Agronomic Applications of Mycorrhiza in Climate Change

Anindya Bhattacharyya and Tanaya Das

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Anindya Bhattacharyya[1] and Tanaya Das*[2]

A B S T R A C T

Climate change has a profound impact on global crop production. Abiotic stress, such as higher temperature, elevated CO_2, alteration in precipitation, including increased or decreased rainfall, flooding, and drought, not only affect a plant's morphology or biochemistry but also affect its biotic interactions, such as interactions with beneficial mycorrhizae. Associated with most plant roots, mycorrhizae provide an enhanced surface area for nutrient and water uptake from the soil, promoting plant health. They can mitigate both abiotic and biotic stress by inhibiting anomalous pathways by producing a variety of compounds and defence mechanisms. Mycorrhiza can improve fruit quality, flowering, enhancing seed germination rate and pollination. Mycorrhiza-based agriculture is booming today due to it being natural, eco-friendly, and cost-effective. The present review focuses on natural systems such as mycorrhizae for sustainable agriculture. It aims to understand the underlying molecular mechanisms that mycorrhiza uses to counteract stress. It also delves into mycorrhiza's applications as a biofertilizer, bioinoculant or bioprotectant. The ultimate goal of the review is to emphasize the role of mycorrhiza as a naturally occurring tool that can aid plants to manage stress under the global change regime and enhance the yields.

Key words: Abiotic stress, Biotic stress, Climate change, Mycorrhiza, Sustainable agriculture

In 2050, there will be 9.9 billion people on earth, up from 7.8 billion in 2020 [1]. According to another study, the global population will be between 8.4 and 8.7 billion in 2030, 9.4 to 10.2 billion in 2050, and approximately 9.6 to 13.2 billion in 2100 [2]. Therefore, almost a 70% increase in food production is necessary. Developing countries will need almost double their food production [3]. Climate is one of the major factors by which crop production is regulated. Agriculture faces major challenges due to global climate change. The average temperature rises when greenhouse gases are released into the atmosphere. High temperature may cause heatwaves, altered precipitation, floods, and droughts. Climate change, like droughts, floods, or heavy rainfall may cause degradation of land, accumulation of salt in the soil, loss of nutrients from soil resulting in less productivity. It indicates that there is a strong relationship between climate change and agriculture [4]. Ray *et al*. indicated that Europe, Southern Africa and Australia received mostly negative effects due to global climate change. A decreased crop yield by 6.3-21.2% in western and southern Europe was observed. This data indicates that the risk of food insecurity has been associated with climate change in most

food-insecure countries [5]. These abnormalities in climate change have been associated with the development of abiotic and biotic stress in plants. Hence, a few strategies are urgently required to eradicate food insecurity by alleviating the impact of climate change on crop production. Therefore, the development of stress-tolerant plants is a sustainable approach to survive in extreme and harsh environments [4].

Soil, a very complex medium, supports growth for plants consisting of the solid phase of minerals derived from rock and organic materials derived from the decomposition of plants and animals by microorganisms, the liquid phase of water or soil solution, gases and living organisms including bacteria, fungi, algae, protozoa and earthworms etc [6]. Firstly, the nutrients must be released into the soil water followed by up taking by plant roots. Hence, one of the crucial factors for the growth of the plants is the absorption of nutrients by the root system of the plants. Root architecture is essential for maximum absorption of nutrients and water. Mycorrhizae, fungal associations provide enhanced volume around the roots of a plant to uptake water, nutrients mainly P and N. In addition to, nutrient uptake mycorrhizal association can combat different environmental stresses faced by plants [7]. Hence, mycorrhiza (arbuscular mycorrhizal fungi) is considered to be a biofertilizer [8]. Because biofertilizer not only provides good and healthy soil and crop health but also is an eco-friendly approach.

The objective of this review is to decipher mycorrhiza, a natural association with plants for survival strategy by mitigating the stress associated with global climate change. Hence, the present review at first highlights the stress that occurs in plants due to climate change. Then, how mycorrhiza

* **Tanaya Das**
  ✉ tanayadas1981@gmail.com

[1] Department of Biochemistry, Gurudas College, Kolkata - 700 054, West Bengal, India

[2] Department of Biochemistry, West Bengal State University, Kolkata - 700 126, West Bengal, India

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mitigates the stress and the molecular mechanism behind it are also focused on. This review also enlightens mycorrhiza as a biofertilizer and bioprotectant for plants. The field that needs more work to explore the interaction of mycorrhiza with plants under stress conditions is also discussed. These gaps will surely open up a new area for future research.

How climate change afflicts plants

Acclimatization to climate change and ensuring food security for the future have become major challenges throughout the world in the current situation. Climate change describes a rise in greenhouse gases (CO_2), a rise in temperature, precipitation alteration, flood or drought etc. An increment of the earth's temperature by 0.14°F or 0.08°C per decade since 1880 has been observed in the report. Since 1981,

it has risen by 0.32°F or 0.18°C per decade [9]. Excess heat results in the development of seasonal extreme temperatures, heavy rainfall. Heavy rainfall, rising sea level, higher flood level, erosion of coastal area, storm surge, strong winds, tornado, cyclones are generally hazards associated with climate variability in the coastal areas. The intrusion of seawater (saline water) into groundwater, surface water, and land, mainly soil has jeopardized crop production, leading to lowered coastal agricultural productivity [10]. Climate change has been thought to be associated with an alteration in plant growth, productivity, etc. A reduction of crop yield across the world was observed due to abrupt climate change and is presented in (Table 1). Climate change results in the development of abiotic and biotic stresses which are accompanied by alteration in plant physiology as well as morphology (Fig 1).

