

Plant $\delta^{15}\text{N}$ values along a fog gradient in the Atacama Desert, Chile

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The Atacama Desert is characterized by a fog zone occurring between 500 and 800 m elevation. We hypothesized that atmospheric deposition from marine sources was the primary source of nitrogen for plants in the fog zone, and so the $\delta^{15}\text{N}$ of plants should differ between those above and below that zone. No significant differences in leaf $\delta^{15}\text{N}$ values were detected among the three locations. The $\delta^{15}\text{N}$ values for non-nitrogen fixing species (6–12‰) were substantially more positive than that of atmospheric deposition (–1‰) suggesting immediate assimilation of nitrogen from fog was not an important source of plant nitrogen.

Keywords: Atacama Desert; atmospheric deposition; desert ecology stable isotopes; nitrogen cycle; fog gradient

Introduction

The Atacama Desert of Chile is one of the driest regions in the world. Mean annual precipitation can be as low as 0.6 mm and periods without precipitation of up to 8 years are not uncommon (Rundel *et al.* 1991). The maritime influence on the climate of the region results in a persistent fog zone along the coastal ranges that is bounded above (800 m) and below (300 m) by extremely arid zones (Rundel & Mahu, 1976). The moisture gradient causes large changes in plant coverage over a short distance (Rundel & Mahu, 1976). The fog zone is characterized by relatively high plant coverage (> 50%) and a lush growth of epiphytic lichens, while coverage above and below the fog zone is generally less than 5% and epiphytic lichens are absent (Rundel, 1978; Rundel *et al.*, 1991). The extent to which atmospheric nitrogen deposition from the marine sources contributes to soil mineral resources, and ultimately to productivity in these regions, is unclear.

The isotopic composition of nitrogen in plants and soils can provide valuable information on inputs and subsequent nitrogen transformations within an ecosystem (Nadelhoffer & Fry, 1988; Evans & Ehleringer, 1993). Nitrogen input into a community occurs through biological nitrogen fixation and atmospheric deposition. The contribution of symbiotic nitrogen fixation to the total nitrogen in a plant can be estimated by measuring the $^{15}\text{N}/^{14}\text{N}$ composition (Shearer & Kohl, 1986). Isotopic ratios are expressed in delta

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notation ($\delta^{15}\text{N}$) relative to the atmospheric-air standard (Mariotti, 1984) as:

$$\delta^{15}\text{N} = \left(\frac{R_{\text{sample}}}{R_{\text{standard}}} - 1 \right) \times 1000\%$$

where R_{sample} and R_{standard} are the molar ratios of $^{15}\text{N}/^{14}\text{N}$ of the sample and standard, respectively. By definition, the isotopic composition of the atmosphere is 0‰ (Mariotti, 1984). Discrimination against ^{15}N during nitrogen fixation is small, and so the $\delta^{15}\text{N}$ value of a plant that receives nitrogen solely by symbiotic nitrogen fixation is near 0‰. In contrast, the isotopic composition of the plant-available mineral nitrogen within the soil is often enriched in ^{15}N (Virginia & Delwiche, 1982; Shearer & Kohl, 1986), and so the $\delta^{15}\text{N}$ of plants that are not capable of symbiotic nitrogen fixation is usually greater than 0‰. Therefore, the fractional contribution of biologically-fixed nitrogen and soil available nitrogen to a plant can be estimated by two-end member linear mixing models (Shearer & Kohl, 1986). This approach has been used to examine the role of nitrogen fixation in numerous ecosystems (see Shearer & Kohl, 1986; 1988; Virginia *et al.*, 1988), including regions of North America (Virginia & Delwiche, 1982; Shearer *et al.*, 1983), South America (Ehleringer *et al.*, 1992), and Africa (Schulze *et al.*, 1991).

