Moderate disturbances and shrub protection enhance perennial grass recruitment in northern Patagonia

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ABSTRACT

Seedling recruitment of perennial grasses (PGR) and annual species (ASR) were registered on each microsite. PGR was similar on the leeward side, suggesting that shrubs generate similar microsites for their establishment per se as a result of an elevated seedling mortality (Fenner, 2000; Fenner and Thompson, 2005). In the Monte desert, cattle are known to induce cascading effects on perennial grass fitness, through processes such as changing the pollinator assembly (Tadey, 2008; Vázquez and Simberloff, 2004), removing inflorescences before seeds set, and reducing spike production following grazing (Kröpfl et al., 2007; Pol et al., 2014). Meanwhile, annual species tend to maintain their elevated seed production under disturbances and might take advantage in grazed sites (Grime, 1977).

In the Monte desert, vegetation is distributed in patches (‘islands’) surrounded by a bare soil matrix (or interpatches) (Aguiar and Sala, 1999). These patches are dominated by shrub species, with other functional groups growing under their canopy (Funk et al., 2018). Shrubs enhance local growth conditions through the accumulation of nutrients (Fuentes et al., 1986; Soriano and Sala, 1986) and provide protection against wind erosion, desiccation, and defoliation (Acosta and Agüero, 2001; Aguiar and Sala, 1994; Fuls, 1992). This protection enhances seed rain produced by species growing under the canopy (Soriano and Sala, 1986). Furthermore, patches act as seed traps collecting propagules.

1. Introduction

Grazing and fire promote changes in ecosystem structure and function by means of an increase in the heterogeneity of plant community and a modification in resource release (Pickett and White, 1985). These are the main disturbances in semiarid grasslands (Oesterheld et al., 1999) and, particularly, in Argentinean Patagonia (Gittins et al., 2011). There, during the last 100 years, introduced cattle have changed grazing intensity and also altered fire regimes (Kitzerberger et al., 2005; Peter et al., 2013). The occurrence of summer wildfires is common in this system (Kröpfl et al., 2007), but the use of prescript fires as a tool to reduce shrubs and enhance perennial grass cover prevents severe accidental fires (Bran et al., 2007; Peléz et al., 2010). Despite this, only a few studies have been focused on the effects of grazing and fire on seedling recruitment in these semiarid shrublands (Bisigato and Bertiller, 2004a; Franzese and Ghermandi, 2012; Gonzalez and Ghermandi, 2012).

Seedling recruitment is affected by a combination of processes and its limitation might be the consequence of a poor soil seed bank caused by low seed production or dispersal, restrictions in seed germination caused by high seed senescence and mortality or restrictions in seedling establishment per se as a result of an elevated seedling mortality (Fenner, 2000; Fenner and Thompson, 2005). In the Monte desert, cattle are known to induce cascading effects on perennial grass fitness, through processes such as changing the pollinator assembly (Tadey, 2008; Vázquez and Simberloff, 2004), removing inflorescences before seeds set, and reducing spike production following grazing (Kröpfl et al., 2007; Pol et al., 2014). Meanwhile, annual species tend to maintain their elevated seed production under disturbances and might take advantage in grazed sites (Grime, 1977).

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transported by animals and wind (Acosta and Agiero, 2001; Aguilar and Sala, 1994; Fuentes et al., 1986). On the other hand, as most shrub species have a dense and unpalatable canopy, grazing pressure is higher in interpatch areas, and this suggests that patch formation could be a result of grazing (Allington and Valone, 2013).

