporation from transpiration in the total evapotranspiration flux is through the use of stable isotopes of trapped vapor. *Wang and Yakir* [2000] employed this approach in a wheat field in Israel, concluding that soil evaporation only accounts for ~3% of midday evapotranspiration. Stable isotopes can be used for this distinction because different fractionation effects result from evaporation and transpiration. During evaporation, there is an enrichment of the lighter isotopes

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(^{1}H and ^{16}O) in vapor water as their heavier counterparts preferentially remain in the liquid phase [*Dansgaard*, 1964; *Majoube*, 1971]. This enrichment of heavier isotopes in soil water can reach up to 60‰ in relation to soil water in deeper soil profiles as it was found in unvegetated sand dunes [*Barnes and Allison*, 1988]. The enrichment of heavier isotopes at shallow depths is particularly characteristic of arid and semiarid regions [*Mathieu and Bariac*, 1996; *Walker et al.*, 1989; *Zimmermann et al.*, 1967] and results in profiles of soil water having high isotopic values in the topsoil and then gradually decreasing with depth. Tropical regions also exhibit a decreasing trend in isotopic values for soil water with depth, but the difference between values in the topsoil and those at depth is not as pronounced as in arid regions. For example, *Jackson et al.* [1995] reported a 20‰ difference in a soil profile of the lowlands of Panama.

[4] The other important flux of water (and energy) from terrestrial ecosystems to the atmosphere is plant transpiration. Phenomenological models [e.g., *Ball et al.*, 1987] predict that transpiration rates are directly proportional to photosynthesis rates and humidity, and inversely proportional to the partial pressure of carbon dioxide. General circulation models have illustrated the significance of transpiration in climate change [e.g., *Betts et al.*, 1997]. For instance, simulations of the replacement of tropical forests by pastures in Amazonia yielded a 30% decrease in evapotranspiration which resulted in a 2.5°C increase in mean surface temperatures and in a ~25% decrease in annual precipitation [*Shukla et al.*, 1990]. The potential impact of reduced transpiration on the regional climate of Amazonia as shown by these model results points, therefore, to the importance of assessing the factors that control transpiration fluxes in climate change studies.

[5] Multiple studies have measured no change in isotopic value as water passes from soil into plant roots [*Dawson and Ehleringer*, 1991; *Wershaw et al.*, 1966; *White et al.*, 1985; *Zimmermann et al.*, 1967]. Plants can access water throughout the soil profile, depending on the prevailing soil water potential and soil moisture content [*Kramer and Boyer*, 1995] as well as root placement. Thus the isotopic composition of sap water reflects the proportion of water taken from each soil level as well as the isotopic composition of that water. For example, *Jackson et al.* [1995] used an isotopic profile for soils of the lowlands of Panama in order to determine plant's water source from within the profile. The authors discovered that deciduous species in this semi-evergreen forest withdraw water from shallow (<40 cm) depths, whereas evergreen species have access to all soil horizons in the studied 120-cm soil profile.

[6] During photosynthesis, a significant component of sap water is lost when the opening of stomata facilitates the transfer of water from plants to the atmosphere. While this transpired water has isotopic values falling within the analytical uncertainty of those of sap water [*Yakir and Sternberg*, 2000], water remaining in leaves undergoes significant fractionation that results in an enrichment of the heavier isotopes in leaf water [*Wang and Yakir*, 2000]. The extent of this enrichment has been demonstrated to be affected by both local climatic and physiological conditions, including temperature, humidity, and transpiration rates [*Roden and Ehleringer*, 1999; *Yakir and Sternberg*, 2000]. Although the relative proportion of hydrogen lost in the vapor phase may vary as photosynthesis progresses, experimental studies show that plants take about 2–3 hours to reach isotopic steady state conditions [*Roden and Ehleringer*, 1999]. At this point, δD values for leaf water remain constant until photosynthesis ceases at the end of the photoperiod.

[7] In this study, we determined the distribution of hydrogen isotopes in soils and plants for three deciduous forests during early spring and summer to evaluate the influence of temperature, precipitation, and humidity on isotope abundances within this ecosystem of the North American continent. This evaluation is possible due to presence of a significant rainfall and humidity gradient along the ~500-km transect determined by the sites. Moreover, an assessment of the effect of environmental conditions (e.g., temperature, humidity, phenology) in the distribution of stable isotopes in the studied forests can provide information of the potential effects of these environmental parameters on evapotranspiration fluxes. This information could presumably be incorporated in modeling efforts to improving gas exchange and heat flux estimations.

2. Location, Materials, and Methods

[8] Sites possessing similar climate, vegetation, and proximity to the Mississippi River (Figure 1) were selected for this study in order to maintain a suite of common site characteristics. The studied sites (Figure 1) include Lake Chicot State Park in the state of Arkansas (33°22′16″N, 91°11′42″W), Natchez State Park in Mississippi (31°35′53″N, 91°12′06″W), and Saint Bernard State Park in Louisiana (29°51′40″N, 89°53′57″W). The climate at all three sampling sites is characterized as humid-subtropical. During the growing season of 1997, there was a latitudinal temperature gradient of 5°C and a rainfall gradient of 13.5 cm in March. Mean daily temperatures in March increased southward from 14.1°C at Lake Chicot (AR) and 16.2°C at Natchez (MS), to 19.4°C at Saint Bernard (LA), while precipitation rates decreased southward in March from 23.5 cm at AR and 17.1 cm at MS to 10.0 cm at LA. All three sites had similar native vegetation consisting of deciduous hardwood trees [*Thompson et al.*, 1999]. Regionally abundant species included elm (*Ulmus americana*), maple (*Acer saccharinum*), oak (*Quercus nigra*), and dogwood (*Corpus drummondi*). For this study, the same trees (Table 1) were sampled early (March) and late (June) in the growing season of 1997 to evaluate the effect of environmental parameters (i.e., rainfall, humidity, and temperature) on plant transpiration. Herbaceous plants were also collected in March and June (Table 1) to assess the dependence of transpiration rates on plant size. Different herbaceous specimens had to be studied in March and June as the plants identified in March were dead in July.

