Reduced herbivore pressure under rainy ENSO conditions could facilitate dryland reforestation

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Abstract

Most semi-arid and arid regions around the world have lost a major part of their original vegetation. Restoration of once shrublands and woodlands is often challenged by low seedling establishment success due to water stress and herbivory. In some regions, increased rainfall during El Niño Southern Oscillation (ENSO) events can significantly stimulate plant recruitment. However, recruitment seems to be strongly modulated by herbivore pressure. Also, seedling establishment in arid ecosystems can be facilitated by adult trees and shrubs whose canopies contribute to improve seedling water relations. We performed a field experiment to test the role of small mammalian herbivores and shade availability during simulated rainy ENSO conditions on the growth and survival of *Prosopis chilensis* saplings in semi-arid Chile. When mammalian herbivores were absent, sapling survival increased from 25% under simulated strong ENSO rain to 60% under very strong rainy events. This positive effect of increased water availability was over-ruled by strong herbivory of mainly introduced European rabbits (*Oryctolagus cuniculus*) and hares (*Lepus europaeus*). Most saplings died when herbivores were present. Shade availability did not significantly improve plant growth and survival. Our results support the hypothesis that rainy years such as those associated to ENSO events could improve the possibilities for successful tree reforestation in semi-arid ecosystems when combined with a reduction in herbivore pressure.

Keywords: Ecosystem restoration; Facilitation; Herbivore; *Prosopis chilensis*; Resource pulse; Semi-arid ecosystem

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1. Introduction

Dryland degradation is one of the most serious global environmental problems (Millennium Ecosystem Assessment, 2005). Restoration of arid and semi-arid shrublands and woodlands is often stimulated through tree reforestation but water limitation makes it often unsuccessful and costly (Whitford, 2002). In many arid and semi-arid regions, inter-annual variability in precipitation is strongly associated to El Niño Southern Oscillation (ENSO). Increased rainfall during ENSO events is crucial for plant recruitment and productivity in these systems (Holmgren et al., 2001, 2006) and may cause long-lasting effects on dryland vegetation depending on the prevalent herbivore pressure (Holmgren and Scheffer, 2001). Indeed, several field studies have found successful recruitment of woody vegetation during rainy ENSO events (Nicholls, 1991; Brown et al., 1997), especially when herbivores were excluded (Austin and Williams, 1988; Bowers, 1997). Even relatively inconspicuous animals such as small rodents might interact strongly with rainfall effects in regulating plant biomass in dry ecosystems. For example a large-scale field experiment conducted in northern Chile since 1989 has shown that shrub and perennial cover can increase significantly either when rodent herbivores are directly excluded, or when predators (birds of prey and foxes) are allowed to prey on these (Gutiérrez et al., 1997).

Holmgren and Scheffer (2001) hypothesized that increased tree and shrub establishment during rainy ENSO events could be improved by controlling main herbivores thereby facilitating a switch of degraded semi-arid ecosystems towards a more productive state. Because of positive feedbacks, a more productive state would tend to be maintained despite the relatively short duration of the rainy pulse that triggered the increase in primary productivity. This is an attractive hypothesis with large applied implications since ENSO events are potentially predictable several months in advance and model forecasts are steadily improving (Goddard et al., 2001).

In addition to increased water availability and reduced herbivory, plant shade often facilitates the successful establishment of new trees and shrubs in arid and semi-arid ecosystems (Holmgren et al., 1997). Nurse plants shade usually provides a more benign microclimate (Joffre and Rambal, 1988; Del Pozo et al., 1989) that reduces seedling thermal and water stress (Valiente-Banuet and Ezcurra, 1991; Aguiar and Sala, 1994). This facilitating role of shade, however, may become less crucial during rainy ENSO years when water availability is not a strong limiting factor.

This study aims to test the role of small mammalian herbivores and shade during simulated rainy ENSO conditions for tree recruitment. We performed our field experiments with *Prosopis chilensis* (Mol.) Stuntz saplings, a native tree species which was widely distributed in arid and semi-arid Chile before indiscriminated logging and grazing reduced the population to scattered adult individuals (Arancio et al., 2001).

2. Material and methods

2.1. Study site

The study site was located within a private farm (Fundo El Salitre), 85 km south of La Serena and 25 km from the highway (30°41′S, 71°37′W), in north-central Chile. This site has a south-east orientation on a gentle slope (10°, 200 m elevation) and is currently being used for livestock grazing. The vegetation is dominated by xerophytic shrubs. The climate is semi-arid mediterranean with 90% of the precipitation falling in the austral winter months (May–September); summer months are warm and dry. Between 1989 and 2003, mean annual precipitation in Fray Jorge was 145.4 ± 31.3 mm (1 S.E.). The accumulated rainfall in 2002 was 337.2 mm which was three times the average value, as a result of an ENSO event (McPhaden, 2004). In 2003 the accumulated rainfall was 92.9 mm.

