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Carbon and nitrogen dynamics in a sandy groundwater-coupled ecosystem in the Monte Desert, indicated by plant stable isotopes

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ABSTRACT

The high productivity of sandy groundwater-coupled woodlands in the Monte Desert is exploited by local pastoralist communities for fuel, domestic use, and manure accumulation and export to irrigated oases. We explored processes and species that could replenish C and N losses from the ecosystem using stable isotopes of plants and nutrient analysis of soils. Foliar ^{15}N natural abundances, which were lower in *Prosopis flexuosa* plants and C4 grasses from dune flanks, indicate that these plants may fix atmospheric N_2. Groundwater availability did not decrease water use efficiency (indicated by similar foliar $\delta^{13}C$ in dune flanks and interdune valleys), suggesting that the higher stomatal conductance allowed by the additional water source and reported in previous studies is coupled with higher photosynthetic rates, increasing productivity in interdune valleys. Water use efficiency and N stable isotopes of *P. flexuosa* responded to temporal changes in precipitations, suggesting rapid shifts of N sources, to uptake of recently mineralized soil N (higher $\delta^{15}N$ and lower $\delta^{13}C$ after rain events). Soil heterogeneity was low, except for ammonium and moisture in interdune valley soils. This study allows us to hypothesize that carbon is replenished in interdune valleys by increasing photosynthetic rates, and N is replenished by N_2 fixation done by young *P. flexuosa* plants and grasses from dune flanks.

1. Introduction

Arid groundwater-coupled ecosystems have a higher productivity than ecosystems in arid areas that only rely on precipitation (Contreras et al., 2011). Phreatophyte *Prosopis flexuosa* woodlands in the Monte Desert (NE Mendoza, Argentina) have a relatively high productivity, which has been used for fuel, vineyard and railroad construction in the past, and is currently used by pastoralist communities for local consumption of wood and forage, and exports of manure to irrigated oases (Villagra et al., 2009, 2005; Alvarez et al., 2009a, 2006; Torres, 2008). Currently wood extraction is only allowed for fuel and construction material of the local communities (Gobierno de la República Argentina, 2009). Recent studies suggest that a moderate extraction and commercialization of dry wood from multi-stemmed trees may be a sustainable economic activity for local communities (Alvarez et al., 2011). Other studies designed to evaluate the ecological consequences of these extraction activities indicate negative effects on flower pollinator visits, positive effects on seed production of *P. flexuosa*, and no effects on soil nutrients and understory vegetation (Vazquez et al., 2011). The consumption of forest resources may cause an imbalance of carbon and nitrogen, if not replenished by inputs to the ecosystem, so it is important to identify and quantify C and N input and export mechanisms.

Carbon stocks may be replenished by the high productivity of phreatophyte plants, while N stocks may be replenished by biological N_2 fixation. Carbon fixation by photosynthesis is primarily limited by water in this arid ecosystem, but shallow groundwater in interdune valleys (6–15 m depth, Aranibar et al., 2011) provides an additional water source for deep rooted trees such as *P. flexuosa*, *Prosopis alpataco*, *Larrea divaricata*, and others (Jobbágy et al., 2011). Groundwater availability increased stomatal conductance and changed other physiological characteristics of *P. flexuosa* in

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interdune valleys (Giordano et al., 2011), which probably decreased water use efficiencies. With respect to N inputs, modeling estimates indicate negligible atmospheric deposition of N in these non-industrialized areas (Galloway et al., 2004). Biological soil crusts are present in these ecosystems and may contribute to N inputs, especially in undisturbed sites where they are not destroyed by livestock (Aranibar et al., 2003a; Gómez et al., 2012). The legume *P. flexuosa* is the dominant tree of these phreatophyte forests, and it could form nodules of N_2 fixing bacteria. *P. flexuosa* seedlings from the Monte Desert nodulated in laboratory conditions (Morales, 1992), as other *Prosopis* species in arid areas around the world (Felker and Clark, 1980; Geesing et al., 2000). However, soil nitrogen inhibits N_2 fixation, as shown by decreasing N_2 fixation of *Prosopis glandulosa* plants under high soil nitrate concentrations in arid areas of Texas (Geesing et al., 2000). *Acacia drepanolobium* also decreased N_2 fixation near fertile termite mounds in East African savannas (Fox-Dobbs et al., 2010), and *Prosopis* species of the Monte Desert decreased nodulation in soils with high soil N contents (Morales, 1992). Grasses with the C4 metabolism may also associate with non-symbiotic N_2 fixing bacteria, obtaining N recently derived from atmospheric N_2 (Abbadie et al., 1992; Aranibar et al., 2008; Swap et al., 2004). Because nitrogen fixation is an energy demanding process, only individuals with poor access to soil available nitrogen (ammonium and nitrate) would likely invest in N_2 fixation (Rastetter et al., 2001).

Different processes that could replenish C and N losses to the ecosystem are not homogeneous in time and space. Photosynthesis and N_2 fixation depend on the availability of soil resources and plant characteristics (i.e, photosynthetic metabolism, root distribution), which vary with species, landscape positions, and plant ages. The landscape of these phreatophyte forests is characterized by dune-interdune systems, with dispersed livestock settlements (Goirán et al., 2012), which generate gradients of groundwater and nutrient availability. Previous studies indicate that interdune valleys have higher contents of organic matter, higher availability of water, nitrogen, and phosphorus, larger trees, which grow at a faster rate, and higher vegetation cover than dune flanks (Guevara et al., 2010; Aranibar et al., 2011; Jobbágy et al., 2011; Giordano et al., 2011). Mineral nitrogen availability was highly variable in time and space, but exposed soils in dune flanks showed much lower nitrate concentrations than in valleys (Guevara et al., 2010). In addition, wind and water erosion probably transport surface soil and litter from dunes to valleys, as suggested by the finer sediments found in valleys (Guevara et al., 2010). Nitrate accumulated in corrals is leached to groundwater (Meglioli et al., 2013), and it could be transported by groundwater flow to surrounding areas, providing an additional source of nitrogen to phreatophyte plants in nearby interdune valleys. The low N availability in dune flanks may encourage the necessary investment on N_2 fixation, while the higher N availability in valleys may inhibit it.

The spatial heterogeneity associated with dispersed woody plants has been proposed to increase water and nutrient use efficiency at the ecosystem scale (Aguiar and Sala, 1999). Biological activity is localized under woody canopies where nutrient inputs and soil moisture are higher (Cesca et al., 2012; Rossi and Villagra, 2003). Groundwater subsidies can affect patterns of heterogeneity, concentrating biological activity under productive phreatophyte canopies, or increasing productivity of the whole ecosystem (i.e., by hydraulic lift), with a consequent decrease of soil patchiness. Changes of spatial heterogeneity may affect resource use strategies, such as absorption, nutrient and water use efficiency, and investment in symbiotic and non-symbiotic associations.

