ISSN print: 0258-5936 ISSN online: 1819-4087



# Review THE AGRICULTURE, SALINITY AND ARBUSCULAR MYCORRHIZAL FUNGI: A NEED, A PROBLEM AND AN ALTERNATIVE

#### Revisión bibliográfica

## La agricultura, la salinidad y los hongos micorrízicos arbusculares: una necesidad, un problema y una alternativa

#### Laura R. Medina García

ABSTRACT. Among the adverse conditions of farming systems, salinity is the most influential factor on the establishment of human populations. Salinity inhibits plant growth and productivity, induces osmotic imbalances relationships between soil and plants and in the metabolism of these. Stress tolerance in plants is a complex phenomenon involving many changes at the biochemical and physiological level. The mechanisms behind stress tolerance seem to be affected by the colonization of arbuscular mycorrhizal fungi, numerous studies demonstrating that inoculation with these fungi improving plant growth under salt stress, so the knowledge of the interactions between different AMF species and soil conditions leading to the establishment of better adapted populations and more effective to ensure the benefits of symbiotic association under these conditions.

**RESUMEN**. Entre las condiciones adversas de los sistemas agrícolas, la salinidad es el factor que más ha influido sobre el establecimiento de las poblaciones humanas. La misma inhibe el crecimiento de las plantas y su productividad, induce desequilibrios en las relaciones osmóticas entre el suelo y las plantas y en el metabolismo de estas. La tolerancia al estrés en la plantas es un fenómeno complejo que involucra numerosos cambios a nivel bioquímico y fisiológico. Los mecanismos detrás de la tolerancia al estrés parecen estar afectados por la colonización de los hongos micorrízicos arbusculares. Demostrando numerosos estudios que la inoculación con estos hongos mejora el crecimiento de las plantas bajo estrés salino; por lo que el conocimiento de las interacciones entre distintas especies de HMA y las condiciones edáficas lleva al establecimiento de poblaciones mejor adaptadas y más efectivas que garanticen los beneficios de la asociación simbiótica en estas condiciones.

Key words: biofertilizers, abiotic stress, fungi

Palabras clave: biofertilizantes, estrés abiótico, hongos

#### INTRODUCTION

In nature, plants are exposed to many stress conditions that retard their development and reduce yields. One of the most widespread agricultural problems is salt accumulation in soil surface (1).

Instituto Nacional de Ciencias Agrícolas (INCA), Gaveta Postal 1, San José de las Lajas, Mayabeque, Cuba, CP 32 700.

⊠ laura@inca.edu.cu

Salinity completely affects a third portion of all irrigated lands in areas with water shortage, high temperatures, high evapotranspiration or when a deficient irrigation is managed by farmers. In addition, due to decrease of available water sources, the use of saline water for irrigation is almost inevitable (2).

In general, salinity inhibits plant growth and its productivity.

High salinity induces unbalanced osmotic relationships between soil, plants and their metabolism. There is a group of factors that enhances plant tolerance against salinity; their application to plants can provide better resistance to salt stress and help improve crop productivity under these conditions (3, 4).

Stress tolerance in plants is a complex phenomenon that involves numerous biochemical and physiological changes; however, the mechanisms behind stress tolerance seem to be affected by arbuscular mycorrhizal fungus (AMF) colonization (5).

Arbuscular mycorrhizal symbiosis is an obvious result from the interaction between plant roots and fungus; it is an excellent example of great morphological disorders undergone by roots to get adapted to a symbiont. AMF receives plant photosynthates; meanwhile the plant improves its ability to take up nutrients, water and enhances both its abiotic and biotic stress tolerance (6, 7).

Several studies have shown that fungal inoculation improves plant growth under salt stress conditions (4, 8). This can be attributed to an increased mineral nutrient absorption, such as phosphorus (P), zinc (Zn), copper (Cu) and iron (Fe). There is some evidence that AMF protects leaf metabolism from sodium (Na) toxicity (9, 10).

Salt stress affects plant growth and its damages on plant metabolic activity may change according to AMF use; thus, it is necessary to perform deeper studies on the selection of effective AMF strains, so as to improve plant development under such stress conditions.

#### **SALINITY**

Among all adverse farming system conditions, salinity is the most influencing factor on the establishment of human populations, as there are historical records of migrations caused by arable soil salinization (11).

Salinity is a serious problem for agriculture, mainly in arid and semi-arid regions. The total soil area affected in the world is of 831 million hectares, including 397 and 434 million hectares of saline and sodic soils, respectively (12).

Soils with salinity problems are located in places where evaporation is greater than rainfall (13); therefore, the most affected climatic areas by salts are situated in arid, semiarid and steppe areas, where evaporation is dominant.

The most influencing factors on saline soil formation are: topography, biological activity, climatic conditions, geomorphological processes of sedimentation, erosion, material redistribution and changes in surface as well as underground water, besides some human actions, such as tillage, irrigation with low water quality and use of chemicals (14-17).

Irrigation with water containing salts have an unavoidable effect on higher salt concentration in plant root zone (18), which depends on several factors, including the quantity and quality of irrigated water, irrigation method and adequate drainage (14, 19, 20).

