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MITIGATION OF DROUGHT STRESS IN *Solanaceae* VEGETABLES THROUGH SYMBIOSIS WITH PLANT GROWTH - PROMOTING BACTERIA AND ARBUSCULAR MYCORRHIZAL FUNGI. A REVIEW

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Abstract

Plants constitute dynamic systems with different strategies to face biotic and abiotic stress. Water deficit is one of the most challenging abiotic factors increased by climate change, affecting seriously the quality of soils and crop yields, decreasing photosynthetic rate, increasing the accumulation of free radicals, and modifying root morphology. In this regard, the potential role of the host plant - arbuscular mycorrhizal fungi (AMF) and plant growth-promoting bacteria (PGPB) interactions within the rhizosphere in the alleviation of drought stress is being deeply studied. These symbiotic relationships not only allow a major nutrient and water uptake, but also could be integrated as a sustainable approach to improve the growth and productivity of crops under water scarcity conditions. A better comprehension of the mechanisms of these synergies between PGPB and AMF with plants is becoming an important key to develop effective applications of these natural symbiosis. In this work, the highlighted knowledge concerning these associations and their effect in the response of plants under drought stress have been reviewed, focusing on the interactions described in Solanaceae vegetables, one of the most relevant crops in the Mediterranean area.

Key words*: arbuscular mycorrhizal fungi, drought tolerance, plant biostimulants, plant growth - promoting bacteria, symbiosis.*

INTRODUCTION

There is an increasing need for rising crop yield to sustain the growing global population, ideally with a reduction of the impact on agroecosystems and human health (Colla & Rouphael, 2015). A promising and resilient farming strategy which is being widely studied is the use of plant biostimulants (PBs). A plant biostimulant (PB) is any beneficial substance and/or microorganism for plants without corresponding to nutrients, soil improvers or pesticides (Colla & Rouphael, 2015; Du Jardin, 2015). These products represent a non-polluting organic approach to boost plant growth, nutrient use efficiency (NUE), flowering, fruit set, fruit quality, crop yield and to relieve the effect of biotic and abiotic stress conditions (Barea et al., 2005; Bona et al., 2017; Colla & Rouphael, 2015).

Arbuscular Mycorrhizal Fungi (AMF) and Plant Growth-promoting bacteria (PGPB), in addition to other beneficial microorganisms, constitute the microbial biostimulants subgroup (Du Jardin, 2015). Numerous studies have demonstrated their efficiency to improve fruit quality and yield, as well as to reduce damage caused by biotic and abiotic stresses, through their interaction with plant roots (Berta et al., 2014; Noceto et al., 2021; Parada et al., 2018).

AMF are symbiotic associations established between different soil fungi and plants. These fungi belong to the phylum *Glomeromycota* (Schüßler et al., 2001), being obligate biotrophs which establish symbiotic interactions with most land plant species (Smith & Read, 2008). AMF colonize root system of plants through infected roots, spores, or hyphae, modifying the normal root architecture (Smith & Read, 2008), characterised by the formation of arbuscules in root cortical cells (Strullu-Derrien et al., 2016). In this regard, AMF allow a better water and some nutrients uptake from soil (Helber et al., 2011), such as potassium (K), nitrogen (N), and mainly phosphorus (P) (Asrar et al., 2014; Qiu et al., 2022), which stimulate plant growth and yield (Kheyri et al., 2022), improve crop quality (Kheyri et al., 2022) and enhance photosynthesis rate (Ran et al., 2021). AMF association also influences the normal plant metabolism and hormones biosynthesis (Campo & San Segundo, 2020) and improve the defence capability to biotic (Klinsukon et al., 2021) and abiotic stress (Figure 1) (Borde et al., 2017).

PGPB are root - associated plant - growth promoting bacteria that establish symbiosis with many different crops (Rai et al., 2021). PGPB stimulate plant development and growth by improving mineral nutrition through the phosphate solubilization, the nitrogen fixation or the iron chelation via siderophores (Gamalero & Glick, 2011), as well as producing plant growth phytohormones, such as cytokinins, auxins and gibberellins (Liu et al., 2013; Luziatelli et al., 2021). PGPB are also able to provide some resistance or tolerance to different abiotic and biotic factors due to reducing stress – ethylene, and synthetising different bioactive compounds (Figure 1) (Kim et al., 2022; Rossi et al., 2021). PGPB include different genera, such as *Arthrobacter*, *Enterobacter*, *Acinetobacter*, *Pseudomonas*, *Serratia*, *Streptomyces*, *Ochrobactrum*, *Bacillus*, etc. (Ribeiro et al., 2022; Siebielec et al., 2021; Ummara et al., 2021; Wang et al., 2022).

