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Interactive effects of soil-dwelling ants, ant mounds and simulated grazing on local plant community composition

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Abstract

Interactions between aboveground vertebrate herbivores and subterranean yellow meadow ants (*Lasius flavus*) can drive plant community patterns in grassland ecosystems. Here, we study the relative importance of the presence of ants (*L. flavus*) and ant mounds under different simulated grazing regimes for biomass production and species composition in plant communities. We set up a greenhouse experiment using intact soil cores with their associated vegetation.

We found that plant biomass production in the short term was affected by an interaction between simulated grazing (clipping) and ant mound presence. Clipping homogenized production on and off mounds, while in unclipped situations production was higher off than on mounds. During the experiment, these differences in unclipped situations disappeared, because production on unclipped mounds increased. Plant species richness was on average higher in clipped treatments and patterns did not change significantly over the experimental period. Plant community composition was mainly affected by clipping, which increased the cover of grazing-tolerant plant species. The actual presence of yellow meadow ants did not affect plant community composition and production.

We conclude that the interaction between ant mounds and clipping determined plant community composition and biomass production, while the actual presence of ants themselves was not important. Moreover, clipping can overrule effects of ant mounds on biomass production. Only shortly after the cessation of clipping biomass production was affected by ant mound presence, suggesting that only under low intensity clipping ant mounds may become important determining plant production. Therefore, under low intensity grazing ant mounds may drive the formation of small-scale plant patches.

Zusammenfassung

Die Interaktionen zwischen oberirdisch aktiven, herbivoren Wirbeltieren und der unterirdisch aktiven Gelben Wiesenameise (*Lasius flavus*) können die Muster von Pflanzengemeinschaften in Graslandökosystemen bestimmen. Wir untersuchten die relative Bedeutung des Vorhandenseins von Ameisen und Ameisenhügeln bei unterschiedlichen simulierten Beweidungssystemen für die Biomasseproduktion und Artenzusammensetzung. Wir installierten ein Gewächshausexperiment mit intakten Bodenkernen und ihrer jeweiligen Vegetation.

Wir fanden, dass die Biomasseproduktion der Pflanzen kurzfristig von der Interaktion zwischen simulierter Beweidung (Schnitt) und dem Vorhandensein von Ameisenhügeln beeinflusst wurde. Der Schnitt glich die Produktion auf Ameisenhügeln

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und abseits davon einander an, während bei unbeschnittenen Proben die Produktion abseits der Hügel höher war als auf diesen. Während des Experiments verschwanden diese Unterschiede in den unbeschnittenen Behandlungen, weil die Produktion auf unbeschnittenen Ameisenhügeln anstieg.

Der Artenreichtum der Pflanzen war im Durchschnitt höher in den beschnittenen Behandlungen, und diese Muster änderten sich nicht wesentlich während der Dauer des Experimentes. Die Zusammensetzung der Pflanzengemeinschaft wurde hauptsächlich durch das Beschneiden beeinflusst, wodurch der Deckungsgrad beweidungstoleranter Arten zunahm. Die tatsächliche Anwesenheit der Gelben Wiesenameise beeinflusste die Zusammensetzung und Produktion der Pflanzengemeinschaft nicht.

Wir schließen, dass die Interaktion zwischen Ameisenhügeln und Beschneiden die Zusammensetzung und Produktion der Pflanzengesellschaft beeinflusste, während die Anwesenheit von Ameisen nicht wichtig war. Darüberhinaus kann das Beschneiden den Einfluss von Ameisenhügeln auf die Biomasseproduktion übertönen. Schon kurz nach Beendigung des Beschneidens wurde die Biomasseproduktion durch das Vorhandensein von Ameisenhügeln beeinflusst, was nahelegt, dass Ameisenhügel nur bei geringer Beschneidungsintensität einen wichtigen Einfluss auf die Pflanzenproduktion nehmen. Deshalb könnten Ameisenhügel bei geringer Beweidung die Bildung kleinräumiger Pflanzenformationen steuern.

Keywords: Aboveground–belowground interactions; Herbivores; *Lasius flavus*; Vegetation composition; Simulated grazing; Multivariate analysis; Principle response curves (PRC)

Introduction

Aboveground and belowground components of terrestrial ecosystems are linked by plants. Consequently, the interaction between aboveground and belowground organisms is an important driver of plant community composition and structure (Wardle et al. 2004). Aboveground and belowground herbivores directly reduce plant biomass, thereby altering the competitive ability of plant species and hence plant community composition (van der Putten & Peters 1997; Olff & Ritchie 1998). Moreover, aboveground–belowground interactions modify soil nutrient cycling which feeds back to plant growth and community composition (Bardgett & Wardle 2003).

The interaction between aboveground vertebrate herbivores and subterranean yellow meadow ants (*Lasius flavus*) has been identified as an important determinant of plant community composition and heterogeneity in grassland ecosystems (e.g. King 1977a, 1977b; Blomqvist, Olff, Blaauw, Bongers, & van der Putten 2000). Yellow meadow ants are ecosystem engineers that modify biotic and abiotic soil properties (Jones, Lawton, & Shachak 1994). They dig up soil from deeper layers to build nest mounds and thereby create open, competition-free space that can be colonized by plants (King 1977b). Moreover, digging modifies abiotic soil conditions (such as pH, organic matter content, temperature and water availability), changes soil community composition and reduces abundances of plant-parasitic pathogens (Blomqvist et al. 2000; Dauber & Wolters 2000; Dostal, Breznova, Kozlickova, Herben, & Kovar 2005). Also, *L. flavus* 'farm' root aphids (which are root sap suckers) in their nest mounds, from which they harvest honey dew excretion (Pontin 1978), and which they consume as well. This can be viewed as an obligate symbiosis. The honeydew serves as an important food source for yellow meadow ants, in return the ants tend these aphids in their nests by protecting them from enemies, cleaning them from microbes and moving them to suitable root sites (Pontin 1978).

All the changes in biotic and abiotic environmental conditions induced by yellow meadow ants affect plant species directly and indirectly and can alter the plant community composition on mounds (e.g. King 1977a, 1977b; Dean, Milton, & Klotz 1997; Blomqvist et al. 2000; Frouz & Jilková 2008). Both King (1977a, 1977b) and Blomqvist et al. (2000) showed that yellow meadow ants interact indirectly with aboveground vertebrate grazers. When tall grasses become dominant in the absence of vertebrate grazing, ants build higher mounds to keep up with the vegetation height. This is probably done to maintain sufficient solar radiation reaching the soil surface, thus to regulate the temperature in the mound. In turn, altered ant activity and mound structure may influence plant growth.

It has been acknowledged that plant community changes on mounds of yellow meadow ants are driven by changes in biotic and abiotic soil conditions as the result of soil heaping by the ants (King 1977a, 1977b; Blomqvist et al. 2000; Frouz & Jilková 2008). The relative importance of the actual presence of the ants themselves on the changes in plant community composition has not been quantified. However, ants could potentially induce changes in plant growth and plant species composition by tending root aphids, which are belowground sap-suckers. Therefore, the aim of our study is to understand whether plant community changes induced by yellow meadow ants are mainly driven through presence of mounds or through the actual presence of the ants themselves. In addition, we investigated how the presence of mounds and of ants themselves interacted with the removal of aboveground plant biomass. We address the following questions (1) do ants alter plant community production and species composition predominantly by building nest mounds (and their associated effects on soil properties) or does the actual presence of the ants themselves affect the plant community as well (for example by tending root aphids)? and (2) how does the