All those processes induced by shrubs combined with the effects of different land use histories result in a heterogeneous soil seed bank spatial distribution (Edwards and Crawley, 1999; Caballero et al., 2008; Leder et al., 2017) and may promote uneven seedling recruitment. Other forces, as predominant wind direction, may affect the protective function of the shrub, so in addition to the general patch-interpatch heterogeneity of arid land vegetation, differences between microsites under shrub canopy must be considered (Bistagato et al., 2009; Bussola et al., 2012; Caballero et al., 2008; Soliveres et al., 2015). In this sense, Whitford (2002) proposed a process promoted by the wind in which soil particles, leaves, and small stems, are deposited on the leeward side of vegetation patches. This process may promote differences in seed bank abundance and microenvironmental conditions among microsites and affect seedling recruitment, especially in grazed sites in which interpatches have a low plant cover and are prone to wind erosion (Chartier and Rostagno, 2006; Parizek et al., 2002; Funk et al., 2018). But on the other hand, after fire occurrence, wind promotes the redistribution of nutrients, organic matter and seeds from patches to interpatches (Boo et al., 1996; Ravi and D’Odorico, 2009; Rostagno et al., 2006). This process might homogenize patch-interpatch conditions and reverse the grazing effect, reducing differences among microsites regarding seedling recruitment.

Our main objective was to understand seedling recruitment dynamics and shrub patch effects on this process in a complex system as the Monte desert. We designed a study that included different disturbance intensities and contrasting microsites in each patch along a transect defined by the predominant wind direction. We tested three hypotheses:

**Hypothesis 1.** Predominant wind effect combined with grazing by domestic livestock, a disturbance that promotes vegetation and soil seed bank loss in interpatches, deteriorates safe microsites for seedling recruitment at the windward side of shrubs, reinforcing the patch-interpatch structure in the Monte system.

**Hypothesis 2.** Post-fire wind erosion, a disturbance that redistributes nutrients and propagules from patches to interpatches, homogenizes the distribution of safe microsites for seedling recruitment.

**Hypothesis 3.** Grazing decreases perennial plants reproductive performance and has a negative effect on perennial grass seedling recruitment. Fire promotes propagules and nutrients redistribution, which causes the opposite effects.

2. Materials and methods

2.1. Study area

The study area was located in the Adolfo Alsina Department (40° 40′ S, 64° 10′ W), Río Negro province, Argentina. The climate is subtemperate dry, with warm summers (mean temperature 24 °C) and mild winters (mean temperature 7 °C). Mean annual precipitation ranges from 300 to 350 mm, with high variability within and between years (Godagnone and Bran, 2009). The annual precipitation for the sampling period was 357 mm, slightly higher than the mean value. A moderate north-westerly wind occurs throughout the year (Godagnone and Bran, 2009). The topography is uniformly flat and soils are classified as Ari-disolos (Godagnone and Bran, 2009). Natural vegetation in the area is characterized by a shrubland steppe, corresponding to the Monte Phytogeographical Province, South District, North Patagonia Sub-district (Roig et al., 2009); with a herbaceous layer of predominately winter-growing grasses. This community is dominated by Larrea divaricata Cav., Chusquira erinacea D. Don and Condalia microphylla Cav. in the shrub layer, and Nassella tenuis (Phil.) Barkworth in the herbaceous layer. Perennial grasses Poa ligularis Nees ex Steud., Pappostipa speciosa (Trin. and Rupr.) Romasch., Nassella longiglumis (Phil.) Barkworth, and annual species Schismus barbatus (L.) Thell (non-native), Erodium cicutarium (L.). l’Her. ex Ait. (non-native), and Daucus pusillus Michx. are also commonly found in the herbaceous layer (Cabrera, 1971). Adolfo Alsina Department has almost 100 years of extensive grazing history, with an average stocking rate of ≈0.18 sheep ha⁻¹ (Peter et al., 2015).

2.2. Sampling design

The study area was a 30 × 10 km vegetation unit and comprised several ranches. Grazing intensities were selected using the piosphere criteria (Bistagato et al., 2005). Piospheres are the radial grazing intensity gradients developed in arid lands by cattle concentration in some places, as water points (Chillo et al., 2015). Grazing impact is higher as the distance to the water point decreases (D’Odorico et al., 2013). With this in mind, seven areas with different land use histories related to grazing intensity and summer wildfire occurrence were selected using the same classification employed by Peter et al. (2013) (Table 1).

