Journal of Ecology

British Ecological Society

Journal of Ecology 2016, **104**, 1608–1617 doi: 10.1111/1365-2745.12643

Plant–soil feedbacks: role of plant functional group and plant traits

Roeland Cortois[1], Thomas Schröder-Georgi[2,3], Alexandra Weigelt[2,3], Wim H. van der Putten[1,4] and Gerlinde B. De Deyn[5]*

[1]Department of Terrestrial Ecology, Nederlands Instituut voor Ecologie NIOO KNAW, NL-6700 AB, Wageningen, The Netherlands; [2]Department of Special Botany and Functional Biodiversity, Institute of Biology, University of Leipzig, D-04103 Leipzig, Germany; [3]German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig, Leipzig, Germany; [4]Laboratory of Nematology, Wageningen University, NL-6700 ES, Wageningen, The Netherlands; and [5]Department of Soil Quality, Wageningen University, NL-6700 AA, Wageningen, The Netherlands

Summary

1. Plant–soil feedback (PSF), plant trait and functional group concepts advanced our understanding of plant community dynamics, but how they are interlinked is poorly known.

2. To test how plant functional groups (FGs: graminoids, small herbs, tall herbs, legumes) and plant traits relate to PSF, we grew 48 grassland species in sterilized soil, sterilized soil with own species soil inoculum and sterilized soil with soil inoculum from all species, and quantified relative growth rate (RGR), specific leaf area (SLA), specific root length (SRL) and per cent arbuscular mycorrhizal fungi colonization (%AMF).

3. Plant growth response to the plant species' own soil biota relative to sterilized soil (PSFsterilized) reflects net effects of all (generalist + specialized) soil biota. Growth response to the plant species' own soil biota relative to soil biota of all plant species (PSFaway) reveals effects of more specialized soil organisms.

4. PSFsterilized showed that graminoids and small herbs have a negative and tall herbs a positive response to their own soil biota, whereas legumes responded neutrally. However, PSFaway showed that on average, all plant FGs benefitted from growing with other species' soil biota, suggesting that pathogens are more specialized than plant growth-promoting soil biota. Feedback to plant growth from all soil biota (PSFsterilized) was stronger than from more specialized soil biota (PSFaway) and could be predicted by SRL and especially by %AMF colonization. Species with high SRL and low %AMF colonization when grown in away soil experienced most negative soil feedback.

5. *Synthesis.* Plant species from all plant FGs grow better in soil from other species because of less net negative effects of soil biota (in graminoids), or because of more net positive soil biota effects (in tall herbs). Explorative plant species (high SRL, low %AMF colonization) suffer most from negative feedback of all soil biota, whereas more resource conservative species (low SRL, high %AMF colonization) benefit from soil feedback of all soil biota. These findings help to understand replacement of explorative species during succession. Moreover, we suggest a potentially larger role for species with positive feedback than for species with negative feedback to contribute to maintain plant community productivity of diverse communities over time.

Key-words: above-ground–below-ground interactions, below-ground traits, biodiversity–ecosystem functioning, functional traits, mycorrhizal fungi, plant–soil feedback, plant–soil interactions, soil legacy effects, soil microbes, trait-based ecology

Introduction

Interactions between plants and soil organisms are known to be important determinants of plant performance, affecting plant population and community dynamics (Wardle *et al.* 2004; Bever *et al.* 2010). During the last two decades, the reciprocal interactions between plants and soil biota, named plant–soil feedback (PSF), rapidly gained interest as a mechanism that may explain species invasion, plant diversity–productivity relationships and the maintenance of diversity through promoting plant coexistence (Bever *et al.* 2010; van der Putten *et al.* 2013). As those papers point out, most

*Correspondence author. E-mail: gerlinde.dedeyn@wur.nl

studies on PSF effects have focused on feedbacks via plant pathogens and mutualists that suppress or stimulate plant growth, respectively. All these individual influences add up to net PSF effects, which can be negative, neutral or positive.

Meta-analytical studies have shown that the direction and effect sizes of PSF effects governed by soil microbiota appear to differ between plant functional groups (Kulmatiski *et al.* 2008; Meisner *et al.* 2014). Specifically, graminoids and early-successional plant species show predominantly negative PSF, likely due to the build-up of host-specific plant pathogens (Kardol, Bezemer & van der Putten 2006; Kulmatiski *et al.* 2008). In contrast, late-successional species are slower growing, have positive PSF (Kardol, Bezemer & van der Putten 2006) and tend to benefit more from AMF (Koziol & Bever 2015) than early secondary successional species. Recent work also shows that large plants suffer stronger negative PSF than smaller plants, which prevents large plants to become dominant, especially in species-rich grassland systems with low land-use intensity (Heinze *et al.* 2015). In addition to plant functional groups (FGs), plant functional traits can capture important differences between species both across and within plant FGs and can thereby help to explain and predict PSF effects. However, despite the growing attention for plant traits that are related to plant interactions with below-ground biota (Bardgett, Mommer & de Vries 2014), there is still little known about which functional plant traits may predict PSF effects (Bever, Westover & Antonovics 1997; van der Putten *et al.* 2013).

Plant trait frameworks are mainly based on principles of resource capture, abiotic stress (in)tolerance, competitive ability and dispersal strategies (e.g. Grime 1977; Tilman 1988; Craine 2009; Díaz *et al.* 2016). Consequently, plant traits may be used to predict effects of plants on ecosystem processes (Violle *et al.* 2007; De Deyn, Cornelissen & Bardgett 2008; Lavorel & Grigulis 2012; Baxendale *et al.* 2014) and plant performance along environmental gradients (Lavorel & Garnier 2002). It is well recognized that trade-offs may exist between plant resource capture through investment in acquisitive traits and vulnerability to natural enemies (e.g. Herms & Mattson 1992; van der Putten 2003; Rasmann *et al.* 2011). For example, plant growth rate may trade-off with increased rate of herbivory on leaves (e.g. Coley 1988; Fine *et al.* 2006) and roots (Bauerle *et al.* 2007). In general, plant species can be regarded as being 'slow' with low relative growth rate (RGR), low specific leaf area (SLA) and low specific root length (SRL) or 'fast' with high RGR, SLA and SRL (Grime *et al.* 1997; Westoby *et al.* 2002; Tjoelker *et al.* 2005; Reich 2014). Plants with a 'slow' strategy like late-successional species are considered to be resource conservative and well defended, whereas plants with a 'fast' strategy like early-successional species have rapid resource acquisition but are generally poorly defended. It can thus be expected that plant species with high SLA, SRL and RGR suffer more from negative PSF than plant species with low SLA, SRL and RGR.

Recent studies that aimed to predict PSF from plant traits focused on litter and decomposer community-mediated PSF (Orwin *et al.* 2010; Baxendale *et al.* 2014). These studies showed that traits of fast versus slow-growing plant species differentially influenced PSF via nutrient cycling-related mechanisms through litter quality and decomposition (Baxendale *et al.* 2014). To what extent plant traits can also predict PSF effects generated via all soil microbiota, including pathogens, mutualist and saprotrophs remains to be tested. A recent modelling study, however, showed that the role of litter traits in PSF depended on the presence of pathogens and mycorrhizal fungi with a minor role for litter traits when pathogens are present (Ke, Miki & Ding 2015). That study also demonstrated the importance of the balance between pathogens and mycorrhizal fungi for the outcome of PSF effects, under the assumption that mycorrhizal fungi act in a mutualistic way through nutrient provision to plants.