Human activity has enlarged salinity areas by expanding irrigated lands as a result of developing great hydrological projects, which have led to changes in water and salt balance of hydrogeological systems. According to a study performed at the United Nations University, about 62 million hectares (20 %) of irrigated lands are affected in the world, exceeding 45 million hectares in the 1990s (21).

### PLANTS AND SOIL SALINITY

The most common salinity effect on plants is that it reduces its development, due to a decreased osmotic potential of the medium and, consequently, of soil water potential, a specific toxicity usually associated with excessive Na<sup>+</sup> and Cl<sup>-</sup> absorption, a nutritional unbalance caused by salt ion interference of essential nutrients and the above effects combined. As a result of these primary effects, other secondary stresses often occur, such as oxidative damage<sup>A</sup> (22).

#### WATER ABSORPTION

One of the most obvious salt stress effects is that it reduces water absorption capacity, which may be observed through water stress effects, such as a reduced leaf expansion and loss of turgor (23).

A plant cell exposed to saline medium balances its hydric potential by losing water, resulting in a decreased osmotic potential and turgor. This situation leads to chemical signals (higher intracellular free Ca<sup>2+</sup>, ABA synthesis, etc.) that trigger further adaptive responses<sup>A</sup>.

Macroscopic changes observed under salinity conditions, such as reduced leaf area and root/aerial part relationship, among others, also show a necessary adjustment to recover water balance (24).

A World losing 2,000 hectares of farm soil daily to salt damage [en línea]. Phys.Org, 28 de octubre de 2014, [Consultado: 23 de marzo de 2016], Disponible en: <a href="http://phys.org/news/2014-10-world-hectares-farm-soil-daily.html">httml</a>.

#### ION ABSORPTION

In a saline soil, high Na $^+$  and Cl $^-$  or (SO $_4^{2-}$ ) concentration causes nutrient absorption interference (K $^+$ , Ca $^{2+}$ , NO $_3^-$ ) and prevents their uptake, meanwhile they can reach toxic cytosolic levels to cell metabolism (25).

The root, as the main water and ion absorption organ, is very important for a short or long-term response to salt stress. Abscisic acid (ABA) is synthesized there, which is one of the early stressful signs that is able to produce local (hydraulic conductivity) and distant (stomatal closure) physiological changes (26). Both anatomical and morphological root characteristics can have great influence on the adaptive ability to salinity (27, 28).

#### **N**UTRITIONAL EFFECTS

The presence of salt ions in soil solution, starting from a certain critical concentration level, causes a displacement of plant mineral nutritional balance. This effect occurs in two ways:

- ◆ Soil ionic strength has a direct effect on nutrient absorption and translocation, which is evident because salinity induces phosphorus uptake and accumulation in certain species. This is an osmotic effect that occurs regardless of the type of salt used (29).
- ◆ The most common salinity mechanism that modifies plant mineral nutrition is the direct Cl<sup>-</sup> and Na<sup>+</sup> interaction on nutrient uptake and translocation within the plant (25).

Several studies show that K<sup>+</sup> concentration decreases in the plant when salinity or Na<sup>+</sup>/Ca<sup>2+</sup>

relationship increases in the soil (14, 30-32).

The reduced K<sup>+</sup> absorption by Na<sup>+</sup> is a competitive process in the plant. Although plants have high K<sup>+</sup> selectivity compared to Na<sup>+</sup>, its excessive amounts may have negative effects (33). Despite various studies indicate K<sup>+</sup> absorption and translocation is reduced in plants grown on substrates where Na<sup>+</sup> predominates, there is little evidence demonstrating that K<sup>+</sup> addition improves plant development under these conditions (34, 35).

Apart from this classic ion unbalance, a decreased NO<sub>3</sub>concentration in plants under saline conditions has been widely studied under several experimental conditions with different plant species, such as wheat (Triticum spp L.), barley (Hordeum vulgare L.) and tomato (Solanum lycopersicum Mill) (36-41). However, in spite of the drastic NO<sub>3</sub>-concentration reduction in leaves as a response to salinity, various nitrogenous fractions increase (or at least do not decrease), such as proline content, betaines and amino acids or total soluble proteins (42).

Moreover, NaCl has also proved to induce phosphorus toxicity in some species as corn (Zea mays L.) (43, 44), sesame (Sesamum indicum L.) (45), certain soybean varieties (Glycine max L.) (46) and lupine (Lupinus polyphyllus Lindl.) (47).

Under saline conditions, there may be some problems with micronutrient availability in plants, although the influence of salinity on their concentrations depends either on the plant or the micronutrient involved (48, 49).

## ARBUSCULAR MYCORRHIZAL FUNGI AND SALINITY

Arbuscular mycorrhizal fungi (AMF) are plant root symbionts that can be considered the cornerstone of mutualism in terrestrial ecosystems (50).

Mycorrhizal symbiosis is an ancient relationship. Hyphae and arbuscules have been reported in fossils derived from the early Devonian period and molecular studies suggest Glomal presence about 350-460 million years ago, which evolved along with the plants when they were conquering the Earth (51).

Arbuscular mycorrhizae have been widely described as favoring plant growth (52). Mycorrhizal colonization provokes physical, biochemical and physiological changes in roots, so that it leads to a better overall plant status and helps relief abiotic (heavy metals, salinity) and biotic (pathogen attacks, rhizosphere microbial changes) stress situations (53).

