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Water uptake by plants: perspectives from stable isotope composition

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ABSTRACT

Stable isotope studies of hydrogen and oxygen stable isotope ratios of water within plants are providing new information on water sources, competitive interactions and water use patterns under natural conditions. Variation in the utilization of summer rain by aridland species and limited use of stream water by mature riparian trees are two examples of how stable isotope studies have modified our understanding of plant water relations. Analyses of xylem sap and tree rings have the potential of providing both short-term and long-term information on plant water use patterns.

Key-words: hydrogen isotope; oxygen isotope; ground water; water use; water-use efficiency; water relations; D/H; $^{18}O/^{16}O$.

INTRODUCTION

Field studies aimed at understanding the utilization of belowground resources by plants, such as water and nutrients, have been hampered by a limited ability to assess non-destructively particular characteristics of root systems (e.g. root activities and rooting patterns). Excavation studies provide a one-point-in-time snapshot of root distribution, but may provide very little insight into resource uptake rates or patterns of resource utilization. That is, root presence may not be a reliable indicator of either actual water or nutrient uptake dynamics in either time or space. In this paper, we present evidence to show that at least some of these problems can be resolved by analyses of the stable isotope composition of water at natural abundance levels. Results from isotopic studies over the past 6–8 years are providing new insights into the functioning of roots within the soil profile and of the differential utilization of water by plants within natural communities.

The utility of stable isotopes in water as an avenue for understanding water utilization by plants is based on the fundamental observation that there is no isotopic fractionation of either hydrogen (^1H, ^2H or D) or oxygen (^{16}O, ^{18}O) isotopes of water during water uptake by roots (Wershaw, Friedman & Heller 1966; Allison *et al.* 1984; White *et al.* 1985; Dawson & Ehleringer 1991). Gradients in the isotopic composition of water within soils can arise because of differences in the seasonal input of moisture into the soil (Friedman *et al.* 1964; Gat 1980b; Siegenthaler & Oeschger 1980; Yurtsever & Gat 1980; Ferronsky & Polyakov 1982; Rozanski, Sonntag & Münnich 1982), evaporation in the uppermost surface layers (Allison, Barnes & Hughes 1983; Allison & Hughes 1983; Barnes & Allison 1983), or differences between bulk soil moisture and ground water (Fontes 1980; Gat 1980a). During water transport between the root and the shoot, the isotopic composition (measured as the ratio of heavy to light isotopes) of xylem water remains unaltered from that in the soil, until it reaches tissues undergoing water loss (i.e. leaves or nonsuberized stems), where evaporative enrichment in the heavier isotopes of hydrogen and oxygen takes place. Leaves are the primary site of evaporative enrichment and the magnitude of this enrichment of leaf water is dependent upon humidity gradients, transpiration rate and the isotopic composition of atmospheric water (Dongmann *et al.* 1974; Zundel *et al.* 1978; Leaney *et al.* 1985). The extent of this enrichment varies diurnally. However, if the hydrogen or oxygen isotopic composition of water within xylem sap is analysed before it has been exposed to evaportative processes, this isotopic composition is an integrated measure of overall water uptake, reflecting the various zone(s) and depth(s) from which the plant is currently extracting soil water. As such, stable isotope analyses of source and xylem sap water provide a powerful tool for improving our understanding of active rooting zones and water uptake processes. Such understanding can provide insights into the role of water in influencing ecological and physiological processes.

There are several advantages of stable isotope analyses for use in studies of water uptake by plants. Firstly, there are often large gradients in isotopic composition of water within plant communities. Analysis of stable isotopes in water along these gradients makes it easy to determine which water source(s) is currently exploited by the plant. Secondly, the analysis needs only very small quantities of water, and therefore, is effectively non-destructive. Thirdly, no radioactive or nonradioactive labelling is required to distinguish clearly among

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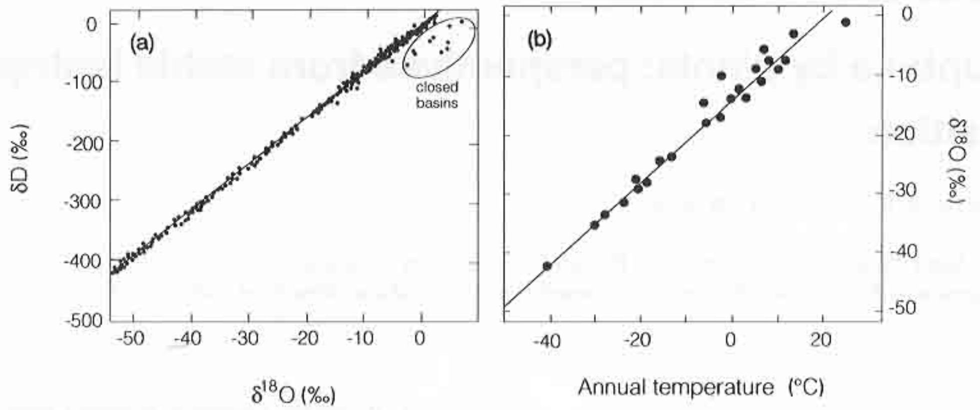

Figure 1. (a) A plot of the relationship between hydrogen and oxygen isotope ratios in precipitation from different global locations; based on a figure from Taylor (1974). The line through these data is known as the Meteoric Water Line (MWL). (b) A plot of the relationship between oxygen isotope ratio of meteoric water and mean annual temperature for different global locations; based on a figure from Fontes (1980).

possible water sources, making it possible to get continuous temporal information not available with labelled approaches.

Isotopic composition for hydrogen or oxygen is expressed in delta notation (δ) as

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

where R_{sample} and $R_{standard}$ are the molar ratios of either D/H (for δD) or $^{18}O/^{16}O$ (for $\delta^{18}O$) of the sample and standard, respectively. The standard is defined as Standard Mean Ocean Water (SMOW) (actually now V-SMOW since the original SMOW has been exhausted) with absolute ratios of D/H equal to 0·00015576 (Hagemann, Nief & Roth 1970) and $^{18}O/^{16}O$ equal to 0·0020052 (Baertschi 1976). The units for hydrogen or oxygen isotope ratios are parts per thousand or more simply 'per mil'. Preparation and measurements of the isotopic composition of water can be completed with as little as $0{\cdot}5 \times 10^{-9}$ m^3 (0·5 μl) (Bigeleisen, Perlman & Prosser 1952; Coleman *et al.* 1982; Wong, Lee & Klein 1987; Ehleringer & Osmond 1989).

