

Does land use change alter water and nutrient dynamics of phreatophytic trees in the Central Monte desert?

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ABSTRACT

In the woodlands of the Central Monte desert (Argentina), phreatophyte vegetation is exposed to different levels of disturbance. Livestock and settlement activity produce mainly nutrient inputs and partial vegetation removal, with a consequent reduction on water use by vegetation. We hypothesize that because of the increased soil water and nutrient resources associated with livestock stations, water stress will be relieved for the remaining *Prosopis flexuosa* trees, favouring water and nutrient status, and plant growth at the plant scale. The goal of this research was to analyse the physiological responses of *P. flexuosa* trees that grow in interdune valleys under different land uses, and the changes in relative importance of environmental factors controlling these responses. We compared the ecophysiological responses of adult *P. flexuosa* trees in two contrasting types of disturbance: disturbed (livestock stations) and relatively undisturbed (control woodlands) stands, in the 2011–2013 growing seasons. Pre-dawn and midday leaf water potential and stomatal conductance were higher in livestock stations than in control woodlands, suggesting a better water status of *P. flexuosa* in livestock stations. Isotopic composition (lower $\delta^{13}\text{C}$, and higher $\delta^{15}\text{N}$) and foliar nitrogen concentration (lower C:N ratios) indicated lower water use efficiency and higher nitrogen absorption from the soil in livestock stations. Both growth of new leaves (foliar area) and the length of young branches were higher in the first season for both land uses, but branch length was higher in livestock stations. This is consistent with the idea that vegetation removal and nutrient contribution of settlement activities improved water and nutrient status of remaining vegetation, and modified the relative importance of factors controlling ecophysiological processes. We concluded that physiological responses and vegetative growth of *P. flexuosa* were not only affected by meteorological conditions (rainfalls, vapour pressure deficit), but also by the ecohydrological changes caused by changes in land use. Copyright © 2015 John Wiley & Sons, Ltd.

KEY WORDS Algarrobo woodlands; disturbed arid land; drought responses; phreatophytes; *Prosopis* woodlands; tree physiology; water relationships

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INTRODUCTION

In arid-semiarid ecosystems, spatial and temporal variability of resources (Noy-Meir, 1973; Evans and Ehlerer, 1994; Aguiar and Sala, 1999) is produced both by natural and anthropogenic causes, generating extreme conditions of supply and demand of resources to plants (Knapp *et al.*, 2008). Human disturbances, including changes in land cover and use, affect plant water use as well as the amount and distribution of soil carbon and other nutrients (Vitousek *et al.*, 1997; Jackson *et al.*, 2000; Finzi *et al.*,

2011; Marchesini *et al.*, 2012). These changes in the hydrological and biogeochemical cycles could influence plant growth and plant ecophysiology (Mooney *et al.*, 1999; Buchmann, 2002).

Physiological processes are the result of the combined effects of physiological and environmental factors (Tuzet *et al.*, 2003; Christmann *et al.*, 2007). For example, stomatal conductances respond not only to shifts in the atmospheric conditions at short time intervals, but also respond to soil moisture conditions through abscisic acid, which is an important regulator of long-term stomatal response under drought stress (Comstock, 2002; Damour *et al.*, 2010; Duursma *et al.*, 2014). In addition, changes in soil resource (water and nutrients) associated with the removal of woody plants in 'livestock stations' (Tolsma *et al.*, 1987; Todd, 2006; Meglioli *et al.*, 2014) can affect

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plant physiological parameters such as growth, conductance, water use efficiency, photosynthesis, nutritional and water status (Mateo *et al.*, 2004).

In water-limited ecosystems, plants with deep roots that are coupled to groundwater present complex links between water, soil and vegetation (Jobbágy *et al.*, 2011; Villagra *et al.*, 2013). During periods of limited soil moisture and nutrients, phreatophytes utilize water at the capillary fringe to mitigate water stress (Gou and Miller, 2013). Moreover, hydraulic redistribution by mesquite roots is a potential mechanism that may provide moisture in the soil surface layers (Caldwell *et al.*, 1998; Hultine *et al.*, 2004; Seyfried *et al.*, 2005). *Prosopis*, distributed in most arid regions around the world, has been well-studied because of their great development of annual biomass (higher than predicted by precipitation) and their ability to survive in areas with very low rainfall (less than 200 mm annually) (Burkart and Simpson, 1977; Adams *et al.*, 2010). Numerous ecophysiological studies for *Prosopis* spp. were first done in the Northern Hemisphere (*Prosopis glandulosa*, *Prosopis velutina*) (Easter and Sosebee, 1975; Nilsen *et al.*, 1983; Sosebee and Wan, 1987; Ansley *et al.*, 1992; Snyder and Williams, 2000; De Soyza *et al.*, 2004) and then in South American arid areas (*Prosopis flexuosa*, *Prosopis chilensis*, *Prosopis alata*, *Prosopis argentea*) (Alvarez and Villagra, 2009; Villagra *et al.*, 2010; Giordano *et al.*, 2011; Vega Riveros *et al.*, 2011; Meglioli *et al.*, 2012). In the Central Monte desert of Argentina, *P. flexuosa* ('algarrobo dulce') is a dominant tree species that grows in dune and interdune valleys (Alvarez and Villagra, 2009).

The phenotypic plasticity and the ecophysiological responses of *P. flexuosa* result from the combination of phreatophytism and drought tolerance (Guevara *et al.*, 2010; Giordano *et al.*, 2011). Measurements of leaf water potential, osmotic potential and turgor potential indicated that growth of *P. flexuosa* trees in the Ñacuñán Biosphere Reserve (Cavagnaro and Passera, 1993) and the interdune valleys of the Telteca Natural Reserve (Giordano *et al.*, 2011) was relatively independent of the amount of summer rainfall. In contrast, growth of adult individuals in dune flanks, disconnected from groundwater, was strongly dependent on summer rainfall (Villagra *et al.*, 2010; Giordano *et al.*, 2011). Stable isotope composition of xylem water, groundwater and precipitation evidence that adult *P. flexuosa* trees from interdune valleys access groundwater, and use water resources from both, the upper soil layers and groundwater (Giordano *et al.*, 2011; Jobbágy *et al.*, 2011). However, groundwater uptake requires extra energy to overcome gravitational force compared with surface soil water uptake (Gou and Miller, 2013). Previous studies, such as the aforementioned, focused mainly on intraspecific comparisons between different landscapes positions, while our understanding of

the ecophysiological responses to changes derived from human activities remains incomplete.

Traditional livestock settlements (livestock stations) produce focused disturbances in the *P. flexuosa* woodlands with direct effects on vegetation structure (reduced coverage and changes of functional group dominance) and soil characteristics (distribution of water and solutes) (Villagra *et al.*, 2009; Goirán *et al.*, 2012; Meglioli *et al.*, 2014). Previous studies in the Central Monte found that constant nutrient deposition and vegetation removal near corrals and other areas where livestock congregate resulted in increased soil nutrient and moisture content, deep drainage of rainfall, nitrate leaching from the surface to the aquifer and lower vegetation cover (Aranibar *et al.*, 2011; Jobbágy *et al.*, 2011; Goirán *et al.*, 2012; Meglioli *et al.*, 2014). Although at the ecosystem scale, livestock effects have negative consequences on groundwater quality and vegetation, the effects can be positive at the plant scale, particularly for the *P. flexuosa* trees that remain in the area.