The objective of this study was to analyze indicators of N and C inputs in an arid ecosystem in the central Monte Desert, where the dominant economic activity of local communities causes C and N exports to irrigated oases. As an initial approach for the region, we use stable isotopes of C and N as indicators of ecosystem processes in different species and landscape units, and to identify potential N_2 fixers. Stable isotopes integrate ecosystem processes over different time scales, and are useful to indicate patterns of C and N cycle and establish research priorities for future studies (Robinson, 2001). Stable isotopes of N were used as indicators of N_2 fixation, assuming that species with lower foliar $\delta^{15}N$ values derive part of their N from recently fixed atmospheric N_2. Stable isotopes of C were used as indicators of water use efficiency. These and previous reports of stomatal conductance were used as indicators of C uptake by photosynthesis in sites with different groundwater access. We hypothesized that N_2 fixation occurs in C4 grasses and young *P. flexuosa* trees, particularly in nutrient poor dune flanks, and that decreased water use efficiencies in interdune valleys would be responsible of the high productivities observed in these landscape positions. Furthermore, we hypothesized that there would be a higher heterogeneity of soil resources in dune flanks during a rainy season, which would stimulate N_2 fixation in these areas, if they are representative of larger time scales. To test these hypotheses, we analyzed foliar $\delta^{15}N$ of vascular plants as an indicator of N_2 fixation, foliar $\delta^{13}C$ as an indicator of water use efficiency in different plant species, and heterogeneity of soil available N and moisture in a dune-interdune system of a relatively undisturbed woodland in the Monte Desert. We predicted a) lower $\delta^{15}N$ in adult *P. flexuosa* plants than in other C3 species, b) lower $\delta^{15}N$ in young than adult *P. flexuosa* plants, c) lower $\delta^{15}N$ in C4 grasses than all C3 species combined, d) higher water use efficiencies of adult *P. flexuosa* trees in dune flanks, and e) higher heterogeneity of nitrate, ammonium and soil moisture in dune flanks.

2. Materials and methods

2.1. Study site

The study site is located in the Telteca Natural Reserve, NE Mendoza (32° 25′42″S 68°00′ 33″ W). The climate is arid, long term (1972–2007) mean annual precipitation is 155 mm, and mean annual temperature is 18.5 °C. Precipitation is concentrated during the summer months, and daily and annual thermal amplitudes are high, ranging from 48 °C absolute maximum to −10 °C absolute minimum (Alvarez et al., 2006). The site has been described in Guevara et al. (2010), and corresponds to site “La Penca” from the Aranibar et al. (2011) study. The landscape is characterized by dune-interdune systems, partially stabilized by the vegetation, composed of fine and very fine sands. These fluvial and aeolian sediments have been reworked by the winds (Aranibar et al., 2011). Low landscape positions (interdune valleys) have surface soils with finer texture, higher organic matter content, and vegetation cover, characterized by larger *P. flexuosa* trees. Bulk densities are slightly different in both topographic positions, with lower values in the interdune valley (1.43 g cm^{-3}, and 1.56 g cm^{-3} in the interdune valley and dune flank, respectively) (Guevara et al., 2010). These trees access groundwater (located at 7 m depth), while trees from dune flanks rely on soil water derived from local precipitation (Jobbágy et al., 2011). The study site is a relatively undisturbed area, which hosted a livestock settlement, composed of a house, a well, and corrals, abandoned approximately five years before the study. Nitrate concentrations in groundwater are low in this site (2.8 ppm, Aranibar et al., 2011), indicating that nitrate leaching was not important when the settlement had livestock, or that groundwater nitrate concentration has been diluted since the settlement was abandoned. Although goats and horses were occasionally seen in the area, the nearest active settlement is located 1 km from the site, behind high sand dunes, reducing the movement of animals to the study site. The effects of wood and shrub removal associated with the abandoned settlement are still evident approximately 50 m around the housing area.

2.2. Plant nutrients and stable isotope composition

Stable isotope composition of foliar N integrate several processes at different spatial and temporal scales (Robinson, 2001). It has been widely used as an indicator of N_2 fixation, because N recently derived from atmospheric N_2 has $\delta^{15}N$ values close to 0‰ (Nadelhoffer and Fry, 1994). In arid areas, where soil N is generally enriched in ^{15}N, N_2 fixation decreases the $\delta^{15}N$ values of organic N in relation to other plants using only soil N (Aranibar et al., 2004). Other processes, such as absorption of ^{15}N depleted nitrate, could also decrease foliar $\delta^{15}N$, because nitrification can deplete nitrate by 15–35‰ with respect to the ammonium source, before it undergoes denitrification (Robinson, 2001). A knowledge of the ecology, history and biology of the system, and testing with other methods are necessary to confirm the occurrence of N_2 fixation. The high temporal and spatial variability of soil $\delta^{15}N$, given by the dynamics of microbiological activity in desert soils associated with pulse events and vegetation patches, the different root profiles, and micorrhizal status make it difficult to estimate the $\delta^{15}N$ of soil N end members, in order to obtain a reasonable quantification of N_2 fixation by natural abundance of ^{15}N (Aranibar et al., 2004; Hobbie et al., 1999; Högberg, 1990; Shearer and Kohl, 1989; Virginia et al., 1989; Wang et al., 2013). Several species present at the sites, including *P. flexuosa*, *L. divaricata*, *Larrea cuneifolia*, *Atriplex lampa* and a few grasses have root systems that allow them to exploit different areas of shallow and deep soils, including groundwater (Barbour et al., 1977; Gonzalez Loyarte et al.,, 2000; Morello, 1958; Passera and Borsetto, 1989; Villagra et al., 2011). Furthermore, the proportion of water derived from groundwater in the study site differs for different species and landscape units (Jobbágy et al., 2011), indicating variations in root systems and soil N sources. For these reasons, we could not select a reference plant and N end members to quantify N_2 fixation. Instead, we aimed to identify possible species and sites where N_2 fixation may occur, based on foliar $\delta^{15}N$ of different plants, landscape units, and sampling times.

With respect to carbon uptake, foliar $\delta^{13}C$ of C3 plants is commonly used as an indicator of water status during the leaf life period (Ehleringer and Cooper, 1988; Farquhar and Richards, 1984; Leffler and Evans, 2001). $\delta^{13}C$ of assimilated carbon varies according to the ratio of substomatal to ambient CO_2 concentration (*ci/ca*), mainly determined by stomatal conductance and photosynthetic rates, reflecting the trade-off between assimilation rate and water loss, i.e., water-use efficiency (WUE) (Farquhar et al., 1982, 1989). We assumed that internal conductance (from stomatal cavity to sites of carboxylation) does not significantly affect the relationship between WUE and $\delta^{13}C$, because of the lack of specific data on the species and region studied, and the strong controls of water availability on the ecophysiology of these arid ecosystems. However, variations of internal conductance among species could decouple WUE and $\delta^{13}C$, and should be considered in future ecophysiological studies (Warren and Adams, 2006). Foliar $\delta^{13}C$ often correlates with atmospheric conditions, such as vapor pressure deficit (Bowling et al., 2002), and it changes at short temporal scales in response to air temperature and humidity (Aranibar et al., 2006). In this study, we use $\delta^{13}C$ of C3 plants as an indicator of integrated water use efficiency in different species, landscape units, and sampling times.

