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Effects of plant–soil feedback on tree seedling growth under arid conditions

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Abstract

Aims

Plants are able to influence their growing environment by changing biotic and abiotic soil conditions. These soil conditions in turn can influence plant growth conditions, which is called plant–soil feedback. Plant–soil feedback is known to be operative in a wide variety of ecosystems ranging from temperate grasslands to tropical rain forests. However, little is known about how it operates in arid environments. We examined the role of plant–soil feedbacks on tree seedling growth in relation to water availability as occurring in arid ecosystems along the west coast of South America.

Methods

In a two-phased greenhouse experiment, we compared plant–soil feedback effects under three water levels (no water, 10% gravimetric moisture and 15% gravimetric moisture). We used sterilized soil inoculated with soil collected from northwest Peru (*Prosopis pallida* forests) and from two sites in north-central Chile (*Prosopis chilensis* forest and scrublands without *P. chilensis*).

Important Findings

Plant–soil feedbacks differed between plant species and soil origins, but water availability did not influence the feedback effects. Plant–soil feedbacks differed in direction and strength in the three soil origins studied. Plant–soil feedbacks of plants grown in Peruvian forest soil were negative for leaf biomass and positive for root length. In contrast, feedbacks were neutral for plants growing in Chilean scrubland soil and positive for leaf biomass for those growing in Chilean forest soil. Our results show that under arid conditions, effects of plant–soil feedback depend upon context. Moreover, the results suggest that plant–soil feedback can influence trade-offs between root growth and leaf biomass investment and as such that feedback interactions between plants and soil biota can make plants either more tolerant or vulnerable to droughts. Based on dissecting plant–soil feedbacks into aboveground and belowground tissue responses, we conclude that plant–soil feedback can enhance plant colonization in some arid ecosystems by promoting root growth.

Keywords: biomass allocation • dry forest • facilitation • *Prosopis* • South America • water pulse

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INTRODUCTION

Drylands cover ~41% of the earth's surface (Millennium Ecosystem Assessment 2005). In these arid and semiarid ecosystems, water availability is not only low but it is also highly variable in time and space (Schwinning and Sala 2004). Rainfall events create water pulses that affect plant recruitment and performance (Chesson *et al.* 2004; Holmgren *et al.* 2001; Holmgren, Stapp, *et al.* 2006). How plants use these water pulses depends on several factors, including inherent plant adaptations to water use efficiency and drought (Lambers *et al.* 1998), as well as interacting environmental conditions affecting plant growth rate (Holmgren, López, *et al.* 2006). Biotic interactions such as plant competition (Chesson *et al.*

2004; Gebauer *et al.* 2002), facilitation (Jankju-Borzelabad and Griffiths 2006) and herbivory (Holmgren, López, *et al.* 2006; Holmgren, Stapp, *et al.* 2006; Scheffer *et al.* 2008) affect plant responses to rainfall.

Soil organisms can also affect plant responses to water availability. For example, water uptake and transport by plants can be reduced by soil pathogens and enhanced by vesicular-arbuscular mycorrhizal fungi (Augé 2001). Plants and soil organisms are in constant interaction, also called plant–soil feedback (Bever 2003; Bever *et al.* 1997; Van der Putten 2003). In this process, a plant, or a population of plants, modifies the composition of the soil community. This change in the soil community affects in turn the growth and survival of individual plants. The feedback between plants and soil organisms can be positive, neutral or negative. In the case of positive plant–soil feedback, a plant increases the abundance of a microbial community that increases the growth of that plant (Bever *et al.* 1997). In the case of negative feedback, on the other hand, soil organisms hamper the performance of the plant species involved, which causes the relative rate of plant population growth to decrease over time (Bever *et al.* 1997). The feedback between plants and soil organisms is a major driver of plant community assembly and functioning. For example, plant–soil feedback plays an important role in plant succession (Kardol *et al.* 2006; Van der Putten *et al.* 1993), the invasion of exotic plant species (Callaway *et al.* 2004; Kulmatiski *et al.* 2006; Mangla *et al.* 2008; Reinhart *et al.* 2003; Van der Putten *et al.* 2007) and plant community assemblage and ecosystem development (Bever 2003; Bezemer *et al.* 2006; Casper and Castelli 2007; Reynolds *et al.* 2003; Scheublin *et al.* 2007). Although poorly explored, plant–soil feedbacks seem to play an important role in arid ecosystems (Van der Putten *et al.* 2007) and may become severe when plants are growing under water stress (Brady 1990; Huxman *et al.* 2004; Van der Putten and Peters 1997).