Drought stress is one of the most harmful abiotic factors on Earth, causing physiological, biochemical and molecular alterations in plants (Figure 1) (Wang et al., 2022), limiting plant development, growth and yield (Sharma & Dubey, 2005). To cope with water loss, plants must regulate stomata closure to avoid major metabolism alterations (Prasch & Sonnewald, 2015).

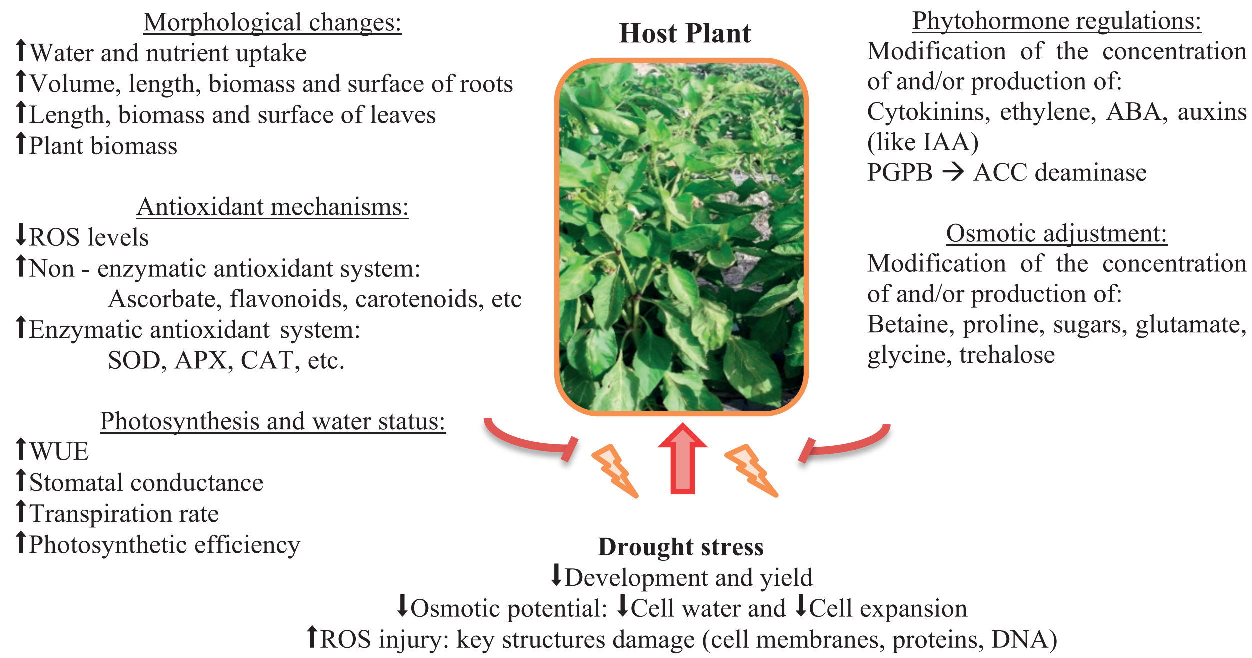

Figure 1. Effects of drought on plants and the mechanisms developed by AMF and PGPB to alleviate water deficit injury. The up and down arrows are indicative of increase or decrease of that element or process. ROS: Reactive oxygen species, SOD: Superoxide dismutase, APX: Ascorbate peroxidase, CAT: catalase, WUE: Water Use Efficiency, ABA: Abscisic Acid, IAA: Indoleacetic acid, ACC deaminase: 1 - aminocyclopropane - 1 - carboxylic acid deaminase

Moreover, drought causes relevant oxidative damage, involving rising levels of reactive oxygen species (ROS) (Figure 1) (Smirnof, 1993). Although plant cells have complex antioxidants mechanisms against ROS injury, when concentration exceeds the tolerance range, these compounds could severely damage key structures, like cell membranes, proteins and DNA (Prasch & Sonnewald, 2015).

