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Grass competition surpasses the effect of defoliation on a woody plant invader

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ABSTRACT

Woody encroachment in grasslands represents a global phenomenon with strong consequences on ecosystem functioning. While the causes triggering this process can be multiple, there is consensus on the fact that anthropogenic activities play a central role in woody expansion. In particular, the loss of grass cover increases the chances of woody invasion, whereas the role of defoliation is less known. In this study our objective was to assess the simultaneous effect of competition generated by resident vegetation and woody seedling defoliation on the growth and survival of *Gleditsia triacanthos* seedlings, a woody invader in Argentina. We established a factorial pot experiment with two main factors: *Gleditsia* defoliation (2 levels: with and without defoliation) and pasture competition (3 levels: without pasture, clipped pasture and intact pasture). Our results showed that pasture competition reduced *Gleditsia* survival and tree growth, but that the effect of tree defoliation on tree growth depended on the magnitude of pasture competition. More widely, our results stress the existence of a hierarchy order of factors controlling *Gleditsia* establishment (survival + growth): grass competition was the main control and tree defoliation became important only in the absence of competition. This evidence suggests that maintaining a competitive grass cover along with a frequency of tree defoliation could diminish tree establishment in herbaceous communities.

1. Introduction

Woody encroachment in grasslands and savannas is a well documented phenomenon occurring around the globe (Anadón et al. 2014; Archer, 1994; Archer et al. 1988; Browning et al. 2008; Chaneton et al. 2012; Roques et al. 2001). Changes in the local and regional propagule pressure, disturbance regime and climatic variability are invoked as some of the main factors contributing to the ongoing process of woody encroachment (Archer, 1994; Bredenkamp et al. 2002; Lockwood et al. 2007; Midgley and Bond, 2001; Van Auken, 2000). The increase of woody vegetation have several consequences on community diversity (Ratajczak et al. 2012; Van Auken, 2009), ecosystem productivity (Hughes et al. 2006) and biogeochemical cycles (Archer et al. 2001; Hibbard et al. 2001; Knapp et al. 2008). Further, increase in woody cover directly affects livestock production by diminishing grass cover and also makes it difficult to maintain roads, corridors and associated agricultural environments (Anadón et al. 2014; Ghersa et al. 2002).

Several studies have demonstrated that successful woody establishment in grasslands and savannas is affected by grass competition (Grellier et al. 2012; Mazía et al. 2001, 2010; Ward and Esler, 2011) and also by seed and seedlings consumers (Archer, 1995; Grellier et al. 2012; Busch et al. 2012; Macias et al. 2014; Tjelele et al. 2015). Livestock and wild herbivores may influence tree recruitment through two opposite ways. First they may promote woody encroachment by selectively consume grasses and relaxing competitive interactions between herbaceous and woody plants (Archer, 1995; Grellier et al. 2012). Second, they may also act as a barrier to tree recruitment by consuming woody seedlings and/or by repeated mechanical damage or defoliation events (Bond, 2008; Chauchard et al. 2007; Macias et al. 2014; Riginos and Young, 2007; Roques et al. 2001).

Many studies have showed that woody plants have a variety of mechanisms of tolerance which allow them to resprout after defoliation (Haukioja and Koricheva, 2000; Strauss and Agrawal,

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1999). Tolerance to defoliation depends on the accumulated reserves which vary according to the environmental conditions (Kozlowski et al. 1991) and also with the bud bank and the foliar area retained after defoliation (Weltzin et al. 1998). Surprisingly, despite of tolerance is a key aspect in the life span of a woody plant, the ecological literature has focused more on herbaceous than on woody plants responses (Boege and Marquis, 2005; Haukioja and Koricheva, 2000). In particular, there exists scarce knowledge on how selective woody or grass defoliation may affect the process of tree establishment in grasslands and pastures.

Here we propose three conceptual models to explain the impact of woody seedlings defoliation across a gradient of grass competition (Fig. 1). In the first model the effect of defoliation and competition are additive, implying that the magnitude of the negative effect of repeated defoliation does not varies through the gradient of competition (Fig. 1a). This scenario might occur when the availability of resources is not sufficient to offset the loss of biomass, independently of the magnitude of grass competition. The second scenario presents a model of interaction where the magnitude of the negative effect of defoliation could be greater as grass competition increases (Fig. 1b). This could be the case when compensation only occurs when competition is not strong enough, at the lower extreme of the gradient. In turn, the third model suggests that the magnitude of the negative effect of repeated defoliation decreases through the gradient of competition (Fig. 1c). This could be the case when the effect of grass competition is so strong in suppressing woody seedling growth that defoliation would be irrelevant. These predictions have two important assumptions: a-competition and defoliation have both, a negative impact on the performance of a woody seedling; b-the chance of recovering after defoliation depends on the woody reserves, which will be out under the more competitive environment. In the last case, we assume a tradeoff between competitive ability and tolerance to defoliation (Coley and Barone, 1996; Maschinski and Whitham, 1989; Strauss and Agrawal, 1999).

