

Plant-soil feedback in herbaceous species of Mediterranean coastal dunes

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Abstract: Plants induce soil heterogeneity that can affect species coexistence. In this work, the soil heterogeneity induced by the growth of 9 species selected from Mediterranean vegetation of coastal dunes was studied in controlled conditions. We investigated the effect of the grown plants on soil characteristics (pH, electrical conductivity, NO₃⁻, and NH₄⁺) and performance of 4 target species (*Dactylis hispanica*, *Melilotus neapolitana*, *Petrorhagia velutina*, and *Phleum subulatum*). Plant growth and survival were affected by soil history in species-specific ways, showing a high variability of both parameters, with survival ranging from 100% to 0%. Soil history did not affect soil pH and conductivity but dramatically changed the availability of mineral nitrogen forms. However, for all plant species, growth and survival results were unrelated to the measured soil characters. Other factors, such as accumulation of allelopathic compounds and/or changes in soil microbial communities, may explain the observed effects. The experimental results, demonstrating a widespread occurrence of plant-soil feedback, show the importance of this process also in species-rich herbaceous Mediterranean vegetation.

Keywords: allelopathy, coexistence, species diversity, soil history, soil-borne pathogens

INTRODUCTION

Small-scale heterogeneity of the underground environment is important for community ecology because it can affect the performance of individual organisms and thus also species coexistence at the community level (HUSTON 1994). Both in terms of species coexistence and successional dynamics, local plant-induced environmental heterogeneity created by individual plants has been indicated as an under-investigated issue (TILMAN & PACALA 1993).

Differences in plant responses to both spatial and temporal environmental heterogeneity have been reported in relation to nutrient distribution and water availability (HODGE 2004). Moreover, in the last decades, growing evidence demonstrated that also

plants profoundly modify the soil through several mechanisms, such as excretion of organic compounds from roots (NEUMANN & MARTINOIA 2002), accumulation of plant litter (EHRENFELD et al. 2005), changing the soil microbial community (KLIRONOMOS 2003) or depleting the available soil nutrients (TILMAN 1988). The plant-induced soil heterogeneity, in turn, affects plant growth, thus producing the so-called plant-soil feedback (BEVER et al. 1997). In general terms, plant-soil feedback effects can range from positive to strongly negative (BONANOMI et al. 2005). Recent studies have demonstrated that both types of feedback seriously affect the structure and organization of plant community. Positive feedback, mostly mediated by water and nutrient accumulation, is important in resource-limited ecosystems, such as arid grasslands and nutrient-limited savannas (RIETKERK et al. 2004). It produces there, for example, the “islands of fertility” phenomenon (BONANOMI et al. 2008). Negative plant-soil feedback occurs in several ecosystems, such as coastal sand dunes during primary succession (VAN DER PUTTEN et al. 1993), temperate grasslands (KLIRONOMOS 2002; KARDOL et al. 2006), and temperate and tropical forests (RIS LAMBERS et al. 2002). Several mechanisms have been proposed to explain this negative feedback, e.g. soil nutrient depletion, increased inoculum of soil-borne pathogens (PACKER & CLAY 2000), changes in soil microbial community composition (KLIRONOMOS 2003), and phytotoxicity resulting from plant litter decomposition (BONANOMI et al. 2011). Furthermore, model studies demonstrate that species-specific negative feedback, by creating unsuitable conditions for conspecifics and providing habitat for other species, allows for species coexistence through reciprocal indirect facilitation (BONANOMI et al. 2005).

Despite the evidence of the widespread occurrence of positive and negative plant-soil feedback and of its role in species-poor sand dune communities in North Europe (VAN DER PUTTEN et al. 1993), no published studies have been available so far for species-rich herbaceous communities of Mediterranean sand-dunes. Mediterranean herbaceous communities frequently occur in the post-disturbance gaps of Mediterranean macchia, and are dominated by many short-lived species growing in nutrient-poor and dry habitats. This work was aimed to investigate if various herbaceous Mediterranean species induce plant-soil feedback on the scale of individuals and how this, in turn, can affect species survival and growth under standardized and controlled environmental conditions.

Three main questions have been addressed by this work:

- (i) Does plant growth build up positive or negative plant-soil feedback in sand-dune Mediterranean grassland?
- (ii) Does plant-soil feedback affect species survival and growth in species-specific ways?
- (iii) Are changes in nutrient availability responsible for the observed plant-soil feedback?