Table 1 Reduction of crop yield across the world was observed due to abrupt climate change

| S. No.	Name of the crop	Stress associated with climate change	Reference
1	Declination of mean yield of wheat in Germany, in the period of 1994-2009	Heat stress	[185]
2	Increase of wheat loss risk by 20% would be experienced in USA and Canada	Drought stress moves from moderate to Exceptional	[186]
3	Increase of rice lowering risk by 20% shown in India and Vietnam	Drought stress moves from moderate to Exceptional	[186]
4	Production of soyabean would decrease by 52% in Brazil	Under moderate drought condition	[186]
	Production of soyabean would decrease by 71% in Brazil	Under exceptional drought condition	
5	Reduction of maize and soybean yield in USA in the most year from 1980-2019	Heat stress	[187]
6	Reduction in winter wheat yield in the middle and lower reaches of the Yangtze River	Excessive rainfall	[188]
7	Risk of yield loss of maize in US is 64.3%, 69.9%, 73.6%, 78.1%	Under moderate, severe, extreme, exceptional drought case	[189]
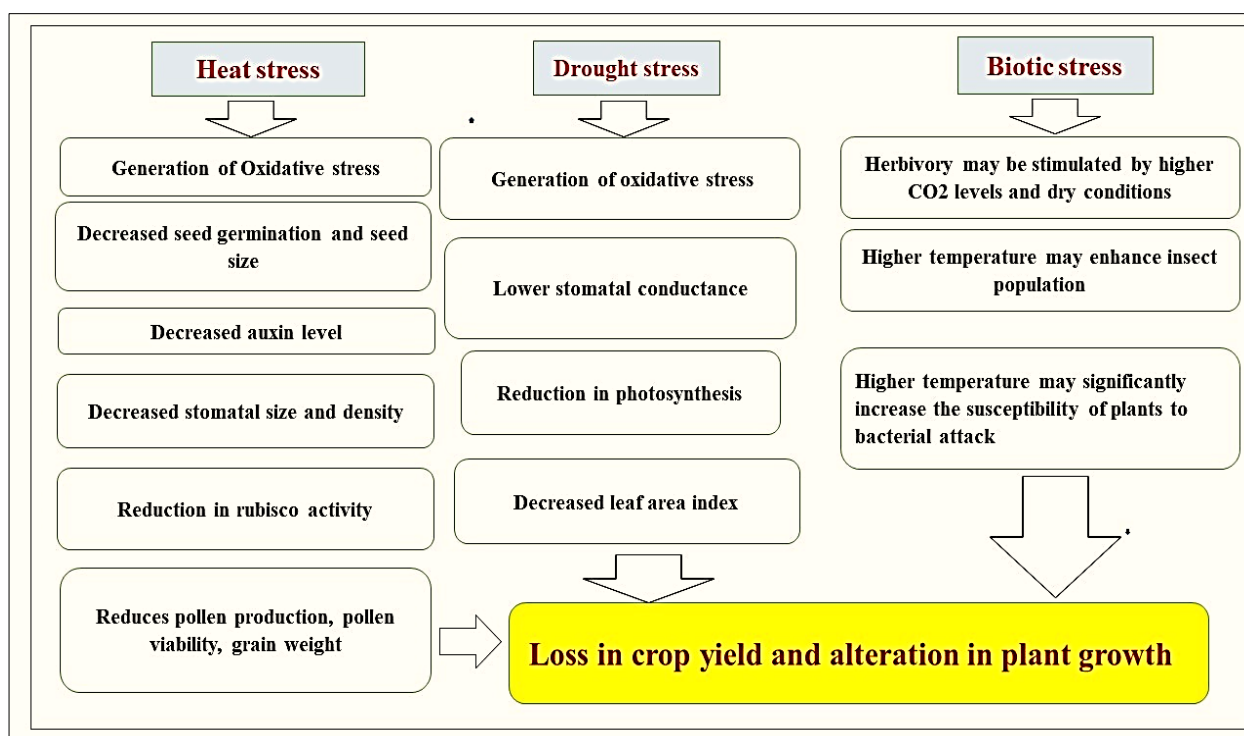
Fig 1 Effect of climate change on plants
Heat stress, drought stress and biotic stresses are responsible for alteration in plants in various levels including morphological, physiological levels. These changes ultimately lead to reduction in plant growth and followed by less production in yield

Modifications occurring in plant
A. *Plant developmental stage*

Climate change has a profound effect on plant population dynamics by influencing seed germination through seed maturation and persistence of the seed in the soil [11]. Itoh *et*

al. showed that the seed germination rate decreased as the temperature increased. The root length of maize plantlets was also found to be decreased at high temperatures [12]. High-temperatures have a negative effect on crop productivity. Early seed development in some crops may be sensitive to abnormal

environmental conditions. Seed size and fertility may be reduced due to heat stress during this stage, leading to a reduction in productivity [13]. Temperature also has an impact on the flowering stage of a plant. Earlier flowering was associated with higher temperatures, whereas late-flowering was associated with less precipitation [14]. The elevated temperature had been associated with decreased auxin levels in developing anther of barley and Arabidopsis. High temperature also caused a reduction in the expression of the auxin biosynthesis gene, YUCCA. Abortion of pollen development may occur through tissue-specific auxin reduction [15]. Pollen germination is affected by high temperatures. Prolonged high temperatures harmed sexual reproduction by lowering germination [16]. Floral buds and flowers are aborted due to the high temperature in peas. The abortion frequency of floral bud in pea may be significantly high under the short duration of heat stress [17]. In addition to heat stress, during the seedling stage, prolonged and severe water stress damaged the structure of the photosynthetic membrane, leading to a reduction in chlorophyll content in maize [18]. Lowered plant height and leaf area development were reported during vegetative and tasseling stages under water stress [19].

B. *Morphological changes*

Various morphological changes have been observed in plants due to climate change. Plant cell walls become wrinkled and loose when turgor pressure is decreased due to severe drought, and this will lead to a reduction in the number and size of the leaves [20]. Elevated CO_2 increases the thickness of the cell wall [21]. Various effects can be observed in the case of stomatal size and density. Stomatal size was found to be decreased at higher temperatures in *S. rehderianum* whereas stomatal density was significantly decreased in *S. superba* [22]. Decreased stomatal opening and stomatal aperture were observed in one cultivar of Rhododendron when exposed to a higher temperature [23]. Smaller internode containing sugarcane plants were observed at high temperatures [24]. Leaf area index is lowered due to water stress [18]. Expansion of cells is impaired when the leaf is exposed to heat stress [25]. Reduced fruit firmness, as well as decreased acid concentration are observed in apples at high temperatures [26].