ISOTOPIC VARIATION AMONG WATER SOURCES

The stable isotopic composition of atmospheric water is a function of temperature and depletion of isotopes that occurs as an air mass moves over continental land masses (Craig 1961; Dannsgaard 1964; Friedman *et al.* 1964; Yurtsever & Gat 1980; Ingraham & Taylor 1991). Precipitation falling as rain is enriched in the heavier isotopes of both hydrogen and oxygen when compared to snow (Fig. 1), primarily because of differences in the vapour pressures of heavier and lighter water (i.e. DHO versus H_2O and $H_2{}^{18}O$ versus $H_2{}^{16}O$). This leads to marked differences between the isotopic composition of precipitation falling in summer and winter and across latitudinal and elevational gradiens (Craig 1961; Dansgaard 1964; Yurtsever & Gat 1980). The isotopic composition of ground water (unless ancient) is a weighted average of annual precipitation inputs. Stable isotopes of oxygen and hydrogen stable isotopes in precipitation are linearly related (Fig. 1; known as the 'Meteoric Water Line', MWL), such that the hydrogen isotopic ratio, δD, of water is,

$$\delta D = 8 \cdot \delta^{18}O + 10‰$$

(Craig 1961). The isotopic composition of waters from springs and closed, inland basins may differ from the MWL because of evaporative enrichment. Variation in these sources of fresh water can be as large as 200‰ in a single location (Dansgaard 1964).

In contrast, coastal plant communities are influenced by gradients of salinity. Changes in isotopic composition of saline water are associated with differences in the proportions of oceanic and fresh water (Sternberg & Swart 1987; Sternberg *et al.* 1991). Water from the ocean is enriched in the heavier isotopes of O and H when compared to fresh water and these differences may be used to detect plant utilization of one source or the other (Sternberg & Swart 1987; Sternberg *et al.* 1991). In addition, many coastal areas of the world have fog, a source of water that is thought to be important for plants (e.g. the Atacama and Peruvian Deserts, Rundel *et al.* 1991). Fog is depleted in the heavier isotopes relative to the water source from which it was formed (Ingraham & Matthews 1988, 1990), and should be detectable if it is absorbed. While it has been argued that fog precipitation can comprise a third or more of annual precipitation in many coastal regions, its importance as a water source for plants remains unquantified (see Ingraham & Matthews 1988).

The ability to switch rapidly among different water sources could put a plant at an advantage if competition for water occurs within the ecosystem. In a study of soil

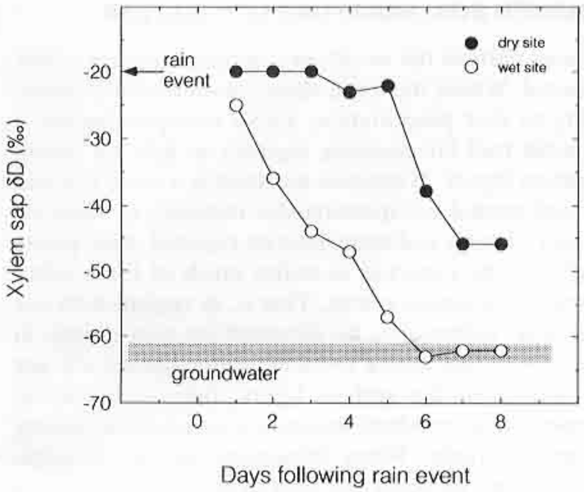

Figure 2. Time course of the hydrogen isotope ratio of xylem sap in eastern white pine (*Pinus strobus*) following a summer rain event; based on data from White *et al.* (1985). Trees at the wet site had access to a secondary ground water source, whereas trees on the dry site did not have access to the ground water.

moisture utilization by eastern white pine (*Pinus strobus*) in the eastern United States, White *et al.* (1985) showed that water extraction switched between deep and surface soil layers, depending on the recent history of precipitation events (Fig. 2). Immediately following a rain event, the white pine trees utilized moisture from surface layers wich had an isotopic signature similar to that of the recent precipitation event. However, as surface soil layers dried out, there was a progressive decrease in the δD of water contained within the stem xylem sap, indicating a switch from surface soil moisture to deeper soil layers. In those sites where ground water was close to the surface, δD switched from that of surface moisture back to that of the ground water. At those sites where the trees did not have access to ground water, the δD values of sapwood water switched from that of the past rain event to that of the heartwood, indicating a movement of water out of the heartwood into the sapwood (Fig. 3). These data illustrate the capacity of heartwood to relinquish water during periods when no rain occurs (no surface water source) or during periods of water deficit. Thus, stable isotopic approaches provided valuable insights into water movement through these plants.

DEEP WATER UTILIZATION BY PERENNIAL VEGETATION

If the long-term stability of a water source is a major factor influencing the survival of plants in natural ecological situations, individuals capable of utilizing deeper soil layers should be favoured over those solely dependent on surface soil layers, especially when exposed to water deficits. Large oscillations in water content are more likely in upper surface layers by either evaporation or water uptake by plants than in deeper soil layers (layers likely to be buffered by ground water recharge). Any drought, regardless of its frequency, should also strongly infuence utilization of soil moisture from deeper soil layers (assuming that roots penetrate to these layers), and thus, could be a strong selective agent on water uptake characteristics in plants. While such a pattern might be expected (as shown above in the pine example), the lack of surface moisture utilization by plants is unexpected. Recent studies have demonstrated the lack of surface moisture utilization during summer by a number of dominant perennials in different ecosystems, regardless of their water potentials.