MATERIALS AND METHODS

Study site

The research was carried out at the “Castel Volturno” Nature Reserve, a flat coastal area of ~268 ha north of Naples in southern Italy (40°57'N; 1°33'E). The area

is located on stabilized dunes of alluvial deposits and loose siliceous-calcareous sand, with a maximum elevation of 9 m above sea level. The climate is typically Mediterranean, with precipitation mostly occurring in autumn and winter, with a dry period in summer. The soil is rather homogeneous, with 97.1% sand, 1.25% loam, and 1.6% clay, poor in organic matter and nutrients.

The vegetation can be characterized as low Mediterranean scrubland with scattered post-fire disturbance gaps dominated by annual herbs and bryophytes. Species richness of the herbaceous community on a small scale was high, with an average of 24 ± 5 species at 0.25 m^2 . The most frequent species were the grasses *Phleum subulatum*, *Dactylis hispanica*, the forbs *Petrorhagia velutina*, *P. saxifraga*, *Carex distachya*, *Bellis perennis*, *Lobularia maritima*, *Teucrium chamaedrys*, *T. polium*, and the nitrogen-fixing legumes *Melilotus neapolitana* and *Medicago minima*.

Soil history generation

In relation to their cover values in the study area, 9 coexisting herbaceous species (Table 1) were selected for soil history generation. This method, although creating a simplified rooting environment, is widely accepted (KLIRONOMOS 2002; BONANOMI & MAZZOLENI 2005; PETERMANN et al. 2008) because it allows investigation of the soil heterogeneity induced by root systems of each plant species without the confounding factors of above-ground litter and other root systems.

Seeds of the 9 selected species and soil samples were collected in the field in the autumn of 2004. The collected seeds were put in paper bags, transported to the laboratory, and stored at room temperature. About 100 kg of soil were sampled within the topsoil (0–20 cm in depth) after litter removal at the soil surface. The following day, the soil was sieved in the laboratory (mesh size <2 mm). Pots (12 cm across, 15 cm deep) were filled with 400 g of a mixture of the dry soil and perlite (4:1, v/v). Ten different soil treatments were established by growing the 9 species as mono-cultures and using bare soil as the control. Seeds of all species were sown in the pots (30 seeds of only one species per pot). After 21 days, germinated seedlings of each species were thinned to a density of 3 plants/pot. Plants were watered daily with distilled water at field capacity without addition of nutrient solution. Pots were weeded weekly to avoid the emergence of seedlings of other species from the soil seed bank. Irrigation was maintained for 90 days and then stopped to dry the soil until plant death, which occurred within 15 days. Dry above-ground biomass was removed by cutting at the soil surface, without any soil disturbance. The pots containing the soil and the residual dead roots of the different species were used to establish the growth experiment.

Growth experiment

In this experiment we used the 10 groups of pots differing in soil history (Table 1), i.e. the control pots with bare soil and the pots labelled with 9 names of species grown in the pots in the first experimental phase described above. Four of the 9 plants were chosen as target species (Table 1) on the basis of their different growth forms. In all soil types, 3 individual plants of one target species were grown in each soil type for 10 weeks. The experiment was organised according to a completely randomised block design with 4 target species and 10 soil types in 12 replicates, i.e. in a total of

Table 1. Target species utilized for the growth experiment and species utilized for soil history generation

Target species	Soil history	Species growth forms
	Control (bare soil)	
	<i>Bellis perennis</i> L.	Perennial forb
	<i>Carex distachya</i> Desf.	Perennial sedge
<i>Dactylis hispanica</i>	<i>Dactylis hispanica</i> Roth	Perennial grass
	<i>Globularia maritima</i> L.	Perennial forb
<i>Melilotus neapolitana</i>	<i>Melilotus neapolitana</i> Ten.	Annual legume
	<i>Petrorhagia saxifraga</i> L.	Annual forb
<i>Petrorhagia velutina</i>	<i>Petrorhagia velutina</i> Guss	Annual forb
<i>Phleum subulatum</i>	<i>Phleum subulatum</i> (Savi) Asch et Gr.	Annual grass
	<i>Teucrium chamaedrys</i> L.	Dwarf shrub

480 pots ($4 \times 10 \times 12$). Pot distribution was randomly rearranged within the greenhouse every week.

Seedlings were obtained from germinated seeds in 9-cm Petri dishes with wet filter paper by incubation in a growth chamber at $+25^{\circ}\text{C}$ for 48 h. Next, 3 seedlings were transplanted into 1-cm-deep holes in a triangular design into each pot. Withered seedlings were replaced within the first 48 h. Plants were irrigated daily with distilled water without any fertilizer for 70 days. The whole experiment was conducted in a growth chamber in the spring of 2005, with temperature ranging from 20 to 28°C and natural day length.

