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Refuse dumps from leaf-cutting ant nests reduce the intensity of aboveground competition among neighboring plants in a Patagonian steppe

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ABSTRACT

In arid environments, the high availability of sunlight due to the scarcity of trees suggests that plant competition take place mainly belowground for water and nutrients. However, the occurrence of soil disturbances that increase nutrient availability and thereby promote plant growth may enhance shoot competition between neighboring plants. We conducted a greenhouse experiment to evaluate the influence of the enriched soil patches generated by the leaf-cutting ant, *Acromyrmex lobicornis,* on the performance of the alien forb *Carduus thoermeri* (Asteraceae) under different intraspecific competition scenarios. Our results showed that substrate type and competition scenario affected mainly aboveground plant growth. As expected, plants growing without neighbors and in nutrient-rich ant refuse dumps showed more aboveground biomass than plants growing with neighbors and in nutrient-poor steppe soils. However, aboveground competition was more intense in nutrient-poor substrates: plants under shoot and full competition growing in the nutrient-rich ant refuse dumps showed higher biomass than those growing on steppe soils. Belowground biomass was similar among focal plants growing under different substrate type. Our results support the traditional view that increments in resource availability reduce competition intensity. Moreover, the fact that seedlings in this sunny habitat mainly compete aboveground illustrates how limiting factors may be scale-dependent and change in importance as plants grow.

1. Introduction

Competition is a widespread interaction in natural plant communities mainly determined by the availability of aboveground (light) and belowground (water and nutrient) resources (Grace and Tilman, 1990; Kiær et al., 2013). Aboveground, an individual plant may trigger shoot competition by blocking the light of neighboring plants. For example, the fastest growing trees rapidly acquire a dominant height, decreasing the performance of slower ones by overshadowing (Schwinning and Weiner, 1998); rosette plants or plants with expansive cups intercept a greater amount of light and thus may reduce the growth of their neighbors (Kleunen et al., 2001). Belowground, in response to adjacent individuals, plants can alter the length, density, and spatial distribution of their roots to reach nutrient or water patches (Jose et al., 2006). Although plants compete simultaneously for resources above and below ground, the spatial separation between roots and shoots has promoted the study of above and below competition separately (e.g., Cahill, 1999; Song et al., 2006; Wang et al., 2014). However, competition for light can affect root performance and vice versa, and the relative importance of both types of competition may be influenced by resource availability (Morris, 2003).

Classical ecological theory proposes that the strength of competition depends on resource availability (Grime, 1979; Tilman, 1988; Goldberg, 1990); under nutrient-poor conditions more intense competition is expected between neighboring plants (e.g., Rebele, 2000; Pugnaire and Luque, 2001). However, there are contrasting opinions about the impact of enhanced nutrient availability on plant competition outcomes (Cahill, 1999: Morris, 2003; Wang et al., 2015). Some studies propose that competition may be stronger in nutrient-rich than in nutrient-poor sites because higher nutrient availability triggers plant growth, which in turn, increases root and shoot competition levels (Grime, 1973, 1979). Other studies propose that the negative effects of competition remain constant along a gradient of nutrient availability because plants shift from root to shoot competition as nutrients increase (e. g., Wilson and Tilman, 1993). The particular case of intraspecific competition is even more controversial. Despite that conspecifics can be expected to have similar physiological needs and ways to access resources (Morris, 2003; Farrer and Goldberg, 2011; Roiloa et al., 2014), the evidence is also contrasting. For example, under intraspecific competition, *Cunninghamia lanceolata* had less growth and biomass accumulation at the individual level and this negative effect was larger in poor soil fertility compared to more nutritious soils (Dong et al., 2016).