AMF has the ability to protect plants from salinity stress; however, its mechanisms are not so clear, partly because there are few studies about AMF effects on plant growth under salinity conditions and its effects upon mycorrhizal colonization. Nevertheless, some available data indicate these fungi have the potential of improving salt tolerant crop benefits when selected and combined adequately (54).

The existence of AMF under saline environments is

well known, where salt tolerant plants can have a better early growth (55, 56).

It is considered that AMF improves mineral nutrient supply to plants in saline soils, especially phosphorus, which tends to be precipitated by other ions, such as Ca<sup>2+</sup>, Mg<sup>2+</sup> and Zn<sup>2+</sup> (5, 57-59).

In addition to nutritional improvement, AMF benefits some physiological processes, as plant water absorption capacity, increases root water conductivity and promotes osmotic balance adaptation as well as carbohydrate composition (60, 61). Thus, these fungi mitigate the adverse effects of excessive salt accumulated in roots (9).

The role of mycorrhizae under saline conditions is still incomplete. A few studies have demonstrated its effects on osmotic adjustment (61, 62), but all of them have been focused on low salinity; therefore, it would be interesting to perform new experiments under different salinity situations to explain its role.

A discussion on AMF ecology under a saline environment may be confused, due to the need to distinguish between biotic and abiotic effects on fungus distribution and its relative abundance (63). No mycorrhizal colonization is observed when sodium is higher than 3 131 mg g<sup>-1</sup> in the soil, but there have been root-colonized plants and arbuscular mycorrhizal fungus spores in habitats of saline soils with electrical conductivity exceeding 185 dS m<sup>-1</sup> (56).

Several studies report the identification of AMF species in saline soils. The positive identification of these fungi into

species is a difficult and highly specialized process that can be impossible when the material is collected in these soils (56).

Salinity effects on arbuscular mycorrhizal formation should include its influence on host plant growth. Root colonization levels are reduced when soil salinity is higher, perhaps because of physiological changes caused by direct symbiotic effects or indirect fungal effects provoked by other soil parameters, such as pH, texture, organic matter, aeration, clay content, physical and chemical soil characteristics as well as biotic factors (64).

## AMF USED AS AN ALTERNATIVE FOR AGRICULTURAL PRODUCTION UNDER SALINITY CONDITIONS

Although there is evidence that mycorrhizal symbiosis affects and regulates several mechanisms involved in plant tolerance to salinity, many physiological aspects and the molecular basis of this regulation are unknown. However, the ecological significance of mycorrhizal association to plant survival and growth under salt stress conditions is widely demonstrated; therefore, it is important for agriculture under this condition.

In a study performed with AMF inoculation in pepper plants (Capsicum frutescens L.), a higher growth and yield was observed by reducing sodium in leaves, also increasing membrane stability and essential inorganic nutrient concentrations (65).

AMF improved harmful salinity effects on plant growth and nutrition of pepper (Capsicum annuum L.) at lower Na concentrations in leaf tissues and relieved salinity impact on membrane stability; besides, it delayed senescence syndrome in these plants (66).

Inoculated grapevines (Vitis vinifera L.) recorded significant increases of volume and root length, leaf number per plant, leaf area and dry weight, as well as chlorophyll levels compared to non-mycorrhized plants under salinity conditions (67).

In tomato plants (Solanum lycopersicum Mill) grafted to become more salinity resistant, the use of AMF-inoculated rootstocks increased total and commercial yield, besides improving quality parameters, such as high vitamin C and low acid contents (68).

Mycorrhized trifoliate orange (Poncirus trifoliataL.) seedlings showed more efficient antioxidant defense systems that provided better protection against salinity damages; in addition, malondihaldeide and hydrogen peroxide contents in leaves of mycorrhized plants were significantly lower (69).

Two leguminous crop species of *Myrica esculenta* (Buch.) and *Syzygium cumini* (L.), where the effects of different salinity levels were tested on growth, nodulation and nitrogen fixation proved that co-inoculation of rhizobia together with AMF showed the best results in all cases (70).

A greenhouse study was conducted to determine the effects of increasing salt (NaCl)

concentrations on mycorrhized and non-mycorrhized leguminous crop species of Strophostyle shelvola (L.). Data showed evidence of significantly higher chlorophyll content, dry weight and root nodule number of mycorrhized plants than non-mycorrhized ones. High salt concentrations had a negative effect on growth, but they were partially mitigated by AMF (71).

These and other studies have reported agricultural benefits of AMF inoculation in areas affected by high salt levels and the importance of studying this fungal ecology in saline soils, in order to identify the most efficient strains for agriculture under these conditions.

#### CONCLUSIONS

Experimental results confirm that AMF enables to alleviate adverse salinity effects by means of improving water intake and nutrient absorption, especially P through colonized plant roots. Moreover, it is able to enhance photosynthetic efficiency reduction, gas exchange and membrane disorders by applying various mechanisms; thus, the proper AMF management has the potential to enable and improve agriculture in salinity-affected areas, using a natural process that plants have employed since the planet was colonized.