Before the start of the experiment, 5 g of soil were taken from 12 pots selected at random for each soil history for soil analysis. Electrical conductivity, pH, and concentration of extractable NO_3^- and NH_4^+ in potassium sulphate were measured (CASTALDI & ARAGOSA 2002).

During the experiment, plant mortality for each species in each soil type was monitored after 14, 35, 53, and 70 days from the beginning of the experiment. At the end of the experiment, i.e. after 70 days of growth, roots of individual plants were separated and cleaned from soil by washing with tap water. Next, above-ground and underground dry biomass of each living plant was measured after desiccation at $+105^{\circ}\text{C}$ for 72 h.

Statistical analysis was done by one-way analysis of variance (ANOVA) on log-transformed data as required for normalization. Simple regression analysis was applied to test the relationships between the measured soil variables and species biomass and survival in the different soil types.

RESULTS

Plant growth of the 4 target species was significantly affected by soil history (ANOVA $P < 0.01$ for all species; Fig. 1). The growth of the grass *Dactylis hispani-*

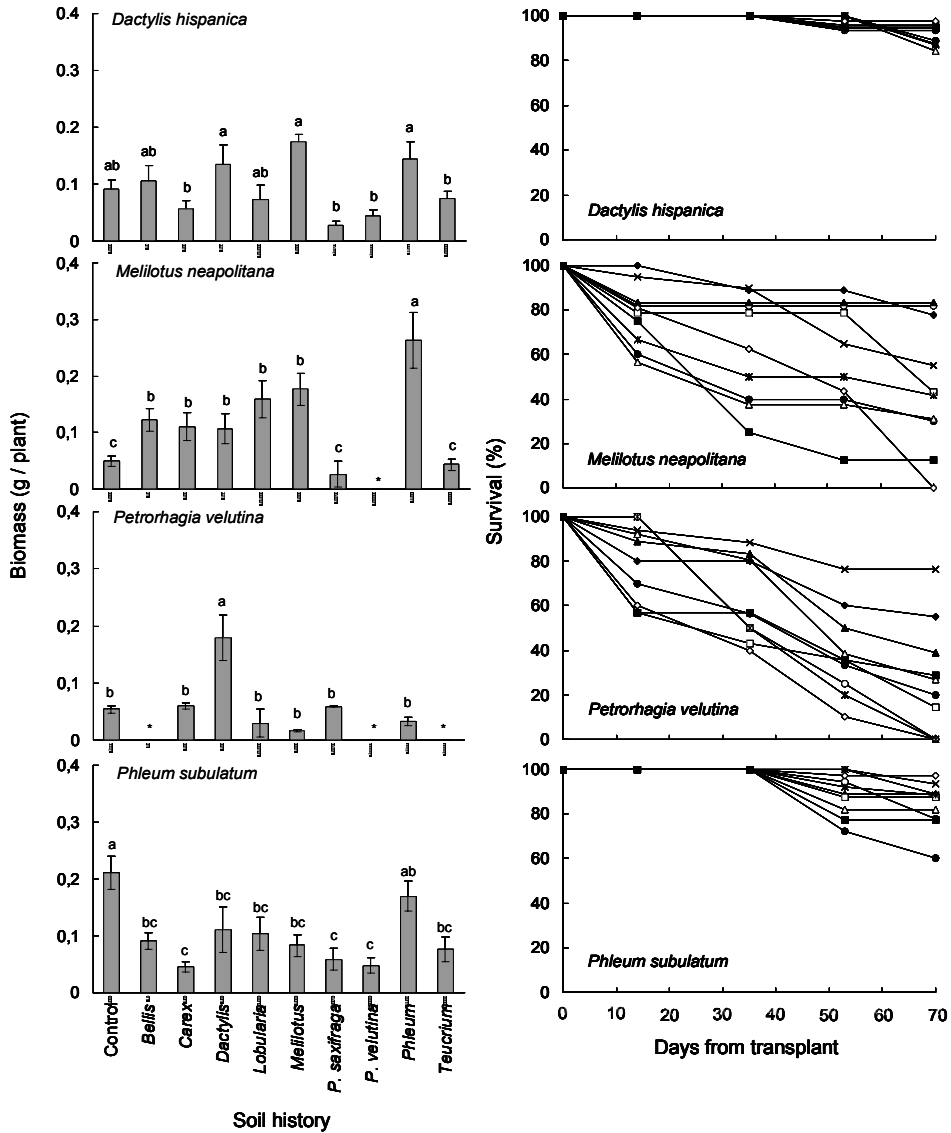


Fig. 1. Plant growth (left column) and survival (right column) of *Dactylis hispanica*, *Melilotus neapolitana*, *Petrorhagia velutina* and *Phleum subulatum* in the 10 soil types during the growth experiment. For plant growth, different letters indicate significant differences (Duncan test; $P < 0.05$), bars indicate