



Geomorphology and soils control vegetation heterogeneity through differential species establishment at an arid ecotone



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ABSTRACT

The influence of geomorphology on the distribution of plant communities in arid landscapes has long been recognized. However, the mechanisms behind this influence still remain unexplored in most cases. At the southern Monte – Patagonia ecotone, communities belonging to both biogeographical regions coexist, but are confined to specific landforms. Bars are dominated by *Larrea divaricata*, which is typical of the Monte, while topographically lower channels are dominated by *Chuquiraga avellanadae*, which is more related to Patagonia. We aimed to evaluate whether these species differed in their ability to establish in different landforms, thereby defining the species distribution across this ecotone. We used a greenhouse experiment to examine the role of soil from different landforms (bars and channels) and microsities (mounds and interspaces), with different levels of water availability to examine seedling establishment and growth of these two species. We recorded three-times greater establishment of *Chuquiraga avellanadae* than *Larrea divaricata* in channels and the average biomass of *Chuquiraga avellanadae* in channel mound soils was more than twice that in other soils. Establishment of *Larrea divaricata* was higher in bar soils but there was no survival in channel interspace soils. We found no overall effect of water availability. Our results indicate that species distribution in this landscape is partly a result of processes operating at early stages of plant life.

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1. Introduction

Geomorphology is among the most important factors influencing vegetation heterogeneity at landscape scales in arid ecosystems (Wysocki et al., 2011). Landforms and their soil properties are associated with changes in the physiognomy of the vegetation and its floristic composition and variation (Ponce et al., 1994). Previous studies carried out in the Chihuahuan desert (Bestelmeyer et al., 2006; Buxbaum and Vanderbilt, 2007), Sonoran Desert (McAuliffe, 1994), Iran (Zare et al., 2011), Patagonia (Palacio et al., 2014) and the Tanami Desert (Dunkerley, 2002) have found that different communities occupy specific landforms, which commonly exhibit distinct soils. However, as the majority of these studies is correlative, the mechanisms behind the association between plant communities and landforms remain unclear in most of the cases.

Additionally, both physical as well as chemical characteristics of

surface soil are strongly influenced by vegetation cover at smaller spatial scales (e.g. microsities) (Mazzarino et al., 1998). Sediments and plant debris carried by water and wind became trapped under shrub canopies (Schlesinger et al., 1996). As a result, soil mounds that originated under vegetation have markedly different characteristics compared with unvegetated interspaces (Buis et al., 2010). In addition to soil differences, microsities located under plant canopies (i.e. mounds) are environments of lower temperature and water evaporation (Moro et al., 1997) as well as seed accumulation (Bertiller, 1998). All these differences may make mounds more favorable microsities for seedling establishment than interspaces (Shumway, 2000). However, under some circumstances, these positive effects are counteracted by competition with established vegetation, reducing the positive effects of mounds in less favorable microsities (Cipriotti and Aguiar, 2015).

Ecotones, the transitional area between different landforms, are characterized by marked differences or gradients in soil type and water availability (McAuliffe, 1994; Wysocki et al., 2011; Warman et al., 2013). Similar differences in water availability have been reported between microsities (Cortina and Maestre, 2005; Magliano

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et al., 2015). In general, soil water infiltration is greater in areas of low relief and at vegetated patches, particularly if precipitation events are intense. Water availability is a fundamental component of plant establishment, and even small differences in soil moisture can drive differences in species recruitment both at landscape (Yang et al., 2010) and microsite scales (Owens et al., 1995).

Plant establishment has been studied extensively at the plant or microsite scale in arid and semi-arid environments (Facelli, 1994). At landscape scales, however, studies have tended to focus on the adult plant growth stage with few studies of establishment at the early plant stages across different landforms. Our study examines the effects of soil heterogeneity (at landscape and microsite scales) and water availability on seedling establishment of two species characteristic of two different landforms in the southern Monte/Patagonia ecotone. We used a glasshouse experiment to test the hypothesis that species distributions in the landscape reflect their ability to establish in different soil types.

