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Interactive effects of above- and belowground herbivory and plant competition on plant growth and defence

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Abstract

Competition and herbivory are two major factors that can influence plant growth and plant defence. Although these two factors are often studied separately, they do not operate independently. We examined how aboveground herbivory by beet armyworm larvae (*Spodoptera exigua*) and belowground herbivory by wireworms (*Agriotes lineatus*) influenced competition between the plant species *Jacobaea vulgaris* and *Leucanthemum vulgare* exposed to three competition levels (no, intra-, and interspecific competition). In addition, we studied the effects of herbivory and competition on pyrrolizidine alkaloid (PA) concentrations in leaves of *J. vulgaris*. For *J. vulgaris*, aboveground herbivory significantly reduced shoot biomass while belowground herbivory increased root biomass. Biomass of *L. vulgare* was not affected by herbivory. Competition caused a reduction in biomass for both plant species, but herbivory did not affect the outcome of the competition. However, competition significantly influenced the amount of leaf damage experienced by the plants. A *L. vulgare* plant had significantly less damage from aboveground herbivores when grown together with *J. vulgaris* than when grown alone or in intraspecific competition, while a *J. vulgaris* plant experienced lowest damage in conditions of intraspecific competition. The total PA concentration in *J. vulgaris* leaves was highest for plants exposed to interspecific competition. Root herbivory caused an increase in the relative concentration of N-oxides, the less toxic form of PAs, in leaves of plants that were grown without competition, but a decrease in plants exposed to competition. Our study shows that competition and herbivory but also the type of competition and whether herbivory occurs above- or belowground, all influence plant performance. However, overall, there was no evidence that herbivory affects plant–plant competition.

Zusammenfassung

Konkurrenz und Herbivorie sind zwei wichtige Faktoren, die das Pflanzenwachstum und die pflanzliche Verteidigung beeinflussen. Auch wenn die beiden Faktoren oft getrennt untersucht werden, wirken sie nicht unabhängig voneinander. Wir untersuchten, wie oberirdische Herbivorie durch Zuckerrübenraupen (*Spodoptera exigua*) und unterirdische Herbivorie durch Schnellkäferlarven (*Agriotes lineatus*) die Konkurrenz zwischen *Jacobaea vulgaris* und Leucanthemum vulgare beeinflussten, die drei Konkurrenzszenarien ausgesetzt waren: keine Konkurrenz, intra- und interspezifische Konkurrenz). Zusätzlich untersuchten wir die Effekte von Herbivorie und Konkurrenz auf die Konzentrationen von Pyrrolizidinalkaloiden (PA) in den Blättern von *J. vulgaris*. Bei *J. vulgaris* reduzierte oberirdische Herbivorie signifikant die oberirdische Biomasse, während

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unterirdische Herbivorie die Wurzelbiomasse erhöhte. Die Biomasse von *L. vulgare* wurde durch Herbivorie nicht beeinflusst. Konkurrenz führte bei beiden Pflanzenarten zu einer Reduktion der Biomasse, aber die Herbivorie beeinflusste nicht das Ergebnis der Konkurrenz. Indessen beeinflusste die Konkurrenz signifikant das Ausmaß der Blattschäden an den Pflanzen. Eine Leucanthemum vulgare-Pflanze erlitt signifikant geringere Schäden durch oberirdische Herbivoren, wenn sie zusammen mit *J. vulgaris* wuchs, als wenn sie allein oder zusammmen mit Artgenossen wuchs, während eine *J. vulgaris*-Pflanze den geringsten Schaden bei intraspezifischer Konkurrenz erlitt. Die gesamte PA-Konzentration in den Blättern von *J. vulgaris* war am höchsten bei Pflanzen in interspezifischer Konkurrenz. Wurzelfrass verursachte eine Zunahme der relativen Konzentration von N-Oxiden, der weniger toxischen Form der PA, in Blättern von Pflanzen, die ohne Konkurrenz wuchsen, aber eine Abnahme bei Pflanzen unter Konkurrenzbedingungen. Unsere Untersuchung zeigte, dass Konkurrenz und Herbivorie, aber auch der Typ der Konkurrenz und ob die Herbivorie ober- oder unterirdisch erfolgte, die Wuchsleistung der Pflanzen beeinflusste. Indessen gab es keinen Hinweis auf einen Effekt der Herbivorie auf die Konkurrenz zwischen Pflanzen.