2.1. Climate

[9] The climate at the studied sites was subtropical with cool, dry winters and humid, hot summers. Temperatures in

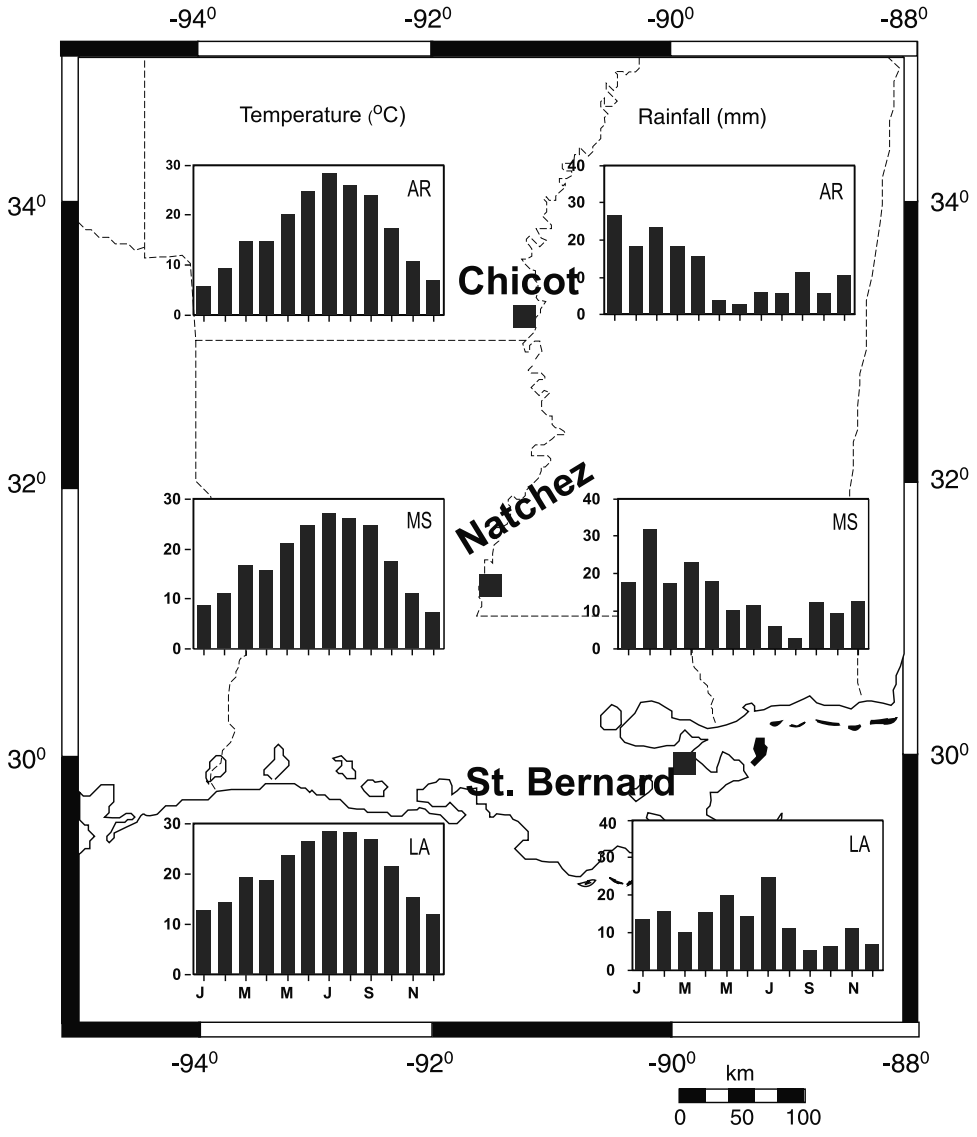

Figure 1. Location of the three studied sites (Lake Chicot State Park in Arkansas, Natchez State Park in Mississippi, and Saint Bernard State Park in Louisiana), showing the variability of temperature and rainfall for 1997.

the studied area ranged from an average summer high of about 30°C to an average winter low of 0–5°C. A larger temperature gradient across the sites occurred in spring in relation to the gradient observed in summer (Figure 1). Spring precipitation in the southern states of the United States was more abundant than summer precipitation as a result of the atmospheric instability produced by the confluence of the upper level jet stream and moist air from the

Table 1. Studied Species at Three Selected Sites in Arkansas (AR), Mississippi (MS), and Louisiana (LA) During the 1997 Growing Season

	Trees	Small Plants
AR	Dogwood (*Corpus drummondi*)	Honeysuckle (*Lonicera sempervirens*)
	Sugar Gum (Liquidambar styracifua)	White Clover (*Trifolium repens*)
	Water Oak (Quercus nigra)	
MS	Dogwood (*Corpus drummondi*)	Fern (*Polystichum acrostichoides*)
	Sugar Gum (*Liquidambar styracifua*)	Mayapple (*Podophyllum peltatum*)
	Magnolia (Magnolia grandiflora)	
	Elm (*Ulmus Americana*)	
LA	Dogwood (*Corpus drummondi*)	Honeysuckle (*Lonicera sempervirens*)
	Maple (*Acer saccharinum*)	Fern (*Thelypteris simulata*)
	Oak (*Quercus nigra*)	

Gulf of Mexico. Although spring rainfall at the studied sites was higher than summer rainfall, spring precipitation varied along the studied sites. This variability resulted from a more southerly position of the upper jet stream in spring that generated a 13.5-cm rainfall gradient in March as more rainfall at the AR site occurred with respect to the other sites (Figure 1). In the summer, the upper jet stream moves northward and the temperature gradient between seawater and the land decreases, resulting in air stagnation. At this time, precipitation preferentially occurred at coastal areas, like the LA site, thereby causing a small rainfall gradient with higher rates increasing southward in the studied area (Figure 1). The inversion of rainfall gradients between March and June (i.e., highest at AR in March and at LA in June) was employed in this study to evaluate latitudinal variations in plant response to rainfall patterns.

2.2. Collection of Plant Tissues

[10] Five or six nonirrigated, naturally occurring specimens were sampled at each site to compare plant water sources. Tissues from both large trees and small, low-lying, herbaceous plants (Table 1) were collected to assess water source and evaluate the dependence of transpiration rates on plant size. Leaf and stem tissues were clipped from the selected plants at least three hours after sunrise to ensure the establishment of isotopic steady state conditions [*Flanagan et al.*, 1991]. At least three replicates of stem and leaf tissue were randomly collected from each specimen to assess isotopic variability in each plant. Upon collection, plant tissues were rapidly placed in 22-mL borosilicate vials and packed as tightly as possible with plant tissues to reduce headspace. Vials were then tightly closed with Teflon-sealed caps to prevent evaporation, and wrapped in parafilm to secure the caps, thereby avoiding accidental opening of the vials while being transported. Vials containing plant tissues were stored on ice in the field and kept at ~3°C in the laboratory to retard microbial decomposition.

2.3. Sampling of Soils

[11] Prior to sampling, the soil litter layer (O horizon) was removed to avoid contamination by water from living plant material. A standard soil auger was used to collect soil samples at 25-cm increments. From each extruded section, homogenized aliquots of soil were taken in order to ensure a representative sample of the entire section. Borosilicate vials with a 22-mL capacity were completely filled with soil samples to eliminate headspace, capped with Teflon-seals, and covered with parafilm. Capped vials containing soil samples were kept on ice in the field and maintained at ~3°C in the laboratory prior to water extraction.

2.4. Rainfall Collection

[12] Precipitation was collected in non-evaporating rain gauges at each site. Each gauge consisted of a short-stemmed Nalgene funnel with a wide-mouth diameter of 6 cm fitted to a 3.8-L Nalgene bottle with about 0.5 m of flexible Tygon tubing. Prior to installation, a fine mesh was placed on the funnel to prevent introduction of large particles such as leaf fall, insects and other debris. About 100 mL of silicone oil was poured in the collection bottles to prevent evaporation of collecting precipitation. The gauges were erected at each site in March of 1997. After 3 months of collection, rainwater in the bottles was gently mixed and sampled with a syringe, avoiding the silicone oil layer. Borosilicate vials were filled with sampled rainwater, capped, wrapped in parafilm, and refrigerated at ~3°C. After sampling and discarding residual fluid in the rain gauge, the collection bottles were thoroughly rinsed. Silicone oil was replaced and the gauges were erected to collect precipitation for another 3-month period, after which the sampling procedure was repeated.

