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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.

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 the species that conditioned the soil will be influenced most strongly by plant–soil feedback. Specifically, we expected that when the conditioning plant species exhibits negative intraspecific plant–soil feedback this will reduce its competitiveness when interacting with another plant species. Alternatively, we expected that positive intraspecific feedback will enhance competitiveness and that both responses may depend on the sign and strength of the interspecific feedback.

Materials and methods

To examine how plant–soil feedback of 10 early secondary succession plant species influences competition with the early successional species *J. vulgaris*, we conducted a greenhouse experiment that consisted of two phases.

Phase 1: Soil conditioning

We used 10 grassland species that all co-occur with *J. vulgaris* in restoration grasslands on former arable fields in the Netherlands (four forbs: *Achillea millefolium, Myosotis arvensis, Taraxacum officinale, Tripleurospermum maritimum*, four legumes: *Vicia cracca*, *Vicia sativa* subsp. *nigra*, *Trifolium dubium*, *Trifolium repens*, and two grasses: *Agrostis capillaris, Anthoxanthum odoratum*). In March 2012, soil was collected from a depth of 5–20 cm below soil surface in an ex-arable field (Mossel, Ede, The Netherlands) located on sandy loam in the central part of the Netherlands that was abandoned in 1995. The field soil was sieved using 0.5 cm mesh size to remove coarse fragments and homogenized. The soil was then separated in four parts that served as replicates. Half of the soil of each replicate was sterilized by γ-irradiation (minimally 25 KGray). A total of 120 pots (10 species × 3 plant treatments (as described under the heading Phase 2: feedback phase) × 4 replicates) of 1 L each were then filled with 1000 g of soil. We used a mixture of 500 g field soil and 500 g sterilized soil in order to standardize the background soil and ensure that there were enough nutrients (released through sterilization) for plant growth. The remaining sterilized soil was stored at room temperature in sealed bags to be used for Phase 2.

Seeds were obtained from specialized suppliers that provide seeds collected from wild plants (Cruydt-hoech, Assen, The Netherlands; B&T World seeds, Paguignan, France). All seeds were surface-sterilized (1 min in 2% sodium hypochlorite solution), rinsed and sown on glass beads. The glass beads were moistened with deionized water and placed in a germination cabinet (16/8 light/dark photo regime at 22/18 °C). One week after germination, seedlings were placed at 4 °C until transplanting to pots. Seedlings were transplanted in monocultures with five seedlings in each pot. The pots were placed randomly in the greenhouse. All pots were watered every second day and the initial soil moisture level was re-set to 17% (w:w) once a week by weighing. Dead seedlings were replaced during the first week of the experiment. Seedlings that emerged from the seed bank of the soil were removed manually. After eight weeks, the aboveground biomass was harvested by cutting the shoots at the soil surface. The main roots, and rhizomes were removed and the soil in each pot was then homogenized.

Phase 2: Feedback

The conditioned soil from each pot was mixed (1:1 ratio) with the stored sterilized bulk soil, in order to have ample volume of soil for plant growth and available nutrients coming from the sterilized soil. Soil from each pot was split in two halves. One half was used to test specific plant–soil feedback effects, whereas the other half was used to create control soil. To avoid pseudoreplication, we did not mix soil from the individual replicate pots. The control soil consisted of a mixture of soils conditioned by each of the 10 plant species and was mixed while keeping the four replicates separate. Therefore, each control soil had 5% of own soil (1:1 dilution of 10%), but previous work has shown that such low inoculation dosage may have little and non-significant effect on a plant species (Van der Putten, Van Dijk & Troelstra 1988). The advantage of the current approach is that all comparisons with the control treatment are based on identical soils. plant–soil feedback was tested using three plant treatments: (1) one seedling per pot of each of the 10 species; (2) one *J. vulgaris* seedling grown with one seedling of the 10 competitors per pot (interspecific competition); (3) one *J. vulgaris* seedling per pot; all in control and conditioned soil.

There were 240 pots in total: 10 plant species × 3 plant treatments × 2 soil conditioning types × 4 replicates. For treatment 3 (one *J. vulgaris* seedling per pot), there were 40 pots filled with the control soil that was conditioned keeping four replicates separately (10 pots for each replicate). We allocated one pot of each of the four replicates to each of the 10 species-specific soils (i.e. 4 unique control pots for each species-specific soil). Climatic conditions in the greenhouse were as described for the conditioning phase. Eight weeks after transplanting, all plants were harvested. Aboveground plant material was oven-dried (70 °C) for 3 days and weighed.

