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Original article

Influence of two bacterial isolates from degraded and non-degraded soils and arbuscular mycorrhizae fungi isolated from semi-arid zone on the growth of *Trifolium repens* under drought conditions: Mechanisms related to bacterial effectiveness

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ABSTRACT

The limited growth and nutrition of plants growing in semi-arid zones may be overcome by the inoculation with selected soil microorganisms [bacteria or arbuscular mycorrhizal fungi (AMF)]. In this article we investigate how autochthonous AM fungi and the two most abundant cultivable bacterial groups, isolated from dried degraded (B1) and non-degraded (B2) soil, affect *Trifolium repens* growth under water limiting conditions. On the other hand, and with attempt to characterize biochemically both isolates, we also analysed the indole acetic acid (IAA) and proline production as well as the antioxidant response of both isolates subjected to an increasing osmotic stress degree caused by Polyethylene glycol (PEG). When the bacteria were grown in axenic culture at increasing osmotic stress caused by PEG levels (from 0 to 30%) they show different osmotic response. B2 produced the highest IAA and proline amount under the strongest stress condition (30%). Similarly, under 30% PEG, B2 showed 6 times less CAT and two times more APX than B1 while SOD resulted similar in both strains. Bacterial CAT and APX activities were more sensitive than SOD to osmotic stress which is an indication of bacterial response to drought and reflect the diversity and intrinsic osmotic stress tolerance of these both bacteria. AMF or bacterial inoculated plants widely decreased stomatal conductance and increased the relative water content, both values are important for plants growing in soil with water limitation.

1. Introduction

Drought stress is one of the most important factors limiting plant growth and yield in many areas of the earth. Water limitations reduce nitrogen and carbon metabolism and these processes lead to change plant physiology [1,2] and photosynthetic activity [3–5]. The mechanism of plant drought tolerance may involve promotion of root extension, allowing an efficient water uptake [6,7]. Thus, an alternate plant strategy for coping with water deficiencies is the interaction with beneficial soil microorganism.

In general, productivity and quality of soils depends on the microbial functionality [8,9]. Plants can interact with several soil microorganisms including bacteria having plant growth promoting (PGP) abilities and/or mycorrhizal fungi that enhance plant water uptake and nutrition status, improving plant stress tolerance [9,10]. It is known that PGP microorganisms can increase plant growth by increasing the nutrients availability in the rhizosphere and also may enhance the plant hormones production such as IAA [11,12]. Arbuscular mycorrhizal fungi (AMF) symbiotically associated with plant roots are known to enhance plant growth under drought conditions by increasing nutritional status and water uptake [13,14]. However, osmotic stresses may reduce microbial activities and as a consequence, to reduce also plant productivity [15,16]. Limitation in soil water content causes a series of reactions in plants like stomatal closure that limits CO_2 fixation. After some time, lack of water in the growing medium causes poor nutrients diffusion in soil which has important detrimental effects on plant growth.

It is well documented that drought exert, at least part, of their effects by causing oxidative damage. Oxidative damage is caused by reactive oxygen species (ROS) that can react with a large variety of biomolecules causing irreversible damage and leading to cell necrosis and death [17–19]. Hence, because ROS are toxic but also participate in signalling events, living organisms are equipped with at least two different mechanisms to regulate their intracellular

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ROS concentrations by scavenging ROS: one enabling the fine modulation of low levels of ROS for signalling purposes [peroxidase (POX), superoxide dismutase (SOD), and catalase (CAT)], and one regenerating the oxidized antioxidants [ascorbate peroxidase (APX)] [20]. Recently, we were able to characterize several arbuscular mycorrhizal ROS scavenging systems showing enhanced activities in response to abiotic stress [21–23]. However, as far as we know, there is very limited information about the oxidative response of the PGP microorganisms in response to specific environmental adverse conditions such as drought.

In the present study we investigates at increasing osmotic stress level, induced by polyethylene glycol (PEG), the antioxidant response (SOD, CAT and APX activities) as well as the bacterial production of IAA and proline. These parameters were correlated with the bacterial effectiveness in plant growth, nutrition and water uptake.

2. Materials and methods

Two independent experiments were carried out in this study. Firstly in a bioassay microcosm experiment was tested for studying the abilities of autochthonous bacteria from degraded or non-degraded soil or AMF to increase plant growth under water stress conditions.