Grazed treatments were located in 600 ha paddocks. Heavily grazed (HG) and moderately grazed (MG) sites were in the same paddock, but 2000 m apart from each other. Burned grazed (BG) and burned ungrazed (BU) sites were separated by a wire fence. The recently burned grazed (B7) was moderately grazed and was affected by a wildfire in the summer of 2007 (six years before sampling). Sites HG, MG, and UG were located in a farm separated by less than 30 km from another farm that contained the other four treatments. The LU site was a 40 years exclosure, and D. Obscura and D. Cavato were excluded from grazing again since then. Three years after the summer wildfire occurrence in 2002, a five-year drought event took place, and the mean annual rain ranged from 35% to 75% of the annual average (Funk et al., 2012).

Previous studies in the same land use histories and area showed a decrease in grass cover and richness associated with intense grazing and a compensation of these negative effects related to post-fire recovery (Peter et al., 2013). Studies in similar systems also suggested that after fire occurrence wind contributes to the redistribution of propagules and nutrients that were accumulated under shrub canopy (Boo et al., 1996; Ravi and D’Odorico, 2009; Rostagno et al., 2006), homogenising vegetation cover. Considering the previous information provided by Peter

<table>
<thead>
<tr>
<th>Land use history</th>
<th>Acronym</th>
<th>Post-fire recovery years</th>
<th>Distance to the watering point</th>
<th>Grazing history</th>
<th>Disturbance intensity</th>
</tr>
</thead>
<tbody>
<tr>
<td>Ungrazed</td>
<td>UG</td>
<td>50 years enclosure</td>
<td>null</td>
<td></td>
<td>low</td>
</tr>
<tr>
<td>Long grazed</td>
<td>LU</td>
<td>40 years enclosure,</td>
<td>overgrazed for one year in 2008</td>
<td>low</td>
<td>medium</td>
</tr>
<tr>
<td>Burned ungrazed</td>
<td>BU</td>
<td>11 years</td>
<td>11 years</td>
<td>medium</td>
<td>medium</td>
</tr>
<tr>
<td>Burned grazed</td>
<td>BG</td>
<td>&lt;600 m</td>
<td>grazed by sheep</td>
<td>high</td>
<td>high</td>
</tr>
<tr>
<td>Recently burned</td>
<td>B7</td>
<td>six years &gt;2500 m</td>
<td>grazed by sheep</td>
<td>medium/high</td>
<td>very high</td>
</tr>
<tr>
<td>Moderately grazed</td>
<td>MG</td>
<td>≥2500 m</td>
<td>grazed by sheep</td>
<td>high</td>
<td></td>
</tr>
<tr>
<td>Heavily grazed</td>
<td>HG</td>
<td>&lt;600 m</td>
<td>grazed by sheep</td>
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</tr>
</tbody>
</table>
et al. (2013) and our general knowledge of the study site, a gradient according to the disturbance intensity was established (Table 1).

To estimate seedling recruitment, five shrub patches with a radius greater than one meter were randomly chosen as experimental units on each land use history area. Patches were nonspecific and consisted of different shrub species. Following the pattern used to sample soil seed bank in the area (Leder et al., 2017), seven microsites were located on each patch along an east-to-west (leeward-windward) transect. One microsite was located at the shrub trunk side, two on the shrub edges, two at middle distances between the edges and the trunk, and two in interpatch areas at the same distance from the edge as the middle microsites (n = 35). Each patch was separated from another patch by at least one meter and was carefully chosen in order to assure that the microsites located outside the canopy did not overlap with those from other patches.

Once the microsites were selected, a grid with 10 × 10 4 cm² squares was placed on each one and was permanently marked with metal spikes. At that time, grasses with more than three tillers, shrubs, and sub-shrubs with secondary growth and/or plants that had fructified (with rests of the inflorescence) were identified and tagged as ‘adults’, to avoid registering them as recruiters on the following visits (Bisigato and Bertiller, 2004b). Microsites were sampled on the first two weeks of each month, starting after the autumn rains, from April 2013 to March 2014. In each visit, all seedlings were identified to species level when possible and were classified by functional group and by native/non-native species. In this way, data consisted of the number of squares in which each species (group or taxa) was present in that sampling date and this was used as a proxy of seedling abundance.

2.3. Statistical analyses

Few species were consistent in their appearance between and within sites, so statistical analyses were carried out over species data summed up into two functional groups: perennial grasses (all native species), and annual herbs = grasses (annuals, with three non-native and nine native species). Shrubs = subshrubs as a functional group were not statistically analysed because data was scarce.

