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Mycorrhizal Symbiosis for Better Adaptation of Trees to Abiotic Stress Caused by Climate Change in Temperate and Boreal Forests

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Global climate changes have serious consequences on natural ecosystems and cause diverse environmental abiotic stressors that negatively affect plant growth and development. Trees are dependent on their symbiosis with mycorrhizal fungi, as the hyphal network significantly improves the uptake of water and essential mineral nutrients by colonized roots. A number of recent studies has enhanced our knowledge on the functions of mycorrhizal associations between fungi and plant roots. Moreover, a series of timely studies have investigated the impact and benefit of root symbioses on the adaptation of plants to climate change-associated stressors. Trees in temperate and boreal forests are increasingly exposed to adverse environmental conditions, thus affecting their durable growth. In this mini-review, we focus our attention on the role mycorrhizal symbioses play in attenuating abiotic stressors imposed on trees facing climatic changes, such as high temperatures, drought, salinity, and flooding.

Keywords: mycorrhizal symbioses, trees, climate change, environmental abiotic stress, high temperature, drought, salinity, flooding

INTRODUCTION

Plant growth and development are dependent on intimate interspecific interactions and co-adaptation between plant species and soil microorganisms, and will be increasingly affected by environmental and climatic changes (van der Putten, 2012; Steidinger et al., 2019; Suz et al., 2021; Van Nuland et al., 2021). Trees, requiring sustained growth in fluctuating environmental conditions, are particularly vulnerable to increasing stress. Functional plant-microbe interactions are determinant drivers for plant adaptation to environmental stressors, among them severe and frequent climate-caused factors (Gehring et al., 2017; Lau et al., 2017). Such increasing abiotic stress conditions include high temperature waves associated with increasing solar radiation (Teskey et al., 2015), intensifying periods of drought (Cook et al., 2018), high levels of salinity (Corwin, 2021), and unpredictable events of flooding (Alfieri et al., 2017; Tabari, 2020; **Figure 1A**). Often, these conditions are tightly connected to poor soils with nutrient shortages. In temperate and boreal forest ecosystems, belowground beneficial interactions with plant roots are dominated by