Data and statistical analysis

Plant–soil feedback was calculated according to Brinkman, Van der Putten, Bakker, and Verhoeven (2010) as

$$\text{feedback} = \ln\left(\frac{\text{biomass}_{\text{conditioned}}}{\text{biomass}_{\text{control}}}\right)$$

$\text{biomass}_{\text{conditioned}}$ represents the biomass of an individual plant when grown alone in conditioned soil, and $\text{biomass}_{\text{control}}$ represents the average biomass of plants grown alone in control soil.

In order to test whether plant–soil feedback affects interspecific competition intensity, competitiveness was calculated using a log-response ratio (Hedges, Gurevitch, & Curtis 1999; Weigelt & Jolliffe 2003), so that:

$$\text{competitiveness} = \ln\left(\frac{\text{biomass}_{\text{competition}}}{\text{biomass}_{\text{alone}}}\right)$$

$\text{biomass}_{\text{competition}}$ represents the biomass of an individual plant grown in a pot with interspecific competition, either grown in conditioned or in control soil, and $\text{biomass}_{\text{alone}}$ represents the average biomass of an individual plant when grown alone in control soil.

All data were analyzed using SPSS 19 (IBM, Chicago, IL, USA). Data were checked for homogeneity of variance using Levene's test and for normality by inspection of the normal-probability plot. To test the intra- and interspecific plant–soil feedback effect for plants that were grown without competition, data were analyzed using nested ANOVA with the factor type of plant–soil feedback (intraspecific or interspecific) nested in the factor of soil (conditioning by 10 species). For each individual species, we used a one-sample *T*-test to analyze whether the plant–soil feedback effect differed from zero.

To examine whether the effects of soil conditioning on competitiveness of *J. vulgaris* and on competitiveness of the 10 species differed in conditioned and control soil, data were analyzed using nested ANOVA with the factor soil (conditioned or control) and the factor competitor (*J. vulgaris* or other species) nested into the factor plant pair (ten combinations of *J. vulgaris* with one of the 10 neighbours). Independent sample *T*-tests were used to compare for each species the difference in competitiveness between conditioned and control soil. To determine whether there was a relationship between competitiveness or biomass of *J. vulgaris* and competitiveness or biomass of the competing species, and how this was affected by soil conditioning, we used analysis of covariance using averages for each species combination. The relationship between plant–soil feedback and competitiveness was analyzed using linear regression and means for each species/soil. Multiple regression analysis was used to determine the relative importance of (i) interspecific plant–soil feedback of *J. vulgaris* and (ii) competitiveness of the 10 species against *J. vulgaris*.

Results

Overall, the intra- and interspecific plant–soil feedback effects differed significantly (nested ANOVA, $F_{10,58} = 7.34$, $P = 0.041$). Soil conditioning by the 10 plant species caused significant and species-specific differences in interspecific plant–soil feedback on *J. vulgaris* ($F_{9,30} = 7.34$, $P < 0.001$). *V. cracca* caused significantly positive feedback on *J. vulgaris*, whereas the feedback effects on *J. vulgaris* of *M. arvensis*, *A. odoratum*, *A. capillaris*, and *A. millefolium* were significantly negative (Fig. 1A). The intraspecific plant–soil feedback effects did not differ among the 10 species ($F_{9,30} = 0.91$, $P = 0.53$). *A. millefolium* had a strong direct negative feedback that differed significantly from zero (Fig. 1B). The intraspecific plant–soil feedback effects of the other nine species were not significantly different from zero (Fig. 1B).