For leaf nutrient and isotopic analysis, we collected plant leaves from adult trees (*P. flexuosa*, *Capparis atamisquea*), shrubs (*Lycium tennuispinosum*, *L. divaricata*, *Tricomaria usillo*, *Bouganvillea spinosa*, *Ximenia americana*), and grasses (*Bouteloa barbatum*, *Sporobolus rigens*, *Panicum urbilleanum*, *Aristida* sp., *Trichloris crinita*, and *Setaria leucophylla*) in December 2007 (spring, before the first rains of the season, $n = 38$), February 2008 (summer, onset of growing and rainy season, $n = 48$), and April 2008 (fall, end of growing season, before litter fall, $n = 20$), with a total of 106 plant samples. These samples were collected in plants growing in the interdune valley ($n = 69$) and in the dune flank ($n = 37$). We collected a minimum of 10 leaves from each plant during each sampling period, covering different exposures and heights, in order to average the variability given by sun exposure. Leaves from the same plant were composited into one sample per individual. We also collected leaves of seedlings and young individuals of *P. flexuosa* in the interdune valley during the onset of the growing season (February, 2008), registering the diameter at the base of the trunk (dbt). The leaves were stored in paper bags, air dried in the field, and oven dried at 60 °C in the laboratory, upon return from the field. All leaves collected from each plant were ground until the sample was homogeneous, and sent to the University of Arkansas Stable Isotope Laboratory for $\delta^{13}C$, $\delta^{15}N$, %C and %N analysis. The samples were analyzed on a Delta Plus Isotope Ratio Mass Spectrometer coupled with an elemental analyzer, with an overall precision better than 0.2‰ for C and 0.4‰ for N. Natural abundance of stable isotopes are expressed in the delta notation.

Foliar C:N ratios, $\delta^{13}C$, and $\delta^{15}N$ data of different plants were analyzed with linear models (glm function in R), considering sampling time (December, February, and April), landscape unit (dune flank and interdune valley), photosynthetic metabolism (C3 and C4), dbt class of *P. flexuosa* (adults: dbt $\geq$ 10 cm, young: 5 $<$ dbt $<$10 cm, juveniles: 1 $<$ dbt $\leq$ 5, and seedlings: dbt $\leq$ 1 cm), and species (*Prosopis* vs non *Prosopis*) as different fixed factors, in different models according to the predictions to be tested. For adult *P. flexuosa* plants, we used models that explained response variables (foliar C:N ratios, $\delta^{13}C$, or $\delta^{15}N$) as a function of sampling time and landscape unit. For all *P. flexuosa* plants, including different ages, we used models with the effect of sampling time, age, and the interaction among sampling time and age. For plants with the C3 metabolism, we compared *P. flexuosa* with other C3 plants, considering landscape unit and sampling time as additional fixed factors. For all adult plants, we included photosynthetic metabolism (C3 and C4) as a fixed factor, in addition to landscape unit and sampling time. The glm models provided the *t* student and *p* values for each fixed factor. We considered significant effects of a fixed factor on a response variable when the *t*-student absolute value was higher than 2, and the *p* value was lower than 0.05.

2.3. Soil nutrients and vegetation description

We estimated differences in vegetation between the dune flank and interdune valley with vegetation transects and remote sensing. We used a Landsat 5 Thematic Mapper scene (path 231 row 083) acquired on March 8th, 2011 (NASA Landsat Program, 2013), which was radiometrically corrected to surface reflectance using the COST approach (Chavez, 1996). We obtained an average value of SATVI (Soil Adjusted Total Vegetation Index, Marsett et al., 2006) and NDVI (Normalized Difference Vegetation Index) in an area of 57 pixels of 30 × 30 m in the dune and interdune valley used for plant and soils sampling.

$$\mathrm{SATVI} = (\rho_{\mathrm{SWIR}} - \rho_{\mathrm{SWIR}})/(\rho_{\mathrm{SWIR}} + \rho_{\mathrm{Red}} + \mathrm{L})(1 + \mathrm{L}) - \rho_{\mathrm{SWIR2}}/2$$

$$\mathrm{NDVI} = (\rho_{\mathrm{NIR}} - \rho_{\mathrm{Red}})/(\rho_{\mathrm{NIR}} + \rho_{\mathrm{Red}})$$

Where ρ_{SWIR}, ρ_{SWIR2}, ρ_{Red} and ρ_{NIR} are the reflectances in the shortwave infrared (band 5 and band 7), red (band 3), and near infrared (band 4) in the TM sensor, respectively. Previous work has shown that SATVI is the most sensitive index to vegetation cover in the study area (Goirán et al., 2012).

In addition, two 50-m transects were placed, one in the valley and one in the dune flank of the study site, in January 2010. A 1.5 m metal needle was placed every 50 cm, perpendicular to the ground, and the type of vegetation (species) and number of times that vegetation touched the needle were registered. Total vegetation cover was calculated as the percentage of points where either plants or litter were present. Soil samples were collected with a soil core every 50 cm along the transects, from 0 to 20 cm depth. A subsample of approximately 100 g was weighted and oven dried at 100 °C to determine gravimetric soil moisture. Soil available nitrogen was determined in soil extracts by spectrophotometry with a HACH DR2800 spectrophotometer. For ammonium determinations, soil extracts were prepared with 10 g of soil and 50 ml of 2N KCl (two normal potassium chloride), shaken for 30 minutes, filtered, and frozen until analysis, with a modified indophenol method (HACH, 2009). Nitrate concentrations were determined in soil extracts of 5 g of soil and 25 ml of extracting solution, composed of 2.5 g of $CuSO_4 * 5H_2O$ (Copper(II) sulfate pentahydrate), 0.15 g of Ag_2SO_4 (silver sulfate), 0.62 g of BO_3H_3 (boric acid) in 1000 ml of deionized water. Soil extracts were shaken during 1 hour, filtered, and frozen until analysis. Nitrate concentrations were determined by spectrophotometry with the cadmium reduction method, after adjusting to pH 7 with 1% NaOH (sodium hydroxide). Soil nutrient and moisture data were analyzed with semivariograms in order to detect spatial autocorrelation. The empirical semivariograms for soil nutrient and moisture data from the dune and interdune valley were built, previously evaluating the distributional assumptions (stationary and continuity) and performing a logarithmic transformation of the original data when necessary.

We calculated all pair-wise distance between sampling sites for different lag-distances between 0.5 and 15 m for nitrate, ammonium and soil moisture in both, the dune and the interdune valley, and we calculated the omni-directional semivariograms for each lag-distance using the classical estimator (Webster and Oliver, 2007):

$$\gamma(h) = \frac{1}{2N(h)} \sum_{i=h}^{N(h)} (Z_i - Z_{i+\Delta h})^2$$

where $\gamma(h)$ represents the semivariance calculated for a specific spacial distance h, and Z represents the random variable, nitrate, ammonium or moisture content at point i and $i+\Delta h$. $N(h)$ is the number of all pairs of points separated by distance h. Then, we obtained the empirical omni-directional semivariograms for each zone (dune flank and interdune valley), we fitted different models (i.e. exponential, spherical, and Gaussian) and chose the best model according to the residual square sum.