#### **BIBLIOGRAPHY**

- Kausar, A.; Ashraf, M. Y.; Ali, I.; Niaz, M. y Abbass, Q. "Evaluation of sorghum varieties/lines for salt tolerance using physiological indices as screening tool". *Pakistan Journal of Botany*, vol. 44, no. 1, 2012, pp. 47–52, ISSN 0556-3321, 2070-3368.
- Alrahman, N. M. A.; Shibli, R. A.; Ereifej, K. y Hindiyeh, M. Y. "Influence of Salinity on Growth and Physiology of in Vitro Grown Cucumber (Cucumis Sativus L.).". Jordan Journal of Agricultural Sciences, vol. 1, no. 1, 19 de agosto de 2010, pp. 93–106, ISSN 1815-8625.
- 3. Ashraf, M. y Foolad, M. R. "Roles of glycine betaine and proline in improving plant abiotic stress resistance". *Environmental and Experimental Botany*, vol. 59, no. 2, marzo de 2007, pp. 206-216, ISSN 0098-8472, DOI 10.1016/j. envexpbot.2005.12.006.
- 4. Al-Karaki, G. N. "Response of Wheat and Barley during Germination to Seed Osmopriming at Different Water Potential". *Journal of Agronomy and Crop Science*, vol. 181, no. 4, 1 de noviembre de 1998, pp. 229-235, ISSN 1439-037X, DOI 10.1111/j.1439-037X.1998. tb00422.x.
- Al-Karaki, G. N. "Growth of mycorrhizal tomato and mineral acquisition under salt stress". *Mycorrhiza*, vol. 10, no. 2, agosto de 2000, pp. 51-54, ISSN 0940-6360, 1432-1890, DOI 10.1007/ s005720000055.
- Aggarwal, A.; Kadian, N.; Neetu, K.; Tanwar, A. y Gupta, K. K. "Arbuscular mycorrhizal symbiosis and alleviation of salinity stress". Journal of Applied and Natural Science, vol. 4, no. 1, 2012, pp. 144-155, ISSN 0974-9411.
- Rabie, G. H. y Almadini, A. M. "Role of bioinoculants in development of salt-tolerance of Vicia faba plants under salinity stress". African Journal of Biotechnology, vol. 4, no. 3, 2005, p. 210, ISSN 1684-5315.

- Tian, C. Y.; Feng, G.; Li, X. L. y Zhang, F. S. "Different effects of arbuscular mycorrhizal fungal isolates from saline or nonsaline soil on salinity tolerance of plants". *Applied Soil Ecology*, vol. 26, no. 2, junio de 2004, pp. 143-148, ISSN 0929-1393, DOI 10.1016/j.apsoil.2003.10.010.
- Giri, B. y Mukerji, K. G. "Mycorrhizal inoculant alleviates salt stress in Sesbania aegyptiaca and Sesbania grandiflora under field conditions: evidence for reduced sodium and improved magnesium uptake". Mycorrhiza, vol. 14, no. 5, 23 de octubre de 2003, pp. 307-312, ISSN 0940-6360, 1432-1890, DOI 10.1007/s00572-003-0274-1.
- 10. Yano, M. A. M.; Saggin, O. J. y Costa, M. L. "Tolerance of mycorrhized banana (*Musa* sp. cv. Pacovan) plantlets to saline stress". *Agriculture, Ecosystems & Environment*, vol. 95, no. 1, abril de 2003, pp. 343-348, ISSN 0167-8809, DOI 10.1016/S0167-8809(02)00044-0.
- 11. James, D. W.; Hanks, R. J. y Jurinak, J. J. Modern irrigated soils [en línea]. edit. John Wiley & Sons, 1982, 235 p., ISBN 978-0-471-06351-3, [Consultado: 23 de marzo de 2016], Disponible en: <a href="http://www.cabdirect.org/abstracts/19820308987.html">http://www.cabdirect.org/abstracts/19820308987.html</a>.
- 12. Hasanuzzaman, M.; Nahar, K.; Alam, M. M.; Bhowmik, P. C.; Hossain, M. A.; Rahman, M. M.; Prasad, M. N. V.; Ozturk, M. y Fujita, M. "Potential Use of Halophytes to Remediate Saline Soils". *BioMed Research International*, vol. 2014, 6 de julio de 2014, ISSN 2314-6133, DOI 10.1155/2014/589341, [Consultado: 23 de marzo de 2016], Disponible en: <a href="http://www.hindawi.com/journals/bmri/2014/589341/abs/">http://www.hindawi.com/journals/bmri/2014/589341/abs/</a>>.
- 13. Wicke, B.; Smeets, E.; Dornburg, V.; Vashev, B.; Gaiser, T.; Turkenburg, W. y Faaij, A. "The global technical and economic potential of bioenergy from salt-affected soils". *Energy & Environmental Science*, vol. 4, no. 8, 2 de agosto de 2011, pp. 2669-2681, ISSN 1754-5706, DOI 10.1039/C1EE01029H.