Many plant species associate with arbuscular mycorrhizal fungi (AMF), which can stimulate plant growth both via enhancing nutrient acquisition (Smith & Read 2010) and by plant protection against root pathogens (Newsham, Fitter & Watkinson 1995). The benefits of colonization by AMF to plant growth, however, remain hard to predict and may even be negative when AMF act as parasites (Johnson, Graham & Smith 1997; Hoeksema *et al.* 2010). Moreover, PSF effects mediated by AMF can vary from positive to negative, with positive PSF when plant species promote their own most beneficial AMF, and negative PSF when the AMF beneficial to their competing plant species are promoted (Bever 2002; Bever *et al.* 2010). Also the relation between AMF and root traits is not straightforward (Maherali 2014) and dependent on other soil biota (Newsham, Fitter & Watkinson 1995). However, it has been proposed that plant species with low SRL gain greater benefits from AMF than plant species with high SRL because of larger benefits of enhanced nutrient access, at least when pathogen pressure is relatively low (Newsham, Fitter & Watkinson 1995; Blumenthal *et al.* 2009; Smith & Read 2010; Yang *et al.* 2015). It is well known that legumes benefit not only from AMF, but also from N_2-fixing symbiotic bacteria. It can therefore be expected that legumes generate a positive PSF by stimulating their beneficial soil-borne microbes (Wagg *et al.* 2015).

Plant–soil feedback can be studied in a variety of ways depending on the research focus, and with that the experimental methods used to quantify PSF and the type of statistical analysis performed (Brinkman *et al.* 2010). Plant species responses to their own soil biota can be tested relative to sterilized soil (PSFsterilized) or relative to soil biota from other plant species (PSFaway). These two types of PSF values have both been used in meta-analyses (Kulmatiski *et al.* 2008; Meisner *et al.* 2014), without further distinction between them. However, the biological interpretation of these two types of PSFs differs: PSFsterilized reflects net effects of all soil biota from the species' own soil, which include generalists as well as more specialized soil biota, whereas PSFaway compares the impact of soil biota from own soil with that of soil biota from other species' soil. Species suffering from their own soil biota (i.e. have negative PSFsterilized) can benefit from growing in other species' soil (i.e. have negative PSFaway) through dilution of specific pathogens. However,

also plant species benefitting from their own soil biota (i.e. have positive PSFsterilized) may benefit less from their own soil biota than from those from other plant species (i.e. have negative PSFaway) and can hence be promoted in other species' soil relative to growth in their own soil (Bever 2002; Bever *et al.* 2010). To date, it is unknown how plant responses to all soil biota and to more specific soil biota are related and whether plants with different traits or different plant FGs show distinct responses.

Here we examine how plant FGs and plant traits may be indicative of PSF effects resulting from net effects of all soil biota (PSFsterilized) and those resulting from more specialized soil organisms (PSFaway). Based on current literature, we tested the idea that for co-occurring grassland species, PSFsterilized and PSFaway differ between plant FGs and that plant traits also contribute to predicting PSF effects. We also expect that PSFsterilized and PSFaway have the same sign (positive or negative) based on the idea that plant species are generally expected to stimulate their own pathogens or own most beneficial organisms more than other plant species do. We specifically tested the hypotheses that (i) graminoids and tall herbs have negative PSFsterilized and PSFaway, (ii) legumes have positive PSFsterilized and PSFaway and (iii) across-plant FGs species with traits targeting rapid resource acquisition (high RGR, SLA, SRL, low AMF%) will have more negative PSF compared to species with more resource conservative traits.

Materials and methods

STUDY SYSTEM

The plant species used for the plant–soil feedback (PSF) experiments are typical for mesophilic Central-Western European grasslands (Table S1 in Supporting Information). We used 48 of 60 plant species that are also being used in the Jena biodiversity experiment (Roscher *et al.* 2004), because there were insufficient seedlings of 12 plant species due to poor germination. Seeds were provided by commercial suppliers who collected seeds from wild populations in Germany. The soil (Eutric Fluvisol, developed from loamy sediments) for the PSF experiment was collected from the Jena field site (Jena, Thuringia, Germany, 50°55′ N, 11°35′ E) (Roscher *et al.* 2004). A two-stage PSF experiment was carried out in pots in a climate-controlled glasshouse in which we tested growth of the 48 species in three soils: (i) soil conditioned by conspecifics (own soil), (ii) a mixture of all 48 species-specific conditioned soils (away soil) and (iii) sterilized soil. In all treatments, we used sterilized soil inoculated with living (treatments i and ii) or sterilized conspecific soil inoculum (treatment iii), as this approach causes the lowest potential for confounding effects due to sterilization-induced nutrient flushes (Troelstra *et al.* 2001). To determine the plant traits relative growth rate (RGR), specific root length (SRL) and specific leaf area (SLA), individuals of all species were grown in additional experiments under controlled conditions in the Botanical garden of Leipzig University and in a glasshouse of NIOO-KNAW at Wageningen, The Netherlands (see below for details). In brief, the traits SLA and SRL were quantified on mature plants grown in non-sterilized soil from the Jena experiment (Schroeder-Georgi *et al.* 2016), and RGR was quantified using the total (above- and below-ground combined) dry biomass increase per unit of time of seedlings of 1 and 3 weeks that were grown in the soil mixture of all plant species (i.e. away soil). This soil of the PSF experiment contained on average over all plant species 35.8 ± 0.7 mg kg^{-1} $NH_4^+ + NO_3^-$-N and 29.9 ± 0.1 mg kg^{-1} P-Olsen and soil pH-H_2O of 7.7. This soil can be classified as moderately fertile and similar to the field conditions in the first years of the Jena experiment (Roscher *et al.* 2004; Oelmann *et al.* 2011). The %AMF colonization was quantified in roots of plants grown in own soil and in away soil. The abiotic conditions in these soils were similar given that they originated from the same field, and for all the species, each trait (SLA, SRL, RGR) was quantified on plants grown in the same soil (mixed field soil or away soil) in order to obtain standardized values for all plant species. As the %AMF colonization may depend on whether plant species grow in own or away soil, we included results of both.

PLANT–SOIL FEEDBACK

Plant germination

In December 2010, plant seeds were surface-sterilized by soaking in 5% or 25% household bleach (5% sodium hypochlorite solution) for 30 s; 25% household bleach was used when 5% bleach was not a sufficient concentration to prevent fungal infection of seeds. The sterilized seeds were rinsed with demineralized water and placed in a growth cabinet (16-h/8-h 22 °C/16 °C light/dark) on water-saturated glass beads in plastic boxes closed with a transparent plastic lid. Based on Roscher *et al.* (2004), prior to germination, some seeds were scarified or treated with gibberellic acid (Sigma Chemical co., St. Louis, MO, USA). After germination, which took 3–12 days, seedlings were transferred to a climatized room at 4 °C and 16-h/8-h light/dark conditions, which kept them all in the same post-germination stage until planting.

Soil conditioning phase

At the end of December, 384 pots of 1.5 L each were filled with 1500 g of soil, consisting of a mixture of 80% sterilized soil and 20% unsterilized soil (based on dry soil weight). Pots were arranged in the glasshouse (16-h/8-h light/dark) in eight replicate blocks. Two seedlings per species were planted per pot, and pots were spatially randomized within blocks. Soil moisture level was reset to 25% (w/w) by adding demineralized water until pots were at preset weight equivalent to 30% moisture. This was repeated every second or third day. After 2 months of growth, plants were harvested and the soil was collected from each pot individually in order to be used in the feedback phase. During harvest, above-ground biomass was clipped and dried at 70 °C for minimally 72 h. Adhering soil was shaken off roots before rinsing with tap water and drying them at 70 °C for minimally 72 h.

Soil from each plant species was stored separately in plastic bags at 4 °C. Cross-contamination of soils from different plant species during harvest was avoided by cleansing all used material in 70% ethanol in between working steps. A 50-mL subsample was taken from all plant species-specific conditioned soils and dried at 40 °C during 72 h in order to analyse nutrient concentration and moisture content. Plant-available P was determined according to Olsen *et al.* (1954). Soil mineral N was extracted by shaking 10 g (dry weight) soil with 50 mL 1 M KCl for 2 h. NH_4^+-N and NO_3^--N were determined calorimetrically in the KCl extract.

