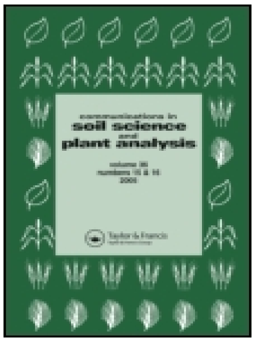

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Mycorrhizal Inoculation and High Arsenic Concentrations in the Soil Increase the Survival of Soybean Plants Subjected to Strong Water Stress

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*Soybean (*Glycine max *L.) cropping is increasing in marginal environments, including water-limited lands, some of which are loaded with arsenic (As). Plants inoculated with mycorrhiza increased their tolerance to water stress. We studied the effect of a sudden and severe water stress on soybean inoculated with the mycorrhizal fungus* Glomus intraradices *in soils with increasing concentrations of As. Soybean plants were grown in greenhouse with adequate water supply for 60 days. Irrigation was stopped completely and soil abruptly reached the permanent wilting point. Most inoculated plants survived under such limiting water stress, but noninoculated plants were clearly affected. Arsenic showed a negative effect on plant growth but improved plant survival under this severe water stress. It seems that the negative effects of As on plant water equilibrium explain why plants affected by As survived extreme water stress events.*

Keywords Arsenic in soils, mycorrhiza, soybean, wilting point

Introduction

Arbuscular mycorrhizal fungi (AM) occur in almost all climates and habitats (Ortas 2008; Smith and Read 1997). They are the most common soil microorganisms that can establish mutual symbioses with terrestrial plants, including nearly all economically important crops. The host plants benefit from the association with the fungi, enhancing their tolerance to abiotic strains and improving plant growth under conditions of water stress (Augé 2001; Zhao and He 2007). Water stress, either permanent or transient, is almost universal, and periods of drought may occur frequently even in regions characterized by high annual rainfall. Water stress is a major abiotic factor that limits agricultural crop production (Bohnert and Bressan 2001). Thus, soil water has been intensively studied for a long time and their status has been measured in different categories, such as field capacity and permanent wilting point (PWP). PWP is defined as the percentage of remaining water when the soil dries and it is retained with a suction force of 1500 kPa (Soil Science Society of America 1997). At this point, most plants wilt without recovery. During a drought, this point could be reached in part of the soil profile and crop production is usually affected. In extreme cases, all the soil dries up to PWP

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and crops die (Brouwer, Goffeau, and Heibloem 1985). The occurrence of extraradical mycelia allows roots greater access to soil water, improving its absorption and plant metabolism, even in drought conditions (Augé 2004). The effects of mycorrhiza on soybean plants subjected to water stress have been studied by several authors (Busse and Ellis 1985; Tjondronerogo and Gunawan 2000; Ruiz-Lozano et al. 2001; Porcel and Ruiz-Lozano 2004).

Soybean (*Glycine max* L.) is one of the main crops in the world and its production has doubled in the past two decades, following worldwide food demand (Eickhout, Bouwman, and van Zeijts 2006). Because this crop can grow under a wide range of environments and management systems, it increases the pressure on the world's arable land. For this reason, soybean cropping is advancing on marginal environments, including water-limited lands, and is thus subjected to frequent drought conditions. In various areas of the world, groundwater is loaded with arsenic (As) (Smedley and Kinniburgh 2002). The irrigation with such water and other geogenic and anthropogenic sources increases the As concentration in soils. The problem of cropping in those contaminated soils has been widely documented (Heikens, Panaullah, and Meharg 2007; Lavado and Reinaudi 1986). Plants exposed to high As levels suffer oxidative stress and show toxicity symptoms, decreases in root and aerial biomass growth and yield, and in some cases even death (Abedin, Feldmann, and Meharg 2002). Arsenic-treated plants suffer a decrease in leaf water potential, transpiration rate, and stomata conductance and a slight decrease in relative water content (Stoeva, Berova, and Zlatev 2005). However, there is no clear knowledge about the effects of extreme water stress on mycorrhiza-inoculated soybean when the crop is subjected to simultaneous effect of As in the soil. Our objective was to evaluate the survival of soybean plants (*Glycine max* L.) inoculated with the mycorrhizal fungus *Glomus intraradices* in soils with increasing concentrations of As and subjected to a sudden and severe water stress.

