



Research article

Abiotic factors affect the recruitment and biomass of perennial grass and evergreen shrub seedlings in denuded areas of Patagonian Monte rangelands



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ABSTRACT

Assessing the ability of key species to cope with environmental stresses in disturbed areas is an important issue for recovery of degraded arid ecosystem. Our objective was to evaluate the effect of soil moisture, exposure to UV radiation, and presence/absence of litter with different chemistry on soil N, recruitment and biomass of seedlings of perennial grass (*Poa ligularis* and *Nassella tenuis*) and evergreen shrub species (*Atriplex lampa* and *Larrea divaricata*) in denuded areas. We carried out a microcosm experiment with soil blocks (28 cm depth) sowed with seeds of the target species, subjected to different levels of litter type (perennial grass-evergreen shrub mixture, evergreen shrub mixture, and no litter), UV radiation (near ambient and reduced UV), and soil water (high: 15–25% and low 5–15%). Periodically, during 6 months, we assessed soil-N (total and inorganic) at two depths and species seedling recruitment at microcosms. Additionally, emerged seedlings of each species were transplanted to individual pots containing soil and subjected to the same previous factors during 12 months. Then, all plants were harvested and biomass assessed. Only inorganic soil-N at the upper soil varied among treatments increasing with the presence of evergreen shrub litter, exposure to ambient UV, and high soil water. Inorganic soil-N, promoted by near ambient UV and high soil water, had a positive effect on recruitment of perennial grasses and *A. lampa*. Both litter types promoted the recruitment of perennial grasses. Evergreen shrub litter and high soil water promoted the recruitment of *L. divaricata*. Seedling biomass of perennial grasses increased with high soil water and reduced UV. Ambient UV had positive or null effects on biomass of evergreen shrub seedlings. High soil water increased biomass of *L. divaricata* seedlings. We concluded that soil water appeared as the most limiting factor for seedling recruitment of all species whereas inorganic soil N limited the recruitment of the small-seeded perennial grasses and *A. lampa*. Ambient UV had negative effects on seedling biomass of perennial grasses. These complex relationships among abiotic factors and seed and plant traits should be taken into account when planning management actions after disturbances.

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1. Introduction

Livestock grazing affects the structure and functioning of plant communities in arid and semiarid rangelands, shifting vegetation from stable states with high cover of perennial grasses to alternative stable states dominated by shrubs or annual species with a significant increase in the size of denuded areas (Ares et al., 1990;

Bestelmeyer et al., 2015; Fick et al., 2016; Milchunas and Lauenroth, 1993; Okin et al., 2009). In this context abiotic drivers are relevant and ecosystem changes may be difficult or impossible to reverse towards desirable states without an active human intervention (Fick et al., 2016; James et al., 2012, 2013).

Plant regeneration by seeds is an essential process to restore plant species diversity, and community structure and dynamics in disturbed arid ecosystems of the world where the majority of plant species reproduce by seeds (Bertiller and Carrera, 2015; Grime and Hillier, 2000; Larson et al., 2015). Accordingly, seed availability across space and time is the first step for plant cover recovery in these environments (De Falco et al., 2009; Fick et al., 2016). A

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second step is that seeds reach safe microsites for germination and plant establishment (Bertiller and Carrera, 2015; Fick et al., 2016; Larson et al., 2015). The early stages in plant development are expected to be more sensitive to environmental variability than adult stages, and consequently represent a major constraint for plant regeneration processes (Walk et al., 2011; Wellstein, 2012). Early processes such as seedling emergence may have different abiotic drivers that those leading to the later seedling survival and biomass accumulation (Fay and Schultz, 2009; Lloret et al., 2004).

The increase in the size of denuded areas due to disturbance is associated with a major incidence of abiotic factors over biotic factors related to the established vegetation such as the facilitation/competition balance (Fick et al., 2016; Mollard et al., 2014; Schlesinger et al., 1990). Negative interactions with established plants may constitute a main biotic control for plant reestablishment processes in small soil gaps or vegetated areas (Funk et al., 2008; Hulvey and Aigner, 2014; Luzuriaga et al., 2012) where microclimatic conditions, soil resources (water, nutrients), and protection from herbivores are more favorable than in denuded areas for seedling emergence and survival, and biomass accumulation (Barberá et al., 2006; Bertiller et al., 2002; Mollard et al., 2014; Smit et al., 2006).

Litter accumulation on the soil surface could improve the microenvironmental conditions in denuded areas since this layer may reduce soil temperature fluctuation, and increase soil water conservation, microbial activity and nutrient levels thus promoting plant regeneration processes (Loydi et al., 2013; Xiong and Nilsson, 1999). However, the presence of litter could have facilitative to inhibitory effects on seedlings depending on either the amount (physical effect) or the chemical properties (Hovstad and Ohlson, 2008; Rotundo and Aguiar, 2005). Additionally, C/N ratios or the presence of secondary compounds in litter could influence microbial litter decomposition thus favoring either microbial N release or N immobilization processes (Arriaga and Maya, 2007; Bosco et al., 2016; Gartner and Cardon, 2004). However, litter N dynamics in arid ecosystems may be decoupled from microbial processes due to abiotic processes such as photo-degradation (Brandt et al., 2010; Parton et al., 2007). Decomposition and N release processes in litter layers, depending on their chemistry, may be differentially affected by abiotic factors such as soil water content and exposition to UV radiation (Bosco et al., 2016) with different effects on seedling establishment.