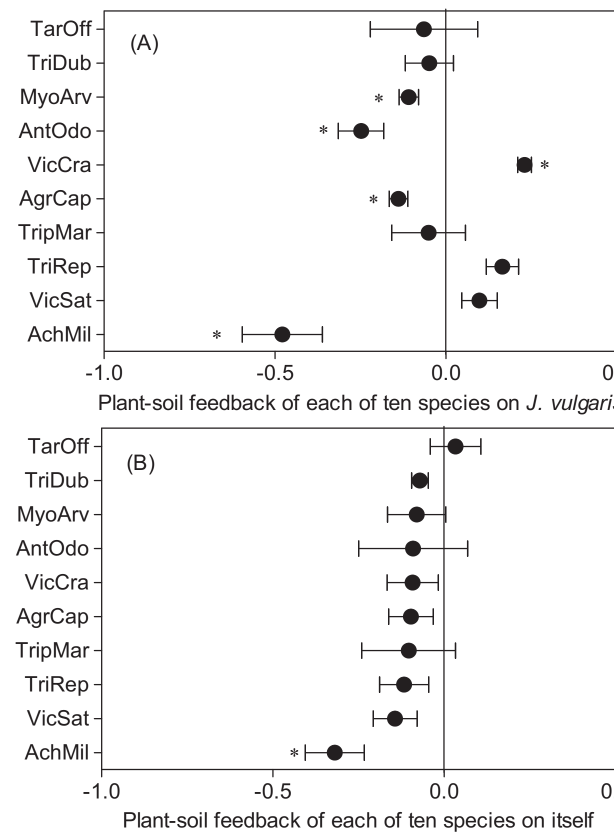

Fig. 1. Plant–soil feedback effect of soil conditioning by each of 10 plant species on (A) *Jacobaea vulgaris* (interspecific feedback), and (B) on themselves (intraspecific feedback). * indicates significant difference from zero at $P < 0.05$. Data are mean ± SE.

The competitiveness of *J. vulgaris* and the 10 species differed significantly ($F_{10,\ 111} = 20.10$, $P < 0.001$, Fig. 2A versus Fig. 2B), and depended greatly on the species *J. vulgaris* was competing with (plant pair: $F_{9,111} = 4.13$, $P < 0.01$). Soil conditioning influenced both magnitude and direction of the effects (soil × competitor: $F_{10,\ 111} = 5.58$, $P < 0.001$). Soil conditioning by *T. dubium, A. odoratum*, and *A. capillaris* enhanced competitiveness of *J. vulgaris* relative to competitiveness in control soil (Fig. 2A). In contrast, soil conditioning by *A. millefolium* decreased competitiveness of *J. vulgaris*. The competitiveness of *T. officinale* and *A. odoratum* was decreased by soil conditioning compared with control soil (Fig. 2B). The effect of soil conditioning on competitiveness was less strong for the 10 species that conditioned the soil than for *J. vulgaris* (Fig. 2B versus Fig. 2A), as indicated by the stronger absolute effect (independent of the sign of the effect) of soil conditioning on competitiveness of *J. vulgaris* compared with the other species (Fig. 2C).

There was a significantly ($F_{1,16} = 8{,}51$; $P = 0.01$) negative relationship between the competitiveness of the 10 species and the competeveness of *J. vulgaris*, and this

Table 1. Results of a multiple linear regression analysis testing the effects of interspecific plant–soil feedback, and competitiveness of 10 conditioning species on competitiveness of *J. vulgaris* in conditioned soil.

Parameters	Coefficients	Standardized coefficients	Overall R^2	Overall F value
Intercept	-1.703^{***}		0.84	18.28
Plant–soil feedback of *J. vulgaris* when grown alone	1.617^{**}	0.63		
Competitiveness of the conditioning species	-1.389^{**}	−0.63		

$^{**}P<0.01$.
$^{***}P<0.001$.

relationship was not influenced by soil conditioning ($F_{1,16}=10.21$, $P=0.65$; Fig. 3A). Interestingly, this relationship could not be explained by negative effects of plant size on competition, as there was no evidence for a negative relationship between the biomasses of two competing species ($F_{1,16}=2.62$, $P=0.13$; Fig. 3B). Furthermore, there was a positive relationship between the interspecific plant–soil feedback effect on *J. vulgaris* and its competitiveness in conditioned soil ($F_{1,8}=6.40$, $P=0.035$, Fig. 4A), as well as in control soil ($F_{1,8}=9.00$, $P=0.017$, Fig. 4B). Multiple linear regression showed that the competitiveness of *J. vulgaris* was related to both interspecific plant–soil feedback effect and the competitiveness of the 10 species (Table 1). In contrast, there was no significant relationship between intraspecific plant–soil feedback effects of the 10 species and their competitiveness in both conditioned ($F_{1,8}=1.16$, $P=0.31$, Fig. 4C) and control soil ($F_{1,8}=0.33$, $P=0.58$, Fig. 4D). Therefore, in the present study interspecific plant–soil feedback effects appeared to be more important to the outcomes of competition than intraspecific feedback effects of the conditioning species.