The *Solanaceae* family is characterised by its wide variability and distribution around the world (Coelho et al., 2017). The genera *Solanum* represents the largest and the richest of the family (Bohs, 2007), where economically important species, such as tomato, eggplant and potato are included (Basu & De, 2003). The interest of this family also lies in pharmacological relevant species belonged to *Atropa*, *Solanum*, *Capsicum* or *Datura* genera (Shah et al., 2013), other economically valuable crops, like peppers (Basu & De, 2003) and species with ornamental uses, such as petunias (Basu et al., 2014).

Numerous scientific sources of information have reported valuable knowledge about the effects of AMF and PGPB in *Solanaceae* crops in the last decades, demonstrated their potential behaviour to alleviate multiple biotic and abiotic stresses. In this regard, this review aims to gather the most up-to date information and results for AMF and PBPG applications on the most economically important *Solanaceae* crops to reduce the harmful stress of water deficit.

STRATEGIES OF AMF - MEDIATED WATER DEFICIT STRESS TOLERANCE

AMF play a key role in the ecological balance maintenance of ecosystems, especially in arid areas (Cheng et al., 2021). The mechanisms involved in the enhancement of drought tolerance in plants by AMF are complex to elucidate and understand, producing multiple and variable responses in plants (Figure 1) (Cheng et al., 2021).

Effects of water deficit on AMF colonization

In response to water deficit, AMF can perform the anastomosis function, i.e. the capability to trigger the inter-individual fusion of vegetative cells, allowing to rebuild a disrupted mycelium after facing water stress (Bahadur et al., 2019). Moreover, the development of extraradical hyphal network of AMF outside the plant root system can contribute about the 20% of total water uptake by the plant host (Ruth et al., 2011). However, different studies have also shown negative effects of drought stress not only on the AMF colonization, but also during the post-colonization and the extraradical mycelium formation (Bahadur et al., 2019), difficulting the proper establishment of AMF - plant symbiosis. In this regard, Xu et al. (2018) observed that the inoculum of *Rhizophagus intraradices* added to wild - type (*wt*) tomato plants, as well as to ABA - deficient mutant not-abilis (*not*) tomato plants, had a colonization rate higher under water scarcity than in full water regime. Bitterlich et al., (2018) quantified an increase in the root colonization intensity by *Funneliformis mosseae* in tomato plants under drought. The same patter was observed by Leventis et al., (2021) in tomato F1 hybrid plants, inoculated with *Rhizophagus irregularis* and *Funneliformis mosseae*, which showed a two - fold increase in root colonization under drought conditions. Tallapragada et al. (2016) also reported a significant enhancement in the colonization percentage of *Rhizopagus fasciculatum* after drought management in sweet pepper plants. However, contrary results were reported by Duc et al. (2018), who quantified and important decrease in the inoculation rate of *Septoglomus constrictum* and *Septoglomus deserticola* after drought treatment in tomato plants. The same result was reported by Yooyongwech et al. (2016), who detected in two different potato varieties, inoculated with a mix of *Glomus* sp. and *Acaulospora* sp., a significant reduction in the inoculation rate after water stress.

AMF - Assisted drought stress tolerance by morphological changes

The effects of AMF symbiosis on plants root morphology have been widely studied (Saia et al., 2020). Thus, AMF allow a better distribution and penetration of plant root systems in soil, in addition to the promotion of some root traits, such as the volume, length, biomass and surface area (Liu et al., 2016). These modifications could maintain a balanced nutrient and water uptake in host plants under drought (Bahadur et al., 2019).