The success of plant survival in contrasting soil microsites may differ among different plant species depending on their functional traits (Gilardelli et al., 2015; Navas et al., 2010). Perennial grasses and shrubs are the dominant plant life forms in arid ecosystems (Bär Lamas et al., 2016; Navas et al., 2010). In general, perennial grasses are opportunistic species with shallow rooting depth and active growth usually coupled with water inputs in the upper soil whereas shrubs with deep or dimorphic root systems and high diversity of structural and chemical defenses against water shortage, UV radiation exposure and herbivory develop vegetative growth decoupled from water inputs (Bertiller et al., 1991; Carrera et al., 2003; Navas et al., 2010). Therefore, shrub species may be better able to colonize large denuded areas with low fertility and harsh microclimatic conditions than perennial grass species (Bertiller and Bisigato, 1998). However, species of the same life form in arid environments may have differences in functional traits among them (Bär Lamas et al., 2016). Moreover, some studies found adaptive or plastic differences in functional traits within the same perennial grass species in arid environments (Moreno and Bertiller, 2015; Valladares et al., 2007).

Knowledge about the capabilities of different key species to cope with environmental filters imposed by land degradation after disturbance is an important issue in relation to the recovery of

degraded areas in arid ecosystems (James et al., 2011; Madsen et al., 2016) but this topic still remains as one main issue of research in restoration ecology (Gilardelli et al., 2015; Hulvey and Aigner, 2014; Larson et al., 2015). The aim of this study was to evaluate the capability of seedlings of dominant species of the main plant life forms in arid ecosystems (perennial grasses and evergreen shrubs) to cope with different abiotic environments (conditioned by soil moisture, exposure to UV radiation, and presence/absence of litter mixtures with different chemistry) in areas denuded by disturbances. We hypothesized that differences in seedling recruitment and biomass accumulation induced by different abiotic scenarios in the regeneration microsites will be less between species of the same life form than between life forms (Fig. 1). We predicted that soil water content has a direct effect on plants promoting recruitment and growth of perennial grass species while evergreen shrub species are less dependent of this factor. Soil water content exert an indirect effect on recruitment and growth throughout litter decomposition mediated by microbial activity with higher soil water content promoting soil microbial activity. The incidence of UV radiation impacts directly on seedling recruitment and growth with negative effects on perennial grass species (low concentration of protective compounds) but with negligible effects on evergreen shrub species (high concentration of protective compounds), while impacts indirectly on both life forms throughout litter photo-degradation. Litter presence has a direct positive effect on seedling recruitment of perennial grass species by improving seedbed microclimate conditions while bare soil impacts negatively on this life form. The presence or absence of litter has lower impact on evergreen shrub than on perennial grass species. Litter chemistry modulates soil N availability, being recruitment and growth of perennial grass species higher dependent on soil N availability than evergreen shrub species. Litter with low C/N ratio and high concentration of secondary compounds (- C/N; + secondary compounds) releases inorganic N to soil throughout microbial activity while litter with high C/N ratio and low concentration of secondary compounds (+C/N, - secondary compounds) immobilizes N in microbial biomass.

2. Materials and methods

2.1. Study area and species

The study area is located in the southern portion of the Monte Pytogeographical Province (Patagonian Monte), Argentina. Mean annual temperature is 13.4°C, mean annual precipitation is 235.9 mm and mean annual speed of wind (prevailing from west-southwest) is 4.6 m s⁻¹ (22-year average, Centro Nacional Patagónico, 2009). Soils are a complex of Typic Haplocalcids and Typic Petrocalcids (del Valle, 1998; Soil Survey Staff, 1998). Vegetation corresponds to the shrubland of *Larrea divaricata* Cav. and *Stipa* spp. (León et al., 1998). Perennial grasses and shrubs are the main plant life forms and are arranged in a patchy structure (dominated by shrubs) covering less than 40% of the soil alternating with denuded areas (Bertiller and Ares, 2011). Within this area, we selected six representative study sites of at least 3 ha each (minimal area *sensu* Mueller-Dombois and Ellenberg, 1974) with large denuded areas (>2 m in diameter without vegetation cover) induced by sheep grazing (43° 06' 13.4S, 65° 43' 51.3W; 150 m a.s.l.; 43° 08' 52.0S, 65° 42' 49.6W; 151 m a.s.l., 42° 11' 38.7S, 64° 59' 37.3W; 75 m a.s.l.; 42° 12' 27.8S, 64° 59' 34.5W; 94 m a.s.l. and 42° 12' 13.7S, 64° 58' 55.6W; 92 m a.s.l.) or fire disturbances (42° 49' 15.6S, 65° 00' 24.5W; 63 m a.s.l.). Additionally, we selected a further study site characteristic of the Patagonian Monte located at 42° 47' 10.4S, 65° 00' 28.2W; 5 m a.s.l. to perform the manipulative experiments. This site was characterized by large denuded areas

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