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Refuse dumps from leaf-cutting ant nests reduce the intensity of above-ground 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