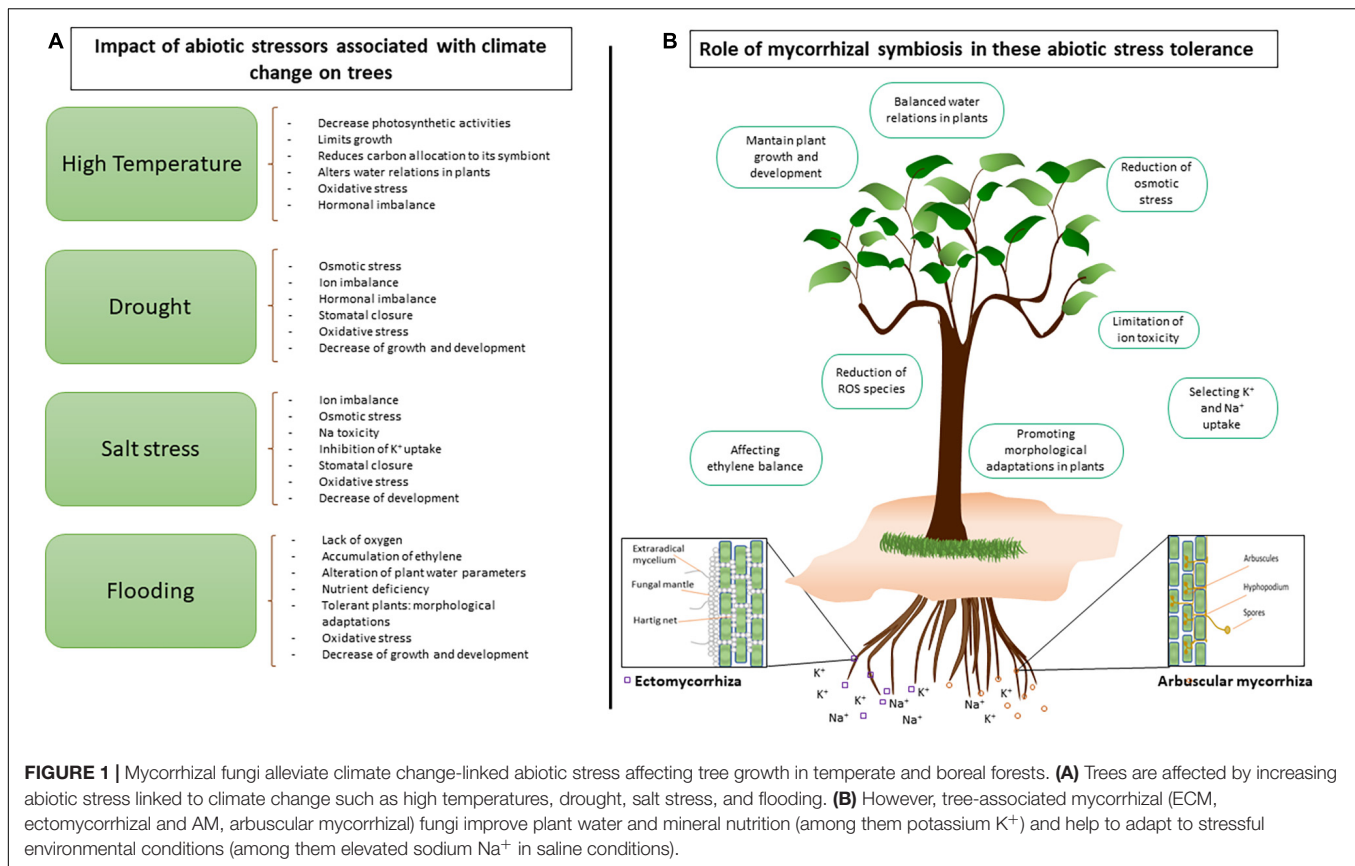


FIGURE 1 | Mycorrhizal fungi alleviate climate change-linked abiotic stress affecting tree growth in temperate and boreal forests. **(A)** Trees are affected by increasing abiotic stress linked to climate change such as high temperatures, drought, salt stress, and flooding. **(B)** However, tree-associated mycorrhizal (ECM, ectomycorrhizal and AM, arbuscular mycorrhizal) fungi improve plant water and mineral nutrition (among them potassium K⁺) and help to adapt to stressful environmental conditions (among them elevated sodium Na⁺ in saline conditions).

mycorrhizal symbioses. Trees are dependent on mycorrhizal fungi because they rely on the hyphal network, extending the root area of exploration beyond the rhizosphere, to increase the acquisition of essential macro- and microelements and water by colonized roots (Smith and Read, 2010; Becquer et al., 2019; Xu and Zwiazek, 2020).

Aside from the well described contribution to plant nutrition (Garcia et al., 2016, 2020), these root-associated beneficial symbionts are expected to improve the ability of their host trees to adapt to the stressor associated with climate change (Classen et al., 2015; van der Linde et al., 2018). Ectomycorrhizal (ECM) and arbuscular mycorrhizal (AM) fungi are widely associated with trees in natural forests and plantations (Figure 1B). ECM fungi, interacting with 60% of all trees (Steidinger et al., 2019) form a fungal sheath around fine roots, thus protecting the plant root and mediating direct interactions with the soil. AM fungi are more present in tropical environments than temperate and boreal forests, but do interact with several tree species, such as poplars (Fang et al., 2020), alders (Kilpeläinen et al., 2019), eucalyptus (Adjoud et al., 1996), or olive trees (Calvo-Polanco et al., 2016).

Herewith, we summarize recent reports on the role mycorrhizal symbioses play in tree growth and survival under increasingly prevalent climate change-driven abiotic stress conditions in temperate and boreal forests. In particular, we focus on publications, mainly from last few years, concerning those stressors that pose the most significant and increasing threat, namely high temperatures, drought, salinity, and flooding.

PLANT TOLERANCE TO ABIOTIC STRESS MEDIATED BY MYCORRHIZAL INTERACTIONS

Global climate change is primarily described by quantification of CO₂ rise causing increase of mean temperatures. Other abiotic stresses, such as drought, salt stress or flooding, are tightly linked and affect plants and associated microorganisms (Figure 1). Whether CO₂ rise will affect mycorrhizal tree symbioses in an indirect way by more carbon uptake (Godbold et al., 1997), other consequential stressors deteriorating plant growth might be alleviated by beneficial microbial root associations.