I) First, non-inoculated control plants and plants inoculated with one of two autochthonous bacterial isolated originating from degraded or non-degraded soil, were assayed in a microcosm experiment. Mycorrhizal inoculated plants were also assayed. These treatments were replicated five times with a total of 20 pots placed in a random complete block design.

II) In a second bioassay, these two bacterial isolates were assayed in axenic medium to test indole acetic acid (IAA) and proline production as well as antioxidant enzymatic activities (SOD, CAT, APX) under increasing levels of polyethylene glycol (PEG) (0, 15% or 30%) in the culture medium. The PEG levels were selected in a previous unpublished study in which a greater PEG level highly decreased bacterial counts in the growing medium. The two bacterial isolates without PEG and at the two PEG levels were replicated three times with a total of 18 tubes.

2.1. Study sites

The experimental area where samples were collected was located in Benslimane (Morocco) Tetraclinis woodland (co-ordinates: N 33 40 665, W 00 700 525, 191 m above sea level). The climate is semi-arid Mediterranean with an average annual rainfall of 577 mm and a mean annual temperature of 17.8 °C. The substratum is schistose with a neutral to neutral-alkaline pH and low amounts of nitrogen and phosphorus, respectively 800% and 2.10 mg/kg of soil and organic matter rate between 1.2 and 4.8% [24].

In non-degraded soil having a rich vegetation cover (80%) was represented by the association of trees, shrubs and herbaceous plants: *Geranium molle*, *Fedia pallescens*, *Fraxinus xanthoxyloide*, *Pistacia lentiscus*, *Lavandula multifida*, *Asphodelus microcarpus*, *Olea europea*, *Ononis natrix*, *Sonchus oleraceus*, *Achyrantes sicula*, *Scolymus hispanicus*, *Anagallis arvensis*, *Evax pygmaea*, *Asplenium onopteris* and *Tetraclinis articulata*.

In degraded soil having a low vegetation cover, the percentage of vegetation cover didn't exceed 30% and shrubs were the most representatives of this area: *L. multifida*, *Olea. oleaster*, *Cistus. monspeliensis*, *S. hispanicus*, *P. lentiscus*, *A. arvensis* and *T. articulata*. The pedological soil characters of degraded soil 1 were: pH 7.69; clay 29%; silt 26%; sand 45%; organic matter 1.22%; N total 0.48‰; Assimilable P (mg/100) 1.49 and those of non-degraded soil 2 were: pH 8.20; clay 33.13%; silt 40.96%; sand 25.8%; organic matter 4.83%; N total 1.12‰; assimilable P (mg/100) 2.71.

2.2. Soil microorganisms

The soil samples for microbial isolation and inocula production were taken from the rhizosphere of plants growing in degraded or non-degraded soil located in a semi-arid mediterranean soil in Benslimane (South west of Morocco). A mixture of rhizosphere samples from several *T. articulata* plants were selected from degraded and non-degraded area. They were immediately transported to the laboratory in plastic bags at ambient temperature and humidity and kept at four degrees upon arrival under the laboratory before to be processed. The most abundant bacterial isolates from degraded (B1) or non-degraded (B2) soil were selected for the further studies as follow: 1 g of homogenized rhizosphere soil from *T. articulata* grown in degraded or non-degraded zone was suspended in 100 ml of sterile water (dilution 10^{-2}) and 1 ml of this suspension was serially diluted to reach dilutions 10^{-4}–10^{-7}. These dilutions were plated in agar nutrient broth Difco medium (8 g l^{-1}) that contained meat extract (3 ml^{-1}) and peptone gelatine (5 g l^{-1}) and cultivated for 48 h at 28 °C. Once selected the most abundant bacterial isolate from each soil (probably *Bacillus* sp. based on be Gram + rod-shaped, spore-forming and other morphological characteristics) they were grown in corresponding 250 ml flasks containing 50 ml of nutrients broth medium in shake culture for 48 h at 28 °C.

Seedlings were inoculated with 0.5 ml of each one of the bacterial culture suspension (10^8 cfu ml^{-1}) per pot. In control, non-inoculated treatments, 0.5 ml of sterilized bacterial culture was added.