2. Materials and methods

2.1. Study area and species description

The ecotonal area between southern Monte and Patagonia represents intermediate characteristics between the hotter and drier conditions that characterize the Monte Region at a country level and the colder and less xerophytic climate which is typical of the Patagonia Region. The presence of this ecotone has been attributed to geomorphology (Casalini, 2016). There, landscape structure is defined by an ancient alluvial fan of the Chubut River that is characterized by anastomosing systems of channels and bars (González Díaz and Di Tommaso, 2011). On topographically higher bars, plant communities are dominated by *Larrea divaricata* which is representative of the Monte Region, while on topographically lower channels, communities are dominated by *Chuquiraga avellanadae*, more related to the Patagonia Region. Although dominant species differ between landforms, some individuals of *C. avellanadae* are found on bars. In contrast, *L. divaricata* is absent from channels (Casalini, 2016).

Larrea divaricata Cav. (Zygophyllaceae) is an evergreen shrub typical of the west arid region of South America, from Peru to southern Monte in Argentina (Correa, 1988). The tallest individuals reach 3 m high and roots may reach the same depth belowground (Bertiller et al., 1991). *Chuquiraga avellanadae* Lorentz (Asteraceae), of narrower distribution, can be found from Mendoza to Santa Cruz in Argentinean Patagonia (Correa, 1988). Individuals are semi-spherical evergreen shrubs of 1 m high with roots 1.5 m deep (Bertiller et al., 1991).

2.2. Seed and soil sampling

Seeds and soil samples were collected from a representative area in north-east Chubut Province, Argentina (42°55'S, 65°05'W). Soil from the top 20 cm was collected in each landform (channels and bars) and microsite (mounds and interspaces among them). Mature fruits of *C. avellanadae* and *L. divaricata* were hand-collected before dispersal and stored in darkness at room temperature.

2.3. Soil attributes

Gravel was separated with a 2 mm mesh sieve. Five samples of each soil type were gathered for physical and chemical analysis. Sieved dried soil of each landform and microsite combination was settled in 2 L plastic pots (N = 40 pots per soil type).

Soil particle size distribution was determined using the hydrometer method (Bouyoucos, 1962). Total nitrogen was measured

by Micro-Kjeldahl (Page et al., 1982) and electrical conductivity was assessed electrometrically in saturation extracts (Richards, 1974). Field capacity was estimated by measuring the amount of water held in the soil of 12 control pots, 3 by soil type, which had been fully wetted, covered and weighed after 2 days of drainage. Wilting point was assumed to be equal to residual soil moisture (Houser et al., 2001). The difference between field capacity and wilting point corresponded to the maximum water availability for each soil type, called available water-holding capacity (Birkeland, 1984).

2.4. Experimental settings

We used a greenhouse study to evaluate the role of soil type and water supply on the growth of *Chuquiraga avellanadae* and *Larrea divaricata* seedlings. Seeds of both species (achenes in *C. avellanadae*) were placed in Petri dishes on moist filter paper at room temperature and watered daily with distilled water. Seeds of *L. divaricata* were subjected to a previous scarification process to break primary seed dormancy. After emergence of the cotyledons, seedlings were immediately transplanted in the pots. Pots were settled within a greenhouse under natural light in a random arrangement and re-randomized daily during the experiment. When a transplanted seedling died it was replaced by a recently emerged seedling. Seedlings alive after a month were considered established.

Established seedlings were assigned to two groups with different water supply regimes. These regimes differed in the lowest soil water content reached by pots before re-irrigation took place. Pots in the “frequent water supply regime” were irrigated whenever their water content dropped below the value corresponding to two thirds (66%) of their available water holding capacity, while in the “sporadic water supply regime” irrigation only took place when the water content dropped below one third water holding capacity (33%). This experimental approach takes into account differences in atmospheric demand as well as differential water-use by plants from different species and soil types (Cella Pizarro and Bisigato, 2010). Thus, there were 16 treatments resulting from the combination of two levels of each factor: species, landform, microsite and water supply regime. Originally each treatment contained 10 replicates. Because some plants died during the experiment the number of individuals at harvest time was lower in some treatments.

Mean daily maximum/minimum temperatures during the whole experiment were 31.6 + 0.4°C/14.3 + 0.3 °C and the photoperiod ranged between 12 and 15 h. Water used for watering pots was tempered inside the greenhouse to avoid changes in temperature in irrigated pots, which could cause additional effects (Passioura, 2006).