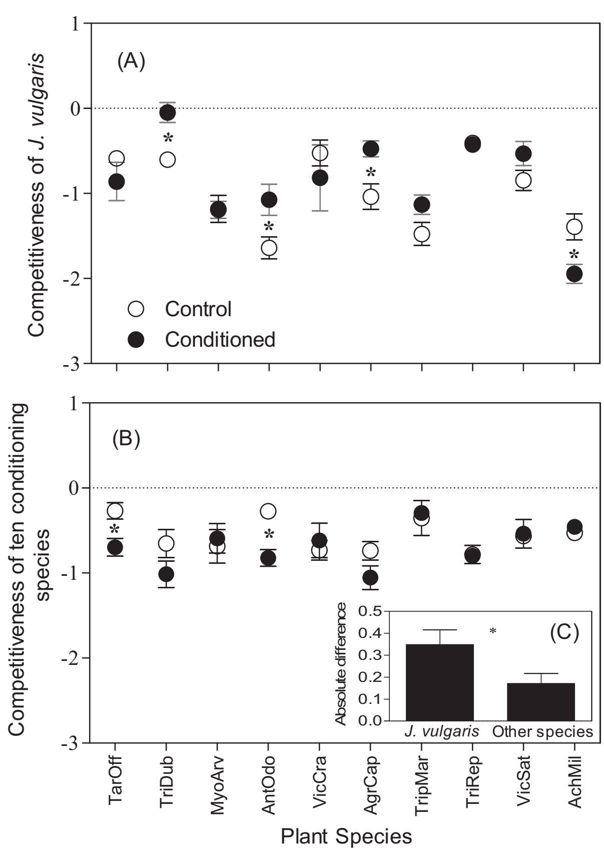

Fig. 2. Competitiveness in conditioned and control soils of (A) *J. vulgaris*, and (B) 10 conditioning species. Absolute difference in competitiveness between conditioned and control soil for *J. vulgaris* and the conditioning species (C: the inset in B). Asterisks indicatesignificant difference ($P<0.05$) between conditioned and control soil in (A) and (B) and between *J. vulgaris* and the other species in (C). Data are mean ± SE.

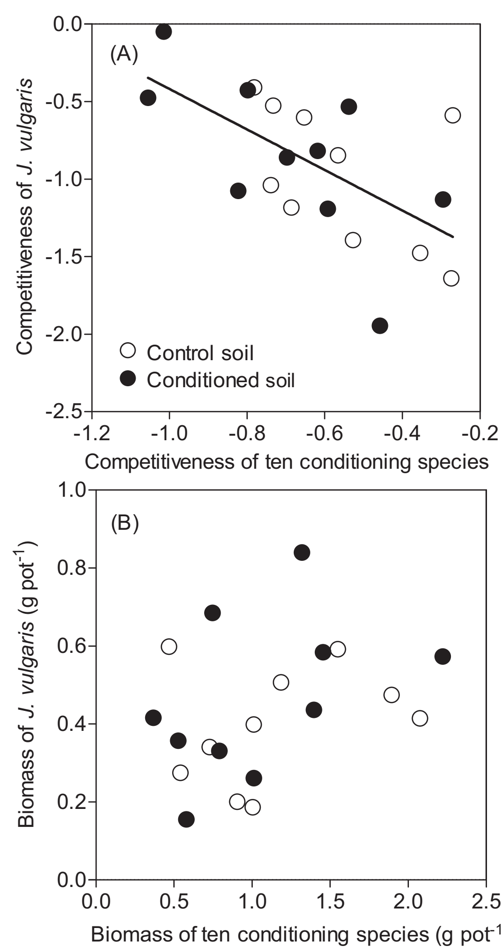

Fig. 3. Relationship between (A) competitiveness of 10 conditioning species and competitiveness of *J. vulgaris*, and (B) plant biomass of the conditioning species and biomass of *J. vulgaris* in control and conditioned soil.