Native mycorrhizal inoculum also coming from degraded area of Benslimane was multiplied in an open pot culture of maize and *Trifolium repens* for six months. After this time the AMF inoculum consisted of soil, spore, hyphae and mycorrhizal root fragments. Five grams of this AMF inoculum (a mixture of *Glomus* species), having a richness of an average of 30 spores g^{-1} and root fragments with 75% of colonized roots length were applied below the seedlings of the *T. repens* plants in the appropriate pots. AMF inoculum was a mixture stable over time of a morphologically distinct *Glomus* species. The non-mycorrhizal treatments received the same amount of autoclaved inoculum together with a 2-ml aliquot of a filtrate (<20 μm) of the AM inoculum to provide a general microbial population free of AMF propagules.

Each one of these three treatments plus untreated control was replicated five times.

2.3. Test soil

The experimental soil was collected from a mediterranean arid region in the east of Spain. The calcareous loamy soil was sieved (2 mm), diluted with quartz-sand (<1 mm) (1:1 soil:sand v/v) and sterilized by steaming (100 °C for 1 h each 24 h along 3 d consecutively) and distributed in pots containing 500 cc capacity. The soil pH was 7.2 (water) and contained 1.6% organic matter. Nutrient concentrations were: 2.1 mg kg^{-1} N; 1.7 mg kg^{-1} P ($NaHCO_3$-extractable P); 0.8 mg kg^{-1} K. The soil texture was made up of: 57.8% sand, 19% clay and 23.2% silt [25].

2.4. Plant and growth conditions

T. repens seeds were surface-sterilized with 2.5% Sodium hypochlorite and pre-germinated in Petri-dishes on humid filter paper. Twenty-day old seedlings were transplanted (4 plants per pot) into

pots containing 500 g of experimental soil–sand mixture. At transplanting time seedlings were inoculated with autochthonous AMF inoculum or with autochthonous bacteria (B1 or B2). Plants were grown under controlled climatic conditions (18–24 °C, with a 16/8 light/dark period and 60–50% of relative humidity). A photoperiod of 16 h at a photosynthetic photon flux density (PPFD) of 500 μmol m^{-2} s^{-1} as measured with a light meter (model LI-188B; Licor Inc., Lincoln, NE, USA) was maintained along the experiment by supplementary light to compensate natural illumination.

Soil moisture was measured with a ML2 Theta Probe (AT Delta-T Devices Ltd., Cambridge, UK) as previously described [13]. Water was supplied daily to maintain soil at field capacity during the first 2 weeks after planting. Then, plants were allowed to dry until soil water content reached 75% field capacity. The soil water content was measured daily with the ThetaProbeML2 before re-watering (at the end of the afternoon), reaching a minimum soil water content ranging from 65 to 70% field capacity. The amount of water lost was added to each pot in order to keep the soil water content at the desired level of 75% field capacity [13]. Plants were maintained under such conditions for an additional 15 days before harvesting.

2.5. Plant biomass analyses

At harvest (3 months after sowing), the root system was separated from the shoot, weighed, dried in a forced-draught oven at 70 °C for 2 d. Shoot concentrations of K were determined by flame photometry and P by the method described [26]. B, Fe, Cu, Mn, Zn, Ca, Mg, Na and S were also measured after wet digestion of the air-dried plant samples with HNO_3 + H_2O_2 by inductively coupled plasma atomic emission spectrometry (ICP-AES) [27].

Shoot N and C concentrations were determined by Dumas methodology [28].

Water content (WC) was calculated on the basis of loss of weight on drying as follow: (Fresh weight − Dry weight)/Fresh weight. Stomatal conductance was measured in five plants of each treatment by using a porometer system (Porometer AP4, Delta-T Devices Ltd, Cambridge, UK) following the user manual instructions. Stomatal conductance measurements were taken in one leaflet of each plant at midday.

2.6. Symbiotic development

The percentage of mycorrhizal root length infected was estimated by visual observation of fungal colonization after boiling washed roots in 10% KOH and staining with 0.05% trypan blue in lactic acid (v/v) [29]. Quantification was carried out using the grid-line intersect method [30].

2.7. Production of indole-3-acetic acid and proline by bacterial isolates under increasing polyethylene glycol (PEG) concentrations

The bacterial isolates were cultivated at 28 °C in 75 ml sterile nutrients broth (Difco) medium supplemented with 0, 15 or 30% of PEG in order to induce osmotic stress. The production of indole-3-acetic acid (IAA) by these bacteria under increasing PEG concentrations was determined using the Salper reagent [31]. Three millilitres of fresh Salper reagent was added to free-cell supernatant and kept in complete darkness for 1 h and the optical density at 535 nm was measured in each treatment. A standard curve was prepared for IAA (Sigma, USA). In the same growing medium the proline accumulation was estimated by spectrophotometric analysis at 515 nm [32].

