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Unraveling the AM fungal community for understanding its ecosystem resilience to changed climate in agroecosystems

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Abstract

The changing global climate affects the agroecosystem making it challenging to achieve the world's sustainable development goals. Among the facets of belowground microbial communities, the arbuscular mycorrhizal fungi (AMF) hold an important place. They represent the most common symbiont phylum colonizing more than 80% of the plant families and are likely to be affected by global climate change. These fungi facilitate plant's mineral acquisition, improving growth and protecting them from biotic and abiotic stresses. The elevated carbon dioxide (eCO_2) level, temperature, increased nitrogen and phosphorus deposition influences the plant phenology and AMF functioning through changes in diversity and community composition of AMF. The interaction effects of soil management practices due to climate change affect the system productivity and perturb mineral cycling. Understanding the carbon and nitrogen cycling of an agro-ecosystem and its associated AMF communities concerning ecosystem productivity is the need of the hour. Plant-fungal associations require a more environment resilient approach to ameliorate the effect of anthropogenic changes in carbon and nitrogen cycles. Since AMF communities alter due to local environmental conditions and land-use changes, the most adapted community may help in predicting the mycorrhizal responses to chemical fertilizers, eCO_2, temperature and drought. In this review, we aimed at investigating (i) the diversity and community composition of AMF in relation to the change in crop and soil management practices, and (ii) how the adapted AMF communities may perform in maintaining the ecosystem resilience of these agroecosystems under climate change conditions. Hence, AMF-plant symbiosis can be effectively integrated into global climate change models. Eventually, the ecosystem resilience will be better understood to exploit the resident AMF communities to offset some of the detrimental effects of anthropogenic environmental change.

Keywords AMF community · climate change · global warming · Glomalin

1 Introduction

Global climate change caused by anthropogenic activities such as the intensification of agriculture, fossil fuel combustion and excess use of chemical fertilizers has increased the emissions of nitrogenous gases such as nitrous oxide, oxides of nitrogen, ammonia and, CO_2. Due to change in precipitation regimes, for instance the current level of CO_2 has increased from 280 ppm of preindustrial regimes to 400 ppm, which has contributed to global warming effects (Betts et al. 2016; Behera et al. 2013; IPCC 2013; Weltzin et al. 2003). In general, global climate change is known to affect terrestrial plants, microorganisms, and change the composition of soil communities which are involved in the functioning of various soil ecosystems (Pugnaire et al. 2019) As per the IPCC report (2014), the expected global

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climate change includes an increase in temperature and changes in rainfall regimes which shift the range of species, altering plant's distribution and associated rhizospheric microbial communities. Ultimately, the shifting of adapted associations under global climate change will modify the outcome of plant-soil microbe interactions.

Arbuscular mycorrhizal fungi (AMF), are the most common association forming a symbiotic relationship with roots of more than 80% terrestrial plant species (Classen et al. 2015; Smith and Read 2008). AMF are obligate symbionts providing nutrients to the plants in exchange for carbon (C) and are mostly affected due to global climate change. These fungi are functionally important and offer a wide range of benefits to their hosts including enhanced nutrient uptake (Bagyaraj et al. 2015; Smith et al. 2011), pathogen resistance (Cameron et al. 2013), heavy metal tolerance (Hildebrandt et al. 2007), soil C sequestration (Rillig et al. 2004; Wang et al. 2017; Parihar et al. 2020; Solaiman 2014), improved water relations (Auge, 2001) and drought alleviation (Mathimaran et al. 2017) while being influence and affecting other soil biotas (Drigo et al. 2010; Nuccio et al. 2013; Gupta et al. 2018). Therefore, the research on AMF in relation to environmental changes is imperative, because AMF may help to either mitigate or intensify climate change under future ecological conditions.

AMF distribution is primarily influenced by abiotic factors (drought, rainfall, flood, eCO_2 and temperature), and the biotic environment (Rasmussen et al. 2018; Vályi et al. 2016). AMF play an essential role in ecosystem resilience by facilitating species-species interactions between the nurse and facilitated plants (Song et al. 2010; Cheng et al. 2012; Montesinos-Navarro et al. 2019) and nutrient changes in soils (van der Heijden, 2008). Global climate change has direct and indirect effects on AMF communities due to the shift in plant phenology (Augé et al., 2001; Rillig et al. 2002a; Singh et al. 2010). As per earlier reports, higher temperature and low moisture levels alter the root-associated microbial community composition, which was found to increase plant growth, and influence AMF colonization (Augé 2001; Gavito et al. 2000, 2002). Seasonal fluctuations in rainfall patterns (Hazard et al. 2013; Alguacil et al. 2015) and temperature (Dumbrell et al. 2011) also influence the AMF development in the soil. AMF diversity and colonization pattern were greatly affected by phenological soybean growth stages, and the rhizosphere was found to be mainly dominated by *Glomus* followed by *Acaulospora* and *Gigaspora* species (Buade et al. 2020). In addition, the levels of available nitrogen (N; Velázquez et al. 2018), phosphorus (P; Zhao et al. 2017), soil pH (Melo et al. 2017), soil moisture (Deepika and Kothamasi 2015) and organic matter (Wang et al. 2015) may also influence the AMF community. Although many reports are available on mycorrhizal responses to global climate change (Begum et al. 2020; Saleh et al. 2020; Del Buono 2021; Wang et al. 2021), the information on the anthropogenic component of global climate change concerning changed crop and soil management practices on the diversity and community composition of AMF is scanty. The diversity and species composition of plant communities can also influence the abundance, diversity and species composition of AMF communities (Oehl et al. 2003; Landis et al. 2004). The higher temperature and CO_2, droughts, floods, nutrient level of N and P shift the distribution of AMF community, cooperate with the newly evolved species, and established synergistic interaction for sustaining the agroecosystems. Therefore, AMF are an essential component for predicting the terrestrial ecosystems functioning in relation to climate change (Drigo et al. 2008). AMF are ecologically important and may have an enormous impact on ecosystem responses (Fig. 1). They directly influence the individual plants and indirectly influence the plant processes such as plant dispersal and community interactions (Johnson et al. 2013a; Treseder, 2016). The selection of appropriate local native AMF and their production in sufficient quantity and improved quality are critical issues for their application in agriculture, particularly under global climate change (Berruti et al. 2016). Native AMF strains appear to be physiologically, ecologically and genetically more adaptable to the changing environment and could be more stable to their host plants (de Oliveira et al. 2017; Hart et al. 2018). However, previous research suggested AMF communities were not resilient (Gavito et al. 2008), but later on it was validated that AMF communities of tropical dry forest ecosystem are resilient and prove to land-use change and management practices (Carrillo and Gavito 2018). Hence, it becomes pertinent to study the AMF community composition and identify the well-adapted resilient AMF communities to the changed climatic conditions for sustaining the productivity under different agroecosystems (Table 1).

