Carbon isotope ratios of Atacama Desert plants reflect hyperaridity of region in northern Chile

Las tasas de los isótopos de carbono en plantas del Desierto de Atacama, reflejan la hiperaridez de esta zona en el norte de Chile

JAMES R. EHLERINGER[1,5], PHILIP W. RUNDEL[2,6],
BEATRIZ PALMA[3,7] and HAROLD A. MOONEY[4,8]

[1]Stable Isotope Ratio Facility for Environmental Research Department of Biology
University of Utah Salt Lake City, Utah 84112 USA
[2]Department of Biology University of California Los Angeles, California 90024, USA
[3]Ciencias Básicas, Facultad de Agronomía, Universidad de las Américas, 948 Manuel Montt, Santiago
[4]Department of Biological Sciences Stanford University Stanford, California 94305, USA
[5]E-mail:ehleringer@bioscience.utah.edu, [6]rundel@biology.ucla.edu,
[7] bpalma@uamericas.cl, [8]hamooney@jasper.stanford.edu

ABSTRACT

Leaf carbon isotope ratios were measured on plants from the coastal portions of the Atacama Desert at Pan de Azúcar and Paposo, Chile. Most species possessed C_3 photosynthesis, although there were several CAM species, indications of some facultative CAM species, and only one C_4 species. The carbon isotope ratios of the C_3 plants are unusually high, even for species from arid ecosystems. These observations indicated that C_3 species of the Atacama Desert were characterized by very low intercellular CO_2 concentration that averaged between 159 and 190 ppm, depending on the severity of the drought.

Key words: Atacama Desert, carbon isotope ratio, desert ecology, intercellular carbon dioxide concentration.

RESUMEN

Se midieron las tasas de isótopos de carbono en hojas de plantas de la región costera del Desierto de Atacama, Parque Nacional Pan de Azúcar y Paposo, Chile. La mayoría de las especies corresponden a plantas C_3; se observó numerosas especies CAM, algunas CAM facultativas y una sola especie C_4. Las tasas de isótopos de carbono son infrecuentemente altas en plantas C_3, aun en plantas de ecosistemas áridos. Estas observaciones indican que las especies C_3 del Desierto de Atacama se caracterizan por tener concentraciones muy bajas de CO_2 intercelular, entre 159 y 190 ppm, y que estos dependen de la severidad de la sequía.

Palabras clave: Desierto de Atacama, tasa de isótopos de carbono, ecologia desértica, concentración de dióxido de carbono intercelular.

INTRODUCTION

Water and plant growth are inextricably linked to each other. Nowhere are these relationships more evident than in arid lands, where primary productivity is driven by pulses of infrequent precipitation events (Noy-Meir 1973). As a consequence, primary productivity is often directly proportional to the seasonal amounts of precipitation (Hadley & Szarek 1981, Le Houeroux 1988, Turner & Randall 1989, Smith & Nowak 1990). Limited moisture availability not only constrains rates of primary productivity to those brief periods when soil moisture is adequate, but there is often a greater water-use efficiency by plants in arid zones (Ehleringer et al.

1992). That is, the ratio of photosynthesis (A) to transpiration (E) on an instantaneous basis or the ratio of biomass produced to water consumption on a long-term basis is typically greater in arid zone plants than in those from more mesic habitats (Stanhill 1986, Turner 1986, Ehleringer et al. 1992).

In recent years, numerous studies have shown that the carbon isotopic composition of leaf material in C_3 species can been used as a long-term indicator of plant water-use efficiency (Farquhar et al., 1989). Discrimination against $^{13}CO_2$ during both diffusion and CO_2 fixation processes within the leaf results in a lower ^{13}C composition in plant materials than in atmospheric CO_2. The carbon isotope ratio of a leaf ($\delta^{13}C_p$) can be described as

$$\delta^{13}C_p = \delta^{13}C_{air} - a - (b - a)\frac{c_i}{c_a}$$

where $\delta^{13}C_{air}$ is the carbon isotope ratio of the air, a is the fractionation associated with the slower diffusion of $^{13}CO_2$ through the stomata, b is the isotopic fractionation associated with RuBP carboxylation, and c_i and c_a are the intercellular and atmospheric CO_2 concentrations, respectively. The carbon isotope ratio of a leaf is related to water-use efficiency (ratio of instantaneous photosynthesis (A) to transpiration (E) in that

$$\frac{A}{E} = \frac{\left(c_a\ 1 - \frac{c_i}{c_i}\right)}{1.6v}$$

where v is the leaf-to-air water mole fraction gradient. While water-use efficiency analyses must assume that u and therefore leaf temperature are equivalent among species being compared, leaf temperatures are usually not sufficiently different to affect broad relationships between carbon isotope ratio and water-use efficiency (Ehleringer et al. 1992).