2.8. Antioxidant enzymatic activities

Total superoxide dismutase (SOD) activity (EC 1.15.1.1) [33] was measured on the basis of SOD's ability to inhibit the reduction of nitroblue tetrazolium (NBT) by superoxide radicals generated photochemically. One unit of SOD was defined as the amount of enzyme required to inhibit the reduction rate of NBT by 50% at 25 °C. Catalase (CAT) activity (EC 1.11.1.6) was measured as described [34]. Consumption of H_2O_2 (extinction coefficient of 39.6 mM^{-1} cm^{-1}) at 240 nm for 1 min was monitored. The reaction mixture consisted of 50 mM phosphate buffer (pH 7.0) containing 10 mM H_2O_2 and 100 μl of cell extracts in a 2 ml volume. APX activity (EC 1.11.1.11) was measured in a 1 ml reaction volume containing 50 mM potassium phosphate buffer (pH 7.0), 0.1 mM hydrogen peroxide and 0.5 mM ascorbate. The H_2O_2 was added to start the reaction, and the decrease in absorbance at 290 nm was recorded for 1 min to determine the oxidation rate for ascorbate [35].

2.9. Statistical analysis

Five replicates were made per treatment and data were subjected to analysis of variance. Differences between means were analysed by Duncan's multiple range test ($P \leq 0.05$). For the percentage values, the data were arcsin square transformed before statistical analysis.

3. Results

3.1. Shoot and root weight

Bacterial inoculation by the most abundant isolates from degraded (B1) or non-degraded area (B2) positively affected the growth of plants; particularly plants shoot (Fig. 1). As well, mycorrhizal plants produced a shoot and root development with 132% (shoot) and 95% (root) of increase over non-inoculated control plants.

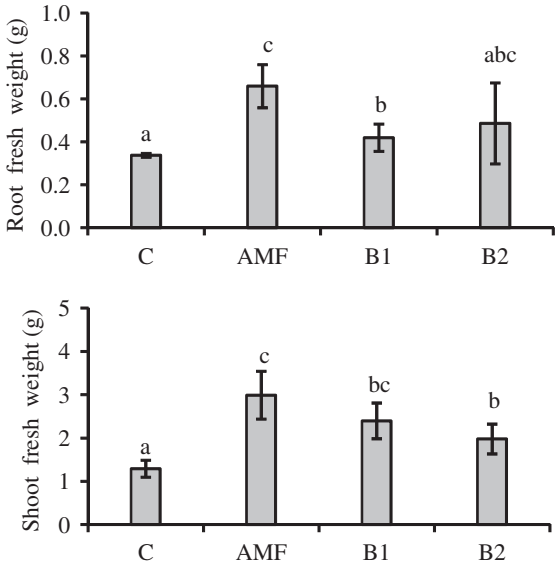

Fig. 1. Shoot and root weight (g) of non-inoculated plants (C), single inoculated plants with AM fungi (AMF), bacteria from degraded soil (B1) or bacteria from non-degraded soil (B2) under drought conditions. Values having a common letter are not significantly different ($P < 0.05$) as determined by Duncan's multiple range test ($n = 5$). Columns represent mean + S.E.

