Austral Ecology A Journal of ecology in the Southern Hemisphere

Austral Ecology (2018) **43**, 280–287

Land degradation affects shrub growth responses to precipitation in a semiarid rangeland of north-eastern Patagonia (Argentina)

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Abstract Arid land degradation diminishes the proportion of precipitation conducted to infiltration and increases the proportion lost to run-off and evaporation. Consequently, we expect that the effects of annual precipitation on shrub growth vary with land degradation as a result of changes in soil available water. *Chuquiraga avellanedae* is the dominant shrub and the main indicator of land degradation in semiarid rangelands of north-eastern Patagonia. We chose two communities with a different degree of land degradation: an herbaceous steppe with shrubs (HSS) and a degraded shrub steppe (SS). Vegetative growth of *C. avellanedae* was determined non-destructively using a double-sampling approach. Soil water content was estimated for the two communities using a soil water balance model. Linear regressions were used to evaluate the relationships between shrub growth and (i) annual precipitation and (ii) mean available water during the period of high vegetative growth in the soil layer that each plant community concentrates their roots. In SS, with elevated clay content, there were more roots of *C. avellanedae* in the upper layers of soil while in HSS, with coarse-textured soil, *C. avellanedae* had more roots in deeper layers. Vegetative growth of *C. avellanedae*, both in HSS and SS communities, was positively related to annual precipitation but, for a given precipitation, *C. avellanedae* presented higher vegetative growth in HSS than in SS. We also found a positive relationship between vegetative growth and soil available water, and this relationship did not differ between communities. SS presented lower water availability because of lower infiltration rates. Our results showed that, irrespective of the degree of land degradation, plants respond directly to water content of the soil layers where most roots are present at a specific window of time.

Key words: annual precipitation, clay-enriched soil, infiltration, shrub growth, soil degradation, soil water availability.

INTRODUCTION

Identifying species-level responses of primary production to precipitation is essential for improving our knowledge of the mechanisms influencing the carbon cycle (Liu *et al.* 2012). One of the general patterns in ecology is the correlation between mean annual precipitation and mean above-ground primary production (Webb *et al.* 1978; Sala 2001; Muldavin *et al.* 2008). However, when this relationship is evaluated at a site level considering yearly precipitation and production data, it is not strong enough, suggesting that there are other variables that influence plant production (Oesterheld *et al.* 2001; Knapp *et al.* 2002; Fay 2009). Recent studies have suggested that soil attributes can influence the responses of vegetation to changes in precipitation (Friedley *et al.* 2011; Bisigato *et al.* 2013; Fernandez-Going & Harrison 2013).

Soil water availability for plant growth is not exclusively a function of precipitation patterns, but it is also deeply linked to edaphic properties (Noy-Meir 1973; McAuliffe 1994; Parker 1995; Hamerlynck *et al.* 2000; Fravolini *et al.* 2005). On the one hand, fine-textured (clay-rich) soils limit the wetting front to the upper soil layers contrary to coarse-textured (sandy) soils where rain water infiltrates deeply into the soil profile (Fravolini *et al.* 2005). On the other hand, clay-rich soils hold more moisture than sandy soils (Laio *et al.* 2001; English *et al.* 2005). Nevertheless, the retentive properties of clay-rich soils imply that water in drying clay soils is harder to extract for plants than water in sandy soils (Sperry & Hacke 2002; Fensham *et al.* 2015). Thus, soil hydraulic characteristics intervene in the dynamics of water uptake by plants during the growing season (Fravolini *et al.* 2005). Recently, Sponseller *et al.* (2012) highlighted that assessing the responsiveness of dominant plant functional groups to variation in precipitation patterns and to local soil characteristics

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Accepted for publication October 2017.

doi:10.1111/aec.12563

continues to be a research priority in arid and semiarid regions.

