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Plant and soil responses to mycorrhizal fungi and rhizobacteria in nodulated or nitrate-fertilized peas (*Pisum sativum* L.)

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Abstract Rhizosphere organisms affect plant development and soil stability. This study was conducted to determine the effects of a vesicular-arbuscular mycorrhizal (VAM) fungus [*Glomus mosseae* (Nicol. & Gerd.) Gerd. and Trappe] and a rhizobacterium (*Bacillus* sp.) on nitrate-fertilized or nodulated pea (*Pisum sativum* L.) plants and on the status of water-stable soil aggregates. The plants were grown in pots in a yellow clay-loam soil, and inoculated with the VAM fungus and the rhizobacterium, with one of the two, or with neither. The *Bacillus* sp. and *G. mosseae* did not affect shoot dry mass in nodulated plants. Under N fertilization, the VAM fungus enhanced plant growth, while the rhizobacterium inhibited shoot growth, VAM root colonization, and nodule formation, but enhanced the root:shoot and the seed:shoot ratios. The inhibition of shoot growth and of root colonization appeared to be related. The water stability and pH of the VAM soils were higher than those of the non-VAM soils. The rhizobacterium enhanced the water-stable aggregate status in the non-VAM soils only. Under both N-nutrition regimes, the soils had the greatest proportion of the water-stable aggregates when inoculated with both rhizo-organisms and the lowest when colonized by neither. The two rhizo-organisms affected both plants and soil, and these effects were modified by the source of N input through N_2 fixation or fertilization.

Key words *Bacillus* · *Glomus* · Mycorrhiza · *Pisum sativum* · Plant response · Rhizosphere · Root nodule · Soil aggregation · Soil pH · Symbiosis

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Introduction

N_2 fixation by root nodules is so important to legumes and to associated plants in intercropping or crop-rotation systems (Heichel and Barnes 1984) that its effect on soil stability is rarely considered (Alberts and Wendt 1985). Adverse effects of N_2-fixing legumes on soil aggregation (Alberts et al. 1985), however, may be a matter of concern for agrosystem stability (Bethlenfalvay and Schüepp 1994).

The effects of the soil biota on both plants and soil (Plankhurst and Lynch 1994) are modified by farming practices (Rovira 1994). Organic farmers rely on natural products and on the activities of beneficial soil organisms to support plant growth (Macgregor 1994). The effects of such plant symbionts (e.g., rhizobia, VAM fungi) may be modified by other associated organisms (Paulitz and Linderman 1991). Although the latter are generally evaluated by plant response alone (Mahaffee and Kloeppner 1994), they may be equally important to soil stability (Foster 1994). The literature of microbial effects on plant or soil (Pfleger and Linderman 1994) is voluminous, but studies of both together are rare (Andrade et al. 1995).

The purpose of our experiment was to evaluate the effects of two plant symbionts (*Rhizobium* and VAM fungus) and an associated rhizobacterium on each other, on plant development and on soil aggregation under two N regimes (N_2 fixation or fertilization), and to determine if rhizobacterium effects on plant and soil were direct or mediated by the VAM fungus or the root nodules.

Materials and methods

Experimental design and statistics

The experiment was designed as a 2×2×2 factorial with N nutrition, VAM colonization, and inoculation with a rhizobacterium as factors. Experimental units (plotted plants) were arranged randomly and rearranged twice weekly. The main effects were (1) nodulation or nitrate fertilization, (2) the presence (+VAM) or absence (–VAM) of a VAM

fungus, and (3) inoculation with a rhizobacterium or its absence. The resulting eight treatments were replicated five times. The results were evaluated by analysis of variance.