standard error ($n=12$), asterisks indicate treatments with 100% plant mortality. In survival diagrams, bare soil is represented by x, *Bellis* by hollow circles, *Carex* by solid circles, *Dactylis* by hollow triangles, *Lobularia* by solid triangles, *Melilotus* by hollow squares, *Petrorhagia saxifraga* by solid squares, *P. velutina* by hollow diamonds, *Phleum* by solid diamonds, and *Teucrium* by asterisks.

ca was higher after cultivation of the same species, *Phleum subulatum* or *Melilotus neapolitana*, while lowest after growth of *Carex distachya*, *Petrorhagia velutina* and *P. saxifraga* and *Teucrium chamaedrys*. The legume *M. neapolitana* grew better after *Phleum subulatum* and worst in bare soil and after *Petrorhagia velutina*, *P. saxifraga*, and *T. chamaedrys*. Very poor growth was reported for *P. velutina* in all soil types, with the exception of the *D. hispanica* soil. Finally, *Phleum subulatum* grew well in bare soil and after cultivation of the same species, while poorly after *C. distachya*, *Petrorhagia velutina*, and *P. saxifraga*.

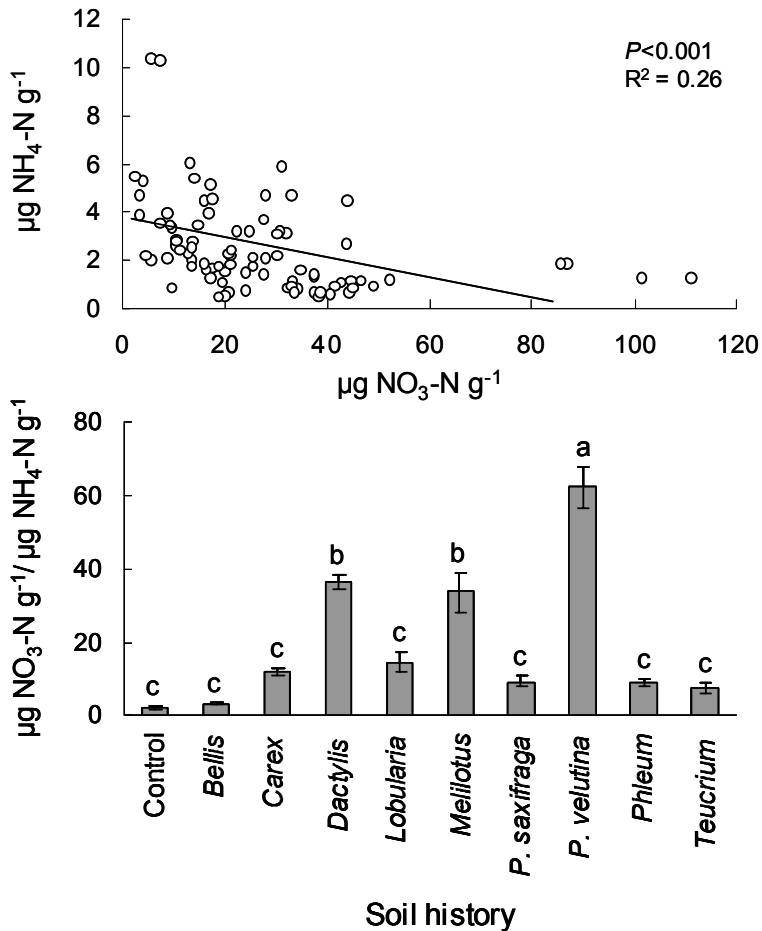


Fig. 2. Regression analysis for soil nitrate and ammonium concentration in relation to soil history (above, the levels of statistical significance are indicated in the graph), and effect of soil history on the ratio between nitrate and ammonium in the soil immediately before the growth experiment. Values are means \pm standard error of 10 replicates. Different letters indicate significant differences (Duncan test $P < 0.05$)