2.2. Experimental design

We designed a factorial experiment with three factors: water, herbivory, and shade. Treatments were applied to plots of $6 \times 6\,m^2$, arranged in five blocks. Treatments were arranged in a split-plot design, with water being the whole unit and herbivory and shade the sub-units. Water treatments were: watered (natural rainfall plus 150 mm irrigation to simulate an average El Niño year) and not watered (only natural rainfall). However, due to heavy natural rainfall, our actual water treatments simulated conditions of strong (337 mm) to very strong rainy years (487 mm). Water was collected from a nearby river (Limarí River), pumped through a PVC piping to the experimental plots, and sprinkled through nine microjets per plot. The irrigation scheme simulated the natural seasonal rainfall pattern described for this region (López-Cortes and López, 2004). We controlled potential runoff water effects by installing metal plates to a depth of 20 cm around each plot and leaving a strip of 5 cm above ground.

Herbivory treatments were: presence (open-access plots) and absence (closed-access plots) of small mammalian herbivores. All large herbivores (such as domestic livestock) were excluded using a 800 m-perimeter fence around the whole experimental setting. This fence allowed the free transit of small mammals (rodents, rabbits, and hares). To exclude these small herbivores from the experimental plots, we used an extra 2-m high galvanized fence (0.5 cm mesh), buried 30 cm into the ground, and with 25 cm strip flashing at the upper part of the fence.

Shade treatments were: shaded and unshaded. Black shading nets (50% irradiance reduction) were placed at 1.5 m high over the experimental plots and additional netting on the sides to avoid lateral light infiltration. We removed the above-ground biomass of all woody shrubs present to avoid uncontrolled effects on shading or water hydraulic lift (Squeo et al., 1999).

2.3. Plantation and sampling

Twenty-five 9-months old *P. chilensis* saplings, obtained from a greenhouse of CONAF (Chilean Forest Service), were planted in each experimental plot following a grid of 5×5 points with 1-m distance between plants. Initial plant height varied between 45 and 50 cm. During planting days (mid May 2002), plants in the herbivore open-access plots were temporarily protected through fences that were removed at the start of the experiment. Monthly, from June 2002 to April 2004, we monitored survival of all 25 plants in each experimental plot and measured plant growth (stem height, stem basal diameter, and number of leaves) of the nine plants growing in the plot centre. By mid-April 2004, we harvested the above-ground biomass (i.e. leaf and stem material) of the nine central plants, which was weighted after oven-drying at 50 °C for 72 h.

2.4. Statistical analysis

Treatment and time effects were analysed using Analysis of Variance for repeated measures (rmANOVA) taking into account the block split-plot experimental design to use the proper error terms (Zar, 1999). Plant growth variables (stem height, stem diameter, number of leaves, and biomass) were $\ln(x+1)$ transformed prior to statistical analysis to account for large variances and comply with a normality distribution assumption. For the same reason, plant survival percentages were transformed to arcsin square roots.

3. Results

By April 2004, plant survival was 45% in the closed-access plots compared to only 0.6% (three out of 500 plants) in the open-access plots (Fig. 1a; $F_{(1,24)} = 84.17$; $p < 0.0001$). Within the closed-access plots, survival of watered plants was more than twice as high as the unwatered ones (Fig. 1a). We did not find significant effects of shade on plant survival ($F_{(1,24)} = 0.22$; $p = 0.6397$). There was a significant interaction between water and herbivore treatments (Fig. 1a; $F_{(1,24)} = 4.75$; $p = 0.0394$), but all other interaction treatments were not statistically significant ($p > 0.05$).

Exclusion of herbivores had a clear effect on stem height within less than 2 months after the beginning of the experiment (Fig. 2a, $F_{(1,24)} = 1480.95$; $p < 0.0001$). Most stems were trimmed by herbivores in the open-access plots, either leading to total destruction or to only very short stems. Although rainfall in 2002 was high, irrigation had a significantly positive effect on stem height (Fig. 2a; $F_{(1,4)} = 10.15$; $p = 0.0333$). We found a water × herbivory treatment effect (Fig. 2a; $F_{(1,24)} = 7.20$; $p = 0.0130$) whereas shade had no effects on plant height ($F_{(1,24)} = 0.04$; $p = 0.8443$). Stem diameter responded in a similar way. In the closed-access plots, plants had wider stems than those growing in the open-access plots (Fig. 2b; $F_{(1,24)} = 25.08$; $p < 0.0001$). Also, stem diameter was wider for watered plants than for unwatered ones ($F_{(1,4)} = 9.23$; $p = 0.0305$). Shade had no effect on stem diameter ($F_{(1,24)} = 1.17$; $p = 0.2909$).

