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Local variation in conspecific plant density influences plant–soil feedback in a natural grassland

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Abstract

Several studies have argued that under field conditions plant–soil feedback may be related to the local density of a plant species, but plant–soil feedback is often studied by comparing conspecific and heterospecific soils or by using mixed soil samples collected from different locations and plant densities. We examined whether the growth of the early successional species *Jacobaea vulgaris* in soil collected from the field is related to the local variation in plant density of this species. In a grassland restoration site, we selected eight 8 m × 8 m plots, four with high and four with low densities of *J. vulgaris* plants. In 16 subplots in each plot we recorded the density and size of *J. vulgaris*, and characteristics of the vegetation and the soil chemistry. Soil collected from each subplot was used in a greenhouse pot-experiment to study the growth of *J. vulgaris*, both in pure field soil and in sterile soil inoculated with a small part of field soil.

In the field, flowering *J. vulgaris* plants were taller, the percentage of rosette plants was higher and seed density was larger in High- than in Low-density plots. In the pot experiment, *J. vulgaris* had a negative plant–soil feedback, but biomass was also lower in soil collected from High- than from Low-density plots, although only when growing in inoculated soil. Regression analyses showed that *J. vulgaris* biomass of plants growing in pure soil was related to soil nutrients, but also to *J. vulgaris* density in the field.

We conclude that in the field there is local variation in the negative plant–soil feedback of *J. vulgaris* and that this variation can be explained by the local density of *J. vulgaris*, but also by other factors such as nutrient availability.

Zusammenfassung

Verschiedene Studien haben dargelegt, dass unter Feldbedingungen das Pflanze-Boden-Feedback mit der lokalen Dichte der Pflanze in Verbindung stehen könnte, aber das Pflanze-Boden-Feedback wurde oft untersucht, indem konspezifische und heterospezifische Böden miteinander verglichen wurden oder indem gemischte Bodenproben von verschiedenen Standorten und Pflanzendichten benutzt wurden. Wir untersuchten, ob das Wachstum der frühen Sukzessionspflanze *Jacobaea vulgaris* in im Freiland gesammelten Böden mit der Variation in der lokalen Dichte dieser Art in Beziehung steht. In einem rekultivierten Grasland wählten wir acht 8 m × 8 m große Probeflächen aus, vier mit hoher und vier mit geringer Dichte von *J. vulgaris* mit jeweils 16 Unterprobeflächen. Hier registrierten wir die Dichte und Größe der *J. vulgaris*-Pflanzen, sowie Eigenschaften der Vegetation und Daten zur Bodenchemie. Boden von jeder Unterprobefläche wurde in einem Topf-Experiment im Gewächshaus verwendet, um das Wachstum von *J. vulgaris* sowohl in reiner Freilanderde als auch in steriler Erde, die mit einer geringen Menge Boden aus dem Freiland inokuliert war, zu untersuchen.

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Im Freiland waren auf Flächen mit hoher Pflanzendichte die blühenden *J. vulgaris*-Pflanzen größer und der Anteil von Rosettenpflanzen sowie die Samendichte höher als auf Flächen mit geringer Pflanzendichte. Im Topf-Experiment zeigte *J. vulgaris* ein negatives Pflanze-Boden-Feedback, aber die Biomasse war ebenfalls geringer in Erde von Flächen mit dichtem Pflanzenbestand als in Erde von Flächen mit geringer Pflanzendichte – allerdings nur bei inokulierter Erde. In Regressionsanalysen zeigte die Biomasse der *J. vulgaris*-Pflanzen eine Beziehung zu den Nährstoffgehalten, wenn sie in reiner Erde wuchsen, aber auch eine Beziehung zur Pflanzendichte im Freiland.

Wir schließen hieraus, dass es im Freiland eine räumliche Variation des negativen Pflanze-Boden-Feedbacks gibt und dass diese Variation durch die lokale Dichte von *J. vulgaris* aber auch durch andere Faktoren wie die Nährstoffverfügbarkeit erklärt werden kann.