The 4 target species differed also in survival (Fig. 1). It was high for *D. hispanica* and *Phleum subulatum* and generally low but highly variable (depending on soil history) for *M. neapolitana* and *Petrorhagia velutina* (Fig. 1). In relation to soil history, *D. hispanica* had the lowest survival after growth of the same species, *T. chamaedrys* and *L. maritima*, and the highest in the control and *P. velutina* soil. As regards *Phleum subulatum*, the lowest survival was observed in the *C. distachya* soil, followed by the *Bellis perennis* and *P. saxifraga* soils, while the highest survival was recorded in the control and *P. velutina* soil. The legume *M. neapolitana* showed marked survival variability among soil types: higher than 80% in the *B. perennis* and *L. maritima* soils and very low (0% and 12%, respectively) in the *P. velutina* and *P. saxifraga* soils. *M. neapolitana* survival was lower than 50% also in the *C. distachya*, *D. hispanica*, *T. chamaedrys* and *M. neapolitana* soils (Fig. 1). Finally, also *P. velutina* showed a high variability in survival among soil types, ranging from 76% in bare soil to complete mortality in the *P. velutina*, *B. perennis* and *T. chamaedrys* soils. Survival of *P. velutina* was higher than 50% only in the control and in the *P. subulatum* soil (Fig. 1). *M. neapolitana* and *P. velutina* seedlings showed widespread damping-off symptoms, i.e. softness of plant tissue followed by wilting and plant death.

Soil history significantly affected nitrate and ammonium concentration and the ratio between these ions (Fig. 2), but not pH and conductivity (Table 2). Moreover, soil nitrate was negatively correlated to ammonium concentration (Fig. 2). Regression analysis between soil parameters and species biomass and survival in each soil type does not show any significant relationship (data not shown).

Table 2. Effect of soil history on pH, electrical conductivity, and nitrate and ammonium concentration immediately before the growth experiment. Values are means \pm standard error of 12 replicates. Different letters indicate significant differences (Duncan test, $P < 0.05$)

Soil history	pH	Electrical Conductivity	Nitrate	Ammonium
		(mS cm ⁻¹)	($\mu\text{g NO}_3\text{-N g}^{-1}$)	($\mu\text{g NH}_4\text{-N g}^{-1}$)
Control	8.01 \pm 1.1 a	0.13 \pm 0.01 a	57.00 \pm 6.43 a	4.79 \pm 0.37 a
<i>Bellis perennis</i>	8.08 \pm 1.2 a	0.17 \pm 0.02 a	7.71 \pm 1.68 c	3.79 \pm 0.39 a
<i>Carex distachya</i>	7.87 \pm 1.1 a	0.40 \pm 0.10 a	12.70 \pm 1.09 c	4.11 \pm 0.36 a
<i>Dactylis hispanica</i>	8.06 \pm 1.3 a	0.53 \pm 0.11 a	28.87 \pm 2.20 b	0.81 \pm 0.08 c
<i>Lobularia maritima</i>	7.94 \pm 0.6 a	0.36 \pm 0.09 a	23.69 \pm 4.22 b	1.83 \pm 0.21 b
<i>Melilotus neapolitana</i>	7.82 \pm 0.5 a	0.56 \pm 0.13 a	45.86 \pm 7.25 a	1.50 \pm 0.16 bc
<i>Petrorhagia saxifraga</i>	7.85 \pm 1.0 a	0.37 \pm 0.11 a	14.53 \pm 1.16 c	1.75 \pm 0.19 b
<i>Petrorhagia velutina</i>	7.86 \pm 0.9 a	0.56 \pm 0.09 a	56.06 \pm 8.47 a	0.91 \pm 0.09 c
<i>Phleum subulatum</i>	7.92 \pm 1.2 a	0.32 \pm 0.08 a	29.07 \pm 3.36 b	3.25 \pm 0.27 a
<i>Teucrium chamaedrys</i>	8.01 \pm 1.2 a	0.43 \pm 0.12 a	21.00 \pm 2.60 b	4.51 \pm 1.05 a

DISCUSSION

Our results demonstrate that both positive and negative plant-soil feedback occurs in the early development stage of coastal dune plant communities. To our knowledge this is the first experimental evidence of plant-soil feedback in a sand beach coastal Mediterranean plant community. The observed plant-soil feedback profoundly affected plant performance, suggesting a potential role in driving population dynamics in further stages of succession. These results, although obtained by a short-term pot experiment, help to understand better the dynamics in natural plant communities.