In this context, we hypothesize that because of the observed increase in soil water and nutrient resources associated with livestock stations, water stress will be relieved for the remaining *P. flexuosa* trees, favouring water and nutrient status, and plant growth at the plant scales. In addition, because soil moisture differs in both land uses, we postulated that physiological adjustments (e.g. stomatal conductance) by *P. flexuosa* trees should change in response to internal and external controls. Thus, atmospheric controls will be more important in livestock stations because soil water availability is not limiting in those sites. The ecophysiological changes will be reflected by the following predictions: (1) lower water stress, indicated by higher leaf water potential, lower foliar $\delta^{13}\text{C}$ and higher stomatal conductance, (2) better nutritional status, indicated by foliar N content, (3) weaker relationships between ecophysiological variables (stomatal conductance and leaf water potential) and soil moisture, (4) stronger relationships between ecophysiological variables (stomatal conductance and foliar $\delta^{13}\text{C}$) and atmospheric conditions (air vapour pressure deficit), and (5) higher vegetative growth of new leaves and branches in *P. flexuosa* trees from livestock stations than in those from control woodlands.

MATERIALS AND METHODS

Study area

The study sites are located in the Telteca Reserve, approximately 120 km northeast of Mendoza city, Argentina. The study area, located in the Central Monte desert, is comprised of vast sandy aeolian plains with lowland (interdune valleys) and upland (dunes) areas. The climate is arid with hot summers (48 °C absolute maximum) and cold

(-10°C absolute minimum), dry winters. The mean annual temperature is 18.5°C and the mean annual precipitation is 156 mm, with precipitation occurring almost exclusively during the spring and summer (from October to March) (Meglioli, 2015). Livestock stations and relatively undisturbed woodlands are located in interdune valleys, where groundwater is found at depths of 6–15 m.

The shrubby steppe dominated by *Zygophyllaceae* and the open woodland dominated by *P. flexuosa* DC (Fabaceae, Mimosoidae) are the characteristic plant communities of the Central Monte (Rundel *et al.*, 2007). *P. flexuosa*, growing as either a tree reaching 10 m in height, or a large shrub, is a facultative phreatophyte with an extended root system which acquires water from relatively shallow groundwater resources (Alvarez and Villagra, 2009). Although individuals of *P. flexuosa* live in different topographic positions of the landscape (dune crests, midslopes, footslopes and interdune valleys), only adult individuals on the lowland areas were sampled in this study.

Experimental design

In four paired valleys of livestock stations and relatively undisturbed ‘control’ woodlands from the Telteca Reserve, we compared the vegetative growth and physiological status of *P. flexuosa* trees which, based on their large size, extensive root systems and previous stable isotope studies, are coupled to groundwater. Three paired sites were

described by Meglioli *et al.* (2014) in a previous study (site 1: ‘La Primavera’; site 2: ‘Las Delicias’ and site 3: ‘Las Hormigas’). We also added one livestock station (site 4: ‘Las Cañas’; $32^{\circ}25'49.4''\text{S}$, $68^{\circ}02'22.0''\text{W}$) with its paired control woodland ($32^{\circ}25'03.5''\text{S}$, $68^{\circ}03'27.3''\text{W}$) (Figure 1). Table I provides a description of the vegetation structure, the manure deposition, the inter-tree distance and the depth to the water table at each study site. Livestock stations had lower total vegetation cover (mainly shrubs and forbs-grasses) and higher manure cover than control woodlands. Moreover, distances from a *P. flexuosa* tree to its nearest woody plant, an indicator of tree density, were greater in livestock stations. The depths to water table are similar for both land uses, ranging from 8.2 to 9.7 m.

We selected five erect adult individuals in each study site ($n=40$). Measurements were performed at eight sampling times 14 to 15 February 2011, 19 to 20 April 2011, 01 to 03 December 2011, 13 to 14 March 2012, 18 to 19 April 2012, 13 to 15 December 2012, 22 to 23 March 2013 and 29 to 30 April 22013. Because of logistic limitations it was not possible to perform all measurements at all sites on all dates.

Environmental measurements

Monthly rainfall and temperature throughout the experimental period were recorded from the meteorological station, ‘El Pichón’ ($32^{\circ}22'59.0''\text{S}$; $68^{\circ}03'14.0''\text{W}$), at the Telteca Reserve. To obtain a better environmental

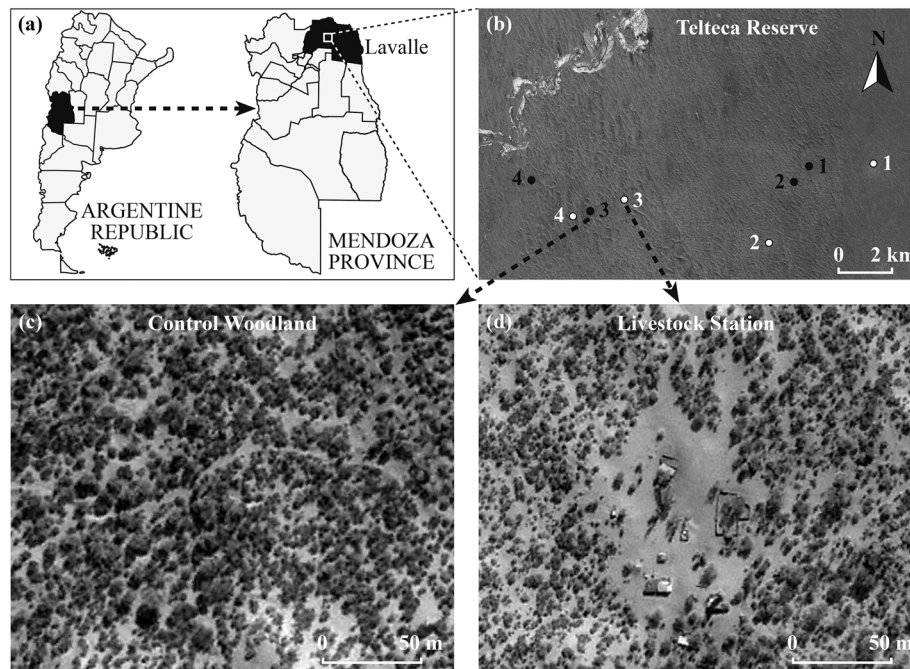


Figure 1. Maps of the Argentine Republic (a) and Mendoza Province (b). A satellite image marks the location of the control woodlands (black mark) and the livestock stations (white mark) in the Telteca Reserve (c). Satellite images with zoom of a control woodland (d) and of paired livestock station (e). Source for the satellite images was Google Earth <http://earth.google.es>.

Table I. Description of each study site.

| Site characterization | Control woodlands | | | | Livestock stations | | | |
|--|-------------------|--------|--------|--------|--------------------|--------|--------|--------|
| | Site 1 | Site 2 | Site 3 | Site 4 | Site 1 | Site 2 | Site 3 | Site 4 |
| Total vegetation cover, % ^a | 68.3 | 60.7 | 65.0 | 60.0 | 7.7 | 39.3 | 14.0 | 26.7 |
| Trees cover, % ^a | 33.0 | 32.7 | 29.3 | 47.0 | 7.7 | 38.7 | 13.0 | 24.0 |
| Shrubs cover, % ^a | 23.3 | 34.0 | 44.3 | 36.0 | 0.0 | 2.7 | 2.0 | 1.0 |
| Forbs-grasses cover, % ^a | 36.0 | 27.3 | 4.0 | 19.0 | 0.0 | 1.0 | 0.0 | 5.3 |
| Manure cover, % ^a | 2.7 | 3.3 | 2.3 | 3.0 | 18.3 | 23.3 | 27.7 | 27.0 |
| Inter-tree distances, m ^b | 2.8 | 4.8 | 5.1 | 5.1 | 8.0 | 13.6 | 10.2 | 9.4 |
| Groundwater depth, m ^c | 8.4 | 9.5 | 9.7 | — | 9.6 | 8.3 | 9.6 | 8.2 |

^a Data indicate average percent covers, obtained with the point-quadrat method using three 30-m linear transects at each site.

^b Data indicate mean distances, at soil level, from the trunk of the *P. flexuosa* tree to the trunk of the nearest woody plant neighbour. Measurements were done on five individuals at each site.