We analysed recruitment dynamics searching for overall changes in seedling emergence between consecutive months. Given that we were interested in describing a general tendency, we used mean values from all the microsites and all the land use histories. When data met the normality requirement consecutive months were compared with Student’s t tests (t), and when the requirement was not reached (even if data were transformed), Wilcoxon’s test (W) was used.

Differences in seedling recruitment between sites and microsites were tested using data of the month with the highest seedling recruitment for annuals and with data of the end of the sampling period for perennial grasses (because those seedlings were considered to be ‘recruited’). To test our third hypothesis about the opposite effects between grazing and fire we performed a factorial analysis using data from sites UG and BU (burned and unburned ungrazed sites), and BG and HG (burned and unburned grazed sites). Homoscedasticity was tested with Levene’s test. Data were transformed when needed in order to meet ANOVA (F) requirements, when these requirements were not met data were analysed using Kruskal-Wallis nonparametric test (H).

Given that we could not identify the species of all the perennial grass seedlings, we did not include an analysis of the dominant species of this group. To identify which annual species dominated seedling recruitment, Student’s t tests were performed comparing the two species with the highest number of seedlings on each land use history. When data did not meet the normality requirement, Wilcoxon’s test was used.

All the statistical analyses were carried out using InfoStat software (Di Rienzo et al., 2011).

3. Results

According to the first and second hypotheses, which postulate changes related to grazing and fire respectively, results are shown with both disturbances mixed in the gradient of land use histories presented in Table 1.

3.1. Recruitment dynamics

Perennial grass recruitment started at the end of the autumn (June 2013). It showed a significant increase in June and July, and this tendency remained until the middle of the spring (October 2013) when recruitment reached its maximum (Fig 1a, Table 2). Starting in October, a mortality increase was observed, especially in December 2013, at the end of the spring. A second and smaller perennial grass recruitment
Fig. 2. Mean perennial grass seedling abundance (seedling/m² ± SE) between sites with different land use histories. Different letters indicate significant differences between land use histories for each microsite (p < 0.05). UG: ungrazed site, LU: long ungrazed with grazing event, BU: burned ungrazed site, BG: burned grazed site, B7: burned in 2007 and grazed site, MG: moderately grazed site, HG: heavily grazed site. A: windward interpatch, B: windward border microsite, C: windward middle microsite, D: trunk, E: leeward middle microsite, F: leeward border microsite, G: leeward interpatch.
Regarding perennial grasses in different land use histories, comparisons between microsites in each land use history did not show any significant differences between them. Nevertheless, seedling recruitment between land use histories showed different results depending on the microsite from which each comparison was made. On the under-canopy windward microsites, recruitment was lower in the heavily grazed (HG) and ungrazed (UG) sites, and higher in the ungrazed sites that had a disturbance background (LU and BU) (Fig. 2). On the other hand, exposed microsites (interpatches) and wind-protected microsites (T, ML, and BL) did not show significant differences in perennial grass seedling recruitment between land use histories (Fig. 2). All perennial grass species recruited were native.

Addressing our third hypothesis, we detected a positive effect of fire on perennial grass recruitment (Fig. 3), as seedlings number was higher in burned sites regarding their grazing treatment.

Annual plant recruitment only showed significant differences between microsites in BG and MG. The highest annual plant recruitment in BG occurred in the leeward interpatch and the lowest in the windward border, the trunk, and the leeward middle microsite (Fig. 4a, $F = 4.282, p = 0.003$). In MG annual plant seedlings abundance was maximum in the leeward middle microsite and minimum in the windward middle and border (Fig. 4b, $F = 3.848, p = 0.006$).

As a general tendency, annual plant recruitment was higher in grazed sites (Fig. 5), where non-native species dominated seedling recruitment (Table 3). Meanwhile, less disturbed sites (e.g., ungrazed) showed lower annual plant recruitment (Fig. 5) and were dominated by native species (without non-native as co-dominant species in sites that presented low or moderate disturbances) (Table 3).