In this regard, tomato F1 hybrid plants inoculated with *R. irregularis* and *F. mosseae* showed a relevant increase in shoot growth, leaf surface and roots dry weight compared to non-inoculated plants under water deficit (Leventis et al., 2021). Duc et al. (2018) observed in tomato plants with *S. constrictum* an increase in root and shoot dry weights than non-inoculated plants under drought. Bitterlich et al. (2018) reported an increase in the leaf and root areas as well as in the root volume density of tomato plants inoculated with *F. mosseae* after water stress. Krishna et al. (2018) detected in hot pepper plants inoculated with *Glomus coronatum* a higher increase in root biomass compared to non-inoculated ones under 60%

and 40% field capacity (FC). Enjili et al. (2018) reported a major number of leaves, and a higher fresh and dry weight of fruits in inoculated sweet pepper plants with *Glomus intraradices* under water deficit conditions. Tallapragada et al. (2016) also observed in sweet pepper plants colonised by *R. fasciculatum* an increase in root length and weight, as well as in shoot length and weight under drought compared to non-inoculated plants. Badr et al. (2020) reported in eggplant F1 hybrid plants, inoculated with *G. intraradices,* an important increase in yield average and in total dry biomass compared to non-inoculated plants after a reduction of irrigation. Swetha & Padmavathi (2020) observed in plants of two eggplant cultivars, inoculated with *Piriformospora indica*, a significant increase in the root and shoot lengths, as well as in the dry weight of root and shoots. The number of leaves and the leaf surface area were also increase by AMF compared to non-inoculated plants under drought. In potato crop, Yooyongwech et al. (2016) reported in plants of potato variety Tainung 57, colonised by a mix of *Glomus* sp. and *Acaulospora* sp., a significant increase in both tuber fresh weight and in the number of leaves compared to non-inoculated plants under drought. Regarding nutrient absorption, Xu et al. (2018) inoculated *wt* and *not* tomato plants with *R. intraradices*, reporting higher P levels in shoots of *wt* plants under both water regimes, whereas *not* plants did not showed relevant effects. Leventis et al. (2021) reported that inoculated tomato hybrid plants with *R. irregularis* and *F. mosseae* showed an increase in P levels in both water regime. Badr et al. (2020) quantified in eggplant hybrid plants with *G. intraradices,* a total N and P content in fruits and shoots significantly higher than in non-inoculated plants under water deficit. Yooyongwech et al. (2016) observed in two potato varieties inoculated with *Glomus* sp. and *Acaulospora* sp., a significantly increase in the leaf P content compare with non-inoculated plants.

AMF - Assisted drought stress tolerance by enhancing antioxidant mechanisms

Some AMF species are interesting candidates for reducing or neutralizing the harmful impact of the accumulation of ROS (Nath et al., 2016). This effect may be the result of increased root hydration due to the AMF hyphae water absorption and its transfer to root cortical cells (Boutasknit et al., 2020). However, the reduction of ROS levels in inoculated plants may also result from the enhancement of non-enzymatic and enzymatic antioxidant defence systems (Zou et al., 2021). The non-enzymatic antioxidants include ascorbate (ASC), flavonoids, carotenoids, or glutathione (GSH); whereas enzymatic antioxidants involve superoxide dismutase (SOD), ascorbate peroxidase (APX), catalase (CAT), glutathione peroxidase (GPX) or guaiacol peroxidase (G-POD) (Kamali & Mehraban, 2020; Karimkhani et al., 2021; Xiao et al., 2022). Some evidence also suggests that AMF antioxidant system promotes the alleviation of oxidative stress in plants (Zou et al., 2021).

In this regard, Duc et al. (2018) observed in tomato plants with *S. constrictum* a reduction in the oxidative damage by drought due to an increase in leaf and root POD, SOD and CAT activities compared to non-inoculated plants. Tallapragada et al. (2016) reported in sweet pepper plants colonised with *R. fasciculatum* an increase in CAT activity, as well as a decrease in GPX activity under drought conditions. Swetha & Padmavathi (2020) also observed in two eggplant cultivars an increase in GPX and CAT activities compared to non-inoculated plants with *P. indica* under water scarcity. Yooyongwech et al. (2016) reported in plants of the potato variety PROC 65-3, inoculated with *Glomus* sp. and *Acaulospora* sp., a significantly major total carotenoids level compared to non-inoculated plants under drought.

