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Alleviation of salt stress by arbuscular-mycorrhizal *Glomus* species in *Lactuca sativa* plants

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Improved salt tolerance of mycorrhizal plants is commonly attributed to their better mineral nutrition, particularly phosphorus. However, the effect of arbuscular-mycorrhizal (AM) fungi on salt tolerance may not be limited to this mechanism. We investigated the possibility that non-nutritional effects of AM fungi, based on proline accumulation or increased photosynthesis and related parameters, can influence the tolerance of lettuce (*Lactuca sativa* L.) to salinity. Three levels of salt (3, 4 and 5 g NaCl kg^{-1} dry soil) were applied and plants were maintained under these conditions for 7 weeks. The salt-treated AM plants produced greater root and shoot dry weights than unfertilized or P-fertilized non-AM controls. With increasing salinity, both shoot and root dry weights were reduced, but this decrease was greater in uninoculated plants. In particular, shoot dry weight was not reduced in *G. fasciculatum*-colonized plants as a consequence of salt, whereas in uninoculated plants it was reduced by about 35% at the highest salt level. Proline accumulation was considerably lower for P-amended non-AM and for AM plants except for *G. mosseae*-colonized plants than was the case for unamended plants. Transpiration, carbon dioxide exchange rate (CER), stomatal conductance and water use efficiency (WUE) were higher in mycorrhizal plants. At 5 g NaCl kg^{-1}, both photosynthesis and WUE increased by more than 100% in mycorrhizal treatment relative to uninoculated plants. The contents of phosphorus of P-fertilized non-AM plants was similar to or higher than those of *G. mosseae*- and *G. fasciculatum*-colonized plants. Plants colonized by *G. deserticola* had the highest P-content regardless of salt level. Hence, the effect of *G. mosseae* and *G. fasciculatum* on salt tolerance in this experiment could not be attributed to a difference in the P content. The mechanisms by which these two fungi alleviated salt stress appeared to be based on physiological processes (increased CER, transpiration, stomatal conductance and WUE) rather than on nutrient uptake (N or P).

Key words – Arbuscular-mycorrhizal *Glomus* species, *Lactuca sativa*, lettuce, salinity, stress.

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Introduction

Saline soils occupy over 7% of the earth's land surface, and crop production on these soils is relatively low (Jain et al. 1989). Soil properties that inhibit or reduce plant survival and development include unfavourable pH, imbalance of essential ions and altered soil structure, factors which reduce aeration and water holding capacity (Bettenay 1986). Probable causes of salt toxicity in various plants involve ionic and osmotic effects. Ionic effects include interference with essential ions and a lowering of the net rate of photosynthesis. Osmotic effects are associated with inhibition of cell wall extension and cellular expansion, leading to reduced plant growth (Lewis et al. 1989).

The introduction of arbuscular-mycorrhizal (AM) fungi to sites with saline soil may improve early plant tolerance and growth (Jain et al. 1989). Although improved salt tol-

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erance of mycorrhizal plants can be related to enhanced mineral nutrition, particularly phosphorus (Graham 1986), the effect of these fungi on salt tolerance may not only be limited to this mechanism. Hence, in a study of the interaction between AM fungi and salinity it is essential to determine if the effect of the fungus on P uptake is the primary mechanism by which it is able to increase salt tolerance or whether this effect is due to additional or alternative mechanisms. Arbuscular-mycorrhizal fungi may influence plant hormones (Danneberg et al. 1992) or improve water uptake (Ruiz-Lozano and Azcón 1995). Other mechanisms may include osmotic adjustment, which assists in the maintenance of leaf turgor, and effects on physiological processes such as photosynthesis, transpiration, conductance and water use efficiency.

One of the best-known responses of plants to drought and other stresses is the accumulation of soluble, low-molecular-mass solutes such as proline (Paleg et al. 1984). Photosynthesis is also greatly affected by salinity because of stomatal closure (Taleisnik 1987). Dawson and Gibson (1987) reported a salinity-induced decrease in the photosynthetic rates of wheat and barley, while the water use efficiency (WUE) was only marginally affected. The transpiration per unit leaf area in several crops has been shown to decrease in response to increasing salinity (Hoffman and Phene 1971). Osmotic adjustment, as well as increased photosynthesis, may enable salinized plants to maintain better turgor and growth during periods of stress.

