



# Interspecific competition of early successional plant species in ex-arable fields as influenced by plant–soil feedback

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## Abstract

Plant–soil feedback can affect plants that belong to the same (intraspecific feedback) or different species (interspecific feedback). However, little is known about how intra- and interspecific plant–soil feedbacks influence interspecific plant competition. Here, we used plants and soil from early-stage ex-arable fields to examine how intra- and interspecific plant–soil feedbacks affect the performance of 10 conditioning species and the focal species, *Jacobaea vulgaris*. Plants were grown alone and in competition in both conditioned and control soils. Overall, plant–soil feedback of the 10 plant species influenced the competitiveness of *J. vulgaris* more strongly than their own competitiveness. However, effects depended on species combination: competitiveness of *J. vulgaris* was significantly enhanced by interspecific plant–soil feedback from *Anthoxanthum odoratum*, *Agrostis capillaris*, and *Trifolium dubium*, and significantly decreased by interspecific feedback from *Achillea millefolium*. Intraspecific feedback from *Taraxacum officinale* and *A. odoratum* decreased their competitiveness with *J. vulgaris*. There was a positive relationship between the strength of interspecific feedback and competitiveness of *J. vulgaris* in conditioned soil. Multiple linear regression showed that the competitiveness of *J. vulgaris* in conditioned soil was determined by interspecific feedback and competitiveness of neighbour plants. The positive relationship between interspecific feedback and competitiveness in control soil suggests that the soil feedback effect of the competing species on *J. vulgaris* can build up quickly during competition. We conclude that the effect of plant–soil feedback on interspecific competition may be due to either legacy effects of plant species previously colonizing the soil, or immediate interspecific feedback of the competing plant species via the soil. Therefore, our results suggest that plant–soil feedback can influence interspecific plant competition through a multitude of intra- and interspecific plant–soil interactions both from predecessors, and from the currently competing plant species.

## Zusammenfassung

Pflanze-Boden-Feedback kann Pflanzen beeinflussen, die zur selben Art (intraspezifisches Feedback) oder zu unterschiedlichen Arten (interspezifisches Feedback) gehören. Indessen ist wenig darüber bekannt, wie intra- und interspezifisches Pflanze-Boden-Feedback die interspezifische Konkurrenz zwischen Pflanzen beeinflussen. Wir studierten diese Feedbacks an zehn konditionierenden Arten und der Zielart *Jacobaea vulgaris* mit Pflanzen und Boden von kürzlich aufgegebenen Ackerflächen. Die Pflanzen wurden allein und in Konkurrenz und in konditioniertem und nicht konditioniertem Boden kultiviert.

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Insgesamt beeinflussten die Pflanze-Boden-Feedbacks der zehn Pflanzen die Konkurrenzfähigkeit von *J. vulgaris* stärker als ihre eigene Konkurrenzfähigkeit. Indessen variierten die Effekte mit der Artenkombination: Die Konkurrenzfähigkeit von *J. vulgaris* wurde signifikant durch interspezifisches Pflanze-Boden-Feedback von *Anthoxanthum odoratum*, *Agrostis capillaris* und *Trifolium dubium* gestärkt und signifikant durch interspezifisches Feedback von *Achillea millefolium* verringert. Intraspezifisches Feedback von *Taraxacum officinale* and *A. odoratum* reduzierte ihre Konkurrenzfähigkeit mit *J. vulgaris*. Es bestand eine positive Beziehung zwischen der Stärke des interspezifischen Feedbacks und der Konkurrenzfähigkeit von *J. vulgaris* in konditioniertem Boden. Multiple lineare Regressionsanalyse zeigte, dass die Konkurrenzfähigkeit von *J. vulgaris* in konditioniertem Boden durch interspezifisches Feedback und die Konkurrenzfähigkeit der Nachbarpflanzen bestimmt war. Die positive Beziehung zwischen interspezifischem Feedback und Konkurrenzfähigkeit in Kontroll-Boden legt nahe, dass sich der Effekt des Boden-Feedbacks der konkurrierenden Arten auf *J. vulgaris* schnell während der Konkurrenz aufbauen kann. Wir schließen, dass der Einfluss des Pflanze-Boden-Feedbacks auf die interspezifische Konkurrenz entweder auf ein langfristiges Nachwirken der Pflanzenarten, die in der Erde wuchsen, zurückzuführen sein könnte oder auf unmittelbares interspezifisches Feedback der konkurrierenden Pflanzenart über den Boden. Somit legen unsere Ergebnisse nahe, dass Pflanze-Boden-Feedback die interspezifische Konkurrenz zwischen Pflanzen durch eine Vielzahl von intra- und interspezifischen Pflanze-Boden-Interaktionen beeinflussen kann, sowohl durch Vorgänger als auch durch die aktuell konkurrierenden Pflanzenarten.