^c Data indicate water table levels, taken from a borehole at each site. Reported data represent mean values in the period 2011–2014.

characterization, in livestock stations 1 (32° 24' 45.1" S; 67° 54' 53.8" W) we installed air temperature (C°) and relative humidity (%) sensors, which record daily measurements using a HOBO Pro Data Logger. This additional station was useful to describe diurnal fluctuations of vapour pressure deficit (*VPD*) for each physiological sampling day. Air temperature and relative humidity data were used to calculate the *VPD* using a calculation given by Murray (1967).

Soil water content (θ) under the canopy, 1 m North of each tree trunk, of *P. flexuosa* was determined for samples (100 g) collected at 0.25-m, 0.5-m and 1.0-m depths with a hand soil auger. We determined gravimetric water content after drying the soil samples in the laboratory at 105 °C for 48 h. Soil samplings were performed only under tree canopies in order to avoid variability among soil microsites, but previous studies found that the difference between land uses occurs in all microsites (Meglioli, 2015).

Physiological measurements

Plant water status was assessed by measurements of leaf water potential (Pre-dawn and midday) and leaf conductance to water vapour (morning and midday). For logistic reasons (accessibility to sampling sites) the measurements were done during two consecutive days at the same time of day, in an effort to ensure similar sampling conditions for each paired site. So, sites 1 and 2 were sampled the same day, and sites 3 and 4 the following day. The order of sampling was selected randomly for the different sampling times.

Leaf water potential. Pre-dawn (Ψ_{PD} , 4:00 to 6:30 h) and midday (Ψ_{MD} , 13:00 to 15:30) leaf water potentials were determined with a pressure chamber (Scholander *et al.*, 1965). For each individual, we cut two terminal twigs (>2-mm diameter) with new expanded leaves, and placed them in plastic bags until analysis, which was done within

one hour of collection. We used the averaged data of each individual for further analyses.

Leaf conductance to water vapour. Morning (8:00 to 10:00 h) and midday (12:00 to 14:00 h) leaf conductance to water vapour (*gs*) were assessed using two steady-state diffusion porometers (SC-1, Decagon Devices, Pullman, WA, USA). We measured two or three abaxial leaves from each individual since December 2011. Measurements were almost simultaneously determined with the two porometers, with at most 15-min differences between paired sites. In order to compare measurements between two porometers, we converted conductance values using simple linear regressions, which were obtained, prior to sampling, by simultaneous measurements on the same leaves of other species. In March 2012 and March 2013, only morning *gs* measurements from two paired sites were analysed because the other sites were measured outside the established sampling schedule. Statistical analyses were computed for the mean values from each site.

Leaf nutrients and isotopic measurements

Variation in the isotopic composition of nitrogen among plants could be used to infer different acquisitions of plant resources, biological N fixation and translocation to the leaves (Amundson *et al.*, 2003). Carbon isotope discrimination of whole leaves can be used as an indicator of water-use efficiency in C3 plants (Ehleringer and Cooper, 1988; Ehleringer *et al.*, 1992) because of isotopic fractionation and changes of intercellular leaf CO₂ concentration during photosynthesis. We evaluated foliar natural abundance and concentration of stable carbon and nitrogen isotopes of *P. flexuosa*. We sampled mature leaves at two sampling times each growing season, trying to obtain two different leaf cohorts, representing different environmental conditions as in Giordano *et al.* (2011). The first sampling of each growing season (December)

generally represents carbon fixed during dry periods, before the onset of the seasonal rains, while the second cohort (February–March) represents carbon fixed under more humid conditions. Next, we sampled mature leaves at the beginning and onset of each growing season during the experimental period (12 to 13 February 2011, 02 to 03 December 2011, 14 to 15 March 2012, 14 to 15 December 2012 and 20 to 22 March 2013).

We randomly collected 20–30 expanded leaves (located 2 to 3 m above ground) in each tree, including leaves from different expositions. Composite leaf samples were stored in paper bags, air dried in the field, oven-dried at 60 °C for 24 h in the laboratory, and finally ground with a mill. Isotopic compositions of dry leaf samples were analysed with a Delta Plus Isotope Ratio Mass Spectrometer in the Stable Isotope Laboratory at University of Arkansas (United States) and reported in the delta notation, considering Pee-Dee Belemnite (PDB) and atmospheric N₂ as standards for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, respectively (Mateo *et al.*, 2004). The obtained variables include $\delta^{13}\text{C}$, $\delta^{15}\text{N}$ and C:N ratio. The overall precision of the determinations was better than 0.2 per mil for $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$.

Vegetative growth measurements

Vegetative growth was evaluated by measuring the length of young branches and the leaf surface area at the end of the growing seasons (March 2012 and March 2013).

Young branches. We randomly selected 15 red–green young branches that were actively growing (located 2 to 3 m above the ground surface) from each tree and measured the length (cm) of the current years' growth, recorded the number of nodes per branch (n) and calculated the internodal length (cm) by using the ratio between the length of branches and the number of nodes.

Leaf surface area. We randomly sampled 10 to 15 mature leaves for each individual. The fully expanded and complete leaves were preserved inside plastic bags with wet paper and immediately measured in the laboratory after return from the field. We measured the leaf surface area (cm²) using a LI-3000A Portable Area Meter.

Statistical analyses

We compared the effects of land use and sampling time on soil moisture, vegetative growth and physiological variables of *P. flexuosa* using generalized linear mixed models (GLMM). For each model, we considered land use (livestock stations versus control woodlands) and sampling times (eight levels) as fixed factors, and sites (1, 2, 3 and 4) as random factors (with individuals nested within site). We ran models with and without the interaction between fixed factors, and we then selected the best model using Akaike's

information criterion (*AIC*) index, with a $dAIC > 2$. All variables followed a Gaussian distribution, except for number of nodes per branch, which followed a Poisson distribution. To run the models we used 'glmer' function of lme4 package (Bates and Maechler, 2009) of R implemented in Infostat software (Di Rienzo *et al.*, 2013).

Water relations of *P. flexuosa* for both land uses were tested using multiple linear functions between physiological variables and several environmental factors. Thus, the soil water content controls (*S*) were established from the relationships among plant water potential (Ψ_{PD} and Ψ_{MD}) and midday *gs* with soil moisture. The plant water status control (*P*) and the atmospheric demand control (*A*) were evaluated from the relationships between midday *gs* with Ψ_{PD} and air *VPD* respectively. To evaluate the relative importance (or strength of association) of internal (*P*) and external controls (*S* and *A*) on midday *gs*, we generated multiple models for each land use type (Control woodlands or Livestock stations). The selection of the best models and parameter estimation was performed for each analysis by the inference of multiple models (Burnham and Anderson, 2002). We considered additive combinations of fixed effects and models with different combinations of factors that were scored according to *AIC* weights (*wAIC*). The relative importance of each control (*S*, *P* and *A*) was calculated adding the *wAIC* of each model that included the parameter in the set of models. Candidate models that differed from the *AIC* of the best-fitting model (*AICc*) by < 4 were retained for the mean parameter estimation which was obtained using weighted model-averaging. Parameters were estimated by restricted maximum likelihood (REML) using the MuMIn package (Barton, 2014). In the analyses, we used individuals that included all variables measured for the same sampling time. All analyses were performed in R (R Development Core Team, 2013).

In order to evaluate controls on the water use efficiency of *P. flexuosa* for both land uses, we also analysed the linear regression and correlation between foliar $\delta^{13}\text{C}$ and air *VPD*, considering mean *VPD* from 8:00 to 14:00 h during the previous 30 days of each foliar sampling time, assuming that the carbon present in the sample was mainly fixed during morning to midday hours (based on Giordano *et al.*, 2011) of the previous month.