The purpose of this experiment was to study the possibility of non-nutritional effects of AM fungi, based on proline accumulation or increased gas exchange and WUE, on the salinity tolerance of *Lactuca sativa*. Non-mycorrhizal, but P-fertilized, plants of comparable size and P content were established prior to imposition of salinity stress in an attempt to produce a proper control. We evaluated whether plants inoculated with an appropriate arbuscular-mycorrhizal fungus are better able to withstand salt stress as a result of mechanisms based on physiological processes rather than on uptake of nitrogen or phosphorus.

Abbreviations – AM, arbuscular-mycorrhizal fungi; CER, CO_2-exchange rate; WUE, water use efficiency.

Materials and methods

Experimental design and statistical analysis

The experiment consisted of a randomized complete block factorial with two factors: (1) mycorrhizal treatment consisting of three *Glomus* species or two nonmycorrhizal treatments, one P-fertilized non-AM and one unfertilized non-AM, and (2) three salt concentrations 3, 4 and 5 g NaCl kg^{-1} dry soil, sequentially added as a water solution. Five replications per treatment were made to give a total of 75 pots (one plant per pot).

Data were subjected to analysis of variance (ANOVA) with AM treatment and salt level as factors. When the main effect was significant ($P < 0.05$), differences among means were evaluated for significance by Duncan's multiple range test in an orthogonal design. For the percentage values, arcsin transformation was made before the statistical analysis.

Soil and biological material

Loamy soil was collected from the grounds of the Zaidin Experimental Station (Granada), sieved (2 mm), diluted with quartz-sand (<1mm) (1:1, soil:sand, v/v) and sterilized by steaming (100°C for 1 h per day during 3 days). The soil had a pH of 8.1; 1.81% organic matter, nutrient concentrations (mg kg^{-1}): 2.5 N, 6.2 P ($NaHCO_3$-extractable P), 132.0 K. The soil was composed of 35.8% sand, 43.6% silt and 20.5% clay. Electrical conductivity was 0.7 dS m^{-1}. Pots were filled with 500 g of the sterilized soil/sand mixture. Mycorrhizal inoculum for each endophyte were bulked in an open pot culture of *Allium cepa* L. and consisted of soil, spores, mycelia and infected root fragments. The AM species, from the Zaidín Experimental Station collection (Ruiz-Lozano et al. 1995a), were *Glomus mosseae* (Nicol. and Gerd.) Gerd. and Trappe, *Glomus fasciculatum* (Thax. sensu Gerd.) Gerd. and Trappe and *Glomus deserticola* (Trappe, Bloss and Menge). Five grams of inoculum possessing similar characteristics (an average of 30 spores g^{-1} and 75% of infected roots) of the three *Glomus* isolates were added to each pot. Four lettuce seeds were planted directly above the inoculum or soil (in controls), and thinned after emergence to one seedling per pot. Controls received 5 ml of an inoculum filtrate that was sieved through a 25-µm filter, in an attempt to provide similar microbial populations in all treatments (excluding AM fungi).

Growth conditions

The plants were grown in a controlled environmental chamber with day/night temperatures of 25/15°C, 70/80% relative humidity (RH) and a photoperiod of 14 h provided by fluorescent (24-F96T12VHO/CW) and incandescent (45–40 W) Sylvania and Phillips lamps, respectively. Photosynthetic photon flux (PPF) was ca 500 µmol m^{-2} s^{-1}. Plants were established for one month prior to salinization. Three concentrations of saline solution (low, medium and high) were applied by appropriate dilutions of 2 *M* NaCl. The concentration of NaCl was increased gradually to 3 (low), 4 (medium) and 5 (high) g NaCl kg^{-1} dry soil, applied on alternative days to avoid osmotic shock. Electrical conductivity of the soil after application of the salt was 2.5, 3.2 and 4.0 dS m^{-1}, respectively. Plants were maintained at these conditions for 7 weeks.

Plants were fertilized with Hewitt's (Hewitt 1952) nutrient solution (10 ml pot^{-1} $week^{-1}$) lacking P. For P-fertilized plants, P was supplied as KH_2PO_4 (7 mg pot^{-1} $week^{-1}$). This rate was selected to match the effects on growth of the fungi, thereby being an appropriate control

Tab. 1. Shoot and root dry weight (g plant^{-1}) of uninoculated or mycorrhizal-colonized lettuce plants grown at three levels of salinity (3, 4 and 5 g NaCl kg^{-1}). Within each parameter, means followed by the same letter are not significantly different ($P < 0.05$) as determined by Duncan's multiple-range test (n = 5).

