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Review

Arbuscular mycorrhizal fungal responses to abiotic stresses: A review

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ABSTRACT

The majority of plants live in close collaboration with a diversity of soil organisms among which arbuscular mycorrhizal fungi play (AMF) an essential role. Mycorrhizal symbioses contribute to plant growth and plant protection against various environmental stresses. Whereas the resistance mechanisms induced in mycorrhizal plants after exposure to abiotic stresses, such as drought, salinity and pollution, are well documented, the knowledge about the stress tolerance mechanisms implemented by the AMF themselves is limited. This review provides an overview of the impacts of various abiotic stresses (pollution, salinity, drought, extreme temperatures, CO_2, calcareous, acidity) on biodiversity, abundance and development of AMF and examines the morphological, biochemical and molecular mechanisms implemented by AMF to survive in the presence of these stresses.

Contents

1. Introduction

Abiotic stresses, such as drought, salinity, extreme temperatures and exposure to pollutants result in the deterioration of the soil and present serious threats to agriculture because they are considered as the primary cause of crop yield loss worldwide (Wang et al., 2003). Fortunately, some telluric beneficial microorganisms, particularly bacteria and fungi, have the ability to overcome the detrimental effects and to ameliorate plant performance under stress environments (Levy et al., 1983). Among them, arbuscular mycorrhizal fungi (AMF), belonging to the Glomeromycota phylum, form symbioses with the roots of over 80% of terrestrial plant species (Smith and Read, 2008). These fungi are known to improve plant growth and health by enhancing mineral nutrition and by increasing tolerance to abiotic and biotic stresses (Clark and Zeto, 2000; Turnau and Haselwandter, 2002). The resistance mechanisms of mycorrhizal plants to abiotic stress, such as drought, salinity and pollution, have been recently reviewed in depth by different authors (Abdel Latef and Miransari, 2014; Cicatelli et al., 2014; Miransari, 2011; Porcel et al., 2012; Seguel et al., 2013; Wu et al., 2013a,b). However, despite the ubiquity of

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Table 1
Examples of AMF species isolated from forest and grassland in absence of stress. All species have been named according to the current classification.

Environment	Order (number of species)	Major species	References
Evergreen and deciduous forests, and grassland areas, Chile	Diversisporales (13), Glomerales (10), Gigasporales (4), Archaesporales (3)	*Acaulospora alpina, Acaulospora mellea, Claroideoglomus etunicatum, Glomus macrocarpum*	Castillo et al. (2006)
Tropical, boreal and deciduous forest	Glomerales (9), Gigasporales (2)	*Rhizophagus irregularis, Rhizophagus fasciculatus, Funneliformis mosseae*	Öpik et al. (2006)
Grassland, Mongolia	Glomerales (13), Diversisporales (1), Gigasporales (1)	*Funneliformis geosporum, Glomus albidum, Claroideoglomus etunicatum*	Su and Zhu (2008)
Boreonemoral forest, Estonia	Glomerales (13), Diversisporales (7), Gigasporales (2)	*Claroideoglomus claroideum, Claroideoglomus etunicatum, Glomus lamellosum, Glomus luteum*	Öpik et al. (2009)
Forests and grasslands, China	Glomerales (23), Diversisporales (13), Pacisporaceae (2), Giga porales (1), Archeosporales (1)	*Acaulospora laevis, Acaulospora scrobitulata, Funneliformis mosseae*	Gao et al. (2010)
Forests and grasslands, El Palmar National Park, Argentina	Diversisporales (13), Glomerales (10), Gigasporales (8), Archeosporales (1)	*Claroideoglomus claroideum, Claroideoglomus etunicatum, Glomus microaggregatum*	Velázquez and Cabello (2011)
Forests and grasslands, India	Glomerales (48), Diversisporales (11), Gigasporales (5), Archeosporales (1),	*Rhizophagus fasciculatus, Funneliformis geosporum, Funneliformis mosseae*	Lakshmipathy et al. (2012)
Prairie sites, Canada	Glomerales (7), Diversisporales (5), Gigasporales (3)	*Redeckera pulvinatum, Claroideoglomus claroideum, Acaulospora nicolsonii, Acaulospora gedanensis, Scutellospora pellucida*	Stover et al. (2012)
Grass, scrub, secondary forest and mature forest in southern Brazil	Glomerales (38), Diversisporales (21), Gigasporales (7), Archeosporales (1), Paraglomerales (1)	*Acaulospora mellea, Acaulospora scrobitulata, Claroideoglomus claroideum, Claroideoglomus etunicatum, Funneliformis mosseae, Glomus macrocarpum*	Zangaro et al. (2013)
Forested habitats, Estonia	Glomerales (7)	*Rhizophagus fasciculatus, Rhizophagus irregularis, Glomus macrocarpum*	Moora et al. (2014)