Several studies have established that carbon isotope ratios of arid land species were heavier (more positive) than from more mesic environments (Ehleringer & Cooper 1988, Ehleringer at al. 1992, Sharifi & Rundel, 1993). These low carbon isotope ratios are thought to be driven by strong evaporative gradients and low precipitation amounts, which result in increased stomatal closure and low intercellular CO_2 values (Rundel et al. 1980). In support of this, Stewart et al. (1995) have recently shown a strong relationship between overall carbon isotope ratios at the community level and annual precipitation inputs, leading to the expectation that plants in very arid sites such as the Atacama Desert should be characterized by low intercellular CO_2 values.

We tested this hypothesis by measuring carbon isotope ratios of leaves of the dominant species from the Atacama Desert, the most arid region in the world (Rundel et al. 1991). We sampled common species from the more arid portions of this hyper-arid region, spanning from coastal sites below the fog zone and extending up through and above the fog zone that bathes plants along the coastal range.

METHODS

Plants were sampled on the coastal plains at Pan de Azúcar, Chile (lat. 26° S, long. 71° E) and along an elevational transect at Paposo, Chile (lat. 25° S, long. 71° E). This area was covered in floristic studies by Johnson (1929, 1936). Plant taxonomy used here, however, follows that used in Rundel et al. (1996). Plant identification followed Johnson (1929, 1936). At each sampling site, all of the dominant species present were sampled. Each sample consisted of a bulk collection of 10-30 leaves from 5 different individuals at the site. Sampling took place in October 1978, December 1987, July, 1989, and December 1990. Leaves were air dried in the field, stored in envelopes, and then dried in a convection oven at 70 °C for 48 h upon returning to the laboratory.

Carbon isotope ratios ($\delta^{13}C$) were determined separately on dried leaf tissues that had been ground into a fine powder with a mortar and pestle. A 2- to 3-mg subsample of the tissue was combusted in an elemental analyzer coupled to an isotope ratio mass spectrometer (delta S, Finnigan MAT, Bremen, Germany). The long-term, absolute repeatability of out laboratory standard (Utah cabbage) was ± 0.11‰ (1 SD). Data are presented relative to the international Pee Dee Belemnite standard.

RESULTS

With limited exceptions, most of the species exhibited carbon isotope ratios consistent with C_3 photosynthesis (Tables 1 & 2). Carbon isotope ratios of these C_3 species across sampling dates ranged from a high of -19.6‰ (*Nolana mollis* at Pan de Azúcar in October 1978) to a low of -28.7‰ (*Argythamnia canescens* near Paposo in December 1987). While most values ranged between -25‰ and -21‰,

TABLE 1

Leaf carbon isotope ratios (‰) of common, dominant species in the Atacama Desert of northern Chile. Samples were collected December 3-4, 1987 during an extremely wet growing season.

Tasas de isótopos de carbono (‰) en las especies más comunes y dominantes en el norte de Chile. Las muestras se recolectaron entre el 3 y 4 de diciembre de 1987, período extraordinariamente húmendo.