Fungal species	Shoot			Root		
	3	4	5	3	4	5
Control (uninoculated)	0.97d	0.66e	0.65e	0.20gh	0.16hi	0.13i
P-fertilized (uninoculated)	1.01d	0.84d	0.66e	0.22fg	0.15i	0.15i
G. mosseae	1.81a	1.47bc	1.39bc	0.47a	0.33cd	0.28ef
G. fasciculatum	1.52b	1.45bc	1.49bc	0.31de	0.28ef	0.26ef
G. deserticola	1.54b	1.53b	1.31c	0.40b	0.35bc	0.26ef

for the mycorrhizal plants (Ruiz-Lozano and Azcón 1995).

Measurements

At harvest (11 weeks after planting), the root system was separated from the shoot and dry weights were determined after drying in a forced drought oven at 70°C for two days.

Visual observation of AM infection was made by clearing washed roots in 10% KOH and staining with 0.05% trypan blue in lactophenol (v/v) according to Phillips and Hayman (1970). Quantification was made by the line-intercept method of Giovannetti and Mosse (1980). An average of 300 root pieces per plant and 5 plants per treatment were examined.

Rates of transpiration, CO_2 exhange, stomatal conductance and water use efficiency were determined at the end of the experiment at 1180 µmol m^{-2} s^{-1} (PPF) using a halogen lamp and a portable, integrated infrared CO_2 analyzer (Analytical Development Company, Hoddesdon, UK, model LCA-3). Measurements were made 2 h after irradiation. Proline content was determined colorimetrically (Bates et al. 1973). The total plant content of N (micro-Kjeldahl) and P (Olsen and Dean 1965) were measured.

Results

Prior to addition of salt, only the unfertilized non-AM plants were smaller than plants of other treatments (data not shown). After salt applications, the shoot dry weight of unfertilized non-AM plants decreased with increased salinity (Tab. 1). For these plants, the growth decreased by 32% at both medium and high salt levels in comparison to 3 g NaCl kg^{-1}, while in P-fertilized non-AM plants the reduction was significant (35%) only at the highest salt level. In mycorrhizal plants the shoot growth reduction, with respect to the lowest salt level, was significant only in plants colonized by *G. mosseae* and *G. deserticola*. Growth reduction in *G. mosseae*-colonized plants, at medium and high NaCl, was 19 and 24%, respectively. Plants colonized by *G. deserticola* displayed reduced growth (15%) at the highest NaCl level. Neither shoot nor root growth was reduced in *G. fasciculatum*-colonized plants as a consequence of salt application.

At all salt levels, mycorrhizal plants grew more than unfertilized and P-fertilized non-AM plants. At the lowest level of salt, the effect of AM treatments on shoot dry weight (relative to P-fertilized non-AM control) was an increase of 79, 50 and 52% for *G. mosseae*-, *G. fasciculatum*- and *G. deserticola*-colonized plants, respectively. At the highest levels of salinity shoot dry weight of AM-colonized plants increased by over 100%. Phosphate application did not affect shoot growth at high NaCl, and it did not affect root growth at any NaCl level. At low and medium salt treatments, root dry weight responded to the species of colonizing mycorrhizal fungus. *G. fasciculatum*-colonized plants had lower root dry weights than *G. mosseae*- or *G. deserticola*-colonized plants (Tab. 1).

No mycorrhizal infection was found in control plants and the degree of mycorrhizal colonization was not significantly affected by salt level in the medium (Tab. 2). Under all salt treatments the degree of infection by *G. deserticola* was highest.

Tab. 2. Proline concentration (nmol [g FW]$^{-1}$) and mycorrhizal colonization (percentage of root lenght) in uninoculated or mycorrhizal lettuce plants grown at three levels of salinity (3, 4 and 5 g NaCl kg^{-1}). Within each parameter, means followed by the same letter are not significantly different ($P < 0.05$) as determined by Duncan's multiple-range test (n = 5).