In a riparian ecosystem in the Intermountain West of the United States, Dawson & Ehleringer (1991) demonstrated that mature trees growing in or in close proximity to a perennial stream used little or none of that stream's water. Using hydrogen isotope analysis of source waters and the water extracted from xylem sap of different sized riparian trees, they demonstrated that the trees were not using stream water during the peak of the growing season, but instead used ground water (Fig. 4). Our interpretation of these data is that for riparian trees inhabiting arid or semi-arid regions of the world, surface water sources (streams or precipitation) may be of limited importance to the long-term summer water balance because they are unreliable, while ground water represents a more reliable water source. If utilized, ground water could have a significant impact on rooting patterns and plant water relations. This hypothesis suggests primary investment in the development of a single root system penetrating to deeper, more reliable, water sources could represent a higher survival probability, even for riparian trees, than allocating carbon to

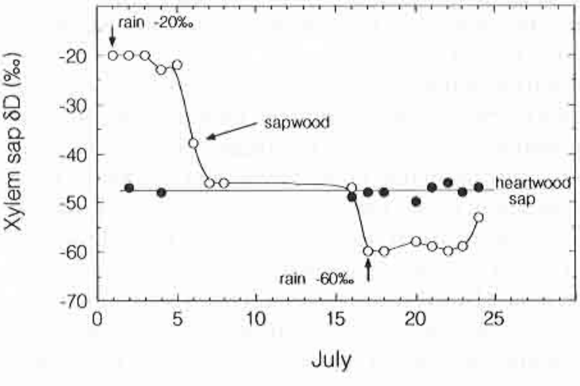

Figure 3. Time course of the hydrogen isotope ratio of xylem sap in eastern white pine (*Pinus strobus*) growing on a dry site following two summer rain events which differed in their hydrogen isotope ratio. Shown also is the time course of the hydrogen isotope ratio of heartwood sap; based on data from White *et al.* (1985).

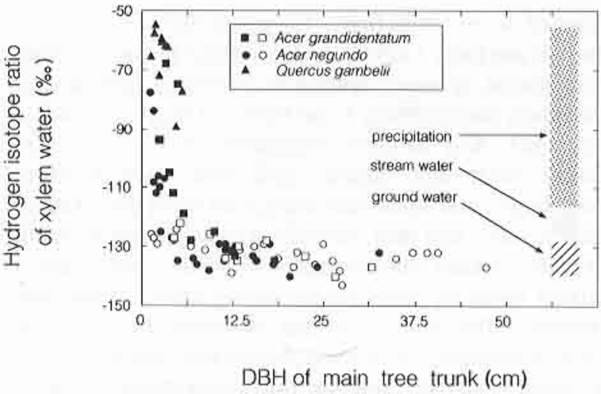

Figure 4. The hydrogen isotope ratio of xylem sap of three tree species as a function of tree size. Trees were sampled in Red Butte Canyon, Utah, during the summer growing season. Trees were growing immediately adjacent to a stream (○) or away from the stream (●). Shown also are the long-term spring and summer values for possible water sources: local precipitation, stream water and ground water. Based on data from Dawson & Ehleringer (1991).

develop both surface and deep roots, if availability of moisture in surface layers is variable.

Recently, two other studies have confirmed these patterns in different ecosystems. Busch, Ingraham & Smith (1992), studying the dominant riparian trees (*Populus fremontii*, *Salix goodingii* and *Tamarix ramosissima*) along the Colorado River in the western United States, and Thorburn, Walker & Hatton (1992), studying *Eucalyptus camaldulensis* along the flood plains of the River Murray in Australia, found that riparian trees were using ground water and not surface stream water. Smith *et al.* (1991) evaluated water sources for a number of species along and near a small perennial montane creek inn the eastern Sierra Nevada of California. Early in the season, the mean δD values suggested that upper surface layers were utilized by the species under investigation; later in the season, ground water was the primary water source.

Riparian habitats can experience large changes in stream discharge rates during the lifetime of most trees. For instance, the courses of streams and rivers often change during major flood events and discharge rates can become quite low or cease all together during extreme droughts. If riparian trees were entirely dependent on surface moisture, their life expectancy might be determined by the time between stream course changes. To persist through such fluctuations in surface moisture availability, utilization of moisture from deep layers may be a necessity. The isotopic studies cited above show that these riparian species were utilizing soil moisture from deeper soil layers. What was perhaps unexpected is the apparent lack of utilization of surface or stream water by mature riparian trees during the growing season.

SUMMER SOIL MOISTURE UTILIZATION

In most parts of the world, precipitation input is highly seasonal. Where there is a strong summer/winter bimodality to that precipitation, stable isotopes provide a valuable tool for assessing capacity to take up recent moisture inputs. If summer moisture is a small fraction of total annual precipitation (for instance, in Mediterranean climates and many interior regions), then plants might not be expected to utilize much of these infrequent precipitation events. That is, in regions with dry summers, carbon may be allocated for root growth in such a way that active roots for water uptake are not maintained in the surface layers, but occur only in deeper soil layers where moisture is most reliable during summer periods. When infrequent summer precipitation events do occur, the lack of an active upper root layer would prevent water uptake from that layer. As average summer precipitation increases along a precipitation cline, at some point precipitation becomes sufficiently predictable, or achieves some minimal threshold, so that plants develop a dimorphic root system (Fig. 5) consisting of two zones of active roots, one in the upper soil layers capturing summer precipitation and a second deeper zone for utilizing the more reliable ground water. The presence of a dimorphic root system depends upon the predictability of moisture sources, and the costs associated with producing and maintaining these roots. Although fine root turnover at a high rate may represent a significant cost to plants in their carbon balance, differential root development for water uptake could put plants at a selective advantage if the reliability of surface moisture is variable. Nonetheless, some roots may remain active near the surface, because of their role in active mineral nutrient uptake rather than water uptake *per se* (functional specialization).

Flanagan & Ehleringer (1991) evaluated water uptake patterns in a semi-arid pinyon-juniper ecosystem site in southern Utah, which received between 30 and 40% of its annual moisture during the summer months. *Chrysothamnus nauseosus* (rabbitbrush) and *Juniperinus*

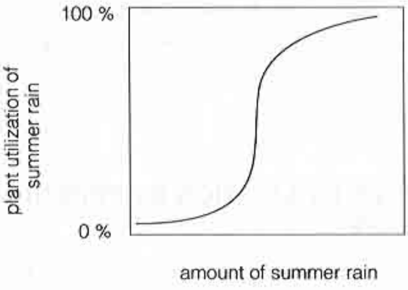

Figure 5. A conceptual model of the relationship between amount or predictability of summer precipitation and plant utilization of that summer precipitation in climates where both winter-spring and summer precipitation are received.