Paposo, 50 - 130 m

Ephedra breana	-24.9
Fagonia chilensis	-24.3
Heliotropium pycnophyllum	-25.3
Nolana aplocaryoides	-25.3
Nolana paradoxa	-22.3
Polyachyrus cinereus	-25.5
Tetragonia maritima	-22.3

Paposo, 490 - 650 m

Alstroemeria paupercula	-26.9
Argylia radiata	-25.4
Argythamnia canescens	-28.7
Balbisia peduncularis	-25.7
Cistanthe grandiflora	-22.1
Cynanchum boerhaviifolium	-25.2
Dioscorea sp.	-25.9
Euphorbia lactiflua	-22.7
Frankenia chilensis	-24.1
Heliotropium taltalense	-27.3
Hoffmanseggia gracilis	-27.7
Leucheria modesta	-28.9
Lycopersicum chilensis	-24.3
Malva parviflora	-24.4
Mentzelia chilensis	-24.8
Nicotiana solanifolia	-24.0
Nolana leptophylla	-24.2
Oxalis gigantea	-25.5
Oxalis sp.	-27.1
Polyachyrus cinereus	-25.4
Proustia ilicifolia	-25.9
Schizanthus laetus	-22.7
Sicyos baderoa	-25.6
Solanum flexuosum	-23.8
Sonchus asper	-25.1

Stachys pannosa	-26.7
Tetragonia macrocarpa	-23.3
Tropaeolum tricolor	-25.5

Paposo, 770 - 840 m

Adesmia sp.	-22.9
Alstroemeria graminea	-27.1
Cistanthe sp.	-18.0
Chaetanthera limbata	-22.6
Chenopodium hastatum	-22.4
Cotula coronopifolia	-26.4
Cristaria integerrima	-24.6
Cruckshanksia pumila	-25.1
Cryptantha sp.	-24.2
Lycium deserti	-28.1
Nolana aplocaryoides	-21.3
Nolana crassulifolia	-24.3
Oxalis paposana	-25.7
Plantago litorea	-27.2
Reyesia chilensis	-24.5
Viola asterias	-24.0
Viola polypoda	-24.7

Paposo, 920 - 1010 m

Cistantheamaranthoides	-19.7
Dinemandra ericoides	-24.9
Loasa fruticosa	-24.2
Malesherbia humilis	-22.8
Nolana leptophylla	-20.9
Nolana divaricata	-21.3
Nolana sedifolia	-23.6
Perityle emoryi	-23.2
Tetragonia maritima	-21.7
Viola polypoda	-23.6

TABLE 2

Mean carbon isotope ratio values (‰) for leaves of common species
from Pan de Azúcar, Chile sampled across several years.

Valores de las tasas de los isótopos de carbono (‰) en hojas de las especies más comunes recolectadas
en diversos años, en el Parque Nacional Pan de Azúcar, Chile.

	October 1978	December 1987	July 1989	December 1990
Astragalus coquimbensis	-20.9			
Atriplex clivicola	-13.7	-14.8	-14.0	
Cistanthe amarantoides	-22.2	-16.6		
Cistanthe grandiflora	-21.4			
Copiapoa cinerea columna-alba	-12.5			
Cristaria integerrima	-26.1	-25.3		
Deuterochonia chrysantha	-13.8	-13.4		
Dinemandra ericoides	-22.6	-22.6	-22.9	
Eremocharis fruticosa	-24.6	-26.2	-24.9	-23.1
Gypothamnium pinifolium	-25.4	-25.4	-24.4	-24.7
Heliotropium pycnophyllum	-25.3	-26.2	-25.2	-24.0
Heliotropium lineariifolium	-26.0	-24.0	-24.9	
Nolana aplocaryoides	-21.1			
Nolana crassulifolia	-21.3	-22.7		
Nolana elegans	-20.1	-19.6		
Nolana mollis	-19.8	-23.1	-21.2	-21.4
Nolana paradoxa	-21.6			
Nolana sp.	-22.2	-21.0		
Ophryosporus triangularis	-23.7	-24.8	-23.5	-22.7
Polyachyrus cinereus	-23.9	-24.5	-24.4	-25.4
Senecio myriophyllus	-22.8	-22.6		
Tetragonia maritima	-20.9	-22.5	-20.3	-20.0

several species had leaves with carbon isotope ratios of ~-20‰ (*Nolana elegans, N. leptophylla, N. mollis, N. paradoxa, N. peruviana,* and *Tetragonia maritima*). While it is not possible to exclude the possibility that some of these *Nolana* may have had limited CAM activity, nocturnal field studies of other *Nolana* species in north-central Chile indicate that CAM is not present (Rundel and Palma, unpublished data). Similarly, field studies with *T. maritima* and with other species of *Tetragonia* in arid regions of South Africa suggest an absence of CAM in this genus (Rundel, unpublished data). No clear patterns between life form and carbon isotope ratio were evident in these data and there were no statistically significant differences in the carbon isotope ratios of ephemeral and woody vegetation at any of the sites.