The response of arid plant communities to rainfall can be intriguingly different. For instance, tree and shrub recruitment can be highly correlated with rainfall pulses in some systems but not correlated with rainfall in other systems (Holmgren, López, *et al.* 2006). Regional differences between ecosystems have been explained mostly in terms of intrinsic differences between plant species (Chesson *et al.* 2004) or the interplay between climate patterns, plant growth rates and the effect of herbivores (Holmgren, López, *et al.* 2006; Scheffer *et al.* 2008). In this paper, we assess how plant–soil feedbacks may influence the growth of seedlings of two tree species occurring in two South American arid ecosystems. The tree species are known to respond distinctively to rainfall availability: tree recruitment during rainfall pulses is highly successful in northwest Peru compared to central Chile, which has been explained by the combined effect of faster plant growth rates and lower grazing pressure in Peru (Holmgren, López, *et al.* 2006). These differences in plant growth rate have been attributed to higher temperatures during rainy pulses since common garden experiments demonstrated no interspecific differences in plant growth rate (Squeo *et al.* 2007). Here, we test the hypothesis that plant–soil feedback interactions affect tree seedling growth in arid conditions. In particular, we predict that seedling growth would increase in sterilized soils as potential soil pathogens would have been removed allowing a larger positive effect of water pulses on seedling growth. To test this hypothesis, we performed a greenhouse experiment to examine the role of plant–soil feedbacks on tree seedling growth and the way it is modified by soil origin and water availability.

MATERIALS AND METHODS

Study sites

The study site in Peru was located within the University of Piura campus (5°10′S, 80°37′W) situated in Piura, northwest Peru. Soils are sandy, alkaline (pH = 8.4) and poor in organic matter (0.12%) (Squeo *et al.* 2007). The site is covered by a *Prosopis pallida* forest with few *Acacia* tree species and other shrubs. *Prosopis pallida* (Fabaceae) is a native tree species, able to grow under very arid conditions with at least 50–250 mm rainfall annually (Pasiecznik *et al.* 2001). It can grow in nutrient-poor soils where its roots fix nitrogen in association with rhizobial bacteria (Pasiecznik *et al.* 2001). It is a fast-growing tree with roots able to reach deep water sources ~25 m below the surface (Pasiecznik *et al.* 2001). In northern Peru, most of the rain falls in the summer months between December and May. Mean annual precipitation is ~50 mm (1961–83) (Bernex de Falen and Reves 1988), with high interannual variation (e.g. ranging from 2.8 mm in 1996 to 1 639 mm in 1998). Mean annual temperature is 24°C, the warmest month is February and the coolest month is August (Bernex de Falen and Reves 1988).

The study site in Chile was located in Fray Jorge in north-central Chile, 85 km south of La Serena (30°41′S, 71°37′W). The site is situated in a private farm that is currently being used for livestock grazing, next to the Fray Jorge National Park. The soil profile is characterized by an organic top layer under which loamy soil material is found (Squeo *et al.* 2007). The soil is rich in calcium carbonate, has a neutral pH (6.8) and relatively high concentrations of organic matter (3.12%) (Squeo *et al.* 2007). The vegetation is dominated by xerophytic shrubs. *Prosopis chilensis* trees do not currently occupy this site but adjacent to the private farm are small remnant populations. *Prosopis chilensis* is native to Chile and considered to have a regionally vulnerable conservation status (Squeo *et al.* 2001). It is also a nitrogen-fixing tree (Franco and De Faria 1997). The climate is semiarid Mediterranean with 90% of the rainfall being concentrated in the winter months between May and September. Mean annual precipitation is 147 mm (1983–2003). Longer meteorological records from La Serena (85 km north) report a mean precipitation of 114.4 mm (1878–1998; Soto and Ulloa 1997). Mean annual temperature is 13.6°C, the warmest month is January and the coolest is July (López-Cortés and López 2004).