Biomass production of the tested plants was significantly affected in the soil after cultivation of conspecifics as well as heterospecifics. However, the observed growth of each species appears idiosyncratic, with no general response of the 4 species to the 10 soil types. In previous studies, plant-soil feedback was found to be primarily negative towards conspecifics (review in MAZZOLENI et al. 2007; KULMATISKI et al. 2008), with variable effect on heterospecifics, ranging from positive to strongly negative (KLIRONOMOS 2002). In this study, the grasses *Dactylis hispanica* and *Phleum subulatum* and the annual legume *Melilotus neapolitana* do not provide evidence of negative feedback to oneself, which contrasts with the forb *Petrorhagia velutina*. Furthermore, we also demonstrated that the plant-soil feedback induced by heterospecifics profoundly affected both plant growth and survival. For instance, after *P. velutina* cultivation, the survival of *Phleum subulatum* and *D. hispanica* was higher than 90%, whereas no *M. neapolitana* and *Petrorhagia velutina* plants survived after the same soil history. However, the effects of soil history on plant survival and growth are difficult to generalise because they seemed strictly species-specific. The only general trend was the poor performance of almost all species after cultivation of *C. distachya* and both *Petrorhagia* species. Interestingly, in this study the 2 grass species *Phleum subulatum* and *Dactylis hispanica* did not suffer negative feedback. This contrasts with a previous study, where the grassland species *Holcus lanatus* showed a dramatic growth decrease in the soil where the same species was cultivated earlier (BONANOMI & MAZZOLENI 2005).

The “black box approach” of the soil history experiment did not allow us to identify the specific mechanism(s) responsible for the observed survival and biomass patterns. However, the changes in abiotic soil properties produced by the plant-soil feedback (EHRENFELD et al. 2005) appear to be of minor importance because no changes in pH and conductivity were recorded and the significant changes in NO_3^- and NH_4^+ were unrelated to survival and plant growth. These last results are surprising because mineral nitrogen is the most limiting nutrient in the studied plant community (CASTALDI & ARAGOSA 2002). Interestingly, the level of soil NO_3^- was significantly negatively correlated to NH_4^+ concentration. These results suggest that culturing of the different species affects in a species-specific way the nitrification process. The capability of several plant species to inhibit the nitrification process is well known (MAO et al. 2006), but the relevance of this process for plant community dynamics is still poorly understood despite the earlier RICE'S (1984) suggestion that the inhibition of nitrification could affect the successional dynamics. On the other hand, changes in availability of other soil nutrients, such as phosphorus and potassium, should play

a role in plant succession. However, starting from soil with very low organic matter content reduced the potential differences in nutrient mineralization by soil organic matter.

Alternatively, the different soil history effects should be related to specific shifts in the soil microbial community composition, as reported in previous studies (e.g. KLIRONOMOS 2002). Changes in the soil microbial community can arise when the presence of specific plant roots, root exudates, and decaying root litter causes a selective increase or decrease in the density of specific soil microbes. The changes can induce negative feedback if they produce a relative increase in host-specific pathogens (VAN DER PUTTEN et al. 1993; BEVER et al. 1997). Positive feedback arises if favourable effects of some microorganisms on plant performance, e.g. of symbiotic arbuscular mycorrhizal fungi or N-fixing bacteria, are enhanced (KLIRONOMOS 2003). For instance, the absence of particular symbionts, such as N-fixing bacteria, is involved in the poor establishment of plant legumes (LARSON & SIEMANN 1998). In this experiment, the poor growth of *M. neapolitana* in the bare soil (control) may be related to a low inoculum of N-fixing bacteria, compared to the *M. neapolitana* soil. However, the pervasive seedling dumping-off and plant wilting of *P. velutina* in the *P. velutina* soil suggests an accumulation of species-specific soil-borne pathogens. Finally, the effect of soil history may be potentially attributable also to the release of allelochemicals during root decay because a previous study demonstrated that 6 of the 9 species utilized in this study has in vitro allelopathic effects (BONANOMI et al. 2006).

In conclusion, this study demonstrated the pervasiveness of plant-soil feedback in a Mediterranean coastal dune plant community. This result is consistent with evidence reported for North European coastal sand dunes (VAN DER PUTTEN et al. 1993). The existence of both positive and negative plant-soil feedback profoundly affected plant performance, with a potential role in plant coexistence. However, future studies are needed to understand how the plants modify the soil microbial communities and how these changes, in turn, interact with observed modifications in nutrient availability and the activity of soilborne pathogens (BONANOMI et al. 2007).

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