C. *Physiological changes*
a) *High-temperature stress*

High-temperature stress due to climate change has a significant effect on plant physiology. The thylakoid membrane of the chloroplast of plants and photosystem II, along with the oxygen-evolving complex is susceptible to high-temperature injury. The oxygen-evolving complex may undergo heat-inactivation directly. The enzymes involved in carbon fixation may be damaged by high temperatures. Heat stress also has another physiological effect by inhibiting photosynthesis. Heat-shock proteins (HSP) are induced by high-temperature stress. Heat stress is also accompanied by water stress [6]. Rubisco activity is reduced and the oxygen evolving complex (OEC) of photosystem II (PSII) is damaged at higher temperature stress [27-28]. High temperatures can alter respiration, water relations, photosynthesis, membrane stability, hormone levels, and the levels of primary and secondary metabolites [29]. Lowered electron transport, damaged photosystem and activation of the glycolate pathway were observed under heat stress which was more than 12 hours [30]. High temperatures are associated with altered in crop yields and plant growth; generation of reactive oxygen species (ROS) results in oxidative stress development [31]. Elevated temperature also reduces pollen production, pollen viability and grain weight

[32-33]. Heat stress also has an impact on biomass. The biomass of maize is decreased under high-temperature stress [34]. Under warming and warming conditions, along with reduced rainfall conditions, a decreased net photosynthesis rate was observed in *H. squamate* shrub. Warming conditions appeared to reduce leaf nitrogen and phosphorus content per unit area, as well as shoot biomass production [35]. Elevated temperatures are also responsible for increasing transpiration in plants [36].

A small temperature change has a great impact on the quality of fruits, vegetables, aromatic and medicinal plants, tea and coffee. The report showed that high-temperature caused adverse effect on potatoes, vegetables, apples, mustard, wheat, peas and tea in the state of Himachal Pradesh in India, in March 2004. Approximately 20%-60% yield loss was noticed based on the crop [37]. Heatwaves and droughts contributed to crop production losses ranging from 2.2% to 7.3% from 1964 to 1990 and 1991 to 2015. This data indicates that the severity of climate change on crop production has almost tripled in Europe within 50 years [38]. Heat stress was able to reduce the number of rice grains per plant as well as grain weight, as a result, the yield was lowered [39]. Grain yield, mean grain weight, and grain number were appeared to be reduced after exposure to elevated temperatures and drought. Elevated temperatures also lead to water stress [40]. Metabolism is also affected by high temperatures. High temperatures also lowered the transcript of starch synthase in wheat endosperm [41]. Lu *et al*. investigated the expression pattern of 23 genes involved in starch biosynthesis in wheat grain under high temperatures. 22 genes among the 23 genes were found to be downregulated when exposed to high temperatures (HT) [42]. An increase in 1°C of temperature decrease around 9% yield of maize [43].

b) *Water stress*

Alteration in precipitation may cause flooding or water deficits (drought). Both are responsible for developing water stress in plants. Desiccation may alter the integrity of the membrane, leading to membrane damage. Water stress also affects photosynthesis. Closure of stomata, which may arise due to a shortage of water leads to a reduced supply of carbon dioxide, the raw material of photosynthesis. Oxygen stress is generally associated with flooding because of the limitation of oxygen due to waterlogging in the roots. The function of roots may be hampered due to a shortage of oxygen, nutrient uptake [6]. Oxidative stress is also associated with drought stress [44]. Decreased shoot growth along with lower stomatal conductance was accompanied by a 10-20% reduction in photosynthesis in *H. squamatum* under reduced rainfall (RR) conditions [35]. Drought stress also affects the total chlorophyll concentration in leaves [45].

In 2007, around 15,000 hectares (ha) of the wheat crop were destroyed by untimely rains or hailstorms in the states of Uttar Pradesh, Punjab, and Haryana in India in the Rabi season [46]. Excessive rainfall decreases crop yield and crop growth. Excessive rainfall causes a reduction in maize yield in the United States and may be one of the major causes of damage recently in the United State [47]. Excessive rainfall leads to flood situation causing a huge loss in paddy crop in South Gujrat of India [48]. Reduced wheat yields in the Northwest part of India during 2000 were analyzed. It was found that decreased rainfall in the monsoon season leads to a shortage of groundwater and surface water during the cultivation of wheat (November-March) might be one of the factors for the reduction in yield. High temperatures combined with a shortage of water play a critical role in the yield reduction of wheat [49].

c) *Biotic stress*

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Climate change is considered to enhance the susceptibility of disease in plants in several ways. Climate change is associated with increasing herbivory. Herbivory may be stimulated by 2 to 4 times in the presence of higher CO_2 levels and dry conditions, resulting in a slower growth rate [50]. When plants meet pathogens like bacteria, viruses, or insects, they cause destruction of the plant's health, leading to the generation of biotic stress. Climate change may accelerate the exposure of this pathogen to plants. A variety of defence mechanisms are activated after the response of pathogens [6]. The rising temperature may enhance insect population, leading to crop damage [46]. Drought stress also stimulates the growth of the insect community. Leaf yellowing, accumulation of osmolytes like proline and inositol may play an important role in attracting insects in drought-stressed plants [51]. The jasmonic acid pathway is considered to be a key regulator of plant defence systems to protect against herbivorous arthropods. A higher level of CO_2 can lower the jasmonic acid defence signaling pathway [52]. Biotic stress, either from plant disease or exposure to insects, may be enhanced by high- stress [6]. When Arabidopsis was exposed to 30°C rather than 23°C, bacterial growth could be increased up to 30-fold, and diseased associated chlorosis was enhanced. A pathway, a defence mechanism against pathogen was found to be compromised at higher temperatures like 30°C. This result indicates that higher temperature may significantly increase the susceptibility of plants to bacterial attack [53].

Pollination is considered to be an essential mechanism for the plant's reproductive process. Pollinators like bees play a significant role in pollination. Pollination is also an important parameter for global crop production [54]. The plant uses several parameters like the colour of flowers, size, and shape for attracting pollinators. Climate change has a great effect on pollination by affecting pollinators. Warm temperatures were proposed to reduce floral signal, thereby lowering accessibility to pollinators. When the temperature rose from 21°C to 26°C, bumblebees visited flowers four times less frequently. This study indicates that the pollination rate may be reduced because of lower flower visitation [55].

d) *Elevated CO_2 level related stress*

Under elevated CO_2 levels both positive and negative effects can be observed. The response of plants to internal CO_2 levels varies. Photosynthesis and CO_2 fixation are increased, whereas photorespiration, transpiration, and stomatal conductance are decreased in the presence of CO_2 levels [7]. Elevated CO_2 levels may be responsible for more insect damage in crops by providing more sugar to insects [46]. Under the elevation of CO_2 levels nutrients like calcium, phosphorus, iron, zinc, potassium, and protein are found to be reduced levels in many crops Although carbohydrate levels are increased in plants under higher concentrations of CO_2, the level of nitrogen is decreased leading to disbalance in the C-N ratio [56]. Stomatal density was found to be reduced at a higher level of CO_2 [57]. Soybean reproductive development was slowed overall at high CO_2 levels [58].