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Instead, nitrogen addition significantly increased intraspecific competitive intensity of *Alternanthera philoxeroides*, but not in its native congener *A. sessilis* (Wang et al., 2015). In summary, even among plants from the same species, there is no consensus whether high nutrient availability should reduce or increase the negative effects of competition (e.g., reduced growth and/or reproduction). In addition, the relative importance of root and shoot competition at different nutrient levels has been studied mainly through experiments with commercial fertilizers (e.g., Lamb et al., 2007; Bartelheimer et al., 2010). Since in nature nutrient-rich patches often come from organic matter, more realistic experiments should employ organically derived nutrient patches rather than commercial fertilizers (Tibbett, 2000). Here we evaluated how increases in nutrient availability affect the strength of shoot and root competition using refuse materials of leaf-cutting ants, a substrate well known for its high levels of nutrients (Farji-Brener and Werenkraut, 2015).

In Patagonian steppes, as in other arid lands, nutrient-poor soils and limited water availability coupled with high sunlight availability at ground level (due to tree scarcity) suggest that plant competition takes place mainly belowground (Fowler, 1986; Wilson, 1988). In this "ocean" of low nutrient availability there are "fertility islands" which can promote plant growth, potentially enhancing the importance of aboveground competition. In northern Patagonia, the leaf-cutting ant *Acromyrmex lobicornis* accumulates organic waste piles around their nests (hereafter, refuse dumps), which are several times richer in C, N, P, Ca, K, Mg and Na than non-nest soils (Farji-Brener and Ghermandi, 2008). Previous studies showed that these nutrient-rich patches increased seedling density and plant performance of the thistle *Carduus thoermeri*, promoting the invasion potential of this alien species into natural protected areas (Farji-Brener and Ghermandi, 2000, 2004, 2008, Farji-Brener et al., 2010). However, the typically high thistle density and large size of the plants that occur in the ant refuse dumps may stimulate competition among neighboring plants, counterbalancing the known positive effect of a nutrient-enriched substrate on plant performance. To determine whether the soil disturbances generated by *A. lobicornis* increase or decrease the strength of competition among neighboring thistles could be relevant to both theoretical and applied ecology. This knowledge will provide evidence regarding the relationship between resource availability and competition in natural conditions and it could reveal whether competition among neighboring plants affects the potential of ant nests as source of biological invasions in this region.

We compared the influence of the naturally increased soil nutrients of ant nests on the performance of the alien herb *C. thoermeri* under different scenarios of intraspecific competition. We conducted a greenhouse experiment in which we grew individuals of *C. thoermeri* in the absence of competition (controls), with only root competition, with only shoot competition and in full competition under two substrate types: nutrient-rich patches generated by *A. lobicornis* and natural nutrient-poor soils from the Patagonian steppe. Three possible scenarios (i. e., hypotheses) were possible: i) if enhanced nutrient availability reduces intra-specific competition (as classical theory suggests), we expect that the presence of neighbors reduce the growth of the focal plants more in the nutrient-poor control soils than those growing in the nutrient-rich refuse dumps; ii) if enhanced nutrient availability triggers overall plant growth and thus stimulates competition we expect that the presence of neighbors affects focal plants growth in refuse dumps more that those growing in control soils; and iii) if enhanced nutrient availability stimulates a shift from root to shoot competition, we expect that the presence of neighbors affects the aerial biomass of focal plants growing in refuse dumps more than those growing in control soils.

2. Materials and methods

2.1. Studied species

Acromyrmex lobicornis (Formicidae) is the only leaf-cutting ant species inhabiting NW Patagonia (Farji-Brener and Ruggiero, 1994) and an important component of the semi-arid steppes of the region because of its role as soil ecological engineer (Tadey and Farji-Brener, 2007; Farji-Brener et al., 2010). The ant workers collect and transport vegetal material of a wide variety of plants into their nest for growing a symbiotic fungus that is the food for the ant brood. As a consequence of this fungus-growing activity, the colony generates a large amount of organic waste (hereafter, refuse dump), which accumulates in piles on the soil surface near the nest entrances. These refuse dumps contain up to 800% higher nutrient levels and better water retention capacity than adjacent, non-nest soils; and are usually colonized by alien plant species, which grow better and produce more seeds than in the typical nutrient-poor soils of the arid steppes (Farji-Brener and Ghermandi, 2004, 2008; Farji-Brener et al., 2010).