AMF - Assisted drought stress tolerance by differential regulation of phytohormones

AMF symbiosis has also shown the ability to reduce the harmful effects of water deficit by modifying the endogenous phytohormonal levels (Bahadur et al., 2019), such as cytokinins, ethylene, abscisic acid (ABA), or auxins like indoleacetic acid (IAA) (Fernández-Lizarazo & Moreno-Fonseca, 2016). Abscisic acid (ABA), induces stomatal closure to reduce water loss by transpiration and the expression of different stress - related genes (Bahadur et al., 2019; Zhang et al., 2006), and it may be also involved in the proper symbiosis establishment (Etemadi et al., 2014). It has also been observed the increase of ABA content in plants due to it induction by AMF under drought, reducing water loss by transpiration through the stomatal closure (Jia-Dong et al., 2019); though, other studies have detected higher ABA levels in non-colonized root plants (Song et al., 2020). However, in both type of cases, the colonized plants showed a higher drought tolerance than non-colonized plants.

In this regard, Xu et al. (2018) observed that inoculation with *R. intraradices* up-regulated the expression of different genes involved in ABA signalling pathway, such as 14-3-3 genes, related to stomatal behaviour, in *wt* tomato plants, whereas stomata of *not* plants remained opened.

AMF - Assisted drought stress tolerance by osmotic adjustments

Osmotic stress participates in the inhibition of cell growth due to the restriction of the cell expansion (Bahadur et al., 2019). To reduce osmotic stress, plant cells promote osmotic adjustments, that involve organic solutes, like sugars, proteins, proline, etc., as well as inorganic solutes, such as Ca^{2+}, Mg^{2+}, K^{+}, etc. (Ozturk et al., 2021). Osmotic adjustments maintain the water potential gradient, favouring the proper water flow from soil into roots (Zhang et al., 2016). It has been reported that AMF colonized plants are favourable to make osmotic adjustments under water deficit stress owing to a major concentration of solutes (Zou et al., 2021).

However, other studies have reported contrary results, due to AMF symbiosis seemed to reduce the presence of different solutes, such as sugars or proline (Manoharan et al., 2010; Wu et al., 2017). These reductions could be the result of a higher drought tolerance in colonized plants (Liu et al., 2016). Proline is an important osmoprotectant that avoids the denaturation of different enzymes and other proteins, as well as it scavenges hydroxyl radical (Chaves et al., 2003; Ruiz-Lozano, 2003). Proline concentration has shown a variable behaviour in AMF colonized plants, increasing, reducing or maintaining its concentration under water deficit (Al-Arjani, 2020; Pons et al., 2020; Yooyongwech et al., 2013).

Thus, Krishna et al. (2018) reported in *G. coronatus* - inoculated hot pepper plants that the ion-leakage range was the half of the range observed in non-inoculated plants. The same drought alleviation sign was observed under 40% FC, when the ion leakage range had a reduction of more than ten percent than non-inoculated ones. Enjili et al. (2018) reported a lower proline content in sweet pepper plants with *G. intraradicese* than non-inoculated plants under drought, whereas Swetha & Padmavathi (2020) observed in two eggplant cultivars, inoculated with *P. indica*, an increase in the proline content compared to non-inoculated plants under water deficit.

AMF - Assisted drought stress tolerance by modifying plant water status and photosynthesis

AMF - plant symbiotic interactions allow plants to tackle drought stress by modifying their root structure and plant water relations (Pavithra & Yapa, 2018). Thus, this improvement in plant water status by AMF may enhance the water use efficiency (WUE), as well as may increase transpiration rate, photosynthetic efficiency or stomatal conductance (Begum et al., 2019; Fernández-Lizarazo & Moreno-Fonseca, 2016). Moreover, different authors have reported that AMF - inoculated plants showed a lower photoinhibition and photosynthetic apparatus injury (Fernández-Lizarazo & Moreno-Fonseca, 2016).