[13] Water samples were also collected from local wells to evaluate isotopic composition of groundwater systems. Prior to sampling, water was allowed to flow for several minutes through the outlet of the wells to ensure collection of representative samples. Borosilicate vials were then filled with groundwater, tightly capped, covered with parafilm, and refrigerated at ~3°C.

2.5. Water Extraction

[14] Water was extracted from plant tissues and soil material under vacuum according to methods fully described and tested previously [*Jahren*, 1996]. Briefly, vials containing plant and soil samples were cracked, rapidly introduced in pyrex tubes, and attached to a vacuum line. The pyrex tubes with the cracked vials were immediately immersed in liquid nitrogen for 30 min to freeze all contained tissue and soil water. Upon freezing, the line was pumped to vacuum and any remaining noncondensable gases were removed from the entire apparatus. Liquid nitrogen was then replaced with a water bath maintained at 100°C for 6 hours. Water evolving from plant tissues and soil material was cryogenically trapped, and subsequently thawed outside the vacuum line. Extracted water was then stored in tightly capped vials until isotopic analysis.

[15] Extracted water was analyzed for D/H ratios by online chromium reduction on a Micromass Isoprime instrument, in keeping with methods described fully elsewhere [*Morrison et al.*, 2001]. Briefly, water aliquots were introduced into a chromium reactor (ChromeHD™) using a liquid autosampler (Euro AS 300). Temperature in the reactor was kept at 1050°C, allowing a rapid reduction of water to hydrogen. Evolved hydrogen gas in then carried by a stream of He gas into the mass spectrometer. Isotopic results are reported in the standard per mil notation (‰) relative to standard mean ocean water (VSMOW) with an analytical uncertainty, as determined by at least three isotopic determinations of each sample, better than 1.5‰ for δD. Isotopic variability as established by the analysis of three different samples was better than 3‰ for rainwater, better than 5‰ for water extracted from soil material, and better than 8‰ for water extracted from plant species.

3. Results

3.1. Precipitation

[16] A 7‰ gradient in δD values for rainwater existed along the studied transect from March to June of 1997, with values decreasing to the north. This deceasing trend in δD values took place while the amount of rainfall received between March and June of 1997 increased with latitude (Figure 1). A similar decrease of δD values landward has

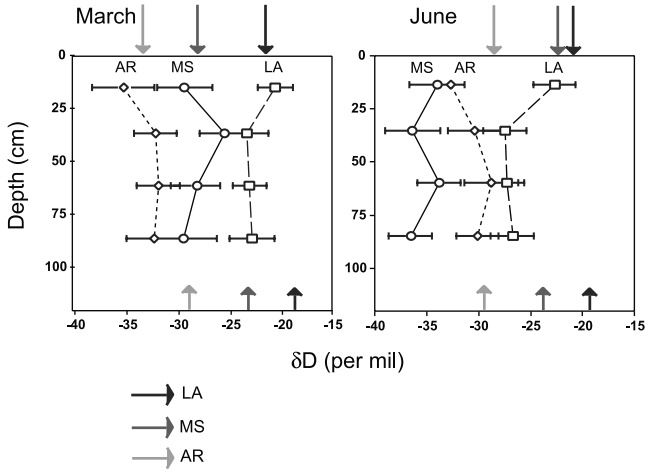

Figure 2. Stable hydrogen isotopic composition (δD) of soil water with depth in the studied sites for the months of March and June, 1997. Arrows pointing down correspond to the mean δD value for rainwater, whereas arrows pointing up indicate the mean δD value for groundwater at the sites.

been observed in other continental localities (e.g., Africa and South America [*Bowen and Wilkinson*, 2002]) and it is referred to as the "continental effect" [*Dansgaard*, 1964]. The progressive decrease in isotopic values for rainwater results as the heavier isotopes are preferentially incorporated in the liquid phase as air parcels move landward. Values of δD for rainwater along the studied transect showed a somewhat reversed trend from June to September: δD values at AR were higher by 9‰ with respect to those at LA, but δD values at MS and AR overlapped.

3.2. Soil Water

[17] A comparison of δD values for water extracted from two adjacent soil profiles at each of the three studied localities yielded a reproducibility that is within the analytical uncertainty (<5‰) of duplicate measurements. The exception, however, was soil water extracted in the upper 25 cm at AR and that extracted from the 75–100 cm interval at MS in March. The variability between two adjacent soils was 8‰ and 7.5‰, respectively. The isotopic composition of soil water extracted from samples collected in March at the three sites showed no significant variability with depth (Figure 2). In June, a small variability (<5‰) in δD values with depth was observed at AR and MS. However, δD values in the upper 25 cm at LA in June were 6‰ higher with respect to those obtained for the deeper horizons.

[18] In general, the isotopic composition of soil water at the three sites fell within the isotopic variability of that for rainwater in March (Figure 2). This was not the case in June, when δD values of rainwater were typically higher than those of soil water (Figure 2). The difference between δD values for rainwater and for soil water in the upper 25 cm was less than 5‰ at AR and less than 15‰ at MS.

3.3. Plant Tissues

[19] In March, δD values for stem-extracted water at AR ranged from −20‰ to −25‰, with the exception of dogwood specimens that exhibited an average value of −35‰ (Figure 3). δD values for stem water in plants at MS also had a narrow range (−28‰ to −35‰), with the exception of elm stem water that showed an average value of −40‰. Tree species at LA showed consistent stem water isotopic values of −30‰. In contrast, small plants at LA showed a wider range of δD values, varying from −25‰ for honeysuckle stem water to −40‰ for fern stem water (Figure 3).

[20] In June, while stem water in the studied trees at AR showed δD values of −30‰, the studied small plants showed δD values ranging from −15‰ for stem water in buttercup specimens to about −35‰ for honeysuckle stem water (Figure 3). Trees at MS had stem water with isotopic compositions varying from −20‰ to −25‰. The exception to this pattern is elm stem water that exhibited an isotopic composition of −30‰. Stem water in fern specimens at MS showed a higher δD value of −10‰. δD values for stem water in trees at LA ranged from −25‰ to −28‰, but stem water in small plants at LA exhibited values from −18‰ to −28‰ (Figure 3).