To calculate the empirical semivariograms and fit the models we used the Gstat package (Pebesma, 2004) in *R* statistical environment (R Core Team, 2012). For the data that were not autocorrelated (i.e., nitrate concentration), we analyzed the effect of landscape units, soil moisture, and number of vegetation touches above the sampling point with a generalized linear model (glm function in R).

3. Results

Adult individuals of *P flexuosa* (dbt ≥ 10 cm) showed a significant variability of stable isotope composition among different sampling times, and insignificant differences for plants located in dune flanks and interdune valleys (Fig. 1, Table 1). Foliar $\delta^{13}C$ values were higher, and foliar $\delta^{15}N$ values were lower in December, before the first rains, than in the other sampling times, while C/N was lower in the onset of the growing/rainy season in February (Fig. 1).

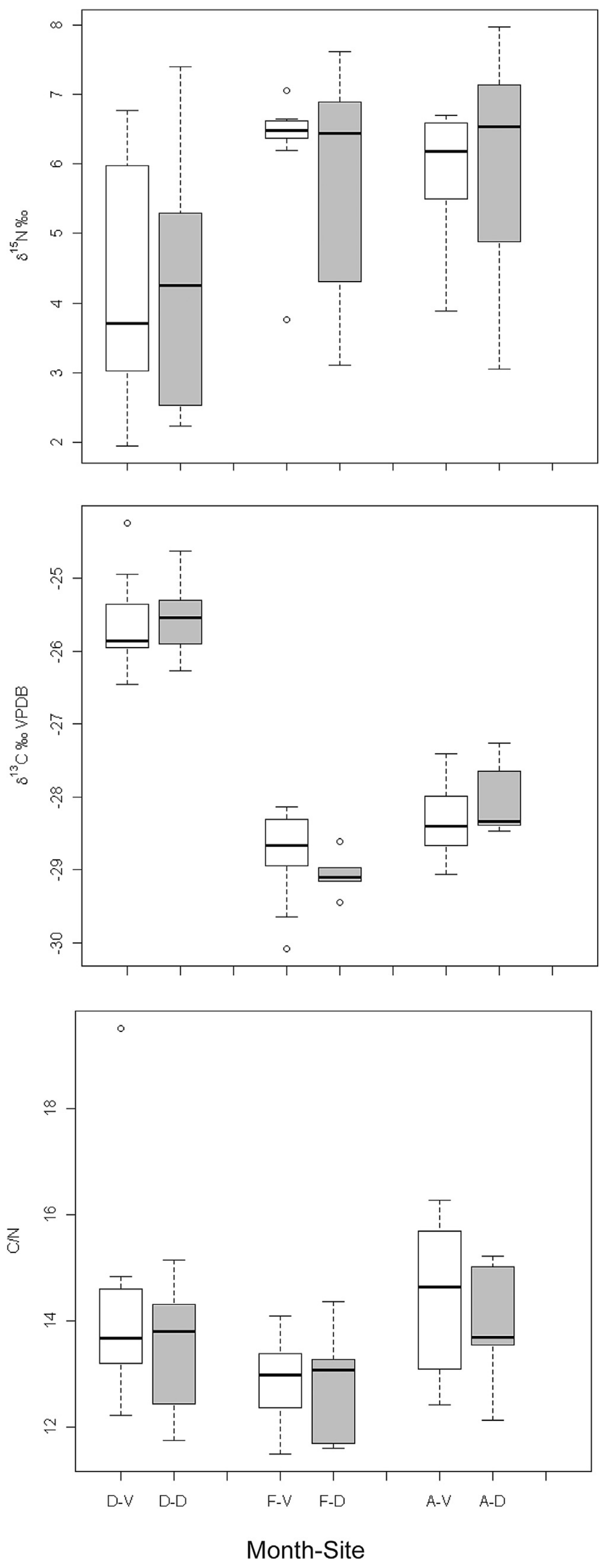

Fig. 1. Foliar $\delta^{15}N$, $\delta^{13}C$ and C/N of adult *Prosopis flexuosa* plants in three sampling times (D = December, F=February, A = April) and two landscape positions (V = interdune valley, white boxes, D = dune flank, gray boxes).

Table 1

Results from the generalized linear models, showing *t*-student and *p values* (in parenthesis) calculated with the glm function for the effect of different factors on foliar stable isotope composition and C:N ratios. Significant differences between the factor categories (highlighted in bold) are indicated by *p values* lower than 0.05. One, two and three asterisks indicate *p values* lower than 0.05, 0.01, and 0.001, respectively.

Factor categories	Foliar δ^{13}C	Foliar δ^{15}N	Foliar C/N
Sampling time and landscape effects on adult Prosopis flexuosa trees (dbt $\geq$ 10)			
Sampling time: Dec 07 – April 2008	**9.8 (2.1e-12***)**	**−2.4 (0.02*)**	−0.4 (0.71)
Sampling time: Feb 2008 – April 08	−1.9 (0.07)	0.5 (0.65)	**−2.7 (0.01*)**
Landscape: dune flank – interdune valley	0.8 (0.43)	0.1 (0.93)	−0.9 (0.4)
Age effects on all Prosopis flexuosa plants from interdune valleys			
Age: dbt class	−0.4 (0.68)	**−2.4 (0.02*)**	**3.9 (4.1 e-4***)**
Sampling time: Dec 07 – Feb 08	**−8.3 (7.95e-10***)**	**−2.5 (0.02*)**	1.7 (0.1)
Interaction (dbt*sampling time)	1.8 (0.08)	**3.0 (4.5 e-3**)**	**−2.4 (0.02*)**
Species effect (Prosopis vs other C3 plants) on adult plants			
Species: *P. flexuosa* – other species	**−4.1(1.51 e-4***)**	**3.5 (9.6 e-4***)**	**4.3 (8.7e-05***)**
Landscape: dune flank – interdune valley	−1 (0.32)	−1.3 (0.19)	1.6 (0.12)
Sampling time: Dec 07 – Feb 08	**−8.5 (5.34e-11***)**	**2.8 (0.007**)**	**−2.4 (0.02*)**
C3 vs C4 metabolism effect on adult plants			
Metabolism: C4 – C3		**−2.3 (0.02*)**	**3.6 (5.33 e-4***)**
Landscape: Dune flank – interdune valley		**−2.4 (0.02*)**	1.2 (0.23)
Sampling time: Dec 2007 – Feb 2008		**2.2 (0.03*)**	**−2.8 (0.01**)**

P. flexuosa plants with different dbt classes, indicative of age, did not show clear differences in δ^{13}C values (Fig. 2, middle panel). Plants with lower dbt (juveniles and seedlings) had lower δ^{15}N and higher C/N than larger plants (adults and young) suggesting the occurrence of N_2 fixation in younger plants (Fig. 2, top and bottom panels, and Table 1). This pattern was clear in December, before the rains, but not in February, as reflected by the significant interaction between sampling time and dbt class (Fig. 2 and Table 1).