AMF in harsh environments and the important potential of these symbiotic fungi to protect plants against several stresses, little is known today concerning the mechanisms implemented by AMF themselves to tolerate the deleterious effects induced by stresses. The present review aims to give an up-to-date overview of current knowledge of the morphological, biochemical and molecular mechanisms set up by the AMF to survive in adverse conditions such as pollution, salinity, drought, extreme temperature, CO_2, calcareous, and acidity.

2. Impact of abiotic stress on AMF biodiversity and abundance

Despite the widespread distribution of AMF in several ecosystems, less than 250 species have been described to date (Öpik et al., 2013). However, it is evident that the overall AMF biodiversity is underestimated (Wang and Li, 2013). Indeed, our understanding of AMF species diversity depends to a large extent on the development of methodology and on the application of new techniques. The diversity of AMF varies greatly and their distribution is affected by various factors including soil, host plant, environmental conditions and agricultural practices (Hayman, 1982; Wang and Li, 2013). The AMF diversity found in non-disturbed soils (forest, grassland) is generally high (Table 1): up to 43 AMF taxa per habitat were recorded in grassland and 52 AMF taxa in forests (Zangaro et al., 2013). *Funneliformis mosseae*, *Claroideoglomus claroideum* and *Claroideoglomus etunicatum* were found with different techniques of identification (morphological or molecular, such as denaturing gradient gel electrophoresis, restriction fragment length polymorphism, cloning and sequencing, pyrosequencing) as major species in many studies (Table 1).

However, in soils exposed to abiotic stress, AMF diversity is generally lower than in non-disturbed soils, with a predominance of *Glomeraceae* (Table 2). These AMF species show an opportunistic behavior, because they invest their energy mainly in the production of many offspring, and have evolved characteristics that are advantageous in adverse environments (Sýkorová et al., 2007). As an example, *Rhizophagus irregularis* is a rapid colonizer of plant roots and generates high number of spores in a short time period. Moreover, Declerck et al. (2001) showed that in *Glomeraceae* the production of spores occurred in parallel to root growth, suggesting a direct investment of carbon in spore formation. To occur in various habitats, AMF species must have also physiological and genetic characteristics which enable them to survive in different environmental conditions (Picone, 2000; Silva et al., 2010). Even though AMF are sensitive to environment (Mosse et al., 1982), some individual species or isolates are very widely distributed and can tolerate different environmental conditions (Stahl and Christensen, 1991). Indigenous AMF ecotypes result from long-term adaptation to soils with extreme properties (Sylvia and Williams, 1992). Several studies have shown that *Glomus* species are typical of semi-arid Mediterranean ecosystems and are able to grow under high salinity (Ferrol et al., 2004; Juniper and Abbott, 2006; Requena et al., 1996; Sánchez-Castro et al., 2012a, b). *F. mosseae* has a global distribution and tolerates different environmental conditions (Stahl and Christensen, 1991; Öpik et al., 2006). This species is the typical early stage colonizer and appears to be adapted to frequent soil disturbance (Sýkorová et al., 2007), including hydrocarbon (Huang et al., 2007a,b), fungicide (Ipsilantis et al., 2012) and trace metal pollutions (Abdel-Azeem et al., 2007; Hassan et al., 2011; Ortega-Larrocea et al., 2010; Zarei et al., 2010), salinity (Krishnamoorthy et al., 2014), drought (Mohammad et al., 2003; Panwar and Tarafdar, 2006; Tian et al., 2009; Verma et al., 2008) or cold (Gai et al., 2009). A predominance of *Funneliformis geosporum* was observed in several salt marshes (Carvalho et al., 2003; Hildebrandt et al., 2007; Sonjak et al., 2009; Wilde et al., 2009).

3. Impact of abiotic stress on AMF development and morphological adaptations

Even if AMF are ubiquitous in terrestrial ecosystems including disturbed soils (Enkhtuya et al., 2002), many studies (listed in Table 3a and 3b) have shown that the main stages of the AMF development cycle (germination, colonization, extraradical hyphal elongation and sporulation) could be hampered by the presence of different abiotic stresses.