Biological materials

Pea (*Pisum sativum* L., cv. Lincoln) seeds were germinated, selected for uniformity after 4 days, planted, and thinned from four to one plant per pot. The isolate of the VAM fungus [*Glomus mosseae* (Nicol. & Gerd.) Gerd. and Trappe] was originally obtained from Barbara Mosse, Rothamsted, UK, and cultured for several years at the Estación Experimental del Zaidín (EEZ), Granada, Spain, in local soil and different host plants. At least 1000 spores and sporocarps and 500 heavily colonized root fragments were mixed into the soils of each pot before planting. Sievings (30 µm diameter) of the VAM inoculum free of VAM propagules were added to all soils in water suspensions (100 ml).

The rhizobacterium (*Bacillus* sp. strain BH-II) was isolated from spores of *G. mosseae* and cultured as described previously (Andrade et al. 1995). It has not been found on other VAM fungi tested under the same conditions (G. Andrade unpublished data), and may be a preferential associate of *G. mosseae*. The American Type Culture Collection (Rockville, Md.) failed to identify this organism to species, but established closest (though weak) resemblance with *Bacillus megaterium* or *Bacillus simplex*. Suspensions of this organism (20 ml, 10^9 ml^{-1}) were applied at planting to stems and to the soil surface and mixed into the soil to a depth of 2–3 cm.

Half of the seedlings were inoculated at planting with suspensions of *Rhizobium leguminosarum*, strain 128C53, obtained originally from the Nitragin Co., Miwaukee, Wis., and cultured at the EEZ. Cultures were prepared on nutrient-agar slants and applied in aqueous suspension (10 ml, 10^8 cells ml^{-1}) to the seedling stems at the soil surface. All treatments not inoculated with any of the three organisms received autoclaved media equivalent to the inocula.

Soil and growth conditions

The yellow clay-loam soil (sand, 42%; silt, 40%; clay, 18%; pH 7, H_2O, 1:1) had organic matter and $NaHCO_3$-extractable P contents of 3.2 g kg^{-1} and 21 mg kg^{-1}, respectively. It was air-dried, crushed, sieved (2 mm) to eliminate large crumbs, and mixed with coarse sand (2–3 mm). The mix (soil:sand, 1:1, v:v) was autoclaved for 1 h on 3 consecutive days.

The plants were grown in pots (700 g growth medium) from January to March in a greenhouse in Granada, Spain. Half of the plants were watered from below with tap water to field capacity (nodulated plants) and the other half with tap water and a nutrient solution [4 mM $Ca(NO_3)_2$, once a week]. The solution contained sufficient N to suppress nodulation and to produce growth equal to that of the nodulated plants (for the treatment with VAM and rhizobacteria). The temperature was controlled (15/32°C, night/day), but varied more widely with occasional control failure. The days were generally sunny throughout the experimental period.

Assays

Roots were separated from the sand-soil mix by crumbling and shaking. Root fragments were collected from the crushed medium, washed together with the roots, dried (70°C, 2 days), and weighed. The root nodules, seeds, and shoots were dried and weighed separately. Root samples for VAM determination were cleared in 5% KOH (90°C, 30 min) washed (H_2O), acidified (0.01 *N* HCl, 1 h), stained with trypan blue (0.05%) in water/lactic acid/glycerol (1:1:2, 90°C, 15 min), and assayed for percent VAM colonization by the gridline-intersect method (Ambler and Young 1977).

Soils were separated from the roots, air-dried, and dry-sieved to eliminate crumbs and sand >2 mm, and to separate the rest into fractions of particle sizes <0.5 and >0.5 mm. The fraction of particle size <0.5 mm was used to determine soil pH (H_2O). These small-particle soil fractions from the replicates within treatments were then combined, mixed, and used to prepare slurries for a count of colony-forming units of organisms. Dilutions of the slurries through 10^{-5} were made to estimate the presence and survival of the inoculated rhizobacterium (Andrade et al. 1995).