In this way, tomato plants with *R. irregularis* and *F. mosseeae* showed an important increase in WUE compared to non-inoculated plants under drought (Leventis et al., 2021). Duc et al. (2018) quantified in tomato plants with *S. constrictum* a stomatal conductance (gs) value almost twice as high as gs detected in non-colonised plants under drought, as well as an increase in leaf water potential, in relative water content and in maximal photochemical efficiency of photosystem II under water stress. Bitterlich et al. (2018) also reported in tomato plants with *F. mosseae* an enhancement in the plant available water content. Krishna et al. (2018) observed in *G. coronatus* - inoculated hot pepper plants that chlorophyll stability index (CSI) was significantly higher than in non-inoculated ones under water scarcity. It was reported in sweet pepper plants with *G. intraradicese* higher chlorophyll contents than in non-inoculated plants under drought (Enjili et al., 2018). Badr et al. (2020) also quantified in F1 hybrid aubergine plants with *G. intraradices*, a significant increase in WUE compared to non-inoculated plants, and the gs and photosynthetic rate (Pn) in inoculated plants showed a significant lower reduction in contrast with non-inoculated ones under water deficit conditions. Swetha & Padmavathi (2020) observed in two eggplant cultivars with *P. indica* an increase in the relative water content, as well as in the total chlorophyll content compared to non-inoculated plants under drought regime. Yooyongwech et al. (2016) observed the same pattern in potato varieties Tainung 57 and PROC 65-3, inoculated with a mix of *Glomus* sp. and *Acaulospora* sp., which showed a significant increase in total chlorophyll in inoculated plants compared to non-inoculated ones under drought. Moreover, inoculated PROC 65-3 plants had a significant increase in photon yield of PSII, as well as in the net photosynthetic rate (Pn) compared to non-inoculated plants under water stress.

STRATEGIES OF PGPB - MEDIATED WATER DEFICIT STRESS TOLERANCE

PGPBs are microorganisms which inhabit the rhizosphere, where their metabolic activity is usually promoted by plant root exudates (Xiong et al., 2020). These microorganisms lend plants some growth - promoting benefits by root colonization, using either their own metabolism or by acting on the plant metabolism (Figure 1) (Kabiraj et al., 2020). As with AMF mechanisms, the strategies used by PGPBs to alleviate drought stress in plants are complex and not clearly elucidated.

Effects of water deficit on PGPB colonization

It has been reported that the intensity and duration of water deficit stress may affect the efficiency of the benefits of PGPB (Ngumbi & Kloepper, 2016). PGPB survival can be also seriously affected by the presence or not-presence of host roots. Thus Wang et al. (2019) quantified survival rates of up to 40% in *Bacillus amyloliquefaciens* 54 of colonized roots after drought stress compared to 6.25% of bacteria without PGPB root inoculation. Tallapragada et al. (2016) reported that tomato plants inoculated with *Burkholderia seminalis* showed a higher colonization rate after drought stress management compared to full irrigation. However, Evseeva et al. (2019) reported a negative effect of drought over the survival rate of *Azospirillum brasilense* Sp245 and *Ochrobactrum cytisi* IPA7.2 in potato plants.

PGPB - Assisted drought stress tolerance by morphological changes

Plants perform different strategies to face drought injury, involving not only root morphology alterations, but also the production of root exudates, which one of its aims is the attraction of soil bacteria (Mohammadipanah & Zamanzadeh, 2019). PGPB can also produce and release different enzymes, phytohormones and secondary metabolites, which tend to promote the proper development of shoots, as well as to reduce the growth of primary roots, while the number and length of lateral roots tend to increase (Ahluwalia et al., 2021; Vacheron et al., 2013) under drought.

Thus, Tallapragada et al. (2016) observed in tomato plants inoculated with *B. seminalis* a significant increase in root length and weight, as well as in shoot length and weight under water deficit. Vigani et al. (2019) reported that the inoculation of *Bacillus subtilis* and *Paenibacillus illinoinensis* in pepper plants increased both fresh and dry weights compared to non-inoculated plants under drought. Tallapragada et al. (2016) showed than bell pepper plants with *B. seminalis* increased both shoot length and weight, as well as the root length compared to non-inoculated plants after water stress. Fathalla and Sabry (2020) also observed in eggplant with *Pseudomonas putida* SAB10 and *Pseudomonas palleroniana* SAW21 a significant increase in plant length and weight, as well as in root and shoot dry weights, being significantly higher in both type of inoculated plants compared to control plants under drought.