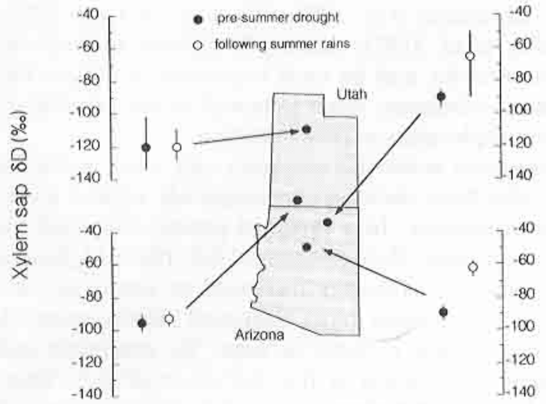

Figure 6. The hydrogen isotope ratio of xylem sap of populations of juniper trees measured in early summer before summer rains occurred and then after the summer rains have fallen. Data were collected from four sites in Utah and Arizona and represent a north-south gradient of increasing fraction of summer rainfall. Circles represent mean values and the vertical bar represents the range of values at that site. Based on data in Gregg (1991).

osteosperma (Utah juniper) did not utilize summer precipitation during the year of study: the δD of xylem sap remained close to that of the ground water (effectively the same as the winter recharge precipitation). In contrast, *Pinus edulis* (pinyon pine) and *Artemisia tridentata* (sagebrush) did utilize summer precipitation. In a follow up study, Flanagan, Ehleringer & Marshall (1992) showed that the Utah juniper would take up summer precipitation in some situations, but that the xylem sap of the rabbitbrush retained the same δD as the ground water source.

Gregg (1991) provided evidence of a cline in the capacity of juniper trees to respond to summer moisture. Along a geographical gradient, where the fraction of summer precipitation varied between 18 and 40%, Gregg (1991) observed that juniper trees on sites with reliable summer precipitation utilized summer precipitation, whereas those on predictably dry summer sites did not respond to summer precipitation (Fig. 6). It is not surprising that there is ecotypic variation in root structure along a geographical gradient, but the suggestion of a lack of an inducible response to summer rains (Gibson & Nobel 1986) by these aridland plants is unusual. In a related study from the Mediterranean-climate macchia of Italy, Valentini, Scarascia Mugnozza & Ehleringer (1992) observed that *Pistacia lentiscus*, *Phyllirea angustifolia* and *Quercus ilex* responded to summer precipitation, whereas *Q. pubescens* and *Q. cerris* did not. Species that did not respond to summer precipitation had xylem sap δD values equivalent to that of the ground water even after a summer rain event.

Another example of differential species response to summer precipitation was given by Ehleringer *et al.* (1991) in an investigation of water sources of desert species in southern Utah, at a site which received 45% of the annual precipitation during the summer. Whereas the annual species and the single CAM succulent species within the desert community responded and fully utilized summer moisture inputs, that was not the case for perennial species (Fig. 7). Herbaceous species utilized summer precipitation more than woody perennials, and a number of perennials appeared not to utilize summer precipitation at all. Moisture at deeper depths was derived primarily from winter and spring recharge events, and this was reflected in the observed ground water δD values. Spring measurements of water sources confirmed that all species were using the same water source at that time. Thus, it appears that annual, herbaceous and perennial species within the community compete for the same limiting source of water in one growing season (spring), but that herbaceous species have preferential access to a second water source (surface moisture) during the summer growing season.

RELATIONSHIPS BETWEEN WATER SOURCE AND WATER-USE EFFICIENCY

Competition only occurs if a resource, such as water, is present in limited quantities. Thus, the efficiency with which water is used is likely to be dependent on the availability of that resource and on the potential competition for that resource. Water-use efficiency (ratio of photosynthesis to transpiration) should be inversely related to availability and/or reliability of a water source (Farquhar, Ehleringer & Hubick 1989). Using carbon

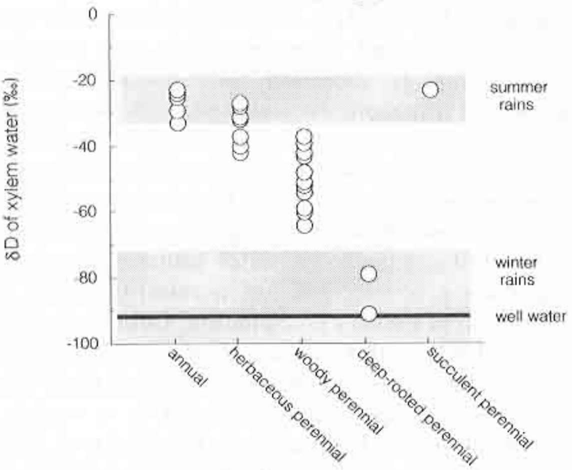

Figure 7. The hydrogen isotope ratio of xylem sap for different species (categorized by life form) at a desert site in southern Utah following summer rains. The gray areas represent the range of hydrogen isotope ratios for both summer and winter rain events. The solid line represents the hydrogen isotope ratio of ground water at this site. Based on a figure and data in Ehleringer *et al.* (1991).

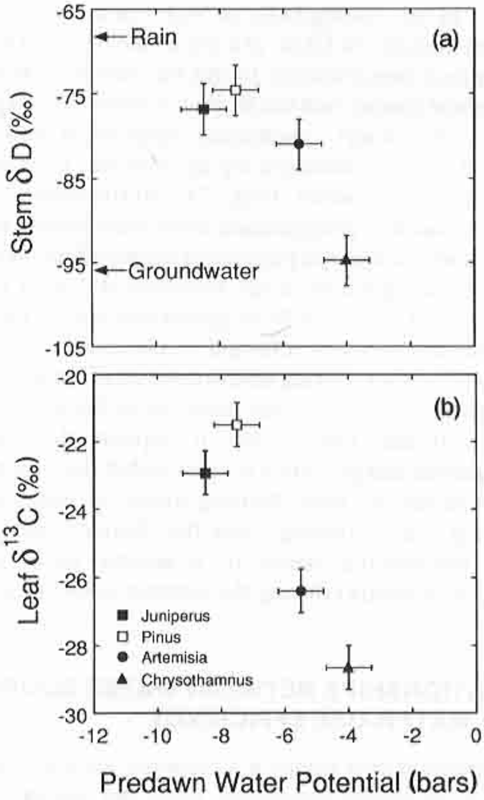

Figure 8. (a) The hydrogen isotope ratio of xylem sap versus predawn leaf water potential for four dominant perennials in a pinyon-juniper woodland in southern Utah following summer rains. (b) The leaf carbon isotope ratio (a measure of water-use efficiency) of those four species also as a function of predawn leaf water potential. Based on a figure in Flanagan *et al.* (1992).