[21] In relation to stem water, leaf water from plants collected in March at all the studied sites showed a strikingly larger enrichment in D in relation to leaf water in June (Figure 3). In March, while δD values for leaf water at AR were enriched by 30‰ to 40‰ in relation to stem water, enrichment in D for leaf water at MS varied from 10‰ to 45‰. The studied tree species at MS had the largest isotopic

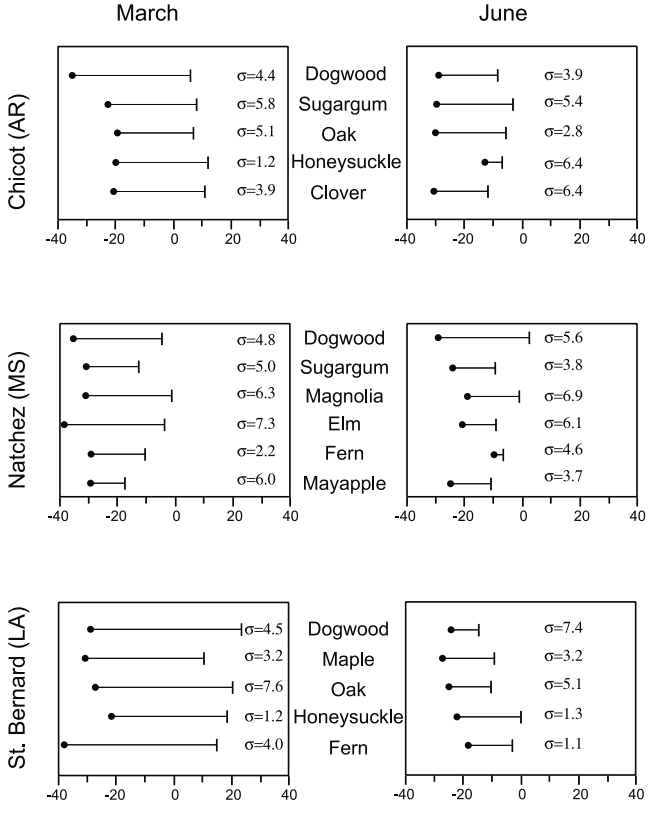

Figure 3. Stable hydrogen isotopic composition (δD) of extracted stem and leaf water for selected plant species at the three studied sites for the months of March and June, 1997.

enrichment. Leaf water extracted from plants at LA exhibited a relatively uniform isotopic enrichment of 45‰ to 55‰ relative to stem water (Figure 3). Conversely, leaf water from plants collected in June showed a wide range of D enrichment, although much smaller in total magnitude than March values, varying from about 5‰ to 25‰ at AR, from about 2‰ to 22‰ at MS, and from about 10‰ to 21‰ at LA (Figure 3).

4. Discussion

4.1. Soil Water

[22] Although the isotopic composition of soil water reflects that of rainwater [*Gat*, 1996], local climate and soil hydrology can cause fractionation of isotopes in soil water [*Zimmermann et al.*, 1967]. Consequently, this isotopic partitioning results in the departure of isotopic values for soil water from those for rainwater. For example, soil water in arid regions exhibit δD values that are significantly higher (by up to 60‰) in relation to the values for rainwater [e.g., *Barnes and Allison*, 1988; *Walker and Brunel*, 1990]. These processes altering the isotopic composition of soil water appear to have had a minor effect on the soils sampled in March at the three studied sites as indicated by the similarity of δD values for soil water, groundwater, and rainwater (Figure 2). These values, falling within the analytical uncertainty, indicate that the ratio of precipitation to evaporation was high enough to result in little isotopic enrichment of soil water. In contrast, the isotopic composition of soil water in June was typically depleted in D relative to rainwater and groundwater in the studied area.

[23] One of the most investigated processes affecting isotopic abundance in soil water is evaporation. A number of studies [*Allison and Hughes*, 1983; *Hsieh et al.*, 1996] show that intense evaporation in arid regions results in a rapid decrease of isotopic values for soil water with depth as water in the upper horizons preferentially loses the lighter isotopes in the vapor phase. For example, *Allison and Hughes* [1983] showed that soil water extracted from the upper 20 cm in arid regions of Arizona was enriched in D by about 30 to 40‰ with respect to water in the deeper soil horizons. The soils in the studied transect, however, showed a variability in δD values for soil water of less than 8‰, indicating that evaporation was limited or that water recharge was sufficient to erase any evaporative signal from the upper soil horizons. The probable exceptions are the soil profiles at LA. The upper horizons of these soils were enriched in D with respect to the deeper horizons in June and March (Figure 2), probably indicating evaporative loss of the lighter isotope. Interestingly, the isotopic composition of soil water in the same profiles at LA remained relatively unchanged from March to June, despite the 11‰ increase in δD values of rainwater during the same time period. The resemblance of soil water δD values in March and June points, therefore, to the significance of spring rain on recharging porous spaces with meteoric water. The same effect was also observed in soils at the other two localities in June, but with less intensity. While δD values for rainwater increased by about 5‰ from March to June, isotopic values for soil water in June were typically depleted in D with respect to rainwater. The apparent persistence of spring rainwater δD values in soil water throughout the growing season of 1997 in the studied soil profiles suggests a "memory effect" in soil water. Under this process, the isotopic signature of strong rain events is retained in soil water as abundant percolating water remain in the soil column for an extended period of time. It is likely that spring rainfall is the most important event in the recharge of soil and groundwater reservoirs, considering that precipitation in March accounts for up to 40% of the annual source of water in the studied region. This spring recharge process explains the resemblance of isotopic values for soil water, rainwater, and groundwater in March as a result of abundant rainfall. The isotopic signature of these early spring rain events persisted during the growing season, explaining the depletion of D in soil water for June relative to rainwater.

[24] The persistence of isotopic signature of March rainfall in June is probably the result of changing water percolation and mixing properties in the soils. We propose that the abundant early spring rainfall in the studied area was sufficient to push previous soil water down (piston-like flow), recharging both soil porous spaces and groundwater reservoirs with new meteoric water. This recharge mechanism explains, for instance, that soil water at LA in March showed values close to those in June, despite the enrichment in D of June rainwater. In contrast, late spring/summer rainfall was insufficient at AR and LA to completely replace soil water, resulting in soil water within the upper 50 cm depleted in D with respect to summer rainwater. The insufficient replenishment by late summer rainfall would be particularly accentuated in deep soil horizons and would cause preservation of the isotopic signal of previous rain events, thereby explaining the similarity in δD values between soil water below 50 cm and early spring rainwater at LA and MS. Supporting this argument, *Tang and Feng* [2001] found that soil water in the upper 20 cm of a profile in New Hampshire (USA) was depleted in the heavier isotopes in relation to summer precipitation, while deep soil water carried the isotopic signature of summer rainwater from previous years. These authors explain these observations in terms of a preferential flow mechanism in which relatively immobile water was inefficiently replaced by percolating (mobile) water from relatively week rain events. *Tang and Feng* [2001] also propose a piston-flow mechanism to explain the isotopic resetting of soil water in spring when abundant precipitation infiltrated the soil, replacing winter water with new meteoric water.