The present review provides a comprehensive up-to-date knowledge on the AMF communities against global climate change underlying drivers especially, rising CO_2, higher temperature, N deposition, drought and precipitation. Further, deciphering the resilient and dominant AMF communities may determine the plant community structure under global climate change scenarios for mitigating the adverse effects of global climate change.

2 Global climate change and global warming are the key drivers of AMF community and resilience to its functioning

Since, global climate change affects AMF, the functional outcome of any change in AMF communities also influences the mechanisms through which global climate change operates. Typically, eCO_2 enrichment generally increases the biomass of roots and mycorrhizal fungi (Rillig et al. 2002a; Drigo et al.

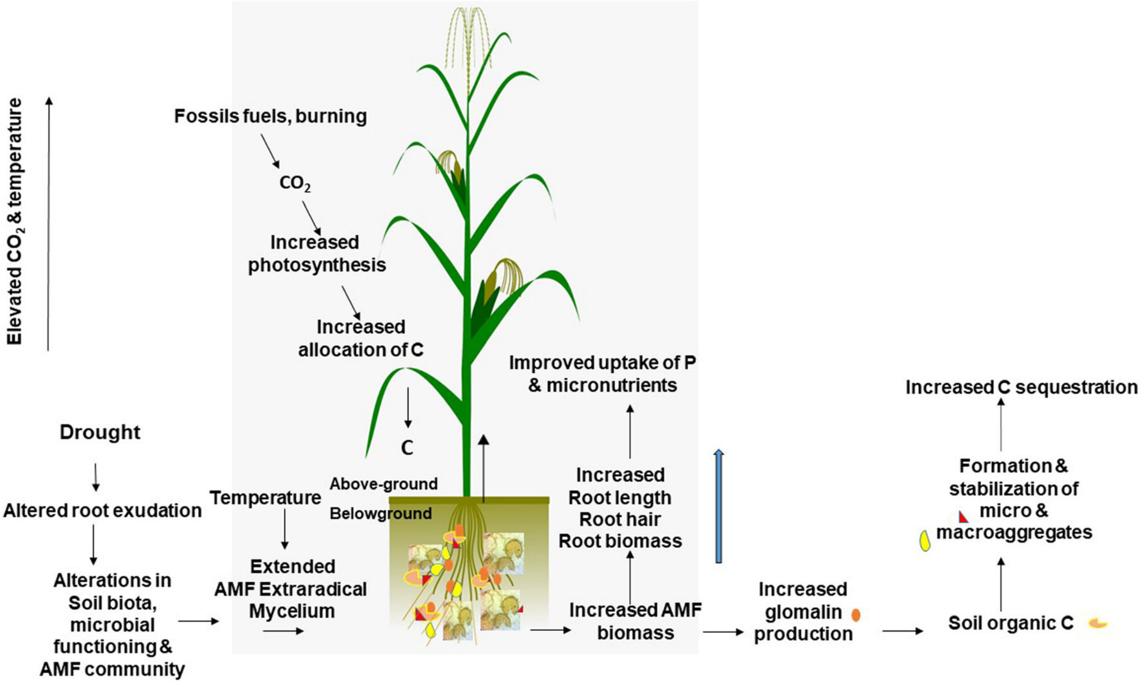

Fig. 1 The effect of elevated CO$_2$, higher temperature, drought warming on plants –microbe interaction, AMF and extraradical mycelium (modified from Compant et al. 2010)