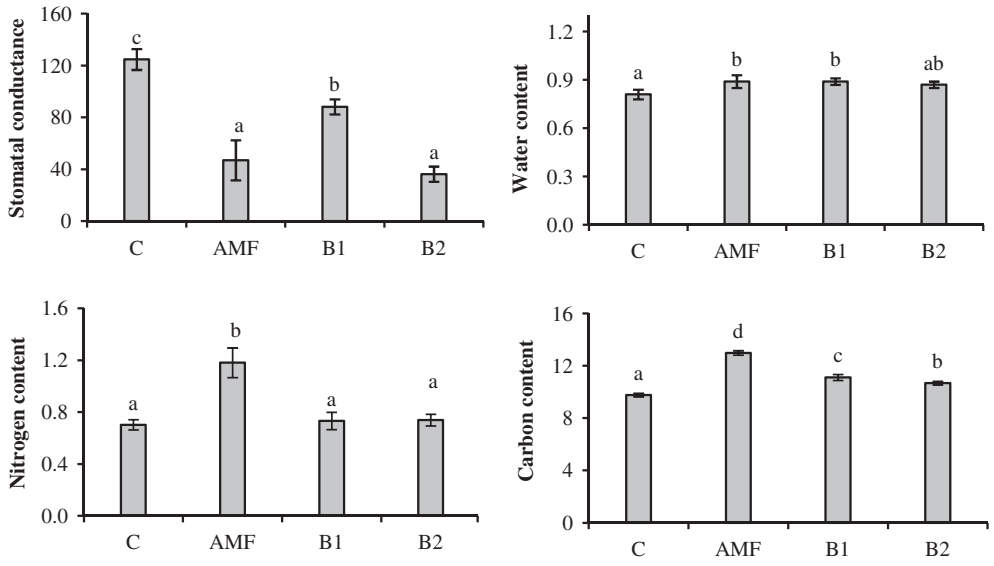

Fig. 2. Stomatal conductance (mmol H_2O m^{-2} s^{-1}), water content (g H2O/g FW), nitrogen and carbon content (mg) in non-inoculated plants (C), single inoculated plants with AM fungi (AMF), bacteria from degraded soil (B1) or bacteria from non-degraded soil (B2) under drought conditions. Values having a common letter are not significantly different ($P < 0.05$) as determined by Duncan's multiple range test ($n = 5$). Columns represent mean + S.E.

3.2. Stomatal conductance and water content

All the microbial treatments applied decreased the stomatal conductance under drought conditions (Fig. 2). The most efficient treatments in decreasing this value were AMF or B2 inocula that caused less than half stomatal conductance than control non-inoculated plants (Fig. 2). Non-significant differences in stomatal conductance between plants inoculated with bacteria from non-degraded soil or mycorrhizal fungi were found.

The effectiveness of these bacteria or AMF was also evident on the plant water content (Fig. 2). Water content was the lowest in non-inoculated plants (0.88 g H_2O/g FW) and the highest in bacterial inoculated or AMF colonized plants. This microbial effect on this relevant physiological value is very important in plant growing in soils with water limitation.

3.3. Nutrient concentrations

Non-significant differences in N content were found in plants inoculated with B1 or B2 but AM-colonization was the treatment that increased it in a highest extent (Fig. 2). Similarly, the highest C content was observed in plants inoculated with AMF but whatever inocula applied increased C content in plants (Fig. 2).

Most of the content of elements showing in Figs. 3 and 4 were increased in inoculated plants particularly Mn, Fe, B and Cu as micronutrients and P and S as macronutrients. Mycorrhizal colonization was the most effective treatment in increasing plant nutrition and B1 resulted more active than B2 in enhancing Ca, K, Fe and Mn contents.

3.4. Production of IAA

In axenic culture the highest IAA production was observed by B2 at the highest PEG concentration applied (30%). Nevertheless, the IAA production was greater in B1 than in B2 culture, in control and 15% PEG treated bacteria (Fig. 5). The IAA production by B1 ranged from 0.49 μg ml^{-1} (without PEG) until 0.54 μg ml^{-1} (with 30% PEG) and in the case of B2 the IAA accumulation was 0.26 μg ml^{-1} (without PEG) until 1.14 μg ml^{-1} in presence of 30% PEG (Fig. 5).

3.5. Production of proline

Proline production by B2 was higher than by B1 in all the PEG concentration assayed in the culture medium ranging from 0.49 to 1.02 μg ml^{-1} (B1) and from 0.9 to 1.76 μg ml^{-1} (B2) (Fig. 5). As consequence of PEG application, proline production increased in both bacteria reaching the highest accumulation at 30% PEG. The highest proline production particularly by B2 (from non-degraded soil) under the greatest PEG concentration is indicative of the strong bacterial responses to the osmotic stress caused by PEG application (Fig. 5).