isotope discrimination to estimate long-term water-use efficiency, Ehleringer *et al.* (1991) observed that water-use efficiency and water potential were negatively related; that is, increased water-use efficiency was associated with more stressed plants with more negative water potentials. While reduced water-use efficiency was also correlated with utilization of summer rains, the repeated negative correlation between water potential and water-use efficiency during spring growth, when all plants utilized the same water source, suggests that water-use efficiency was not necessarily linked with utilization of summer precipitation. DeLucia & Schlesinger (1991) and Flanagan *et al.* (1992) have also observed a negative relationship between plant water-use efficiency and water potential in a variety of perennial species. In the study by Flanagan *et al.* (1992), one of the species (*Chrysothamnus nauseousus*) was phreatophytic and did not utilize any summer precipitation; this species had the lowest water-use efficiency (Fig. 8). These data add further to a growing body of evidence showing that life expectancy is inversely related to water-use efficiency across a range of agricultural and ecological situations (Ehleringer & Cooper 1988; Ehleringer *et al.* 1990; Ehleringer & Cook 1991; Smedley *et al.* 1991), making it difficult to evaluate which variables may be most important in influencing water-use efficiency, water potential or life expectancy without exploratory experimentation.

Long-term water-use efficiency and water potential have also been shown to be negatively related under saline conditions. In a series of papers, Guy and his coworkers (Guy, Reid & Krouse 1980, 1986a,b) showed that water-use efficiency increased as plants became more water stressed under increased salinity stress. A similar situation is likely to occur for mangrove and hammock vegetation at the marine–freshwater interface. Using both hydrogen and oxygen isotope ratios of xylem sap, Sternberg & Swart (1987) and Sternberg *et al.* (1991) have shown differential utilization of sea water and fresh water by different species within these adjacent plant communities. In all species, there was a significant relationship between the isotopic composition of water in the xylem sap and leaf water potential. The more negative water potentials were associated with plants that used sea water as a water source. Andrews, Clough & Muller (1984), Rodelli *et al.* (1984), and Goldstein *et al.* (1989) have also measured the carbon isotope composition of leaves of mangroves and demonstrated that water-use efficiency (as estimated by carbon isotope ratio) was greater in those species occupying the more saline habitats, consistent with the above studies by Sternberg and colleagues.

While it would facilitate our understanding of water relations if there were always a relationship between water source and water potential, the results of Smith *et al.* (1991) suggest caution. In their study, there were no changes in predawn water potential, yet there was a gradual change from surface water to ground water sources. Furthermore, differences among species in water potential could arise from differences in hydraulic conductivity of xylem (Tyree & Sperry 1989) and have very little to do with the source of water. In such cases, plants could be utilizing the same water source, but operating at very different leaf water potentials because of differences in transpiration rate, xylem structure or leaf elastic/osmotic properties.

WATER SOURCE INFORMATION IN TREE RINGS

Variation in the hydrogen and oxygen isotopic composition of cellulose from tree rings has been shown in numerous studies (Schiegl 1974; Gray & Thompson 1976; Epstein, Thompson & Yapp 1977; Fehri & Letolle 1979; Burk & Stuiver 1981; Gray & Song 1984; Edwards & Fritz 1986). Early in these studies, it became clear that some of the hydrogen in cellulose was exchangeable and that only nitrated cellulose was useful for environmental reconstruction (Epstein, Yapp & Hall 1976; Epstein *et*

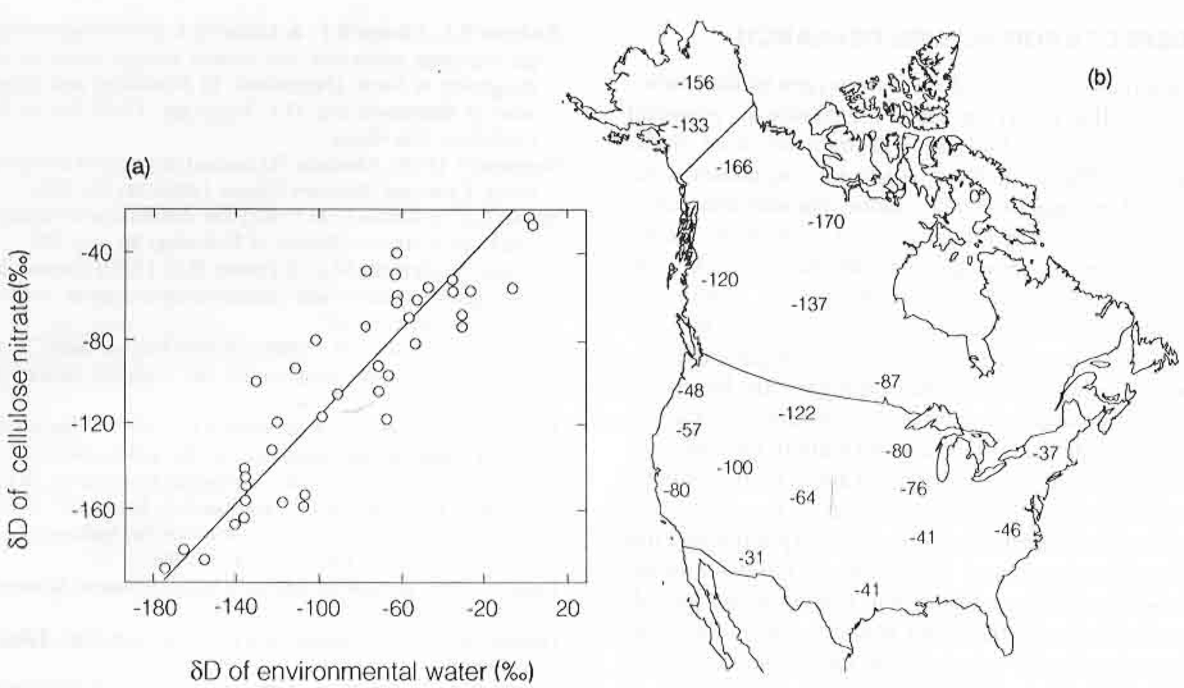

Figure 9. (a) The correlation between hydrogen isotope ratio of cellulose nitrate of tree rings of selected tree species and the hydrogen isotope ratio of local precipitation. Based on a figure in Yapp & Epstein (1982b). (b) The distribution of hydrogen isotope ratios in cellulose nitrate of tree rings of selected tree species across North America. Based on a figure in Yapp & Epstein (1982a).