- 14. Janzen, H. H. y Chang, C. "Cation Nutrition of Barley as Influenced by Soil Solution Composition in a Saline Soil". Canadian Journal of Soil Science, vol. 67, no. 3, 1 de agosto de 1987, pp. 619-629, ISSN 0008-4271, DOI 10.4141/ cjss87-058.
- 15. Pessarakli, M. Handbook of Plant and Crop Stress. 3.ª ed., edit. CRC Press, 16 de noviembre de 2010, 1248 p., ISBN 978-1-4398-1399-7.
- 16. Suárez, D. "Soil salinization and management options for sustainable crop production". En: Pessarakli M., Handbook of Plant and Crop Stress, edit. CRC Press, 16 de noviembre de 2010, pp. 169-203, ISBN 978-1-4398-1399-7.
- 17. Nagaz, K.; Masmoudi, M. M. y Mechlia, N. B. "Impacts of irrigation regimes with saline water on carrot productivity and soil salinity". *Journal of the Saudi Society of Agricultural Sciences*, vol. 11, no. 1, enero de 2012, pp. 19-27, ISSN 1658-077X, DOI 10.1016/j. jssas.2011.06.001.
- Tedeschi, A. y Dell'Aquila, R. "Effects of irrigation with saline waters, at different concentrations, on soil physical and chemical characteristics". Agricultural Water Management, vol. 77, no. 1–3, 22 de agosto de 2005, pp. 308-322, ISSN 0378-3774, DOI 10.1016/j. agwat.2004.09.036.
- Prendergast, J. B. "A model of crop yield response to irrigation water salinity: theory, testing and application". *Irrigation Science*, vol. 13, no. 4, marzo de 1993, pp. 157-164, ISSN 0342-7188, 1432-1319, DOI 10.1007/BF00190030.
- 20. Noborio, K. y McInnes, K. J. "Thermal Conductivity of Salt-Affected Soils". Soil Science Society of America Journal, vol. 57, no. 2, 1993, pp. 329-334, ISSN 0361-5995, DOI 10.2136/ sssaj1993.03615995005700020007x.
- 21. Lax, A.; Diaz, E.; Castillo, V. y Albaladejo, J. "Reclamation of physical and chemical properties of a salinized soil by organic amendment". Arid Soil Research and Rehabilitation, vol. 8, no. 1, 1 de enero de 1994, pp. 9-17, ISSN 0890-3069, DOI 10.1080/15324989309381374.

- 22. Hasegawa, P. M.; Bressan, and R. A.; Zhu, J.-K. y Bohnert, H. J. "Plant Cellular and Molecular Responses to High Salinity". *Annual Review of Plant Physiology and Plant Molecular Biology*, vol. 51, no. 1, 2000, pp. 463-499, ISSN 1040-2519, DOI 10.1146/annurev. arplant.51.1.463.
- 23. Zhu, J. K. "Genetic Analysis of Plant Salt Tolerance Using Arabidopsis". Plant Physiology, vol. 124, no. 3, 11 de enero de 2000, pp. 941-948, ISSN 1532-2548, DOI 10.1104/ pp.124.3.941.
- 24. Bray, E. "Responses to abiotic stresses". En: eds. Buchanan B. B., Gruissem W., y Jones R. L., Biochemistry and Molecular Biology of Plants, edit. Wiley, Chichester, West Sussex, Hoboken, NJ, 2000, pp. 1158–1203, ISBN 978-0-943088-39-6.
- 25. Chinnusamy, V.; Jagendorf, A. y Zhu, J. K. "Understanding and Improving Salt Tolerance in Plants". *Crop Science*, vol. 45, no. 2, 2005, p. 437, ISSN 1435-0653, DOI 10.2135/cropsci2005.0437.
- 26. Marschner, H. Marschner's Mineral Nutrition of Higher Plants. edit. Academic Press, 8 de agosto de 2011, 668 p., ISBN 978-0-12-384906-9.
- 27. Reinhardt, D. H. y Rost, T. L. "Salinity accelerates endodermal development and induces an exodermis in cotton seedling roots". *Environmental and Experimental Botany*, vol. 35, no. 4, octubre de 1995, pp. 563-574, ISSN 0098-8472, DOI 10.1016/0098-8472(95)00015-1.
- 28. Hartung, W.; Sauter, A. y Hose, E. "Abscisic acid in the xylem: where does it come from, where does it go to?". *Journal of Experimental Botany*, vol. 53, no. 366, 1 de enero de 2002, pp. 27-32, ISSN 0022-0957, 1460-2431, DOI 10.1093/jexbot/53.366.27.
- 29. Maggio, A.; Hasegawa, P. M.; Bressan, R. A.; Consiglio, M. F. y Joly, R. J. "Review: Unravelling the functional relationship between root anatomy and stress tolerance". Australian Journal of Plant Physiology, vol. 28, no. 10, 1 de enero de 2001, pp. 999-1004, ISSN 0310-7841.