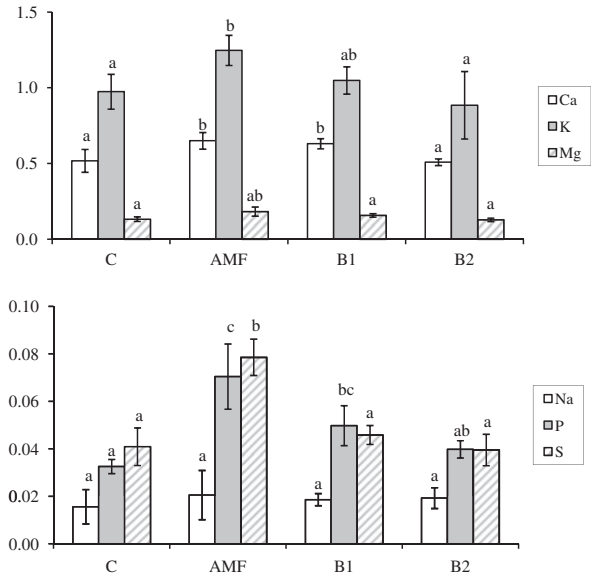

Fig. 3. Elements (Ca, K, Mg, Na, P and S) content (mg) in non-inoculated plants (C), single inoculated plants with AM fungi (AMF), bacteria from degraded soil (B1) or bacteria from non-degraded soil (B2) under drought conditions. Values having a common letter are not significantly different ($P < 0.05$) as determined by Duncan's multiple range test ($n = 5$). Columns represent mean + S.E.

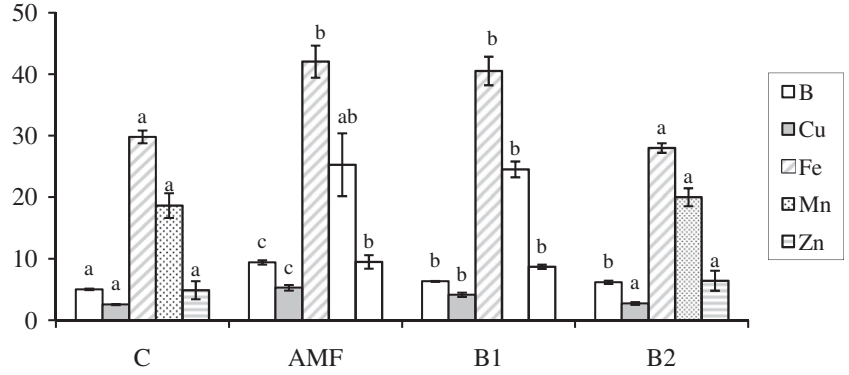

Fig. 4. Elements (B, Cu, Fe, Mn and Zn) content (μg) in non-inoculated plants (C), single inoculated plants with AM fungi (AMF), bacteria from degraded soil (B1) or bacteria from non-degraded soil (B2) under drought conditions. Values having a common letter are not significantly different ($P \leq 0.05$) as determined by Duncan's multiple range test ($n = 5$). Columns represent mean ± S.E.

3.6. Antioxidant activities

Concerning the antioxidant enzyme activities, we observed a high catalase (CAT) activity in B1 in response to high PEG concentration, this activity increase in B1 culture (by 52%) from 0 to 30% PEG. While, a significant down regulation was observed by B2 (by 162%) (Fig. 5). In opposite way, no significant differences in SOD activities were observed between both bacteria in response to the

