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Original article

The role of nurse functional types in seedling recruitment dynamics of alternative states in rangelands

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ABSTRACT

In arid ecosystems, recruitment dynamics are limited by harsh environmental conditions and greatly depend on the net outcome of the balance between facilitation and competition. This outcome can change as a consequence of degradation caused by livestock overgrazing. Also, distinct plant species may show a differential response to a common neighbour under the same environmental conditions. Therefore, ecosystem degradation could affect the net balance of plant-plant interactions, which can also depend on the functional traits of potential nurse species. The aim of this study is to assess the influence of alternative degradation states on *(i)* the density of seedlings of perennial species emerging in four microsite types, and on *(ii)* the relative interaction intensity (RII) between seedlings and potential nurses belonging to three functional types (deep- and shallow-rooted shrubs, and tussock grasses). During three years, we recorded seedling density of perennial species in four alternative degradation states in grass-shrubby steppes from northwestern Patagonia. The density of emerged seedlings of perennial species decreased sharply as degradation increased, showing non-linear responses in most microsites. Seedling density underneath deep-rooted shrubs was higher than underneath shallow-rooted shrubs and tussock grasses. Also, deep-rooted shrubs were the only functional type that recorded seedling emergence in highly degraded states. Deep-rooted shrubs had facilitative effects on the seedlings emerging and surviving underneath them, independently of ecosystem degradation. In contrast, RII between shallow-rooted shrubs and recently emerged seedlings, switched from positive effects in the less degraded states, to negative effects in the most degraded state. Tussock grasses recorded the weakest intensity of facilitative interactions with recently emerged seedlings, switching to competitive interactions as degradation increased. Our results suggest that species with key functional traits should be considered in management and restoration plans for rangelands with different degradation levels, since they have a strong influence in the net outcome of plant-plant interactions and in the recruitment dynamics of arid ecosystems.

1. Introduction

In arid and semiarid ecosystems, plant recruitment is limited by harsh environmental conditions and greatly depends on plant-plant interactions, as facilitation and competition (Whitford, 2002; Padilla and Pugnaire, 2006). Facilitation occurs when an adult plant (i.e., nurse) increases the emergence, survival, growth and/or fitness of spatially associated seedlings (i.e., protégées) (Callaway, 2008). Nurse plants benefit the individuals growing underneath them by: (i) ameliorating extreme microclimatic conditions (i.e., reducing radiation and temperature at ground level, thereby diminishing evapo-transpiration during the day, and decreasing freezing risk during the night); and/or (ii) protecting against herbivores (i.e., many nurse species have spines or other features that deter herbivores, a mechanism known as 'associational resistance') (Callaway, 2008). Conversely, competition occurs when a plant growing close to another decreases the survival,

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growth and/or fitness of its neighbour as a consequence of sharing limited resources (e.g. water, nutrients, light) (Padilla and Pugnaire, 2006). Positive and negative effects occur simultaneously in arid and semiarid ecosystems (*heareafter* 'arid ecosystems'), and thus recruitment dynamics depend on the net outcome of the balance between facilitation and competition (Padilla and Pugnaire, 2006).

The magnitude and even the direction (either positive or negative) of net plant-plant interactions can change as a consequence of ecosystem degradation caused by human activities (e.g. livestock grazing). Overgrazing can, directly and/or indirectly, affect seedling recruitment in arid ecosystems (López et al., 2013). As a consequence of livestock overgrazing, the trampling, consumption of flowers and browsing produced by herbivores directly reduce seedling recruitment, and can affect plant-plant interactions since herbivore pressure will be higher for seedlings growing close to palatable species (Graff et al., 2007). Also, the reduction in vegetation cover, and the increase in soil erosion produced by historical overgrazing can decrease soil water availability, by increasing evaporation and decreasing its storage capacity (Paruelo et al., 1993; Reynolds and Stafford Smith, 2002). Thus, ecosystem degradation can indirectly affect seedling recruitment and plant-plant interactions, because as soil water availability decreases, seedling recruitment decreases as a consequence of increased competition for this limting resource between neighbouring individuals. It has been widely documented that plant-plant interactions can change from negative to positive, or viceversa, in response to increasing abiotic stress or consumer pressure (Bertness and Callaway, 1994; Verwijmeren et al., 2013 and references therein). However, the studies that separately test the effect of abiotic stress and consumer pressure on plant-plant interactions are unrealistic, since abiotic constraints and consumer pressure often co-occur in arid ecosystems (Brooker et al., 2008). In a global context in which a 40% of arid ecosystems are severely degraded (Reynolds and Stafford Smith, 2002; Adeel et al., 2005), mainly as a consequence of livestock overgrazing (Adeel et al., 2005), it would be essential to know the influence of degradation in the recruitment dynamics and in the net balance of plant-plant interactions in rangelands.