- 30. Kronzucker, H. J.; Szczerba, M. W.; Moazami, G. M. y Britto, D. T. "The cytosolic Na\*: K\* ratio does not explain salinity-induced growth impairment in barley: a dual-tracer study using <sup>42</sup>K\* and <sup>24</sup>Na\*". *Plant, Cell & Environment*, vol. 29, no. 12, 1 de diciembre de 2006, pp. 2228-2237, ISSN 1365-3040, DOI 10.1111/j.1365-3040.2006.01597.x.
- 31. Bernstein, N. "Effects of salinity on root growth". En: eds. Eshel A. y Beeckman T., *Plant Roots: The Hidden Half*, edit. CRC Press, Boca Raton, FL, 17 de abril de 2013, pp. 375-391, ISBN 978-1-4398-4648-3.
- 32. Saida, C.; Houria, B. y Mébarek, B. "Interactive effects of salinity and potassium on physiomorphological traits of tomato (Lycopersicon esculentum Mill.; var: heintz)". Agriculture and Biology Journal of North America, vol. 5, no. 3, 2014, pp. 135–143, ISSN 2151-7517, 2151-7525, DOI 10.5251/abjna.2014.5.3.135.143.
- 33. Subbarao, G. V.; Johansen, C.; Jana, M. K. y Kumar Rao, J. V. D. K. "Effects of the Sodium/ Calcium Ratio in Modifying Salinity Response of Pigeonpea (Cajanus cajan)". Journal of Plant Physiology, vol. 136, no. 4, julio de 1990, pp. 439-443, ISSN 0176-1617, DOI 10.1016/S0176-
- 34. Tzortzakis, N. G. "Potassium and calcium enrichment alleviate salinity-induced stress in hydroponically grown endives". *Horticultural Science*, vol. 37, no. 4, 2010, pp. 155–162, ISSN 0862-867X.
- 35. Muhammed, S.; Akbar, M. y Neue, H. U. "Effect of Na/Ca and Na/K ratios in saline culture solution on the growth and mineral nutrition of rice (*Oryza* sativa L.)". Plant and Soil, vol. 104, no. 1, marzo de 1987, pp. 57-62, ISSN 0032-079X, 1573-5036, DOI 10.1007/BF02370625.
- 36. Helal, M.; Koch, K. y Mengel, K. "Effect of Salinity and Potassium on the Uptake of Nitrogen and on Nitrogen Metabolism in Young Barley Plants". *Physiologia Plantarum*, vol. 35, no. 4, 1 de diciembre de 1975, pp. 310-313, ISSN 1399-3054, DOI 10.1111/j.1399-3054.1975.tb03911.x.

- 37. Kafkafi, U.; Valoras, N. y Letey, J. "Chloride interaction with nitrate and phosphate nutrition in tomato (Lycopersicon esculentum L.)". Journal of Plant Nutrition, vol. 5, no. 12, 1 de enero de 1982, pp. 1369-1385, ISSN 0190-4167, DOI 10.1080/01904168209363070.
- 38. Aslam, M.; Huffaker, R. C. y Rains, D. W. "Early Effects of Salinity on Nitrate Assimilation in Barley Seedlings". *Plant Physiology*, vol. 76, no. 2, 10 de enero de 1984, pp. 321-325, ISSN 1532-2548, DOI 10.1104/ pp.76.2.321.
- 39. Chow, W.; Ball, M. y Anderson, J. "Growth and Photosynthetic Responses of Spinach to Salinity: Implications of K\* Nutrition for Salt Tolerance". *Australian Journal of Plant Physiology*, vol. 17, no. 5, 1 de enero de 1990, pp. 563-578, ISSN 0310-7841.
- 40. Massa, D.; Mattson, N. S. y Lieth, H. J. "Effects of saline root environment (NaCI) on nitrate and potassium uptake kinetics for rose plants: a Michaelis—Menten modelling approach". *Plant and Soil*, vol. 318, no. 1-2, 12 de noviembre de 2008, pp. 101-115, ISSN 0032-079X, 1573-5036, DOI 10.1007/s11104-008-9821-z.
- 41. Ali, Y.; Aslam, Z.; Ashraf, M. Y. y Tahir, G. R. "Effect of salinity on chlorophyll concentration, leaf area, yield and yield components of rice genotypes grown under saline environment". International Journal of Environmental Science & Technology, vol. 1, no. 3, 14 de septiembre de 2013, pp. 221-225, ISSN 1735-1472, 1735-2630, DOI 10.1007/BF03325836.
- 42. Feigin, A.; Rylski, I.; Meiri, A. y Shalhevet, J. "Nitrogen: Response of melon and tomato plants to chloride-nitrate ratio in saline nutrient solutions". *Journal of Plant Nutrition*, vol. 10, no. 9-16, 1 de junio de 1987, pp. 1787-1794, ISSN 0190-4167, DOI 10.1080/01904168709363719.
- 43. Bernstein, L. "Effects of salinity and sodicity on plant growth". *Annual Review of Phytopathology*, vol. 13, no. 1, 1975, pp. 295–312, ISSN 0066-4286.