The water-stable aggregates (WSA) were determined according to Kemper and Rosenau (1986) as modified by Andrade et al. (1995). Dry-sieved aggregates (2.0 mm>soil>0.5 mm, 30 g) were immersed in water on a sieve (0.5 mm pores, 10 cm diameter), agitated (16 vertical strokes min^{-1} for 3 min through a 10-cm column of water), dried, and weighed. The fine sand contained in the resulting water-stable particles was determined by dispersing the particles and weighing the remaining sand fraction. Sand-free aggregated materials were reported as a percentage of the total soil.

Results

Plant effects

Plant responses to combinations of *G. mosseae* and *Bacillus* sp. were different in the two N-nutrition treatments: they were uniform in nodulated plants but varied from growth enhancement to inhibition in the fertilized ones (Tables 1 and 2). Although the main effect of N nutrition on shoots was not significant by analysis of variance (Table 1), within fertilized plants all four microbial treatment combinations were different from each other ($P<0.05$) while in nodulated plants they were not ($P>0.16$). Significant main effects of VAM and the rhizobacterium (Table 1) denoted the microbial influence on their host plant's development. Interactions between the main effects (Table 1) indicated changes in the direction of the VAM response and changes in the magnitude of the rhizobacterium response with N nutrition. Root growth (not shown) was also affected by N nutrition (Table 1) and by VAM colonization, but was not affected by the rhizobacterium.

Root:shoot and seed:shoot ratios (Table 2) are parameters of plant development that are of interest in evaluating symbiotic effects on soil stability or plant productivity, respectively. Neither ratio changed significantly in treatments with vs. without the rhizobacterium in nodulated plants. However, both root and seed development of rhizobacterium-inoculated plants increased relative to the shoots in fertilized plants, largely because of the decline in absolute shoot growth. The VAM fungus, in contrast, affected only root:shoot ratios in both N treatments. Thus, the rhizobacterium influenced more than one relationship in plant development but was affected by the form of N nutrition, while the VAM fungus influenced only the root:shoot (but not the seed:shoot) relationship.

N input affected shoot dry mass and root:shoot and seed: shoot ratios in all treatment combinations, except for shoot dry mass in the VAM + rhizobacterium treatment (Table 2). In this latter treatment, the shoot-growth-retarding effects of the *Bacillus* sp. and the shoot-growth-promoting effects of *G. mosseae* may have cancelled each other in the N-fertilized plant, producing growth similar to that of the nodulated plant.

Table 1 Main effects and interactions by analysis of variance of plant, soil, and symbiotic parameters of nodulated or N-fertilized pea plants. The main effects were nodulation or fertilization (*NUT*), colonization by a vesicular-arbuscular mycorrhizal (*VAM*) fungus, and inoculation with a rhizobacterium or its absence (*BAC*). The response variables were root, shoot, and nodule dry mass and root:shoot and seed:shoot ratios, VAM (percent root colonization), WSA (soil aggregates, >0.5 mm) and soil pH

Main effect	Response variables							
	Root	Shoot	Root:S	Seed:S	Nodule	VAM	WSA	Soil pH
NUT	<0.001	0.773	<0.001	<0.001		<0.001	0.020	<0.001
VAM	<0.001	<0.001	0.148	0.652	0.189		<0.001	<0.001
BAC	0.949	<0.001	0.002	0.008	0.003	0.005	0.064	0.009
N×V	0.005	<0.001	0.003	0.677			0.116	<0.001
N×B	0.685	<0.001	<0.001	0.041		0.854	0.433	0.085
V×B	0.989	0.004	0.189	0.661	0.503		0.502	0.980
N×V×B	0.454	0.027	0.153	0.570			0.636	0.473

Table 2 Shoot dry mass and root:shoot and seed:shoot ratios of nitrate-fertilized or nodulated pea plants. The soils were either inoculated with a vesicular-arbuscular mycorrhizal (*VAM*) fungus and a rhizobacterium (+VAM+BAC), with one organism (+VAM–BAC or –VAM+BAC), or were not inoculated (–VAM–BAC). Numbers are means ±SEM of five replications