2008). It is also likely that different AMF species may have a magnitude of variable plant responses (Hart et al. 2018; Gupta et al. 2019). Therefore, most efficacious strains need to be selected under eCO$_2$ and temperature conditions. The higher rainfall alters the AMF community composition directly or indirectly due to change in plant traits related to plant nutrition and water uptake (Deveautour et al. 2018). Changes in the AMF community have been observed in different C$_3$ and C$_4$ genotypes as C$_4$ plants, which have higher assimilation rates and use more CO$_2$ due to kranz anatomy. However, climate change, soil warming or drought stress indirectly affect plants associated with AMF (Auge et al. 2015). The plants under eCO$_2$ decrease their allocation of N-rich metabolites and increase the C rich metabolites allocation to root exudates (Tarnawski and Aragno, 2006). AMF may also be indirectly influenced by global climate change (temperature, rainfall) as it resulted in altered soil properties such as pH and nutrient availability and associated physico-biochemical properties which are the key drivers affecting the AMF communities (Fig. 1). The eCO$_2$ level in the atmosphere influences AMF symbiosis and is crucial for predicting the soil ecosystem changes. Over the past two decades, various studies have been conducted to examine the effect of eCO$_2$ [Evidence from open top chamber (OTC) and free air CO$_2$ enrichment (FACE) experimental studies] on changes in AMF community composition and diversity in a range of systems/practices under different ecosystems (Grover et al. 2015). It is reported that eCO$_2$ brought changes in ecosystem productivity, plant community structure and species composition (Bazzaz 1990). Such changes in the plant community are associated with the AMF community changes (van der Heijden et al. 1998). However, the results are contrasting and variable due to a change in AMF strains and their responses are variable due to the altered conditions (Gavito et al. 2000). It has been shown that plants allocate more C from their photosystem to the growing hyphae and roots under eCO$_2$, which resulted in increased AMF colonization in comparison with ambient CO$_{2.}$ Moreover, eCO$_2$ concentrations help in organic matter degradation, thus generating net C sources rather than C-sinks, which indirectly help mycorrhiza growth (Cheng et al. 2012; Phillips et al. 2012; Parihar et al. 2020). The potential for mitigating rising CO$_2$ levels through increased allocation and storage in mycorrhizas and other belowground C pools is currently debated (Phillips et al. 2012; Verbruggen et al. 2013). However, many studies have been carried out where AMF has been shown to enhance C sink in terms of producing higher amounts of recalcitrant copious sticky glycoproteins called “glomalin” which remains as part of stable C pool (Rillig et al. 2001, 2004; Wang et al. 2017; Parihar et al. 2020). AMF influence agroecosystem directly through mycelium effects by modulating host physiology and resource capture, and indirectly through changes in plant and soil microbial community composition. In addition, the direct effects of the AMF on agroecosystem via mycelium and its products e.g., glomalin becomes significantly important in performing ecosystem services (Rillig 2004a, b) The atmospheric elevated partial pressure of CO$_2$ (pCO$_2$), a higher level of C brought out to adaptive AMF strains, which shift AMF community

Table 1 Recent reports on the impact of agricultural management practices on AMF abundance and community composition under different agro-ecosystems

Agroecosystem/agro-ecological zone	Management practice	Dominant taxa in the AMF communities (species/genera/families)[a]	References
Continuous mono cropping system (China)	Soybean based cropping system	*Funneliformis mossae* and *Glomus*	Cui et al. 2018
Southern Chile	Horticultural agro-ecosystems	*Glomeraceae*	Castillo et al. 2016
Southern-Central zone of Chile	Forest, grassland and wheat agroecosystems	*Acaulosporaceae*	
Metropolitan region of Curitiba, Brazil	Araucaria Nursery seedling	*Glomus, Acaulospora scrobiculata, Dentiscutata heterogama, Glomus spinuliferum*	Vilcatoma-Medina et al. 2018
Coastal temperate mediterranean oceanic region	*Ammophyla arenaria* pioneer plants	*Corymbiglomus pacificum*	Medina et al. 2014, 2015
Temperate and sub-tropical mediterranean climates region	Organic cropping system *Solanum lycopersicum,*	*Glomus* and *Funneliformis*, *Funneliformis geosporus, F. mossae, G.badium, Septoglomus costrictum* and *Claroideoglomus luteum*	Njeru et al. 2015
Temperate grasslands	long-term no-till system	*Septoglomus constrictum*	Maurer et al. 2014
Calcic Chernozem Central Europe	Reduced tillage and fertilizers	*Ambispora fennica, Dominikia bernensis, Dominikia aurea, Scutellospora calospora, Diversispora celata, Funneliformis fragilistratus and Pacispora dominikii*	Baltruschat et al. 2019
Tropical atlantic forests	Crop rotation (sapodilla, rubber tree, mahogany, eucalyptus plantation)	*Acaulospora* spp. and *Glomus* spp.	Pereira et al. 2014
Tropical	Conventional agri practices (Soybean-based cropping system)	*Funneliformis caledonius*	Buade et al. 2020; Zhang et al. 2020
	Maize-Soybean	*Glomus aggregatum, Rhizoglomus fasciculatum, Funneliformis coronatus, Claroideoglomus etunicatum, Glomus* sp *(Glomus-f-Glomeraceae, Paraglomus and Gigaspora*	
Subtropical, warm wet transition zone	Herbs and shrubs with the dominant species herbs such as *Phragmites australis*, *Artemisia halodendron*, and *Solidago canadensis*.	*Glomus* and *Funneliformis mosseae*	Wang et al. 2020
Goa (kodar)	Mono-culture plantation of *Carica papaya L.*	*Acaulospora, Glomus, Gigaspora,* and *Scutellospora. Glomus claroideum*	Sharda and Rodrigues 2008
Tropical agro-ecosystems of African)	Cowpea	*Gigaspora, Sculellospora, Racocetra, Acaulospora, Funneliformis, Rhizoglomus, Glomus* and *Claroideoglomus*	Johnson et al. 2013b
Tropical forest	Conservation-agriculture	*glomoid* and *acaulosporoid spores*	Sharmah and Jha 2014
Annual and perennial herbs	Rainy and dry season Cape goosebery (*Physalis perviana* L.)	*Glomus* species *G. macrocarpum, Diversipora celata* and *Kuklospora colombiana*	Ramírez-Gómez et al. 2019
Semiarid zone	Grasslands Crested wheatgrass *(Agropyron cristatum (L.) Gaertn.)*	*Septoglomus viscosum, Funneliformis mosseae,* and *Simiglomus hoi*	Yang et al. 2010
Azorean islands (Terceira and São Miguel) plants *Picconia azorica*	*Picconia azorica*	*Acaulosporaceae*	Melo et al. 2019
Tropical semi-arid region of NE Brazil	Vegetative mosaic of dry forests, savanna-like shrubland and humid montane forests	*Acaulospora and Glomus*	Vieira et al. 2020
Subtropical agriculture	Maize (Zea mays L.)/soybean (Glycine max L.) intercropping	*Glomus-f-Glomeraceae, Paraglomus,* and *Gigaspora*	Zhang et al. 2020
Therwil near Basel (Switzerland) long-term organic farming	Crop rotation potatoes, winter wheat 2×, beetroots	*Funneliformis mosseae, Acaulospora* and *Scutellospora*	Oehl et al. 2004
Tropical climate	Coffee (*Coffea arabica* L.) Intercropping with corn and beans.	*Acaulospora , Glomus*	Prates Júnior et al. 2019
Tropical agro-ecosystem	combining organic and inorganic fertilization with chemical pest control *(Prunus persica)*	*Glomus, Claroideoglomus, Paraglomus,*	Alguacil et al. 2014
Dry and hot summer mediterranean	Forage rotations (alfalfa-winter cereal rotation, olive orchards and vineyards)	*Funneliformis, Scutellospora*	Pellegrino et al. 2019