The C_4 photosynthetic pathway was uncommon, with but a single species exhibiting carbon isotope ratios consistent with C_4 photosynthesis: *Atriplex clivicola* at Pan de Azúcar (-13.7‰ to -14.8‰). Several of the species exhibited carbon isotope ratios consistent with obligate CAM activity, including *Copiapoa cinerea columna-alba* (-12.5‰) and *Deuterochonia chrysantha* (-13.4‰ to -13.8‰). Several of the herbaceous species exhibited carbon isotope ratios that suggested intermediacy between C_3 and CAM or switching between C_3 and CAM between years. These included *Cistanthe amarantoides* at Pan de Azúcar and Paposo (-16.6‰ to -22.2‰) and *Cistanthe grandiflora* at Paposo (-18.0‰).

Only one species, *N. cf. villosa*, occurred at all points along the coastal transect. Carbon isotope ratios of *N. cf. villosa* leaves were more negative in the fog zone (intermediate altitude), consistent with the notion that this habitat was more humid and possibly less water-stressed (Fig. 1). Coincident with this, carbon isotope ratios of other *Nolana* species were also more positive above and below the fog zone.

At the community level, average leaf carbon was also most negative within the fog zone, with the site above the fog zone averaging a value greater than 2‰ more positive than communities within the fog zone (Fig. 2). Long-term precipitation data were not available for sites along this elevational transect, but it is not unreasonable to expect that the fog zone represented a much wetter habitat within this hyperarid region. Sites above the fog zone were likely the most arid of all, because they have greater solar radiation levels and lower humidities than the coastal plains below the fog belt (Rundel et al. 1991). If this is the case, then community-level variation in leaf carbon isotope ratios
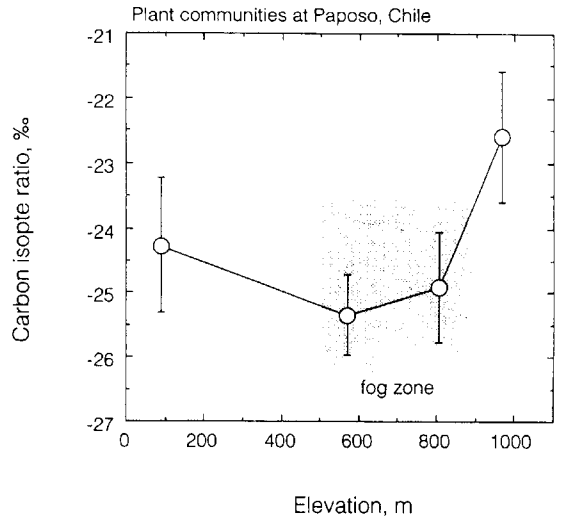

Fig. 2: Changes in the leaf carbon isotope ratios of vegetation along an elevational transect at Paposo, Chile. Plants were sampled in December 1987. Vertical bars indicate ± 1 standard deviation.

Cambios en las tasas de isótopos de carbono en hojas de la vegetación, en un transecto altitudinal en Paposo, Chile.
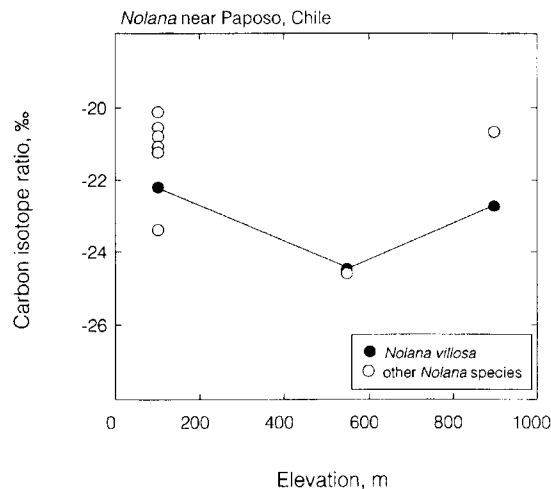
follows a pattern consistent with aridity. Plants from the driest site (above the fog zone) had the most positive carbon isotope ratios, with the mean carbon isotope ratio value for plants above the fog zone translating into a c_i/c_a value of 0.45 and the mean value for plants within the fog zone averaged 0.57. These are unusually low c_i/c_a values when compared to a mean global c_i/c_a value of 0.70 (Farquhar et al. 1989).