Above-ground biomass was significantly higher in the closed-access plots (Fig. 2b; $F_{(1,24)} = 8.64$; $p = 0.0072$) and, within these plots, biomass tended to be higher among watered plants ($F_{(1,24)} = 3.40$; $p = 0.0777$). Only saplings growing in the closed-access plots produced leaves. Watered plants had significantly more leaves than unwatered ones, particularly during the summer months (Fig. 3; $F_{(32,678)} = 1.65$; $p = 0.0144$). Shade did not affect leaf production ($F_{(1,8)} = 0.65$; $p = 0.4447$).

4. Discussion

The field experiment was set up in the year 2002, which was coincident with a rainy ENSO event. Hence, our two water treatments simulated the conditions of a moderate versus a mega-ENSO event. Between 1900 and 2003, the time span during which metereological data for the region have been recorded, the overall highest precipitation was 478 mm during the ENSO event of 1905. This record is very close to the 487.2 mm precipitation of our wet experimental treatment. Unfortunately, we performed the experiment only once during a rainy year which obviously limits our possibilities to make generalizations about the use of rainy ENSO event for reforestation programs. Under our control treatment, simulating a moderate ENSO event, plant survival of protected plants

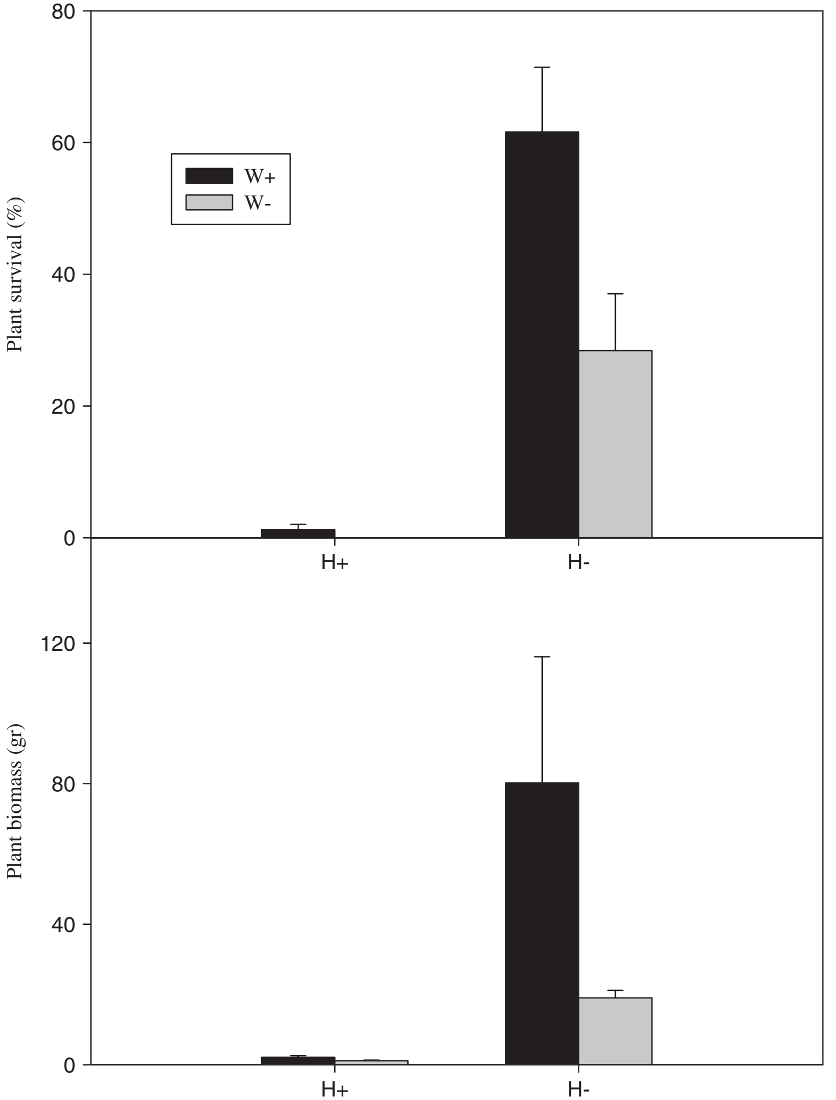

Fig. 1. (a) Survival and (b) above-ground biomass of *Prosopis chilensis* saplings by April 2004. H+: open-access plots to herbivores; H−: closed-access plots to herbivores; W+: irrigated plots simulating a very strong ENSO event; W−: unwatered plots simulating a moderate ENSO event. Data are mean ± 1 S.E.