Land degradation is defined as a 'reduction or loss of the biological and economic productivity' resulting from land uses (mismanagement), or a combination of processes, such as soil erosion, deterioration of soil properties and long-term loss of natural vegetation (Millennium Ecosystem Assessment 2005). Arid land degradation diminishes the proportion of precipitation conducted to infiltration and transpiration and increases the proportion lost to run-off and evaporation (Verón *et al.* 2006; Chartier *et al.* 2013). Previous studies in north-eastern Patagonia found that land degradation was associated with the replacement of herbaceous steppes by shrub steppes, mainly as a consequence of overgrazing by sheep (Beeskow *et al.* 1995; Campanella *et al.* 2016a). This change occurred together with the erosion of superficial soil (Rostagno 1989; Chartier & Rostagno 2006). Shrub steppe soils present areas of exposed clay-rich argillic horizon (Bt horizon) and a shallower A horizon in comparison with herbaceous steppe with shrubs (Chartier & Rostagno 2006; Chartier *et al.* 2011). The loss of the A horizon and the exposure of enriched-clay layers are associated with a reduction in infiltration rates and a rise in run-off (Parizek *et al.* 2002; Chartier *et al.* 2013). *Chuquiraga avellanedae* Lorentz is the dominant shrub and the main indicator of land degradation in the area (Beeskow *et al.* 1995). We hypothesized that land degradation effects on individual plant growth are mostly consequence of its effects on soil water availability. We expect that plant growth responses to precipitation would differ in plant communities exhibiting contrasting degrees of land degradation. We also expect that this difference would be related to soil available water, being lower in degraded communities.

MATERIALS AND METHODS

Site, species and community description

The study was undertaken in the Punta Ninfas area (42°55′S, 64°33′W), a rangeland of north-eastern Patagonia with sheep grazing for more than a century. The climate is arid with a mean air temperature of 12.7°C and a mean annual precipitation of 259.3 mm (considering a 13-year period) (Campanella *et al.* 2016b). The characteristic vegetation is a mosaic of herbaceous and shrub steppes where *C. avellanedae* (quilembai) is the dominant shrub and *Nassella tenuis* (Phil.) Barkworth (flechilla) is the dominant grass (Beeskow *et al.* 1995). Dominant soil in the study area is a Xeric Calciargid with a Xeric Haplocalcid as the subdominant soil (Chartier & Rostagno 2006).

Chuquiraga avellanedae is an evergreen shrub with a peak of biomass growth in spring, when new leaves and stems are produced in a short period. As plant growth is concentrated in a few weeks, it can be expected that water availability during those few weeks have a great influence on its growth. This species exhibits a period of inactivity during winter when temperatures are lowest. The reproductive period occurs in summer (Campanella & Bertiller 2008, 2009).

We chose two communities with a different degree of land degradation: the herbaceous steppe with shrubs (HSS) and the degraded shrub steppe (SS) (Beeskow *et al.* 1995). Both communities differ in soil characteristics and plant cover, which are strongly associated in this ecosystem (Chartier *et al.* 2011). Plant and litter cover are higher in the HSS than in SS, while bare soil and gravel cover show the opposite trend. Also, SS soil has finer texture and presents a shortened A horizon (Chartier & Rostagno 2006). The loss of the A horizon and the formation of desert pavements are good indicators of the erosion process in the study area (Rostagno & Degorgue 2011).

Growth measurements

Shrub growth was determined nondestructively using a double-sampling approach described by Campanella *et al.* (2016b). Data were collected during 6 consecutive years (2011–2016). At mid-December, we measured the length of new shoots in a 15 × 15 cm quadrat in 15 individuals of *C. avellanedae* on HSS and SS. Then, we estimated new biomass using allometric regressions developed for this species (Campanella *et al.* 2016b). Growth was expressed as g m^{-2} canopy $year^{-1}$.

Climatic conditions

During the study period, we recorded precipitation, air temperature and solar radiation with an automatic data logger.

Soil water

Soil water storage was estimated using a soil water balance model developed for Southern Monte and validated against field observations (Bisigato & Lopez Laphitz 2009). The required inputs are daily meteorological data (precipitation, maximum and minimum air temperature and solar radiation), vegetation attributes (plant cover and proportion of roots in each soil layer) and soil attributes (soil water content at field capacity and permanent wilting point, soil texture and gravel content for each soil layer). Precipitation, maximum and minimum air temperature and solar radiation during the study were obtained with the above-mentioned automatic data logger. Soil attributes and the proportion of roots in each soil layer were obtained from soil samples taken from a trench dug next to one individual of *C. avellanedae* in a representative site of each community. Every 10 cm we took soil samples until 80 cm depth. Fine roots (<2 mm diameter) were separated from the soil, washed, dried at 60°C for 48 h and weighted. Soil