[a] Genera and families as presented in Wijayawardene et al. (2020)

composition towards higher pCO_2. Under such conditions, native strains play a crucial role in increasing the N concentration in hosts and maintaining the ecosystem resilience (Jarrell and Beverly 1981; Gamper et al. 2005) e.g., eCO_2 brought changes in the AMF community composition by an increased ratio of Glomeraceae to Gigasporaceae members (Cotton et al. 2015). The members of Glomeraceae dominate in the composition of the AMF communities in vineyards of Oregon State (Schreiner and Mihara 2009), Piedmont (Italy; Balestrini et al. 2010) and Burgundy (France; Bouffaud et al. 2016). Primarily, it has been assumed that eCO_2 increases the C supply to some specific AMF taxa, which resulted in increased abundance along with reduced community evenness, and richness, where intraspecific and interspecific variations were also reported among isolated such as *Glomus claroideum* and *G. intraradices* (Cotton et al. 2015). Contrarily, an increase in the AMF richness arising from C-limitation has also been suggested. Surprisingly, the bulk of studies detected no significant effect of eCO_2 on AMF richness (Antoninka et al. 2011; Cotton et al. 2015; Mueller and Bohannan 2015). Mostly, the impact of eCO_2 on AMF is observed mainly on evenness and not on the AMF community diversity.

2.1 Impact of climate change and global warming on AMF under FACE and OTC conditions

Predicting the productivity potential of agroecosystem's at eCO_2 levels is necessary to understand the interactive effects of eCO_2 with AMF partners and plants uptake of nutrients and growth (Fig. 1). Jakobsen et al. (2016) worked out the effects of eCO_2 up to 900 ppm under FACE on the growth of two host plants e.g., *Medicago truncatula* and *Brachypodium distachyon* differing in P utilization efficiency on AMF symbiosis. They found that the application of AMF at ambient and eCO_2 increased mycorrhizal formation and the growth of *Medicago truncatula* plants at low P conditions Also reported AMF development and function is likely more influenced by the temperature component of climate change than by its (CO_2) component. The eCO_2 had small effects on P acquisition. However, it enhanced the conversion of tissue P into biomass, which indicates no increase of P fertilizers for sustaining the growth of these plants. Similarly, Gamper et al. (2004) assessed the impact of eCO_2 with the partial pressure of CO_2 and N under FACE in a seven-year well-fertilized grass and legume monocultures for AMF symbiosis and nutrient availability. They showed that eCO_2 at a low level of N fertilization marginally increased the AMF root colonization but significantly augmented the production of smaller spores in both the hosts in monocultures. However, larger AMF spores were different in both the hosts. The higher N fertilization decreased the AMF formation in *Lolium perenne* but not in *Trifolium repens*. A ten years experiment of the interaction effect of $eCO_2 \times N$ reported a significant effect of both on AMF (Staddon et al. 2004). However, the eCO_2 and limited N decreased root colonization but increased extraradical hyphae. Understanding of C fluxes in C_3 plants to AMF and subsequent transfer to other rhizosphere microbial communities and in C cycling at eCO_2 are scarce. Drigo et al. (2010) proposed a conceptual model based on a stable isotope tracer study. They observed that under eCO_2 (up to 700 ppm) plant-assimilated C is rapidly transferred to AMF, releasing slowly to the resident niche bacterial and fungal rhizosphere populations. This study helped to understand the C-flow paths in soils and predicts the sustainability of terrestrial ecosystems at eCO_2. The eCO_2 influences on the AMF community dynamics were further assessed in soybean free air concentration enrichment monitored for three growing seasons over five years. It was observed that eCO_2 consistently favored the dominance of *Rhizophagus irregularis* (*Rhizoglomus irregulare*) and not the Gigasporaceae (Cotton et al. 2015).