Leaf carbon isotope ratios of newly produced leaves decreased annually following above average precipitation at Pan de Azúcar in 1987 (Table 2). There was a nearly constant decrease in leaf carbon isotope ratio averaging 0.53‰ per year (Fig. 3). Excluding *Polyachyrus cinereus,* which apparently decreased in its carbon isotope ratio value by 1.5‰, the average Pan de Azúcar species increased its carbon isotope ratio by 2.04‰ in the three-year drought following the 1987 rains. From Eqn 1, this change in carbon isotope ratio translates in an average decrease in leaf intercellular CO_2 concentrations from 190 ppm to 159 ppm.
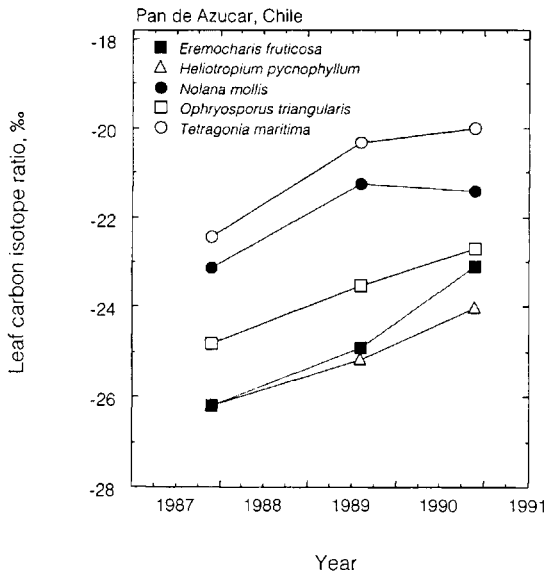

Fig. 1: Changes in the leaf carbon isotope ratios of *Nolana* species along an elevational transect at Paposo, Chile. Plants were sampled in December 1987.

Cambios en las tasas de los isótopos de carbono en hojas de nolanas en un transecto altitudinal en Paposo, Chile. Las muestras se colectaron en diciembre de 1987.

Fig. 3: A time course of leaf carbon isotope ratios in common woody species at Pan de Azúcar, Chile.

Tasas de isótopos de carbono a traves del tiempo (1987 a 1991) en hojas de las especies leñosas más comunes en el Parque Nacional Pan de Azúcar, Chile.

Fig. 4: The relationships between leaf carbon isotope ratios of leaves from common woody species at Pan de Azúcar, Chile between wet (1987) and dry years (1978, 1989)

Relaciones entre las tasas de los isótopos de carbono en un año húmedo (1987) y años secos (1978, 1979) en las plantas leñosas más comunes del Parque Nacional Pan de Azúcar, Chile.

The data in Figure 3 suggest relative rankings of carbon isotope ratio among plants at Pan de Azúcar remained constant through time. This was indeed the case and when carbon isotope ratios in a wet year (1987) were compared to those observed for the same species in dry years (1978 or 1989), there was a highly significant correlation (Fig. 4). These data indicate that different species do have different leaf carbon isotope ratios and that these differences were maintained over time.