al. 1977). Temperature, humidity and other environmental variables have been suggested as contributing to this variation. Epstein and his colleagues (Epstein & Yapp 1976; Yapp & Epstein 1982a,b) suggested that precipitation (environmental water) was the primary variable contributing to the isotopic composition of tree ring cellulose (Fig. 9). While the correlation between precipitation and isotopic composition is strong, it is important to note that no studies to date have continuously monitored both xylem sap and tree-ring cellulose isotopic composition over extended periods. Whereas Yapp & Epstein (1982a,b) observed a good correlation between δD of environmental water and tree-ring cellulose, they also noted that the correlation between δD of cellulose and temperature across sites varied by 5·8‰ °C^{-1}, similar to the variation observed on a global scale for precipitation of 5·6‰ °C^{-1}. The correlation between cellulose δD values and temperature has been confirmed by Gray & Song (1984), who found a slope of 5·5‰ °C^{-1}.

White (1983) measured cellulose nitrate values of tree rings over a 4-year period, during which he also monitored the isotopic composition of summer rain. For trees occurring on dry sites, he found a 1:1 correlation between δD of cellulose nitrate and precipitation. On a wet site, data appeared to deviate most from the 1:1 line during years with heavy spring precipitation, possibly indicating greater utilization of spring recharge during those summers. Further studies of plants inhabiting regions where precipitation falls at two distinct times of the year and phreatophytic plants should help clarify the roles of water source and temperature on the isotopic composition of tree ring cellulose.

The observations of cellulose δD values and precipitation by Yapp & Epstein (1982a,b) show variation about the 1:1 line. This variation may result in part from differences in the seasonal source of water, from contamination by transpiration-enriched water, or from fractionation processes during cellulose formation. Yapp & Epstein (1982a) found that the apparent fractionation between environmental water and cellulose was strongly correlated with humidity (possibly an indicator of the seasonality of precipitation). The biochemical bases of any hydrogen fractionating during cellulose formation are unclear at this time and appear to be either non-existent for stem tissues (as indicated above) or variable within leaf tissues among species (see Yakir chapter in this issue). On the other hand, the process of oxygen isotope fractionation is better understood, and fractionation appears to be 27‰ for all species examined to date (Sternberg & DeNiro 1983; Sternberg, DeNiro & Savidge 1986; Sternberg 1988; Yakir & DeNiro 1990). Thus, while there is a correlation between isotopic composition of precipitation and both δD and δ^{18}O of cellulose, the better mechanistic understanding of oxygen isotope fractionating at present might allow a more quantitative reconstruction of environmental water sources.

PROSPECTS FOR FUTURE RESEARCH

The analysis of either hydrogen or oxygen isotope ratios in water within the xylem sap of plants offers a powerful tool for understanding the dynamics of plant water utilization. These analyses, made in conjunction with studies of leaf gas exchange, water relations characteristics and water-use efficiency, can provide a deeper understanding of how patterns of water uptake can influence patterns of plant performance. Nothing is particularly new about the technology that has not already been previously known by isotope geochemists. However, what is new is that biologists are becoming increasingly aware of how stable isotope analyses at natural abundance levels can contribute to both instantaneous and integrated information about plant performance. Carbon isotopes in organic matter (leaves and tree rings) are providing information on both plant water-use efficiency and stomatal limitations to photosynthesis. Hydrogen and oxygen isotopes in xylem sap are providing information on the water source used by the plant without destructive belowground sampling; analyses of tree rings provide equivalent long-term information. In the near future, it is evident that such isotopic analyses will provide new ecological insights into potential competitive interactions among species in a community, linkages between efficiency of water-use and specific water sources, and linkges between plant performance and landscape hydrology. Quantitative temporal measures of both water sources used by plants and plant water-use efficiency under natural conditions provide an approach through which the impact of episodic events (e.g. droughts and flooding) can be directly assessed.

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REFERENCES

Allison G.B. & Hughes M.W. (1983) The use of natural tracers as indicators of soil-water movement in a temperate semi-arid region. *Journal of Hydrology* **60,** 157–173.

Allison G.B., Barnes C.J. & Hughes M.W. (1983) The distribution of deuterium and ^{18}O in dry soil. *Experimental Journal of Hydrology* **64,** 377–397.

Allison G.B., Barnes, C.J., Hughes M.W. & Leaney F.W.J. (1984) Effect of climate and vegetation on oxygen-18 and deuterium profiles in soils. In *Isotope Hydrology*, pp. 105–122. IAEA, Vienna.

Andrews T.J., Clough B.F. & Muller G.J. (1984) Photosynthetic gas exchange properties and carbon isotope ratios of some mangroves in North Queensland. In *Physiology and Management of Mangroves* (ed. H.J. Teas), pp. 15–23. Dr W. Junk Publishers, The Hague.

Baertschi P. (1976) Absolute ^{18}O content of standard mean ocean water. *Earth and Planetary Science Letters* **31,** 341–344.

Barnes C.J. & Allison G.B. (1983) The distribution of deuterium and O-18 in dry soil. *Journal of Hydrology* **60,** 141–156.

Bigeleisen J., Perlman M.L. & Prosser H.C. (1952) Conversion of hydrogen materials to hydrogen for isotopic analysis. *Analytical Chemistry* **24,** 1356–1357.

Burk R.L. & Stuiver M. (1981) Oxygen isotope ratios in trees reflect mean annual temperature and humidity. *Science* **211,** 1417–1419.

Busch D.E., Ingraham N.L. & Smith S.D. (1992) Water uptake in woody riparian phreatophytes of the southwestern United States: a stable isotope study. *Ecological Applications*, in press.