2.5. Seedling establishment

Each pot and its transplanted seedling was watered daily, and pots allowed to drain freely during the first month of the experiment. Surviving seedlings after this month were considered established. In this way establishment was evaluated in four different soil types (soils from two microsites from two different landforms) for both species using the proportion of seedlings alive one month after transplant.

2.6. Juvenile growth and survival

Plants were harvested five months after establishment, i.e. six months after transplanting. Juvenile survival was calculated as the proportion of plants alive at the end of the experiment, based on the number of established seedlings. Roots were carefully washed

on a fine mesh under a water stream. Each plant was oven dried at 45 °C for 48 h and weighted. Total biomass was then separated into above and below ground biomass.

In addition, three fully expanded leaves of each pot were cut and scanned with a desk-top scanner to measure specific leaf area (SLA), then dried at 45 °C and weighted. Leaf area was measured using a flat-bed scanner and image analysis software.

2.7. Data analysis

All variables were tested for normality with Shapiro-Wilk W test and homoscedasticity of variances by Levene's test. When these assumptions were satisfied, nested ANOVAS were applied to test the effect of the different factors (species, landform, microsite and water supply treatment), and their two- and three-way interactions. Water supply treatment was nested within microsite, which was nested inside the landform, since the nature of microsite levels (mound or interspace) are not the same for the two landforms (channels and bars). Differences among means were evaluated by Tukey's Test. Texture data were arcsine transformed before analysis. Specific leaf area values were inversely transformed in order to meet ANOVA assumptions.

The deviation from homogeneity in seedling establishment and juvenile survival was assessed by binomial Generalized Linear Mixed Models (GLMM) with logit link function. Likewise, differences in total biomass were evaluated by GLMM using gamma distribution with inverse link function. Differences in root mass fraction among treatments were assessed using ANCOVA with total biomass as a covariate. In all cases we first fitted a full model taking into consideration all main effects and their interactions. We then reduced the full models by successive removal of non-significant interactions. All analyses were performed in R (R Core Team, 2014), using the stats (Bates et al., 2015), and car (Fox and Weisberg, 2011) packages.

3. Results

3.1. Soil attributes

Soil texture differed among landforms and microsities (Table 1). Sand content at mounds from channels was the highest and silt content the lowest. Sand content, however, was least in interspaces from the same landform, where clay content was the highest. Channels had denser soils ($F_{1,12} = 6.96, p = 0.02$). Organic carbon was greater in mound soil ($F_{1,8} = 12.82, p < 0.01$). Carbonate content was higher at bars ($F_{1,8} = 9.50, p = 0.01$), with no difference between microsities ($F_{1,8} = 1.73, p = 0.24$). Though mean electrical conductivity values suggested higher salt contents in channel soils, the differences were not statistically significant, probably due to

the high variability amongst samples.

3.2. Seedling establishment

Chuquiraga avellanae had greater seedlings establishment than *L. divaricata* in all soil types ($Z = 3.141, p < 0.01$, Fig. 1). For both species seedling establishment was lower in interspaces from channels, where the difference between species was the highest (more than 11 times higher for *C. avellanae*, interaction landform X microsite: $Z = 2.795, p < 0.01$). In particular, only two of 31 individuals of *L. divaricata* survived at this soil type up to the date of the water supply regime assignment.

3.3. Juvenile survival

Juvenile survival was similar between species but was higher in mounds than interspaces ($Z = 3.900, p < 0.01$), and in bars than in channels ($Z = 2.148, p = 0.03$). No individual of *L. divaricata* survived at interspaces from channels (Fig. 2). Juvenile survival did not differ between water supply regimes.

3.4. Plant biomass and leaf traits

Biomass of *Chuquiraga avellanae* was greatest on mounds within channels (Interaction landform X microsite: $Z = 2.488, p = 0.01$), where average biomass values were more than two times higher than in the rest of soil types (Fig. 3). *Larrea divaricata* reached higher biomasses at mounds from both landforms ($Z = 2.702, p < 0.01$). Total biomass was not affected by water supply regimes.