Increasing Temperatures

Frequency and intensity of high temperatures are increasing due to global warming. It can result in irreversible damages for many tree species, altering their growth and production, and sometimes leading to mortality (Teskey et al., 2015). To date, minimal research has explicitly explored the role of mycorrhizal fungi in heat stress alleviation in trees. Indeed, most studies have focused primarily on how increasing temperatures affect tree and fungal populations individually (Deslippe et al., 2011; Morgado et al., 2015; Treseder et al., 2016). However, the impacts of climate change on tree, fungal, and ecosystem health are connected and interdependent, and mycorrhizal fungi can also be directly affected by increasing soil temperatures

(Kipfer et al., 2010; Gavito and Azcón-Aguilar, 2012). Higher temperatures can lower a tree's photosynthetic activity, thereby limiting its growth and reducing carbon allocation to its ECM symbionts (Fernandez et al., 2017). Recently, Song et al. (2015) examined fungal partner changes in reaction to heat stress in two tree species, Douglas fir (*Pseudotsuga menziesii*) and ponderosa pine (*Pinus ponderosae*), and found that defoliation of the former resulted in stress signaling and resource sharing to the latter. In response to defoliation from heat and insect stress, photosynthetic carbon from *P. menziesii* was transferred to *P. ponderosae* plants via shared mycorrhizal networks (Song et al., 2015). Mueller et al. (2019) investigated growth-promoting effects of mature tree mortality on seedlings of pinyon pines and revealed increases in plant growth after mature trees died, and saw no significant loss of seedling establishment. One reason for this could be the inoculum of ECM symbionts provided by the older trees that the seedlings can utilize for acquiring the newly available resources. This indicates the importance of ECM communities in promoting the success of further generations, even as tree life expectancy may be cut short, as well as their role in promoting growth of other species following mortality. On the other hand, this ecosystem service depends on the presence of compatible species, and mortality from increasing temperatures simultaneous with heat-induced fungal community shifts, may threaten this resilience. Indeed, Fernandez et al. (2017) reported fungal taxonomic changes as a result of warming temperatures. An increased reliance on Ascomycetes and fungi that provided optimum benefits as photosynthesis capacity decreased was observed (Fernandez et al., 2017).

From these observations, it seems imperative that more research is conducted to understand how the positive effects conferred by mycorrhizal fungi will help host trees tackle the upcoming climatic variability. In particular: (i) identifying how ECM fungal communities will evolve, (ii) determining which tree-fungus combinations will be better adapted, and (iii) characterizing the underlying molecular mechanisms in both plant and fungi that prevent deleterious effects triggered by rising soil and ambient temperatures, could be promising ways to explore. Indeed, plant and ecosystem health are facing the pressure of changing global temperatures and will continue to do so to a greater extent in coming years. The respective success of each plant and microbial populations is integral in the success of the other, and further research into how ECM and AM fungi alleviate plant stress to climate change could shed light on how these interdependencies may provide ecosystem resilience through temperature increases.

Drought

Drought stress, partly linked to high temperatures, is one of the major abiotic stressors caused by climate change, and contributes to forest decline at a global level (Choat et al., 2012). Soil water deficiencies diminish plant physiological processes, including photosynthesis, enzyme structure, nutrient uptake and transport, and hormone balancing. This results in the triggering of other stressors such as nutritional, osmotic and oxidative

stress. At the belowground level, roots have developed a variety of strategies to avoid and tolerate drought conditions, including root biomass adjustments, anatomical alterations and physiological acclimation, and interaction with mycorrhizal fungi.

Different mechanisms have been suggested for the improvement of plant drought tolerance by mycorrhizas. The most obvious direct mechanism to cope with water shortage is the increase of the absorbing surface in the soil through the development and ramification of an extraradical mycelium (Bogeat-Triboulot et al., 2004; Ruth et al., 2011; Zhang et al., 2018). Mycorrhizal fungi improve soil aggregate stability thanks to the structure of the hyphal network which, as part of the soil matrix, directly contributes to the formation and maintenance of soil water-macroaggregates (Ji et al., 2019), providing a better infiltration and storage of water. In the case of AM fungi, another well-identified mechanism that improves soil aggregate stability by carbon sequestration is the release of the glycoprotein glomalin by the fungus acting as soil-superglue (Kumar Singh et al., 2020; Cheng H. Q. et al., 2021).