Materials and Methods

Inoculum Preparation

The *Glomus intraradices* inoculum was propagated in 1-L pots with soil, perlite, and vermiculite (1:1:1 ratio) as substrate and using *Trifolium repens* and *Sorghum bicolor* as hosts for a period of 3 months. To test the correct inoculum propagation, wet sieving was carried out (Gerdemann and Nicolson 1963) and a sucrose gradient was then performed (Walker, Mize, and McNabb 1982). Finally, spore morphology was visualized by light microscopy. At the same time, roots were extracted and stained as described by Phillips and Hayman (1970). The inoculum used was composed of spores found in the substrate, small pieces of colonized roots, and mycelia extraradical. Each pot received 11 g of inoculum, containing 141 spores/g dry soil.

Greenhouse Experiment

A greenhouse experiment was carried out using 1-L pots with a substrate composed of sterilized soil and sand (7:3 ratio). The soil used was a loamy A horizon of a Typic Argiudoll (US Soil Taxonomy) from the Solis area in Buenos Aires Province, Argentina (34º 18′ S, 59º 20′ W). The area is devoted to field crops, mainly soybean, maize, and wheat. Soybean was seeded and grown to the R4 stage. The experiment was factorial with five replications and the factors were water stress, AM-inoculated and noninoculated soybean plants, and different levels of As, established by irrigation with As-loaded water. Treatments were T1 (0 As), T2 (0.5 mgAs/l), T3 (1 mgAs/l), T4 (5 mgAs/l), T5 (10 mgAs/l), and T6 (25 mgAs/l). To reach such As concentrations, sodium arsenate was added to the water.

The substrate was kept between 80 and 100% field capacity, and 60 days after seeding, plants were overirrigated and irrigation was then stopped completely. Water content of the substrate in the pots was checked periodically and plants were harvested when they were below the wilting point. This happen 72 h after irrigation stopped.

Determinations

Mycorrhizal Colonization. The percentage of root colonization by arbuscular mycorrhiza was calculated according to the methodology proposed by Mc Gonigle et al. (1990).

Plants. Plant survival was determined at the moment of harvest. After samples were taken to check the water content, soils of the pots were irrigated to field capacity. Those plants that did not recover from water stress were considered dead, while those that reinitiated growth after 24 h were considered to survive. Surviving plants were expressed as percentage of plants alive per total plants per pot. Aerial biomass was harvested and root biomass was extracted in all pots. This material was dried at 70 ºC and weighed. In samples for T1 treatment, calcium (Ca), magnesium (Mg), and potassium (K) were determined using inductively coupled argon–plasma emission spectrometry (ICPES) after acid digestion (Association of Official Agricultural Chemists 1965). Total N in plant samples were determined by the Kjeldahl method and P by wet digestion with a mixture 3:1 ratio (v/v) of nitric acid / perchloric acid ($HNO_3/HClO_4$) concentrate (Jones and Case 1990). Arsenic was determined in sieved and homogenized samples of aerial biomass of the noninoculated plants. Samples were extracted by HNO_3/H_2O_2 acid digestion and As was measured by atomic adsorption (ICP-AES) (United States Environmental Protection Agency 2006).

