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Symposium paper

The Role of AM Symbiosis in Plant Adaptation to Drought Stress

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Abstract

Drought is a worldwide eco-environmental problem and becomes more and more serious in (semi-) arid areas under global climate changes. Drought stress poses detrimental effects on plant growth and development, while plants have evolved a series of mechanisms at the cellular, tissue, and whole-plant level to resist the adverse impacts of drought stress. In this symposium paper, we summarized our recent work on the significance of arbuscular mycorrhizal (AM) symbiosis in plant drought tolerance. Large-scale field investigations in the farming-pastoral ecotone of northern China revealed strong dependency of AM fungal biodiversity and community structure on precipitation and soil properties. By using the bald root barley (*brb*) mutant, we provided direct evidence to demonstrate similar growth dependency of drought-stressed barley on AM fungus as on root hairs, and AM fungus could compensate for the absence of root hairs under drought stress. Moreover, we cloned two functional aquaporin genes (*GintaQPFL* and *GintaQPF2*) from AMF and provided evidence for potential water transport via AMF to host plants. Our recent results proved that AM fungi enhanced the plant drought tolerance through regulating the key functional genes (14-3-3 protein gene and the PIP genes) in ABA signaling pathway. These original work have identified the ecological and physiological significance of AM symbiosis in plant adaption to drought stress, and also laid foundations for further research into the mechanisms underlying the synergetic drought tolerance of AM associations.

Introduction

Arbuscular mycorrhizal (AM) fungi are ubiquitous symbiotic fungi for terrestrial plants. Root colonization to obtain carbohydrates is the foremost strategy for the survival and growth of AM fungi. As reciprocal rewards, mycorrhizal fungal mycelia facilitate root uptake of soil water and mineral nutrients from soil to root (Kiers *et al.* 2011). Mycorrhizal symbiosis substantially improves plant growth and development, particularly under abiotic (e.g., drought) stress conditions (Fig. 1). AM fungal mycelium can extend and cross-link via roots of congeneric species or different plants in a plant community to form common mycelial networks (CMNs). CMNs provide opportunities for material exchange and energy transfer from plant to plant (He *et al.* 2010). Therefore, mycorrhizal symbiosis has the ecological significance in nutrient transfer and carbon sequestration at

global scale, and also has profound impacts on structure and productivity of terrestrial ecosystem, as well as its adaptation and resilience in responses to environmental changes.

In recent years, studies on ecophysiology of AM fungi, particularly against abiotic (e.g., drought) stresses, have become research hotspots in the field of soil biology. Remarkable progresses have been achieved in the fields such as physiological bases of mycorrhizal symbiosis, genetic and metabolic regulations of stressed plants by AM fungi. Simultaneously, applications of mycorrhizal technology show tremendous potential in improvements of agricultural production and eco-environmental protections. In this symposium paper, based on the obtained research findings, we described AM fungi diversity in responses to environmental changes and anthropogenic disturbance in the farming-pastoral ecotone of northern China, then provided molecular and physiological evidence for AM symbiosis improving plant drought tolerance.



Fig. 1. Drought tolerance of tobacco plants was improved by AM symbiosis in a pot experiment. Pots in the left, non-inoculation control; pots in the right, tobacco plants inoculated with AM fungus *Rhizophagus irregularis*.

AM fungal diversity in the farming-pastoral ecotone of northern China

The farming–pastoral ecotone of northern China is the most severely degraded zone in China (Hu *et al.* 2014). The fragile ecosystem is suffering from natural (such as drought and sandstorms) and anthropogenic disturbances (such as overgrazing and unsustainable arable farming). Through large-scale field investigations in the ecotone, we found high AM fungal diversity across different steppe types and strong dependency of AM fungal communities on precipitation. Our results showed that increased precipitation decreased AM fungal biomass and altered the fungal community structure; while MAT, MAP, and soil properties significantly influenced AM fungal community composition (Xiang *et al.*, 2016). Moreover, land use conversion from grassland to farmland significantly reduced AMF richness and also significantly altered AMF community composition through mediations by available phosphorus (P), soil physical and chemical properties (soil texture, soil carbon, nitrogen and soil pH). Land use has a partly predictable effect on AMF communities across this ecologically relevant area of China; high soil P concentrations and poor soil structure are particularly unfavorable to AMF in this fragile ecosystem (Xiang *et al.* 2014).