Carduus thoermeri (nodding thistle, Asteraceae) is one of the most common alien species growing in the nutrient-rich refuse dumps of *A. lobicornis* (Farji-Brener and Ghermandi, 2008). This thistle is a noxious weed of Eurasian origin and has invaded pastures and roadsides areas worldwide (Kelly and Popay, 1985; Popay and Medd, 1995). It is a monocarpic biannual herb that grows in a flat rosette form during the first year, with numerous sharp spines on the leaf borders. In the second year, it bolts and produces one or more stems with distinct purple inflorescences. Individuals reproduce strictly by seed, which can be dispersed by wind using its attached pappus an average of about 1–2 m away from the mother plant (Skarpaas and Shea, 2007) or shed when the capitula drops to the ground below the parent plant (Smith and Kok, 1984). Plants die after flowering.

2.2. Methodology

To evaluate the effect of the nutrient-rich refuse dumps on the performance of the alien herb *C. thoermeri* under intraspecific competition, we performed a greenhouse experiment during the growing season (spring) of 2014. The greenhouse was located in Bariloche, Patagonia, Argentina (41° S, 71′ W), a few kilometers from the east border of the national park Nahuel Huapi, where the studied organisms are common. We randomly collected seeds from several individuals of *C. thoermeri* growing on natural steppe soils near Bariloche city. Seeds were set to germinate in a greenhouse under two substrate types, nutrient-rich refuse dumps (RD) and nutrient-poor steppe soils (SS), in four competition treatments. In the control competition treatment the focal plant was alone, and in the rest of the competition treatments it was located at the center of a pot, surrounded by four neighbors (i.e., a density of 5 plants/300 cm^2). This density simulates well those found in field conditions (AGFB, personal observation, see also Appendix 1).

The four competition treatments were: no competition (focal plants growing without neighbors, NC), root competition (focal plants freely interacting underground but not aboveground, RC), shoot competition (focal plants interacting freely aboveground but not underground, SC) and full competition (focal plants interacting with roots and shoots of neighbors, FC). To impede shoot competition in RC treatments, the focal plant was surrounded with a wire mesh only above ground. To impede root competition in the SC treatment, the focal plant was surrounded by artificial plant neighbors made with plastic plants that had shoot but no roots. The use of artificial plastic plants in experiments to separate below-and above-ground competition is relatively common (Lötscher et al., 2004; Lurling et al., 2006; Nagashima and Hikosaka, 2012), and has weaknesses as well as strengths. In one hand, plastic plants do not change red/far red ratios just as real plants do, and this fact may affects the pattern of above-ground growth (McPhee and Aarssen, 2001; Nagashima and Hikosaka, 2012). However, plastic