Keywords: Aboveground–belowground interactions; Insect–plant interactions; Leaf damage; Pyrrolizidine alkaloids; Root herbivory

Introduction

Plant competition and insect herbivory are two important biotic interactions that can greatly affect plant performance (Rees & Brown 1992; Wardle & Barker 1997; Gurevitch, Morrison, & Hedges 2000; Agrawal 2004; Huang, Carrillo, Ding, & Siemann 2012a). While these two factors are often studied separately, they do not necessarily operate independently. Interactions with plant neighbours, for example, can influence the level of herbivory on a focal plant (e.g. Hambäck & Beckerman 2003; Agrawal 2004; Barbosa et al. 2009). These effects are called associational resistance or susceptibility depending on whether the focal plant experiences less or more herbivory in the presence of another plant (Tahvanainen & Root 1972; Barbosa et al. 2009; Underwood, Inouye, & Hambäck 2014). Numerous studies have shown that herbivory can influence plant–plant competition and the composition of plant communities (Clay, Marks, & Cheplick 1993; Hulme 1996; Carson & Root 2000; Graff, Aguiar, & Chaneton 2007).

Insect herbivory can greatly influence plant competition. Virtually all generalist insect herbivores will preferentially feed on a particular plant species when offered a choice, and individuals of the same plant species often do not experience similar levels of damage when multiple plants are exposed simultaneously to herbivory (Crawley 1997). When two plants that belong to the same species compete, selective herbivory on the larger plant may reduce effects of intraspecific competition. In interspecific competition, such herbivore preferences can mediate coexistence (Crawley 1997). In contrast, preferential feeding by herbivores on the weaker competitor will increase the negative effect of competition and result in plant exclusion (Kim, Underwood, & Inouye 2013). In nature, most plants grow in diverse communities consisting of both conspecific and heterospecific plants, and a plant may be exposed to either intraspecific or interspecific competition depending on the identity of its direct neighbours. Most empirical studies that examined the effects of herbivory on plant competition focused on intraspecific or interspecific competition only, hence an unresolved question is whether the effects of herbivory on a plant are influenced by the type of competition.

Plants interact with both aboveground and belowground herbivores, and the impact of herbivory on competition can greatly depend on whether the plants are damaged aboveground, belowground, or both (e.g. Müller-Schärer & Brown 1995). So far, most studies have focused on the effects of aboveground herbivory on competition. However, root herbivores can also greatly influence plant performance, and the impact of root herbivores may even exceed that of aboveground herbivores (Maron 1998; Blossey & Hunt-Joshi 2003; Wardle et al. 2004). Similar to aboveground herbivores, root herbivores can influence competitive interactions between plants by preferentially feeding on particular plants or plant species, although several studies have also suggested that feeding by root herbivores is less specific than that of aboveground herbivores (reviewed in: van Dam 2009). While the effects of belowground herbivores on plant–plant competition are less well understood than the effects of aboveground herbivory (e.g. Ramsell, Malloch, & Whittaker 1993; Maron 1998), the interactive effects of aboveground and belowground herbivory on competition are even more poorly understood (van Ruijven, De Deyn, Raaijmakers, Berendse, & van der Putten 2005; Huang, Carrillo, Ding, & Siemann 2012b).

Most studies that have examined the effects of herbivory on competition between plants have focused on plant growth, reproduction and survival (e.g. Schädler, Brandl, & Haasse 2007; Suwa & Louda 2012; Kim et al. 2013). However, exposure to herbivory or the presence of a plant neighbour can also influence the defence chemistry of a plant. It is well known, for example, that insect herbivory can induce plant defence responses resulting in e.g. increased levels of secondary plant compounds (Karban & Baldwin 1997). If competition influences the amount of herbivory that a plant experiences, and plant defence induction is related to the amount of