Soils. The substrate was analyzed using standard soil test methods. For the physical properties, we followed the procedures described by Klute (1986): particle-size distribution; clay, silt, and sand (pipette method); water present in pot soil samples; and water content obtained by pressure plate (field capacity, 0.33 kPa) and obtained by pressure chamber (permanent wilting point, 1500 kPa), by drying in an oven at 102–105 ºC. For the physicochemical and chemical properties, we followed the procedures described by Sparks et al. (1996): organic carbon (Walkley and Black), total nitrogen (N) (Kjeldhal), total phosphorus (P) (perchloric acid), organic P (concentrated sulfuric acid), extractable P (Bray and Kurtz 1), cation exchange capacity and exchangeable potassium (K) (extraction with ammonium acetate), extractable sulphur (S) (extraction with potassium chloride), pH in saturation extract, and electrical conductivity in saturation extract. Soil As in bioavailable forms was extracted using a 1.0 M solution of acetic acid and sodium acetate, and filtrates were acidified and quantified by atomic absorption (AA) according to the EPA6010 method (USEPA 2006) ICP-AES.

Statistical Analyses

Results were statistically analyzed by a factorial analysis of variance (ANOVA), after testing the variables for normality and for homogeneity of variance. The statistical software InfoStat was used. When there was a significant effect of the treatment, contrasts

(Tukey's test) were used to compare the means ($P \leq 0.05$). For survival analysis, a Pearson's χ^2 test at the 0.05 confidence level was used. The strength of the associations was determined by Cramer's V associations, which at least relatively strong (Cramer's V > 0.4) were considered.

Results

The soil properties are shown in Table 1. The soil was loam, nonsaline, and neutral with a regular provision of available P, K, and S. The water content found in the pot soils at the end of the experiment was 74.5 g kg^{-1} ± 1.7 in pots with noninoculated plants and 51.5 g kg^{-1} ± 0.30 in pots with inoculated plants. The average concentrations of As in soils after harvest were as follows: T1, 0.6 mg As kg^{-1}; T2, 1.227 mg As kg^{-1}; T3, 1.413 mg As kg^{-1}; T4, 2.937 mg As kg^{-1}; T5, 4.842 mg As kg^{-1}; and T6, 6.747 mg As kg^{-1}. At harvest time, average As concentrations in aerial biomass were as follows: T1, 0.754 mg As kg^{-1}; T2, 0.909 mg As kg^{-1}; T3, 0.956 mg As kg^{-1}; T4, 1.332 mg As kg^{-1}; T5, 1.803 mg As kg^{-1}; and T6, 2.274 mg As kg^{-1}. The chemical composition of soybean showed no significant tendency to be greater in inoculated plants.

Table 2 shows that root colonization with *Glomus intraradices* was more than 64% in inoculated plants. No significant effects of As were observed on mycorrhizal infection. At harvest time, the aerial biomass of noninoculated plants was significantly greater than that of inoculated plants. The effect of soil As concentration on aerial biomass can be separated in two categories: treatments with no or low arsenic concentration (T1, T2, and T3) showed no significant differences among them, whereas treatments with greater As concentration (T4, T5, and T6) showed a significant reduction in aerial biomass. Inoculated plants showed a significant decrease in biomass only in T6 (Table 2). Root biomass also showed differences between noninoculated vs inoculated plants, being lower in the latter. The effect of As was only detected by significant decreases in inoculated plants in T5 and T6.

The survival of soybean plants after the water stress was imposed showed that noninoculated plants died in treatments with no or low As concentrations (T1 to T3). The remaining noninoculated plants with greater arsenic concentration (T4 to T6) showed a high survival rate, from 60 to 100%. All inoculated plants, on the other hand, remained alive irrespective of the As concentration. The living surviving plants ranged from 20% in T1 to 80–100% in the remaining treatments.

Table 1
Average of soil physical and chemical properties rates

Physical and physicochemical properties		Chemical properties	
Clay content	275.0 g kg^{-1}	Soil organic carbon	14.7 g kg^{-1}
Silt content	244.7 g kg^{-1}	Total nitrogen	1.7 g kg^{-1}
Sand content	470.3 g kg^{-1}	C/N ratio	8.6
Water al 0.33 kPa	231.3 g kg^{-1}	Total phosphorus	304.6 mg kg^{-1}
Water at 1500 kPa	99.5 g kg^{-1}	Organic phosphorus	189.1 mg kg^{-1}
Cation exchange capacity	23.7 $cmol_c$ g^{-1}	Extractable phosphorus	35.7 mg kg^{-1}
pH in paste	6.4	Exchangeable potassium	1.4 $cmol_c$ g^{-1}
Electrical conductivity	0.5 dSm^{-1}	Extractable sulfur	12.8 $cmol_c$ g^{-1}