[25] The proposed preservation of early spring isotopic signal of rainwater in soil profiles is not observed, however, in the studied soils at MS. δD values of soil water in June were consistently depleted in D at all depths in relation to isotopic values for soil water in March. We hypothesize that soil texture caused the observed pattern. Soils at MS are coarser grained than the other studied soils, having up to 80% silt content (Figure 4). MS soils probably posses a faster percolation of water and a poorer retention of water as permeability in soils increases with particle sizes. As a result, the residence time of water in the MS soil columns is smaller than that of the other, more impermeable soils at AR and LA. Therefore, the isotopic composition of soil

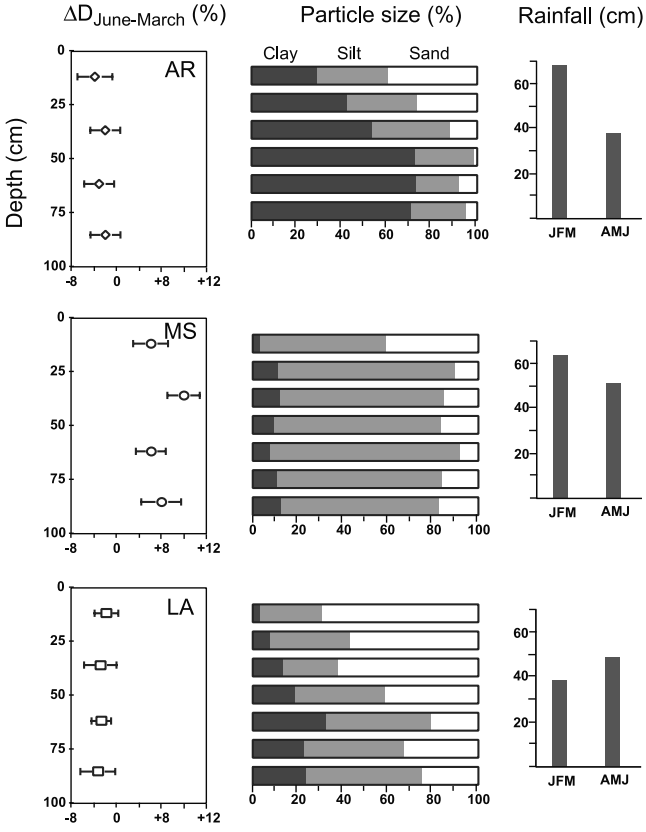

Figure 4. Difference between stable hydrogen isotopic compositions (δD) of extracted soil water for March and those in June at the three studied sites, particle size distribution of soils at the studied sites, and rainfall for March and June. Notice that the largest difference occurs at the MS site, which consists of mostly silt particles.

water in the MS soils probably reflected that of a single rainfall event.

4.2. Stem Water

[26] The isotopic composition of stem water reflects that of soil water and has been used to pinpoint source water for plant communities [*Busch et al.*, 1992; *Dawson and Ehleringer*, 1991; *Feild and Dawson*, 1998; *Grieu et al.*, 2001]. However, plants can draw water from different soil horizons [*Thorburn and Walker*, 1993], making δD values for stem water dependant on the amount of water that is taking up from each horizon and their respective isotopic composition [e.g., *Brunel et al.*, 1997]. Because the isotopic values of soil water from each studied site fall in a small range, it is difficult to establish with relative accuracy the source water for each of the studied species. However, the similarity between δD values for stem water and soil water in the upper 25 cm at MS, and between those for stem water and soil water in the upper 50 cm at LA suggest extraction of water from the upper soil horizons by plants at MS and LA in March. Previous studies have also indicated the potential of shallow soil horizons as major suppliers of water for plants. For example, *Tang and Feng* [2001] showed that water extracted from the upper 20 cm of a soil in a temperate, subhumid region of New Hampshire is the source water for a maple tree (*Acer saccharum*) as indicated by the resemblance in δD values between stem and soil water.

[27] While most studied species withdrew water from the topsoil, elm at MS and fern at LA appeared to extract water from other sources as indicated by the isotopic data. Relative to soil water, stem water in elm and fern was consistently depleted in D by about 8‰ and 10‰, respectively. Similarly, isotopic values for stem water in plants at AR were about 10‰ higher than those measured for soil water in March, with the exception of dogwood that appeared to have soil water in the upper 25 cm as a source. The discrepancy in isotopic values between soil water and stem water in some species (those at AR, elm at MS, and fern at LA) in March points to a yet unidentified source. It is possible that soil inhomogeneity could result in soil water exhibiting dissimilar isotopic values as local hydrological processes differentially fractionate isotopes in soil water [e.g., *Barnes and Allison*, 1988; *Mathieu and Bariac*, 1996]. However, the measured isotopic variability among different profiles at each site is small (Figure 2), making the possibility of isotopically distinct pools of soil water unlikely. Another explanation includes the possibility that the studied species withdraw water from the surface, before infiltration. Our data is unable to identify this source as the measured δD values for rainwater represents the average of numerous events that probably have different isotopic compositions, even varying within the same rain event [*Dansgaard*, 1964; *Salati et al.*, 1979]. Thus, it might be possible that the unidentified water source for those plants with anomalous δD values correspond to rainwater with isotopic signatures different from the weighted δD value. Alternatively, it is possible that the plants showing higher stem water δD values than those measured in soil water were drawing water from a D-enriched uppermost soil horizon. This isotopic enrichment induced by evaporation is, however, unresolved in our soil isotopic data. A possible explanation for the absence of D-enriched soil water in our data could involve our soil sampling protocol of collecting a representative sample of every 25-cm increment.

[28] The isotope data for the month of June suggest that the studied five plant species at LA were also taking up water from the upper 50 cm as indicated by the similarity in isotopic values between soil and stem water. Although δD values for soil and stem water at AR agreed in June, the limited variability in isotopic values with depth precludes an assessment of source water for these plants. In contrast, δD values for stem water at MS were enriched in D by about 13‰ to 18‰ in relation to soil water, indicating that soil water was an unlikely source. A possible source includes rainwater with a probably different isotopic composition than that of the mean value obtained for the March–June period, but with low volume of infiltration to drastically shift the isotopic composition of soil water. Alternatively, it is possible that the D enrichment observed in the MS plants came from soil water enriched in D due to evaporation. Although our water soil isotopic data do not show this enrichment, it is possible that our sampling scheme (i.e., samples from every 25 cm) may have overprinted any

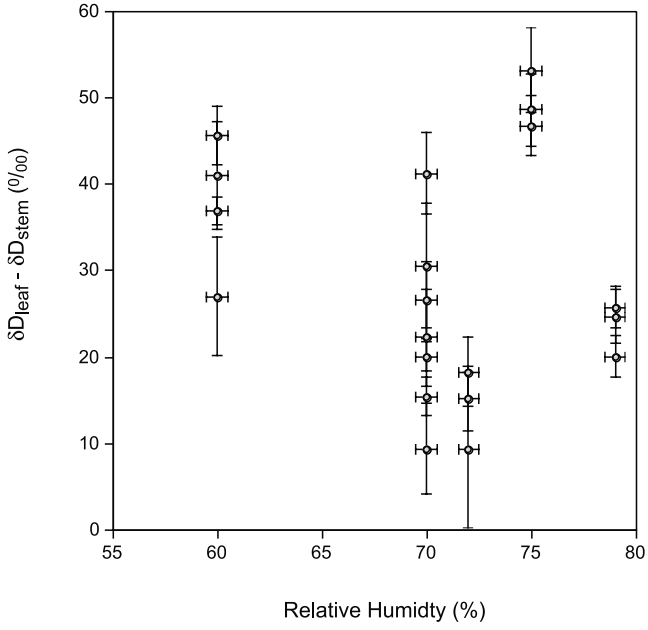

Figure 5. Relationship between relative humidity and the difference of stable hydrogen isotopic compositions (δD) of extracted stem and leaf water for the studied plant species at the three sites.

evaporative enrichment. This would occur when the amount of soil water in the upper centimeters is lower than that of the rest of the collected increment. Unfortunately, no data of soil moisture exists for the studied soil horizons to evaluate this possibility.