Among all C3 plants sampled, *P. flexuosa* had lower δ^{15}N and C/N, and higher δ^{13}C than other species before the rains (December-2007) (Fig. 3). C4 grasses from dune flanks had lower δ^{15}N than C4 plants growing in the interdune valleys, and C3 plants of both landscape units, suggesting the occurrence of N_2 fixation in dune grasses (Fig. 4).

Vegetation cover estimated with vegetation transects was higher in the interdune valley than in the dune flank (Table 2), with 78% cover (69% litter cover) in the interdune valley, and 64% cover (52% litter cover) in the dune flank. Trees were taller in interdune valleys (personal observations). Remote sensing indices followed the same pattern, with higher values for both, SATVI and NDVI in interdune valleys.

Soil moisture was generally higher in interdune valley soils, while nitrate concentrations were higher in dune flank soils, although with a high variability and many outliers (Fig. 5). Soil ammonium and moisture contents were spatially autocorrelated in interdune valleys, at a distance of 7 m and 5 m, respectively. The spatial variability represented 52% of the total variability for ammonium and 70.3% for soil moisture, as shown in the semi-variograms and the best fit models (spherical models for ammonium: range = 7.66, nugget = 0.133, sill = 0.277, Fig. 6c, and for soil moisture: range = 5.05, nugget = 0.041, sill = 0.14, Fig. 6e). Semi-variograms for ammonium concentrations and soil moisture in the dune flank, and nitrate concentrations in both landscape units show only nugget effects, indicating a lack of spatial autocorrelation (Fig. 6a, b, d and f). The linear model for nitrate concentrations, which did not present autocorrelation, indicated a significant effect of landscape units and number of vegetation touches above sampling point, with a higher concentration in the dune flank, and in points with a higher number of vegetation touches above the sampling point (Table 3).

4. Discussion

Among C3 plants, *P. flexuosa* had lower δ^{15}N values than other species, suggesting that it derives part of its N from atmospheric N_2 fixation. Particularly low δ^{15}N values were found in younger individuals, such as a few seedlings and juveniles. After the root system is fully developed, it might be more efficient to absorb soil nitrogen. This agrees with studies of *P. glandulosa*, where tree size was inversely related to the proportion of N derived from biological N_2 fixation (López Villagra and Felker, 1997). The high temporal variability of foliar δ^{15}N in *P. flexuosa* suggests that this species can use different sources of N, according to the availability in the soil related to pulse events, similar to *Acacia* species in the Kalahari desert (Aranibar et al., 2004). Before the rains, *Prosopis* may have reflected previously mineralized N, stored from the previous growing season. After the onset of the rainy season, increasing foliar δ^{15}N values suggest the absorption of recently mineralized N, enriched in ^{15}N by coupled nitrification-denitrification during wet pulses, and ammonia volatilization in drying soils (Mariotti et al., 1981; Robinson, 2001).

Another possible source of N to plants is N_2 fixation by non symbiotic bacteria associated with grass roots. Grasses, particularly *P. urbilleanum*, *Aristida mendocina*, *T. crinita*, and *S. leucophylla* from dune flanks, which have the C4 photosynthetic metabolism in theses arid areas, had lower δ^{15}N values than C3 plants, suggesting the occurrence of atmospheric N_2 fixation. Furthermore, grasses had lower δ^{15}N values in dune flanks than in interdune valleys, indicating higher N_2 fixation rates in dune flanks. Previous studies in the Kalahari and the Lamto savanna (Cote dÍvore) also reported differences between C3 and C4 plants, indicating a lower reliance on recently mineralized N or organic matter for C4 than C3 plants (Abbadie et al., 1992; Aranibar et al., 2008; Swap et al., 2004). Lower δ^{15}N values may also be caused by the absorption of ^{15}N depleted soil N. Grasses from the Kalahari showed a preference for nitrate in drier areas, even when cultivated in greenhouse conditions (Wang and Macko, 2011). Although the temporal and spatial variability of δ^{15}N values of grasses, with lower values in dune flanks before the rainy season, is more indicative of localized N_2 fixation than absorption of depleted nitrate, the occurrence of N_2 fixation in grasses should be tested with other methods (i.e., *in situ* quantifications of N_2 fixation by acetylene reduction assays, or identification of N_2 fixing heterotrophs associated with grass roots), using the species identified in this study as potential N_2 fixers.

The temporal and spatial variability of δ^{13}C and δ^{15}N values in adult *P. flexuosa* trees indicate a dynamic system controlled by summer precipitation, which relieve water stress (indicated by lower δ^{13}C values in the rainy season, February), increase N availability, and enhance microbial processes that enrich soil N sources, such as mineralization, denitrification, and ammonia volatilization

