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An AM fungus and a PGPR intensify the adverse effects of salinity on the stability of rhizosphere soil aggregates of *Lactuca sativa*

Josef Kohler, Fuensanta Caravaca*, Antonio Roldán

CSIC-Centro de Edafología y Biología Aplicada del Segura, Department of Soil and Water Conservation, P.O. Box 164, Campus de Espinardo 30100-Murcia, Spain

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A B S T R A C T

A mesocosm experiment was conducted to examine the effect of an arbuscular mycorrhizal (AM) fungus (*Glomus mosseae* (Nicol & Gerd.) Gerd. & Trappe) and a plant growth-promoting rhizobacterium (PGPR) (*Pseudomonas mendocina* Palleroni), alone or in combination, on the structural stability of the rhizosphere soil of *Lactuca sativa* L. grown under two levels of salinity. The plants inoculated with *P. mendocina* had significantly greater shoot biomass than the control plants at both salinity levels, whereas the mycorrhizal inoculation was only effective in increasing shoot biomass at the moderate salinity level. The aggregate stability of soils inoculated with the PGPR and/or *G. mosseae* significantly decreased with increasing saline stress (about 29% lower than those of soils under non-saline conditions). Only the inoculated soils showed higher concentrations of sodium (Na) under severe saline stress. The severe salinity stress decreased the glomalin-related soil protein (GRSP) concentration, but the highest values of GRSP were recorded in the inoculated soils. Our findings suggest that the use of AM fungi and/or a PGPR for alleviating salinity stress in lettuce plants could be limited by their detrimental effect on soil structural stability.

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1. Introduction

Secondary salinisation of agricultural soils by irrigation is a serious land degradation problem in arid and semi-arid areas, where evaporation greatly exceeds precipitation and salts dissolved in the ground water reach and accumulate at the soil surface through capillary movement. It has been estimated that more than 7 % of the earth is land occupied by saline soil (Tester and Davenport, 2003), rising up to 15 % in arid and semi-arid areas of the world, while salt-affected soils represent about 40 % of the world's irrigated lands (Zahran, 1997). Excessive amounts of salts, mainly sodium (Na) salts, in the soil solution cause numerous adverse phenomena such as destabilisation of soil structure, deterioration of soil hydraulic properties and a considerable reduction in crop yield (Lax et al., 1994; Kohler et al., 2009). Likewise, various authors (Rietz and Haynes, 2003) have also reported negative effects of salinity on soil microbial biomass carbon and enzyme activities.

In semi-arid environments, soil aggregate stability is one of the most important properties controlling the growth of plants which, in turn, protects the soil against water erosion. Thus, the improvement of soil structural stability is of great importance in rendering these degraded, saline soils suitable for agriculture. The contribution of microbial populations, either as free-living organisms or associated with plant roots, and their activities to soil aggregate stability has been stressed by Jastrow and Miller (1991). In particular, the symbiosis between arbuscular mycorrhizal (AM) fungi and plants has been shown to contribute to the stability of soil aggregates, including soils of high salinity such as salt marshes (Caravaca et al., 2005). Arbuscular mycorrhizal fungi primarily influence the stability of macroaggregates (>250 μm), which they are hypothesised to help stabilise via hyphal enmeshment aggregates (Miller and Jastrow, 2000) and by deposition of organic substances (Bearden and Petersen, 2000). A key factor in the contribution of AM fungi to soil aggregation is the production of the glycoprotein glomalin, which acts as an insoluble glue to stabilise aggregates (Gadkar and Rillig, 2006). Operationally defined by the extraction and detection conditions (Wright and Upadhyaya, 1996), it is detected in large amounts in diverse soils as glomalin-related soil protein (GRSP; Rillig, 2004) although the role of GRSP in the stabilisation of saline soils has not been confirmed.

Bacteria associated with the mycorrhizosphere have been suggested to be involved in plant growth and establishment of AM fungi (Larsen et al., 2009). The production of exopolysaccharides (EPSs) by bacterial populations in response to adverse environmental conditions, such as desiccation, has been shown to contribute to soil aggregation, leading to increased water retention

* Corresponding author. Tel.: +34 968 3962 55; fax: +34 968 396213.
E-mail address: jkohler@cebas.csic.es (F. Caravaca).

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in the rhizosphere (Kaci et al., 2005). In previous work, we demonstrated the effectiveness of inoculation with a plant growth-promoting rhizobacterium (PGPR), *Pseudomonas mendocina*, for both soil stabilisation and promotion of soil fertility under non-saline field conditions (Kohler et al., 2006). The study of the antagonistic or synergistic effects of different microbial inoculants, when co-inoculated, is a crucial step in the development of effective host-microorganism combinations. To the best of our knowledge, nothing is known about the interaction of PGPR and AM fungi with respect to soil aggregate stability under induced saline stress.

We hypothesise that inoculation with a PGPR, alone or in combination with an AM fungus, can improve soil physical properties, even under saline stress. To assess this hypothesis, we determined the combined effects of such microbial inoculations on the structural stability of the rhizosphere soil of *Lactuca sativa* under different conditions of soil salinity.

2. Materials and methods

2.1. Soil and plant

An agricultural soil used to cultivate lettuce was collected near Murcia (SE Spain). The climate is semi-arid Mediterranean with an average annual rainfall of 300 mm and a mean annual temperature of 19.2 °C; the potential evapo-transpiration reaches 1000 mm y^{-1}. The analytical characteristics of the agricultural soil used, determined by standard methods (Page et al., 1982), were: pH (1:5 in H_2O) 8.89; electrical conductivity 0.18 dS m^{-1}; TOC 1.80%; total N 2.01 g kg^{-1}; available P, 70 μg g^{-1}; extractable K, 440 μg g^{-1}; cationic exchange capacity, 15 cmol kg^{-1}.