Keywords: *Calluna vulgaris*; Inoculated soil; *Jacobaea vulgaris*; Nutrients; Pure soil; Ragwort; *Senecio jacobaea*; Soil pathogens; Spatial patterning

Introduction

Plants influence the biology, chemistry and structure of the soil they grow in, which in turn, can lead to changes in the performance of plants that grow later in the soil. This process is referred to as plant–soil feedback (PSF) (Bever, Westover, & Antonovics 1997; Ehrenfeld, Ravit, & Elgersma 2005; Kulmatiski, Beard, Stevens, & Cobbold 2008; van der Putten et al. 2013). PSF can be mediated by abiotic soil conditions, such as availability of nutrients, as well as biotic conditions, such as presence of microorganisms (Bezemer et al. 2006b; Kulmatiski et al. 2008). Biotic PSF effects can be highly species-specific, while abiotic PSF effects are often less species-specific (Aerts and Chapin 2000; Reynolds, Packer, Bever, & Clay 2003). PSF can be positive due to increased nutrient availability (Chapman, Langley, Hart, & Koch 2006) or accumulation of mutualistic microorganisms such as arbuscular mycorrhizal fungi (Klironomos 2002). Negative PSFs can arise from nutrient depletion or immobilisation (Ehrenfeld et al. 2005) or the build-up of pathogenic soil microorganisms (Klironomos 2002; Packer and Clay 2000; van der Putten, van Dijk, & Peters 1993).

Several studies have argued that the PSF of a species can explain the abundance of this species in the field (Klironomos 2002; Kulmatiski et al. 2008; Mangan et al. 2010; Reynolds et al. 2003). These studies typically have examined how species-specific PSFs can explain interspecific variation, e.g. between dominant and rare plant species. However, several studies have also argued that for a single plant species, the strength of the PSF may be density-dependent, and hence may depend on the local density of the species in the field. Recently, a large database analysis of more than 200,000 forest plots and including 151 tree species revealed that for most species the establishment of seedlings was negatively affected by the local abundance of this species (Johnson, Beaulieu, Bever, & Clay 2012). These effects are likely mediated by density-dependent effects on soil pathogens. For example, seedling mortality of the tropical tree species *Sebastiana longicuspis* increases at higher local densities of conspecifics and this is caused by soil fungal pathogens (Bell, Freckleton, & Lewis 2006).

Although most of this work has been done with tree species, similar density-dependent PSF may be expected in grasslands (Bever 1994; Klironomos 2002; Petermann, Fergus, Turnbull, & Schmid 2008). Recently, van de Voorde, van der Putten, & Bezemer (2012) compared PSF of the early successional plant *Jacobaea vulgaris* in soil collected from 10 fields where this species occurred in different densities, and showed that indeed PSF was negatively related to the density of this species in the field. Similarly, in a field experiment with sown and unsown plots, *J. vulgaris* grew much better in soil collected from the sown plots where it was rare or even absent, than in soil from the unsown plots where it was present at high densities in the field (Bezemer, Harvey, Kowalchuk, Korpershoek, & van der Putten 2006a). However, in the latter study not only the density of *J. vulgaris*, but also the densities of other plant species differed greatly between sown and unsown plots, and several studies have shown that there are also strong heterospecific effects on PSF (Mangan et al. 2010; van de Voorde, van der Putten, & Bezemer 2011). So far, studies that examined PSF of *J. vulgaris* have used mixtures of soil samples taken from different locations within a field or an experimental plot. The local density of *J. vulgaris* often varies greatly within a single field (Bezemer personal observation). Whether PSF is related to the local density of *J. vulgaris* within a single field has not been tested.

Most studies test biotic PSF in sterile bulk soil inoculated with a small quantity of live field soil (e.g. Bever 1994; Kardol, Bezemer, & van der Putten 2006; Reinhart 2012). The rationale is that soil biota are introduced through the inoculum of live field soil, while the large amount of sterile bulk soil standardises soil nutrient levels across treatments (e.g. Kardol et al. 2006; Troelstra, Wagenaar, Smant, & Peters 2001). Inoculation with field soil, rather than using pure field soil, prevents confounding effects of local differences in soil nutrient availability that may exist in field soil, for example due to local disturbance of the soil. This is particularly important in bioassays where the soil effects on plant performance are tested directly without a conditioning phase (e.g. Bezemer et al. 2006a). However, using inoculated soil does not represent the natural field condition, where plants interact with biotic as well as abiotic components of the soil