Other studies conducted under OTC at eCO_2 and temperature were found to positively influence diversity and community composition of AMF, where *Glomus* spores were found to be most abundant. However, there was a clear difference in the AMF species richness observed at the altered conditions (Asha et al. 2017). When the ambient CO_2 level was increased to 550ppm, a concomitant increase of *Glomus* species (up to 93% of AMF taxa) over the ambient CO_2 (up to 62%) was detected (Klironomos et al. 2005). The relative abundance of sequences putatively identified as *Rhizoglomus irregulare* was also shown to increase from an average of 53% under ambient CO_2 to 73% under eCO_2 (550ppm; Cotton et al. 2015) and an increase in the CO_2 levels to 560ppm lead to a fourfold increase in the spores of *Glomus clarum* (Wolf et al. 2003).

2.2 Impact of temperature on diversity and community composition of AMF

Increased temperatures may generally promote the plant growth by enhancing the photosynthesis, which indirectly supports the development of AMF through the nutrient exchange (Mathur et al. 2018). The selection of ecosystem resilient AMF strains under the changing global climate scenario for promoting the growth is the need of an hour (Fig. 1). It is known that AMF form colonization with most plants and respond to plant growth at higher temperatures (Graham et al. 1982; Fitter et al. 2000). AMF ameliorate the effects of temperature stress due to global climate change on plants by increasing growth and nutrient content (Pischl and Barber 2016). However, these effects do not extend and confer tolerance to plants against herbivorous organisms. The temperature may also significantly alter the structure of the AMF hyphal network, where low temperature (cooled soil) allocate more vesicles (storage) and high temperature (warmed soil) contributes to more extensive extraradical hyphal networks (growth) (Hawkes et al. 2008). The detection of a direct effect of temperature on the extraradical mycelium was investigated in a compartment study to assess the differences in nutrient uptake through AMF species (Jakobsen et al. 1992). This study provided a better understanding of rhizospheric C-allocation and the increased respiration of the extraradical hyphae when the soil temperature is high (Heinemeyer et al. 2006) in conferring the tolerance to plants. The temperature responses of AMF have not been investigated intensively along with eCO_2. The effect of temperature such as extremely low or high temperatures in a given region can considerably reduce the AMF population because no adaptation found in these AMF isolates (*Funneliformis mosseae*) in the soils (Addy et al. 1994;Gavito and Azcón-Aguilar, 2012).Therefore, AMF adapts and confer resilience to themselves against the changed climatic conditions (Al-Karaki et al. 2004). Region-specific AMF strains and their communities need to be identified for their exploitation in sustaining the agroecosystems.

2.3 Impact of nitrogen and phosphorus fertilizers on diversity and community composition of AMF

The continuous application of N and P fertilizers created environmental problems such as reduced biodiversity and suppressed ecosystem functionalities (Socolow 1999). To overcome the ecological issues, beneficial microorganisms in increasing the growth, nutrient availability and sustaining the agroecosystem's productivity are being promoted. In addition, the response of plants to eCO_2, the availability of both N (Daepp et al. 2001) and P (Campbell and Sage 2002) need to be assessed to understand the contribution of AMF in acquiring these nutrients. The exploitation of native AMF forming association with most terrestrial plants is gaining importance in order to provide nutrients and protection even under environmental stress. The effects of N enrichment on AMF are mediated by soil P availability, where N enrichment of P-limited soils was found to increase the biomass of AMF. In contrast, N enrichment of P-rich soils declined the AMF biomass (Johnson et al. 2003). Resource availability affects the plant community composition and, through interactive effects of N, CO_2, and plant diversity, it governs the AMF communities (LeBauer and Treseder 2008). Higher N concentrations increase plant productivity, but decrease the C availability to AMF (Johnson et al. 2003). The impacts of N and rainfall on AMF communities at eCO_2 were assessed in a seven-year field study. It was observed that N application reduced AMF, whereas rainfall increased AMF abundance. The interaction of both N and precipitation mainly altered the AMF community structure than AMF phylogenetic structure (Chen et al. 2017). Cavagnaro et al. (2007) reported that inoculation of AMF in tomato plants grown at eCO_2 showed higher contents of N, P and Zn, when compared to plants grown at under ambient CO_2. However, the response of AMF on N uptake was found to vary with host plants and AMF species used (Chen et al. (2007). For example, AMF colonization enhanced N uptake under eCO_2 in *Plantago lanceolata*, but not in *Festuca arundinacea* plants. The P use efficiency in plants is being modulated through P transformation at eCO_2 condition. Ainsworth et al. (2003) showed a higher photosynthetic rate and plant growth at eCO_2, mediated and metabolized through concentration of the Rubisco enzyme to facilitate C assimilation by autotrophic organisms. It is known that eCO_2 increases the Rubisco concentration to metabolize more inorganic P to transform into organic P. Organic P is needed to synthesize Rubisco which is a major constituent of rRNA involved in the synthesis of Rubisco enzyme (Veneklaas et al. 2012). The eCO_2 increases the grain yield due to an increased P assimilation in the grain (Buddrick et al. 2014). Hence, it is likely that eCO_2 levels increase the Puse efficiency by accumulating a higher proportion of P in plant tissue to further help in the photosynthesis-associated metabolisms and assimilation activities. The AMF diversity and community vary with the type of fertilization. The application of organic manure in maize is regarded as the most critical factor influencing AMF community composition, followed by N and P fertilizer inputs. In another recent study on coffee agroecosystem concentrating on identifying the AMF communities in conventional and organic systems, AMF were affected due to interactive effects of N fertilization with light shade (Aldrich-Wolfe et al. 2020). The higher correlation of AMF community composition in organic manure applied maize rhizosphere activates more AMF species to interact with other species thereby regulating the AMF symbiotic system in maintaining the soil health and productivity of crops (Zhu et al. 2016). There are not many studies available concerning the diversity and community composition of AMF in relation to N and P fertilization at eCO_2. Therefore, further work is needed in this area to harness the potential of stabilized native AMF communities in rationalizing the fertilizer uses without compromising crop productivity.