Feedback phase

All 48 soils from the conditioning phase were split into three equal parts. One part was left untreated and kept separate per species (named own soil), the second part was left untreated and used to prepare a mixture of all soils based on equal dry weight proportions of the species-specific soils (named: away soil), and the third part was kept separate per species and was sterilized by gamma irradiation (25 KGray; named sterilized soil). All soil treatments thus obtained were mixed individually with a sterilized background soil from the Jena experimental field site as 65% sterilized soil and 35% living inoculum soil (of one species or of the mixture of all species) or sterilized inoculum soil (w/w).

To test the plant responses to the soils, seeds of all plant species were germinated as done before, and seedlings were planted in pots with either 550 g of the own, away or sterilized soil inoculum treatment. Treatments were carried out in a randomized block design with eight replicates, resulting in an experimental design of 48 plant species × 3 soil treatments × 8 replicates = 1152 pots. The replicates capture the variation in plant species response to the average legacy left by the species from which the soil inoculum was derived, as the soil from the conditioning phase was pooled per species. All seedlings that died in the first week after planting were replanted and pots were spatially randomized within blocks. Plants were watered every 3 or 4 days using demineralized water to reset moisture to 25% (w/w). After growing for 6 weeks, all plants were harvested as described for the soil conditioning phase, and total dry weight was determined. Plant dry weights in the three soil treatments were used to calculate two PSF values per experimental block as log (total dry weight in soil type X/total dry weight in soil type Y) (Brinkman *et al.* 2010), resulting in a PSF value per block for eight blocks ($n = 8$). For PSFsterilized: X = own soil and Y = sterilized soil and for PSFaway: X = own soil and Y = away soil. We are aware that PSF effects are likely to be inherently time and inoculum density dependent (Kardol *et al.* 2013). However, the duration of the soil conditioning and feedback phase resembled the duration often used in plant–soil feedback experiments with grassland species, while the concentration of soil inoculum we used in the test phase was well comparable to other studies that have reported significant plant–soil feedback effects (Brinkman *et al.* 2010).

TRAIT DATA

Relative growth rate (RGR) was determined in the glasshouse (16-h/8-h light/dark) in soil consisting of 40% away soil inoculum and 60% sterilized Jena soil. To quantify RGR, the proportional total dry weight biomass increase from one-week-old plants grown in cylinder pots of 3 cm diameter × 6 cm depth to 3-week-old plants grown in pots of 7 × 7 × 7 cm was measured (Hendry & Grime 1993). One-week-old plants of all study species were harvested the same day. Three-week-old plants were harvested at three different dates (one replicate block per day), washed free of soil particles and dried at 70 °C for at least 48 h. RGR was calculated as (log W2 – log W1)/(t2–*t*1) (Hendry & Grime 1993), where W1 is total dry weight biomass at $t1 = 7$ days and W2 is total biomass at $t2 = 21$, 23 or 24 days (three replicate blocks).

Specific leaf area and SRL were quantified in a mesocosm experiment, which was conducted outdoors in the Botanical Garden of Leipzig (Germany) in 2011. Each species was represented as five replicates in a randomized block design. Individual plants grew for 12 weeks in separate mesocosms of 60 cm height and 15 cm diameter, filled with a mixture of soil derived from experimental plots of the Jena experiment and sand (20%) (for details, see Schroeder-Georgi *et al.* 2016). Sampling and measurements of SLA followed recommendations of Cornelissen *et al.* (2003). Roots were washed using tap water, fine sieves and forceps. Cleaned roots were scanned and measured using a flat-bed scanner and the software WINRHIZO (Regent Instruments Inc., Quebec City, QC, Canada) to estimate root length. Root mass was measured after drying for 48 h at 70 °C. SRL was then calculated as root length-to-root dry mass ratio.

Arbuscular mycorrhizal fungi (AMF) colonization levels in roots were determined for a random subset of 27 out of the 48 species (six graminoids, ten legumes, three small herbs and eight tall herbs; Table S1 species in bold) due to practical constraints. Root material from plants grown in own soil and grown in away soil (see 'feedback phase' described above) was rinsed free of soil and stored in 50% ethanol. The fungal structures in roots were stained with trypan blue using a standard protocol (Brundrett *et al.* 1996). In short, roots were cut into fragments of approx. 2 cm and cleared in 10% KOH at 90 °C for 20–50 min, depending on root thickness. After rinsing with tap water, roots were acidified in 2% HCl for 1 h and subsequently stored overnight in 0.01% trypan blue in a 5:1:1 mixture of lactic acid, demineralized water and glycerol. Roots were de-stained and stored in 50% glycerol for microscopic investigation. To this end, roots were dispersed in a Petri dish of 5 cm diameter with a counting grid and examined under a microscope with magnification 10 × 40. The AMF colonization percentage of the roots was estimated according to the grid line intersection method (McGonigle *et al.* 1990). Distinction was made between septate and non-septate hyphae and occurrence of arbuscules verified, the latter representing AMF (Hudson 1991).

DATA ANALYSES

The relation between the plant traits SLA, RGR, SRL, %AMF colonization in own soil and in away soil was tested using principal component analysis (PCA) of the standardized traits. To test the effect of plant functional group, PSF type and plant traits on PSF values, we used average values per species for PSFsterilized, PSFaway, SRL, SLA, RGR and %AMF colonization. We subsequently used general linear models with plant functional group (graminoid, legume, small herb and tall herb), PSF type (PSFsterilized or PSFaway) and their interaction as fixed factors and SLA, RGR and SRL as covariates to explain PSF values. For the data subset for which we also had the %AMF colonization values, we included this plant trait also as a covariate. We ran the models without and with covariates to test whether including the traits improved the model. Assumptions for the error distributions were verified using Levene's test for homoscedasticity and Kolmogorov–Smirnov test for normality. Differences among average plant biomass production across all plant species in own, away and sterilized soils were tested using a nonparametric Kruskal–Wallis test across the three groups and Mann–Whitney *U*-test to test differences between groups, because assumptions for parametric testing were not met. We tested whether PSF effects could be attributed to altered nutrient levels (NO_3^-, NH_4^+ and Olsen's P) due to the different plant species' inocula by testing the correlation between PSFsterilized and the difference in nutrient levels in the own versus sterilized soil treatment. PSFsterilized was not related to the difference in nutrient levels between own and sterilized soil for NH_4^+-N ($r = 0.15$, $P = 0.33$), NO_3^--N ($r = -0.08$, $P = 0.62$) and P-Olsen ($r = 0.19$, $P = 0.22$), neither was PSFaway related to the nutrient levels in the soil inocula: NH_4^+-N ($r = 0.07$, $P = 0.64$), NO_3^--N ($r = 0.04$, $P = 0.76$) and P-Olsen ($r = -0.05$, $P = 0.73$). Structural equation modelling (SEM) analyses were performed to test the direct and indirect relations of SRL and %AMF colonization in own and away soil in affecting PSFaway and PSFsterilized. To test the most parsimonious model of the significant models, AIC criteria were used.

Initially, we also tested SEM models with graminoids, SRL and % AMF included, but models with graminoids as parameter were inferior (AIC criteria) so we proceeded with the models with only SRL and %AMF. Statistical analyses were performed using the statistical software R version 3.1.0 (R core team 2013) and SPSS 22 (IBM, New York, NY, USA), and PCA of the plant traits was done using CANOCO 5 [Software for Ordination (version 5.0), Microcomputer Power, Ithaca, NY, USA].

Results

PLANT TRAITS

The PCA analysis of the plant traits SRL, SLA, RGR and % AMF colonization in own and in away soil across the plant species revealed that 49% of the variation in the data could be explained by the first axis and 22% by the second axis (Fig. 1). The main traits driving the first axis were %AMF colonization and SRL, in opposite directions, whereas the second axis was primarily determined by SLA (PCA factor loadings. Table S2). The %AMF colonization in roots of plants grown in own soil was very similar to the %AMF colonization in roots of plants grown in away soil, as can be seen both in the PCA (Fig. 1) and in the bivariate correlation analysis ($R^2 = 0.80$, $P < 0.001$; Fig. S1). Apart from the %AMF colonization in own and in away soil ($r = 0.9$) and between SRL and %AMF colonization ($r = -0.7$ for AMF own and $r = -0.6$ for AMF away), the plant traits were not strongly correlated ($r < 0.5$) (Table S2).