RESULTS

Environmental measurements

Accumulated summer precipitation at the end of the growing season was similar for 2010–2011 (141.3 mm) and 2011–2012 (163.6 mm) periods. However, the 2012–2013 growing season received lower rainfall (125.6 mm) than the historical average values for Telteca Reserve (156 mm annually). In the 2011–2012 growing season,

rainfall events were primarily concentrated in the spring, while in the other growing seasons they fell primarily in summer. In the 2011–2012 growing season, the average monthly temperatures ranged between 5.1 °C and 28.6 °C, with a mean maximum of 36.0 °C for the month of January. In the following growing season (2012–2013), average monthly temperatures showed similar values (fluctuations between 6.2 °C and 28.1 °C), although a high monthly mean (36.1 °C) was recorded in December. Therefore, December 2012 not only received no rainfall but also recorded higher average monthly temperature, determining a relatively dry period (Figure 2).

Diurnal climatic conditions for each date of physiological sampling showed that the VPD values were elevated at the beginning of summer, gradually decreasing with the advance of each growing season. However, VPD were higher in December 2013 compared to December 2012, reaching 6.35 kPa and 5.18 kPa respectively. Vapour pressure deficit also followed a similar pattern of daily fluctuation, reaching maximum values at 17:00 h and minimum values during pre-dawn hours (Figure 3).

Soil water contents under the canopy of *P. flexuosa* were higher in livestock stations than in control woodlands in all depths of the soil profiles, even in surface layers (0.25 m), where variability was higher (Figure 4). Sampling time had

a significant effect on soil water content at all depths, with higher values in December 2011 and April 2012 and lower values in December 2012. The interaction between fixed factors (land use and date) was not significant for any depth (Table II). The fluctuations of soil moisture showed the same pattern in both land uses and differing water availability. These fluctuations of soil moisture were related to rainfall dynamics. Accordingly, the 2011–2012 growing season (December 2011 to April 2012) began and finished with higher soil moisture than the others. The following growing season had lower soil moisture, caused by the low value of accumulated rainfall for that period (December 2012 to April 2013).

Physiological measurements

Pre-dawn leaf water potentials of *P. flexuosa* trees were higher in livestock stations than control woodlands throughout most of the sampling period. The maximum differences in Ψ_{PD} between land uses were 0.34 MPa and 0.32 MPa for March 2012 and December 2012, respectively. In addition, similar mean values for both land uses were obtained in December 2011 and April 2013. Models also showed significant changes associated with time of sampling, with higher average values in April 2011 and December 2011 (ranged from -0.62 to -0.86 MPa) and

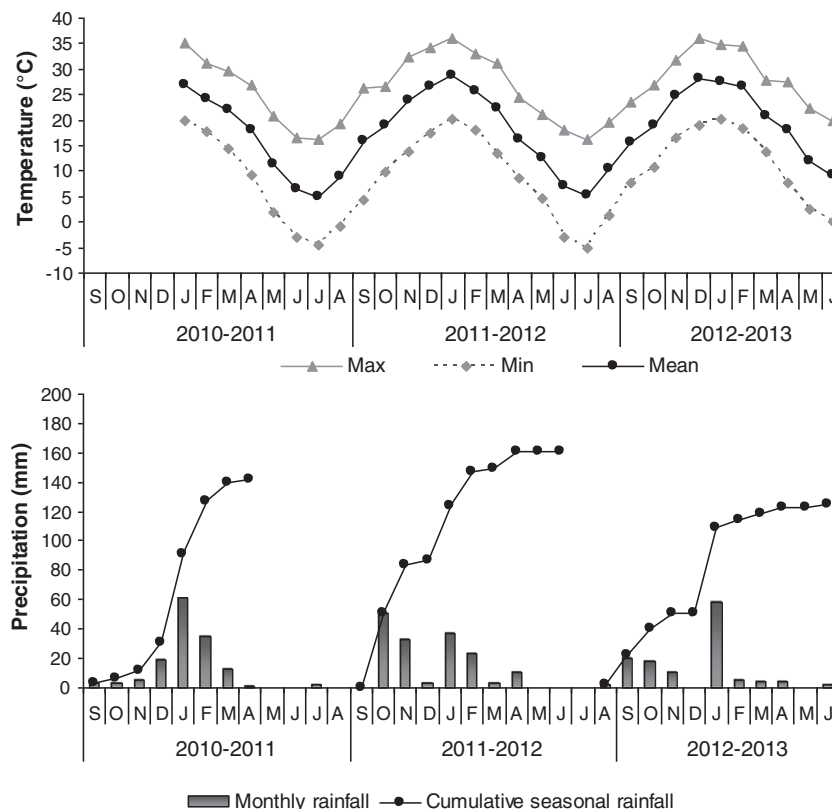


Figure 2. Seasonal climatic conditions throughout the experimental period.

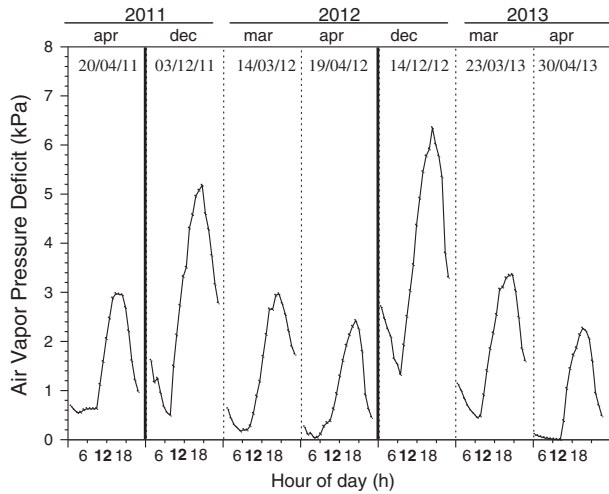


Figure 3. Diurnal fluctuations of vapour pressure deficit for each physiological sampling day. The vertical solid lines indicate the beginning of the growing season.

lower Ψ_{PD} in December 2012 and March 2013 (ranged from -1.82 to -2.15 MPa) (Figure 5a). The interaction between land use and sampling time did not improve the model ($dAIC < 2$, Table II), showing that Ψ_{PD} differences between two land use regimes were relatively constant throughout most of the sampling times. At midday, the individuals of livestock stations had also higher leaf Ψ_{MD} (from -2.97 to 3.96 MPa) than individuals of control woodlands (from -3.26 to -4.38 MPa), with significant differences (Figure 5b). The difference among both land uses appeared to be greater during the last growing season; however, the model without interaction between land use and sampling time had the lowest AIC index (Table II).

Morning leaf conductance to water vapour (g_s) differed significantly with land use (Table I), with higher mean values in livestock stations (97.8 – 202.4 $\text{mmol m}^{-2}\text{s}^{-1}$) than in control woodlands (52.6 – 151.9 $\text{mmol m}^{-2}\text{s}^{-1}$). The highest values in livestock stations, with maximum differences between treatments, were found in April 2012 and March 2013 (Figure 5c). Sampling time had a significant effect on morning g_s (Table II), with the lowest mean value in March 2012 for livestock stations and April 2012 for control woodlands (Figure 5c). Midday g_s showed a significant interaction between both fixed factors. At the beginning of December 2011, midday g_s were higher in *P. flexuosa* trees from control woodlands than in those from livestock stations (Figure 5d). During the start of the dry December 2012, midday g_s did not vary significantly between land use, and the values were lower (90.8 – 96.8 $\text{mmol m}^{-2}\text{s}^{-1}$) than during the other sampling periods (Figure 5d). The best models for g_s were those that included the interaction between both effects (land use and sampling time) (Table II).