N nutrition	Shoot dry mass (g)		Root:shoot ratio		Seed:shoot ratio	
	+VAM	–VAM	+VAM	–VAM	+VAM	–VAM
Nodulated						
+BAC	3.0±0.1	3.2±0.1	0.169±0.017	0.135±0.005	0.623±0.015	0.621±0.016
–BAC	2.9±0.1	3.0±0.2	0.180±0.017	0.144±0.014	0.610±0.017	0.613±0.015
Fertilized						
+BAC	2.9±0.2	2.1±0.3	0.232±0.011	0.224±0.010	0.575±0.009	0.603±0.055
–BAC	4.5±0.2	2.6±0.1	0.152±0.004	0.185±0.005	0.516±0.012	0.514±0.014

Endophyte effects

Root colonization by the VAM fungus was more intensive in plants without than in those with the rhizobacterium in both N treatments, and was significantly smaller in the nodulated than in the N-fertilized roots with or without the rhizobacterium (Table 3). These results indicate antagonism between *G. mosseae* and the *Bacillus* sp., while the differences due to N nutrition may have been due to direct or plant-mediated stimulation of the VAM fungus by $Ca(NO_3)_2$, or antagonism with *Rhizobium* sp. effects on the host plant. The main effects of N nutrition and of the rhizobacterium on VAM colonization were significant, but the lack of interaction (Table 1) indicated similar VAM responses in magnitude and direction to those of fertilization and nodulation.

There was no VAM effect on nodulation in the presence or in the absence of the rhizobacterium (Table 3), but nodulation in the inoculated plants was inhibited both with and without VAM colonization. Thus, the rhizobacterium reduced both nodulation and VAM colonization. Higher levels of Gram-positive organisms (including *Bacillus* sp. BH-II) were recorded in the soils of nodulated plants than in N-fertilized soil, and counts of colony-forming units tended to be highest in the absence of the VAM fungus (Table 4).

Table 3 Development of microsymbionts or symbiotic plant organs in the roots or soils of nodulated or N-fertilized pea plants. Values for vesicular-arbuscular mycorrhiza (*VAM*; percent root colonization) and nodule (dry mass) are the means and SEM of five replications. *Bacteria* denotes Gram-positive organisms (colony-forming units×10^5) and includes *Bacillus* sp. BH-II

Treatment	VAM (%)	Nodule (mg)	Bacteria
Nodulated			
+V+B	30.0±5.6	42±2	3.3
–V+B	0.0	40±4	6.7
+V–B	46.6±4.1	54±3	3.2
–V–B	0.0	48±4	3.8
Fertilized			
+V+B	49.8±5.9	0	1.8
–V+B	0.0	0	2.6
+V–B	64.6±5.7	0	1.6
–V–B	0.0	0	1.8

Soil effects

The percentage of soil aggregated into water-stable particles (>0.5 mm) was significantly greater in +VAM than in –VAM soil of both N treatments (Table 4). There was no significant rhizobacterial effect on water-stable aggregates in +VAM plants, but in –VAM plants aggregation was more pronounced in the presence of the rhizobacterium regardless of N treatment. The VAM + rhizobacterium-inoculated soils had the highest levels of water-stable aggregates in both N treatments and those without either treatment had the lowest levels. Soils of the fertilized +VAM

Table 4 Water-stable aggregates (*WSA*) and soil pH of nodulated or nitrate-fertilized pea plants. Soils were either inoculated with a vesicular-arbuscular mycorrhizal (*VAM*) fungus and a rhizobacterium (+VAM+BAC), with one organism (+VAM–BAC or –VAM+BAC), or were not inoculated (–VAM–BAC). Numbers are the means ±SEM of five replications