Arkhipova et al. (2020) reported in potato plants with *A. brasilense* Sp245 or *O. cytisi* IPA7.2 a significant increase in stem length, as well as in the fresh mass of leaves and roots, especially in IPA7.2 inoculated plants, compared to non-inoculated plants under drought. Evseeva et al. (2019), observed in potato plants with *A. brasilense* Sp245 and *O. cytisi* IPA7.2, a significant increase in shoot length and the number of nodes on shoots, compared to non-inoculated plants under water deficit. Moreover, IPA7.2 inoculated plants showed a significant major leaf wet weight compared to Sp245 - inoculated and non-inoculated plants under drought. Belimov et al. (2015) also reported in potato plants with *Achromobacter xylosoxidans* Cm4 and *Variovorax paradoxus* 5C-2 an increase in tuber yield and tuber number per plant compared to non-inoculated ones under deficit irrigation.

Related to nutrient uptake, Tahiri et al. (2021) observed that inoculated tomato plants with *Acinetobacter* sp. and *Rahnella* sp. showed an increase in shoot Na^{+} and Ca^{2+} levels, as well as root Ca^{2+} levels under drought. Vigani et al. (2019) reported in pepper plants with *B. subtilis* and *P. illinoinensis* a significant increase in root Na^{+} and K^{+} levels compared to non-inoculated plants under water deficit.

PGPB - Assisted drought stress tolerance by enhancing antioxidant mechanisms

It has been observed that PGPB promote plants to increase the accumulation of different antioxidant components, or modify the activity of these compounds under water deficit, resulting in drought tolerance (Gusain et al., 2015; Vurukonda et al., 2016). Thus, an increase in ROS scavenging enzymes, such as APX, GPX and CAT has been observed in inoculated plants under drought, correlating it with a major drought tolerance (Batool et al., 2020). Though, other studies reported contrary results, quantifying a decrease in the antioxidant components in PGPB - plants, which could be indicative of a lower stress level in front of non-inoculated plants under drought (Armada et al., 2014). In both cases, PGPB symbiosis seemed to alleviate plant oxidative damage (Ahluwalia et al., 2021).

PGPB has also shown a role as drought relievers. Thus, Wang et al. (2019) detected in *B. amyloliquefaciens* 54 - inoculated plants higher SOD, CAT, POD and APX activities compared to non – inoculated plants at 7 and 11 days after drought. Mekureyaw et al. (2022) observed in plants with *P. fluorescens* G20-18 an increase in SOD, POX and CAT activities, as well as a major anthocyanin content compared to non-inoculated plants under water deficit. However, Tallapragada et al. (2016) observed a decrease in CAT and GPX in *B. seminalis* - inoculated tomato plants under drought against non-inoculated plants, though plants showed a significant increase in root and shoot dry weights. Bell pepper plants with *B. seminalis* showed an increase in CAT activity, whereas the GPX activity showed a decrease compared to non-inoculated ones under drought.

PGPB - Assisted drought stress tolerance by differential regulation of phytohormones

PGPB can synthetize different phytohormones, promoting the cell division, the tissue growth and the increase of tolerance against variable stresses (Mohammadipanah & Zamanzadeh, 2019). Thus, ethylene is a phytohormone which is released under stress, promoting the ripening of fruits, or determining the gender of plants. Though, an excess of ethylene levels can produce detrimental effects on plants, such as decreasing the proper development of roots and shoots as well as stomatal conductance, and promoting plant death (Ahluwalia et al., 2021). In this regard, IAA is a phytohormone produced by about 80% of PGPB, participating in cell growth and tissue elongation, promoting a higher root surface area (Etesami et al., 2015), and a major nutrient and water uptake (Ngumbi & Kloepper, 2016). PGPB also can increase drought tolerance in host plants through the enzyme synthesis of 1 – aminocyclopropane – 1 – carboxylic acid (ACC) deaminase, reducing ethylene concentration in root system of plants (Saikia et al., 2018). Thus, the increase of IAA and ACC deaminase in PGPB inoculated plants under drought have shown a better plant development, as well as a lower cell damage (Ahluwalia et al., 2021).