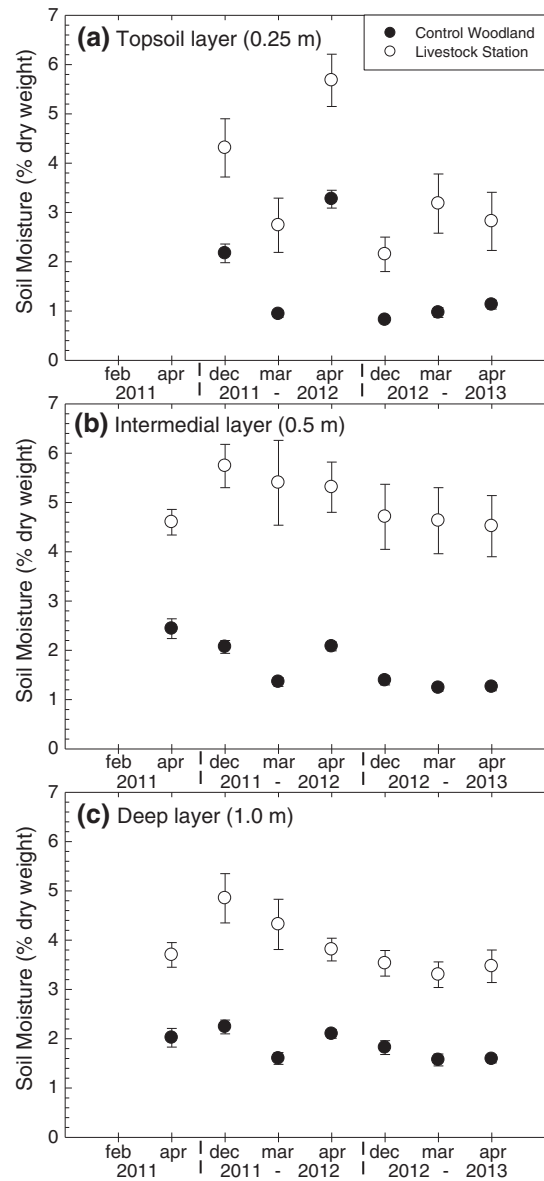


Figure 4. Soil moisture at 0.25 m (a), 0.5 m (b) and 1.0 m (c) depths beneath *P. flexuosa* trees in control woodlands (filled circles) and livestock stations (open circles) during the experimental period. Symbols are means ± 1 s.e.m.

Leaf nutrients and isotopic measurements

In the control woodlands, $\delta^{13}\text{C}$ values ranged from a minimum of -27.5‰ in March 2012 to a maximum of -26.2‰ in December 2012, whereas $\delta^{13}\text{C}$ values in leaves sampled from the livestock stations ranged from a minimum of -27.7‰ in March 2013 to a maximum of -27.0‰ in December 2011 (Figure 6a). The significant interaction between land uses and sampling times indicated that the differences between treatments were lower during the 2011–2012 growing season than in the other growing seasons (Table II). We also found differences in carbon

Table II. Results from generalized linear mixed models (GLMM) for response variables on *P. flexuosa*. We have included Akaike's information criterion (*AIC*) index and *p*-values (*p* < 0.05 as significant), considering land use and date as fixed factors. The best model, indicated by a *dAIC* > 2, is marked in boldface type.

| Variables on <i>P. flexuosa</i> | Models | <i>AIC</i> | Land use | Date | Interaction |
|--|--------|------------|----------|---------|-------------|
| Soil moisture under the canopy | | | | | |
| Layer at 0.25 m (%) | 1 | 333.5 | <0.0001 | <0.0001 | |
| | 2 | 334.2 | <0.0001 | <0.0001 | 0.0995 |
| Layer at 0.5 m (%) | 1 | 238.0 | <0.0001 | <0.0001 | |
| | 2 | 241.2 | <0.0001 | <0.0001 | 0.2432 |
| Layer at 1.0 m (%) | 1 | 173.0 | <0.0001 | <0.0001 | |
| | 2 | 175.4 | <0.0001 | <0.0001 | 0.1777 |
| Physiological | | | | | |
| Pre-dawn water potential (MPa) | 1 | 29.6 | 0.0055 | <0.0001 | |
| | 2 | 27.9 | 0.0055 | <0.0001 | 0.0342 |
| Midday water potential (MPa) | 1 | 259.6 | <0.0001 | <0.0001 | |
| | 2 | 260.0 | <0.0001 | <0.0001 | 0.1053 |
| Morning stomatal conductance (mmol m ⁻² s ⁻¹) | 1 | 1951.0 | 0.0475 | <0.0001 | |
| | 2 | 1942.5 | 0.0475 | <0.0001 | 0.0024 |
| Midday stomatal conductance (mmol m ⁻² s ⁻¹) | 1 | 2147.7 | 0.9475 | <0.0001 | |
| | 2 | 2110.0 | 0.9475 | <0.0001 | <0.0001 |
| Leaf nutrients and isotopic | | | | | |
| ¹³ C/ ¹² C | 1 | 428.4 | <0.0001 | <0.0001 | |
| | 2 | 422.2 | <0.0001 | <0.0001 | 0.0069 |
| ¹⁵ N/ ¹⁴ N | 1 | 646.7 | <0.0001 | <0.0001 | |
| | 2 | 633.9 | <0.0001 | <0.0001 | 0.0004 |
| C:N ratio | 1 | 552.6 | <0.0001 | <0.0001 | |
| | 2 | 553.2 | <0.0001 | <0.0001 | 0.1194 |
| Vegetative growth | | | | | |
| Branch length (cm) | 1 | 9041.8 | 0.0223 | <0.0001 | |
| | 2 | 9042.5 | 0.0223 | <0.0001 | 0.2513 |
| Internodal length (cm) | 1 | 3307.3 | 0.3033 | 0.0001 | |
| | 2 | 3302.6 | 0.3033 | 0.0001 | 0.0182 |
| Nodes per branch (n) | 1 | 1253.6 | 0.0438 | <0.0001 | |
| | 2 | 1253.4 | 0.0438 | <0.0001 | 0.1416 |
| Leaf surface area, one pinnae pair (cm ²) | 1 | 4163.7 | 0.705 | 0.0001 | |
| | 2 | 4164.5 | 0.705 | 0.0001 | 0.2770 |

isotopic composition between leaves of the first (December) and second (March) cohorts, for the two consecutive experimental periods. Leaf $\delta^{15}\text{N}$ values of *P. flexuosa* trees were higher in individuals from livestock stations (from 7‰ to 7.8‰) than in those from control woodlands (from 3.5‰ to 5.7‰). Control woodlands also had greater fluctuations in leaf $\delta^{15}\text{N}$ throughout the sampling period, showing one growing season (December 2011 to March 2012) with $\delta^{15}\text{N}$ values which decreased with the seasonal progress (Figure 6b). However, at the start of the second growing season (December 2012 to March 2013) $\delta^{15}\text{N}$ values were slightly larger than during other sampling times. The interaction between fixed factors yielded better model performance, showing lower *AIC* values (Table II) for leaf $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values. Foliar C:N ratios were lower in livestock stations, but increased with seasonal progress for both land uses (Figure 6c). Models without interaction between fixed factors had lower *AIC* values (Table II).

Relationships between ecophysiological measurements

In control woodlands, the Ψ_{PD} showed a weak positive relationship, with a marginal significance, to soil moisture ($\Psi_{PD} = 0.37 \times \theta - 2.06$; $r^2 = 0.17$; $P = 0.0418$), whereas in disturbed woodlands the Ψ_{PD} did not show relationship with soil moisture ($r^2 = 0.03$; $P = 0.41$). The Ψ_{MD} were not correlated with soil water content under the canopy of trees, both from control woodlands ($r^2 = 0.12$; $P = 0.14$) and from livestock stations ($r^2 = 0.07$; $P = 0.24$).