doi:10.1111/aec.12563

texture was determined by the pipette method (Kilmer & Alexander 1949) and gravel content by passing the air-dried soil samples through a 2-mm sieve. Volumetric water content at field capacity and wilting point were determined with a pressure plate at 0.33 and 15 atmospheres, respectively (Richards & Fireman 1943). Plant cover was obtained from Palacio *et al.* (2014). This one-dimensional model calculates, on a daily basis, soil water depth in each soil layer and losses by evaporation, transpiration and drainage. Available water in each soil layer is obtained subtracting soil water depth at permanent wilting point from current soil water depth. The model included five layers of soil, each 10 cm deep. In its original form the model does not take into account surface run-off, because it was developed for sandy soils. However, as previous studies have demonstrated the existence of run-off in soils of the study area (Parizek *et al.* 2002), we included into the model an additional module to consider it. This module was based on infiltration curves of each community (Parizek *et al.* 2002). On average, run-off accounted for 10% of daily precipitation in the SS; whereas it was negligible in the HSS. Losses by evaporation are only computed from the upper layer. Water lost by transpiration is a function of the potential evapotranspiration and the effective available water, which is the sum of the available water of each soil layer weighted by the root proportion in each soil layer. Flow from the last soil layer downward corresponds to deep drainage. Plant cover is kept constant throughout the simulation.

Statistical analysis

Linear regressions were used to evaluate the relationships between shrub growth and (i) annual precipitation and (ii) mean available water during the period of high vegetative growth in soil layers where plants concentrate their roots. ANCOVA models were used to test whether regression slopes and intercepts differed between plant communities. We considered that the period of high vegetative growth extends from week 39 to 45 (i.e. from the end of September to beginning of November; Campanella & Bertiller 2009). Above-mentioned soil samples were used to identify the soil layers where fine roots are concentrated at each community.

RESULTS

In the SS soil sample with elevated clay content, most of fine roots were found between 10 and 30 cm depth (layers 2 and 3), while in the HSS soil sample with coarse-textured soil, fine roots were concentrated between 30 and 50 cm depth (layers 4 and 5, Fig. 1). Considering total fine root biomass per gram of soil, the soil sample at SS presented a higher amount than the soil sample at HSS (6.91 mg DW roots g^{-1} soil *vs.* 3.88 mg DW roots g^{-1} soil).

The highest annual precipitation occurred in 2013 (354.6 mm) and was 37% above the long-term average of 259.3 mm. In contrast, the lowest annual precipitation occurred in 2015 (175 mm) and was 32% below the long-term average. Years 2011 (220 mm), 2012 (221.8 mm) and 2016 (246.2 mm) were characterized with precipitation scarcely below the long-term average, and at last, 2014 (258.8 mm) was a year with average precipitation (Fig. 2).

Modelled soil water dynamics in the soil layers where roots are concentrated was different for the two communities (Fig 3). Soil layers in HSS (i.e. layers 4 and 5) were recharged in all years with the exception of 2015, which was the year with the lowest annual precipitation. That year, water did not reach layer 5. In contrast, soil layers with highest root biomass in SS (i.e. layers 2 and 3) were only full recharged in 2013 (the year of highest precipitation) and 2014 (the year with the largest precipitation event). At similar precipitation amounts, SS presented lower water availability because of their lower infiltration rates and higher wilting point than HSS (Table 1).

Vegetative growth of *C. avellanedae*, both in HSS and SS communities, was positively related to annual precipitation (Fig. 4a). However, for the same amount of precipitation, *C. avellanedae* exhibited higher vegetative growth in HSS than in SS (Fig. 4a). In other words, the slopes were equal, but the intercepts differed between communities. In contrast, we

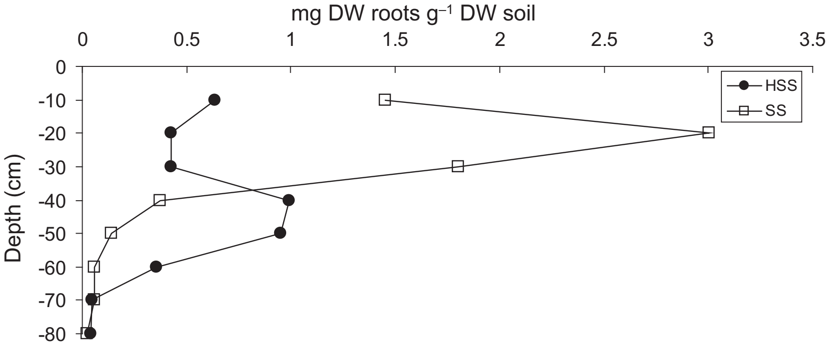

Fig. 1. Vertical distribution of fine roots of *Chuquiraga avellanedae* in the two communities (herbaceous steppe with shrubs (HSS) and shrub steppe (SS)).

