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How does disturbance affect the intensity and importance of plant competition along resource gradients?

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ABSTRACT

Ecologists have long argued about the modification of plant competition along abiotic gradients, and particularly along resource gradients. Through simulations, we evaluated the impact of bramble defoliation by roe deer on the response of oak seedlings to bramble presence along two resource gradients. We set up a controlled experiment crossing: (i) two light availabilities (10% and 30% incident radiation), (ii) two water regimes (normal rainfall and a reduced water regime) and (iii) three bramble defoliation modes (non-defoliated brambles, brambles defoliated in June and brambles defoliated in late July). Control plots contained no brambles. We found that, the intensity of the competition remained constant along the gradients, while the importance of the competition significantly increased with increasing resource availability. Our results further show that bramble defoliation causes a significant decrease in both competition intensity and importance and that the effect depends on both the demographic parameter and the defoliation period. Furthermore, defoliation did not change the patterns of competition intensity and importance along the resource gradients. We emphasize the importance of considering both disturbances, such as deer defoliation, and various demographic parameters related to plant phenology and plant response dynamics in the characterization of plant-plant interactions.

1. Introduction

Inter-specific plant-plant interactions are central to community ecology and are one of the main drivers of plant community structure and composition. Plants interact in many ways, both negatively (competition) and positively (facilitation). They compete for resources such as light, nutrients, and water but can also protect one another from disturbances such as browsing damage, the impact of other competitors or the effects of extreme climates. Plants are also able to provide each other with additional resources, for example by modifying the microbial environment, and through hydraulic lift or canopy leaching (Brooker et al., 2008). Thus, the overall interaction between two plants A and B is the accumulation of all the interactions going on between them (Callaway and Walker, 1997). For these interactions, intensity (amount of reduction or improvement in A's performance as a consequence of B's presence) and importance (the impact of B on A expressed as a proportion of the total environmental impact on A) can be modulated by external forces such as climate or resource availability (Corcket et al., 2003; Brooker et al., 2005). Some studies show that the nature (negative or positive) of interactions varies along productivity gradients: competition is more frequent when the environment is favorable (i.e. productive, with high resource availability). Inversely, facilitation is more often present in harsh conditions (Bertness and Callaway, 1994; Brooker and Callaghan, 1998; Callaway et al., 2002). This theory is called the "stress gradient hypothesis" and concerns a large resource gradient. When focusing on plant competition:

(i) There is some evidence that intensity of competition is more or less constant along a productivity gradient but that the mechanisms driving this competition change. In productive, unstressed systems, plants mainly compete for light and space (aerial competition), whereas in harsh environments (limited soil resources), plants mainly compete for water and/or soil nutrients (root competition) (Tilman, 1987). In contrast, some researchers have shown that plant competition intensity increases with increasing resource availability (Maalouf et al., 2012).

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(ii) As suggested by Brooker et al. (2005), Grime's model argues that the importance of competition is higher in productive environments, and that it increases with resource availability and decreases as environmental severity increases (limited light, water or mineral nutrients and suboptimal temperatures) (Grime, 1977).

As underlined by Brooker et al. (2008), the "clarification of the relationship between interactions and environmental gradients is central for further progress, and necessitates implementation of experiments specifically designed to address this issue". Indeed, even though the impact of resource gradients on plant-plant interactions has been extensively studied, this area of research still remains a topic of considerable debate. Furthermore, there is some evidence that for certain plants, browsing on their neighbors can have more impact than the effect of being browsed themselves (Lagerström et al., 2011). In one study, Brooker et al. (2006) found evidence that a facilitative effect of planting heather with saplings was greatest at an intermediate level of ungulate density. The timing of the damage caused by browsing is of major importance because it conditions the plant's response (compensation) and can cause a "phenological time-lag" (Mower et al., 1997; Freeman et al., 2003). One study does exist on the effect of herbivory on individual plant performances along a resource gradient: The "compensatory-continuum hypothesis" predicts that plants are less able to tolerate herbivory in harsh environments than in rich environments because the low resource availability limits their regrowth after damage (Maschinski and Whitham, 1989). Maalouf et al. (2012) studied mowing effect on plant interaction intensity and importance along a water-availability gradient; they showed that, at very high stress levels, disturbance may accelerate the collapse of the interaction.