Soil collection

Soil was collected from each study site in October 2007. In Peru, we took samples under 10 living adult *P. pallida* trees from the first 50 cm of soil, as close as possible to the roots and the stem of the tree. Under each tree, soil was collected from a minimum of three different spots and bulked so that each tree served as a single replicate. In Chile, we took samples from two plant communities: (i) a scrubland field site where *P. chilensis* trees are currently absent (used in previous experiments by Holmgren, López, *et al.* 2006 and Squeo *et al.* 2007); (ii) underneath adult living *P. chilensis* trees in an area adjacent to the scrubland field site. Collecting in these two different sites allowed assessing the potential changes in soil community produced by the eradication of *Prosopis* trees, which could therefore affect the strength of plant–soil feedbacks on seedling growth. In the scrubland field site, 10 plots of ~4 m^2 were selected randomly. The sampling plots were ~10 meters apart. In each sampling plot, soil was collected from the first 50 cm of soil, as close as possible to the roots of the shrubs. In each sampling plot, soil was collected from a minimum of six different sampling points and bulked so that each sampling plot served as a single replicate. In the adjacent *Prosopis* population, we took samples under 10 living adult *P. chilensis* trees, using an identical soil collection protocol as in Peru. The soil was sieved using a 10-mm mesh to remove coarse roots and stones and homogenized.

Experiment 1: interspecific growth responses

Because soil types in Chile and Peru were different, we designed a pilot experiment to compare the growth responses of the two study species, *P. pallida* and *P. chilensis,* when growing under same abiotic conditions. We carried out a three-way factorial experiment with species (*P. pallida* vs. *P. chilensis*), soil type (sandy vs. sandy loam) and water availability (no water, 10% gravimetric moisture and 15% gravimetric moisture). The treatment combinations were replicated 5 times for a total of 60 experimental pots. The experiment took place in The Netherlands because experimental facilities with the required climate control were not available close to our study sites.

We used two Dutch soils sterilized by gamma irradiation (25 kGy) by Isotron in Ede, The Netherlands, one with a sandy texture and one with a sandy loam texture that had a physicochemical signature resembling the two field soils in South America. We filled pots (7 cm diameter and 40 cm height) with one of the two sterilized soil types. In each pot, one individual germinated seed of either *P. pallida* or *P. chilensis* was planted and grown for 7 weeks. Seeds were hydrated for 16 h at 30°C in demineralized water and then germinated in a petri dish for 2 days prior to planting. Seedlings that died during the first week were replaced. Both tree species were planted on both soil types. We used constant percentages of water in the experiment as this is a very accurate way to define water availability. Soil moisture of the 10% and 15% gravimetric moisture was reset twice a week by weighing each pot and watering with demineralized water. Greenhouse conditions were set at 60% RH, 16 h of light and 8 h of dark with a daytime temperature of 25°C and a nighttime temperature of 16°C. The pots were randomly distributed in replicate blocks over the greenhouse and the pots were moved within blocks and blocks shifted position twice a week to account for any potential microclimatic differences within the greenhouse.