- 44. Gorham, J.; Budrewicz, E.; Mcdonnell, E. y Jones, R. G. W. "Salt Tolerance in the *Triticeae*: Salinity-induced Changes in the Leaf Solute Composition of Some Perennial Triticeae". *Journal of Experimental Botany*, vol. 37, no. 8, 8 de enero de 1986, pp. 1114-1128, ISSN 0022-0957, 1460-2431, DOI 10.1093/jxb/37.8.1114.
- 45. Nieman, R. H. y Clark, R. A. "Interactive Effects of Salinity and Phosphorus Nutrition of the Concentrations of Phosphate and Phosphate Esters in Mature Photosynthesizing Corn Leaves". *Plant Physiology*, vol. 57, no. 2, 2 de enero de 1976, pp. 157-161, ISSN 1532-2548, DOI 10.1104/pp.57.2.157.
- 46. Cerda, A.; Bingham, F. T. y Hoffman, G. J. "Interactive Effect of Salinity and Phosphorus on Sesame". Soil Science Society of America Journal, vol. 41, no. 5, 1977, pp. 915-918, ISSN 0361-5995, DOI 10.2136/sssaj1977.036159950 04100050021x.
- 47. Grattan, S. R. y Maas, E. V. "Interactive Effects os Salinity and Substrate Phosphate on Soybean". Agronomy Journal, vol. 76, no. 4, 8/01 de 1984, pp. 668-676, ISSN 0002-1962, DOI 10.2134/agronj1984.000219620 07600040038x.
- 48. Treeby, M. T. y van Steveninck, R. F. M. "The influence of salinity on phosphate uptake and distribution in lupin roots". *Physiologia Plantarum*, vol. 72, no. 3, 1 de marzo de 1988, pp. 617-622, ISSN 1399-3054, DOI 10.1111/j.1399-3054.1988.tb09172.x.
- 49. El-Motaium, R.; Hu, H. y Brown, P. H. "The Relative Tolerance of Six Prunus Rootstocks to Boron and Salinity". Journal of the American Society for Horticultural Science, vol. 119, no. 6, 11 de enero de 1994, pp. 1169-1175, ISSN 0003-1062, 2327-9788.

- 50. Wimmer, M. A.; Muehling, K. H.; Läuchli, A.; Brown, P. H. y Goldbach, H. E. "Interaction of salinity and boron toxicity in wheat (Triticum aestivum L.)" [en línea]. En: eds. Horst W. J., Schenk M. K., Bürkert A., Claassen N., Flessa H., Frommer W. B., Goldbach H., Olfs H.-W., Römheld V., Sattelmacher B., Schmidhalter U., Schubert S., Wirén N. v, y Wittenmayer L., Plant Nutrition, edit. Springer Netherlands, 2001, pp. 426-427, ISBN 978-0-7923-7105-2, [Consultado: 23 de marzo de 2016], Disponible en: <a href="http://link.">http://link.</a> springer.com/chapter/10.1007/0-306-47624-X\_206>.
- 51. Öpik, M.; Moora, M.; Zobel, M.; Saks, Ü.; Wheatley, R.; Wright, F. y Daniell, T. "High diversity of arbuscular mycorrhizal fungi in a boreal herb-rich coniferous forest". New Phytologist, vol. 179, no. 3, 1 de agosto de 2008, pp. 867-876, ISSN 1469-8137, DOI 10.1111/j.1469-8137.2008.02515.x.
- 52. Mohammadi, G. E.; Rezaee, D. Y.; Prasad, R. y Varma, A. "Mycorrhizal Fungi: What We Know and What Should We Know?" [en línea]. En: ed. Varma A., *Mycorrhiza*, edit. Springer Berlin Heidelberg, 2008, pp. 3-27, ISBN 978-3-540-78824-9, [Consultado: 23 de marzo de 2016], Disponible en: <a href="http://link.springer.com/chapter/10.1007/978-3-540-78826-3\_1">http://link.springer.com/chapter/10.1007/978-3-540-78826-3\_1</a>.
- 53. Smith, S. E. y Read, D. J. "Mycorrhizas in agriculture, horticulture and forestry". En: *Mycorrhizal Symbiosis*, edit. Academic Press, 2008, pp. 144-187, ISBN 978-0-08-055934-6.
- 54. Azcón, A. C. y Barea, J. M. "Applying mycorrhiza biotechnology to horticulture: significance and potentials". *Scientia Horticulturae*, vol. 68, no. 1–4, 3 de marzo de 1997, pp. 1-24, ISSN 0304-4238, DOI 10.1016/S0304-4238(96)00954-5.
- 55. Juniper, S. y Abbott, L. "Vesicular-arbuscular mycorrhizas and soil salinity". *Mycorrhiza*, vol. 4, no. 2, diciembre de 1993, pp. 45-57, ISSN 0940-6360, 1432-1890, DOI 10.1007/BF00204058.