4. Discussion

4.1. Recruitment dynamics

Annual grass seedlings suffered high mortality at the end of spring and beginning of summer probably related to temperature increases. Seedlings that survived through this period reached establishment. A second perennial grass recruitment peak may be related to the occurrence of summer rains and to an increase in seed availability as a result of seed dispersal in the same period (Leder et al., 2015).

Annuals seedling recruitment remained high for several months, and this can be explained by low seedling mortality and/or a high seedling replacement rate. This promotes the persistence of a high annual seedling number until the fructification and senescence season towards the spring.

4.2. Effects of the predominant wind combined with land use histories on seedling recruitment

In relation to perennial grass seedling recruitment, our results do not support our first hypothesis, as we did not find evidence of differences promoted by the combination of grazing and the predominant wind direction on the distribution of safe microsites. Differences founded in perennial grass soil seed bank between microsites in unburned grazed sites (Caballero et al., 2008; Leder et al., 2017; Marone et al., 2004) are not reflected in seedling recruitment. Leeward middle-canopy microsites have higher perennial grass seed bank than borders and interpatches (Leder et al., 2017), but their recruitment is equal.

Regarding the other land use histories, the lack of differences in seedling recruitment between microsites may be explained by (i) the absence of recruitment per se in some sites, probably as a result of a very scarce soil seed bank, as is the case of heavily grazed sites (Leder et al., 2017), or (ii) a high seed supply from patches to interpatches directly through the seed rain combined with similar micro-environments that
Fig. 5. Mean annual species seedling abundance (seedling/m² ± SE) between sites with different land use histories. Different letters indicate significant differences between land use histories for each microsite (p < 0.05). UG: ungrazed site, LU: long ungrazed with grazing event, BU: burned ungrazed site, BG: burned grazed site, B7: burned in 2007 and grazed site, MG: moderately grazed site, HG: heavily grazed site. Different letters indicate significant differences. A: windward interpatch, B: windward border microsite, C: windward middle microsite, D: trunk, E: leeward middle microsite, F: leeward border microsite, G: leeward interpatch.
allow a significant and even recruitment. The second explanation is sustained by the lack of differences in seed rain between patches and interpatches found by Leder et al. (2015) and the capacity of the dominant grass species, Nasella tenuis, to anchor, germinate and establish in unprotected microsites (Distel et al., 1992). On the other hand, the results found in the burned sites seem to agree with our second hypothesis, as we do not find differences among microsites after ten years of post-fire recovery.

Considering a different approach, only under-canopy windward microsites showed differences between land use histories, showing a differential effect of the wind direction related to the microsite. And on the other hand, the lack of differences between land use histories at the leeward microsites might represent evidence of shrub protective effects. These effects might promote a similar aptitude for seedling recruitment among land use histories on the leeward micro-environments. In this sense, it is important to highlight that the differences in perennial grass seedling recruitment between sites were found only at the windward under-canopy microsites.

On the other hand, our results partially agree with our third hypothesis. Because even though fire enhanced perennial grass recruitment, the undisturbed site had also extremely low recruitment, contrary to what we expected. In this sense, three different situations could be proposed to explain the case for each site: (i) Land use histories with a disturbance (considered to have a medium disturbance) might indicate that conditions in the leeward interpatch enhance higher annuals recruitment than those in microsites under shrub canopy. The greatest challenge to maintaining forage grass species in the Monte desert is recruiting new perennial grass seedlings. A better understanding of complex microsite conditions that enhance seedling recruitment can lead to the adoption of management practices that promote favorable microsites and lead to a greater cover of desired species.

On a more promising note, our study also highlights that low-to-medium disturbances (like sites with a long post-fire recovery or grazing events with resting periods) enhance perennial grass seedling recruitment in this semiarid shrubland, especially under-canopy microsites that might provide some kind of shrub protection over the seedlings.

CRediT authorship contribution statement

Cintia Leder: Conceptualization, Methodology, Formal analysis, Investigation, Writing – original draft, Writing – review & editing, Visualization, Project administration. Silvia Torres Robles: Investigation. Guadalupe Peter: Conceptualization, Methodology, Investigation, Writing – review & editing, Supervision, Funding acquisition.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.
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