Experiment 2: plant–soil feedback

Phase 1: soil conditioning

To assess the potential effect of soil microorganisms on seedling growth of *P. pallida* in Peru and *P. chilensis* in Chile, we carried out a second greenhouse experiment. We ran a two-phase experiment, inoculating the soil samples from the three field sites into the same sterilized soils from The Netherlands as used in Experiment 1. These soils had physicochemical properties comparable to the Peruvian and Chilean soils. This use of standard sterilized soil to be inoculated with live soil from the sampling sites has become a standard experimental protocol based on previous work by Van der Putten *et al.* 2007. During transport, the soils were kept under dry conditions to maintain the dormancy of the soil organisms and consequently the biotic composition and the chemical–physical properties of the soil were maintained (Reinhart *et al.* 2003).

Pots (7 cm diameter and 40 cm height) were filled with a mixture of one of the field experimental soils and one of the two sterilized Dutch soils (1 : 4 by weight). Sandy soil from the dunes in The Netherlands was mixed with the Peruvian soil, and sandy loam soil from the Veluwe in The Netherlands was mixed with the Chilean soil. The Dutch soils had been sterilized by gamma irradiation (25 kGy) by Isotron in Ede, The Netherlands, before mixing. This resulted in three soil treatments (one Peruvian soil and two Chilean soils). Initial soil moisture was set at 10% by weight. In each pot, one germinated seed of either *P. pallida* or *P. chilensis* was planted. On the soil inoculated with the Peruvian soil, one seedling of *P. pallida* was planted, and similarly, on the soil inoculated with the Chilean soil, one seedling of *P. chilensis* was planted. Thus, the soils were conditioned only by the plant species that occur naturally on these soils. Seedlings were grown for 7 weeks. Most plant–soil feedback studies of this kind have been of a similar length of time (e.g. Kardol *et al.* 2006). If the experiment would have taken longer, pot limitations would have been unavoidable. Seedlings that died during this growth period were replaced. Seedling mortality was restricted to the first weeks of this growth period. Plants were watered twice a week with demineralized water and initial soil moisture was reset once a week by weighing. Greenhouse conditions were the same as in the first experiment and the pots were distributed and moved as described earlier. After 7 weeks, the seedlings were harvested. The soil was rested for 1 week after which the feedback phase of the experiment started.

Phase 2: assessing plant–soil feedback

The soil of half of the pots of the soil conditioning phase was sterilized by gamma irradiation (25 kGy) by Isotron in Ede, The Netherlands. The remaining pots with conditioned soil were kept in the greenhouse to form the non-sterilized treatment. This experimental design involved three factors: soil origin (Peruvian soil (n = 10), Chilean scrubland soil (n = 10) and Chilean forest soil (n = 7)), water availability (no water, 10% gravimetric moisture and 15% gravimetric moisture) and soil microorganisms (sterilized and non-sterilized), resulting in a total of 162 pots. The direction and strength of the feedback effect was expressed as the relative growth of the *Prosopis* seedlings in the non-sterilized soils compared to the sterilized soils. The feedback effect was calculated as ln[biomass (or length) in the non-sterilized soil/biomass (or length) in the sterilized soil]. As the response variable was a ratio, this reduced the design to a two-factorial experiment with soil origin and water treatment as main factors.

In each pot, one individual germinated seed of one of the tree species (*P. chilensis* or *P. pallida*) was planted and grown again for 7 weeks under the same greenhouse conditions as in the soil conditioning phase. Seedlings that died during the first week of the feedback experiment were replaced. As in the soil conditioning phase, one seedling of *P. pallida* was planted on the Peruvian soil, and similarly, one seedling of *P. chilensis* was planted on the Chilean soil. We only planted each species on its original soil type as this most closely represents the field situation and is thus ecologically meaningful. Seedlings were subject to three levels of water availability: no water, 10% gravimetric moisture and 15% gravimetric moisture. The seedlings that received no water had an initial soil moisture of 10% at the start of phase 2. After 7 weeks, the sandy loam soil had a moisture level of ~7% and the sandy soils ~3%. Soil moisture of the other pots was reset twice a week by weighing and watering with demineralized water. Greenhouse conditions were the same as in the first phase of the experiment and the pots were distributed and moved as described earlier.