Fungal species	Proline			Mycorrhizal colonization		
	3	4	5	3	4	5
Control (uninoculated)	249e	406ab	426a	0d	0d	0d
P-fertilized (uninoculated)	217e	263e	379bc	0d	0d	0d
G. mosseae	178f	239e	343cd	70b	64bc	68bc
G. fasciculatum	245e	250e	309d	69bc	65bc	62c
G. deserticola	154f	170f	185f	87a	83a	83a

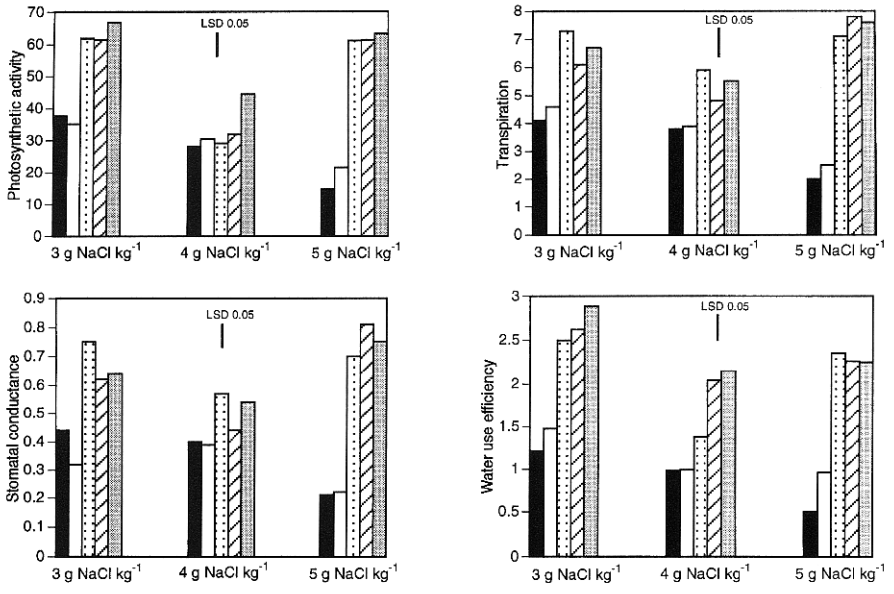

Fig. 1. Photosynthetic activity (μmol CO_2 m^{-2} s^{-1}), transpiration rate (mmol m^{-2} s^{-1}), stomatal conductance (mol H_2O m^{-2} s^{-1}) and water use efficiency (μmol CO_2 mol^{-1} H_2O) of uninoculated (unfertilized ■, and P-fertilized □) or mycorrhizal (*G. mosseae* ⊞, *G. fasciculatum* ▨, or *G. deserticola* ▩) lettuce plants grown at three salinity levels (3, 4 or 5 g NaCl kg^{-1}).

Proline concentrations increased as a consequence of salinity (Tab. 2). However, proline accumulation was considerably less for mycorrhizal (except *G. mosseae*-colonized plants) and P-amended non-AM plants than for the unfertilized non-AM plants. In *G. deserticola*-colonized plants proline did not accumulate significantly with salinity. In the case of *G. fasciculatum*-colonized plants, the increase in proline concentration was significant (26%) at the highest salt level. In contrast, in unfertilized non-AM plants proline increased by 63 and 71% with increasing salinity.

Photosynthetic activity (Fig. 1) was increased by mycorrhization in all cases except at the medium level of salinity, where infection by *G. mosseae* and *G. fasciculatum* did not increase photosynthesis. *G. fasciculatum*-colonized plants also showed no differences for transpiration and stomatal conductance at 4 g NaCl kg^{-1}. At this salt treatment, only plants colonized by *G. deserticola* had an increased photosynthetic rate (46%) as compared with P-fertilized plants. The increase in WUE was 39% (*G. mosseae*), 105% (*G. fasciculatum*) and 124% (*G. deserticola*). At the lowest salt treatment *G. mosseae*- and *G. fasciculatum*-colonized plants stimulated photosynthesis and WUE by over 75% with respect to unfertilized or P-fertilized non-AM plants; *G. deserticola* increased these two parameters by over 90%. At the highest salt treatment, both photosynthesis and WUE values were over 100% in the three mycorrhizal treatments relative to uninoculated P-fertilized plants.

The values of gas exchange parameters in mycorrhizal plants in the highest treatment of salt were considerably greater than in the medium treatment of salt, while in nonmycorrhizal plants these parameters decreased in proportion to increasing salt application.

Table 3 shows that nitrogen content was little affected by mycorrhizal presence at low and medium salt treatments. At the low treatment only *G. deserticola*-colonized plants had less N; at the medium level, it was similar in all treatments. When the salt level was increased to 5 g NaCl kg^{-1}, P-fertilized plants had a higher N content than mycorrhizal and unfertilized non-AM plants. *G. deserticola*-colonized plants had the highest P-content values regardless of salt level. P fertilized plants equalized their P-content with those of plants colonized with *G. mosseae* or *G. fasciculatum* even at the highest level of salt (Tab. 3).