was around 25%. Although we do not know whether this value deviates significantly from the survival rate during a normal dry year, it is much higher than the seedling survival rates observed in other experiments in central Chile (Fuentes et al., 1984). Indeed, the establishment of unwatered seedlings and saplings in reforestation programs is often unsuccessful in north-central Chile (J.M. Torres, personal communication). Interestingly, despite the already high precipitation during this year, additional irrigation had clear positive effects on plant growth and survival when small mammalian herbivores were

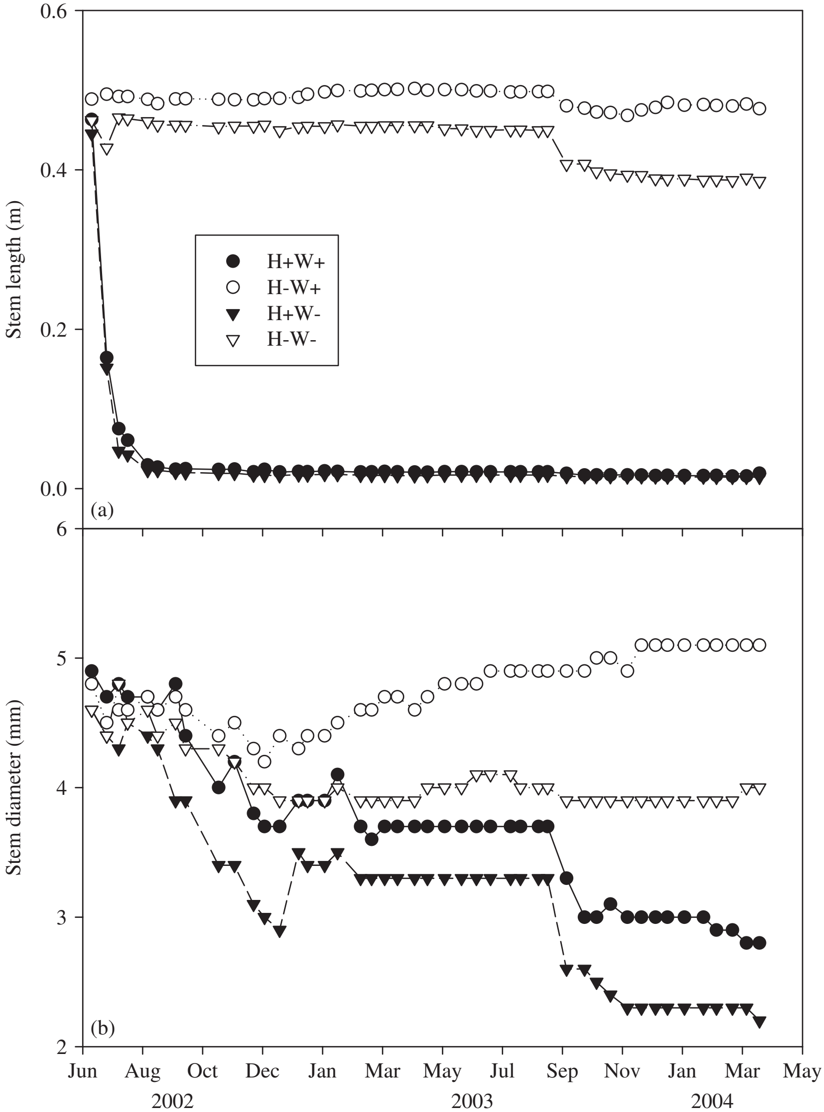

Fig. 2. (a) Mean stem length and (b) mean stem diameter of *Prosopis chilensis* from June 2002 until April 2004. H+: open-access plots to herbivores; H−: closed-access plots to herbivores; W+: irrigated plots simulating a very strong ENSO event; W−: unwatered plots simulating a moderate ENSO event.

excluded from the experimental plots. This can be explained by the high annual water evaporation in this ecosystem, estimated to be close to 1000 mm (F.A. Squeo, unpublished results). Water availability is particularly important during the early establishment phase of *P. chilensis* seedlings and young saplings (Salih, 1998).