Wang et al., (2019) observed in tomato plants with *B. amyloliquefaciens* 54 that *nced1* gene, related to ABA biosynthesis was up –regulated under drought, as well as higher ABA levels, compared to non – inoculated plants under water stress. Tomato plants with *P. fluorescens* G20 – 18 also showed a significant increase in ABA levels under drought (Mekureyaw et al., 2022). Arkhipova et al., (2020) quantified in potato inoculated plants with *A. brasilense* Sp245 or *O. cytisi* IPA7.2 a significant increase in stem IAA levels and a decrease of root IAA content compared to non – inoculated plants under water stress. ABA levels in leaves were also significantly reduced in inoculated plants compared to non – inoculated ones under drought, could being a signal of drought tolerance. Related to cytokinin levels, zeatin derivatives showed in inoculated plants a significant increase in stems compared to non – inoculated plants under drought. Finally, the accumulation of cytokinins isopentenyladenine derivatives showed a significant increase in leaves of Sp245 inoculated plants compared to non – inoculated ones under water scarcity.

PGPB - Assisted drought stress tolerance by osmotic adjustments

PGPB have demonstrated the ability to produce numerous osmoprotectans, increasing their concentration in the soil, which is favourable for the proper performance of osmotic adjustment mechanisms of host plants (Ahluwalia et al., 2021). In this regard, numerous authors have described an increase in proline, betaine, glutamate, trehalose and glycine content under drought in PGPB inoculated plants, promoting greater water deficit tolerance (Li et al., 2020).

Thus, Vigani et al., (2019) showed in pepper plants with *B. subtilis* and *P. illinoinensis* a significant reduction in the proline content against non-inoculated plants under drought. Fathalla & Sabry (2020), also reported in aubergine plants with *P. putida* SAB10 and *P. palleroniana* SAW21 a significant reduction of total proline content in leaves of inoculated plants compared to non-inoculated ones under water stress.

PGPB - Assisted drought stress tolerance by modifying plant water status and photosynthesis

PGPB have different abilities to provide drought tolerance in host plants. PGPB - plant symbiosis has demonstrated to increase photosynthesis rate, involving a mayor root production and a higher plant development (Naylor & Coleman-Derr, 2018).

Some of the strategies that enhance drought tolerance have been elucidated, such as the production of extracellular matrices or biofilms to avoid dehydration of plant root systems (Bhagat et al., 2021; Sandhya et al., 2009). This improvement in plant water status is related with a higher photosynthetic capacity.

In this regard, Wang et al. (2019) reported that tomato plants with *B. amyloliquefaciens* 54 had a higher leaf relative water content (RWC) than non-inoculated plants, due to the formation of biofilm. The root vigor was also improved due to symbiosis, and the stomatal aperture was reduced at 8 and 24 h compared to non-inoculated plants under drought. Mekureyaw et al. (2022) observed in tomato plants with *P. fluorescens* G20-18 an increase in the leaf chlorophyll content after drought stress compared to control plants.

However, gs was reduced in inoculated plants under water stress against non-inoculated plants. This effect in gs was correlated with the increase observed in ABA levels in inoculated plants (Mekureyaw et al., 2022). Vigani et al. (2019) reported in pepper plants inoculated with two different strains, *B. subtilis* and *P. illinoinensis,* a better water status in inoculated plants under drought. The photosynthesis (Pn) and transpiration (E) rates, as well as the stomatal conductance (gs), were also higher in inoculated plants than in non-inoculated ones under stress. Evseeva et al. (2019), observed in potato plants with *A. brasilense* Sp245 and *O. cytisi* IPA7.2, a significantly major content of chlorophyll a in IPA7.2 - inoculated plants compared to non-inoculated ones under water deficit. Belimov et al. (2015) also reported in potato plants with *A. xylosoxidans* Cm4 and *V. paradoxus* 5C-2 an increase in the WUE parameter in both type of inoculated plants compared to non-inoculated plants under drought.

CONCLUSIONS AND PERSPECTIVES

Plants are not autonomous systems in agroecosystems, being involved in numerous symbiotic interactions with different microbes in the rhizosphere, obtaining multiple benefits, such as increasing their tolerance to drought stress. These interactions have also been described in *Solanaceae* crops, like tomato, pepper, eggplant and potato. However, we have observed that there is a lack of information about the role of AMF and PGPB in improving plant status under water deficit in this family of plants compared to other crops.

Due to the increasing water scarcity problems worldwide, the application of AMF and PGPB could be a relevant resilient and sustainable strategy to improve *Solanaceae* production. Therefore, we consider that it is crucial to continue studying and learning about the interactions and effects produced by this kind of microorganisms on these valuable crops.

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