Biomass allocation differed between microsities for both species. Plants from interspaces had a greater proportion of biomass allocated to belowground organs ($F_{1,44} = 15.09, p < 0.01$ for *C. avellanae*; $F_{1,24} = 20.39, p < 0.01$ for *L. divaricata*). Root mass fraction decreased logarithmically with plant size in *C. avellanae*. In *L. divaricata* this fraction increased linearly with total biomass and at higher rates in interspaces ($F_{1,24} = 7.11, p < 0.05$). Thus, the differences in root mass fraction among microsities increased with plant size (Fig. 4).

SLA was higher in *C. avellanae* plants growing at interspace soils ($F_{1,134} = 7.90, p < 0.01$) while *L. divaricata* showed similar values between treatments ($p > 0.10$, Fig. 5). Specific leaf area did not differ between water supply regimes.

4. Discussion

Our results indicate that the association between landforms and plant communities at the Southern Monte-Patagonia ecotone are, at least in part, due to differences in species ability to establish and

Table 1

Mean values and standard error of physical and chemical properties of different soil types (combinations of landform and microsities, $n = 5$). Different letters indicate significant differences ($p < 0.05$) between soil types. EC = electrical conductivity, OC = organic carbon, N_t = total nitrogen.

Attribute	Channel				Bar			
	Mound		Interspace		Mound		Interspace	
	Mean	SE	Mean	SE	Mean	SE	Mean	SE
Sand (%)	84.4 ^a	2.0	61.5 ^c	3.6	78.6 ^{ab}	0.9	76.6 ^b	0.5
Silt (%)	9.2 ^a	0.9	14.6 ^b	1.1	16.6 ^b	0.8	14.7 ^b	0.5
Clay (%)	6.4 ^a	2.3	23.9 ^b	2.6	4.8 ^a	0.8	8.7 ^a	0.5
Bulk density (Mg.m ⁻³)	1.57 ^{ab}	0.03	1.67 ^a	0.05	1.42 ^c	0.01	1.52 ^{bc}	0.06
EC (dS.m ⁻¹)	5.08	0.63	4.73	1.30	4.55	0.39	2.65	1.00
N_t (%)	0.0437	0.003	0.0434	0.004	0.0529	0.005	0.0375	0.005
OC (%)	0.525 ^b	0.056	0.313 ^b	0.069	0.887 ^a	0.094	0.438 ^b	0.048
Carbonate (%)	0.096 ^b	0.020	0.318 ^{ab}	0.165	0.600 ^{ab}	0.222	2.007 ^a	1.188

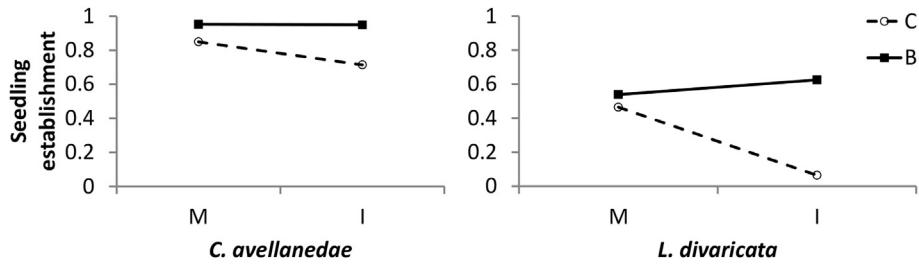


Fig. 1. Seedling establishment (proportion) in each soil type for both species. C = channel, B = bar, M = mound, I = interspace.