In contrast to nitrogen assimilated by symbiotic nitrogen fixation, nitrogen deposited in rainfall, especially from marine sources, is usually depleted in ^{15}N relative to the atmosphere. Rain is the predominant source of nitrogen on successional young sites in Hawaii (Vitousek *et al.*, 1987). Vitousek *et al.* (1989) observed that non-nitrogen fixing plants on these sites had $\delta^{15}\text{N}$ values as negative as -10.1% , and estimated the $\delta^{15}\text{N}$ value of precipitation as -5.1% by measuring the $\delta^{15}\text{N}$ of a non-fixing lichen. Similar negative values for precipitation have been reported by Heaton (1986) for South Africa (-3%) and by Wada *et al.* (1981) for Antarctica (-11 to -24%).

Table 1. The $\delta^{15}\text{N}$ values (‰) of the dominant species along an elevation gradient in the Atacama Desert, Chile. Species were sampled below the Fog Zone (50 m), within the Fog Zone (550 m), and above the Fog Zone (900 m). The mean value for species below the Fog Zone does not include *Astragalus* sp.

Species	Below Fog Zone	Fog Zone	Above Fog Zone
<i>Astragalus</i> sp.	3.8		
<i>Eremocharis fruticosa</i> Phil.	7.4		
<i>Heliotropium pycnophyllum</i> Phil.	11.1		
<i>Heliotropium</i> sp.	10.5		
<i>Nolana aplocaryoides</i> (Gaud.) Johnst.	7.3		
<i>Nolana elegans</i> (Phil.) Reiche	8.8		
<i>Ophryosporus triangularis</i> Meyen	9.4		
<i>Polyachyrus fuscus</i> Meyen	9.5		
<i>Senecio almadeie</i> Phil.	9.5		
<i>Gypothamnium pinifolium</i> Phil.	8.9		6.1
<i>Tetragonia maritima</i> Barn.	10.1		11.9
<i>Nolana villosa</i> (Phil.) Johnst.	8.3	10.5	9.1
<i>Cristaria</i> sp.		8.7	
<i>Euphorbia lactiflua</i> Phil.		10.8	
<i>Heliotropium linariaefolium</i> Phil.		12.6	
<i>Nolana peruviana</i> (Gaud.) Johnst.		10.9	
<i>Oxalis gigantea</i> Barn.		12.0	
<i>Proustia cuneifolia</i> (Phil.) Fabris		8.4	
<i>Loasa</i> sp.			8.6
<i>Nolana</i> sp.			8.7
Location mean	9.2 ± 0.4	10.6 ± 0.6	8.9 ± 0.9

We measured the ^{15}N composition of leaves of dominant species along a fog zone gradient in order to assess the importance of nitrogen fixation and fog as a potential sources of nitrogen input. We hypothesized that plants in the fog zone should have lower $\delta^{15}\text{N}$ values than plants from outside the fog zone, reflecting the $\delta^{15}\text{N}$ of marine sources.

Methods

Plant material for nitrogen isotope analysis was collected below the fog zone (50 m) at Pan de Azucar (26°07'S, 70°40'W), and within (550 m) and above (900 m) the fog zone near Paposo (25°00'S, 70°30'W) in northern Chile. A thorough description of the climate and vegetation of the study sites is provided elsewhere (Rundel *et al.*, 1991). Leaf material was collected from up to four individuals of each species at each site. Leaves were dried at 75°C for at least 48 h and then ground to a fine powder using a mortar and pestle. The ground leaf material was pooled by species for each site for nitrogen isotope analysis.

Samples were prepared for nitrogen isotope analysis following Minagawa *et al.* (1984) and Fiedler & Proksch (1975). Leaf material (100 mg) was placed in a 6 mm Vycor tube with CuO, CaO, and Ag foil. This tube was placed within a 9 mm Vycor tube containing Cu, sealed under vacuum, and heated at 850°C for at least 6 h. The tubes were then allowed to cool slowly for 8 h. The N_2 within the tube was purified by cracking the tube under vacuum and passing the sample gasses through an ethanol-dry ice trap to collect H_2O , and a liquid nitrogen trap to collect CO_2 . The N_2 within the sample was then condensed out on silica gel at liquid nitrogen temperatures. The nitrogen isotope ratio of the purified gas was determined on an isotope ratio mass spectrometer (Delta S, Finnigan MAT). Measurements of organic standards were repeatable to $\pm 0.3\text{‰}$.