4.3. Leaf Water

[29] Values of δD for stem and leaf water differ considerably in the studied area, with leaf water consistently enriched in D relative to stem water (Figure 3). Although no isotopic fractionation occurs during the movement of water from soils to plants [*Zimmermann et al.*, 1967], transpiration changes δD values for leaf water [*Roden and Ehleringer*, 1999; *White*, 1988]. During this process, leaf water is actively moved to evaporation sites (mainly stomata) where it is transformed into vapor phase. Transpiration, therefore, results in the preferential escape of the lighter isotopes and the consequent isotopic enrichment of D in leaf water. *Craig and Gordon* [1965] modeled this kinetic effect on large bodies of water to assess the isotopic composition of water undergoing evaporation. The Craig and Gordon model has been applied to leaf water, assuming that leaves contain well-mixed, isotopically homogenous water [*Farris and Strain*, 1978; *Walker et al.*, 1989].

[30] Although the model predicts increased leaf-water δD with increased humidity, our results showed no direct correlation between the extent of D-enrichment and ambient humidity for 1997 (Figure 5). In fact, leaf water in March was consistently more enriched in D in relation to stem water than June leaf water. This larger March D enrichment occurred irrespective of prevailing precipitation rate, temperature, humidity level, or plant size (Figures 1 and 3). Some models describing plant evaporation [e.g., *Craig and Gordon*, 1965] emphasize the control of the isotopic composition of vapor water on the isotopic composition of leaf water. To assess this effect, we estimated the δD values of vapor water at steady state conditions with our average measured δD values for leaf water using the Craig-Gordon model (Table 2). The δD values for atmospheric water vapor predicted using the Craig-Gordon model exhibited an erratic pattern. If a change in the isotopic composition of atmospheric water vapor is invoked to explain the entire difference between ($\delta D_{leaf} - \delta D_{stem}$) in March versus June, this would imply an increase in the δD value of water vapor of ∼20‰ and ∼37‰, at AR and MS, respectively, and a decrease of ∼35‰ at LA (Table 2). It is difficult to explain the increasing trend in estimated isotopic values for water vapor at AR and MS with the simultaneous decrease in estimated isotopic values for water vapor at LA given that humidity, temperature, and the isotopic composition of rainwater exhibited a consistent trend across the studied transect. Moreover, these estimated δD values of vapor water are out of equilibrium with corresponding groundwater and soil water at the three sites. Although we cannot completely rule out the effect of changing δD values of vapor water on the isotopic composition of leaf water, it is unlikely that the unsystematic changes in the estimated isotopic compositions of vapor water from March to June could account for the observed changes in δD values of leaf water.

[31] Our isotope data indicate that most of the studied species experienced significant evaporative demand in March to produce high leaf δD values, thereby pointing to a common factor. We hypothesize that the large difference in δD values between leaf and stem water in March is caused by plant growth early in the growing season and possibly associated with enhanced transpiration rates. Although enhanced plant transpiration could partially prevent the back diffusion of D-enriched water from the evaporation sites to other sites within a leaf [*Farquhar et al.*, 1993], it is possible that the volume of water diffusing out of the leaf is sufficient to cause increased leaf water δD values as D-enriched water remains in the leaf.

Table 2. Estimated Hydrogen-Isotopic Composition of Vapor Water (δD_v) at Steady State With Measured Hydrogen-Isotopic Compositions of Leaf Water (δD_{lw}) and Steam Water (δD_s) for the Studied Plant Species at the Three Localities[a]

	T, °C	RH, %	δD_s, ‰	δD_{lw}, ‰	δD_v, ‰
			AR		
March	14.6	70	−20 ± 5	+8 ± 4	−120 ± 7
June	24.6	79	−30 ± 5	−8 ± 4	−100 ± 7
			MS		
March	16.8	60	−30 ± 5	−8 ± 5	−160 ± 7
June	24.7	70	−25 ± 7	−5 ± 5	−123 ± 7
			LA		
March	19.4	75	−27 ± 5	+17 ± 4	−88 ± 7
June	24.5	72	−25 ± 5	−10 ± 4	−123 ± 7

[a]Isotopic data represent mean values of the studied plant species and their variability. Estimated δD_v values were calculated with a modified Craig-Gordon evaporation model [*Flanagan et al.*, 1991; *Roden and Ehleringer*, 1999] using monthly mean values of temperature (T) and relative humidity (RH), and assuming a moderate stomatal conductance of 0.3 mol/m^{2}sec.

[32] Supporting our hypothesis of increased transpiration early in the growing season, micrometeorological and flux measurements in a deciduous forest of Tennessee [*Wilson et al.*, 2000] revealed that leaf emergence causes a dramatic increase in transpiration, driving the total evapotranspiration flux from 0.5 mm/day early in spring to 3.0 mm/day after leaf emergence. Moreover, similar results indicating increased transpiration during leaf growth, as determined by increases in latent heat, have been obtained in boreal aspen forests [*Blanken et al.*, 1997], a deciduous forest in Massachusetts [*Moore et al.*, 1996], and a grassland ecosystem in Japan [*Saigusa et al.*, 1998].

[33] Although ambient humidity plays an important role on plant transpiration as documented from micrometeorological measurements in coniferous forests [*Gash et al.*, 1989], savanna vegetation [*Miranda et al.*, 1997], tropical forests [*Grace et al.*, 1995], temperate deciduous stands [*Wilson et al.*, 2000], and temperate grasslands [*Kim and Verma*, 1991]; our results suggest that plant growth could be another important factor controlling plant transpiration on an ecosystem scale. Such a role has been documented in sap measurements of broad-leaved forests [*Kostner et al.*, 1992] and has been proposed on the basis of the established relationship that exists between sapwood area and leaf area [*Whitehead et al.*, 1984].

[34] Our results indicate that while leaf water in the studied sites experienced a large enrichment in D in March, soil water showed little to no enrichment (although it is possible that our sampling scheme did not provide the sufficient resolution to detect an isotopic enrichment). This observation indicates an apparent decoupling between atmospheric evaporative demand and isotopic enrichment in soil water, thereby affecting the partitioning of energy fluxes in the studied forests. Soil evaporation and plant transpiration are the main processes contributing to latent heat flux in forests (although evaporation of water on plant surfaces could also be an important source of latent heat). Our soil water data indicate a similar contribution of latent heat flux from the studied soils during March and June. In contrast, the leaf water data suggest an increased contribution of plant transpiration to latent heat flux in March.