Tab. 3. N and P contents (mg $plant^{-1}$) of mycorrhizal or uninoculated lettuce plants grown at three levels of salinity (3, 4 and 5 g NaCl kg^{-1}). Within each parameter, means followed by the same letter are not significantly different ($P < 0.05$) as determined by Duncan's multiple-range test (n = 5).

Fungal species	N			P		
	3	4	5	3	4	5
Control (uninoculated)	16.3b	13.3cd	15.7b	1.2ef	1.3ef	0.9f
P-fertilized (uninoculated)	15.6bc	11.3d	19.9a	2.3c	1.7cd	1.6de
G. mosseae	15.0bc	13.2cd	12.2cd	2.2c	1.8cd	1.9cd
G. fasciculatum	15.0bc	13.8cd	12.9cd	2.0c	2.0c	1.8cd
G. deserticola	11.6d	12.8cd	11.3d	2.8b	3.2a	2.6b

Discussion

Prior to salt stress phosphate fertilization resulted in plants of equal size but in contrast to mycorrhizal-inoculated plants, could not maintain plant biomass after salt treatment. This demonstrates the beneficial effect of mycorrhizae on the growth of lettuce under stress. Allen and Cunningham (1983) and Hirrell and Gerdemann (1980) have reported similar results in salt grass and onion, respectively.

Addition of various salts to soil is known to influence mycorrhizal colonization negatively (Chambers et al. 1980). However, in this study the level of salt did not affect the colonizing ability of the three fungi. The mycorrhizal infection was presumably already fully established when the salt was applied.

Osmotic adaptation increases the tolerance of plants to water deficit induced by salinity (Rosendahl and Rosendahl 1991). The presence of the AM fungi in the roots may have modified the osmotic potential of the leaves, as they have been shown to influence the composition of carbohydrates (Augé et al. 1987) and the level of proline (Ruiz-Lozano et al. 1995a) in the host plant. In the present study proline content increased with salinity. High levels of proline are known to afford protection to various enzyme systems against dehydration (Paleg et al. 1984). In our study, the increase in proline as a consequence of salinity was considerably lower in plants colonized by *G. fasciculatum* and *G. deserticola* than in uninoculated plants or those colonized by *G. mosseae*. This could indicate that mycorrhizal plants (except *G. mosseae* plants) were less affected by salinity and therefore accumulated less proline.

Data concerning gas exchange and water use efficiency indicate greater tolerance in mycorrhizal than in control and P-fertilized plants. The improved water relations of mycorrhizal plants, which have been found to be unrelated to P nutrition (Augé et al. 1986), could further benefit the water balance of plants exposed to salt stress. Hyphae of mycorrhizal fungi often extend 7 cm or more beyond the rhizosphere into soil and can absorb water and nutrients from the soil solution at different osmotic potentials than those at the root surface (Ruiz-Lozano and Azcón 1995).

At the highest salt level, the rates of CO_2 exchange, transpiration, stomatal conductance and water use efficiency were higher than at the medium one, but only in mycorrhizal plants. This could be due to a 'reaction effect' of AM fungi against the increase in salt. Ruiz-Lozano et al. (1995b) subjected plants to successive drought stress periods of one week duration each and found that photosynthesis and related parameters were greatly decreased when water stress was imposed, but increased again after enhancing the stress.

In conclusion, the three species of AM fungi protected host plants against the detrimental effect of salt in the growth medium. The effects of *G. mosseae* and *G. fasciculatum* on the tolerance to salt cannot be attributed to a difference in the phosphorus content as there were no significant differences in phosphorus among the mycorrhizal and phosphate fertilization treatments. The mechanisms by which these fungi alleviated salt stress appear to be based on physiological processes namely, increased CER, transpiration, stomatal conductance and WUE rather than on uptake of N or P. In contrast, Poss et al. (1985) reported that the main role of *G. deserticola* in improving growth of onion in saline soils was by increasing P accumulation. In agreement with results obtained by Allen and Boosalis (1983) and Ruiz-Lozano et al. (1995b) differences between isolates in their protective effect against drought stress were found.

The present results provide conclusive evidence that mycorrhizal colonization directly promotes physiological processes. These mechanisms are important in the adaptation by mycorrhizal plants to conditions of salt stress. This study suggests that the advantages of arbuscular mycorrhiza for plant development under salt stress is related to the improved physiological status of AM-colonized plants.

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