2.4 Impact of precipitation/rainfall on diversity and community composition of AMF

The mycorrhizal soils had significantly more water stable aggregates and substantially higher extraradical hyphal densities than the non-mycorrhizal soils. However, comparative water relations of both mycorrhizal and non-mycorrhizal soils have not extensively studied (Auge 2001). Variations in water regimes/precipitation influence the soil microbial community (Clark et al. 2009). Changes in rainfall distribution pattern can directly influence the plant communities, diversity and productivity, which alters AMF abundance, functioning and communities at regional scale (Zhang et al. 2016; Johnson et al. 2004). Precipitation alters the root architecture which changes the soil environment and shifts in AMF community associated with changes in root traits (Deveautour et al. 2018). Zhang et al. (2016) examined the direct effect of a gradient of rainfall (50 to 400 mm) on AMF communities associated with dominant plant species in a Tibetan alpine steppe. Among the 31 AMF operational taxonomic units identified, AMF community composition varied significantly among sites but did not differ among plant species. Further, they showed that precipitation directly affected the AMF hyphal length density, and indirectly influenced AMF species richness suggesting the role of water precipitation in driving the AMF communities at the regional scale. The magnitude of AMF responses to confer tolerance in plants against the water stresses differs with the AMF species-plant combinations (Zhang et al. 2016). Under water stress, plants acclimatize native AMF species to survive and proliferate extensive hyphae to acquire more water. It has been shown that during water stress some AMF species may become inefficient in forming colonization in plants (Deepika and Kothamasi 2015). However, under congenial conditions, efficient AMF, which require more C fluxes, may lose their abilities due to insufficient C supply from the host plants (Johnson, 2010). The impacts of drought on AMF abundance and diversity have been reported in a number of studies (McHugh and Schwartz et al. 2015; Martínez-García et al. 2012) On the other hand, higher rainfall conditions also altered the AMF community composition in several studies (Sun et al. 2013; Li et al. 2015; Gao et al. 2016; Deveautour et al. 2018). Deepika and Kothamasi (2015) studied that under flood conditions, the AMF community composition with *Sorghum vulgare* resulted in lowest diversity mainly dominated by two *Acaulospora* phylotypes. An increase of rainfall and relative humidity increased the AMF colonization (Pande and Tarafdar 2004). Changes in AMF formation and an increase in the abundance of one species were observed under increased temperature and precipitation (Sun et al. 2013), and phylogenetic clustering of communities have also been reported (Chen et al. 2017). It was concluded that the plant community influenced the AMF and was closely related with the composition of the AMF community. Rainfall has been observed as a significant driver for AMF spore density, especially of Acaulosporaceae, Diversisporaceae and Glomeraceae, which were positively correlated with abiotic factors. In contrast, members of the Gigasporaceae showed a negative correlation with these climatic variables (Tchabi et al. 2008, Al-Yahya'ei et al. 2011). More studies related to AMF abundance, community composition and associated ecological functions are needed under global climate, change and models covering all the factors of production functions such as rainfall, temperature, seasons etc (Cotton et al. 2018).

2.5 Impact of plant genotypes (C3 and C4 plants) on diversity and community composition of AMF

Plant species are critical in regulating the AMF symbiotic efficacy in C_3 and C_4 plants. Due to climate change, plants are likely to induce changes in physiology and root exudation. Compared to some commonly grown C_3 plants, greater mycorrhizal symbiotic efficacy has been reported in C_4 plants (Hetrick 1991; Wilson and Harnett 1997). In the case of C_4 plants, grasses are categorized as obligate AMF hosts (Hetrick 1991). C_4 plants often benefit more from AMF associations than C_3 plants, partly due to their higher photosynthetic efficiency and greater nutrient demands (Hoeksema et al. 2010). Increasing CO_2 is generally known to enhance plant C fixation, particularly in C_3 plants, and also increase the proportion of fixed C allocated to plant roots (Ainsworth and Long 2005; Drigo et al. 2010). Since C_4 plants have kranz type anatomy that can facilitate two-fold CO_2 fixation hence are more receptive to AMF under eCO_2 and temperature. The AMF mediated drought resistance varies among C_3 and C_4 plant functional groups (Yamori et al. 2014). Single or mixed AMF groups differed in their response, where C_3 plants were positively influenced by *Rhizoglomus irregulare* and compared to other species, C_4 plants benefitted from *Funneliformis mosseae.* Many studies have observed variable responses of AMF to drought conditions, where C_3 species showed higher water use efficiency than C_4 species (Edwards et al. 2010; Worchel et al. 2013; Augé et al. 2015). The mycorrhizal symbiotic efficiency in C_3 and C_4 plants vary depending on the plant species involved. Among C_4 plants, grasses are highly mycorrhizal and exhibited higher mycorrhizal dependency (98 to 99%) than C_3 plants (Hetrick 1991). However AMF colonization seems often to be a rather poor indicator for plant growth promotion (Sharma et al. 1996).

3 Significance of AMF resilience and its functioning in relation global climate change

Global climate change alters the functioning of individual AMF and well-adapted communities. Climate-changing parameters such as eCO_2, temperature, precipitation etc., are known to affect terrestrial plants associated microbial communities including AMF. Previous studies on global climate change with AMF species and their functioning advocates that plant species and abiotic factors are jointly involved in driving the AMF community required to perform various soil eco-functions (Gamper et al. 2005; Klironomos et al. 2005). Together, these studies suggest that eCO_2 concentrations may make AMF communities more effective in some ways, but less effective in another way (Table 1).