High CO_2 levels enhanced rice yield in India, in japonica and hybrid cultivars [59]. Protein concentration was found to be decreased in rice when it was exposed to higher CO_2 levels [60]. Ujiie *et al*. indicated that nutrients like N, S, Mn, and Zn were observed to be lowered in the polished grain of rice by 13.5%, 12.6%, 20.5% and 5.9% respectively at elevated CO_2 levels. Elemental content like Mg, S, Mn of the plant body was also decreased by 28%, 21%, 53% respectively, under enrichment of CO_2 in the plant body [61]. Several factors have been identified as being responsible for the decrease in nutrients in the CO_2-enriched atmosphere. Suppression of shoot nitrate assimilation in various C_3 plants occurred at the elevation of CO_2, resulting in an effect on growth [62]. Plants generally accumulate secondary metabolites when plants are under stress [63]. Total phenolic content in *Zea mays* was increased by 5.13% when the plant was exposed to a higher level of CO_2 [64]. Vary *et al*. [65] concluded that plant-pathogen interactions might be significantly affected by acclimation to higher CO_2 over upcoming decades. Susceptibility to pathogens like *Fusarium verticillioides* was increased when maize was exposed to a high level of CO_2. The combined effect of elevated levels of CO_2 and drought made more susceptible to the proliferation of *Fusarium verticillioides* [66].

D. *Species diversity, richness change*

Global climate change not only affects plant physiology or biotic interactions but also affects diversity, species richness, leading to a disbalance in the function of the ecosystem. Increasing soil temperature contributes to reducing plant α-diversity. Plant species richness is also reported to decrease in warmer habitats [67]. Increased rainfall is responsible for the reduction in diversity [68]. Reduction in water availability may decrease plant diversity [69]. The increased CO_2 level is expected to be involved in the reduction of plant species diversity, and the increased CO_2 level is expected to be involved in the reduction of plant species diversity [68].

I. *Modifications occurring in soil health*
a) *Stress in soil including salinity stress*

Variability in climate has a direct or indirect, permanent or periodical effect on soil structure and function. As a result, plant growth and physiology are also affected by soil stress related to climate change. As rainfall decreases the rate of soil erosion is observed to be lower. Whereas, intensified rainfall causes enhancement in soil erosion [70]. Increased atmospheric temperature generally causes a rise in soil temperature [71]. Salinization in soil generally occurs with the intrusion of seawater [70]. In addition, reduced rainfall or higher evaporation makes the soil saltier [72]. Reduction in crop production occurs if it is grown in a saline environment [73]. Salinity causes a reduction in leaf area and dry matter content [74]. Plant ionic balance is affected because of more generations of ROS by salinity stress. Nutrient uptake and disruption of the membrane are also disturbed due to the impact of salinity. Photosynthesis, transpiration, stomatal conductance, growth, and germination have been affected due to salinity [75]. Reduced leaf chlorophyll concentration was observed when plants were exposed to salinity due to less uptake of Magnesium (Mg) and nitrogen or inhibition of enzymes used for photosynthesis [76].

b) *Stress on soil microbes*

Plant-soil microbe interaction and soil microbe-microbe interaction play a potential role in plant growth and survival. The plant's roots are associated with bacteria and fungi. Soil microbe interaction is also affected by climate change. The relative abundance of soil bacteria is altered when the temperature is increased for a long time [77]. Castro *et al*. observed that a high temperature increases fungal abundance. Bacterial abundance was reported to be augmented when exposed to elevated temperatures and high levels of CO_2. Alteration in precipitation changed the relative abundance of proteobacteria and acid bacterial and fungal community composition. This result concludes that although climate change has an impact on changing bacterial and fungal overall abundance, an alteration in precipitation may have a significant

effect on community composition [78]. According to another study, a bacteria-dominated soil microbial community was observed under higher temperatures [79]. Soil moisture gets reduced with warming [68]. One dominant member of the soil fungal community may be shifted to another one with little change in soil moisture availability. Whereas, the same bacterial community is observed in this case [80]. As soil microbes have a strong impact on plants, alteration in soil-microbe-plant interactions could have a significant role in the plant community and ecosystem [81]. Soil moisture may be increased by a higher level of CO_2 and precipitation, however, warming and drying the moisture content. The effect of drying and warming on soil moisture can be mitigated by elevated levels of CO_2 [82]. This indicates multiple climate change factors are operating simultaneously to interact with each other. This may be a synergistic or contradictory effect on the microbial population.

Mycorrhizal interaction: stress-adaptation strategy?

Mycorrhiza (literally, fungus root) is a root infected fungus. Association between plants and mycorrhiza was first considered by Frank [83]. Around 80% of terrestrial plants have been reported to be associated with mycorrhizal interaction [84]. Reports showed that, evolution of AM symbiosis occurred earlier in land plant, followed by ectomycorrhizal association and ericoid mycorrhiza. Evolution of ectomycorrhizal and ericoid mycorrhiza occurred 100-200 million years and 80 million years ago respectively [85]. Association of AM with land plant took place 450 million years ago. Some fern having longer root hair may be the reason of less dependency with mycorrhiza. Climate change, soil complexity, and increasing habitat are major factors for evolution of later type mycorrhizal association [86]. Mycorrhizae form mutualistic relations with plants. Both plants and fungus are benefitted.

Generally, mycorrhizas are classified into two types – (i) ectomycorrhizae and (ii) endo mycorrhizae. In ectomycorrhiza, mycobiont is found externally, outside of the root tissues. Around 10% of the plants are associated with ectomycorrhiza. Ectomycorrhiza is generally highly branched and short in structure. More than 5000 species of ectomycorrhiza are found in the world. Most of the fungi belong to Basidiomycota. Most genera of plant roots are associated with ectomycorrhiza. Nearly every angiosperm family and most gymnosperms are associated with endomycorrhiza. Hyphae of the endomycorrhiza generally are associated with the cortical cells of the host root very closely. Vesicular arbuscular mycorrhiza (VAM) or arbuscular mycorrhiza (AM) is a specialized endomycorrhiza, found in almost 70% of all plant families. The hyphae of VAM develop a highly branched 'treelike' structure, called arbuscles, by growing between and into the cortical cells of the roots. Sometimes VAM develops vesicles either between or within host cells. Arbuscules and vesicles are effective structures to provide a large surface area for absorption of nutrients and exchange of nutrients between the host plant and mycorrhiza. After the colonization of AM, root morphology may undergo little change. In addition to, another mycorrhiza, ectomycorrhiza has both ectomycorrhiza and endomycorrhiza. Symbiosis is similar to ectomycorrhiza. Orchid mycorrhiza forms roots of the plant in the Orchidaceae family. Imperfect fungus Rhizoctonia generally forms orchid mycorrhiza. They are generally epiparasitic and formless stable associations [6-7].