PSFSTERILIZED AND PSFAWAY

Across all plant species, average plant biomass was significantly affected by the soil treatments (KW $\chi^2 = 6.52$, $P = 0.038$) with largest biomass in sterilized soil, smallest biomass in own soil and intermediate biomass in away soil (Fig. S2; Table S3). Across all plant species, average PSF effects were negative, but PSF effects of individual species ranged from negative to positive. Average PSFsterilized was –0.10 ± 0.05 SE and varied from −0.81 to +0.63, whereas average PSFaway was – 0.09 ± 0.02 SE and ranged from −0.22 to +0.59 (Fig. 2a,b). Overall, the mean of PSFsterilized across the 48 species was only marginally ($P = 0.06$) significantly negative, whereas the mean PSFaway was significantly ($P = 0.0003$) negative (Fig. 2).

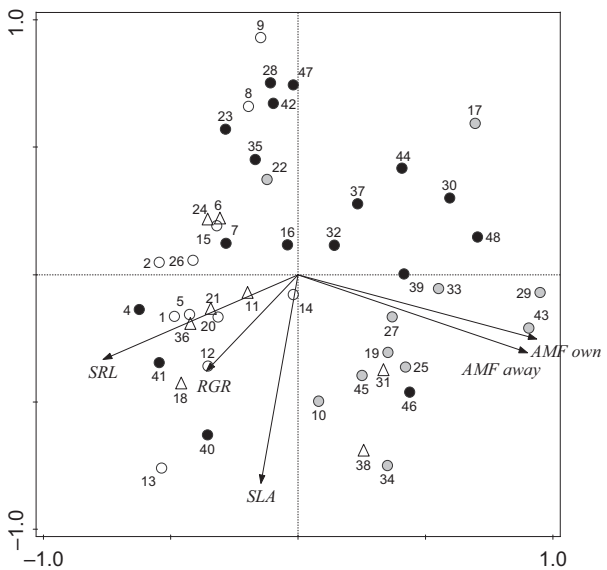

Fig. 1. Principal component analysis of the plant traits specific root length (SRL), specific leaf area (SLA), relative growth rate (RGR), per cent arbuscular mycorrhizal fungi (AMF) colonization in own soil (AMF own) and away soil (AMF away) of the different plant species. Symbol legend: circles white = graminoids, grey = legumes, black = tall herbs, triangles = small herbs. The number indicates the species as listed in Table S1.

PLANT TRAITS AND PLANT FGS PREDICTING PSF

The plant FGs differed significantly in PSF response; however, the magnitude and direction of the PSF effects in the different plant FGs depended significantly on the type of PSF, being PSFsterilized or PSFaway (interaction PSFtype × FG: $F_{3,81} = 5.71$, $P = 0.001$; Table S4). The graminoids showed strong negative PSFsterilized and also small herbs showed a negative PSFsterilized albeit less negative than in the graminoids. Legumes, on the other hand, had a neutral and tall herbs had positive PSFsterilized. In contrast, PSFaway values were similarly negative for all plant FGs (Fig. 3a). Plant traits significantly contributed to explain the variation in PSF values after accounting for differences in PSF between plant FGs (R^2 adjusted = 0.24 without plant traits as covariable; R^2 adjusted = 0.32 with plant traits as covariables). Overall, SRL strongly contributed to explaining the PSF values ($F_{1,81} = 12.77$, $P = 0.001$), whereas PSF was not explained by SLA or RGR (Table S3). The relation between SRL and PSF was significantly negative (Fig. 3b), also when excluding the two PSF data points with highest SRL (being PSFsterilized and PSFaway of *Cardamine pratensis*).

Across the plant species in which %AMF colonization was examined, we found that indeed, the differences of PSF values among plant FGs depended on the type of PSF (interaction PSFtype x FG: $F_{3,42} = 3.435$, $P = 0.025$; Table S5; Fig. S3) in the same way as in the complete data set and that plant traits significantly explained differences in PSF values (R^2 adjusted = 0.29 without plant traits as covariable; R^2 adjusted = 0.45 with plant traits as covariables). However, the only trait significantly contributing to predicting PSF was % AMF colonization in own soil ($F_{1,42} = 6.538$, $P = 0.014$) whereas the other plant traits (SRL, SLA, RGR) did not (Table S5). The relation between %AMF colonization in own soil and PSF was significantly positive (Fig. 3c). Similar results could be obtained using %AMF colonization in away soil, as this value was strongly correlated with %AMF in own soil (Fig. S1). The SEM results showed that PSFaway could not be explained by SRL directly or indirectly via %AMF colonization in away soil (Fig. 4a). In contrast, PSFsterilized was significantly explained by %AMF colonization in away soil, whereas SRL only related significantly to %AMF colonization but not to PSFsterilized (Fig. 4b). Using AIC criteria to reveal the most parsimonious model, we found that PSFsterilized was best explained by %AMF colonization in