3.1 Alleviates drought stress

There are many reports available, where the role of AMF symbiosis in the alleviating drought stress have been spelled out (Mathimaran et al. 2017; Auge 2001; Ruiz-Lozano 2003; Wu et al. 2013; Sharma et al. 2020). AMF confers drought tolerance to plants through various mechanisms such as increased extended hyphal network to absorb more water (Mathimaran et al. 2017), improved plant root architecture and soil properties (Wu et al. 2012), regulating the physiology of plants to perform functions (Yang et al. 2014), regulating plant gene expressions such as aquaporins (Li et al. 2013; Barzana et al. 2014), and osmotic adjustments in plants such enhanced levels of proline, reactive oxygen species (ROS), trehalose sugars (Kaya et al. 2009; Ocon et al. 2007; Sharma et al. 2020). Under drought conditions the interactive effects of plant genotype and AMF richness offset the damage caused due to drought and led to high barley crop yield (Sendek et al. 2019). Recently, Chareesri et al. (2020) showed that under drought, besides increasing the photosynthetic parameters e.g., higher levels of chlorophyll fluorescence in AMF inoculated rice plants were revealed. AMF also increased the levels of abscisic acid (ABA) and indole acetic acid (IAA) in plants under drought. The authors argued that higher response in AMF inoculated rice plants under drought might have been mediated through nutrients and also through the regulation of plant hormones, especially IAA and contributed to a better recovery and resulted in high rice grain yields. This becomes highly relevant under the changing climate, where drought is the critical factor limiting the productivity of the majority of crops. Hence, establishing colonization with resilient AMF species could be essential to regulate and stimulate various mechanisms conferring the drought tolerance in crop plants.

3.2 Stimulation of other plant growth promoting microorganisms (PGPM) and soil biota

Global climate change is altering the plant's behavior and belowground AMF species distributions and interactions with other microbial communities. These beneficial rhizosphere microbes improve crop's nutrient status as described above, facilitate and mobilize soil resources and processes required for sustaining the growth of plants especially under change climate. It is known that environment change through eCO_2, temperature and drought, alter the root exudates composition and induces alterations in the activity, function, abundance and structure of the soil microbial community associated with plants or plant metabolites (Rangel-Castro et al. 2005; Rasche et al. 2009). Shifting of resident AMF species under elevated atmospheric CO_2 conditions are linked with changes in the active bacterial and fungal rhizosphere communities.

Alterations in root exudates include changes in the availability of chemo-attracting or signal compounds as well as a different C/N ratio or nutrient availability (Bansal and Mukerji 1994; Kandeler et al. 2006). The extent of AMF-derived benefits depends on the compatibility of the soil environments including microbes from where the communities were selected and identified. Numerous studies have been conducted on the combined inoculation of AMF with other plant growth promoting bacteria (PGPB) such as *Rhizobium meliloti*, and resulted in higher biomass and grain yield under drought conditions (Panwar 1993; Zoppellari et al. 2014 Valdenegro et al. 2001, Mortimer et al. 2013; Sharma et al. 2016). In a recent review, Sharma et al. (2020) highlighted the role of the tripartite symbiosis of legumes with AMF-rhizobium in conferring the drought tolerance through the trehalose-based mechanism. The community changes at the eCO_2 may substantially affect the diversity and activities of rhizospheric microbes. Therefore, a stabilized resilient combination of AMF (*Glomus clarum*) with PGPB *Bacillus* sp. strains may improve the drought, salt tolerance in plants by increasing chlorophyll, proline and soil aggregates (Kohler et al. 2009, Grover et al. 2015; Diagne et al. 2020). However, studies related to combination of AMF with PGPB particularly at eCO_2 are lacking. Although AMF and other PGPB including endophytes are being used as biofertilizers, phytostimulants, bioprotectants in agriculture (Welbaum et al. 2004; Lugtenberg and Kamilova 2009), the knowledge on how exactly plant-associated microbial communities are being influenced either directly under environmental change or indirectly through changed plant physiology are lacking (Drigo et al. 2008). Therefore, a better understanding of the selection and performance of appropriate ecosystem resilient soil microbiome is needed to mitigate the impacts of global climate change on plant productivity.

3.3 Changes in mycorrhizal dependence and nutrient availability

In general, much work has been carried out in different agroecosystems on how mycorrhizal species are changing their nutritional contribution in plants and gaining significance as potential biofertilizers. However, the information regarding the contribution of AMF to the plant's nutritional requirement under changed climatic conditions is inadequate. AM colonization stimulates plant nutrient acquisition. AMF infect and form a symbiosis with the roots of plants and improves plant growth by supplying N, P, K, Ca and micronutrients including zinc (Zn) and S, as a strategy to obtain essential nutrients from plants (Gupta and Abbott 2020). Thus, AMF provide nutritional support to the plants even under unfitting conditions inside the root cells. AMF produce fungal structures such as arbuscules, which assist in exchanging of inorganic minerals and organic C and P compounds (Li et al. 2016; Prasad et al. 2017; Gupta and Abbott 2020). Under P-limited conditions, mycorrhizal association improves P supply (Bucher 2007, Bagyaraj et al. 2015). For example, Pi uptake rate was markedly enhanced in the AMF-colonized maize, strawberry and onion plants (Garcés-Ruiz et al. 2017; Sharma and Adholeya, 2000 and 2004). It is evident that inoculation with AMF and enforcing the AMF symbiosis can significantly enhance the concentration of various macro and micro-nutrients, which leads to increased photosynthates production and hence increased biomass accumulation (Tchabi et al. 2010; Chen et al. 2017; Mitra et al. 2019; Gupta et al. 2019). Apart from the macronutrients, AMF association has been reported to increase the phyto-availability of micronutrients like zinc and copper (Cu; Smith and Read 2008). AMF inoculation in tomato plants increased leaf area, N, P, K and Ca contents, reflecting enhanced plant growth (Balliu et al. 2015), in chickpea improved growth and increased levels of protein, iron Fe, and Zn (Pellegrino and Bedini 2014) and in soybean enhanced nodulation and physiological status (Sharma et al. 2012, 2016). Increased N in colonized plants by AMF- results in higher chlorophyll contents, as chlorophyll molecules can effectively trap N (De Andrade et al. 2015). It was recently being reported that inoculation with native AMF cause significant alterations in the N contents of crop plants (Turrini et al. 2018). Under the conditions of ambient and elevated CO_2, a substantial improvement in the accumulation C and N and the assimilation of N due to AMF inoculation has been reported (Zhu et al. 2016).