Coleman M.L., Shepherd T.J., Durham J.J., Rouse J.E. & Moore G.R. (1982) Reduction of water with zinc for hydrogen isotope analysis. *Analytical Chemistry* **54,** 993–995.

Craig H. (1961) Isotopic variations in meteoric waters. *Science* **133,** 1702–1703.

Dansgaard W. (1964) Stable isotopes in preciptation. *Tellus* **16,** 436–468.

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

DeLucia E.H. & Schlesinger W.H. (1991) Resource-use efficiency and drought tolerance in adjacent Great Basin and Sierran plants. *Ecology* **72,** 51–58.

Dongmann G., Nurnberg H.W. & Wagner K. (1974) On the enrichment of $H_2{}^{18}O$ in the leaves of transpiring plants. *Radiation and Environmental Biophysics* **11,** 41–52.

Edwards T.W.D. & Fritz P. (1986) Assessing meteoric water composition and relative humidity from ^{18}O and ^{2}H in wood cellulose: paleoclimatic implications for southern Ontario, Canada. *Applied Geochemistry* **1,** 715–723.

Ehleringer J.R. & Cook C.S. (1991) Carbon isotope discrimination and xylem D/H ratios in desert plants. In *Stable Isotopes in Plant Nutrition, Soil Fertility, and Environmental Studies*, pp. 489–497. IAEA, Vienna.

Ehleringer J.R. & Cooper T.A. (1988) Correlations between carbon isotope ratio and microhabitat in desert plants. *Oecologia* **76,** 562–566.

Ehleringer J.R. & Osmond C.B. (1989) Stable isotopes. In *Plant Physiological Ecology Field Methods and Instrumentation* (eds R.W. Pearcy, J.R. Ehleringer, H.A. Mooney & P.W. Rundel), pp. 281–300. Chapman and Hall Ltd, London.

Ehleringer J.R., Phillips, S.L., Schuster W.F.S. & Sandquist D.R. (1991) Differential utilization of summer rains by desert plants: implications for competition and climate change. *Oecologia* **88,** 430–434.

Ehleringer J.R., White J.W., Johnson D.A. & Brick M. (1990) Carbon isotope discrimination, photosynthetic gas exchange, and water-use efficiency in common bean and range grasses. *Acta Oecologia* **11,** 611–625.

Epstein S., Thompson P. & Yapp C.J. (1977) Oxygen and hydrogen isotopic ratios in plant cellulose. *Science* **198,** 1209–1215.

Epstein S., Yapp C.J., & Hall J.H. (1976) The determination of the D/H ratio of non-exchangeable hydrogen in cellulose extracted from aquatic and land plants. *Earth and Planetary Science Letters* **30,** 241–251.

Epstein S. & Yapp C.J. (1976) Climatic implications of the D/H ratio of hydrogen in C-H groups of tree cellulose. *Earth and Planetary Science Letters* **30,** 252–260.

Farquhar G.D., Ehleringer J.R. & Hubick K.T. (1989) Carbon isotope discrimination and photosynthesis. *Annual Review of Plant Physiology and Molecular Biology* **40,** 503–537.

Fehri A. & Letolle R. (1979) Relation entre le milieu climatique et les teneurs en oxygène-18 de la cellulose des plantes terrestres. *Physiologia Vegetale* **17,** 107–117.

Ferronsky V.I. & Polyakov V.A. (1982) *Environmental Isotopes in the Hydrosphere.* John Wiley & Sons, Chichester.

Flanagan L.B. & Ehleringer J.R. (1991) Stable isotope composition of stem and leaf water: applications to the study of plant water-use. *Functional Ecology* **5,** 270–277.

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

Fontes J.C. (1980) Environmental isotopes in groundwater hydrology. In *Handbook of Environmental Isotope Geochemistry. Volume 1. The Terrestrial Environment* (eds P. Fritz & J.C. Fontes), pp. 75–140. Elsevier, Amsterdam.

Friedman I., Redfield A.C., Schoen B. & Harris J. (1964) The variation of the deuterium content of natural waters in the hydrologic cycle. *Reviews in Geophysics* **2,** 177–224.

Gat J.R. (1980a) Groundwater. In *Stable Isotope Hydrology Deuterium and Oxygen-18 in the Water Cycle* (eds J.R. Gat & R. Gonfiantini), pp. 223–240. IAEA Technical Series Report Number 210, Vienna.

Gat J.R. (1980b) The isotopes of hydrogen and oxygen in precipitation. In *Handbook of Environmental Isotope Geochemistry. Volume 1. The Terrestrial Environment* (eds P. Fritz & J.C. Fontes), pp. 21–47. Elsevier, Amsterdam.

Gibson A.C. & Nobel P.S. (1986) *The Cactus Primer.* Harvard University Press, Cambridge, MA.

Goldstein G., Rada F., Sternberg L., Burguera J.L., Burguera M., Orozco A., Montilla M., Zabala O., Azocar A., Canales M.J. & Celis A. (1989) Gas exchange and water balance of a mistletoe species and its mangrove hosts. *Oecologia* **78,** 176–183.

Gray J. & Song S.J. (1984) Climatic implications of the natural variations of D/H ratios in tree ring cellulose. *Earth and Planetary Science Letters* **70,** 129–138.

Gray J. & Thompson P. (1976) Climatic information from $^{18}O/^{16}O$ ratios of cellulose from tree rings. *Nature* **263,** 481–482.

Gregg J. (1991) *The differential occurrence of the mistletoe,* Phoradendron juniperinum, *on its host,* Juniperus osteosperma *in the Western United States.* M.Sc. Thesis, University of Utah, Salt Lake City, UT.

Guy R.D., Reid D.M. & Krouse H.R. (1980) Shifts in carbon isotope ratios of two C_3 halophytes under natural and artificial conditions. *Oecologia* **44,** 241–247.

Guy R.D., Reid D.M. & Krouse H.R. (1986a) Factors affecting $^{13}C/^{12}C$ ratios of inland halophytes. I. Controlled studies on growth and isotopic composition of *Puccinellia nuttalliana. Canadian Journal of Botany* **64,** 2693–2699.

Guy R.D., Reid D.M. & Krouse H.R. (1986b) Factors affecting $^{13}C/^{12}C$ ratios of inland halophytes. II. Ecophysiological interpretations of patterns in the field. *Canadian Journal of Botany* **64,** 2400–2407.