In our study, we examined the impact of ungulate browsing on the modification of the intensity and importance of competition between tree seedlings and shrub thickets along two resource gradients (light and water). We focused on a common case which is widespread in temperate forests - *Rubus sect. fruticosi* (bramble)/*Capreolus capreolus* (roe deer)/*Quercus petraea* (sessile oak). To estimate how competition change with environmental conditions, we set up a controlled experiment crossing two light levels (10 and 30% of incident radiation), and two water regimes (normal rainfall and reduced rainfall). To evaluate how herbivory modifies the competition, we crossed the resource gradients with three modes of bramble defoliation (non-defoliated brambles, brambles defoliated in early June and brambles defoliated in late July). Our work focused on (i) the date of bramble defoliation and (ii) the bramble effect, through bramble LAI, which quantified the bramble defoliation on an annual perspective. This paper explores the following four hypotheses (Fig. 1):

In the absence of disturbance by herbivory - **H1a:** Competition intensity will remain constant along the resource gradient. **H1b:** The importance of competition will increase with resource availability.

In the presence of disturbance by herbivory - **H2a:** Bramble defoliation will decrease the intensity and importance of bramble competition on oak seedlings. **H2b:** These effects will depend on both the defoliation period and the demographic parameter of oak seedlings (height increment, diameter growth, survival and number of live branches).

2. Materials and methods

2.1. Study area

The experiment was conducted under semi-controlled conditions in a plant nursery located in Nogent-sur-Vernisson in the center of France (47°50′06″N 2°45′40″E). The climate is temperate oceanic. The 44-year mean annual temperature was 11.1 ± 0.74 °C, with a mean annual precipitation of 727 ± 142 mm (local weather station data, 1970–2013). For the growing season (April-October), the corresponding annual means for temperature and precipitation were 15.2 ± 0.84 C and 419 ± 106 mm, respectively. The soil

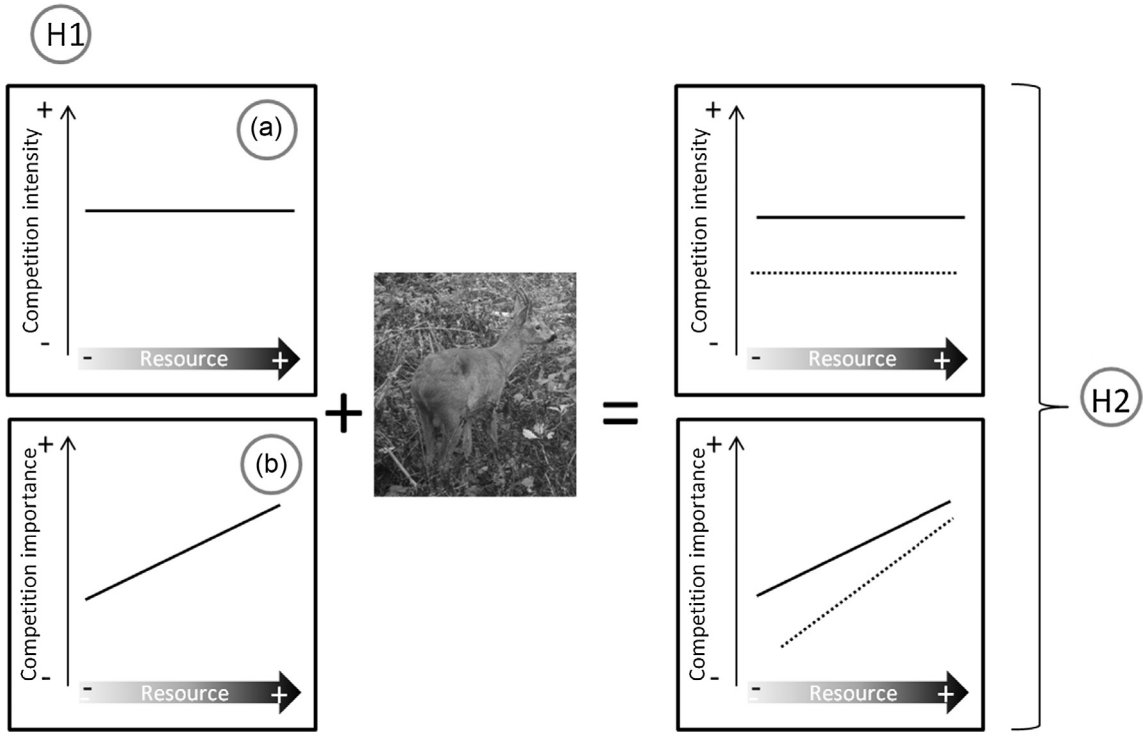

Fig. 1. Theoretical changes in the intensity and importance of plant competition along resource gradients (H1) and (deer) defoliation (H2). Solid lines represent pathways without deer, and dashed lines represent pathways with deer.