Soil and plant measurements

At the end of the soil conditioning phase and after soil sterilization, we analyzed nutrient concentrations (nitrogen, phosphorus and potassium) in each of the three soil types using $CaCl_2$ standard extraction methods (Houba *et al.* 1986) at the Biochemical Laboratory of Wageningen University, The Netherlands. Based on these nutrient concentrations (not reported), 10 ml 0.5 M Hoagland nutrient solution was added to all pots at the start of the feedback phase, to overcome differences in nutrient concentrations due to soil sterilization (Troelstra *et al.* 2001). At the end of the experiments, we harvested all seedlings and measured plant biomass (leaves, stem and roots) as well as stem height and root length. Seedling height was measured from the top to the start of the root. The soil was washed from the roots and all plant material oven-dried at 70°C for at least 72 h before weighing.

Statistical analyses

For the interspecific growth responses experiment, we analyzed the response of leaf biomass, root biomass, total plant biomass, root length and root–shoot ratio through separate factorial analyses of variance (ANOVAs) with three fixed factors: soil type, water treatment and species. Root–shoot ratio was calculated as (root biomass/[stem + leaf biomass]). Data were tested for normality and if necessary, data were $\ln(x + 1)$ transformed to comply with the assumption of normal distributions. The results of the feedback experiment were analyzed in two ways. Firstly, to test if the individual feedback effects were significantly different from zero, we used t-tests for each soil origin and for each variable. Next, to test if there were differences in plant–soil feedback between *P. pallida* grown in the Peruvian soil and *P. chilensis* grown in the Chilean soils and how water availability affected the plant–soil feedbacks, we used a two-way ANOVA with soil origin and water availability as main fixed factors. A different ANOVA was carried out for each of the response growth variables. Differences between treatments were compared by Scheffe *post hoc* tests due to unequal sample sizes. In addition, we compared the growth variables between the sterilized and the non-sterilized soil for the three different soil origins with t-tests and used Mann–Whitney test for variables that did not comply with normal distributions even after transformation (See online supplementary Appendix A). We compared seedling survival across treatments using a chi-square test.

RESULTS

Experiment 1: interspecific growth responses

In this experiment, we tested how seedlings of two tree species from arid areas in western South America responded to soil texture and water availability. The two *Prosopis* species responded similarly to soil type and water availability (ANOVA, $F_{1,48} = 1.475$, $P = 0.230$). Seedlings grown in sandy loam soils had higher leaf biomass and lower root–shoot ratio than seedlings grown in sandy soil (ANOVA, $F_{1,41} = 6.014$, $P = 0.019$; $F_{1,41} = 7.981$, $P = 0.007$, respectively). Water treatment also affected seedling growth; drought resulted in plants with longer roots than 10% gravimetric moisture (ANOVA, $F_{1,41} = 3.642$, $P = 0.035$). Correspondingly, root–shoot ratio was higher in the drought treatment than in soils with 10% or 15% gravimetric moisture (ANOVA, $F_{2,41} = 7.834$, $P = 0.001$).

Experiment 2: assessing plant–soil feedback

We found significant plant–soil feedback effects in the forest soils of both Peru and Chile. Plants grown in the non-sterilized Chilean forest soil produced more aboveground biomass (Fig. 1; $t = 2.033$, $P = 0.059$, d.f. = 16) and root length ($t = 1.898$, $P = 0.076$, d.f. = 16) than those in the sterilized soil. In contrast, the Chilean scrubland soil had a clear neutral feedback for both leaf biomass and root length (Fig. 1; $t = 0.783$, $P = 0.441$, d.f. = 27 and $t = -0.905$, $P = 0.373$, d.f. = 27). We found a different pattern in the feedback response for plants growing in the Peruvian soil. Inoculating non-sterilized Peruvian soil resulted in a negative soil effect on leaf biomass (Fig. 1; $t = -2.923$, $P = 0.007$, d.f. = 28) and a positive effect on root length (Fig. 1; $t = 3.923$, $P = 0.001$, d.f. = 28).