[35] Our suggestion that increased isotopic values of leaf water occur during plant growth as a result of increased evaporative demand has additional implications for global models. The oxygen-isotopic composition ($\delta^{18}O$) of carbon dioxide is currently used to distinguish between photosynthesis and respiration in ecosystems [e.g., *Farquhar et al.*, 1993; *Ciais et al.*, 1997]. Values of $\delta^{18}O$ for respired CO_2 reflect those of soil water and are typically lower than those of CO_2 associated with photosynthesis. Higher $\delta^{18}O$ values for CO_2 associated with photosynthesis result during the isotopic exchange of CO_2 and ^{18}O-enriched leaf water. During photosynthesis, 1/3 of the CO_2 that diffuses into a leaf is carboxylated, while the remaining CO_2 diffuses back out of the leaf. Before diffusing out, an exchange of oxygen isotopes occurs between CO_2 and leaf water, which produces increased $\delta^{18}O$ values for diffusing CO_2. This difference in $\delta^{18}O$ values for CO_2 associated to photosynthesis and those for CO_2 related to respiration has been used in global models to partition net terrestrial ecosystem productivity into gross primary production and ecosystem respiration [e.g., *Farquhar et al.*, 1993]. These models estimate $\delta^{18}O$ values for CO_2 diffusing out leaves by assessing leaf water $\delta^{18}O$ values via the Craig-Gordon model. Although our results do not include leaf water $\delta^{18}O$ values, our data strongly suggest that this evaporation model underestimates the degree of ^{18}O-enrichment in leaf water for deciduous forests during the growing season. In fact, discrepancies between modeled and measured $\delta^{18}O$ values for CO_2 in deciduous ecosystems have already been detected [*Peylin et al.*, 1999], and we propose that may result from accentuated periods of plant growth.

5. Conclusions

[36] Isotopic results indicate a close similarity between δD values for water extracted from soils and those for rainwater in spring. Values for soil water changed little from spring to summer despite a pronounced isotopic enrichment in rainwater during the same time interval. Because spring precipitation makes up 40% to 50% of the annual precipitation budget for the studied region, the persistence of spring isotopic signature in soil water reflects, therefore, a small volume of summer rainfall infiltrating the studied soils. The isotopic composition for soil water shows little vertical variability, indicating little or no evaporative enrichment in the upper horizons despite a significant change in humidity from spring to summer. This observation suggests an uncoupling of the studied soils from atmospheric demands. This conclusion, however, could be tempered by our coarse soil sampling scheme that may have overprint any potential evaporative enrichment.

[37] Isotopic values for stem water are similar to those of the upper soil horizons, with the exception of a few specimens that appear to withdraw water from surface water. Although gradients in temperature and rainfall existed in the studied area and could influence the isotopic composition of leaf water, high δD values for leaf water consistently occurred at the three studied sites in March. These higher δD values for leaf water in spring relative to those in summer reflected a significant evaporative demand earlier in the growing season. We propose that increased evaporative demand was probably prompted by plant growth.

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References

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

Ball, J. T., I. E. Woodrow, and J. A. Berry, A model predicting stomatal conductance and its contribution to the control of photosynthesis under different environmental conditions, in *Progress in Photosynthesis Research*, vol. IV, *Proceedings of the International Congress on Photosynthesis*, edited by J. Biggins, pp. 221–224, Kluwer Acad., Norwell, Mass., 1987.

Barnes, C. J., and G. B. Allison, Tracing water movement in the unsaturated zone using stable isotopes of hydrogen and oxygen, *J. Hydrol.*, *100*, 143–176, 1988.

Betts, R. A., P. M. Cox, S. E. Lee, and F. I. Woodward, Contrasting physiological and structural vegetation feedbacks in climate change simulations, *Nature*, *387*, 796–799, 1997.

Blanken, P. D., T. A. Black, P. C. Yang, H. H. Neumann, Z. Nesic, R. Staebler, G. D. Hartog, M. D. Novak, and X. Lee, Energy balance and surface conductance of a boreal aspen forest: Partitioning overstory and understory components, *J. Geophys. Res.*, *102*, 28,915–28,927, 1997.

Bowen, G. L., and B. Wilkinson, Spatial distribution of $\delta^{18}O$ in meteoric precipitation, *Geology*, *30*, 315–318, 2002.

Brunel, J. P., G. R. Walker, J. C. Dighton, and B. Monteny, Use of stable isotopes of water to determine the origin of water used by the vegetation and to partition evapotranspiration: A case study from HAPEX-Sahel, *J. Hydrol.*, *188–189*, 466–481, 1997.

Busch, D. E., N. L. Ingraham, and S. D. Smith, Water uptake in woody riparian phreatophytes of the southwestern United States: A stable isotope study, *Ecol. Appl.*, *2*, 450–459, 1992.

Ciais, P., et al., A three-dimensional synthesis study of $\delta^{18}O$ in atmospheric CO_2: I. Surface fluxes, *J. Geophys. Res.*, *102*, 5857–5872, 1997.

Craig, H., and L. I. Gordon, Deuterium and oxygen-18 variations in the ocean and the marine atmosphere, in *Proceedings of a Conference on Stable Isotopes in Oceanographic Studies and Paleotemperatures*, edited by E. Tongiorgi, pp. 9–130, Cons. Naz. delle Ric., Lab. Di Geol. Nucl., Spoleto, Italy, 1965.

Dansgaard, W., Stable isotope in precipitation, *Tellus*, *16*, 436–468, 1964.

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

Farquhar, G. D., J. Lloyd, J. A. Taylor, L. B. Flanagan, J. P. Syvertsen, K. T. Hubick, S. Wong, and J. R. Ehleringer, Vegetation effects on the isotopic composition of oxygen in atmospheric CO_2, *Nature*, *363*, 439–443, 1993.

Farris, F., and B. R. Strain, The effect of water stress on the leaf $H_2{}^{18}O$ enrichment, *Radiat. Environ. Biophys.*, *15*, 167–202, 1978.

Feild, T. S., and T. E. Dawson, Water sources by *Didymopanax pittieri* at different life stages in a tropical cloud forest, *Ecology*, *79*, 1448–1452, 1998.

Flanagan, L. B., J. P. Comstock, and J. R. Ehleringer, Comparison of modeled and observed environmental influences on the stable oxygen and hydrogen isotope composition of leaf water in *Phaseolus vulgaris L.*, *Plant Physiol.*, *96*, 588–596, 1991.

Gash, J. H. C., W. J. Shuttleworth, C. R. Lloyd, J. C. Andre, J. P. Goutorbe, and J. Gelpe, Micrometeorological measurements in les Landes forest during HAPEX-MOBILHY, *Agric. For. Meteorol.*, *46*, 131–147, 1989.

Gat, J. R., Oxygen and hydrogen isotopes in the hydrological cycle, *Annu. Rev. Earth Planet. Sci.*, *24*, 225–262, 1996.

Grace, J., J. Lloyd, J. A. McIntyre, A. C. Miranda, H. S. Miranda, I. Wright, and J. Gash, Fluxes of water vapour and carbon dioxide over an undisturbed tropical forest in south-west Amazonia, *Global Change Biol.*, *1*, 1–12, 1995.