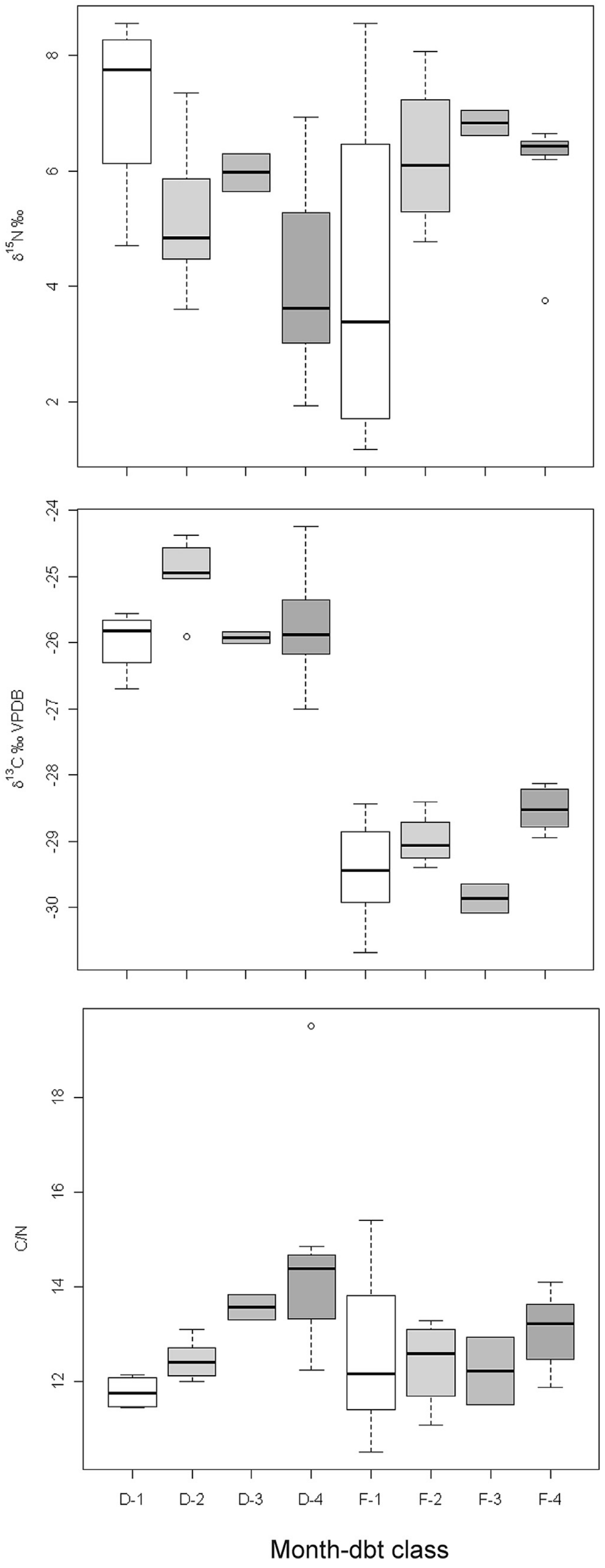

Fig. 2. Foliar $\delta^{15}N$, $\delta^{13}C$ and C/N of *Prosopis flexuosa* with different dbt (diameter at the base of the trunk) classes, in two sampling times (D = December, F=February) located in the interdune valley. Dbt classes correspond to 1-adults: dbt ≥ 10 cm; 2-young: 5 cm < dbt <10 cm; 3-juveniles: 1 cm < dbt ≤ 5 cm; and 4-seedlings: dbt≤1 cm.

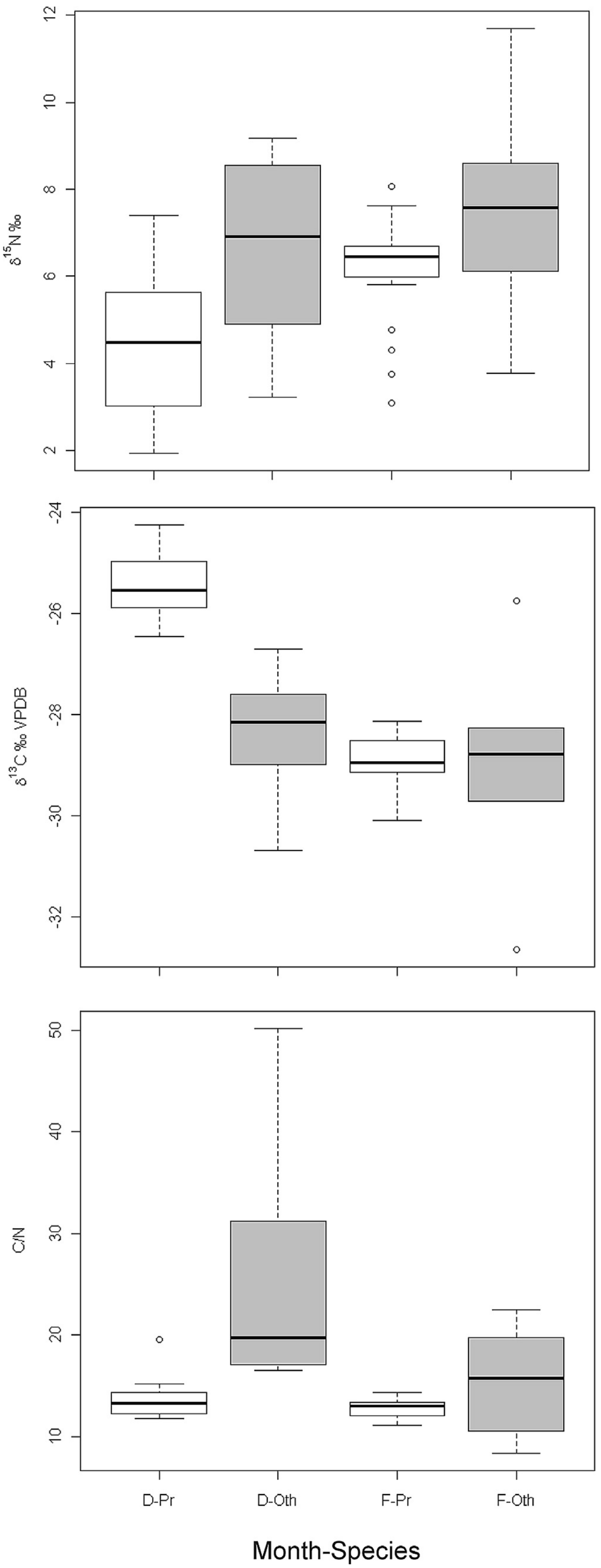

Fig. 3. Foliar $\delta^{15}N$, $\delta^{13}C$ and C/N of *Prosopis flexuosa* (Pr) and other C3 species (Oth) during two sampling periods (D = December, F=February).

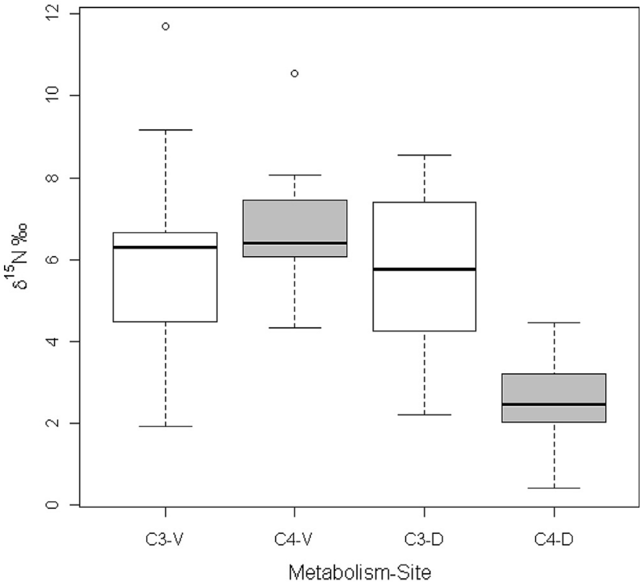

Fig. 4. Foliar $\delta^{15}N$ of C3 and C4 plants located in the interdune valley (V, white boxes), and in the dune flank (D, gray boxes).

(higher $\delta^{15}N$ in the rainy season). Given these responses to environmental changes, it was surprising to find similar water use efficiencies ($\delta^{13}C$ values) in both landscape units, contrary to our predictions. Based on the higher stomatal conductances found in interdune valleys than dune flanks in two occasions (1 day each, in December and February) during the same sampling period (Giordano et al., 2011), we expected groundwater coupling to relieve water stress in interdune valleys. Assuming constant internal conductance of CO_2 from the stomatal cavity to sites of carboxylation for the same species (but see Warren and Adams, 2006), the higher stomatal conductance in interdune valleys found by Giordano et al. (2011), but similar $\delta^{13}C$ in both landscape units found in this study suggest that plants in interdune valleys have higher photosynthetic rates, keeping *ci*/*ca* and water use efficiency constant in both landscape units, at a given sampling time. Leaf orientation, leaflet closure, and higher stomatal density in dune flank trees (Giordano et al., 2011) may also contribute to keep optimal water use efficiencies in both landscape units. The temporal change in $\delta^{13}C$ from dry to wet conditions indicates an atmospheric control of water use efficiency, according to ecophysiological studies in semiarid forests (Aranibar et al., 2006). Probably the phenotypic and physiologic plasticity of *P. flexuosa* allows it to thrive in different landscape units, maintaining internal balance, and increasing CO_2 fixation and productivity in interdune valleys.