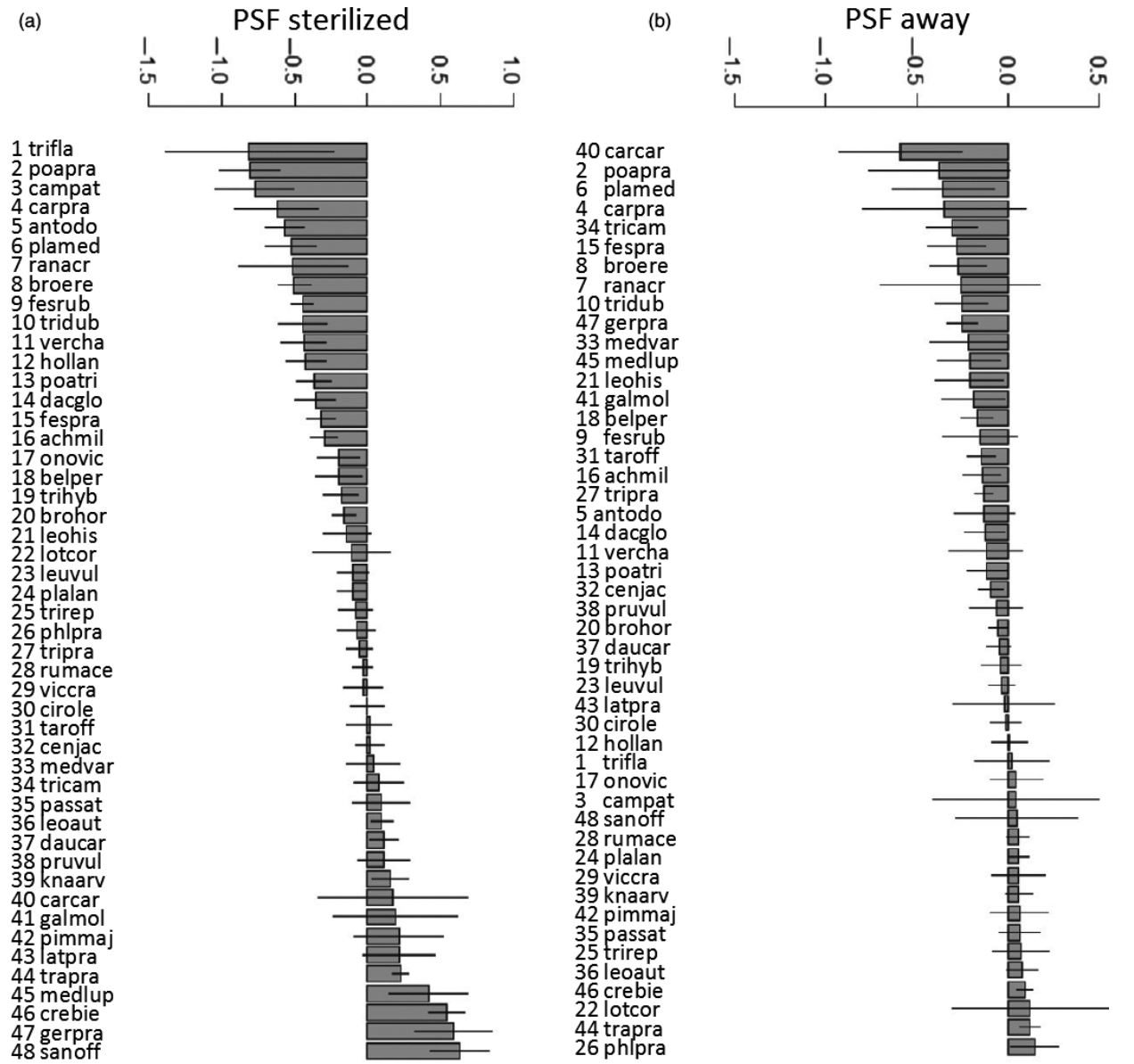

Fig. 2. (a) Plant–soil feedback (PSF)sterilized and (b) PSFaway of the 48 study species. PSFsterilized = log(biomass in own soil) – log(biomass in sterilized soil); PSFaway = log(biomass in own soil) – log(biomass in away soil). Bars are means ± 1 SE, n = 8, label numbers (1–48) indicate the species ranking according to their PSFsterilized, from most negative to most positive (for species full names see Table S1). Overall effects across species are (a) neutral relative to sterilized soil and (b) negative across species in away soil.

away soil (Fig. 4c; AIC = 136; R^2 = 0.36). Performing these SEM analyses using %AMF colonization in own soil instead of %AMF colonization in away soil revealed that both are linked to PSF very much in the same way (results not shown).

Discussion

In support of our first hypothesis, we found that on average, graminoid species responded negatively to feedback from their own soil biota (negative PSFsterilized), and the feedback from their own soil biota was more negative relative to that from away soil biota (negative PSFaway). However, in contrast to our first hypothesis, tall herb species responded on average positively to their own soil biota (positive PSFsterilized) yet less positively to their own soil biota than to away soil biota (negative PSFaway). Legume species responded on average neutral to their own soil biota (non-significant PSFsterilized) and grew less well in own relative to away soil biota (negative PSFaway), which is not in support of our second hypothesis. This result would not be predicted based on well-established strong positive responses of legumes to rhizobia and AMF (e.g. van der Heijden *et al.* 2016). However, many studies on effects of such mutualistic symbionts on legumes have not included plant growth-suppressing soil biota, which were included in our PSF approach. Moreover, the soil we used in our experiment originated from a more fertile grassland system (Oelmann *et al.* 2011), which likely

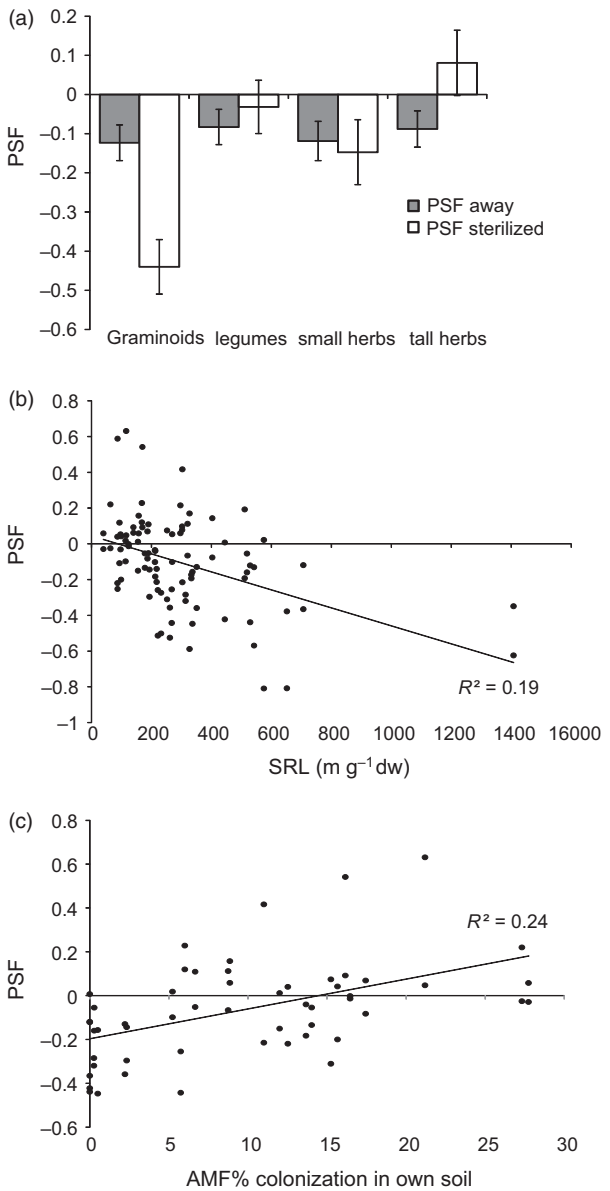

Fig. 3. Plant–soil feedback (PSF) values in relation to (a) PSF type (PSFsterilized or PSFaway) and plant functional group (graminoids, legumes, small herbs, tall herbs), to (b) specific root length (SRL) and to (c) %AMF colonization in own soil. Bars are means ± 1 SE, n = 11 for graminoids and legumes, n = 8 for small herbs, n = 17 for tall herbs; correlation with SRL is based on the average SRL per species across 47 species (the species missing compared to Fig. 2 is *Campanula patula*). Correlation with %AMF is based on the average %AMF colonization per species across the 27 species for which % AMF was quantified. PSF in panel (b) and (c) comprises both PSF types.

results in lower dependency on rhizobia and AMF compared to plants grown in less fertile dune grassland soil (van der Heijden *et al.* 2016). Overall, our results are in line with the results from the same field site (Petermann *et al.* 2008), showing that plant species in the different plant FGs all benefitted from growing in away soil relative to their own soil. For the plants with predominantly negative PSFsterilized, this benefit is likely due to low levels of specialized pathogens or micro-herbivores in the away soil. It has to be noted that despite the fact that the average PSFaway across species per plant FG was negative, some plant species did show a positive PSFaway.

In graminoids, we found stronger negative PSF effects from the species' own soil biota (PSFsterilized) than in the other plant FGs, which supports results of a meta-analysis (Kulmatiski *et al.* 2008). In contrast to the graminoids, tall herbs perceived on average a net benefit of all the species' own soil biota, as indicated by positive PSFsterilized. These results are not in line with Kulmatiski *et al.* (2008) who found negative PSF for all forbs. Our findings differ partly from those of Kulmatiski *et al.* (2008) most likely because we discriminated between the different types of PSF (PSFsterilized and PSFaway) as well as between different groups of forbs (legumes, small herbs, tall herbs). Strikingly, in our experiment, the benefit from the soil biota for tall herbs was equal or was smaller in own as compared to away soil, as indicated by the neutral to negative PSFaway. This result supports the view that beneficial soil biota may be less species specific than pathogenic soil biota and that plant species may benefit more from mutualists from competing plant species than their own (Bever 2002). Indeed, levels of %AMF colonization in own and away soil were strongly positively correlated with a tendency of more colonization in away than in own soil. However, we did not analyse the AMF species composition, or their effectiveness, which may lead to differential benefits even at similar levels of colonization (Klironomos 2003).