Grieu, P., D. W. Lucero, R. Ardiani, and J. R. Ehleringer, The mean depth of soil water uptake by two temperate grassland species over time subjected to mild soil water deficit and competitive association, *Plant Soil*, *230*, 197–209, 2001.

Hsieh, J. C. C., O. A. Chadwick, E. F. Kelly, and S. M. Savin, Oxygen isotopic composition of soil water: Quantifying evaporation and transpiration, *Geoderma*, *82*, 269–293, 1996.

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

Jahren, A. H., The stable isotope composition of the hackberry (*Celtis*) and its use as a paleoclimate indicator, Ph.D. thesis, Univ. of California, Berkeley, Berkeley, Calif., 1996.

Kim, J., and S. B. Verma, Modelling canopy stomatal conductance in a temperate grassland ecosystem, *Agric. For. Meteorol.*, *55*, 149–166, 1991.

Kostner, B. M. M., E. D. Schulze, F. M. Kelliher, D. Y. Hollinger, J. N. Byres, J. E. Hunt, T. M. McSeveny, R. Meserth, and P. L. Weir, Transpiration and canopy conductance in a pristine broad-leaved forest of Nothafagus: An analysis of xylem sap flow and eddy correlation measurements, *Oecologia*, *91*, 330–359, 1992.

Kramer, P. J., and J. S. Boyer, *Water Relations of Plants and Soils*, 495 pp., Academic, San Diego, Calif., 1995.

Majoube, M., Fractionnement en ^{18}O et en deuterium entre l'eau et sa vapeur, *J. Chim. Phys.*, *68*, 1423–1436, 1971.

Mathieu, R., and T. Bariac, An isotopic study (^2H and ^{18}O) of water movements in clayey soils under semiarid climate, *Water Resour. Res.*, *32*, 779–789, 1996.

Miranda, A. C., H. S. Miranda, J. Lloyd, J. Grace, R. J. Francey, J. A. McIntyre, P. Meir, P. Riggan, R. Lockwood, and J. Brass, Fluxes of carbon, water, and energy over Brazilian cerrado: An analysis using eddy covariance and stable isotopes, *Plant Cell Environ.*, *20*, 315–328, 1997.

Moore, K. E., D. R. Fitzjarrald, R. K. Sakai, M. L. Goulden, J. W. Munger, and S. C. Wofsy, Season variation in radiative and turbulent exchange at a deciduous forest in central Massachussets, *J. App. Meteorol.*, *35*, 122–134, 1996.

Morrison, J., T. Brockwell, T. Merren, F. Fourel, and A. M. Phillips, On-line high-precision stable hydrogen isotopic analyses on nanoliter water samples, *Anal. Chem.*, *73*, 3570–3575, 2001.

Peylin, P., P. Ciais, A. S. Denning, P. P. Tans, J. A. Berry, and J. W. C. White, A 3-dimensional study of $\delta^{18}O$ in atmospheric CO_2: Contribution of different land ecosystems, *Tellus, Ser. B*, *51*, 642–667, 1999.

Roden, J. S., and J. R. Ehleringer, Observations of hydrogen and oxygen isotopes in leaf water confirm the Craig-Gordon model under wide-ranging environmental conditions, *Plant Physiol.*, *120*, 1165–1173, 1999.

Saigusa, N., O. Takehisa, and S. Liu, Seasonal variations of the exchange of CO_2 and H_2O between a grassland and the atmosphere: an experimental study, *Agric. For. Meteorol.*, *89*, 131–139, 1998.

Salati, E., A. Dall'Olio, J. R. Gat, and E. Matsui, Recycling of water in the Amazon basin: An isotope study, *Water Resour. Res.*, *15*, 1250–1258, 1979.

Schlesinger, W. H., *Biogeochemistry: An Analysis of Global Change*, 588 pp., Academic, San Diego, Calif., 1997.

Shukla, J., C. Nobre, and P. Sellers, Amazon deforestation and climate change, *Science*, *247*, 1322–1325, 1990.

Tang, K., and X. Feng, The effect of soil hydrology on the oxygen and hydrogen isotopic composition of plant's source water, *Earth Planet. Sci. Lett.*, *185*, 355–367, 2001.

Thompson, S. R., K. A. Anderson, and P. J. Bartle, Atlas of relations between climatic parameters and distributions of important trees and shrubs in North America, *U.S. Geol. Surv. Prof. Pap.*, *1650-B*, 1–423, 1999.

Thorburn, P. J., and G. R. Walker, The source of water transpired by *Eucalyptus camaldulensis*: Soil, groundwater, or streams?, in *Stable Isotopes and Plant Carbon/Water Relations*, edited by J. R. Ehleringer, A. E. Hall, and G. D. Farquhar, pp. 511–527, Academic, San Diego, Calif., 1993.

Walker, C. D., and J. P. Brunel, Examining evapotranspiration in a semiarid region using stable isotopes of hydrogen and oxygen, *J. Hydrol.*, *118*, 55–75, 1990.

Walker, C. D., F. W. Leany, J. C. Dighton, and G. B. Allison, The influence of transpiration on the equilibrium of leaf water with atmospheric water vapour, *Plant Cell Environ.*, *12*, 221–234, 1989.

Wang, X. F., and D. Yakir, Using stable isotopes of water in evapotranspiration studies, *Hydrol. Proc.*, *14*, 1407–1421, 2000.

Wershaw, R. L., I. Friedman, and S. J. Heller, Hydrogen isotope fractionation of water passing through trees, in *Advances in Organic Geochemistry*, edited by G. D. Hobson and G. C. Speers, pp. 55–67, Pergamon, New York, 1966.

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

White, J. W. C., Stable hydrogen isotope ratios in plants: A review of current theory and some potential applications, in *Stable Isotopes in Ecological Research*, edited by P. W. Runderl, J. R. Ehleringer, and K. A. Nagy, pp. 142–162, Springer-Verlag, New York, 1988.

Whitehead, D., P. G. Jarvis, and R. H. Waring, Stomatal conductance, transpiration, and resistance to water uptake in a Pinus sylvestris displacing experiment, *Can. J. For. Res.*, *14*, 692–700, 1984.

Wilson, K. B., and D. D. Baldocchi, Seasonal and interannual variability of energy fluxes over a broadleaved temperate deciduous forest in North America, *Agric. For. Meteorol.*, *100*, 1–18, 2000.

Wilson, K. B., P. J. Hanson, and D. D. Baldocchi, Factors controlling evaporation and energy partitioning beneath a deciduous forests over an annual cycle, *Agric. For. Meteorol.*, *102*, 83–103, 2000.

Yakir, D., and L. Sternberg, The use of stable isotopes to study ecosystem gas exchange, *Oecologia*, *123*, 297–311, 2000.

Zimmermann, U., D. Enhalt, and K. O. Munnich, Soil water movement and transpiration: Changes in the isotopic composition of the water, in *Isotopes in Hydrology*, pp. 567–685, Int. Atom. Energy Agency, Vienna, 1967.

A. H. Jahren, Department of Earth and Planetary Sciences, Johns Hopkins University, Baltimore, MD 21218, USA.

G. Mora, Department of Geological and Atmospheric Sciences, Iowa State University, Ames, IA 50011, USA.