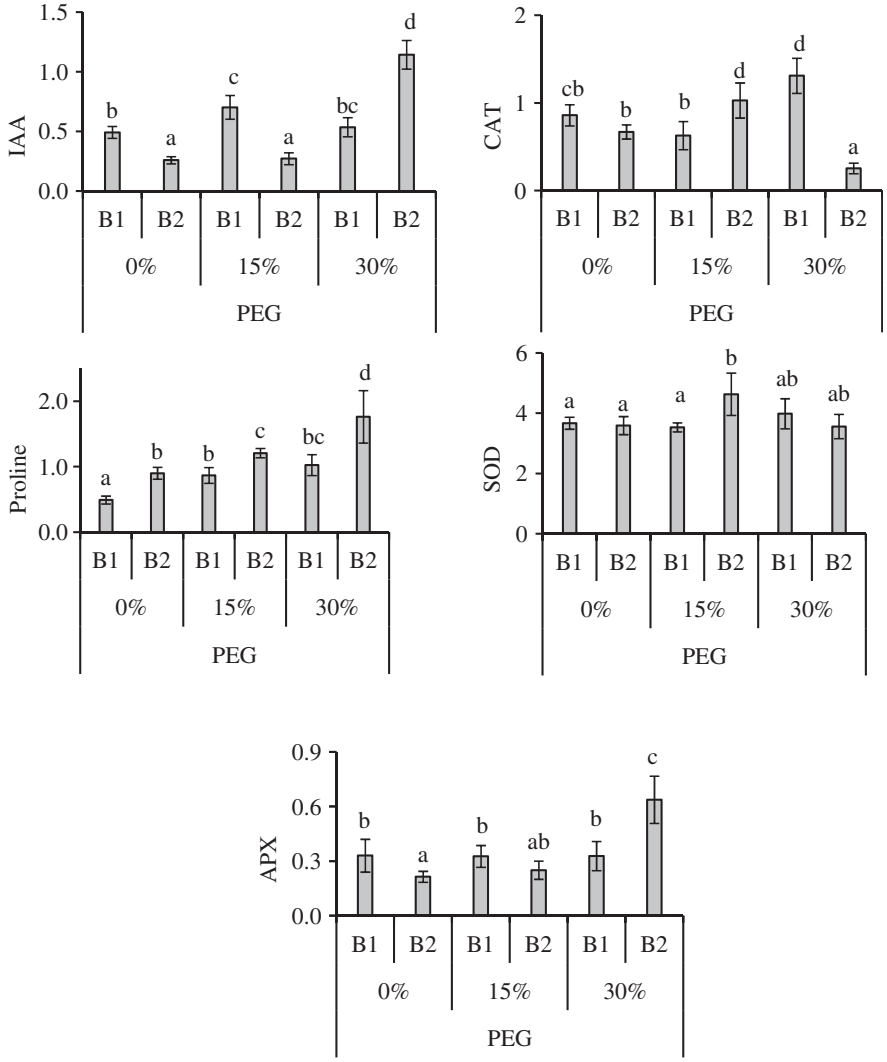

Fig. 5. Indole acetic acid (IAA) μg ml^{-1}; proline μmol mg $protein^{-1}$; catalase (CAT) μmol min^{-1} mg $protein^{-1}$; superoxide dismutase (SOD) min^{-1} mg $protein^{-1}$ and ascorbate peroxidase (APX) μmol min^{-1} mg $protein^{-1}$ by B1 (from degraded soil) and B2 (from non-degraded soil) in axenic medium added of 0, 15 or 30% of polyethylene glycol (PEG). Values having a common letter are not significantly different ($P \leq 0.05$) as determined by Duncan's multiple range test ($n = 5$). Columns represent mean ± S.E.

PEG concentration tested. Increasing PEG content (0–30%) did not significantly change SOD activity (Fig. 3). Regarding APX activity no significant differences were observed in B1 in response to PEG in the medium (Fig. 5). However, a significant difference was observed in the capacity of B2, in comparison with B1, to increase the activity (By 71.5%) of APX in response to 30% PEG (Fig. 5).

4. Discussion

The inoculation of plants with autochthonous bacteria or AM fungi increased plant growth and resistance to water limitation. These microbial inocula provided tolerance against drought stress.

In this study we also investigated some physiological and biochemical bacterial traits under stress conditions of the two most abundant bacterial isolates from degraded (B1) and non-degraded (B2) soil located in the same semi-arid zone in the South West of Morocco. The different microbial abilities could explain also changes observed in plant growth after the inoculation under water stress conditions.

Bacterial isolates exhibiting the highest abilities in increasing proline, antioxidant defence and IAA production as much as increased the osmotic stress in the growing medium would be selected as the best candidates to be inoculated in drought environments.

In the mesocosm experiment under drought conditions both bacterial strains as inoculants were efficient in improving shoot and root growth, however, non-important differences between them were found regarding most of values determined.

The microbial inoculation increased the shoot water content. Concomitantly the stomatal conductance was highly decreased in inoculated plants particularly in those treated with AMF or B2 inoculants. Less stomatal conductance together with a better growth of these inoculated plants under drought conditions indicates a better water use efficiency of these plants [36]. At the same time, the less stomatal conductance of AMF plants could explain their higher shoot water content. Nevertheless, the highest effectiveness of these inocula on plant water acquisition is not always correlated with an enhancement of the nutritional (N, P or K) plant status. The B2 activity seems to be independent of any nutritional effect.