Relative importance of AM fungus and root hairs in plant drought tolerance

AM fungi and root hairs are major contributors to root uptake of soil water and mineral nutrients; so they are closely related with plant water relations and protection of plants against drought stress. However, a relative contribution of AM fungus and root hairs to plant drought tolerance is difficult to distinguish due to unacquirability of bald-root plant mutant. A recent study by Brown *et al.* (2013) demonstrated, by using barley mutants exhibiting different root hair lengths, the importance of root hair length in shoot P accumulation and plant growth under drought stress. Using a bald root barley (*brb*) mutant and its wild type, we provided first and direct evidence to demonstrate that drought-stressed barley shared almost the same growth dependency on AM fungus (*R. intraradices*) as on root hairs; AM fungus could almost compensate for the absence of root hairs under drought-

stressed conditions (Li *et al.* 2014). We outlined the difference in strategies between AM fungi and root hairs to improve plant drought tolerance: *R. intraradices* mainly through an improved uptake of soil water and P, while root hairs probably through an improvement of shoot P nutrition status.

Molecular evidence for potential water transport via AMF to host plants

Water movement in plant roots involves in two main pathways (Steudle 2000): (1) apoplastic water-transport pathway (cell walls); (2) cell-to-cell water-transport pathway from cell to cell via plasmodesmata or cross cell membranes. Under drought stress, water transport via apoplastic pathway is significantly decreased due to stomatal closure-caused decline in leaf transpiration; cell-to-cell transport pathway becomes more important for roots in water uptake and transport. Plants aquaporins (AQPs) are molecular proteinaceous membrane channels that facilitate the membrane transport of water and other small, uncharged molecules such as ammonia and glycerol (Martínez-Ballesta and Carvajal 2016). Maurel *et al.* (2008) previously studied mycorrhizal effects on plant drought tolerance and provided indirect evidence to show that AM fungi can improve plant water status by regulating plant aquaporin activities. However, the molecular basis for direct involvement of AM fungi in plant water relations still has not been established. In a recent study (Li *et al.* 2013), we cloned two full-length aquaporin genes, namely *GintaAQP1* and *GintaAQP2*, by rapid amplification of cDNA 5'- and 3'-ends from an AM fungus, *Glomus intraradices*. The *GintaAQP1* and *GintaAQP2* are the first two functional aquaporin genes from AMF reported to date. The expression of the two genes in arbuscule-enriched cortical cells and extraradical mycelia of maize roots was enhanced significantly under drought stress. Our data strongly support potential water transport via AMF to host plants.

Molecular mechanisms underlying the synergetic drought tolerance of the AM symbiosis

Abscisic acid (ABA) is known as a key hormone in mediating plant response to drought stress (Sah *et al.* 2016).