Midday *gs* of *P. flexuosa* trees did not show a significant response to increasing soil water content for both land uses (Figure 7a). Midday *gs* of *P. flexuosa* trees showed a positive linear response to increasing Ψ_{PD} in control woodlands, which was insignificant in livestock stations (Figure 7b). We also detected a decrease of *gs* as air *VPD* increased in livestock stations (Figure 7c). The model including all parameters (*S*, *P* and *A*) was better (lower

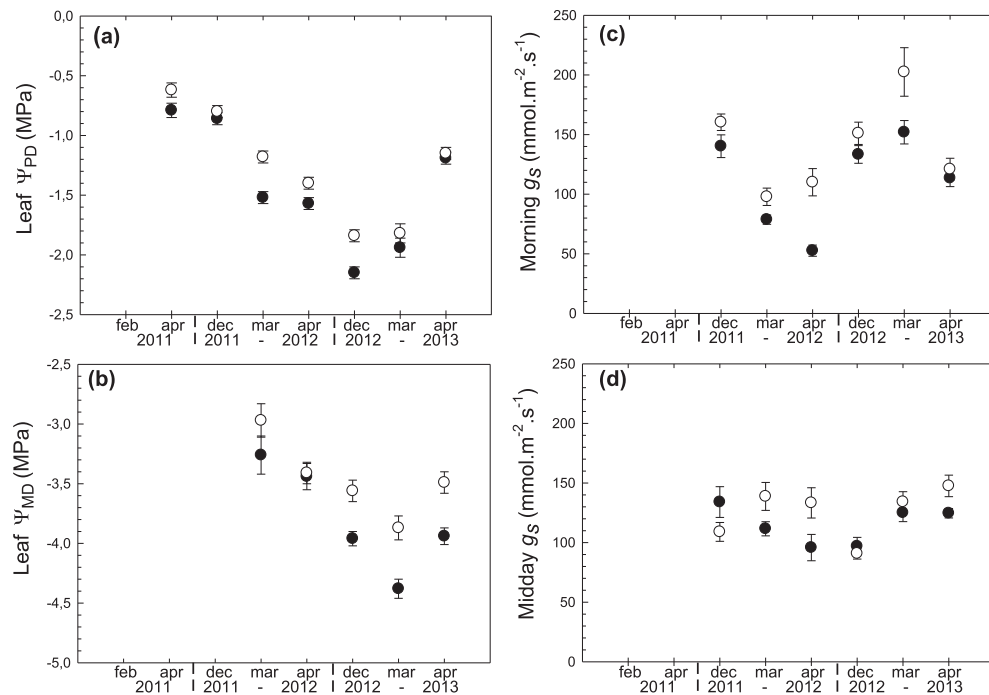


Figure 5. Pre-dawn (a) and midday (b) leaf water potential (Ψ_w), morning (c) and midday (d) leaf conductance (g_s) for *P. flexuosa* in control woodlands (filled circles) and livestock stations (open circles) during the experimental period. Symbols are means \pm 1 s.e.m.

AIC) and had higher weight AIC ($wAIC$) in the set of models for both land uses (Table III).

The parameters with a higher relative importance on midday g_s were plant water status (P) and atmospheric demand (A) for control woodlands and livestock stations, respectively (Table IV).

Water use efficiency

Significant positive linear regressions were observed between foliar $\delta^{13}C$ of *P. flexuosa* and VPD of the previous 30 days in both land uses, although a higher slope and coefficient were found for control woodlands (Figure 8).

Vegetative growth measurements

P. flexuosa had higher young branch length, internodal length and number of nodes per branch in livestock stations than in control woodlands. The differences between the two years were significant for all variables of vegetative growth (Table II), with lower seasonal growth during the second year (Table V).

DISCUSSION

This study contributes to the understanding of how disturbances alter water and nutrient dynamics of phreatophyte vegetation in the Central Monte desert. Phreato-

phytic trees are exposed to different levels of disturbance, because of livestock and settlement activity. Based on our results, livestock stations improved water and nutrient status of the individuals of *P. flexuosa* remaining in these disturbed interdune valleys, in agreement with the postulated hypothesis. A previous study indicated that livestock stations facilitate deep water drainage and nitrate lixiviation into the groundwater, as a result of both, vegetation removal and manure deposition by domestic animals (Meglioli *et al.*, 2014). In the livestock stations, the combination of several factors, such as increased soil nitrate and moisture content, and reduced competition because of lower cover of plants or greater inter-tree distances (Table I), may consequently improve the water and nutrient status of *P. flexuosa* trees. Individuals of this species are able to survive and grow in this arid ecosystem because of their physiological plasticity that allows them to exploit different water and nutrient reservoirs (Guevara *et al.*, 2010; Villagra *et al.*, 2010; Giordano *et al.*, 2011). *P. flexuosa* trees have both, surface (<70-cm depths) and deep roots (>7-m depths), using surface soil and groundwater in the interdune valleys (Guevara *et al.*, 2010; Jobbágy *et al.*, 2011). However, groundwater uptake has a higher energetic cost than soil water uptake for phreatophytic vegetation (Gou and Miller 2013). Therefore, when there is higher surface soil water, *Prosopis* improves water status, because trees tend to take more water from soil layers than from the deep groundwater level.

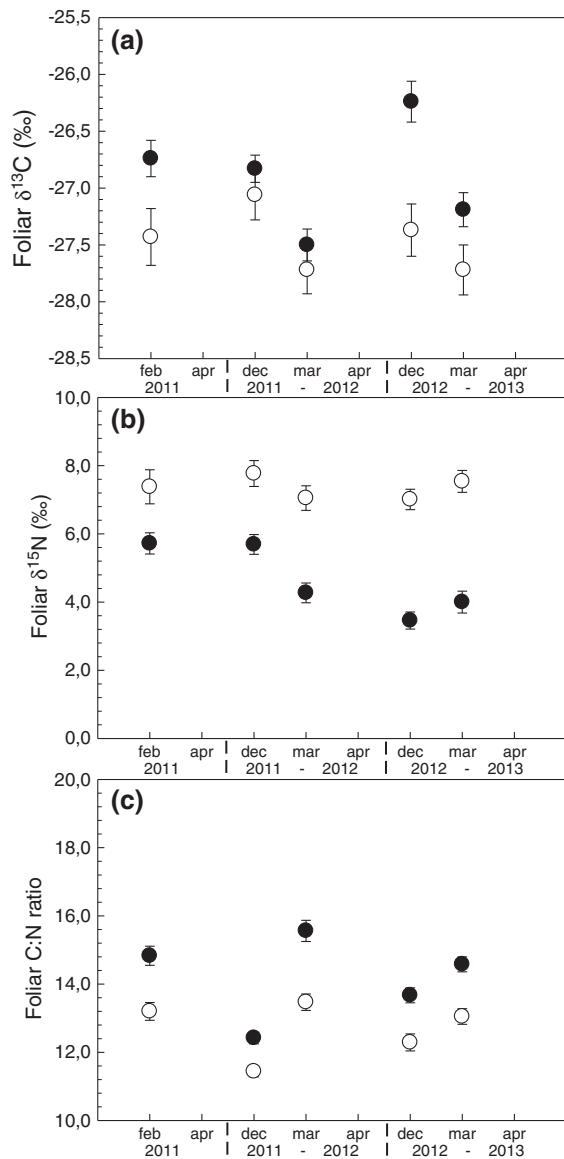


Figure 6. Relative abundance of stable isotopes of carbon (a) and nitrogen (b), and their carbon to nitrogen ratio (c) in leaves of *P. flexuosa* for control woodlands (filled circles) and livestock stations (open circles) during the experimental period. Symbols are means \pm 1 s.e.m.