Hagemann R., Nief G. & Roth E. (1970) Absolute isotopic scale for deuterium analysis of natural waters. Absolute D/H ratio for SMOW. *Tellus* **23,** 712–715.

Ingraham N.L. & Matthews R.A. (1988) Fog drip as a source of groundwater recharge in Northern Kenya. *Water Resources Research* **24,** 1406–1410.

Ingraham N.L. & Matthews R.A. (1990) A stable isotopic study of fog: the Point Reyes Peninsula, California, USA. *Chemical Geology (Isotope Geoscience Section)* **80,** 281–290.

Ingraham N.L. & Taylor B.E. (1991) Light stable isotope systematics of large-scale hydrologic regimes in California and Nevada. *Water Resources Research* **27,** 77–90.

Leaney F.W., Osmond C.B., Allison G.B. & Ziegler H. (1985) Hydrogen-isotope composition of leaf water in C_3 and C_4 plants: its relationship to the hydrogen-isotope composition of dry matter. *Planta* **164,** 215–220.

Rodelli M.R., Gearing J.N., Gearing P.J., Marshall N. & Sasekumar A. (1984) Stable isotope ratio as a tracer of mangrove carbon in Malaysian ecosystems. *Oecologia* **61,** 326–333.

Rozanski K., Sonntag C. & Münnich K.O. (1982) Factors controlling stable isotope composition of European precipitation. *Tellus* **34,** 142–150.

Rundel P.W., Dillon M.O., Palma B., Mooney H.A., Gulmon S.L. & Ehleringer J.R. (1991) The phytogeography and ecology of the coastal Atacama and Peruvian Deserts. *Aliso* **13,** 1–49.

Schiegl W.E. (1974) Climatic significance of deuterium abundance in growth rings of *Picea. Nature* **251,** 582–584.

Siegenthaler U. & Oeschger H. (1980) Correlation of ^{18}O in precipitation with temperature and altitude. *Nature* **285,** 314–317.

Smedley M.P., Dawson T.E., Comstock J.P., Donovan L.A., Sherrill D.E., Cook C.S. & Ehleringer J.R. (1991) Seasonal carbon isotopic discrimination in a grassland community. *Oecologia* **85,** 314–320.

Smith S.D., Wellington A.B., Nachlinger J.L. & Fox C.A. (1991) Functional responses of riparian vegetation to streamflow diversion in the eastern Sierra Nevada. *Ecological Applications* **1,** 89–97.

Sternberg L.S.L. (1988) Oxygen and hydrogen isotope ratios in plant cellulose: mechanism and applications. In *Stable Isotopes in Ecological Research* (eds P.W. Rundel, J.R. Ehleringer & K.A. Nagy), pp. 124–141. Springer-Verlag, New York, NY.

Sternberg L.S.L., Ish-Shalom-Gordon N., Ross M. & O'Brien J. (1991) Water relations of coastal plant communities near the ocean/freshwater boundary. *Oecologia* **88,** 305–310.

Sternberg L.S.L. & DeNiro M.J. (1983) Biogeochemical implications of the isotopic equilibrium fractionating factor between the oxygen atoms of acetone and water. *Geochimica et Cosmochimica Acta* **47,** 2271–2274.

Sternberg L.S.L., DeNiro M.J. & Savidge R.A. (1986) Oxygen isotope exchange between metabolites and water during biochemical reactions leading to cellulose synthesis. *Plant Physiology* **82,** 423–427.

Sternberg L.S.L. & Swart P.K. (1987) Utilization of fresh water and ocean water by coastal plants of southern Florida. *Ecology* **68,** 1898–1905.

Taylor H.P. (1974) The application of oxygen and hydrogen stable isotope studies to problems of hydrothermal alterations and ore deposition. *Economic Geology* **69,** 843–883.

Thorburn P., Walker G. & Hatton T. (1992) Are river red gums taking water from soil, groundwater or streams? In *Catchments of Green*, pp. 37–42. National Conference on Vegetation and Water Management, Adelaide.

Tyree M.T. & Sperry J.S. (1989) Vulnerability of xylem to cavitation and embolism. *Annual Review of Plant Physiology and Molecular Biology* **40,** 19–38.

Wershaw R.L., Friedman I. & Heller S.J. (1966) Hydrogen isotope fractionation of water passing through trees. In *Advances in Organic Geochemistry* (eds G.D. Hobson & G.C. Speers), pp. 55–67. Pergamon Press, Oxford.

White J.W.C. (1983) *The climatic significance of D/H ratios in white pine in the northeastern United States.* Ph.D. Thesis, Columbia University.

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

Wong W.W., Lee L.S. & Klein P.D. (1987) Oxygen isotope ratio measurements on carbon dioxide generated by reaction of microliter quantities of biological fluids with guanidine hydrochloride. *Analytical Chemistry* **59,** 690–693.

Valentini R., Scarascia Mugnozza G.E. & Ehleringer J.R. (1992) Hydrogen and carbon isotope ratios of selected species of a mediterranean macchia ecosystem. *Functional Ecology* **6,** 627–631.

Yakir D. & DeNiro M.J. (1990) Oxygen and hydrogen isotope fractionation during cellulose metabolism in *Lemna gibba* L. *Plant Physiology* **93,** 325–332.

Yapp C.J. & Epstein S. (1982a) Climatic significance of the hydrogen isotope ratios in tree cellulose. *Nature* **297,** 636–639.

Yapp C.J. & Epstein S. (1982b) A reexamination of cellulose carbon-bound hydrogen δD measurements and some factors affecting plant-water D/H relationships. *Geochimica et Cosmochimica Acta* **46,** 955–965.

Yurtsever Y. & Gat J.R. (1980) Stable isotopes in atmospheric waters. In *Stable Isotope Hydrology Deuterium and Oxygen-18 in the Water Cycle* (eds J.R. Gat & R. Gonfiantini), pp. 103–142. IAEA Technical Series Report Number 210, Vienna.

Zundel G., Miekeley W., Grisi B.M. & Förstel H. (1978) The $H_2{}^{18}O$ enrichment of leaf water of tropic trees: comparison of species from the tropical rain forest and the semi-arid region in Brazil. *Radiation and Environmental Biophysics* **15,** 203–212.

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