Mycorrhizal colonization also has the ability to modify the root architecture to both enhance soil aggregate stability and increase the water and nutrient absorbing surface area, especially under drought conditions. For example, several studies in trifoliolate orange suggested that mycorrhizal trees possess greater root hair growth to tolerate drought stress (Wu et al., 2016; Zou et al., 2017; Liu et al., 2018; Zhang et al., 2019). ECM fungi are reported to trigger structural changes in the root system of poplar trees by inducing lateral root formation (Felten et al., 2009; Wu et al., 2012). Finally, the modulation of root water transport under drought conditions in mycorrhizal plants has been commonly attributed to the aquaporin-mediated transport, as mycorrhizal colonization has been often shown to affect plant aquaporin gene expression (Calvo-Polanco et al., 2016, 2019; He et al., 2020).

In addition to the increased water uptake, mycorrhizal symbioses can indirectly improve nutrient acquisition under drought (Lehto and Zwiasek, 2011; Ouledali et al., 2018; Behrooz et al., 2019; Boutasknit et al., 2020). This is not only due to the increased absorption area of mycorrhizal roots, but also to factors such as the improved secretion of phosphatase to the soil, either directly by the extraradical hyphae as described for *Rhizophagus clarus* (Sato et al., 2019), or by stimulating the exudation of root phosphatase as observed in mycorrhizal citrus trees (Cheng H. Q. et al., 2021). These mechanisms could stimulate the decomposition and acquisition of organic orthophosphate and might thus partially alleviate the plant responses to drought stress.

Finally, mycorrhizal symbiosis also triggers numerous biochemical and physiological modifications in the plants that enhance plant drought tolerance. For example, some reports exist about the enhanced production of enzymatic (He et al., 2020; Huang et al., 2020) and non-enzymatic (Essahibi et al., 2018) antioxidants in mycorrhizal trees such as carob, trifoliolate orange and apple trees under drought conditions. These enzymes and compounds may decrease the oxidative damage in the structure of carbohydrates, lipids, proteins, and DNA that result from

prolonged drought exposure. It has also been suggested that mycorrhizal symbiosis has the potential to lower the osmotic damage through the accumulation of soluble sugars and proline (Yin et al., 2018; Behrooz et al., 2019; Boutasknit et al., 2020; Huang et al., 2020; Wang et al., 2021). Similarly, the water-use efficiency is in most cases improved in colonized plants, as observed in AM poplar and in ECM pine and oak trees exposed to drought (Li L. et al., 2021; Li M. et al., 2021; Li Y. et al., 2021). This could be related to a better modulation of stomata closure and abscisic acid concentration and signaling (Wang et al., 2017; Ouledali et al., 2018; Chen et al., 2020).

Salt Stress

Climate change-associated salinity stress causes land degradation, decreased crop yields, and afforestation, thus severely impacting the global economy (Leisner, 2020; Zandalinas et al., 2021). In addition, due to deep changes in environmental conditions and the expansion of irrigated land (>20% worldwide), the negative impact of salinity is considerably increasing and will continue to do so (Yuan et al., 2016). Excessive sodium (Na^+) in soil competes for potassium (K^+) uptake by plant roots due to ion similarity (Liang et al., 2018; Wu, 2018). Moreover, within the cytoplasm, Na^+ has toxic effects on cellular functions and enzyme activation. Several endangered tree species (Bothe et al., 2010) evolved adaptations (Kijowska-Oberc et al., 2020), such as the exclusion or accumulation of the excess of Na^+ within the different plant tissues (Ottow et al., 2005; Thiem et al., 2018), the control of transpiration (Negrão et al., 2017), or the increase of vessel frequencies (Janz et al., 2012).

Although many plant species have evolved salt tolerance mechanisms, interaction with soil microorganisms, and particularly mycorrhizal fungi, can greatly improve plant growth and development under saline conditions (Weissenhorn, 2002; Yi et al., 2008; Yang et al., 2014; Hrynkiewicz et al., 2015; Zwiazek et al., 2019; Klinsukon et al., 2021). Improved water (Lee et al., 2010) and nutrient (Li et al., 2012) uptake, as well as the exclusion of Na^+ from roots and, consequently, shoots by mycorrhizal fungi are mechanisms that have been proposed to contribute to salt stress tolerance in colonized trees (Guerrero-Galán et al., 2019).