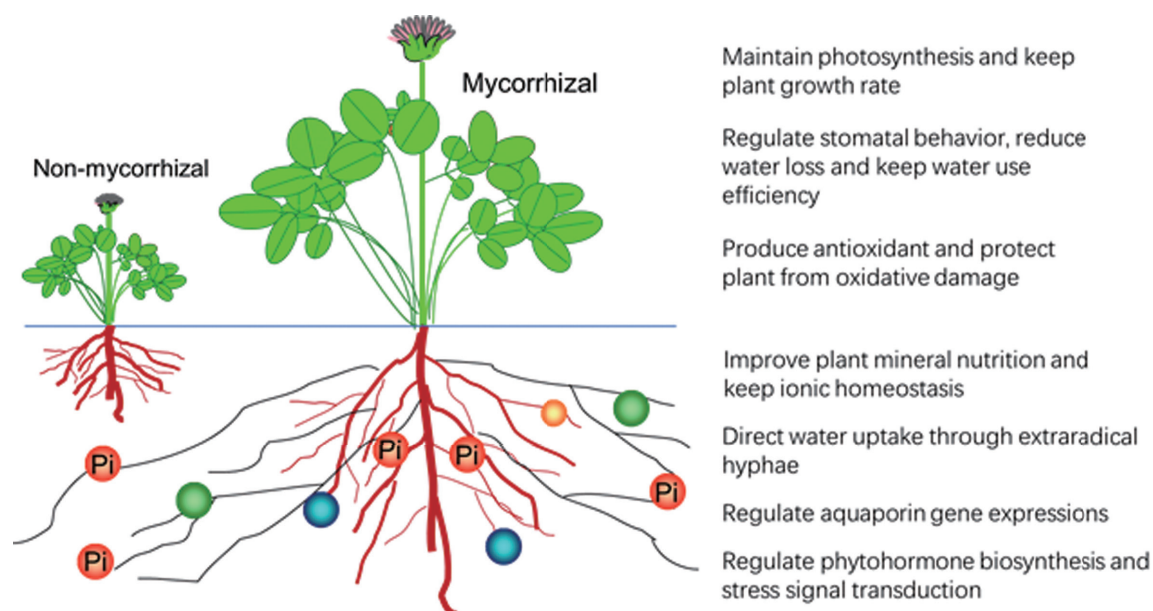


Fig. 2. Physiological mechanisms underlying the improved drought tolerance of host plants by AM symbiosis.

Drought stress can first induce ABA synthesis in roots; then through ABA-dependent signaling pathway or converging with ABA-independent pathways, the stress signal is quickly transduced and triggers plant genetic and subsequently physiological responses (Knight and Knight 2001). AM fungi have been postulated to regulate expression of drought-responsive genes in the ABA-dependent signaling pathway (Ruiz-Lozano 2003). Our recent results supported the postulation and proved that AM symbiosis could improve plant water relations and plant drought tolerance through regulation of the 14-3-3 genes in the ABA signaling pathway. In a split-root experiment, we found that AM fungi simultaneously up-regulated the expression of plant genes encoding D-myoinositol-3-phosphate synthase (IPS) and 14-3-3-like protein GF14 (14-3GF) (Li *et al.* 2016), which were responsible for ABA signal transduction, leading to activation of 14-3-3 protein and aquaporins in *R. intraradices*, and finally improved plant water relations. Co-expression of IPS and 14-3GF is potentially responsible for the crosstalk between maize plant and *R. intraradices* under drought stress. Based on transcriptome and metabolome analysis, our results proved that AM fungi can promote the synthesis and transport of lignin and strengthen the cell wall through regulating the phenylpropane synthesis. The genes involved in glycolysis were up-regulated by AM fungi to promote the decomposition of carbohydrates and fatty acids metabolism, finally leading to improved plant drought tolerance. Meanwhile, the AM fungi themselves can potentially achieve enhanced drought tolerance through stimulating glycolysis and P450 metabolism (unpublished data).

In summary, together with previous studies, our work clearly demonstrated that AM symbiosis can effectively improve plant performance under drought stress. Mycorrhizal fungi may modulate plant physiological responses to water deficiency, e.g. regulate stomatal behavior (possibly through regulating phytohormone biosynthesis and ionic homeostasis), reduce water loss and keep water use efficiency; produce antioxidant and protect plant from oxidative damages, and

consequently protect photosynthetic system and maintain plant growth rate. On the other hand, extraradical hyphae of AM fungi can access water resources unavailable for roots and directly take up and transport water to plants, which involves regulation of AM fungal aquaporin genes and directly contributes to improved plant water relations under drought stress (Fig. 2). The beneficial effects AM symbiosis on plant drought tolerance strongly supported the potential use of AM fungi for sustainable agriculture and also ecological restoration of degraded ecosystem in the drought stressed area. However, further research is still needed to deep into the molecular mechanisms of synergetic drought tolerance of AM fungi and their host plants. There is also a need of field trials to demonstrate AM functions under natural conditions.

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