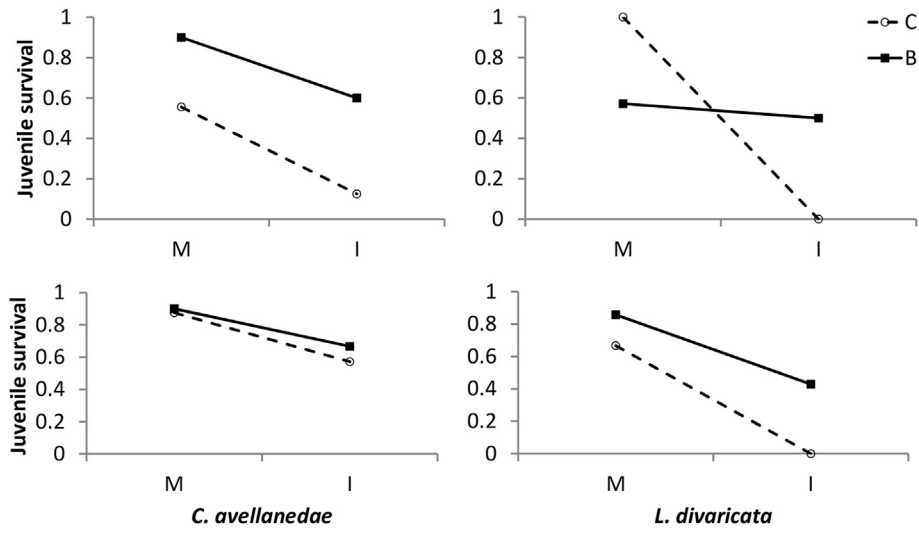


Fig. 2. Juvenile survival (proportion) in each soil type and water supply regime. C = channel, B = bar, M = mound, I = interspace. Upper panels correspond to frequent water supply regime, while lower panels correspond to sporadic water supply regime.

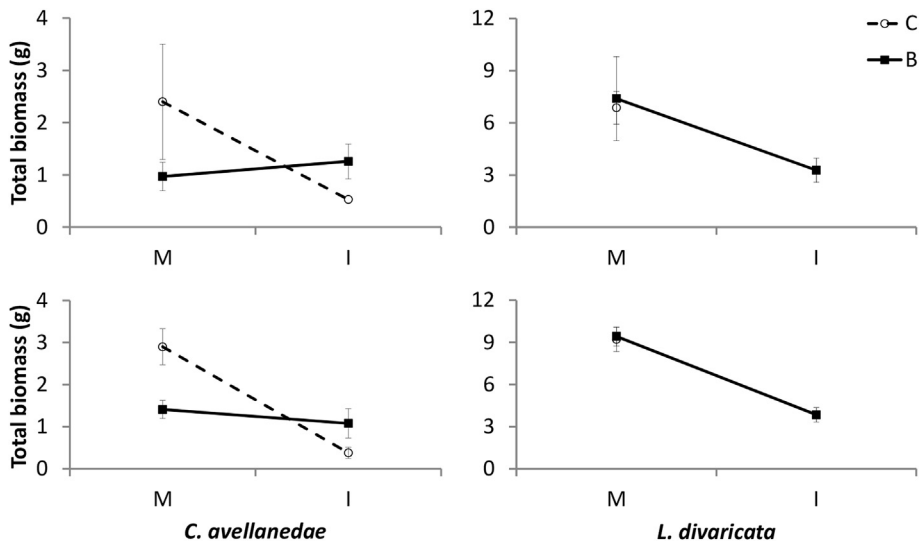


Fig. 3. Average values (\pm standard error) of total biomass for each species in each soil type and water supply regime. C = channel, B = bar, M = mound, I = interspace. Upper panels correspond to frequent water supply regime, while lower panels correspond to sporadic water supply regime.

grow in soils of each landform (Figs. 1–3). *Chuquiraga avellaneda* was able to establish and grow successfully in all soils and treatments, whereas *L. divaricata* did not survive at channel interspaces, where sand content is the lowest and clay content the highest among soil types (Table 1). Thus, this study identifies the probable

causes of the absence of *L. divaricata* from channels and consequently goes beyond the descriptive association of species with landforms. Although previous studies exemplifies the strong relationship between geomorphology, soil development and vegetation patterns in arid and semi-arid environments (e.g. Hamerlynck