doi:10.1111/aec.12563

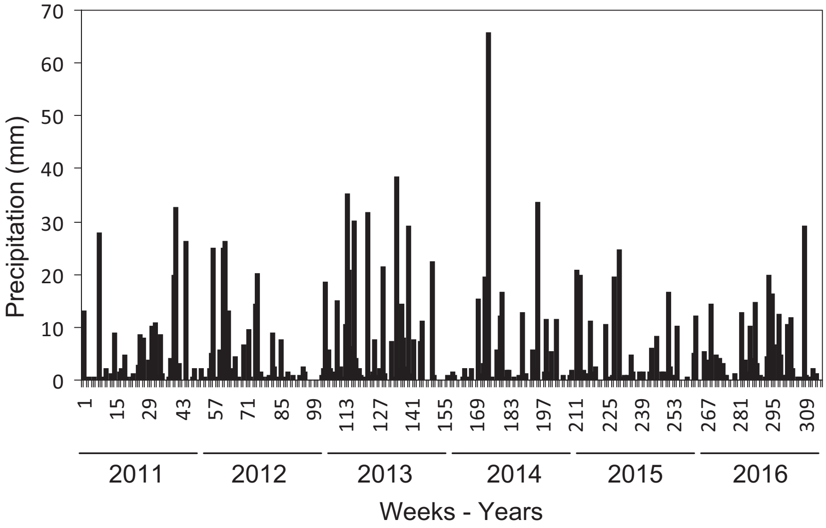

Fig. 2. Precipitation during the studied period (2011–2016).

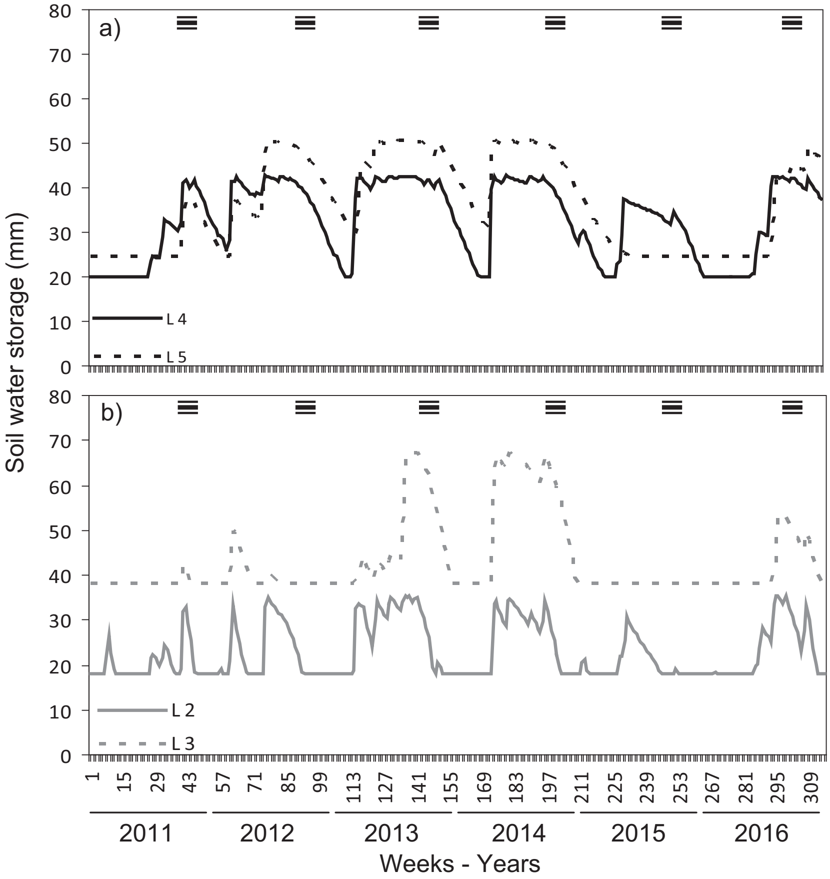

Fig. 3. Modelled soil water dynamics in the layers of soil that *Chuquiraga avellanedae* concentrates their roots. In herbaceous steppe with shrubs (a), L4 = layer 4 (30–40 cm depth) and L5 = layer 5 (40–50 cm depth), and in shrub steppe (b), L2 = layer 2 (10–20 cm depth) and L3 = layer 3 (20–30 cm depth). The period of high vegetative growth (weeks 39–45) is indicated with horizontal lines at the top of the panels.