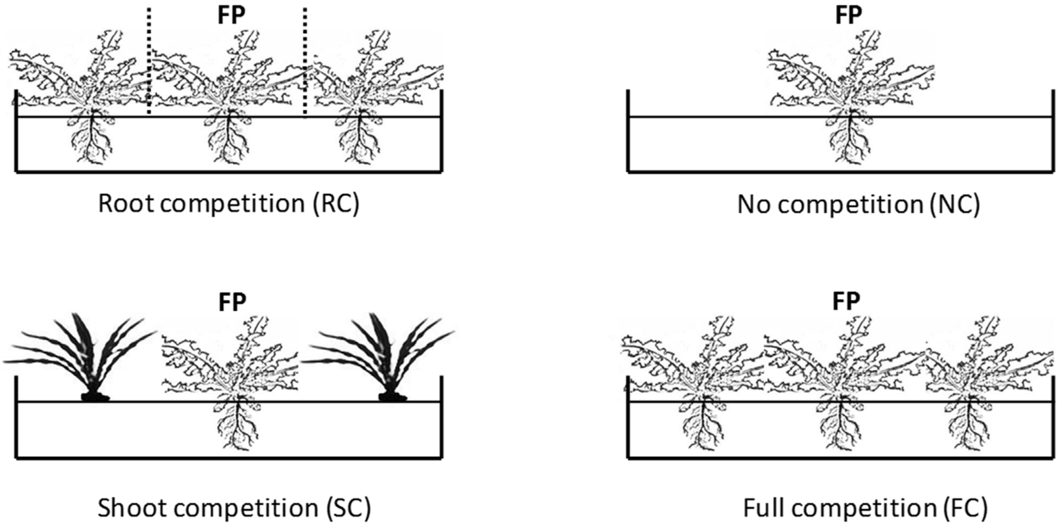

Fig. 1. Scheme of the experimental design showing the four competition treatments; no competition (NC, focal plants growing without neighbors), root competition (RC, focal plants freely interacting underground but not aboveground), shoot competition (SC, focal plants interacting freely aboveground with two plastic plants but not underground) and full competition (FC, focal plants interacting with roots and shoots of neighbors). Each rectangle represents a pot 15 × 20 cm and in the center is the focal plant (FP). Only two of the four competitor neighbor plants are shown (lateral view). Plants at these four competition treatments were assigned at two soil fertility conditions (nutrient-poor steppe soils and nutrient-rich ant refuse dumps). See text for a detailed description of the experimental design.

plants successfully intercept light quantity, which greatly affects shoot growth (Nagashima and Hikosaka, 2012) evading use of belowground partition techniques, which are used to prevent root competition but may affects plant growth and does not necessarily limit root access to resources (McPhee and Aarssen, 2001). Accordingly, and despite their potential limitations, we consider the use of plastic plants an appropriate way to stimulate aboveground competition for light, ensuring the absence of belowground competition. Overall, in the RC treatment the focal plant could interact only with its neighbors belowground, whereas in SC treatment only aboveground (Fig. 1).

Both substrates (nutrient-rich refuse dumps and nutrient-poor soil) were field collected from randomly selected ant nests and surrounding non-nest soils. All ant nests were established in bare soils (i. e., not associated with shrubs). Each soil and refuse sample were a homogenized mix of four subsamples of soil or refuse material. In the lab we filled pots (plastic containers 15 cm deep and 15 cm × 20 cm at the top) with each substrate type (refuse dumps or control soils). In the center of each pot we put a seed of *C. thoermeri* (the focal plant) and assigned the pots to different competition treatments. Initially we assigned 60 focal plants per competition treatment/substrate (i.e., 240 pots under each substrate type; a total of 480 pots). However, the final number of replicates in each treatment depended on the germination success and seedling survivorship. The final number of replicates for each treatment were 52 in NC ($N = 13$ refuse dump, $N = 39$ steppe soil), 37 in SC ($N = 8$ refuse dump, $N = 29$ steppe soil), 23 in RC ($N = 7$ refuse dump, $N = 16$ steppe soil) and 91 in FC treatment ($N = 37$ refuse dump, $N = 54$ steppe soil). All pots were regularly watered and kept at field capacity for 6 months. At the end of the experiment (summer of 2015), we harvested each focal plant, separated it into aboveground and belowground biomass, and weighed after drying at 60 °C for 48 h.

2.3. Data analysis

We compared the plant biomass using two-way factorial ANOVAs with type III sum of squares (SS) for unbalanced design. Competition scenario (with four levels: FC, RC, SC and NC) and substrate type (with two levels: nutrient-poor steppe soils versus nutrient-rich ant refuse dumps) were considered fixed factors. Shoot and root biomass were the response variables. Data was log transformed to meet the ANOVA assumption (see Appendix 1). A posteriori comparisons between treatments were carried out using post-hoc Duncan tests where appropriate.