Table 2

Average and standard deviation of percentage of mycorrhizal colonization, plant biomass, and survival of soybean plants subjected to severe water stress and increasing concentrations of As [means ± SE ($n = 5$) in the same row with different letters differ significantly ($P < 0.05$)]

		Treatments					
Parameter	Inoculation	T1	T2	T3	T4	T5	T6
Root colonization (%)	No	0.0 ± 0.0 a	0.0 ± 0.0 a	0.0 ± 0.0 a	0.0 ± 0.0 a	0.0 ± 0.0 a	0.0 ± 0.0 a
	Yes	77.62 ± 6.01 a	69.88 ± 24.55 a	76.33 ± 11.36 a	69.27 ± 6.34 a	70.00 ± 9.64 a	64.05 ± 6.86 a
Dry aerial biomass (g plant^{-1})	No	5.10 ± 0.64 a	4.54 ± 0.35 a	4.32 ± 0.36 a	3.65 ± 0.33 b	3.69 ± 0.20 b	3.35 ± 0.75 c
	Yes	4.25 ± 0.34 a	4.06 ± 1.25 a	3.99 ± 0.61 a	3.61 ± 0.28 a	3.93 ± 0.51 a	3.14 ± 0.35 b
Dry root biomass (g plant^{-1})	No	1.20 ± 0.21 a	1.96 ± 0.31 a	2.03 ± 0.37 a	1.96 ± 0.41 a	1.51 ± 0.20 a	1.17 ± 0.30 a
	Yes	1.05 ± 0.27 a	0.87 ± 0.12 a	1.29 ± 0.35 a	1.12 ± 0.26 a	0.65 ± 0.14 b	0.78 ± 0.23 b
Plant survival (%)	No	0	0	0	60	60	100
	Yes	20	80	100	80	80	100

Table 3

Average and standard deviation of the content of calcium, magnesium, potassium, nitrogen and phosphorous in the soybean aerial and root biomass. Significant differences ($P < 0.05$) as assessed by Tukey test

Parameter	Inoculation	Ca^{++}	Mg^{++}	K^{+}	N	PP
Aerial biomass	No	7.09 ± 0.89 a	1.32 ± 0.16 a	3.63 ± 0.29 a	1.37 ± 0.17 a	0.78 ± 0.09 a
	Yes	6.07 ± 0.49 a	1.23 ± 0.09 a	5.13 ± 0.65 b	4.46 ± 0.36 b	0.72 ± 0.05 a
Root biomass	No	0.55 ± 0.09 a	0.32 ± 0.05 a	0.68 ± 0.12 a	0.18 ± 0.03 a	0.15 ± 0.02 a
	Yes	0.41 ± 0.10 a	0.35 ± 0.09 a	0.99 ± 0.25 a	0.21 ± 0.05 a	0.19 ± 0.04 a

Table 3 shows the content of Ca^{2+}, Mg^{2+}, and K^{+} in both the aerial and root biomass. The quantities of Ca^{2+} and Mg^{2+} in inoculated and noninoculated plants were similar. The K^{+} content was significantly greater in the aerial biomass of inoculated plants. The inoculated plants also showed significantly greater N content in aerial biomass but no differences were found in root biomass. Moreover, no significant differences were found in the P content in aerial and root biomass in both inoculated and noninoculated plants.