DISCUSSION

O'Leary (1988) and Farquhar et al. (1989) examined variation in the carbon isotope ratios of a large number of C_3 species and concluded that the average leaf carbon isotope ratio was close to -28‰. Plants from desert ecosystems are known to have more positive values than the global average (Ziegler et al. 1981,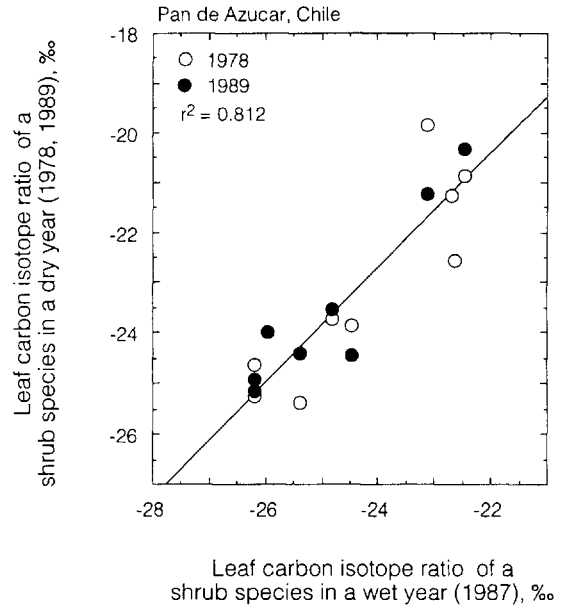 Ehleringer 1989, Ehleringer et al. 1993, Sharifi & Rundel 1993; Evans & Ehleringer 1994). However, the very positive carbon isotope ratios of plants from the coastal portions of the Atacama Desert are more positive on average than have been described from other desert ecosystems. Physiologically, one consequence is that leaves of plants within the hyperarid Atacama Desert have c_i/c_a values averaging as low as 0.45. The impact of such low c_i/c_a values on photosynthetic gas exchange is that photosynthetic rate will likely be substantially depressed because of stomatal limitations, since leaf N contents of Atacama Desert species are similar to leaves of desert shrubs from other ecosystems (Rundel et al. 1980). Although gas exchange rates are unknown for Atacama Desert shrubs, it is likely that maximum gas exchange rates will be low given the very positive carbon isotope ratios and moderately low leaf N contents.

The lack of any difference in the carbon isotope ratios of annual-ephemeral and

perennial species contrast with patterns observed in other ecosystems, where carbon isotope ratios of shorter-lived organisms are usually more negative than observed in longer-lived perennials (Ehleringer & Cooper 1988, Smedley et al. 1991). In this study, there were no significant differences among annuals, shorter-lived herbaceous species, and longer-lived perennials. All have very positive carbon isotope ratios, suggesting very low operational leaf intercellular CO_2 concentrations. Perhaps in this hyperarid region, tolerating water stress is such a dominant factor in a plant's life cycle that few opportunities exist with abundant soil moisture to allow expression of high leaf intercellular CO_2 concentrations.

There is often the mis-perception that deserts are dominated by C_4 species. Clearly on a species richness basis this is not the situation in the Atacama Desert, where only a single C_4 species was observed in our samples. Based on the full flora of Pan de Azúcar (Rundel et al. 1996), C_4 metabolism is restricted to the genus *Atriplex* and several grasses including the common *Distichlis spicata* (saline habitats) and *Eragrostis attenuata* (fog zone). The absence of any summer precipitation and low summertime temperatures are likely to be the key factors not favoring C_4 plants in this environment. Even CAM did not play a major role within these communities on a species richness basis, although a number of herbaceous species had carbon isotope ratios indicative of facultative CAM. Arroyo et al. (1990) had earlier noted that both *Cistanthe* (reported as *Calandrinia* and *Philippiamra*) had isotope ratios suggesting that this was the case. Mooney et al. (1974) had compared increases in the abundance of CAM along gradients of decreasing precipitation in coastal portions of coastal California - Baja California and northern Chile. However, our study site extends into a drier region than characterized by the Mooney et al. (1974) study, where C_3 photosynthesis re-emerges as the dominant photosynthetic pathway under these extremely arid conditions.

The Atacama Desert represents the extreme end of an aridity gradient which is currently the driest terrestrial region on this planet. Long-term climatic trends in the southern part of the Atacama Desert during this century indicate a continued decrease in mean annual precipitation (Burgos et al. 1991, Santibanez & Uribe 1994). The basic plant photosynthetic response to such conditions appears to be C_3 photosynthesis and with leaves that exhibit unusually low intercellular CO_2 concentrations. Whether such a response represents an adaptation to these unusual conditions or reflects the severe constraints imposed by a hyperarid environment is unknown at this time. Future ecophysiological studies of Atacama Desert plants should focus on the factors resulting in such low leaf intercellular CO_2 concentrations.

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