Improved acquisition of K^+ as an essential macroelement by AM and ECM fungi (Garcia and Zimmermann, 2014; Frank and Garcia, 2021) helps maintain a desirable K^+/Na^+ ratio. By contrast, the mobilization of Na^+ and chloride (Cl^-) by plant roots was attenuated by the presence of mycorrhizal fungi, particularly under salt stress (Giri et al., 2007; Calvo-Polanco et al., 2008; Hrynkiewicz et al., 2015; Garcia et al., 2017; Hashem et al., 2018; Abdelhamid et al., 2019). To elude the translocation of excessive Na^+ in photosynthetic organs, plants have adopted mechanisms to store Na^+ in intraradical mycelium or in root cell vacuoles (Acosta-Motos et al., 2020). Moreover, defense mechanisms using antioxidant enzymes in plants might be improved by AM symbiosis lifting up their activities to mitigate salt stress, like catalase, peroxidase, glutathione reductase, superoxide dismutase, and ascorbate peroxidase. Ait-El-Mokhtar et al. (2019) demonstrated this mechanism when *Phoenix dactylifera* L. was colonized

by AM fungi in salt stress conditions. Improvement of physiological plant parameters by AM and ECM symbioses has been shown by several studies in recent years, however, mechanisms have been discussed mainly for AM symbioses in non-woody plants (Porcel et al., 2012; Evelin et al., 2019). In trees, Behmanesh et al. (2019) reported that pistachio seedlings (*Pistacia vera* L.) inoculated by *Rhizophagus irregularis* (formerly *Glomus intraradices*) and *Glomus mosseae* displayed improved vegetative growth, chlorophyll contents, and less deposition of Na^+ in shoots as compared to non-inoculated seedlings. Similar findings were reported by Frosi et al. (2018), when *Cenostigma pyramidale* was inoculated with AM fungi *Acaulospora longula* and *Claroideoglomus etunicatum*. Increases in shoot dry weight and chlorophyll contents, and less accumulation of Na^+ and Cl^- in photosynthetic organs were reported. Salt tolerance of almond rootstocks was increased by the AM fungi *R. intraradices* and *Funneliformis mosseae* through the improvement of diverse physiological parameters like chlorophyll, soluble sugars and proline content, osmotic parameters, and increased activity of antioxidant enzymes (Shahvali et al., 2020).

Likewise, several studies have shown improved salt tolerance in ECM trees as in white spruce in association with *Hebeloma crustuliniforme* (Muhsin and Zwiazek, 2002). When *Coccoloba uvifera* L., inoculated by *Scleroderma bermudense*, was grown in up to 500 mM of salt, the plants exhibited improved growth, water uptake, and shoot phosphorus and K^+ concentrations, while the upward movement of Na^+ and Cl^- ions was limited in comparison to non-inoculated plants (Bandou et al., 2006). Improved ECM-driven uptake of essential nutrients along with water was observed in poplar roots colonized by *Paxillus involutus* under saline conditions (Luo et al., 2011). Involvement of aquaporin-mediated water transport was shown in jack pine in association with *Suillus tomentosus* (Lee et al., 2010). A recent study revealing improved growth of *Alnus glutinosa* when inoculated by the ECM strain *P. involutus* OW-5 under saline conditions, showed proline accumulation in plant tissues that acts as an endogenous osmotic regulator to tolerate salt stress effects (Thiem et al., 2020).

Altogether, mechanisms behind plant salt tolerance in AM and ECM symbiosis are rather complex, including several direct and indirect effects, and need further studies.

Flooding

Extreme precipitation and floods are expected to intensify due to climate change (Alfieri et al., 2017; Tabari, 2020), with consequences in the structure, function and production of forest ecosystems, and their interactions with soil microorganisms (Barnes et al., 2018). The adaptation of plants to flooding is dependent on the accumulation of ethylene within the plant tissues (Reynoso et al., 2019). In the most tolerant species, plants display extensive morphological modifications, such as the formation of aerenchyma (Sou et al., 2021) and adventitious roots, the reduction of the endodermis (Calvo-Polanco et al., 2012; Voesenek and Bailey-Serres, 2015), and the formation of hypertrophied lenticels (Fougny et al., 2007).