Results and discussion

The $\delta^{15}\text{N}$ values for the species at each location indicate that neither symbiotic nitrogen fixation nor immediate assimilation of nitrogen deposited from fog were important sources of nitrogen input along the fog gradient. The $\delta^{15}\text{N}$ values for the species at each location were significantly above 0‰ (Table 1). The $\delta^{15}\text{N}$ value measured on *Tillandsia landbeckii* Phil., a plant without roots and relying solely on atmospheric deposition, was -0.3‰ . Although there were general trends for isotopic variation among locations, the mean $\delta^{15}\text{N}$ values at each of the three sites were not significantly different from each other ($p = 0.117$).

The $\delta^{15}\text{N}$ values for all species were greater than 6‰, with the exception of *Astragalus* sp. located below the fog zone. Assuming that $\delta^{15}\text{N}$ for N derived from symbiotic nitrogen fixation is between -2 and 0‰ (Shearer & Kohl, 1986), we estimated that *Astragalus* sp. derives 41–52% of its nitrogen from biological nitrogen fixation. This is well within the range (43–61%) reported by Shearer *et al.* (1983) for nitrogen-fixing species at seven sites in the Sonoran Desert of southern California, but somewhat lower than values (64–96%) found for leguminous species in Baja California, Mexico (Shearer & Kohl, 1986).

The lack of evidence for significant nitrogen fixation or direct uptake of nitrogen contained in fog droplets suggests the primary nitrogen source for plants along the fog gradient is atmospheric deposition that has undergone significant volatilization and/or denitrification. Both processes are accompanied by isotopic fractionation resulting in the residual inorganic nitrogen becoming more enriched in ^{15}N over time (Blackmer & Bremner, 1977; Shearer & Kohl, 1986), and would cause the relatively high plant $\delta^{15}\text{N}$ values observed in the Atacama Desert. Nitrogen fixation by lichens may represent a potential nitrogen source within the fog zone. It is difficult to estimate the contribution of nitrogen from different sources once it has entered the soil because of changes in $\delta^{15}\text{N}$ associated with transformations during the nitrogen cycle (Binkley *et al.*, 1985). However,

a significant input of nitrogen from lichens would be expected to lower the $\delta^{15}\text{N}$ of all species within the fog zone in comparison with the other sites.

The absence of plant species that are capable of symbiotic nitrogen fixation and the dependence upon atmospheric deposition for nitrogen inputs may have important implications for plant nitrogen relations in the Atacama Desert. Measurements of atmospheric deposition are not available for the Atacama Desert, but rates for arid regions of the United States have been estimated at $3 \text{ kg N ha}^{-1} \text{ year}^{-1}$ (Peterjohn & Schlesinger, 1990). Values for the Atacama Desert are likely to be lower, because of fewer precipitation events. This is in contrast to rates of nitrogen input of $25\text{--}40 \text{ kg N ha}^{-1} \text{ year}^{-1}$ that have been measured in other desert ecosystems where significant input occurs from nitrogen fixation (West & Skujins, 1977; Rundel *et al.*, 1982). The low rates of nitrogen input may be exacerbated by subsequent losses to the atmosphere due to volatilization and denitrification. Gaseous nitrogen loss from volatilization and denitrification can be significant in arid environments; Peterjohn & Schlesinger (1990) estimated that gaseous loss of nitrogen accounted for over 70% of annual inputs in North America, and from 75 to 94% of NH_4^+ and NO_3^- experimentally applied to desert ecosystems was subsequently lost to volatilization and denitrification (Westerman & Tucker, 1979; Klubek & Skujins, 1981). The low rates of nitrogen input, coupled with relatively high rates of nitrogen loss, suggest that plant growth may be nitrogen limited in the Atacama Desert even when infrequent rains do occur.

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