3. Results

The type of substrate and competition scenario affected aboveground plant growth (Fig. 2, Table 1a). Focal plants showed 54% more aboveground biomass in nutrient-rich refuse dumps than in nutrient-poor steppe soils. On the other hand, focal plants growing under full and shoot competition showed significantly lower aboveground biomass (52% and 68% less shoot dry mass, respectively) than plants growing alone and under root competition (Fig. 2, Table 1a, all $P < 0.05$, Duncan post-hoc tests). This reduction in plant biomass under full and shoot competition was higher in nutrient-poor substrate than in nutrient-rich refuse dumps (Fig. 2, $P < 0.05$, Duncan post-hoc tests).

The belowground biomass of focal plants was similar in nutrient rich and nutrient-poor substrates, but it was affected by the presence of neighboring plants (Fig. 2, Table 1b). Focal plants showed significantly lower belowground biomass in full and shoot competition (46% and 62% less shoot dry weight, respectively) than plants growing alone (Table 1b, all $P < 0.05$, Duncan post-hoc tests). Also, the presence of neighbors reduced the belowground performance of plants, regardless of whether they were in nutrient-rich refuse dumps or nutrient-poor typical steppe soils (Table 1b).

4. Discussion

The role of resource availability on plant competition has been the subject of controversy (Wilson and Tilman, 1993; Cahill, 1999; Morris, 2003; Roiloa et al., 2014; Wang et al., 2015). Using a natural source of nutrients (ant refuse dumps) we experimentally found that enhanced soil resources reduces the intensity of competition among neighboring plants, a result with theoretical and applied implications. It has been proposed that greater nutrient availability triggers plant growth and consequently a greater demand for resources that promotes higher competition intensity in nutrient-rich rather than in nutrient-poor environments (Grime, 1973, 1979). However, we found ~25% higher shoot biomass in thistles growing under full and shoot competition on the nutrient-rich ant refuse dumps than those growing on the nutrient-poor steppe soils (Fig. 2). Despite plants on refuse dumps showed

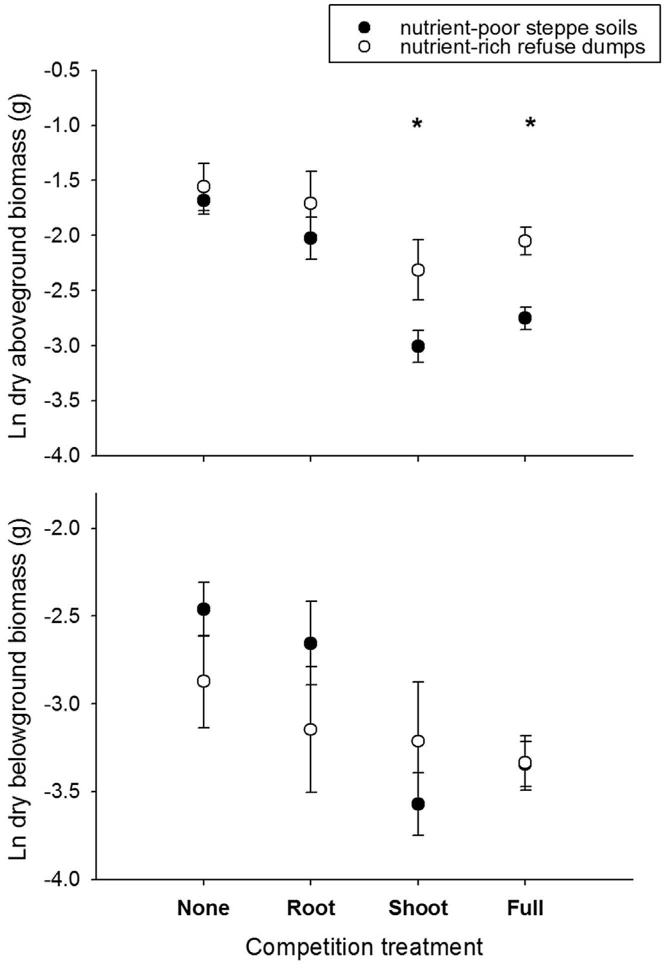

Fig. 2. Above- and below-ground dry biomass (g) of focal plants of *Carduus thoermeri* growing on control soils and ant refuse dumps under four competition treatments (root competition alone, shoot competition alone, full competition, and without competition). Values are mean ± 95% confidence interval. The asterisk indicates significant differences between means ($P < 0.05$, Duncan post-hoc tests).