Discussion

Root colonization indicated that the inoculation was active even in the soils added with As and that AM colonized all soybean roots (alive and dead) throughout the experiment. Soybean plants suffered a sudden strong shortage of water (water contents were 7.45% in noninoculated plants and 5.15% in inoculated plants), clearly below the water content at the PWP (9.95%). This is a severe and limiting situation but it is known that the effects of drought treatments are difficult to standardize due to local environmental characteristics, soil properties, and crop attributes (Panda, Behera, and Kashyap 2004). It is evident that the lack of water in confined volumes is more critical, but the effect of water stress depends greatly on the intensity of the deficit. According to Rimski-Korsakov, Rubio, and Lavado (2009) results in the field and in the pots are similar. In the present case, soybean aerial and root biomass was lower in inoculated plants in opposition to findings of Ahmed et al. (2011) or Li et al. (2011), who found root biomass was increased in inoculated plants. However, other authors found that present results are not uncommon as root biomass was clearly high in noninoculated plants. (Gardezi et al. 2001). The greater N content in aerial biomass of inoculated plants can be explained by the greater absorption and transfer of N via AM extraradical hypha to their host plants in relatively dry agricultural soil (He, Critchley, and Bledsoe 2003).

Inoculated soybean plants subjected to water stress survived, and the adjustment of the osmotic potential by AM is probably one of the most important reasons for the improved ability of the host plant to survive under extreme water stress (Fusconi and Berta 2012). In addition, under drought stress conditions, AM-inoculated plants show a lower transpiration rate than noninoculated plants, which has been related to a significant increase in the leaf absicic acid (Aroca, Vernieri, and Ruiz-Lozano 2008). On the other hand, the potassium (K^{+}) content in plant tissues is related to water uptake by the roots and its function is modified by the arbuscular mycorrhizal symbiosis (Porras-Soriano et al. 2009; Benlloch-González, Fournier, and Benlloch 2010). Potassium plays a critical role in the opening and closing of stomata in plant leaves. Its deficiency can severely impair plant-water relations (Jordan-Meille and Pellerin 2004) and can lead to stomata as well as photosynthetic activity limitations (Bednarz, Oosterhuis, and Evans 1998). The greater contents of K found in inoculated plants agree with results of Querejeta et al. (2007) and Porras-Soriano et al. (2009), who found that greater survival of inoculated plants could be partially linked to a greater content of K in plant tissues.

The increases in As concentration in the soil affect the response of soybean plants, reducing their aerial and root biomass production, in a way similar to that found in other crops (Stoeva, Berova, and Zlatev 2005; Singh et al. 2007) as well as in soybean (Deuel and Swoboda 1972; Lee and Yu 2012). In the present case, the aerial biomass of noninoculated plants was negatively affected when As concentrations in irrigation water exceeded 5 mg As / L^{-1}, which is equivalent to almost 3 mg As kg^{-1} in the soil. Inoculated plants were only affected by irrigation water bearing 25 mg As L^{-1}, a high concentration not found in irrigated areas (Smedley and Kinniburgh 2002). Results indicating that biomass of *G. intraradices*–inoculated soybean plants are affected by As at greater concentrations showed some coincidence with studies carried out by Li et al. (2011) in rice, although results varied according to the plant-fungus combination, and with those by Ahmed et al. (2011) in *G. mosseae*–inoculated lentils (*Lens culinaris* L.).

Plants subjected to high concentrations of As reduced their biomass accumulation, affecting the plant-water relationship. Membranes are vulnerable targets of As-stress-induced cellular damage, which leads to unbalanced nutrient uptake and water content in plant cells, and to a decrease in stomata conductance. The negative effects of As on the transpiration process are probably due to the disturbed uptake and transport of water (Garg and Singla 2011). Also, Stoeva, Berova, and Zlatev (2004) showed that leaf water potential and transpiration rate in beans decrease in As-treated plants and that the relative water content decreases slightly.

Conclusions

Soybean tolerance to water stress improved in arbuscular mycorrhizae–inoculated plants. The significantly greater concentrations of K in inoculated plants plus the adjustment of the osmotic potential and their lower transpiration rate are among the reasons for soybean's ability to survive under extreme water stress. Soybean plants subjected to increasing As concentrations showed a significant survival even in noninoculated plants. The negative effects of As on plants related to water equilibrium and plant water losses could explain why soybean plants affected by As survived under the extreme water stress situation of the PWP.

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