We found that plant traits (quantified on independent plants apart from %AMF) significantly contributed to explaining PSF effects, even when accounting for different plant functional groups. The larger the specific root length (SRL), the more negative PSF, whereas PSF related positively to the %AMF colonization. Contrary to our predictions, we did not find significant correlations between PSF and relative growth rate (RGR), or specific leaf area (SLA), as also supported by the ordination analysis. We expected to find negative correlations if there would be a trade-off between plant resource capture through investment in resource acquisition traits and vulnerability to natural enemies, which would have pointed at coordinated responses to natural enemies of both above-ground and below-ground plant organs (e.g. Mooney 1972; Herms & Mattson 1992; van der Putten 2003; Rasmann *et al.* 2011). A recent study by Koziol & Bever (2015) showed that plant growth rate was negatively correlated with the level of colonization by AMF and with plant growth response to AMF across grassland species from different successional stages, in line with the expectations. In our study, however, above-ground traits (i.e. SLA) and whole-organism traits (i.e. RGR) did not significantly correlate with PSF values. The absence of these relations may be due to the fact that our pool of plant species was restricted to grassland species from mesotrophic grasslands, whereas these relations may only become apparent when including a species pool covering a wider range of plant communities and plant trait values (Díaz *et al.* 2016). In our study, we nevertheless found significant correlations between PSF and the root-related traits SRL and

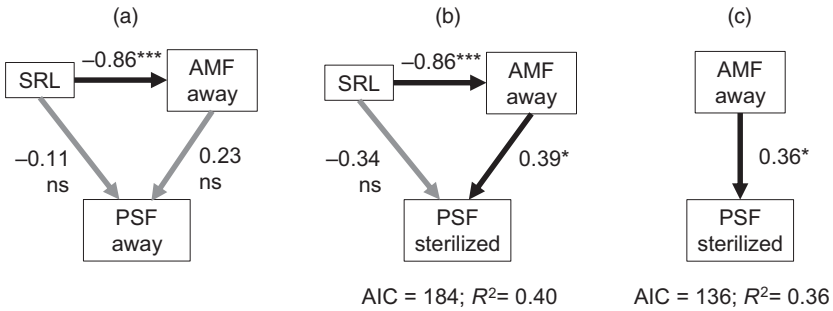

Fig. 4. Structural equation models of direct and indirect interactions between specific root length and %AMF colonization in away soil and (a) Plant–soil feedback (PSF) away and (b) PSFsterilized; and (c) the most parsimonious model (according to AIC) explaining PSFsterilized: simple regression with %AMF colonization in away soil. Grey arrows indicate non-significant relations (ns), and black arrows indicate significant relations with $*P < 0.05$, $***P < 0.001$.

%AMF colonization. These results are well in line with recent work on predictive capacity of above-ground and below-ground plant traits for microbial composition and microbial processes, where root traits showed significant effects, but not shoot traits (Legay *et al.* 2014). Here we show that root traits are also relevant to plant–soil feedback effects.

Previous studies have shown that mycorrhizal benefits to plants are generally higher when SRL is lower (Smith & Read 2010). Our findings that %AMF colonization is positively related to PSF and negatively related to SRL is in line with the idea that AMF may underlie the positive PSF effects and that these occur in species with low SRL. A recent meta-analysis (Maherali 2014), however, challenged this common idea of more benefit of AMF for species with low SRL by showing that there is no consistent correlation between different measures of root coarseness and plant growth response to AMF. The discrepancy may be due to differences in the pool of AMF used in the studies, because it can be expected that the AMF species and plant species were not matched optimally when using non-native inoculum (Maherali 2014). Therefore, we suggest that associations between a plant species and a limited, pre-selected pool of AMF species, as in studies with commercial inoculum, can yield biased results regarding AMF responsiveness of plants in natural systems. In our study, we determined AMF colonization of plants growing in soil that contained a naturally diverse species pool of soil biota, including AMF, collected from the Jena Experiment field site, which is expected to comprise a more diverse pool of AMF as compared to commercial inoculum that usually contains relatively few species (König *et al.* 2010). Testing plant responses in these soils, as we did, might be more indicative for the actual benefits of the plant-AMF symbiosis, because all plants were exposed to their natural AMF assemblages while also interacting with other soil biota (Graham, Eissenstat & Drouillard 1991; Hoeksema *et al.* 2010; Cortois & De Deyn 2012).

The strength of PSFs in our study might have been larger if roots from the conditioning phase had also been included in the soil inoculum, as the roots can serve as a source of mutualists and pathogens. We did not include roots as they also represent a pool of nutrients which, especially for the species with low tissue C:N ratio, could become mineralized during our experiment and thereby interact with the effect of the soil biota (De Deyn, Raaijmakers & van der Putten 2004). As recently proposed by the modelling study of Ke, Miki & Ding (2015), the relation between plant traits and PSF may depend on the presence of pathogens. These authors found that traits of litter decomposability play only a minor role in predicting PSF when plant pathogens are also present. In our experiment, PSFs were mostly negative, pointing at a dominant role of plant pathogens. In that case, the inclusion of litter only would have played a minor role in PSF according to Ke, Miki & Ding (2015).

We acknowledge that we have examined a limited number of plant traits in relation to PSF and that the time span of our experiment was limited. Therefore, we propose that several other functional plant traits are worth exploring further, including chemical and physical plant traits, such as litter C:N ratios of shoot and root and tissue density, as well as that soil biota and litter feedbacks need to be further integrated with their respective temporal dimensions (Kardol *et al.* 2013; Ke, Miki & Ding 2015). It may well be that testing PSF effects over longer time spans will also reveal other plant traits to be important besides SRL and % AMF colonization, such as RGR with faster growing species potentially building up more negative PSF in case pathogen effects dominate. Alternatively, species with high RGR may on a longer term generate positive PSF through nutrient rich litter (Orwin *et al.* 2010; Zhang, van der Putten & Veen 2016) provided pathogen densities remain low (Ke, Miki & Ding 2015). Including structural equation modelling to test direct and indirect impacts of multiple plant traits on PSF will be an asset, yet will require even larger scale PSF tests than in our study. Nevertheless, our data set allowed us to test small SEM models which revealed that SRL did not directly affect PSF but acted rather indirectly on PSF via %AMF colonization. Furthermore, the use of plant traits to predict PSF effects may be applied to the plant intraspecific level as well, as considerable intraspecific variation exists for both plant trait values and PSF effects (Schweitzer *et al.* 2014). This approach would require independent trials of soil conditioning and plant biomass responses, along with the determination of plant traits in the different trials.

In conclusion, our results show that explorative plant species (high SRL, low %AMF colonization) suffer most from negative feedback of all soil biota, whereas more resource conservative species (low SRL, high %AMF colonization) benefit from feedback of all soil biota. This coupling of plant traits to PSF across a wide range of grassland species is a step forward towards making PSF effects more predictable and more connected to plant ecological strategy theory (e.g. Grime 1977) and plant successional dynamics. Moreover, we found that plant species from all plant FGs show enhanced growth in soil from other species because of less net negative effects of soil biota (in graminoids) or because of more net positive soil biota effects (in tall herbs). Altogether, these findings are of direct relevance to biodiversity–ecosystem functioning relations beyond pathogen dilution alone (Maron *et al.* 2011; Schnitzer *et al.* 2011) as they demonstrate that there is potentially a larger role for species with positive feedback than for species with negative feedback to contribute to plant community productivity over time.

Acknowledgements

We are grateful to Amalia Castro and Nasir Uddin for practical assistance. This work was supported by the Deutsche Forschungsgemeinschaft (FOR 1451) and by NWO-ALW VIDI through financial support to G.B.D.D. (grant nr 864.11.003), and NWO additional fund (grant nr 832.13.009) to W.H.v.d.P. NIOO Publication Number 6135.

Data accessibility

Data of SLA and SRL are deposited and accessible at the TRY data base https://www.try-db.org/TryWeb/Home.php (Kattge *et al.* 2011); data of PSF values, RGR and %AMF colonization are deposited in the Jena Biodiversity Experiment data repository http://www.the-jena-experiment.de/Data.html.

References

Bardgett, R.D., Mommer, L. & de Vries, F.T. (2014) Going underground: root traits as drivers of ecosystem processes. *Trends in Ecology & Evolution*, **29**, 692–699.

Bauerle, T., Eissenstat, D., Granett, J., Gardner, D. & Smart, D. (2007) Consequences of insect herbivory on grape fine root systems with different growth rates. *Plant, Cell & Environment*, **30**, 786–795.