Plant–soil feedback was significantly different between the Peruvian soil and the Chilean forest soil for leaf biomass (Fig. 1; two-way ANOVA, $F_{2,65} = 5.123$, $P = 0.009$). The feedback for root length was more positive on Peruvian forest soils than on Chilean scrubland soils (Fig. 1; two-way ANOVA, $F_{2,65} = 6.185$, $P = 0.003$). Plant–soil feedback effects in the two Chilean soils were not significantly different from each other both for aboveground and belowground feedback effects on biomass and length. Water availability had no effect on the strength or direction of the feedback effects (Table 1). As the soil feedback effects are ratios and, therefore, influenced by values in both the numerator and the denominator, we have provided the biomass data in online supplementary Appendix A. Although not all comparisons were significant, these biomass data support the findings in our comparison of ratios: mixed aboveground and belowground feedback effects in the Peruvian forest soil, neutral effects in Chilean scrubland soil and positive aboveground and belowground feedback effects in the Chilean forest soil. Seedling survival was not affected by the biotic conditions of the soil or water availability (chi-square test, $\chi^2 = 0.9998$, $P = 0.9997$, d.f. = 10). At the end of the experiment, seedling mortality was 10% in the sterilized Peruvian soil, 10% in the sterilized Chilean scrubland soil and 29% in the Chilean forest soil for the drying out treatment, while under 10% soil moisture seedling mortality was 14% in the sterilized Peruvian soil, 10% in the non-sterilized Chilean scrubland soil and 14% in the non-sterilized Chilean forest soil. No seedlings died in the 15% soil moisture treatment.

DISCUSSION

Our first experiment tested how soil texture, tree species and water availability affect growth responses of the two *Prosopis* species. The results indicated that the two *Prosopis* species respond similarly when grown under the same abiotic environmental conditions. This is in line with earlier studies

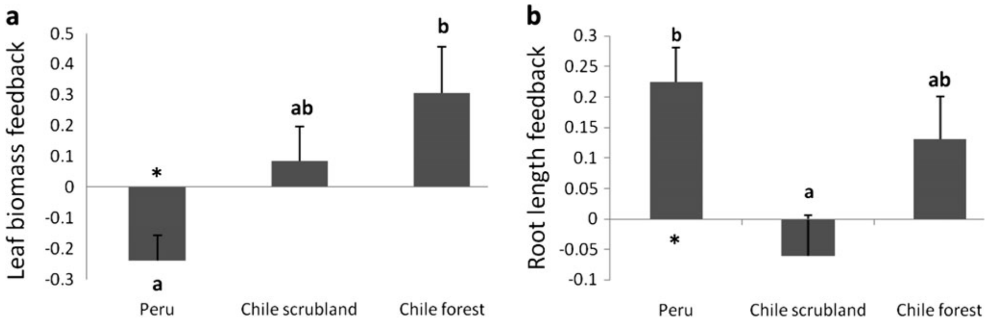

Figure 1: plant–soil feedback effects (mean + 1 standard error) for leaf biomass (a) and root length (b) for seedlings grown in soils of different origin. *Prosopis pallida* seedlings were grown in the Peruvian soils and *Prosopis chilensis* in the Chilean soils. Plant–soil feedback is calculated as ln(non-sterilized soil/sterilized soil). Different lowercase letters above bars indicate significant differences at the $P < 0.05$ level according to a Scheffe *post hoc* test; significant differences (after a *t*-test) of each of the bars from zero are indicated with asterisks (*<0.05).