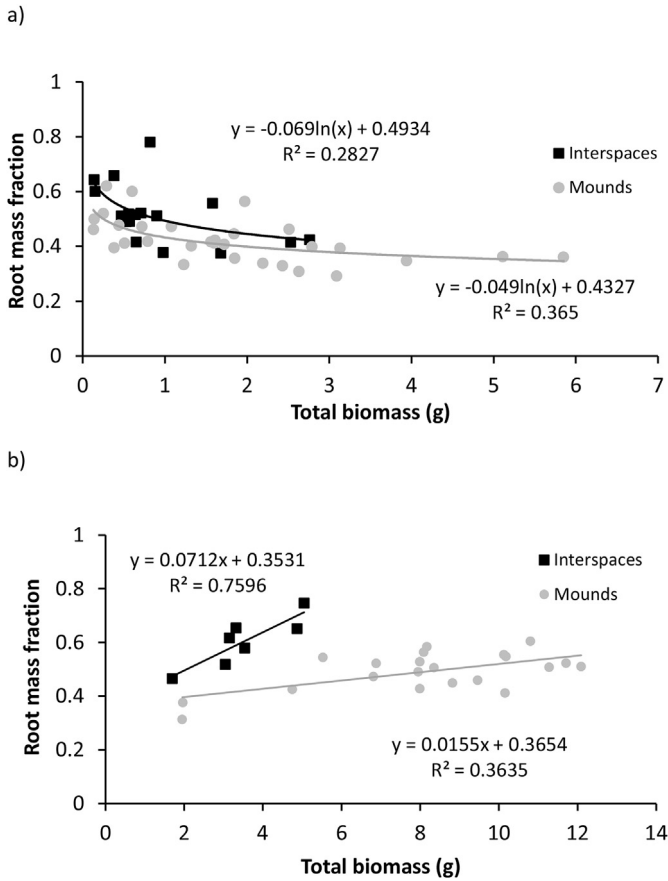


Fig. 4. Allometric relationship between root mass fraction and total biomass of *C. avellanedae* (a) and *L. divaricata* (b).

et al., 2002; Buxbaum and Vanderbilt, 2007), the mechanisms behind the absence of some species from a particular landform have rarely been identified. However, we must recognize that our study is basically focused on the differences of soils between landforms, leaving out other aspects of geomorphology.

Existing studies evaluating the influence of geomorphology on

plants were generally focused on their effects over adult plants. These studies, carried out in other arid ecosystems around the world, showed that adult plant growth (Hamerlynck et al., 2002) and mortality (Hamerlynck and McAuliffe, 2008; McAuliffe and Hamerlynck, 2010) may differ between landforms of the same landscape and/or between soil types of different geological formations. In addition, our results showed that differences among soils from different landforms not only influenced seedling growth and survival, but also species establishment.

Soil from mounds showed evidence of being safe sites for species establishment and growth (Figs. 1–3). The favorable influence of mounds associated with vegetation patches over species establishment and growth manifested in this research are consistent with previous studies in arid and semiarid areas. Several authors have mentioned mounds as high establishment microsites - both in field (Bisigato and Bertiller, 2004) and greenhouse (Bisigato and Bertiller, 1999) experiments - and as microenvironments where plants grow better (Shumway, 2000). Mound advantages have been attributed to multiple factors such as lower bulk density (Callaway, 1995), lower tendency to generate physical crusts (Buis et al., 2010), higher nutrient availability (Mazzarino et al., 1998) and the presence of beneficial microorganisms (Titus et al., 2002).

Both species assigned a higher proportion to belowground biomass in interspaces (Fig. 4). This response is common at low nutrient environments (Shumway, 2000), such as interspaces (Moro et al., 1997). Root mass fraction in *C. avellanedae* became lower with increasing plant size, while this fraction for *L. divaricata*, on the contrary, was higher in bigger plants. These differences between species may reflect diverse allocation strategies early in the life of individuals, but it could also be a consequence of the greater biomass reached by individuals of *L. divaricata*. Future studies should dig deeper on the causes of these differences considering a wider range of biomasses.

Soil from the channel interspaces turned out to be particularly hostile for *L. divaricata*. Although this species can establish itself in soil from the mounds of channels, once the roots extend to depths beyond the sand and litter accumulation layer and reach the underlying soil, analogous to interspace soil, plants would stop growing and would eventually be excluded by competition and/or desiccation. *C. avellanedae*, on the contrary, manages to survive and grow in this soil (yet with high mortality rates and achieving smaller sizes).