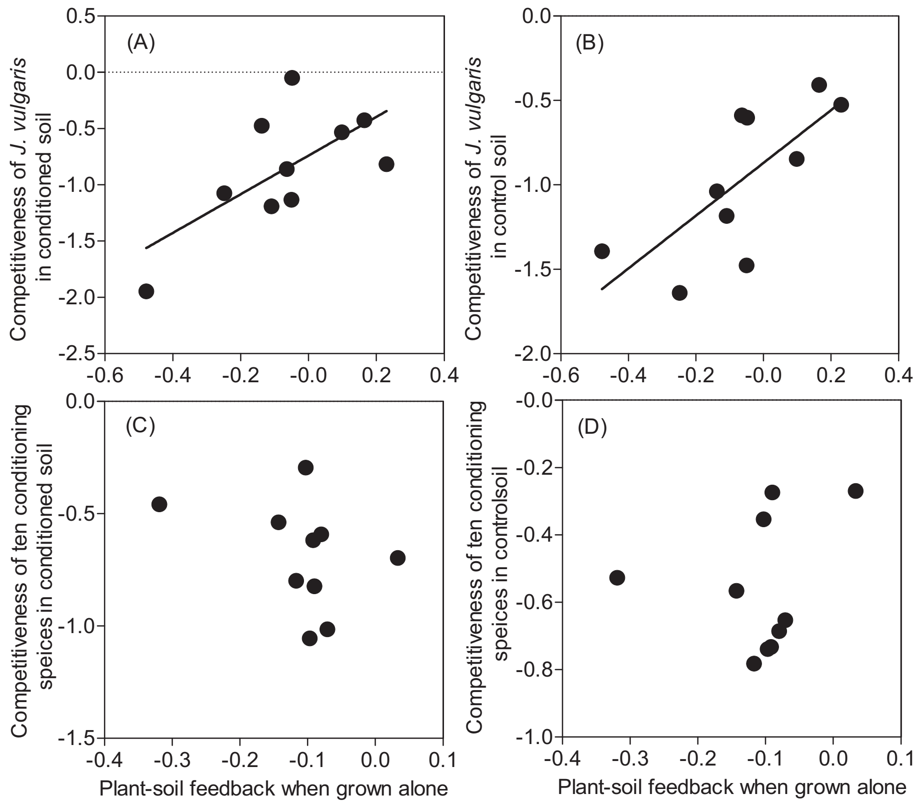

Fig. 4. Relationship between plant–soil feedback on *J. vulgaris* when grown alone and competitiveness of *J. vulgaris* in (A) conditioned soil ($r = 0.67$, $P = 0.035$) and (B) control soil ($r = 0.78$, $P = 0.017$), and plant–soil feedback of 10 conditioning species when grown alone and competitiveness in (C) conditioned soil and (D) control soil.

Discussion

In the present study, we examined how intraspecific and interspecific plant–soil feedback influenced interspecific competition between an early successional plant species and each of 10 co-occurring species. We found that plant–soil feedback of these 10 species had a stronger effect on the competitiveness of *J. vulgaris* than on the competitiveness of the 10 species themselves. Moreover, there was a positive relationship between interspecific plant–soil feedback and interspecific competitiveness of *J. vulgaris* indicating that species with which *J. vulgaris* competes well also promote the growth of *J. vulgaris* through soil feedback. Importantly, we found the competitiveness of *J. vulgaris* in conditioned soil to be determined by both interspecific plant–soil feedback and competitiveness of its neighbour. However, no relationship was observed between intraspecific plant–soil feedback of the 10 species and their competitiveness, so that our main hypothesis, representing the view that intraspecific plant–soil feedback reduces plant competitiveness, was not supported.

J. vulgaris is an early successional plant species, and in the ex-arable fields its abundance peaks relatively soon after establishment followed by a rapid decline (Bezemer, Harvey, Kowalchuk, Korpershoek, & Van der Putten 2006; Van de Voorde et al. 2012). Recently, it has been proposed that the population dynamics of this early successional species may be affected by both intra- and interspecific plant–soil feedback (Van de Voorde et al. 2011). Here, we observed positive and negative feedback effects of the 10 co-occurring species on *J. vulgaris*, whereas intraspecific plant–soil feedback effects of these 10 species were neutral or negative (Fig. 1B). A number of studies have demonstrated that intra- and interspecific plant–soil feedback can have different effects on plant performance (e.g. Van der Putten et al. 1993; Bever 1994 Bever, Westover, & Antonovics 1997; Bever 2003; Van de Voorde et al. 2011). These differences may be due to variation in sensitivity among plant species for soil-borne pathogens (Van der Putten et al. 1993), arbuscular mycorrhizal fungi (Klironomos 2003), or decomposer organisms (Miki, Ushio, Fukui, & Kondoh 2010).