Mycorrhiza forms a mycorrhizal network with two or more plants of the same or different species. Hence, multiple plants along with multiple fungi may interact with each other, resulting in proper fitness for the plants. Both AMF and EMF may form a mycorrhizal network [87]. Plant community structure and composition are also the community of AMF [88]. Colonization of mycorrhiza may be augmented by mycorrhiza helper bacteria (MHB) [89].

a) *Heat stress tolerance by mycorrhizal interaction*

Plants colonization with AMF interaction can be grown easily under high-temperature conditions through nutrient and water absorption, efficiency in photosynthesis, and protection from oxidative damage by AMF [90]. The minimum rate of leaf browning was observed in mycorrhizal plants under heat stress conditions, whereas, non-mycorrhizal inoculated plants exhibited a high rate of leaf browning of 80%-100%. The growth of plants and mineral nutrients were found to be increased under mycorrhizal action. Heat stress was alleviated by AMF through enhanced antioxidative activity [91].

b) *Drought tolerance by mycorrhizal interaction*

Mycorrhizal interaction (AMF) is a well-established strategy to have a significant role in drought tolerance. Mycorrhizal hyphae provide an enhanced surface area to absorb water [92]. Mycorrhizal plants exhibit a higher transpiration rate than nonmycorrhizal plants by several mechanisms. These include- less resistance to water flow in roots and shoots, increased stomatal conductance, increased use of water as leaf area increases [7]. AMF results in increased transpiration rate and stomatal conductance [93]**.** Hence, water stress can be mitigated by water uptake, transpiration, and stomatal conductance. Osmoprotectant proline may be accumulated in plants following AM colonization of the roots under limiting water conditions, providing drought tolerance [94]. Proline may serve as a reservoir of energy during water stress [95]. Biomass and grain yield were found to be increased after colonization with AMF, but soil moisture content did not play a role at all here [96]. Production of antioxidant compounds is associated with AMF colonization to combat oxidative stress induced by water deficiency. In addition, phytohormones like auxin, salicylic acid, jasmonic acid, ABA, ethylene, and cytokinins are produced in AMF-colonized plants under drought stress. AMF also encourages the development of adventitious roots for uptake of water and nutrients to mitigate drought stress [92]. AMF was also able to enhance root hair density and length in trifoliate orange in drought conditions to provide an increased surface area for absorption of water and nutrients [97]. Mycorrhiza inoculated plants showed a higher level of SOD, leaf catalase compared with non-mycorrhizal plants under drought conditions [98]. Hea *et al.* [99] concluded that under drought conditions total plant biomass was enhanced by 48.6% when AMF was associated with trifoliate orange. However, in the case of well-watered conditions, total plant biomass was increased up to 11.9% when inoculated with AMF.

c) *Biotic stress tolerance by mycorrhizal interaction*

Colonization with mycorrhiza decreases biotic stress associated with pathogens like Fusarium, Phytophthora, and Verticillium. Enhanced pathogen resistance may result from increased nutrition, generation of phenolics or isoflavonoids, higher biomass production, providing a mechanical barrier for invasion of root pathogens, and having antibiotic properties of ectomycorrhizal fungi [7]. An enhanced level of compounds has been observed with inoculation with different types of AMF, *A. lingula* and *C. tunicate* in the bark of the stem of *Libidibia ferra*. In comparison to the control, flavonoids concentrations increase by approximately 236% and 186%, respectively, after treatment with *A. lingula* and *C. tunicate*, respectively [100]. Flowering can be promoted by ericoid

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mycorrhizal fungi [101]. The report indicated that mycorrhiza also can increase flower size if the light is sufficient [102].

d) *Salinity tolerance by mycorrhizal interaction*

The generally hot and dry conditions lead to soil more saline. Mycorrhizal interaction with plants is quite able to resist salinity stress. Stimulating uptake of nutrients and maintaining ion balance, accumulation of proline, betaines, abscisic acid, and fructose are good strategies to mitigate the saline stress by AMF [103-104]. AMF was able to enhance protection of *E. Mackie* from moderate salt concentrations (100 and 150 mM) by increasing absorption of nutrients, stimulating photosynthesis, and activation of antioxidant enzymes [105]. AMF was proposed to ameliorate saline stress in tomatoes by reducing oxidative damage and accumulation of proline, and soluble sugar [106]. AMF also mitigates salt stress by decreasing hydrogen peroxide, lipid peroxidation, and electrolyte leakage in the cucumber plant [107].

e) *Photosynthesis and upliftment of the nutritional status*

Ectomycorrhizal plants generally appear to have a greater photosynthesis rate in comparison to nonmycorrhizal plants. Increased photosynthesis in plants with mycorrhizal colonization may be the result of the availability of inorganic phosphate in the leaves, increment of specific leaf area, or increased specific leaf phosphorus. Higher carbon assimilation occurs in plants that are heavily colonized with mycorrhiza than in non-colonized plants [7]. Mycorrhizae are thought to encourage absorption by increasing the root surface. This can be done because of the passing of hyphae having a diameter of 1/10 the diameter of roots in small soil pores. The affinity of the root for phosphorus is increased by the presence of mycorrhiza, resulting in faster movement of phosphorus from the roots. Mycorrhiza has been reported to translocate amino acids from acidic, organic soils and is responsible for assimilation by plants. Not only mycorrhizae are important for the absorption of P or N but also improve in the accumulation of Cu, and Zn [7]. Chlorophyll a, chlorophyll b, Chlorophyll a +b and carotenoid level were found to be increased in plants inoculated with AMF in comparison to non-inoculated plants. The net photosynthetic rate was also significantly enhanced by the presence of AMF [108].

f) *Enrichment in diversity, richness*

Mycorrhiza is known to have a crucial role in plant diversity and community composition. Mycorrhiza regulates plant population, community, and plant coexistence by influencing seed dispersal and seedling establishment, as well as intraspecific and interspecific competition [109]. Plant diversity is enhanced by AMF colonization and plant community composition is also influenced by AMF [110-111].

g) *Mycorrhizal interaction with soil microbiota*

Mycorrhiza can interact with other soil microorganisms, leading to various effects, including competitive or mutually beneficial effects [95]. The rhizosphere microbial population is different from the mycorrhizal inoculated plant from the non - inoculated plant, indicating that mycorrhiza has a role in the soil microbial community [112].