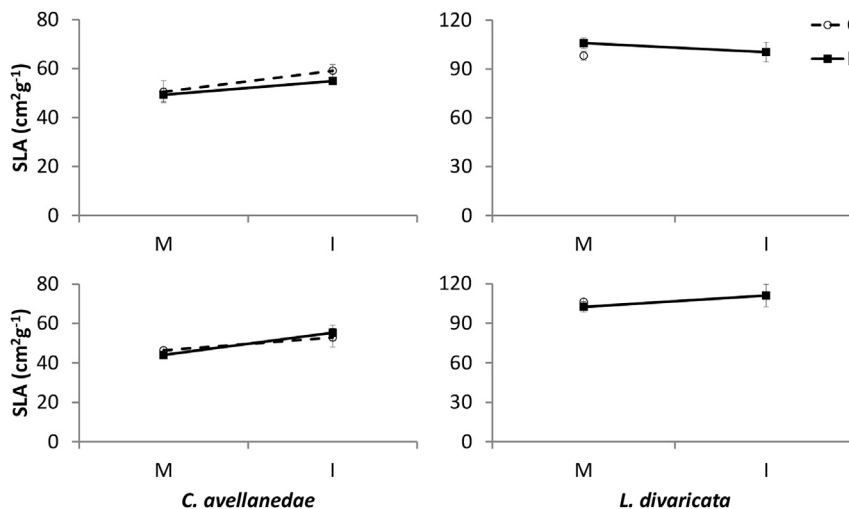


Fig. 5. Average values (\pm standard error) of specific leaf area index (SLA) for each species in each soil type and water supply regime. C = channel, B = bar, M = mound, I = interspace. Upper panels correspond to frequent water supply regime, while lower panels correspond to sporadic water supply regime.

Water availability did not affect any of the studied variables in either species (Figs. 3–5). This kind of answer is not unusual in arid and semiarid environments (Bisigato and Bertiller, 1999; McKiernan et al., 2017), and should not be ignored since this kind of results could advance our quantitative understanding of arid environments (Fernández, 2007). Cella Pizarro and Bisigato (2010) attributed this response to low phenotypic plasticity in young individuals of Patagonian species compared with fast-growing plants from high nutrient availability habitats. Species responsiveness may have been limited by their small size, because in some species, seedlings exhibited less phenotypic plasticity when compared to adult individuals (Schlichting, 1986). In addition, the reduced realism of greenhouse experiments with respect to field experiments could have also contributed to the absence of differences between water supply regimes. In particular, the use of pots limits the volume of soil available for plant exploration (Poorter et al., 2012). These limitations make pots prone to become anoxic environments (Passioura, 2006) and cause soil to dry much faster than under field conditions, thus preventing plants acclimatization to drought. Despite these limitations, greenhouse experiments achieve greater variable control (Fernández, 2010) and the use of plants growing in pots under controlled conditions is an accepted way to evaluate drought effects on plants.

Seedling establishment for *C. avellanadae* was higher than for *L. divaricata* in all soils (Fig. 1). This response is in agreement with the association between seed size and seedling ability to survive in different types of environments (Moles and Westoby, 2004), since *C. avellanadae* seeds (14.15 ± 0.20 mg) are larger compared to *L. divaricata*'s (2.57 ± 0.13 mg). Besides, the lowest SLA values of *C. avellanadae* could be related to their longer leaf lifespan (Campanella and Bertiller, 2009).

Lower biomass produced by *C. avellanadae* in bar mounds compared with the same microsite in channels (Fig. 3) indicates the presence of limiting factors in bars for this species, possibly the presence of soil calcium carbonate (Table 1), or some kind of stimulating factors in channels. In addition, higher biomasses achieved by *L. divaricata* respect to *C. avellanadae* are consistent with higher SLA values in the first species (Campanella and Bertiller, 2009) and could result as competitively disadvantageous for *C. avellanadae* on bars.

In summary, the results support the best performance of *L. divaricata* in bars and give some evidences of enhanced growth of *C. avellanadae* in channels. These results support our hypothesis and are consistent with the differential distribution of species observed in the field but should be complemented with field experiments where intra- and interspecific interactions are also involved and climatic and microclimatic conditions become more complex.

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