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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