139

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CARBON ISOTOPE DISCRIMINATION AND XYLEM HYDROGEN ISOTOPE RATIOS IN DESERT PLANTS

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Abstract

CARBON ISOTOPE DISCRIMINATION AND XYLEM HYDROGEN ISOTOPE RATIOS IN DESERT PLANTS.

Stable isotopic compositions of plant materials were used to address the question of whether variations in water use efficiency were related to possibly different soil moisture sources for common desert perennials in the Sonoran Desert of North America. Leaf carbon isotope discrimination values were used to estimate long term water use efficiency (molar ratio of photosynthesis to transpiration). Soil moisture sources were estimated from D/H ratios of stem waters. Carbon isotope discrimination varied significantly among species within the community, with the highest discrimination values occurring in short lived perennials. Long lived perennials had the lowest carbon isotope discrimination values. Substantial variation also occurred in the xylem D/H ratios, indicating that groups of species were utilizing soil water from different depths within the soil profile. Midday leaf water potential values and D/H ratios in xylem waters were not correlated across species, indicating that leaf water potential alone is not a reliable indicator of the depth in the soil from which a species is extracting water. The variation in carbon isotope discrimination, and thus presumably also in water use efficiency, was not related to the water source used by a species. Leaf type or leaf duration appeared also not to be correlated with either water source or carbon isotope discrimination. Rather it appeared that tree species and shrub species (irrespective of longevity) were utilizing different soil moisture regimes in this habitat. The life expectancy (longevity) of a species was negatively correlated with its carbon isotope discrimination values, suggesting that longer lived species are more conservative in their use of water. In addition, the likelihood of a species utilizing summer precipitation was also inversely proportional to longevity, indicating the more opportunistic nature of shorter lived perennials.

1. INTRODUCTION

Growth and reproduction of plants in arid zones are very much affected by water availability [1]. Since the pioneering studies of Briggs and Shantz [2], there has been a continued interest in relationships between water consumption and growth under arid land conditions, and in particular in the possible role of water use efficiency in the adaptation of different species to droughted conditions. Water use efficiency is the ratio of productivity to water loss by a plant. It is defined on an instantaneous basis as the molar ratio of photosynthesis to transpiration or over the long term as the ratio of biomass produced to water consumed (often termed transpiration efficiency) [3].

A major limitation to progress in our understanding of water use efficiency had been adequate methods for assessing this parameter on large numbers of plants. A major breakthrough occurred when Farquhar and colleagues [4] showed that, on a theoretical basis, carbon isotopic composition ($^{13}C/^{12}C$) should be correlated with both short term and long term integrated estimates of water use efficiency. Since that time, numerous studies have demonstrated that carbon isotope discrimination (Δ) is a reliable indicator of water use efficiency and that there is substantial genetic variation in this character [3] (see paper by Farquhar at this symposium for a further description of Δ [5]).

Our interest was in exploring possible variations in the efficiency of water use among different species in a natural arid land setting through analyses of carbon isotope discrimination. Is it possible that interspecific differences in this character existed among members of the plant community and that they were related to aspects of community structure? Secondly, is it possible that water sources were partitioned within the community and that water use efficiency of different component species was related to water availability? Addressing questions of the water source utilized by plants had proved difficult to evaluate but recent studies [6–8] have shown that there is no fractionation of isotopes during water uptake by roots and therefore the hydrogen isotope ratios (δD) of stem waters are a reliable indicator of the water source(s) being utilized by a plant.

2. METHODS AND STUDY SITE

All studies were conducted on native Sonoran Desert vegetation 9 km west of Oatman, Arizona, United States of America (latitude 34°57′ N, longitude 114°25′ W). This site, typical of the Colorado Desert subdivision of the Sonoran Desert [9], consisted of an active wash microsite, an adjacent shallow-soil slope microhabitat and the alluvial transition zone in between (Fig. 1). The vegetation of the area is typically a mixture of drought-deciduous herbaceous perennials, evergreen and drought-deciduous woody shrub species, and trees and subtrees which are restricted to active wash sites.