Baxendale, C., Orwin, K.H., Poly, F., Pommier, T. & Bardgett, R.D. (2014) Are plant–soil feedback responses explained by plant traits? *New Phytologist*, **204**, 408–423.

Bever, J.D. (2002) Negative feedback within a mutualism: host-specific growth of mycorrhizal fungi reduces plant benefit. *Proceedings of the Royal Society B-Biological Sciences*, **269**, 2595–2601.

Bever, J.D., Westover, K.M. & Antonovics, J. (1997) Incorporating the soil community into plant population dynamics: the utility of the feedback approach. *Journal of Ecology*, **85**, 561–573.

Bever, J.D., Dickie, I.A., Facelli, E., Facelli, J.M., Klironomos, J., Moora, M., Rillig, M.C., Stock, W.D., Tibbett, M. & Zobel, M. (2010) Rooting theories of plant community ecology in microbial interactions. *Trends in Ecology & Evolution*, **25**, 468–478.

Blumenthal, D., Mitchell, C.E., Pyšek, P. & Jarošík, V. (2009) Synergy between pathogen release and resource availability in plant invasion. *Proceedings of the National Academy of Sciences of the United States of America*, **106**, 7899–7904.

Brinkman, P., van der Putten, W.H., Bakker, E.J. & Verhoeven, K.J. (2010) Plant–soil feedback: experimental approaches, statistical analyses and ecological interpretations. *Journal of Ecology*, **98**, 1063–1073.

Brundrett, M., Bougher, N., Dell, B., Grove, T. & Malajczuk, N. (1996) *Working With Mycorrhizas in Forestry and Agriculture*. Australian Centre for International Agricultural Research, Canberra, Australia.

Coley, P. (1988) Effects of plant growth rate and leaf lifetime on the amount and type of anti-herbivore defense. *Oecologia*, **74**, 531–536.

Cornelissen, J., Lavorel, S., Garnier, E., Díaz, S., Buchmann, N., Gurvich, D., Reich, P., Ter Steege, H., Morgan, H. & van der Heijden, M. (2003) A handbook of protocols for standardised and easy measurement of plant functional traits worldwide. *Australian Journal of Botany*, **51**, 335–380.

Cortois, R. & De Deyn, G.B. (2012) The curse of the black box. *Plant and Soil*, **350**, 27–33.

Craine, J.M. (2009) *Resource Strategies of Wild Plants*. Princeton University Press, Princeton, NJ, USA.

De Deyn, G.B., Cornelissen, J.H. & Bardgett, R.D. (2008) Plant functional traits and soil carbon sequestration in contrasting biomes. *Ecology Letters*, **11**, 516–531.

De Deyn, G.B., Raaijmakers, C.E. & van der Putten, W.H. (2004) Plant community development is affected by nutrients and soil biota. *Journal of Ecology*, **92**, 824–834.

Díaz, S., Kattge, J., Cornelissen, J.H.C., Wright, I.J., Lavorel, S., Dray, S. *et al.* (2016) The global spectrum of plant form and function. *Nature*, **529**, 167–171.

Fine, P.V., Miller, Z.J., Mesones, I., Irazuzta, S., Appel, H.M., Stevens, M.H.H., Sääksjärvi, I., Schultz, J.C. & Coley, P.D. (2006) The growth-defense trade-off and habitat specialization by plants in Amazonian forests. *Ecology*, **87**, S150–S162.

Graham, J., Eissenstat, D. & Drouillard, D. (1991) On the relationship between a plant's mycorrhizal dependency and rate of vesicular-arbuscular mycorrhizal colonization. *Functional Ecology*, **5**, 773–779.

Grime, J. (1977) Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. *The American Naturalist*, **111**, 1169–1194.

Grime, J., Thompson, K., Hunt, R., Hodgson, J., Cornelissen, J., Rorison, I., Hendry, G., Ashenden, T., Askew, A. & Band, S. (1997) Integrated screening validates primary axes of specialisation in plants. *Oikos*, **79**, 259–281.

van der Heijden, M.G.A., de Bruin, S., Luckerhoff, L., van Logtestijn, R.S.P. & Schlaeppi, K. (2016) A widespread plant-fungal-bacterial symbiosis promotes plant biodiversity, plant nutrition and seedling recruitment. *ISME Journal*, **10**, 389–399.

Heinze, J., Bergmann, J., Rillig, M.C. & Joshi, J. (2015) Negative biotic soil-effects enhance biodiversity by restricting potentially dominant plant species in grasslands. *Perspectives in Plant Ecology, Evolution and Systematics*, **17**, 227–235.

Hendry, G.A. & Grime, J.P. (1993) *Methods in Comparative Plant Ecology: A Laboratory Manual*. Chapman and Hall, London, UK.

Herms, D.A. & Mattson, W.J. (1992) The dilemma of plants: to grow or defend. *The Quarterly Review of Biology*, **67**, 283–335.

Hoeksema, J.D., Chaudhary, V.B., Gehring, C.A., Johnson, N.C., Karst, J., Koide, R.T., Pringle, A., Zabinski, C., Bever, J.D. & Moore, J.C. (2010) A meta-analysis of context-dependency in plant response to inoculation with mycorrhizal fungi. *Ecology Letters*, **13**, 394–407.

Hudson, H.J. (1991) *Fungal Biology*. CUP Archive, Cambridge, UK.

Johnson, N., Graham, J.H. & Smith, F. (1997) Functioning of mycorrhizal associations along the mutualism–parasitism continuum. *New Phytologist*, **135**, 575–585.

Kardol, P., Bezemer, T. & van der Putten, W.H. (2006) Temporal variation in plant–soil feedback controls succession. *Ecology Letters*, **9**, 1080–1088.

Kardol, P., De Deyn, G.B., Hawkes, C., Laliberté, E. & Mariotte, P. (2013) A hierarchical framework for investigating plant-soil feedbacks in time and space. *Journal of Ecology*, **101**, 309–315.

Kattge, J., Diaz, S., Lavorel, S., Prentice, I.C., Leadley, P., Bönisch, G. *et al.* (2011) TRY – a global database of plant traits. *Global Change Biology*, **17**, 2905–2935.

Ke, P.J., Miki, T. & Ding, T.S. (2015) The soil microbial community predicts the importance of plant traits in plant–soil feedback. *New Phytologist*, **206**, 329–341.

Klironomos, J.N. (2003) Variation in plant response to native and exotic arbuscular mycorrhizal fungi. *Ecology*, **84**, 2292–2301.

König, S., Wubet, T., Dormann, C.F., Hempel, S., Renker, C. & Buscot, F. (2010) TaqMan Real-Time PCR Assays To assess arbuscular mycorrhizal responses to field manipulation of grassland biodiversity: effects of soil characteristics, plant species richness, and functional traits. *Applied and Environmental Microbiology*, **76**, 3765–3775.

Koziol, L. & Bever, J.D. (2015) Mycorrhizal response trades off with plant growth rate. *Ecology*, **96**, 1768–1774.

Kulmatiski, A., Beard, K.H., Stevens, J.R. & Cobbold, S.M. (2008) Plant–soil feedbacks: a meta-analytical review. *Ecology Letters*, **11**, 980–992.