In semi-arid Chile as in other dry environments, seedling survival is usually higher under shrub canopies than in open areas, partly because the adult shrub shade improves seedling water conditions (e.g. Fuentes et al., 1984; Holmgren et al., 1997). However, we found no

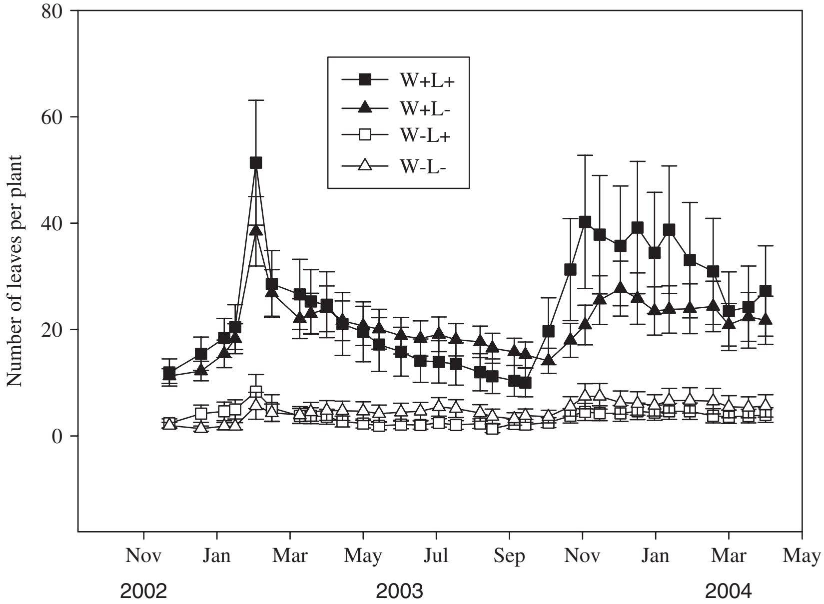

Fig. 3. Number of leaves per *Prosopis chilensis* sapling in the closed-access plots to herbivores from November 2002 to April 2004. W+: irrigated plots; W−: non-irrigated plots; L+: unshaded plots; L−: shaded plots. Data are mean ± 1 S.E.

significant effect of shade on *Prosopis* saplings growth and survival. This might be due to the already high levels of water availability under which we worked, where shade does not significantly contribute to reduce water stress. Indeed, shade is expected to play a less crucial role in moister conditions (Bertness and Callaway, 1994; Holmgren et al., 1997). Neither did Vilela and Ravetta (2000) find significant differences in the height of *P. chilensis* seedlings growing under full irradiance versus 52% irradiance in greenhouse experiments. In contrast, they found that shading could actually reduce the chances of survival, probably due to an increase in shoot/root ratio, and reductions in total biomass and stored carbohydrates.

The positive effect of the simulated rainy ENSO conditions were only observed when plants were protected from herbivores. Small mammals, mainly introduced European rabbits and hares, had the most dramatic effects on sapling survival. Over 90% of the *P. chilensis* plants were killed in the plots accessible to small herbivores during the first 2 months after plantation. At the end of the experiment, only 0.6% had survived in these open-access plots. We are aware that the herbivory impact could be overestimated, since seedlings were planted in high density on a relatively small area which could attract rabbits and hares. However, comparable results have been found in evergreen shrublands (matorral) further south in central Chile. Fuentes et al. (1984) reported that 100% of the *Quillaja saponaria* experimental seedlings were killed by rabbits after 60 days of plantation in open access patches. In Chile, introduced European rabbits (*Oryctolagus cuniculus*) and hares (*Lepus europaeus*) have proven to be extremely harmful to native herbs and shrubs (e.g. Jaksic and Fuentes, 1980, 1991; Fuentes et al., 1984; Holmgren, 2002).

Our results support the hypothesis that tree establishment success can be improved when coupling herbivore control to rainy years such as those associated to ENSO events (Holmgren and Scheffer, 2001). This could have large implications for future restoration programs of original semi-arid shrublands and woodlands. El Niño events have become more frequent in the last decades (Trenberth and Hoar, 1997; Tudhope et al., 2001), and their frequency might increase as a result of global climate warming (Timmermann et al., 1999). We could therefore take advantage of these changes by coupling reforestation programs and herbivore control to inter-annual rainfall variability. ENSO events can be forecasted some months in advance and they could be used to enhance the probabilities of plant establishment at probably lower costs than those involved with traditional restoration programs.

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