N nutrition	WSA (%)		Soil pH	
	+VAM	–VAM	+VAM	–VAM
Nodulated				
+BAC	25.0±3.1	17.6±0.9	7.19±0.02	6.67±0.04
–BAC	22.4±2.0	14.6±1.6	7.20±0.02	6.70±0.03
Fertilized				
+BAC	29.2±1.1	17.9±0.8	7.49±0.01	7.38±0.05
–BAC	28.2±2.3	15.6±1.6	7.59±0.02	7.46±0.04

plants had higher levels of water-stable aggregates with or without the rhizobacterium than those of the nodulated +VAM plants. The water-stable aggregate status of –VAM soils did not change with N treatment, but it improved when colonized with the rhizobacterium (Table 4).

The rhizobacterium had a small, but significant effect on soil pH only in the +VAM soils of the N-fertilized treatment (Table 4). The VAM fungus, in contrast, raised soil pH in all cases, especially in the soils of nodulated plants, which had a significantly lower pH than the soils of the N-fertilized plants in all treatment combinations (Table 4).

There was a direct relationship between the percentage of water-stable aggregates and pH in the soils of both nodulated and N-fertilized plants, which was apparently influenced by the VAM status of these plants: both pH and the percentage of water-stable aggregates were higher in the soil of +VAM than of –VAM plants. The rhizobacterium did not affect pH significantly.

Discussion

Promotion of legume growth by VAM fungi can be remarkable, especially when accompanied by an enhancement of root-nodule activity in low-P soils. In our moderate P soil, the VAM effect on shoot dry mass was small and VAM colonization was inhibited in noculated plants compared to N-fertilized ones. Antagonism between microsymbionts (Bethlenfalvay et al. 1985), or impairment of root colonization by a low rhizosphere pH (Wong and Marschner 1988) may be possible causes. Although both VAM colonization and nodulation were further inhibited in our plants inoculated with the rhizobacterium, no significant bacterial effects on shoot dry mass were recorded in nodulated plants.

While shoot growth was uniform in nodulated plants of the four treatment combinations, the influence of the rhizosphere organisms on water-stable aggregates was diverse. Stronger development of VAM roots (and presumably their associated soil mycelia) encouraged aggregate stability compared to –VAM soils. Both the VAM fungus and the rhizobacterium enhanced aggregation in spite of their apparent antagonism. Such antagonisms between rhizosphere organisms are well-known, but are evaluated usually by plant responses only (Cook and Baker 1983).

Elevated pH in the soils of VAM-colonized plants has been attributed to an increased uptake of counter-balancing anions by these plants (Buwalda et al. 1983). The association of higher soil pH with aggregate stability shown by our data suggests a functional relationship between these soil parameters. However, the literature (Miller and Jastrow 1992) offers little support for it. Although a low soil pH may decrease water-stable aggregate stability by interfering with the bridging of clays and organic materials by polyvalent cations (Oades 1984), it may also increase stability by slowing the degradation of organic stabilizing agents (Martin and Aldrich 1955), and by enhancing the adherence of microbial cells and clay particles to each other (Oades 1984). In general, soil pH appears to affect water-stable aggregates mainly through its effects on microbial activity (Hamblin 1991).

Plant growth promotion by certain rhizobacteria is well-known (Burr and Caesar 1984) and the organisms are used widely to influence plant yield (Stephens 1994). However, characterization of a rhizosphere organism as deleterious or growth-promoting may not do justice to its entire potential range of influence in the plant-soil system. Our *Bacillus* sp. BH-II had diverse effects both above and below ground. To emphasize that such an organism may elicit soil as well as plant responses which may be both positive and negative, we term it an "agrosystem-affecting rhizobacterium" (ASAR). Within the context of sustainability in agriculture, soil responses are of particular interest, if legumes indeed aggravate erosion (Oschwald and Siemens 1976; Zhu et al. 1989). Hence, contributions of rhizobacteria to the agrosystem (Bethlenfalvay and Schüepp 1994) should be evaluated for their impact on plant and soil alike.

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