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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 avellanedae*, 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 microsites (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 avellanedae* than *Larrea divaricata* in channels and the average biomass of *Chuquiraga avellanedae* 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.

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. microsites) (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, microsites 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 microsites 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 microsites (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 microsites (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 avellanedae*, more related to the Patagonia Region. Although dominant species differ between landforms, some individuals of *C. avellanedae* 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 avellanedae* 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. avellanedae* 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 avellanedae* and *Larrea divaricata* seedlings. Seeds of both species (achenes in *C. avellanedae*) 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