Molecular mechanism of stress-adaptation strategy by mycorrhiza

There are several strategies for combating different abiotic and biotic stresses associated with climate change. Different biomolecules, including carbohydrates, proteins, or amino acids that are produced in mycorrhiza, can alleviate stress. In addition, secondary metabolites and phytohormones also participate in mitigating the stress. The basic mechanism of stress tolerance in plants mediated by mycorrhiza is depicted in (Fig 2).
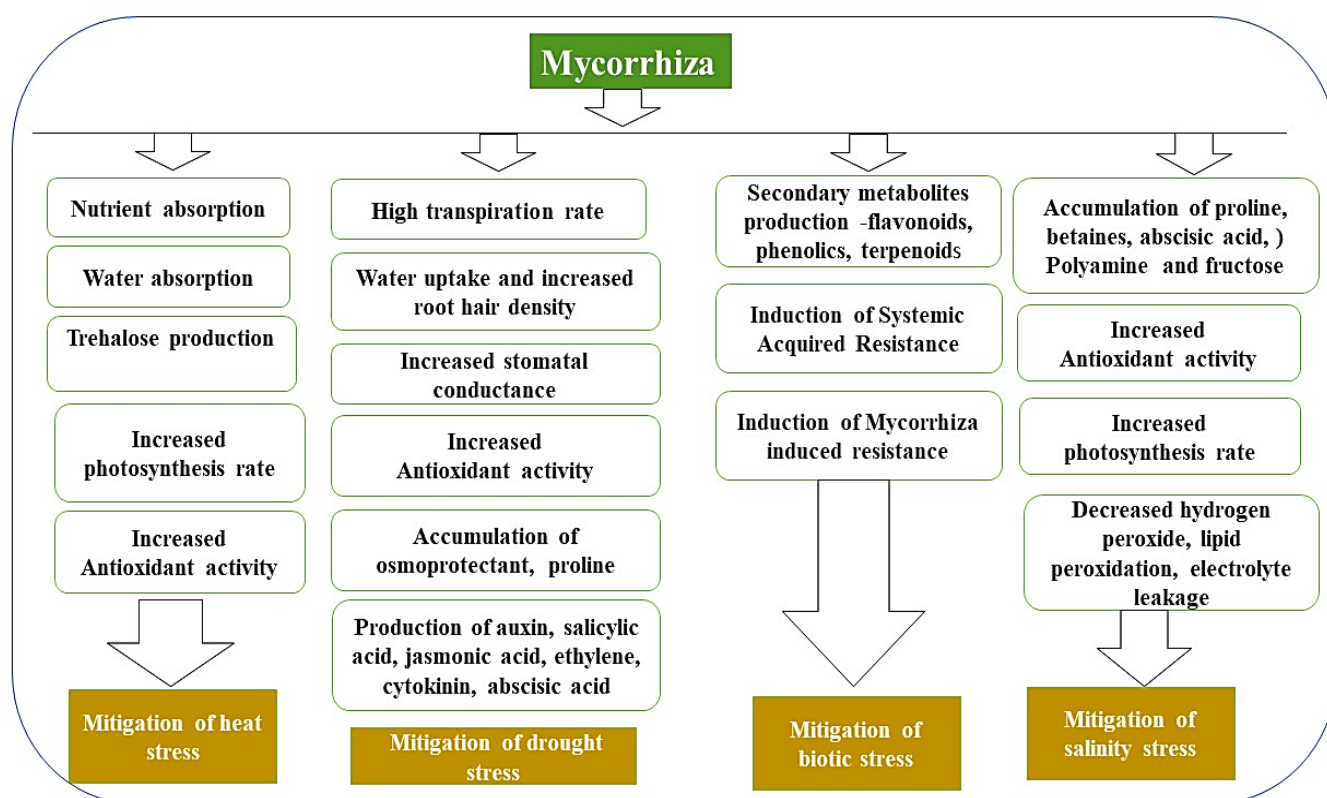

Fig 2 Basic mechanism of stress tolerance in plant mediated by mycorrhiza
Mycorrhiza can mitigate heat stress, drought stress, biotic stress, salinity stress through various ways in plant by improving physiological, morphological condition

i) *Trehalose*

Trehalose is a nonreducing disaccharide having two molecules of glucose joined by α,α-1,1-glycosidic linkage, widely found in fungi. The concentration of trehalose is increased after the colonization of mycorrhizae [113]. Trehalose can inhibit the formation of an aggregation of denatured proteins. It also suppresses protein denaturation in vitro at high temperatures [114]. A higher level of trehalose can be found in cells under heat or chemical stress. The normal concentration of trehalose is observed after stress is over. This data suggests that trehalose of AMF could have a role in the prevention of heat stress [115].

ii) *Proline*

Accumulation of proline has been associated with AMF plants to diminish stress [103]. Proline, low molecular weight compounds cause osmotic adjustment by stabilizing proteins and antioxidant enzymes; scavenging reactive oxygen species (ROS) and maintaining redox balance. In response to osmotic stress or drought stress, accumulation of proline occurs in plants [116]. Elevated proline levels were observed in soybean plants inoculated with AMF compared to non-AM plants at various salinity conditions [117].

iii) *Antioxidant system*

The antioxidant system is another mechanism to protect cells from oxidative damage produced by abiotic stress related to climate change. One of the key factors in reducing ROS accumulation is increased expression of antioxidant enzymes in mycorrhizal plants under heat stress conditions. The activity of SOD was found to be significantly increased in shoot and root, and ascorbate peroxidase was increased when *Asparagus officinalis* L. was exposed to heat stress after inoculation with AMF [91]. According to a study conducted by Hea *et al.* [99] activities of leaf Fe-SOD, Mn-SOD, Cu/Zn SOD, CAT and peroxidase (POD) were thought to be significantly higher by 20.6%, 25.1%, 56.5%, 17.5% and 17.4% respectively in plants inoculated with mycorrhiza under drought condition. Inoculated mycorrhizal plant induced upregulation of the genes of PTFE-SOD, Pt Mn-SOD and PtCu/Zn- SOD under drought conditions. Activities of catalase (CAT), as well as SOD, were appeared to be significantly increased in *Zea mays* when inoculated with AMF under drought [98]. AMF was reported to lower salt stress by reducing hydrogen peroxide and lipid peroxidation by 37.52% and 21.20% in cucumber [107]. Hashem *et al.* indicated that malondialdehyde (MDA), the end product of lipid peroxidation was decreased by 35% when symbiosis with AMF in comparison to control plant [118].