Table 1. Volumetric water content (%) at field capacity (FC), permanent wilting point (PWP) and highest available water capacity (HAW) in the first 5 layers of soil (L) for the HSS and SS communities

Soil depths (cm)	HSS			SS		
	FC	PWP	HAW	FC	PWP	HAW
L1: 0–10	12.60	5.09	7.51	18.42	6.43	11.99
L2: 10–20	14.07	6.03	8.04	**35.78**	**18.22**	**17.56**
L3: 20–30	35.64	18.22	17.42	**68.21**	**38.32**	**29.89**
L4: 30–40	**43.68**	**20.37**	**23.31**	57.62	30.02	27.60
L5: 40–50	**51.99**	**25.06**	**26.93**	48.51	24.92	23.59

Bold indicates soil layers with highest concentration of roots in each community. HSS, herbaceous steppe with shrubs; SS, shrub steppe.

did not find differences in the relationship between vegetative growth and soil available water between plant communities, that is we found similar growth for equal available water irrespective of land degradation (Fig. 4b).

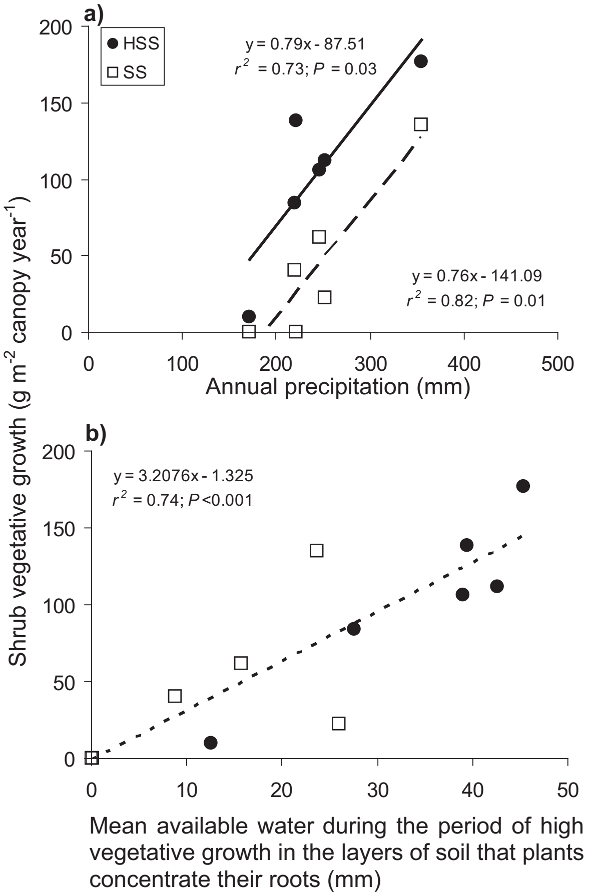

Fig. 4. Relationships between vegetative growth of *Chuquiraga avellanedae* and (a) annual precipitation (mm), and (b) mean available water during the period of high vegetative growth in the soil layer that each plant community concentrates their roots (mm). The solid and dashed straight lines in (a) indicate the linear regressions between vegetative growth and annual precipitation for herbaceous steppe with shrubs (HSS) and shrub steppe (SS), respectively. Dotted line in (b) indicates the regression between vegetative growth and mean available water in soil for both communities.

DISCUSSION

Besides shrub growth was positively related to annual precipitation, which is in accordance with a growing body of site-specific studies that find a stronger relationship between annual precipitation and plant productivity (Lauenroth & Sala 1992; Muldavin *et al.* 2008), *C. avellanedae* growth was higher in the HSS community compared with the SS community. Higher soil available water in HSS than in SS under the same precipitation explained that difference (Fig. 4b), supporting our hypothesis. Previous studies have shown that soils in SS community presents lower infiltration rates than soils in HSS community as a result of the reduction in perennial grasses and litter cover (Parizek *et al.* 2002; Chartier *et al.* 2011; Campanella *et al.* 2015). Moreover, SS community presents clay-enriched surface soils and vesicular crusts as a consequence of land degradation in comparison with HSS community with coarse surface soils (Chartier & Rostagno 2006; Rostagno & Degorgue 2011). However, the consequences on plant growth of these changes were unknown to the present. It is generally accepted that sites with coarse surface textures (5-10 cm depth) tend to be more productive as a consequence of high infiltration and reduction in evaporative losses (Le Hoúerou *et al.* 1988; Sala *et al.* 1988; Epstein *et al.* 1997; Browning *et al.* 2012). In accordance to this, Fensham *et al.* (2015) found lower woody biomass on clay soils than in nonclay soils in Australia. That study strongly suggests that moisture-retentive properties of clay-enriched soils are the main cause of lower woody biomass (Fensham *et al.* 2015). Recently, a regional scale study performed in the United States highlighted the strong control of subsurface soil texture on above-ground productivity (Shepard *et al.* 2015). Our results showed that plants respond directly to water content of soil layers (Reynolds *et al.* 2004; Fernández 2007) where most roots are present at a specific window of time, which may reflect links to plant phenology (Robinson *et al.* 2013). Soil moisture along with precipitation mainly determines plant growth (Pockman & Small 2010; Bisigato *et al.* 2013; Campanella & Bertiller 2013; Kidron & Gutschick 2013).