Plant–plant interactions are widely acknowledged as a principal factor that can determine the relative dominance of species within plant communities (Brooker 2006). Previous studies have shown that effects of plant–soil feedback can be enhanced or eliminated by plant–plant interactions (e.g. Casper & Castelli 2007; Petermann et al. 2008; Hol, de Boer, ten Hooven, & van der Putten 2013; Pendergast, Burke & Carson 2013). Moreover, the response of a plant to intraspecific plant–soil feedback in the absence of competition often does not predict well how plant–soil feedback will affect the performance of that plant species in competition (Casper & Castelli 2007; Shannon et al. 2012), indicating that the effects of plant–soil feedback and plant–plant interactions are not independent. Our study shows that plant–soil feedback is important in determining the outcome of interspecific competition, but the effects of intra- and interspecific feedback differ depending on which plant species interact. This was due to sensitivity of *J. vulgaris* to interspecific plant–soil feedback, which varied from negative to positive depending on the plant species that conditioned the soil. However, competitiveness of the other 10 species was not affected by intraspecific plant–soil feedback. This is probably because the intraspecific plant–soil feedback effects on the 10 plant species were not significantly different from zero, and thus less likely to influence competitiveness of these plant species. It is important to note that the competitiveness of *J. vulgaris* in conditioned soil was also determined by the competitiveness of the other plant species. Taken together, intraspecific competition from neighbour species and their plant–soil effects both can influence the performance of *J. vulgaris*.

Intra- and interspecific plant–soil feedback can influence plant competition through either one of the two competing species, leading to effects ranging from competition to facilitation (Van der Putten 2009). Positive intraspecific plant–soil feedback locally will lead to decreased diversity (Bever et al. 1997), and is likely to contribute to local competitive exclusion (Bever 2003). According to a previous study (Van de Voorde et al. 2011), *J. vulgaris* has strong negative intraspecific plant–soil feedback, which may reduce the performance of this early successional plant species. However, the positive relationship between interspecific plant–soil feedback and competitiveness of *J. vulgaris* in our study suggests that positive interspecific plant–soil feedback may be important in slowing down competitive exclusion, which probably promotes species coexistence in plant communities.

Thus far, attention has focused on how negative plant–soil feedback may decrease species abundance (Klironomos 2002; Mangan et al. 2010; but see Reinhart 2012), or drive succession (Van der Putten et al. 1993; Kardol et al. 2006). Interestingly, our study shows that negative plant–soil feedback does not necessarily lead to reduced competition. For example, the negative intraspecific plant–soil feedback of *A. millefolium* did not affect its competitiveness with *J. vulgaris* in conditioned soil. We observed a negative relationship between the competitiveness of the 10 species and *J. vulgaris*. Hence, the competitiveness of the 10 conditioning species was probably affected by that of *J. vulgaris*, which is influenced by interspecific plant–soil feedback at the same time. Therefore, investigating intra- and interspecific plant–soil feedback effects shows that there are more possible outcomes of plant competition than predicted by intraspecific plant–soil feedbacks or net plant–soil feedback effect based on pairwise designed experiments. Thus, rates and directions of plant community development can only be understood when considering both intra- and interspecific plant–soil feedbacks (Kardol, De Deyn, Laliberte, Mariotte, & Hawkes 2013).

We did not find a significant relationship between biomass of the 10 species and biomass of *J. vulgaris* in control and conditioned soil, which indicates that the outcome of competition was not determined by plant size. The positive relationship between interspecific plant–soil feedback and competitiveness in control soil of *J. vulgaris* (Fig. 4B) may reveal a rapid build-up of plant–soil feedback when two competing species were growing together. This caused an effect similar to interspecific plant–soil feedback of one species to another.

Awareness of the different consequences of intra- and interspecific plant–soil feedback may help to further understand plant population dynamics, community development, and species turnover through time (Fukami & Nakajima 2013). Although some studies have shown that plant–soil feedback changes with competitive context (Casper & Castelli 2007; Shannon et al. 2012), the linkage between plant–plant interaction and strength and direction of feedbacks has been largely overlooked. We conclude that during early secondary succession interactions between one focal plant species and its co-occurring species can be driven by positive or negative intra- and interspecific plant–soil feedback. The resulting process may vary from competition to facilitation. Interspecific plant–plant interactions mediated by plant–soil feedback, as well as intraspecific interactions, therefore, may contribute profoundly to the species composition and to the direction of change therein during early secondary succession.

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