iv) *Polyamine*

Polyamines are polycations that are low molecular weight signaling molecules in plants [119]. Strong salt tolerance can be observed in plants having a good source of polyamine [120]. Protection and preservation of the structure and function of a cell may be obtained by polyamine and its derivatives under stress conditions [119]. Polyamine pools may be used by AMF for plant survival in saline soil. Total free polyamine is higher in plants inoculated with mycorrhiza than in non-mycorrhizal plants. Polyamine also plays a crucial role in root development under salty conditions. This may be one of the strategies to combat salt stress [121].

v) *Phytohormones and Systemic Acquired Resistance (SAR)*

Phytohormones have a crucial role in helping the plant to adapt to stress conditions by inducing various mechanisms. The phytohormones like abscisic acid, jasmonic acid, ethylene,

auxin, salicylic acid, and cytokinin induced by AMF have been observed to have a protective role in drought stress [92]. Abscisic acid, the stress hormone, protects plants from stress by mediating hydraulic features via the expression of aquaporin [122]. Jasmonic acid and salicylic acids (SA) were also higher under salt stress when the plant was colonized by AMF [107]. SA can augment the activity of antioxidant enzymes in plants to ameliorate the abiotic stress of plants [123]. The concentration of pathogenesis-related protein (PR) that has antimicrobial properties can be stimulated by SA [124]. Phytohormones may have an impact on proline metabolism for regulation of salt tolerance, ABA has a role to synthesize L-proline from glutamic acid [119], [125]. Auxin also plays an important role in drought tolerance. Liu et al. reported that AMF (*Funneliformis mosseae*) was thought to induce IAA level in the root of trifoliate orange (*Poncirus trifoliata*) seedlings under drought conditions. Under drought conditions, AMF (*Funneliformis mosseae*) significantly increased the density, growth, and diameter of the root hair in that plant. It is known that root growth is regulated by auxin levels. Hence, an elevated level of IAA might have a role in root hair growth, leading to plant fitness [126]. SAR is long-lasting resistance to the second infection in plants through secondary metabolites, mainly salicylic acid [127-128]. Methyl salicylate (MeSA), a phenolic and volatile compound generated from SA, has been thought to be involved in SAR and plant communication [129-130].

vi) *Secondary metabolites Phenolic compounds, terpenoids*

Defense mechanisms are largely dependent on secondary metabolites. Phenolic acids, which are known as signalling molecules, are the main polyphenols in plants [131]. Phenols are important for the protection of ROS, contributing to stress tolerance [132]. Studies have shown that AMF can increase phenolic compounds in plants [133]. Polyphenol content was enhanced after inoculation with mycorrhiza under saline conditions [134]. Terpenoids also have a crucial role in mitigating abiotic and biotic stress. AMF is known to enhance the production of various terpenoids, including monoterpenes, triterpenoids [135].

vii) *Enhancement in photosynthetic efficiency*

Increased photosynthesis may be due to the high level of chlorophyll content and enzymes like rubisco significantly ameliorating the stress condition. The pigments associated with photosynthesis chlorophyll a, chlorophyll b and carotenoids were reported to be higher in AMF symbiosis plants by 12.8%, 40.2% and 29.1%. Rubisco, one of the prime enzymes for photosynthesis, was also appeared to be increased by 10% in AMF-inoculated plants [118].

viii) *Mycorrhiza induced resistance (MIR)*

MIR can share the characteristics of SAR [136]. Jasmonic acid and its derivatives have a significant role in abiotic stress and biotic stress [137]. Plant-mycorrhizal interaction is capable of inducing a systemic response. Mycorrhiza *Piriformospora indica* contributed to generating a systemic response in *Arabidopsis* through jasmonic acid [138].

Diversity and function of mycorrhizae under abiotic stress caused by climate change

Climate change may affect the community and functions of mycorrhizae. High temperature, high CO_2 levels, flooding, drought, alteration in rainfall may have direct or indirect effects.

High CO_2 level

High CO_2 levels have a strong influence on mycorrhiza. Phosphorus uptake has been increased under the CO_2 enrichment atmosphere in the mycorrhizal plant [139]. The report showed that total mycorrhizal foot length is increased from 3.4 to 6.1 m per plant under higher CO_2 levels [140]. According to another report, the combination of AMF and higher CO_2 level encourage biomass production and photosynthesis as well as the generation of sugar, amino acids (essential and nonessential), unsaturated fatty acids, volatile compounds, flavonoids, and phenolic acids in *T. vulgare*. Hence, functional food value may be improved after inoculation with AMF under elevated CO_2 levels [141]. Hence, effective integration of elevated CO_2 levels and AMF may be one of the most eco-friendly approaches to agriculture in the near future.

High temperature

Various effects have been observed at high temperatures in mycorrhizal diversity and colonization. Warming can cause positive, negative, or neutral effects on AMF colonization. No constant response has been observed in temperature variation [142]. At higher temperatures, the internal and external mycelium of AMF, *Planceolota* grew faster [143]. The ectomycorrhizal fungal community was altered under warming, reduced rainfall, and a combination of warming, reduced rainfall and combination [35].

Alteration in rainfall/water availability

Rainfall also impacts mycorrhizal colonization. Contrast results have been observed in a variety of rainfall conditions. Soil water status influences the colonization of AMF. Reduced AMF colonization was observed under the surplus of water treatment. [144]. The mycorrhizal rate on the root of barley (*Hordeum vulgare* L) was inversely proportional to the average annual rainfall [145]. The composition of AMF may be directly or indirectly affected by changes in water availability. Changing the pattern of rainfall may contribute to alteration in plant community of above ground, diversity, productivity resulting in an indirect effect on AMF [146]. Soil moisture becomes one of the regulators of assembly in the AMF community. If the soil moisture is around 15-20%, a high diversity of AMF has been observed [147]. Flooding conditions may develop oxygen deficiency, leading to anaerobic conditions. Hence, colonization of AMF in flooded soil was observed to be less because the anaerobic condition is not suitable for the development and survival of AMF [95].