Lavorel, S. & Garnier, E. (2002) Predicting changes in community composition and ecosystem functioning from plant traits: revisiting the Holy Grail. *Functional Ecology*, **16**, 545–556.
Lavorel, S. & Grigulis, K. (2012) How fundamental plant functional trait relationships scale-up to trade-offs and synergies in ecosystem services. *Journal of Ecology*, **100**, 128–140.
Legay, N., Baxendale, C., Grigulis, K., Krainer, U., Kastl, E., Schloter, M., Bardgett, R., Arnoldi, C., Bahn, M. & Dumont, M. (2014) Contribution of above-and below-ground plant traits to the structure and function of grassland soil microbial communities. *Annals of Botany*, **114**, 1011–1021.
Maherali, H. (2014) Is there an association between root architecture and mycorrhizal growth response? *New Phytologist*, **204**, 192–200.
Maron, J.L., Marler, M., Klironomos, J.N. & Cleveland, C.C. (2011) Soil fungal pathogens and the relationship between plant diversity and productivity. *Ecology Letters*, **14**, 36–41.
McGonigle, T., Miller, M., Evans, D., Fairchild, G. & Swan, J. (1990) A new method which gives an objective measure of colonization of roots by vesicular-arbuscular mycorrhizal fungi. *New Phytologist*, **115**, 495–501.
Meisner, A., Hol, W.G., de Boer, W., Krumins, J.A., Wardle, D.A. & van der Putten, W.H. (2014) Plant–soil feedbacks of exotic plant species across life forms: a meta-analysis. *Biological Invasions*, **16**, 2551–2561.
Mooney, H. (1972) The carbon balance of plants. *Annual Review of Ecology and Systematics*, **3**, 315–346.
Newsham, K., Fitter, A. & Watkinson, A. (1995) Arbuscular mycorrhiza protect an annual grass from root pathogenic fungi in the field. *Journal of Ecology*, **93**, 991–1000.
Oelmann, Y., Buchmann, N., Gleixner, G., Habekost, M., Roscher, C., Rosenkranz, S., Schulze, E.-D., Steinbeiss, S., Temperton, V.M., Weigelt, A., Weisser, W.W. & Wilcke, W. (2011) Plant diversity effects on aboveground and belowground N pools in temperate grassland ecosystems: development in the first 5 years after establishment. *Global Biogeochemical Cycles*, **25**, GB2014, 1–11.
Olsen, S., Cole, C., Watanabe, F. & Dean, L. (1954) *Estimation of Available Phosphorus in Soils by Extraction with Sodium Bicarbonate*. USDA Circular Nr 939. US Gov. Print. Office, Washington, DC, USA.
Orwin, K.H., Buckland, S.M., Johnson, D., Turner, B.L., Smart, S., Oakley, S. & Bardgett, R.D. (2010) Linkages of plant traits to soil properties and the functioning of temperate grassland. *Journal of Ecology*, **98**, 1074–1083.
Petermann, J.S., Fergus, A.J.F., Turnbull, L.A. & Schmid, B. (2008) Janzen-Connell effects are widespread and strong enough to maintain diversity in grasslands. *Ecology*, **89**, 2399–2406.
van der Putten, W.H. (2003) Plant defense belowground and spatiotemporal processes in natural vegetation. *Ecology*, **84**, 2269–2280.
van der Putten, W.H., Bardgett, R.D., Bever, J.D., Bezemer, T.M., Casper, B.B., Fukami, T. *et al.* (2013) Plant-soil feedbacks: the past, the present and future challenges. *Journal of Ecology*, **101**, 265–276.
R Core Team (2013) *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria.
Rasmann, S., Bauerle, T.L., Poveda, K. & Vannette, R. (2011) Predicting root defence against herbivores during succession. *Functional Ecology*, **25**, 368–379.
Reich, P.B. (2014) The world-wide 'fast–slow' plant economics spectrum: a traits manifesto. *Journal of Ecology*, **102**, 275–301.
Roscher, C., Schumacher, J., Baade, J., Wilcke, W., Gleixner, G., Weisser, W.W., Schmid, B. & Schulze, E.-D. (2004) The role of biodiversity for element cycling and trophic interactions: an experimental approach in a grassland community. *Basic and Applied Ecology*, **5**, 107–121.
Schnitzer, S.A., Klironomos, J.N., HilleRisLambers, J., Kinkel, L.L., Reich, P.B., Xiao, K., Rillig, M.C., Sikes, B.A., Callaway, R.M., Mangan, S.A., van Nes, E.H. & Scheffer, M. (2011) Soil microbes drive the classic plant diversity-productivity pattern. *Ecology*, **92**, 296–303.
Schroeder-Georgi, T., Wirth, C., Nadrowski, K., Meyer, S.T., Mommer, L. & Weigelt, A. (2016) From pots to plots: hierarchical trait-based prediction of plant performance in a mesic grassland. *Journal of Ecology*, **104**, 206–218.
Schweitzer, J.A., Juric, I., van de Voorde, T.F.J., Clay, K., van der Putten, W.H. & Bailey, J.K. (2014) Are there evolutionary consequences of plant-soil feedbacks along soil gradients? *Functional Ecology*, **28**, 55–64.
Smith, S.E. & Read, D.J. (2010) *Mycorrhizal Symbiosis*. Academic Press, London, UK.
Tilman, D. (1988) *Plant Strategies and the Dynamics and Structure of Plant Communities*. Princeton University Press, New York, NY, USA.
Tjoelker, M.G., Craine, J.M., Wedin, D., Reich, P.B. & Tilman, D. (2005) Linking leaf and root trait syndromes among 39 grassland and savannah species. *New Phytologist*, **167**, 493–508.
Troelstra, S., Wagenaar, R., Smant, W. & Peters, B. (2001) Interpretation of bioassays in the study of interactions between soil organisms and plants: involvement of nutrient factors. *New Phytologist*, **150**, 697–706.
Violle, C., Navas, M.L., Vile, D., Kazakou, E., Fortunel, C., Hummel, I. & Garnier, E. (2007) Let the concept of trait be functional! *Oikos*, **116**, 882–892.
Wagg, C., Boller, B., Schneider, S., Widmer, F. & van der Heijden, M.G.A. (2015) Intraspecific and intergenerational differences in plant-soil feedbacks. *Oikos*, **124**, 994–1004.
Wardle, D.A., Bardgett, R.D., Klironomos, J.N., Setälä, H., van der Putten, W.H. & Wall, D.H. (2004) Ecological linkages between aboveground and belowground biota. *Science*, **304**, 1629–1633.
Westoby, M., Falster, D.S., Moles, A.T., Vesk, P.A. & Wright, I.J. (2002) Plant ecological strategies: some leading dimensions of variation between species. *Annual Review of Ecology and Systematics*, **33**, 125–159.
Yang, H., Zhang, Q., Dai, Y., Liu, Q., Tang, J., Bian, X. & Chen, X. (2015) Effects of arbuscular mycorrhizal fungi on plant growth depend on root system: a meta-analysis. *Plant and Soil*, **389**, 361–374.
Zhang, N., van der Putten, W.H. & Veen, G.F. (2016) Effects of root decomposition on plant–soil feedback of early- and mid-successional plant species. *New Phytologist*, doi:10.1111/nph.14007.

Received 8 February 2016; accepted 12 July 2016
Handling Editor: Marcel van der Heijden

Supporting Information

Additional Supporting Information may be found in the online version of this article:

Figure S1. Relation between %AMF colonization of plants grown in own soil and in away soil, $n = 27$.

Figure S2. Average plant biomass across all species in response to own, away and sterilized soil inoculum. Bars are means ± 1 SE, $n = 375$. Different letters indicate treatments are significantly different ($P < 0.05$).

Figure S3. PSF values across the species in which AMF colonization was determined in relation to PSF type (PSFsterilized or PSFaway) and plant functional group (graminoids, legumes, small herbs, tall herbs).

Table S1. Plant species names: abbreviations, full Latin name and plant functional group FG: Gr = graminoid, Sh = small herb, Th = Tall herb, Lg = legume. Rank number indicates the species ranking according to their PSFsterilized, from most negative to most positive as shown in Figure 2. In bold the species in which %AMF colonization in roots grown in own and away soil was quantified.

Table S2. Loadings of the factors on the first two principal component axes.

Table S3. Average plant biomass (g dw ± 1 SE) per plant species grown in own soil (Own), soil of all species (Away) and in sterilized soil (Sterilized).

Table S4. General linear model testing effects of PSF type, plant functional group (FG), their interaction and the plant traits SLA, RGR, SRL on PSF values.

Table S5. General linear model effects of PSF type, plant FG, their interaction and of plant traits SRL, SLA, RGR, %AMF colonization in own soil (AMF own) on PSF values.