In order to evaluate the ability of these ecosystems to provide C and N to the local community and irrigated oases, C and N inputs and outputs given by nitrogen fixation (by symbiotic associations with *P. flexuosa*, non-symbiotic associations with grasses, and by biological soil crusts), groundwater nitrate uptake, net ecosystem carbon exchange, fuel consumption, and manure exports should be quantified. Biological N_2 fixation of potential N_2 fixers, identified in this study, could be quantified using reference plants with similar root systems in nearby positions, and $\delta^{15}N$ analysis of soil organic and inorganic N end members.

Table 2
Vegetation cover, SATVI and NDVI in the interdune valley and dune flank analyzed. For SATVI and NDVI, mean and standard error of 57 pixels are indicated.

Landscape unit	Vegetation cover, %	SATVI	NDVI
Interdune valley	78	0.07 ± 0.01	0.27 ± 0.03
Dune flank	64	0.04 ± 0.01	0.21 ± 0.02

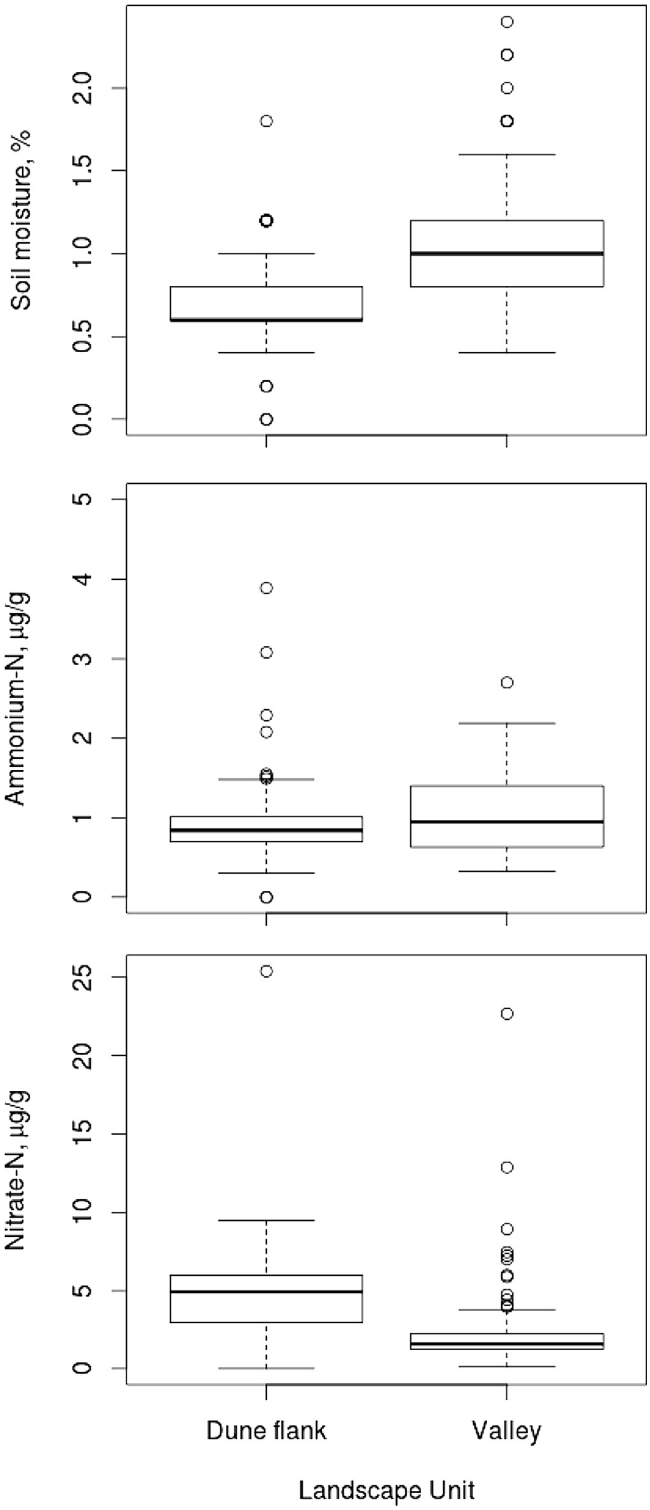

Fig. 5. Soil moisture, ammonium and nitrate contents in the dune and interdune valley. Boxplots indicate the median, first and third quartiles; whiskers extend to the most extreme data point, which is no more than 1.5 times the interquartile range from the box; circles indicate outlying data points falling beyond whisker limits.