Carbon isotope discrimination (Δ) was measured on bulked, dried leaf samples from ten separate plants of each species. Carbon isotope ratios of combusted tissues [10] were converted to discrimination values [3] using an atmospheric $\delta^{13}C$ value of $-8‰$ (on the PDB scale). For hydrogen isotope ratio determination of xylem tissues, non-green stems were first vacuum distilled and then the hydrogen in

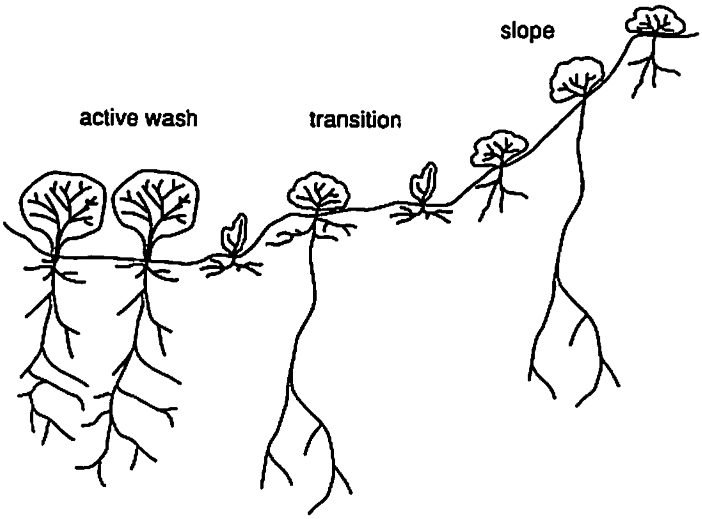

FIG. 1. Cross-section of active wash, transition and slope microhabitats in the desert. The alluvial deposits are substantially deeper in transition and active wash sites. Infrequent stream flow occurs only in the active wash sites.

extracted water was converted to diatomic hydrogen [11]. Values of δD are expressed relative to the SMOW standard. All isotopic analyses were made on a Finnigan MAT Delta S isotope ratio mass spectrometer. Leaf water potentials were measured at midday under typical spring field conditions using a Scholander type pressure chamber.

3. VARIATION IN CARBON ISOTOPE DISCRIMINATION

Carbon isotope discrimination was measured on the dominant species in the active wash, transition and slope microhabitats (Fig. 1), which in effect formed a decreasing water availability gradient because of differences in soil depth. Over a 6‰ difference in Δ occurred among species occupying this gradient (Fig. 2). Carbon isotope discrimination was positively correlated with expected soil moisture availability, indicating that species in wetter microhabitats had lower water use efficiencies. Leaf type or leaf duration appeared also not to be correlated with either water source or carbon isotope discrimination. Of ecological interest, Δ values of species within a microhabitat were inversely related to the life expectancy of the shrub [12]. Longer lived species were more conservative in their efficiency of water use than shorter lived species. Even though there was environmental variation in Δ associated with differences in microhabitat, the inverse relationship between Δ and

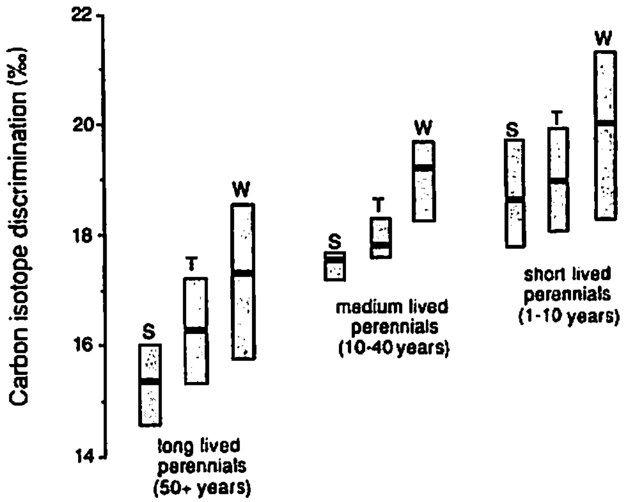

FIG. 2. Ranges of carbon isotope discrimination values for different perennial species occupying wash (W), transition (T) and slope (S) microhabitats at Oatman, Arizona, within the Sonoran Desert. Horizontal bars indicate the average value for all species within a category. Modified from Ehleringer and Cooper [12].

life expectancy held across microhabitats. Similar negative correlations between life expectancy and Δ have recently also been observed among species in grassland communities [13] and between cultivars of common bean [14].

The patterning of Δ values among species was maintained through time (Fig. 3). Carbon isotope discriminations of species sampled in 1987 (a relatively wet year) were highly correlated with those later sampled in 1990 (a relatively dry year). That the slope of this relationship was less than 1 indicated that plasticity occurred in Δ in response to environmental change and that low water use efficiency species were more responsive than high water use efficiency species to the drier conditions prevailing in 1990. However, the more important observation was that the rankings or differences among species were maintained. That is, short lived perennials with a low water use efficiency became more water use efficient under drier conditions, but still did not attain as high a water use efficiency as longer lived species within the community.