Plant responses in arid/semiarid ecosystems are mainly controlled by precipitation pulses, the unpredictable nature of soil moisture dynamics (Porporato *et al.*, 2004; Potts *et al.*, 2006; Knapp *et al.*, 2008), and by integrated effects of community composition, competition, nutrient limitations, seasonality, phenology, plant age and the prevailing environmental conditions (Ehleringer and Cooper, 1988; Ogle and Reynolds, 2004; Faustino *et al.*, 2011). When shallow soil water has been depleted, permanent groundwater is used by phreatophytic trees to maintain physiological processes during drought periods (Nilsen *et al.*, 1981; Nilsen *et al.*, 1983; Sosebee and Wan, 1987). Particularly, the utilization of summer rains by desert plants

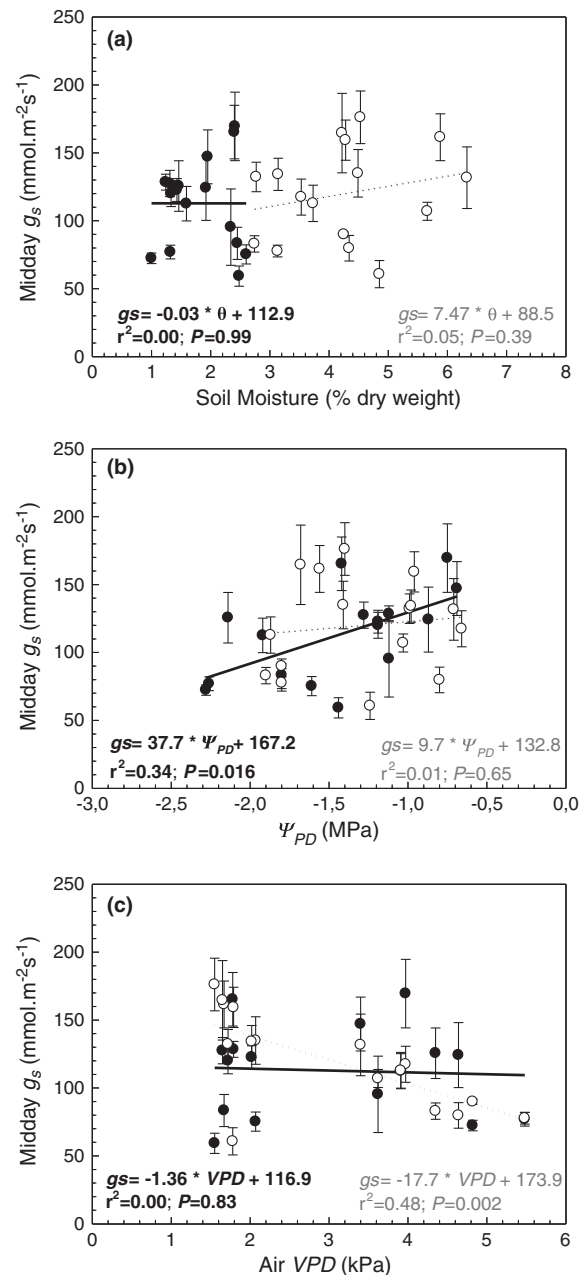


Figure 7. Relationships between the midday leaf stomatal conductance (mean \pm s.e.m.) with (a) the soil moisture, (b) the pre-dawn leaf water potential and (c) the air vapour pressure deficit for *P. flexuosa* in control woodlands (filled circles) and livestock stations (open circles). Solid and dotted lines are the trend of linear regressions for control woodlands (black equations) and livestock stations (gray equations) respectively.

is life-form dependent. Deeply rooted woody perennials should be relatively less affected by precipitation regime change than shallow-rooted life forms, as grasses and forbs (Ehleringer *et al.*, 1991). Our research shows that, despite the access to groundwater by *P. flexuosa* trees in lowlands (Giordano *et al.*, 2011; Jobbágy *et al.*, 2011), the physiology and the vegetative growth of this species were

Table III. Model selection statistics for midday leaf stomatal conductance to evaluate the effects of different controls on individuals of *P. flexuosa* in control woodland (a) and livestock station (b).

| Models | <i>S</i> | <i>P</i> | <i>A</i> | df | <i>AIC</i> | <i>dAIC</i> ^a | <i>wAIC</i> ^b |
|-----------------------------------|----------|----------|----------|----|------------|--------------------------|--------------------------|
| (a) Control woodland individuals | | | | | | | |
| 8 | + | + | + | 7 | 814.6 | 0.00 | 0.672 |
| 4 | + | + | | 6 | 817.0 | 2.38 | 0.205 |
| 7 | | + | + | 6 | 818.5 | 3.89 | 0.096 |
| 3 | | + | | 5 | 821.1 | 6.45 | 0.027 |
| 6 | + | | + | 6 | 832.1 | 17.49 | 0.000 |
| 2 | + | | | 5 | 834.4 | 19.82 | 0.000 |
| 5 | | | + | 5 | 835.9 | 21.28 | 0.000 |
| 1 | | | | 4 | 838.2 | 23.63 | 0.000 |
| (b) Livestock station individuals | | | | | | | |
| 8 | + | + | + | 7 | 801.9 | 0.00 | 0.635 |
| 7 | | + | + | 6 | 803.8 | 1.82 | 0.256 |
| 6 | + | | + | 6 | 806.2 | 4.27 | 0.075 |
| 5 | | | + | 5 | 807.9 | 5.92 | 0.033 |
| 4 | + | + | | 6 | 830.2 | 28.22 | 0.000 |
| 3 | | + | | 5 | 831.9 | 30.01 | 0.000 |
| 2 | + | | | 5 | 836.1 | 34.12 | 0.000 |
| 1 | | | | 4 | 837.9 | 35.92 | 0.000 |

Effects tested in models: *S*, soil water content (soil moisture); *P*, plant water status (pre-dawn leaf water potential); *A*, atmospheric demand (air vapour pressure deficit).

^a *dAIC* is the difference in *AIC* among candidate models.

^b Models were ranked using Akaike weights (*wAIC*).

also regulated by local meteorological conditions, through their impact on soil water availability and atmospheric demand (Figure 5, Table V).

For our study sites, *P. flexuosa* trees of livestock stations are subjected to prolonged superficial soil wetness, and increased nutrient availability compared to trees of control woodlands which may decrease surface resources more quickly because of local competition for water and

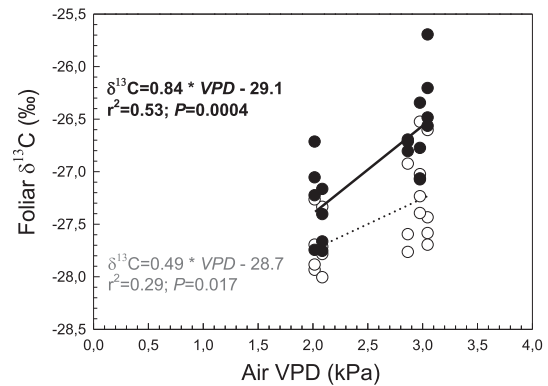


Figure 8. Relationships between leaf stable carbon isotope composition (mean \pm s.e.m.) and air vapour pressure deficit (average of climatic conditions during previous 30 days to each isotopic sampling) for *P. flexuosa* in control woodlands (filled circles) and livestock stations (open circles). Solid and dotted lines are the trend of linear regressions for control woodlands (black equation) and livestock stations (gray equation) respectively.

nutrients. The effect of soil water was evident in the slightly higher Ψ_{PD} and Ψ_{MD} and lower foliar $\delta^{13}C$ in livestock stations trees observed during most of the experimental period. These observations agree with field experimental studies for *P. glandulosa*, in which surface water contents were manipulated to create different soil moisture levels (e.g. irrigation, rainout), showing decreasing leaf Ψ_{PD} with decreasing volumetric soil water contents (Ansley *et al.*, 1992). According to our results, the slope of the linear regression for control woodlands indicates that an increase in the soil water content of 1% will induce an increase in Ψ_{PD} of 0.37 MPa, whereas for individuals of livestock stations the Ψ_{PD} will tend to remain constant. These findings appear to support the notion of a higher soil water control for trees living in woodlands than trees from livestock stations. However, a low correlation coefficient ($r^2 = 0.17$) did not allow us to be

Table IV. Model-averaged coefficients obtained from the best models (*dAIC*_c < 4) that describe the variation in the midday leaf stomatal conductance of *P. flexuosa* in control woodland (a) and livestock station (b).