- 56.Cho, K.; Toler, H.; Lee, J.; Ownley, B.; Stutz, J. C.; Moore, J. L. y Augé, R. M. "Mycorrhizal symbiosis and response of sorghum plants to combined drought and salinity stresses". *Journal of Plant Physiology*, vol. 163, no. 5, 3 de marzo de 2006, pp. 517-528, ISSN 0176-1617, DOI 10.1016/j. jplph.2005.05.003.
- 57.Al-Karaki, G. N. y Clark, R. B. "Growth, mineral acquisition, and water use by mycorrhizal wheat grown under water stress". *Journal of Plant Nutrition*, vol. 21, no. 2, 1 de febrero de 1998, pp. 263-276, ISSN 0190-4167, DOI 10.1080/01904169809365401.
- 58.Al-Karaki, G. N.; Hammad, R. y Rusan, M. "Response of two tomato cultivars differing in salt tolerance to inoculation with mycorrhizal fungi under salt stress". *Mycorrhiza*, vol. 11, no. 1, mayo de 2001, pp. 43-47, ISSN 0940-6360, 1432-1890, DOI 10.1007/s005720100098.
- 59. Aliasgharzadeh, N.; Rastin, S. N.; Towfighi, H. y Alizadeh, A. "Occurrence of arbuscular mycorrhizal fungi in saline soils of the Tabriz Plain of Iran in relation to some physical and chemical properties of soil". *Mycorrhiza*, vol. 11, no. 3, 2 de marzo de 2014, pp. 119-122, ISSN 0940-6360, 1432-1890, DOI 10.1007/s005720100113.
- 60. Porras, S. A.; Soriano, M. M. L.; Porras, P. A. y Azcón, R. "Arbuscular mycorrhizal fungi increased growth, nutrient uptake and tolerance to salinity in olive trees under nursery conditions". *Journal of Plant Physiology*, vol. 166, no. 13, 1 de septiembre de 2009, pp. 1350-1359, ISSN 0176-1617, DOI 10.1016/j. jplph.2009.02.010.
- 61. Rosendahl, C. N. y Rosendahl, S. "Influence of vesicular-arbuscular mycorrhizal fungi (*Glomus* SPP.) on the response of cucumber (*Cucumis sativus* L.) to salt stress". *Environmental and Experimental Botany*, vol. 31, no. 3, julio de 1991, pp. 313-318, ISSN 0098-8472, DOI 10.1016/0098-8472(91)90055-S.

- 62. Sharifi, M.; Ghorbanli, M. y Ebrahimzadeh, H. "Improved growth of salinity-stressed soybean after inoculation with salt pretreated mycorrhizal fungi". *Journal of Plant Physiology*, vol. 164, no. 9, 5 de septiembre de 2007, pp. 1144-1151, ISSN 0176-1617, DOI 10.1016/j.jplph.2006.06.016.
- 63. Giri, B. y Mukerji, K. G. "Improved growth and productivity of Sesbania grandiflora Pers. under salinity stress through mycorrhizal technology". Journal of Phytological Research, vol. 12, no. 1-2, 1999, pp. 35–38, ISSN 0970-5767.
- 64. Neumann, P. M.; Azaizeh, H. y Leon, D. "Hardening of root cell walls: a growth inhibitory response to salinity stress". *Plant, Cell & Environment*, vol. 17, no. 3, 1 de marzo de 1994, pp. 303-309, ISSN 1365-3040, DOI 10.1111/j.1365-3040.1994.tb00296.x.
- 65. Duvert, P.; Perrin, R. y Plenchette, C. "Soil receptiveness to VA mycorrhizal association: Concept and method". *Plant and Soil*, vol. 124, no. 1, mayo de 1990, pp. 1-6, ISSN 0032-079X, 1573-5036, DOI 10.1007/BF00010924.
- 66. Selvakumar, G. y Thamizhiniyan, P. "The effect of the arbuscular mycorrhizal (AM) fungus Glomus intraradices on the growth and yield of chilli (Capsicum annuum L.) under salinity stress". World Applied Sciences Journal, vol. 14, no. 8, 2011, pp. 1209–1214, ISSN 1818-4952.

- 67. Beltrano, J.; Ruscitti, M.; Arango, M. C. y Ronco, M. "Effects of arbuscular mycorrhiza inoculation on plant growth, biological and physiological parameters and mineral nutrition in pepper grown under different salinity and p levels". *Journal of soil science and plant nutrition*, vol. 13, no. 1, marzo de 2013, pp. 123-141, ISSN 0718-9516, DOI 10.4067/S0718-95162013005000012.
- 68. Derbew, B.; Mokashi, A.; Patil, C. y Hegde, R. "Effect of Mycorrhizal Inoculation at Different Salinity Levels on Root Colonization, Growth and Chlorophyll Content of Different Grape Rootstocks (Vitis spp)". Tropical Agricultural Research and Extension, vol. 10, no. 0, 26 de abril de 2010, pp. 79-82, ISSN 1391-3646, DOI 10.4038/tare.v10i0.1875.
- 69. Oztekin, G. B.; Tuzel, Y. y Tuzel, I. H. "Does mycorrhiza improve salinity tolerance in grafted plants?". Scientia Horticulturae, vol. 149, 4 de enero de 2013, pp. 55-60, ISSN 0304-4238, DOI 10.1016/j.scienta.2012.02.033.
- 70. Wu, Q. S.; Zou, Y. N.; Liu, W.; Ye, X. F.; Zai, H. F. y Zhao, L. J. "Alleviation of salt stress in citrus seedlings inoculated with mycorrhiza: changes in leaf antioxidant defense systems". *Plant Soil Environ*, vol. 56, no. 10, 2010, pp. 470–475, ISSN 1214-1178.
- 71. Bhushan, G.; Sharma, S. K.; Sagar, P.; Seth, N. y Singh, A. P. "Role of arbuscular mycorrhiza fungi on tolerance to salinity of the tree legume *Albizia lebbeck* (L.) inoculated by *Rhizobium*". *Indian Journal of Pharmaceutical and Biological Research*, vol. 2, no. 1, 2014, pp. 45-50, ISSN 2320-9267.

Received: December 12, 2014 Accepted: November 10, 2015