A plant strategy for drought stress tolerance is to enhance CO_2 assimilation [37] and this activity was observed in inoculated plants in the present study. The greatest water content found in inoculated plants may be the results of increasing water use efficiency as consequence of the relative improvement in intracellular CO_2 and partial stomatal closure [38].

Curiously, AMF are sink for photosynthetic products in the symbiosis and about 4–20% of the total C fixed is used by fungal partner in the root [39]. In this study the fungal C demand did not result a cost of symbiotic status since the real symbiotic cost was highly compensated by the mycorrhizal activity.

The ability of B2, from non-degraded soil, to increase in greatest extent the production of proline and IAA at the highest level of PEG inducing osmotic stress in the culture medium would account for compensation of the bacterial lack osmotic tolerance and thus may represent its ability to enhance plant tolerance to these stressed osmotic conditions. Comparatively B1, from a degraded soil, was more adapted to the osmotic conditions and consequently weaker changes in proline and IAA production were observed in response to stress (PEG) conditions applied.

The bacterial response (in terms of IAA and proline productions) to the highest osmotic stress by PEG application resulted greater in the bacterial strain B2. The proline production could induce the adjustment of cell osmotic potential which is very important as cellular adaptation process to maintain cell integrity under severe osmotic stress conditions. By such mechanism bacterial cells can cope with the osmotic stress. This bacterial capacity may enhance its competitive advantage under osmotic stress conditions.

It has been reported that elevation of free auxin was dependent on the stress strength [40]. Recently, an increasing amount of auxins evidence has emerged indicating that auxin, indoleacetic acid, play an important role in stress response [41,42]. In parallel proline accumulation is one of the mechanisms involved in stress responses and drought tolerance was enhanced in plants with elevate proline content [43]. But the enhancement of both compounds (proline and IAA) was dependent on the stress strength as our results show regarding the less tolerant bacterial isolate B2.

In this study, the cellular proline production was used to identify the bacterial stress symptoms after PEG treatment. The highest amount of proline produced by bacteria from non-degraded soil indicates a greater stress response in this bacterium. This proline value correlated with a strong negative regulation of catalase but an enhancement of APX activity. The efficient destruction of O^{2-} and H_2O_2 generated under stress requires the action of several antioxidant enzymes acting in synchrony. It is assumed [44] that hydroxyl radical and singlet oxygen are so reactive that their production must be minimized. The chief toxicity of O^{2-} and H_2O_2 is thought to reside in their ability to initiate cascade of reactions that results in the production for hydroxyl radicals capable to cause oxidative damage [45].

The low CAT activity of B2 in response to high PEG level precludes a direct role of this enzyme in the protection against oxidative injury in these bacteria. Nevertheless, an alternative mode of H_2O_2 destruction is peroxidases productions which are found throughout the cell and have a much higher affinity for H_2O_2 than CAT [46]. In fact B2 exhibit a marked increase of APX activity in response to 30% PEG.

The bacterial strains here assayed differ on antioxidant enzyme activities particularly at the highest stress level. Bacteria (B2), from non-degraded soil, which showed the highest APX and the lowest CAT under the highest stress (30% PEG) was not the most effective in improving plant water content or nutrients acquisition.

Under 30% PEG B2 had 6 times less CAT and 2 times more APX than B1 whereas, the SOD resulted quite similar between both strains. Differences in such antioxidant activities reflected the physiological diversity and intrinsic osmotic stress tolerance of these bacteria. B2, from non-degraded soil, may need to be adapted to the oxidative stress produced by PEG (30%) through a higher APX activity and a low CAT activity. Diversity and stress tolerance of these bacteria implied that they may play a multifaceted role to sustain plant and soil health. Mechanisms and factors affecting drought tolerance and environmental adaptation by bacteria cannot be easily resolved because of the multiplicity of factors involved. The bacterial or AM activities on plant growth enhancement and the increased water content as affected by the specific bacterial or AMF inoculation may be considered as a promising strategy to promote plant growth and water stress tolerance under water limited conditions.

5. Conclusions

This study demonstrates that bacterial osmotic stress tolerance in term of oxidative response, and proline and IAA production differs between isolates from degraded and non-degraded environment. We observed that the highest IAA and proline production by B2 in axenic culture may be correlated with the plant growth promotion under drought conditions. These to easy assayable compounds can be used as markers to select potential soil bacterial strains suitable to induce plant growth under drought conditions.

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