Distinct plant species may show a differential response to a common neighbour under the same environmental conditions (Maestre et al., 2009a). This could be because the species that co-occurr in a given community have different above- and below-ground traits which make them functionally different. Distinct functional traits could be beneficial, or even detrimental, for the same neighbour. For example, the different degree of palatability of nurse species, determined by the presence or abscence of mecanical or quemical defenses, will differentially affect the emergence and/or survival of protégées. Thus, non-palatable nurse species can benefit protégées growing beneath them by deterring herbivores or lowering consumer pressure (Graff et al., 2007). Also, depending on the depth of the radicular system, water competition between neighbouring individuals can increase, or even, decrease. Competition for water will be higher for individuals whose roots are overlapped, than for those whose roots explore different soil layers. Although, the net balance of plant-plant interactions could depend on above- and below-ground traits of plant species, we do not know studies focusing on the functional types of nurse species (*sensu* Sala et al., 1997) as a determinant of the net outcome of plant-plant interactions in arid ecosystems.

While there is broad consensus in the scientific community that facilitation strongly modulates recruitment dynamics in arid ecosystems, facilitative interactions have not yet been explicitly considered in the conceptual framework of degradation (Verwijmeren et al., 2013). In this sense, the aim of this study is to assess the influence of alternative degradation states in seedling recruitment dynamics considering different functional types of potential nurse plants. To do this, we used grass-shrubby steppes of northwestern Patagonia as a model-system, and during three years we evaluated the recruitment dynamics of perennial species in four alternative degradation states. Specifically, we assessed the influence of alternative degradation states on *(i)* the interannual density of seedlings emerging in different microsite types and on *(ii)* the relative interaction intensity between seedlings and potential nurses belonging to three functional types.

2. Materials and methods

2.1. Study area

The study was carried out in Pilcaniyeu, at a 7800 ha field station belonging to Estación Experimental Agropecuaria Bariloche from the Instituto Nacional de Tecnología Agropecuaria (INTA), located in Río Negro, Argentina (41° 01′ 42″ S, 70° 35' 21" W). Climate is characterized by cold wet winters (coldest month mean temperature is 2.1 °C) with temperate dry summers (hottest month mean temperature is 15 °C). Mean annual precipitation is 265 mm ± 82.5, and more than 70% of the precipitation falls during autumn and winter (López, 2011; Appendix A, Fig. A.1). As in other arid and semi-arid regions, annual precipitations are highly variable (Noy-Meir, 1973; Whitford, 2002), alternating years with precipitations near the historical average, and years with precipitacions below- and above-average (Bustos, 2006; López, 2011). We studied the grass-shrubby steppe of *Poa ligularis* and *Mulinum spinosum*, a community of high forage value within the Western Patagonian District of the Patagonian Steppe. Soils are shallow, with a sandy surface layer and a clay-rocky sub-superficial layer (Lores et al., 1983). The main species are tussock-grasses (*P. Ligularis* and *Pappostipa speciosa* var. *speciosa*), and deep- and shallow-rooted shrubs (*M. spinosum* and *Senecio filaginoides*, respectively), forming grass and/or shrub patches immersed in a bare soil matrix (Aguiar and Sala, 1999; López et al., 2013). Patch dimensions vary from 0.15 to 1.5 m in width and from 0.1 to 1.2 m in height.

2.2. Functional types

To study the influence of alternative degradation states on recruitment dynamics of perennial species, we divided the dominant species of the grass-shrubby steppe from the western Patagonian District in functional types based on two criteria, which can influence the net outcome of plant-plant interactions in arid ecosystems: (a) above ground traits mainly associated with the ability to deter herbivores, as the presence of mechanical or quemical defenses; and (b) below ground traits that mainly determine plant-plant water relations which are extremely important in arid ecosystems, because water is the most limiting resource (Sala et al., 1997). Several studies suggest that shrubs can be potential nurses in arid lands (Gómez Aparicio et al., 2004), and it has also been documented facilitation by grasses (Maestre et al., 2001). Therefore, we selected the main shrub (*M. spinosum* and *S. filaginoides*) and tussock-grass (*P. ligularis* and *P. speciosa* var *speciosa*) species. Shrub species were assigned to different functional types, as they differ in their above- and below-ground functional traits, whereas grass species were grouped together in one functional type due to their functional similarities (Table 1).

2.3. Experimental design

At three sites we identified four alternative degradation states of vegetation (I-IV, *sensu* Bonvissuto et al., 1993), separated by at least one critical threshold (López et al., 2013). Specifically, states I and II