Morphological differences in the root system between communities suggest that *C. avellanedae* can adapt phenotypically to maximize water use. There are evidences that desert shrubs can morphologically

doi:10.1111/aec.12563

adjust their root systems maximizing water availability (Donovan & Ehleringer 1994; Schwinning & Ehleringer 2001; Xu *et al.* 2007). In the same way, the root system of a phreatophyte tree (*Prosopis flexuosa*) of the Monte Desert (Argentina) presented a great phenotypic plasticity when growing in different soil environments (Guevara *et al.* 2010). We found that in clay-enriched soil, more roots were found in the top soil. Generally, on sand-rich soil, water is accessible to plants at greater depths, whereas on clay-rich soil, water is available at surface (English *et al.* 2005). This was in agreement with the suggestion that plant rooting depths could be limited by infiltration depths (Schenk & Jackson 2002).

Although 2014 was an average precipitation year, it had the largest precipitation event throughout the study. Event size affects the temporal persistence of available water (Noy-Meir 1973) and the depth of water storage, heavy rains penetrated deeper on the soil layers (Sala & Lauenroth 1982). Also, the season during which the precipitation event occurs controls the extent of water infiltration (Loik *et al.* 2004). Large precipitation events during cold months are more effective recharging soil layers (Coronato & Bertiller 1997; Bisigato & Lopez Laphitz 2009).

The two communities are mixed in the landscape, they are subject to similar climatic conditions, and therefore, differences in growth among plants are more related to variation in water availability. Other authors highlighted that soil texture and local topography rules small-scale patterns of water availability to plants following precipitation events (McAuliffe 1994; Hamerlynck *et al.* 2004; Pockman & Small 2010; Sponseller *et al.* 2012). Similarly, soil characteristics can control the phenology of tropical trees (Cardoso *et al.* 2012), *Larrea tridentata*'s physiological responses (Hamerlynck *et al.* 2000) and grass cover (English *et al.* 2005). It is important to highlight that understanding shrub growth responses to precipitation within the context of land degradation will be important to predict the potential impacts of climate change.

We must recognize some limitations of our study. First, our study lacks of soil profile replication. However, soil characteristics coincided with previous studies in both communities indicating representativeness (Chartier & Rostagno 2006; Chartier *et al.* 2011). Second, our study only encompasses aboveground growth. Future studies should also consider belowground growth as plants could be allocating more carbon to belowground structures in SS. In fact, total root biomass is greater in SS (Fig. 1). Third, we did not prove that plants in SS were subjected to a higher water stress than plants growing in HSS. Future studies should include measures of stomatal conductance or changes in leaf water potential, among others. Finally, soil water availability was not measured; it was estimated with a soil water balance model. However, this model was validated against field data when developed (Bisigato & Lopez Laphitz 2009), and the use of soil water balance models is generally accepted to study soil water effects on plant growth in arid ecosystems (Paruelo & Sala 1995; Flerchinger & Pierson 1997; Rodriguez-Iturbe *et al.* 1999; Reynolds *et al.* 2000).

In conclusion, in both communities, there were positive linear responses to annual precipitation but *C. avellanedae* presented lower growth in SS compared to HSS. This is attributable to lower water availability in those soils through less infiltration. Thus, vegetative growth of *C. avellanedae* in response to precipitation was mediated by land degradation. Our results also showed that plants responded directly to water content of the soil layers where most roots were present at a specific window of time.

ACKNOWLEDGEMENTS

We thank Romina D'Agostino, Cristian Barrionuevo and Romina Palacio for their field assistance. We express gratitude to R. de Vries and Don Lopez who allowed access to the study area (Ea. Bahia Cracker). This research was supported by PIP 11220120100592 of the National Research Council of Argentina (CONICET) and PICT-2013 No. 1876 of the National Agency for Scientific and Technological Promotion.

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