Table 1: effect of soil origin and water availability on plant–soil feedback

	Soil origin					Water availability					Interaction, soil × water	
Variable	Peru	Chile scrubland	Chile forest	$F_{2,65}$	P	Dry out	10%	15%	$F_{2,65}$	P	$F_{4,65}$	P
Shoot length	0.02 ± 0.04	0.14 ± 0.07	0.30 ± 0.12	2.611	0.081	0.23 ± 0.08	0.02 ± 0.06	0.14 ± 0.08	2.20	0.12	0.98	0.43
Root length	0.22 ± 0.06	−0.06 ± 0.07	0.13 ± 0.07	6.185	0.003*	0.06 ± 0.08	0.11 ± 0.06	0.11 ± 0.07	0.40	0.67	2.36	0.06
Stem biomass	0.01 ± 0.08	0.12 ± 0.13	0.54 ± 0.25	2.641	0.079	0.33 ± 0.13	0.05 ± 0.13	0.15 ± 0.16	1.22	0.30	1.06	0.39
Leaf biomass	−0.24 ± 0.08	0.09 ± 0.11	0.31 ± 0.15	5.123	0.009*	0.10 ± 0.09	−0.09 ± 0.11	0.03 ± 0.14	0.78	0.46	0.96	0.44
Root biomass	−0.12 ± 0.12	−0.01 ± 0.13	0.23 ± 0.24	0.918	0.404	0.12 ± 0.14	−0.04 ± 0.13	−0.06 ± 0.17	0.53	0.59	0.70	0.60
Aboveground biomass	−0.17 ± 0.08	0.10 ± 0.11	0.39 ± 0.18	4.246	0.018*	0.17 ± 0.10	−0.05 ± 0.11	0.06 ± 0.14	0.96	0.39	1.02	0.41
Total biomass	−0.17 ± 0.09	0.07 ± 0.11	0.32 ± 0.20	2.980	0.058	0.15 ± 0.11	−0.07 ± 0.11	0.02 ± 0.15	1.02	0.37	1.22	0.31

Plant–soil feedback effects (mean ± standard error) for *Prosopis* seedlings grown in soils of different origins and under different water treatments. *Prosopis pallida* seedlings were grown in the Peruvian soils and *Prosopis chilensis* in the Chilean soils. Feedback is estimated for each response variable as ln[non-sterilized soil/sterilized soil]. Results of two-factorial ANOVA, asterisk signs indicate significant P values ($P < 0.05$).

reporting no difference in growth rates between these two species (Holmgren, López, *et al.* 2006; Squeo *et al.* 2007). However, soil type did affect seedling growth. Plants grown in the sandy soil had a higher root–shoot ratio than those grown in the sandy loam soil, showing that the tree seedlings produced proportionally more roots in sandy soil. Water availability also affected seedling growth as root length increased with decreasing water availability. Root elongation has been identified as one of the most important plant traits explaining higher seedling survival to drought (León *et al.* 2011; Padilla and Pugnaire 2007).

Our plant–soil feedback experiment showed that soil biota, developing in the root zone of *Prosopis* plants, have the potential to influence plant biomass production of the next generation seedlings and that this feedback can be expressed differently in aboveground and belowground plant growth. The second separate experiment indicated that *P. chilensis* had a somewhat positive plant–soil feedback in the loamy Chilean forest soil for both leaf biomass and root length, that *P. chilensis* had a neutral plant–soil feedback in the loamy Chilean scrubland soil for both leaf biomass and root length and that *P. pallida* had a negative plant–soil feedback for leaf biomass and a positive plant–soil feedback for root length in the sandy Peruvian soil. These findings of mostly neutral and positive plant–soil feedback contrast with our hypothesis that seedling growth would increase in sterilized soils as potential soil pathogens would have been removed. Plant–soil feedback effects are net effects of pathogens, symbionts and decomposer organisms (Bever *et al.* 1997). If the soil feedback effects are positive, as in some of our comparisons, it will mean that the symbionts have overruled the effects of the pathogens. Although plant–soil feedback effects are often documented in temperate biomes, where they are usually negative (Petermann *et al.* 2008), there are very few reports from arid ecosystems (Kulmatiski *et al.* 2008; Van der Putten *et al.* 2007). We found that plant–soil feedback affected plant performance and biomass allocation differently depending on soil origin.