3.4 Improved soil aggregation, stability and soil sequestration

AMF activities vary with the way plants behave under the changed environment and soil conditions. Elevated atmospheric CO_2 leads to C fixation by plants and more significant transfer of C to growing roots in the soil and stands as one of the most significant factors in AMF functioning. Plants invest additional C in their AMF partner, and AMF through their extended hyphal network facilitates C transport and take part in C cycling thus becoming ecologically crucial in sustaining the productivity of agroecosystems (Parihar et al. 2020).

AMF produce large amounts of copious recalcitrant glycoproteins known as “glomalin” which are hydrophobic, insoluble and significantly important in stabilizing soil aggregates (Wright and Upadhyaya 1998, Rillig 2004a). The greater stability of aggregates leads to larger amounts of protected organic C in terrestrial ecosystems (Wright and Upadhyaya 1998; Singh 2012; Wang et al. 2015; Gupta 2020; Gupta and Abbott 2020). AMF influence soil aggregate stability and long-term C and N storage through glomalin (Wright and Upadhyaya 1998). Glomalin also responds to plant species and land-use changes (Rillig et al. 2002b, 2003). However, glomalin concentration in the soil varies and is responsive to AMF species, crop and soil management practices, e.g. crop rotations, tillage, etc. (Agnihotri et al. 2018), and factors of global climate change e.g., elevated atmospheric CO_2, warming (Rillig et al. 2002a). Rillig et al. (2001) demonstrated the role of AMF-mediated glomalin in soil aggregate water stability. They suggested that glomalin should be used as a useful indicator in assessing the impacts of global climate change based on altered aggregate stability. Nautiyal et al. (2019) recently showed that the glomalin concentrations and soil aggregation varied across different cropping systems. They observed that glomalin content (total and easily extractable) was positively correlated with soil organic C. Long back, Rillig et al. (1999) observed that when compared to ambient $CO_{2,}$ the glomalin production and soil aggregation increased at higher CO_2 indicating the role of AMF in capturing C. Thus, under eCO_2, the soils can retain large amounts of C through the production of glomalin, which can sequester C and may help in mitigating the effects of eCO_2 (Zhang et al. 2015). To simulate eCO_2 in different agroecosystems, systematic long-term field studies are needed to establish and predict the contribution of AMF in sequestering soil C.

The adoption of appropriate agriculture management practices can contribute to the mitigation of climate change. Conservation agriculture, for example zero tillage (ZT) practice has been shown to increase soil organic carbon and improve soil quality and glomalin pool (Gathala et al. 2011; Agnihotri et al. 2021). The C sequestration varies with the cropping system and tillage practices (Aryal et al. 2015). This may result in changes of the microbial community composition, e.g. AMF biomass. In one of the long-term field trial in India (over 20 years) where maize–wheat and cotton–wheat production systems under zero tillage system showed more C-sequestration than the rice-wheat system under the same practice indicating the role of crop sequences and soil management practices in C cycling. Since AMF are ecologically crucial in maintaining C balance and C storage for the future (Parihar et al. 2020). Furthermore, an assay for extraction and quantification of higher recovery of glomalin in soil and roots should be optimized to decipher the role of AMF in C cycling and soil processes (Holatko et al. 2021).

4 Conclusions and future prospects

The impact of anthropogenic changes on the current and future global environment is unprecedented; therefore, a holistic and comprehensive approach is required to mitigate these adverse effects. AMF are widespread and highly responsive to the changing environment. This review provides an understanding of the impacts of climatic change and associated crop and soil management practices on AMF symbiosis for ecosystem resilience. Given the massive importance of these fungi in ecosystems, there is a need to include them in global climate change models. The use of real-time data in the models will help to formulate strategies for sustaining the ecosystem services and food grain production for the future. The shreds of evidence from climate change studies indicate the shaping up of the AMF communities. However, native AMF are not sufficiently considered, both fully exploited in sustainable crop and soil management practices.

Soil and crop management practices, e.g. doses of fertilizers, use of C_3 or C_4 plants, need to be customized to adopt AMF favoring systems to eventually help in sustaining the productivity of agroecosystems through mitigating the effects of climate change. However, to arrive at a logical conclusion, long-term field studies across the agroecosystems are needed in different climatic situations to elucidate the potential of AMF in mitigating the anthropogenic perturbations and sustaining the below-ground ecosystem services systematically. Such studies will help to generate data on the contribution of AMF and associated practices for predicting their role in sustaining the productivity in different agroecosystems for the future.

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