4. VARIATION IN XYLEM D/H RATIOS

Given that annual precipitation appeared to have a significant impact on Δ values, we examined possible interactions between Δ, leaf water potential (a measure of water stress) and δD of stem waters (a measure of water source). Precipitation

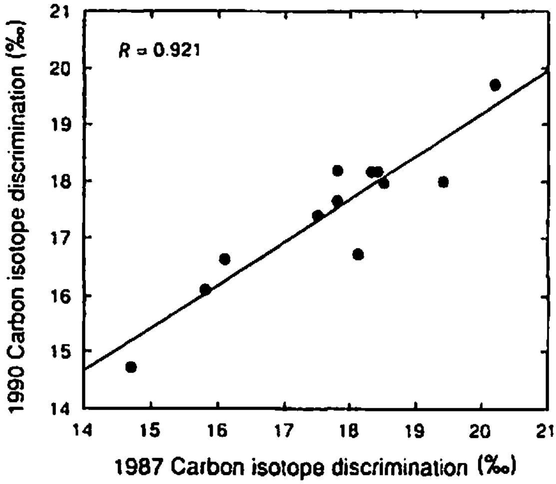

FIG. 3. Correlation between carbon isotope discrimination values measured on 12 different perennial species in 1987 and again in 1990. Data are for species occupying wash and slope microhabitats at a Sonoran Desert site near Oatman, Arizona.

in the study region falls primarily in November and March [15, 16]. These winter-spring rains have an average δD value of −100‰. Summer rains (July-September), which typically have an average δD value of −40‰, are sporadic and typically account for only about 25% of the annual precipitation. The δD of groundwaters, which averages approximately −100‰, reflects this primary winter recharge. Summer rains, however, appear to play an important role in promoting establishment of perennials and in allowing short lived perennials to persist between years [9].

The years 1987, 1988 and 1990 differed in the extent of summer precipitation, with successive years becoming progressively wetter. However, no summer rains occurred in 1989. The utilization of summer precipitation by different perennial species within the community reflected life history differences (Table I, Fig. 4). Under limited summer rains (such as in 1987), short lived perennials, presumably with a greater proportion of surface roots, utilized the summer rains, whereas long lived perennials (primarily trees) used little if any of this summer precipitation. As the intensities of the summer rains increased in the successive years, so did the utilization of this rain by different life forms. However, even under the wetter conditions of 1988 and 1990 when short lived perennials were fully utilizing summer rains as their water source, the longer lived, more conservative water use efficiency perennials were on average obtaining only 50–75% of their water from the upper soil layers.

There was no significant relationship between the water sources utilized by species within the community and the levels of water stress experienced by these

TABLE I. HYDROGEN ISOTOPE RATIOS OF COMMON PERENNIAL SPECIES FROM ACTIVE WASH AND SLOPE MICROHABITATS WEST OF OATMAN, ARIZONA, USA

Species	Life form	δD (‰)
Active wash		
Acacia greggii Gray	Winter-deciduous tree	−87 ± 3
Cassia covesii Gray	Drought-deciduous herb	−68
Cercidium floridum Benth.	Drought-deciduous tree	−83 ± 4
Chilopsis linearis (Cav.) Sweet	Winter-deciduous tree	−77 ± 3
Eriogonum inflatum T. & G.	Drought-deciduous herb	−63
Hymenoclea monogyra T. & G.	Drought-deciduous tree	−67 ± 3
Hymenoclea salsola T. & G.	Drought-deciduous shrub	−67 ± 2
Senecio douglasii DC.	Drought-deciduous shrub	−65 ± 0
Slope		
Ambrosia dumosa Gray	Drought-deciduous shrub	−65 ± 1
Encelia farinosa Gray	Drought-deciduous shrub	−59 ± 8
Ephedra viridis Cov.	Evergreen shrub	−69 ± 1
Eriogonum fasciculatum Benth.	Drought-deciduous shrub	−64
Larrea divaricata Cav.	Evergreen shrub	−67 ± 6
Sphaeralcea ambigua Gray	Drought-deciduous herb	−61 ± 7

Note: Data are means ± SD (n = 3-5) for samples collected in March 1990 at the peak of the winter season vegetative growth period, except for single sample observations.

species (Fig. 5). This result is interesting because it indicates that water potential measurements alone are not a reliable indicator of the depth from which a plant is extracting soil moisture. The lack of a significant correlation between leaf water potential and δD when species across all microhabitats are considered is likely the result of differences in the extent of canopy development and of differences in the xylem hydraulic architecture among species, both of which will influence the water stress experienced by the plant independent of water source considerations.