| Parameter | Estimate | E.E. | z Value | Pr(> z) | CI 2.5 % ^a | CI 97.5% ^a | Importance ^a |
|-----------------------------------|----------|-------|---------|----------|-----------------------|-----------------------|-------------------------|
| (a) Control woodland individuals | | | | | | | |
| (Intercept) | 165.64 | 23.30 | 6.96 | <2e-16 | 119.01 | 212.27 | |
| <i>S</i> | -4.73 | 7.82 | 0.59 | 0.55 | -20.39 | 10.93 | 0.87 |
| <i>P</i> | 34.92 | 9.01 | 3.79 | 0.00 | 16.87 | 52.96 | 1.00 |
| <i>A</i> | 2.23 | 3.65 | 0.59 | 0.54 | -5.08 | 9.55 | 0.76 |
| (b) Livestock station individuals | | | | | | | |
| (Intercept) | 183.37 | 19.71 | 9.11 | <2e-16 | 143.93 | 222.81 | |
| <i>S</i> | -1.69 | 2.76 | 0.60 | 0.54 | -7.22 | 3.83 | 0.71 |
| <i>P</i> | 5.43 | 9.12 | 0.58 | 0.56 | -12.83 | 23.70 | 0.89 |
| <i>A</i> | -16.84 | 2.99 | 5.50 | <2e-16 | -22.84 | -10.85 | 0.99 |

^a We include the lower (2.5%) and upper limit (97.5%) of confidence intervals (CI), and the relative importance of each parameter (*S*: soil water content; *P*: plant water status; *A*: atmospheric demand).

Table V. Vegetative growth of *P. flexuosa* in control woodlands and livestock stations at the end of two growing seasons.

| Variables | March 2012 | | March 2013 | |
|---|-------------------|------------------|-------------------|------------------|
| | Livestock station | Control woodland | Livestock station | Control woodland |
| Branch length (cm) | 29.81 (1.36) | 25.23 (1.27) | 22.94 (1.37) | 19.74 (1.27) |
| Internodal length (cm) | 3.45 (0.11) | 3.15 (0.13) | 3.53 (0.11) | 3.51 (0.13) |
| Nodes per branch (n) | 8.57 (0.35) | 7.88 (0.33) | 6.71 (0.28) | 5.78 (0.25) |
| Leaf surface area, one pinnae pair (cm ²) | 7.28 (0.31) | 6.96 (0.30) | 6.58 (0.29) | 6.56 (0.27) |

Data represent mean values \pm 1 s.e.m. between brackets.

conclusive with this point, as observed in other studies for *P. glandulosa* (Ansley *et al.*, 1992). The relationship among water use and water conservation in plants is controlled by both, atmospheric demand and soil water content (Comstock, 2002; Duursma *et al.*, 2014).

As expected, the leaf *gs* in the livestock stations were higher than in control woodlands, but the responses were not constant during sampling time. This may be indicative that *P. flexuosa* may have developed different stomatal behaviours in response to environmental conditions. The different responses of stomatal conductance to leaf water status and atmospheric demand suggest that the combination of hydraulic and atmospheric factors influenced *P. flexuosa* stomatal behaviour, as in other *Prosopis* species from drylands (Wan and Sosebee, 1991; Elfadl and Luukkanen, 2006; Resco *et al.*, 2009). The positive linear relationship between midday *gs* with leaf Ψ_{PD} suggests that leaf conductance of control woodland trees is strongly related to an internal physiological variable (leaf water status) (Figure 7b). Conversely, leaf *gs* in trees at the livestock station sites had the best fit with the air *VPD* (Figure 7c). This suggests that internal signals in trees from livestock station, with better leaf water status, will be less important, and, therefore, these individuals were more sensitive to atmospheric conditions. These results support the explanation suggested by Comstock (2002) who said that stomatal behaviour and transpiration are influenced by the integration of numerous signals such as chemical (root water status), hydraulic signals (leaf water potential) and atmospheric signals. A current review on mesophyll conductance in different plant groups showed responses to several internal and external factors which operate both, in the long (days, weeks) and short (seconds, minutes) term (Flexas *et al.*, 2008; Damour *et al.*, 2010). Thus, Ansley *et al.* (1992) found that stomatal behaviours of *P. glandulosa* (in north Texas) were positively related to soil moisture, and that the rapidity of responses was also delayed in the more highly stressed individuals.

Leaf $\delta^{13}C$ across the growing seasons allowed us to assess the integrated physiological dynamics for *P. flexuosa*. Assuming that $\delta^{13}C$ is an indirect measure of trade-off between photosynthesis and transpiration during

the period of leaf life (Ehleringer, 1989), our findings suggest that trees in livestock stations had lower water use efficiency (more negative $\delta^{13}C$ values) than trees in undisturbed woodlands (Figure 6a). In addition, the temporal variability of $\delta^{13}C$ values also shows that the difference in water use efficiency between land uses increased during the drier periods, although individuals of control woodlands had greater $\delta^{13}C$ values when *VPD* was higher (Figure 8). Different responses to *VPD* may indicate that trees in control woodland may be experiencing water stress compared to trees that have access to soils with higher moisture. Leaf $\delta^{13}C$ during photosynthetic gas exchange is influenced by changes in environmental conditions, including air temperature, *VPD* and soil water availability (Alstad *et al.*, 2007).

Nutritional status of *P. flexuosa* was better in trees living in livestock stations, indicated by lower C:N ratios. Moreover, these values increased with the seasonal progress for both land uses (Figure 6c), suggesting that trees reabsorb nitrogen before leaf fall. Foliar $\delta^{15}N$ values in individuals from livestock stations were higher during all the experimental period than in those from control woodlands (Figure 6b). Considering that significant isotopic fractionation does not occur during the plant resource uptake (Evans and Ehleringer, 1994), this finding possibly indicates an acquisition of soil nitrogen enriched in ^{15}N by gaseous losses, such as ammonia volatilization, and coupled nitrification–denitrification (Amundson *et al.*, 2003). In the livestock stations, constant nutrient deposition by goats and cattle increase soil nutrients. Leaf $\delta^{15}N$ values of plants reflect the net effect of a range of processes, including the $\delta^{15}N$ signatures of multiple sources of nitrogen, mycorrhizal associations, temporal and spatial variation in nitrogen availability and changes in metabolic requirements by the plant (Dawson *et al.*, 2002). Our findings of foliar $\delta^{15}N$ support the idea that *P. flexuosa* can use different sources of N (Aranibar *et al.*, 2014), according to the N availability in the soils. Furthermore, the decrease of $\delta^{15}N$ values with season progress in control woodlands during a year of low precipitations suggests the occurrence of N_2 fixation under conditions of low N availability.

According to previous studies for the study area (Jobbágy *et al.*, 2011; Goirán *et al.*, 2012; Meglioli *et al.*, 2014) and to this research, we highlight that land use change alters water, carbon and nitrogen fluxes in Monte Desert. The ecohydrological consequences occur at different temporal and spatial scales. Livestock stations represent a relatively small portion of total land area, but this study contributed to understand the effects of the vegetation removal on *P. flexuosa* trees, at the plant spatial scale. We found improved water and nutrient status of remaining trees in the disturbed woodlands. Our research did not address the responses of individuals over long time periods, and did not allow us to estimate the time required to observe these consequences after establishment of the livestock stations. The analysed livestock stations were established more than 80 years ago.

In conclusion, the ecophysiological responses of *P. flexuosa* in the lowlands were not only affected by meteorological and soil conditions, but also by land use changes caused by livestock activities in the Monte desert. The woody vegetation remaining in livestock stations appears to grow under a less stressful environment as a result of vegetation thinning and nutrient input by livestock. As a consequence, trees can increase the vegetative growth (branch length) because of higher soil resources (water and nutrient) (Villagra *et al.*, 2013; Meglioli *et al.*, 2014). Therefore, the negative effects of human disturbances, such as the reduction of native vegetation because of grazing or cutting of plant species by the local settlers, may be partially offset at the plant scale, in *P. flexuosa* individuals by increasing vegetative growth.

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