We tested these ideas through a manipulative pot experiment using *Gleditsia triacanthos* (honey locust, hereinafter *Gleditsia*) as a model of woody plant invader. This tree is one of the most aggressive and difficult to eradicate invasive species in Argentina (Mazía et al. 2001, 2010; Ghersa et al. 2002). In previous work we showed that different factors affect the initial phase of *Gleditsia* seedling establishment in grasslands. In particular, inter-annual climatic variability (Mazía et al. 2010), disturbance regime (Chaneton et al. 2004; Mazía et al. 2010), competition from resident vegetation (Mazía et al. 2001, 2013) and seed granivory (Busch et al. 2012; Muschetto et al. 2015) in a direct or indirect way negatively affected *Gleditsia* seedling establishment (see Chaneton et al. 2012).

We examined the simultaneous effects of competition and defoliation on the establishment of *Gleditsia* seedlings. During one growing season, we analyzed the effect of defoliation on survival and growth across a gradient of grass competition generated by clipping the aerial biomass of a polyphitic pasture. Previous studies have showed that first grow season is crucial to the successful tree recruitment in pampean grasslands communities (Mazía et al. 2001, 2010). After this critical period *Gleditsia* mortality is extremely low, reflecting the survival during the initial phase of tree recruitment (Chaneton et al. 2012). Through making this experiment under controlled conditions we represented a simplified model of ecological communities which do not attempt to reproduce all natural processes occurring under field conditions. As a consequence, others factors not considered (e.g. seed dispersal, trampling as well as nutrient deposition) might also affect the probabilities of woody establishment under natural conditions (Augustine and McNaughton, 2004; Tjelele et al. 2015).

Our working hypothesis was that the magnitude of the effect of seedling defoliation varies through the gradient of grass competition. This hypothesis raises two possible predictions which are an increased or decreased defoliation effect as pasture competition increase (Fig. 1b and c respectively).

2. Materials and methods

2.1. Experimental design

We conducted a garden experiment at the Faculty of Agronomy, University of Buenos Aires (34° 35′ 32″ S; 58° 29′ 16″ O). The experiment followed a factorial design with two main factors: *Gleditsia* defoliation (2 levels: with and without defoliation) and pasture competition (3 levels: without pasture, clipped pasture and intact pasture). These six treatments were disposed in 10 complete blocks. Treatments of pasture competition implied an increasing gradient of above and below pasture biomass (see below).

In September 2012, 60 pots (13.5 dm^3) were filled with fertile soil and sand (2/3–1/3, respectively) to improve drainage conditions. Twenty pots were left intact and weekly weeded (no competition) while forty were sown with a poliphytic pasture (50% of *Trifolium pratense*, 25% *Dactylis glomerata* and 25% *Bromus catharticus*). Pasture composition is the most frequently used by rangers in the Pampas. Seeds were provided by Administration de Campos (Ea. San Claudio, UBA, Carlos Casares) and tested for germination rate. To standardize the initial conditions of the experiment before *Gleditsia* planting, a first cut to all sown pots was applied to a height of 8 cm. This height corresponds to the lower limit used in rotational grazing (*Rodriguez*, personal

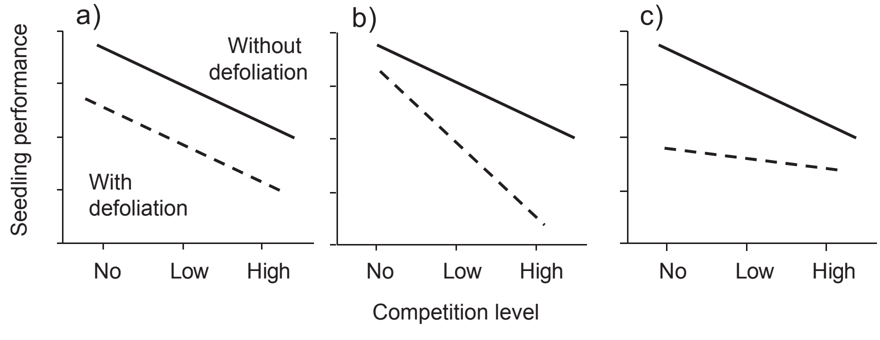

Fig. 1. Conceptual models for the performance of tree seedlings under the effect of defoliation (continuous vs. dashed lines) along an increasing gradient of competition (no competition, low competition and high competition). These models assume that both, competition and defoliation have a negative effect, but that this effect may vary. a) The negative effect of defoliation is constant under different levels of competition; there is no interaction between these factors. b) The effect of defoliation increased with the gradient of competition. c) The effect of competition surpasses the negative effect of defoliation.