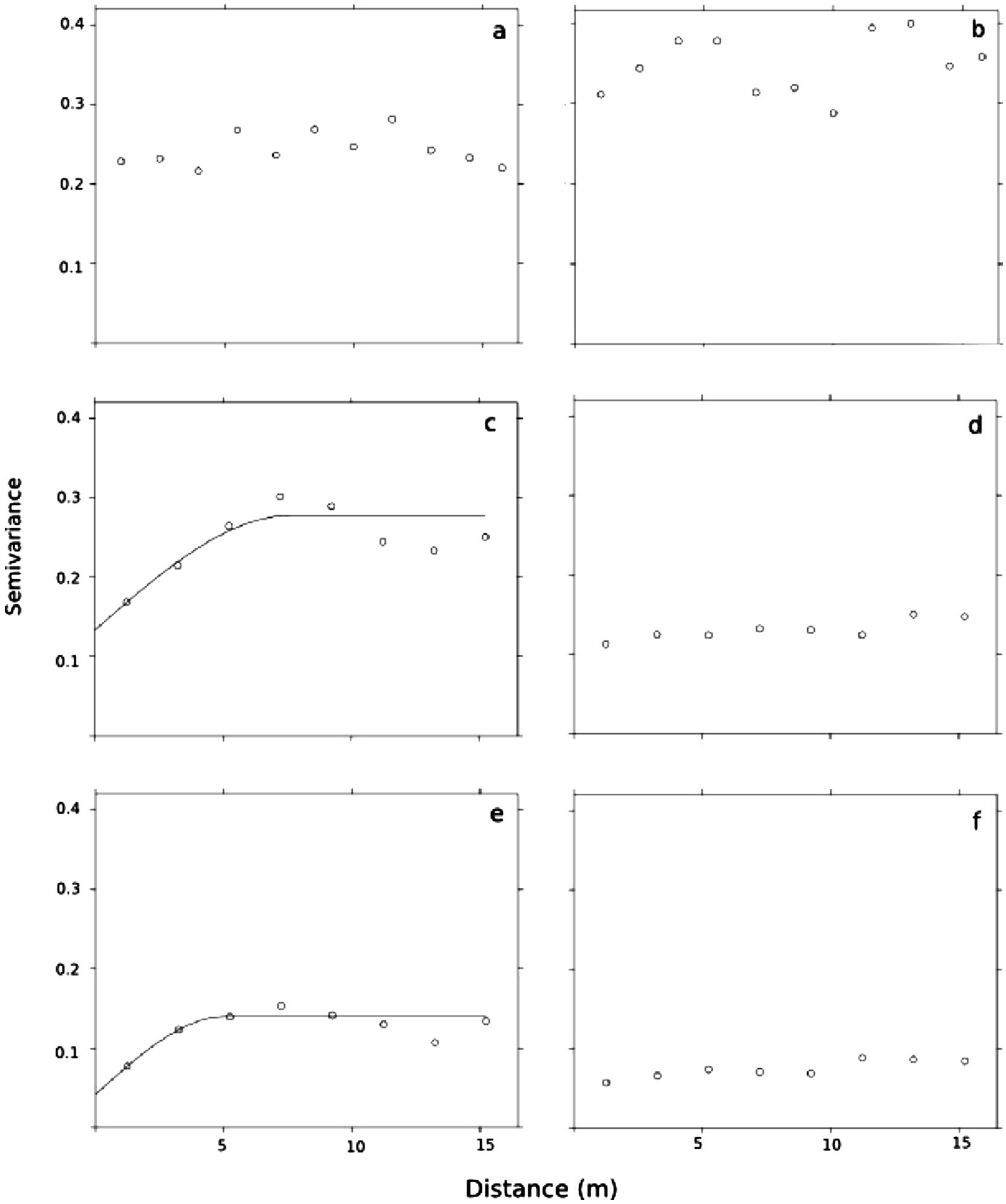

Fig. 6. Empiric semi-variograms of soil variables: nitrate in top panels (a and b), ammonium in medium panels (c and d), and moisture in bottom panels (e and f) for the interdune valley (left panels a, c, and e) and dune flank (right panels, b, d, and f) soils. Adjusted semivariogram models are shown for ammonium (c) and moisture (e) of the interdune valley.

The lack of spatial autocorrelation in nitrate from both landscape units, and soil moisture and ammonium from the dune flank, contrary to our predictions, suggests that the landscape is not dominated by fertility islands, probably reflecting a low degradation of the system. These data do not support the idea that soil heterogeneity in dune flanks encourages N_2 fixation. Soil nitrate and ammonium sampled at a single time may not reflect N availability during the entire growing season, given the high temporal variability of soil mineral N. However, the low heterogeneity found in this study agrees with studies in relatively undisturbed areas of the Kalahari (Feral et al., 2003) and the Monte Deserts (Abril et al., 2009), which did not find a large heterogeneity in soil nutrients and organic matter. Other studies describe large differences among soil nutrients and organic matter concentration, and litter inputs in distinct vegetation patches, such as under tree/shrub canopies and open spaces, especially during the rainy season (Abril et al., 2009; Alvarez et al., 2009b; Aranibar et al., 2003b, 2011; Guevara et al., 2010; Vazquez et al., 2011). However, these distinct patches may not represent the dominant landscape features in the study site and other woodlands, where vegetation cover is high, and numerous life forms, such as several species of trees, shrubs, grasses and forbs overlap. Above ground diameters of shrub and tree canopies generally exceed 1 m in these woodlands, decreasing the extension of bare soil patches. Belowground areas of influence are much higher than above ground for *P. flexuosa*, *L. cuneifolia*, *Bulnesia retama*, and probably most plants of interdune valleys (Abril et al., 2009; Guevara et al., 2010; Rossi and Villagra, 2003), homogenizing the distribution of mineralized nitrogen. Runoff and subsurface transport given by the convective characteristics of precipitation in the area, with intense and short events, may further homogenize

Table 3
Results from the generalized linear model showing t-student and *p values* (in parenthesis) from the glm function for the effect of different factors on soil nitrate concentrations. Significant effects of different factors (highlighted in bold) are indicated by *p values* lower than 0.05. One, two and three asterisks indicate *p values* lower than 0.05, 0.01, and 0.001, respectively.

Factor	t-student *(p value)*
Landscape unit: dune flank − interdune valley	**−5.9 (1.31e-08***)**
Vegetation (number of vegetation touches above sampling point)	**3.1 (2.13e-3**)**
Soil moisture	0.0 (0.97)

soil nitrate. The significant effect of vegetation on nitrate concentration (i.e., reported in the linear model) suggests an association between these two variables, although the high vegetation cover and the other processes mentioned above maintain a relatively low heterogeneity of soil resources.

The spatial autocorrelation of ammonium in the interdune valley may reflect processes related to its output from the system, such as ammonia volatilization in drying alkaline soils (Schlesinger and Peterjohn, 1991), affected by temporally variable soil moisture conditions, instead of its production. The similar scale of autocorrelation for ammonium and soil moisture (between 5 and 7 m) supports this idea. The presence of large and tall trees in interdune valleys, and the occurrence of hydraulic lift by phreatophyte plants may increase soil moisture content and heterogeneity, which would affect ammonia volatilization rates. The lack of spatial autocorrelation in dune flanks, contrary to our prediction, may also be given by the sampling scale, every 50 cm, which does not capture small fertility patches associated with grasses. In the Chihuahuan desert grasslands, soil nutrients were autocorrelated at spaces of 20 cm (Schlesinger et al., 1996).

Differences of nutrient dynamics between high and low topographic positions have been described in other systems, where surface runoff dominates nutrient transport (Puigdefábregas, 2005; Tongway and Ludwig, 1990). In the study site, where precipitation is scarce, N fixed to organic matter and litter may be transported to low topographic positions by aeolian processes, as suggested by the finer texture of interdune valley sediments, and nitrate may be transported by subsurface water flow (Aranibar et al., 2011). Furthermore, rooting patterns of *P. flexuosa* are different in both landscape units, with a higher horizontal extension in interdune valleys (up to 19 m from the trunk) than in dune flanks, where roots concentrate below the canopies (Guevara et al., 2010). Our and previous findings allow us to hypothesize that higher biological N_2 fixation in dune flanks, and the patchy root system may cause a transport of N to interdune valleys by nitrate leaching, subsurface transport, and wind erosion. The higher productivity observed in interdune valleys may be sustained not only by groundwater access, but also by nitrogen fixed in dune flanks and transported to valleys, causing a positive reinforcement of dune-interdune differences of vegetation structure and productivity. Tracing experiments using ^{15}N labeled nitrate could be used to test the occurrence of N transport from dune flanks to interdune soils and plants.

5. Conclusions

Dune and interdune valleys in the Monte Desert showed differences in N cycling, with higher indications of N_2 fixation in dune flanks. Young *P. flexuosa* plants and C4 grasses from dune flanks may derive part of their nitrogen from biological N_2 fixation, while adult *P. flexuosa* plants in interdune valleys seem to absorb mainly recently mineralized soil N, during pulses of water availability. *P. flexuosa* showed a clear response to changes in atmospheric conditions, decreasing water use efficiency and increasing N content during the rainy season, but showed similar characteristics in high and low landscape positions. Groundwater access did not change *P. flexuosa* water use efficiency, suggesting that both, photosynthesis and stomatal conductance are higher where groundwater is available, resulting in a higher productivity in interdune valleys as reflected by remote sensing indices.

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