The plant used in the experiment was lettuce (*L. sativa* L. cv. Tafalla). Seeds of lettuce were grown for 15 days in peat substrate under nursery conditions, without any fertilization treatment.

2.2. Microorganisms

The AM fungus used was *Glomus mosseae* (Nicol & Gerd.) Gerd. & Trappe, obtained from the collection of the experimental field station of Zaidín, Granada. The *Glomus* species was multiplied in pots using a mixture of sterile sepiolite/vermiculite (1:1, v:v) as growing substrate and *Sorghum* sp. as host plant. Trap cultures were maintained under greenhouse controlled conditions for 4 months. The AM fungal inoculum consisted of a mixture of rhizospheric soil from the trap cultures containing spores, hyphae and mycorrhizal root fragments and was stored in polyethylene bags at 5 °C. The inoculum was subjected to a most probable number test (Sieverding, 1991) to determine potential infectivity and to equalize application doses. The source of inoculum had a potential infectivity of about 35 infective propagules g^{-1} inoculum.

The PGPR strain *Pseudomonas mendocina* Palleroni was obtained from Probelte, S.A., Murcia, and was selected on the basis of its ability to produce siderophores. The *P. mendocina* was grown in a medium (nutrient broth, Scharlau Chemie, Spain) composed of meat and yeast extracts, peptone and sodium chloride, for 2 days at room temperature on a Heidolph Unimax1010 shaker. The bacterial culture was centrifuged at 2287 × g for 5 min at 2 °C and the sediment was re-suspended in sterilized tap water. The bacterial suspension contained 10^9 colony forming units (CFU) mL^{-1}.

2.3. Microbial inoculation and salt stress treatments

The experiment was a mesocosm assay, conducted as a randomized factorial design with two factors and five-fold replication. The first factor had seven levels: control soil, soil inoculated with the AM fungus *G. mosseae*, soil inoculated with the bacterium *P. mendocina*, the combination of soil inoculated with the bacteria *P. mendocina* and with *G. mosseae* and a soil fertilized with inorganic fertilizer. The second factor had three levels of salt stress: non-salt stress, moderate and severe salt stress. Five replicates per treatment were set up, making a total of 105 pots.

Seven hundred grams of substrate, consisting of soil and vermiculite at a ratio of 2:1 (v:v) sterilized by autoclaving at 105 °C for 60 min in three consecutive days, were placed in 1-L pots. *L. sativa* seedlings were transplanted to the pots (one per pot). The AM inoculum was mixed with the potting substrate, at a rate of 5% (v/v). The same amount of the autoclaved inoculum was added to non-AM plants, supplemented with a filtrate (Whatman no. 1 paper) of the culture to provide the microbial populations accompanying the AM fungi. The plants were inoculated with *P. mendocina* twice during the growth period. The dose of inoculum applied corresponded to 10^{10} CFU per plant. Fertilized plants received 10 ml of Long Ashton Nutrient Solution on two occasions (μg mL^{-1}): 175.9 nitrogen, 156.2 potassium, 160.2 calcium, 98.4 sulphur, 11.7 sodium, 5.4 chlorine, 5.0 iron-chelate sequestrene, 0.54 manganese, 0.54 boron, 0.10 copper, 0.06 zinc, 0.006 molybdenum and 40 phosphorus. Two concentrations (2 g and 4 g NaCl kg^{-1} soil) of saline solution were applied to the saline pots. The NaCl concentration was gradually increased until reaching the required salinity of NaCl for each concentration, applied over four consecutives days to avoid osmotic shock. A plastic bag was put underneath each pot to collect excess water due to drainage. This water was reapplied to the respective pot. All seedlings were grown for five weeks without any fertilizer treatment (except fertilized seedlings). The experiment was conducted in a greenhouse, located in the SACE service at the Campus of Espinardo (University of Murcia, Spain). During the experiment, the mean temperature was 22 °C, and the relative humidity was between 60% and 80%. Midday photosynthetically active radiation (PAR) averaged 260 μE m^{-2} s^{-1}.

2.4. Plant analyses

Five weeks after planting five plants per treatment were harvested. The roots were washed free from soil under a stream of cold tap water and fresh and dry (105 °C, 5 h) weights of leaves and roots were recorded.

Roots were subsampled in three 2-cm cross-sections of the upper, middle, and lower root system. To assess colonisation, roots were cleared with 10% KOH and stained with 0.05% trypan blue (Phillips and Hayman, 1970). The percentage of root length colonised by AM fungi was calculated by the gridline intersect method (Giovannetti and Mosse, 1980). Positive counts for AM colonisation included the presence of vesicles or arbuscules or typical mycelium within the roots.

2.5. Soil analyses

At the end of the experiment, rhizosphere soil samples were collected from the pots. To collect the rhizosphere soil the root system with adhering rhizosphere soil was placed into a plastic bag and shaken, thus separating the rhizosphere soil from the root system. Rhizosphere soil samples were air-dried at room temperature and sieved at 2 mm for physical-chemical and chemical analysis or at 0.2–4 mm for aggregate stability.

The percentage of stable aggregates was determined by the method described in Lax et al. (1994). A 4 g aliquot of soil sieved between 0.25 and 4 mm was placed on a small 0.250 mm sieve and wetted by spraying with water. After 15 min the soil was subjected to an artificial rainfall of 150 mL with energy of 270 Jm^{-2}. The remaining soil on the sieve was dried at 105 °C and weighted (P1). The soil was then soaked in distilled water and, after 2 h, passed

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