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**Keywords:** *Jacobaea vulgaris*; Interspecific plant–soil feedback; Intraspecific plant–soil feedback; Plant–soil interactions

## Introduction

Plants can alter the physical, chemical and biological properties of their soil environment, which, in turn, can affect plants that grow later in the soil. These interactions between plants and soil properties are termed plant–soil feedback (Ehrenfeld, Ravit, & Elgersma 2005). The majority of plant–soil feedback studies, mostly done in grasslands and tropical forests, report negative feedbacks of plant species to their conspecifics (Kulmatiski, Beard, Stevens, & Cobbold 2008; Petermann, Fergus, Turnbull, & Schmid 2008; Mangan et al. 2010). Negative feedbacks are known to reduce competitiveness and contribute to plant species replacement (Van der Putten & Peters 1997), leading to a decrease in the abundance and performance over time of many early successional plant species, such as *Jacobaea vulgaris* (Van de Voorde, Van der Putten, & Bezemer 2012). Thus, plant–soil feedbacks can play an important role in shaping the composition of plant communities by determining plant growth, abundance, and succession (Van der Putten, Van Dijk, & Peters 1993; Packer & Clay 2000; Kardol, Bezemer, & Van der Putten 2006; Manning, Morrison, Bonkowski, & Bardgett 2008; Mangan et al. 2010; Van de Voorde, Van der Putten, & Bezemer 2011; Reinhart 2012).

A number of studies have compared intra- and interspecific plant–soil feedback using pairwise feedback design (e.g. Vogelsang & Bever 2009; Kulmatiski & Beard 2011; Shannon, Flory, & Reynolds 2012). Intraspecific feedback focuses on the soil-mediated effects of one plant on the growth of another plant that belongs to the same species. Interspecific feedback focuses on the soil-mediated effect of one plant species on another species (Van der Putten et al. 2013). A recent study on the early successional

plant *J. vulgaris*, for example, showed that both intra- and interspecific plant–soil feedback can greatly affect its biomass production (Van de Voorde et al. 2011). However, it is still largely unknown how interspecific plant–soil feedbacks, both negative and positive, may affect interspecific plant–plant interactions.

When two plants compete, the performance of both individuals can be changed through competition for nutrients, light or space, but also through plant–soil feedback effects. Interestingly, several studies have shown that competition between two plant species (interspecific competition) can be enhanced or eliminated by plant–soil feedback effects (e.g. Van der Putten & Peters 1997; Casper & Castelli 2007; Kardol, Cornips, Van Kempen, Bakx-Schotman, & Van der Putten 2007). When two species compete in soil conditioned by one species, the plant–soil feedback effect of that one plant species can affect the outcome of competition via influencing the performance of itself (intraspecific feedback effect), or the competing species (interspecific feedback effect). However, the relative role of intra- and interspecific plant–soil feedback in plant competition is not well understood.

The aim of the present study was to investigate how plant–soil feedback can influence the competitiveness of both plants that conditioned the soil and the competing species. We used 10 plant species from an early stage of ex-arable field succession (Kardol et al. 2006). First we grew the 10 plant species to condition soils. Then, we examined the importance of intra- and interspecific plant–soil feedback for competitiveness with the early successional plant species *J. vulgaris*. We tested the hypothesis that the competitive ability is affected more by intraspecific than by interspecific plant–soil feedback. Therefore, we expected that when two species compete in conditioned soil the performance of

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