In addition to these plant adaptations, the associated microbiome is crucial. The tolerance of mycorrhizal fungal species to flooding varies according to their host tree species and the severity and length of the stress (Lodge, 1989; Yang et al., 2016; Barnes et al., 2018; Johnson, 2018). In general, AM fungi are believed to be more present in waterlogged environments than ECM fungi, as they have been shown to survive anaerobic conditions due to the presence of well-developed aerenchyma in the roots (Wang et al., 2010). However, recent studies have determined that ECM also display a certain degree of resilience dependent on the species (Cho et al., 2021). Differences between hydrophobic and hydrophilic ECM fungi have been observed (Barnes et al., 2018), and several fungal species recovered after long periods of waterlogged field conditions (Thomas, 2021), as was shown for *Thelephora terrestris*, *Laccaria laccata*, and *H. crustuliniforme* (Stenström, 1991).

The few studies on AM trees under flood conditions are related to improving growth and development (e.g., citrus, peach, or trifoliolate orange trees) by acting on the phosphorus and nitrogen acquisition (Neto et al., 2006; Fougnes et al., 2007; Wu et al., 2012; Zou et al., 2014; Zheng et al., 2020) and on the expression of aquaporins (Cheng X. F. et al., 2021). Even that it is commonly known that ethylene accumulation within the plant tissues is one of the main responses of plants to waterlogged conditions, this information on mycorrhizal trees is largely lacking. Only one study reported for mycorrhizal tomato plants showed that AM fungi reduced root ethylene concentrations, while improving their water status through the action of fungal and tomato aquaporins and the regulation of ACC synthase and oxidase genes (Calvo-Polanco et al., 2014).

In conclusion, there is immense potential to improve our knowledge on how mycorrhizal fungi help trees to cope with flooding events, and their effect in the main mechanism of ethylene regulation for the initial sensing of flood, that involves the oxygen-dependent degradation of group VII Ethylene Response Factor transcription factors and Plant Cysteine Oxidase enzymes (van Dongen and Licausi, 2015). This information will contribute to the development of new technologies and management procedures to overcome flood stress in agricultural and forestry settings.

CONCLUSION

Overall, mycorrhizal fungi have the potential to conserve and restore temperate and boreal forest ecosystems and to maintain sustainable forestry crops under stress due to global changes (Bothe et al., 2010; Field et al., 2020; Li et al., 2020). Numerous studies have shown improved tolerance of mycorrhizal trees to numerous abiotic stresses, such as high temperatures, drought, high salinity, and flooding (Figure 1). In general, the identified mechanisms are similar to those ones found in non-woody plants. However, we need to consider that most of these experiments have been performed with tree seedlings grown in pots under controlled conditions, so further research is required to unravel the underlying mechanisms in natural environments and in mature trees. The influence of natural soil microbiome interactions on complex ecosystem

functioning linked to conditions of climate change has been recently analyzed taking growth and foliar development of a tree species (*Populus angustifolia*) as a model (Van Nuland et al., 2021). Moreover, microbiome manipulation experiments in forest conditions (e.g., adding inoculum of adapted species isolated from not stressed forest environments) could be feasible and bring further insight.

One of the most outstanding particularities of large trees is that they possess a root system that penetrates several meters into the ground. Although mycorrhizas have been commonly described to be mostly concentrated in the top layer of the soil, some reports show that they are also present several meters underground (de Araujo Pereira et al., 2018; Robin et al., 2019). With this respect, further research is required to unravel other relevant roles of mycorrhizas in deeper soil horizons and in large trees, probably more related with ecosystem services, such as carbon storage, that may also help trees to cope with environmental stresses.

Clear evidence exists to consider local beneficial mycorrhizal fungi as an environmentally friendly tool with a high potential to protect trees, from both forest and sustainable agricultural systems, against environmental stressors that will only increase in intensity and frequency due to global climate change. Although our review is focused on the negative effects of climate change on trees, it is worth mentioning that the mycorrhizal fungi decline occurring nowadays might be also linked to climate change (Bennett and Classen, 2020). However, it is unclear if mycorrhizal populations are directly affected by climate change-derived stresses or if, by contrast, they are negatively affected by a lower performance of trees exposed to stresses (Sapsford et al., 2017). Thus, further research is required to decipher the links between trees and mycorrhizal fungi under stress conditions in a climate change scenario in order to design good strategies aimed at supporting the health of both partners, trees and mycorrhizal fungi.

AUTHOR CONTRIBUTIONS

MU, TH-P, HERF, MC-P, KG, and SDZ wrote the manuscript. MC-P, IG, KG, and SDZ revised and supervised this work. All authors contributed to the article and approved the submitted version.

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