Table 1
Results of factorial ANOVA for dry aboveground biomass and dry belowground biomass. Substrate (nutrient-poor steppe soils, nutrient-rich refuse dumps) and competition scenario (no competition, root, shoot and full competition) were designed as fixed effects.

Source	d. f.	MS	*F*	*P*
a) Response variable: Ln dry aboveground biomass (g.)				
Substrate	1	6.576	11.04	< 0.005
Competition	3	8.031	13.48	< 0.001
Substrate * competition	3	0.876	1.47	0.22
Error	196	0.595		
b) Response variable: Ln dry belowground biomass (g.)				
Substrate	1	0.567	0.62	0.43
Competition	3	4.991	5.51	< 0.005
Substrate * competition	3	1.082	1.194	0.31
Error	196	0.906		

greater shoot biomass and thus high potential to overlap with adjacent individuals, their growth were less affected by the presence of neighboring plants than those with lower shoot biomass (and thus lower capacity of overlap neighboring plants) growing on poor soils. This result suggests that the presence of nutrient-rich substrates diminishes the negative effects of competition by making the plants better able to withstand potential competitive stress. Our finding is consistent with other studies that found a decline in the intensity of competition with increments of resources (e.g., Di Tommaso and Aarssen, 1991; Turkington et al., 1993; Davis et al., 1998), and highlights the relevance of limited resource availability on competition strength, as classical ecological theory propose.

Even though light is not considering a limiting resource in arid lands, shoot competition for light appears to be the main mechanism affecting *C. thoermeri* in early stages of its ontogeny. This assumption coincides with other studies in arid lands that found successful *C. thoermeri* establishment was highly dependent on access to light (Han, 2012). The relevance of aboveground competition was supported mainly by our finding of more intense competition when individuals were subject to shoot rather than root competition, especially in plants growing on nutrient-poor soils. Thistles grow exclusively as a flat rosette during their first year of life, so their large leaves can completely cover the leaves of neighboring seedlings, limiting light access and decreasing photosynthetic rate (Appendix 1). Conversely, roots can grow to deeper depths to avoid belowground horizontal overlapping, even in open-habitats such as our study area, where water and soil nutrients have been considered more limiting than light (Fowler, 1986; Wilson, 1988). The fact that in this sunny habitat seedlings mainly compete aboveground illustrates how limiting factors may be scale-dependent and change in importance as plants grow.

Finally, our results may be useful for the improvement of management and conservation strategies. Earlier studies demonstrated that the alien thistle *C. thoermeri* grows better and produces more seeds when established in ant refuse dumps, increasing their potential invasiveness into nearby natural protected areas (Farji-Brener and Ghermandi, 2008). Here we reinforce the idea that *A. lobiornis* nests may be considered as hot spots of alien propagules; their nutrient-rich refuse dumps not only stimulate larger and more productive plants, but also reduce the strength of intraspecific competition among neighbors. Therefore, eradication practices for this alien thistle should focus on plant clusters growing on ant refuse dumps. Our findings highlight the importance of understanding how natural organic soil patches influence competitive interactions among alien plants, affecting both the structure of plant assemblages and the potential spread of alien species.

Statement of authorship

AGFB designed research and performed experiments; AGBF and NL analyzed the data; NL and AGFB wrote the paper; all authors contributed to data interpretation and manuscript revision.

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Appendix A. Supplementary data

Supplementary data related to this article can be found at http://dx.doi.org/10.1016/j.actao.2017.10.009.

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