This effect of soil origin cannot be separated from soil type. Our first experiment indicated that soil texture affects seedling growth and biomass allocation of the *Prosopis* seedlings. The second experiment demonstrated that plant–soil feedback enhanced root elongation in the Peruvian forest soil and leaf production in the Chilean soils. These results suggest that in the Peruvian forest soil, *Prosopis* seedlings invest in root length at the cost of having less leaf biomass, whereas the *Prosopis* seedlings in the Chilean soil would invest in the opposite direction. These contrasting patterns of biomass allocation might be highly relevant for understanding the low survival rates of *Prosopis* seedlings documented for Chile compared to Peru (Holmgren, López, *et al.* 2006; Squeo *et al.* 2007). Since in semiarid ecosystems water is a limiting resource for plant growth, longer roots can enable seedlings to survive under dry conditions (León *et al.* 2011; Padilla and Pugnaire 2007). In contrast, larger leaf biomass production increases transpirational surface and thus plant water demands, which would in combination with shorter roots reduce the chances of survival under drought conditions. This may be one important reason for the low seedling survival rates found in the Chile system despite exclusion of grazing effects (Holmgren, López, *et al.* 2006; Squeo *et al.* 2007). Also long-term monitoring of reforestation projects in Peru suggests larger *Prosopis* recruitment in sandy soils compared to calcareous ones (Sitters *et al.* 2011). Our greenhouse experiments provide some mechanistic basis at the plant level to understand the facilitating role of sandy soils on plant growth.

In our comparison between the Chilean and the Peruvian forest soils, there were two combined factors: tree species and soil type. Our first experiment showed that root growth by both *Prosopis* species was greater in sandy soils than loamy soils. Sandy soil, as occurring in Peru, likely facilitated root elongation, whereas the loamy texture of Chilean soils impeded such plant response. Therefore, the way the plant–soil feedback is expressed could depend on soil texture, with faster root growth in sandy soils and more aboveground biomass allocation in clayish ones. Differences in plant–soil feedback in relation to soil texture have also been suggested by Bezemer *et al.* (2006) who showed that plant–soil feedback patterns in restored chalk grassland differ from restored grasslands on sandy loam soil. One important limitation of our study is the lack of landscape level replication, which requires some caution in generalizing the results across the landscape beyond the scope of our study sites.

There were also differences between the two Chilean sites. Plant–soil feedbacks were neutral in scrubland soils and positive in soils where *Prosopis* trees were present. This suggests that soil communities in *Prosopis* forests may facilitate reestablishment by affecting plant biomass allocation in the early stages of tree growth. Thus far, facilitation is often considered to occur between plant species (Callaway 2007) or between plant species and symbiotic mutualists (Van der Heijden 2004; Van der Heijden *et al.* 2008). Most of the facilitative effects in plant communities have been explained in relation to reductions of water stress, increased nutrient concentrations or reductions of herbivory pressure under the shade of nurse plants (Callaway 2007; Holmgren *et al.* 1997). Our results indicate that soil biota may play a role in plant biomass allocation, thus providing a new explanation why Holmgren, López, *et al.* (2006) and Squeo *et al.* (2007) found low survival rates for *P. chilensis* in Chile on the scrubland site where *Prosopis* is no longer present. Possibly, survival will be more successful when seedlings are planted in sites where *P. chilensis* still occurs as root nodulating bacteria and mycorrhizal fungi could bring about a positive plant–soil feedback between the adult trees and their seedlings.

Conclusions

In our experiments, we found mainly positive plant–soil feedbacks contrasting with the great majority of current research emphasizing the role of negative plant–soil feedbacks in nature. Our results suggest that the expression of a positive plant–soil feedback on biomass allocation patterns has implications for the way plants can deal with drought and potentially also with other disturbances.

SUPPLEMENTARY MATERIAL

Supplementary Appendix A is available at *Journal of Plant Ecology* online.

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