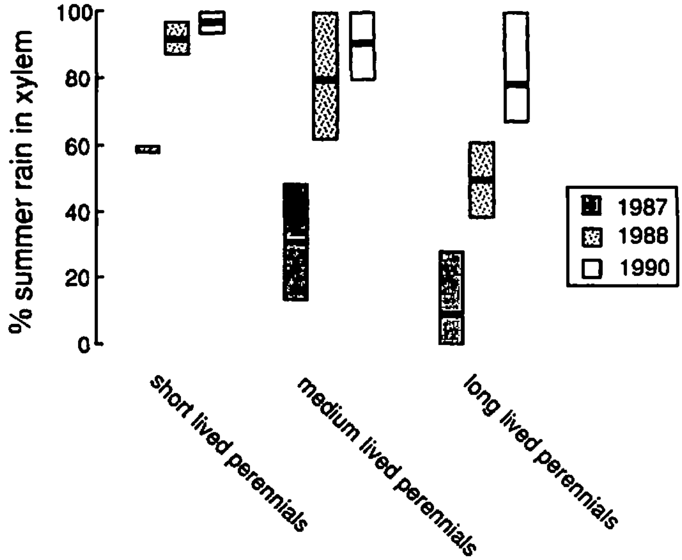

FIG. 4. Ranges of the percentage of xylem water that was derived from summer rain utilized by different categories of desert perennials at Oatman, Arizona, in 1987, 1988 and 1990. Horizontal bars indicate the average value for all species within a category. Values are calculated assuming winter and summer precipitation end points of −100 and −40‰ respectively. Data are for species occupying wash and slope microhabitats at a Sonoran Desert site near Oatman.

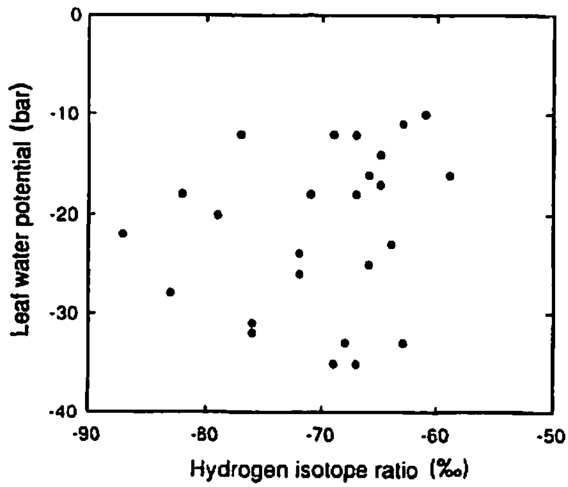

FIG. 5. Correlation between water sources utilized by a species (hydrogen isotope ratio) and the water stress experienced by that species (measured as midday leaf water potential) (1 bar = 10^5 Pa). Data are for species occupying wash and slope microhabitats at a Sonoran Desert site near Oatman, Arizona.

5. COMMUNITY STRUCTURE AND WATER USE

Together the carbon and hydrogen isotopic composition information provides new insights into the structure and possible interactions among different species in a desert community. The more conservative water use efficiency pattern of longer lived species may play a significant role in allowing these species to persist through extended drought periods, especially relative to the lower water use efficiency, shorter lived perennial species. While a priori there need not necessarily be an association between the efficiency of water use and persistence through time (and therefore tolerance of droughts), such a pattern does appear to occur in these desert perennials and this pattern appears to be maintained across years. Since it is known that there are strong competitive interactions among desert perennials [17, 18], it is possible that species-level variations in water use efficiency may play a role in allowing less water use efficient species to get established and successfully compete with established, but more water use efficient species during years of above average precipitation, only to suffer greater mortality rates during years of below average precipitation. The more conservative water use efficiency of long lived species, combined with their reduced dependence on summer precipitation, may be of fundamental importance in allowing these long lived species to persist in the highly unpredictable precipitation regimes that characterize desert environments.

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