Mycorrhiza in agriculture sustainability

i) *As biofertilizer*

Biofertilizers are organisms that are used in increasing soil fertility. They provide several advantages over chemical fertilizers. They are not only eco-friendly but also provide a healthy environment for plants [148]. Another attractiveness of AMF is low cost [149]. There are several reasons for using mycorrhiza as a biofertilizer. Mycorrhiza can augment plant growth and crop yield by providing higher branching of plant roots. It increases the surface area to absorb nutrients and water. Nutrients like phosphorus, nitrogen, calcium, magnesium, potassium, zinc, and copper are absorbed with greater efficiency in plant-associated with mycorrhiza. In addition, the mycorrhizal association also stimulates the photosynthesis and metabolism of the plant [150]. Mycorrhiza is also known to improve phosphorus availability [151]. Mycorrhizal fungi, along with plant growth-promoting rhizobacteria (PGPR), are mainly found in the rhizosphere, a region associated with plant roots and microorganisms in the soil. They are involved in stimulating plant growth, enhancing yield and resistance to stress [152].

Industry based on mycorrhiza as inoculants are growing rapidly. 68 products from 28 manufacturers across Europe, Asia, and North America were investigated by Baisru *et al*. They observed that 100% of products were from the Glomereceae family, and AMF accounted for 44% of the sampled products, and the rest were mixed with other active ingredients. Single species of AMF was around one-third. Nutrients benefits were obtained from around 84% of the products [153]. More than 50% improved crop yield was observed when farmers used chemical fertilizer along with mycorrhiza on asparagus. This resulted in an increased income of farmers by 61% compared to only chemical fertilizer [150]. Mycorrhiza also has a significant role in biological nitrogen fixation by interacting with other biofertilizers and chemical fertilizers. Mycorrhiza and endophytic *H. seropedicae* along with chemical fertilizer are effective strategies for rice grain production, and growth by enhancing nutrient uptake and root growth [154]. AMF has a critical role in intercropping systems. Co-culture with AMF and rhizobium in a soybean/maize intercropping system has been shown to increase yield by increasing soybean nitrogen fixation efficiency and enhancing nitrogen transfer from soybean to maize [155].

ii) *Improving soil health*

Glomalin-related soil protein (GRSP) can be produced by the hyphae of AMF. It has many properties that are key factors for mycorrhizal mediated soil fertility. It is involved in soil aggregation [156]. Generally, glomalin, a glycoprotein glue-like structure, plays a critical component in soil aggregation. Soil particles get together to form soil aggregates in the presence of glomalin-related soil protein [95]. It stimulates polycyclic aromatic hydrocarbon availability in soil [157]. AMF, along with organic matter, enhances the soil quality [158].

iii) *As bioinoculant / co-inoculation with other bacteria*

Recently, fungal inoculants have received significant attention. The use of mycorrhiza-based inoculants like commercial AMF inoculants is increasing day by day in the field of agriculture [159]. In the case of potato production, AMF has been found to increase crop yield [160]. AMF species, *Rhizophagus irregularis* improved cotton growth and yield by increasing P concentration, inducing the expression of a specific phosphate transporter family of genes, and increasing photosynthetic rate [161]. AMF has been co-inoculated with other bacteria to improve crop yield. Synergistic effect of AMF of *Rhizophagus intraradices* and Phosphate solubilizing bacteria *Klebsiella variicola* were reported to augment sunchoke growth and inulin content in pot experiment [162]. Nacoon *et al*. [163] also reported that AMF strain *Rhizophagus intraradices* and Phosphate solubilizing bacteria *Klebsiella variicola* enhanced growth and production of *Helianthus tuberosus* under field conditions. Combined effects of plant growth promoting bacteria (PGPR) rhizobacteria and AMF also have been observed to contribute beneficial role on plant growth and yield. Consortium of PGPR-rhizobia and mycorizha stimulated not only Na, K, P, Ca, N content in shoot but also sugar and protein content in crop, resulting in improving crop nutrition and productivity [164].

iv) *As biocontrol/ bioprotectant*

Protection from soil-borne diseases has become common practice in sustainable agriculture. Mycorrhizal inoculation is known to protect host plants from pathogens. Various strategies

mediated by mycorrhiza have been proposed to protect against pathogens like fungi, nematodes and viruses. Plant tolerance may be carried out by enhanced nutrient absorption and alteration in root morphology. Other options for protecting plants from pathogens include competition for nutrients and space between mycorrhiza and the pathogen, induced systemic response (ISR), and altered rhizosphere interaction [165]. Mould disease induced by air borne-fungal pathogen *Cladosporium fulvum* in tomato was significantly alleviated by mycorrhiza *Glomus mosseae* via stimulating net photosynthesis rate, total chlorophyll content, activities of superoxide dismutase, peroxidase and reducing H_2O_2 and malondialdehyde level [166]. Jasmonic acid (JA) mediated defence was accounted for resistance to nematode [167].

v) *Improving food quality*

Mycorrhiza has a role in improving food quality by enhancing gene expression. The total amino acid concentration of tea leaves was found to be significantly augmented by AMF. AMF also increased the content of total soluble protein, glucose, sucrose, tea polyphenol and flavonoid content of leaf of tea plant [168]. Cu, Fe, anthocyanins and carotenoids were increased in lettuce plants inoculated with AMF [169].

vi) *Restoration of land*

Mycorrhiza has an important role in the restoration of land. Several mechanisms have been reported in this context. Mycorrhizal inoculated plants help in plant establishment. Fungal hyphae are able to form water stable-aggregate. In this way, improvement in quality of soil as well as biological, chemical, and physical properties has been observed [95].

vi) *Crop rotation and mycorrhiza*

Crop rotation plays a critical role in sustainable agriculture because it helps with nutrient supply. The AMF community can be affected by crop rotation and selection of crops. Growth and yield of the following crop may be influenced by preceding crop. High colonization of mycorrhiza has been observed in less dense roots [95]. Higher AMF colonization was observed in wheat after chickpea rotation than canola rotation [170].

vii) *Weed control*

Weeds play an important role in reduction of crop production. Herbicide application is one of the methods to eradicate the weeds. But uses of chemical should be less in order to maintain good environment. Hence, alternative sustainable approach may be the uses of biological agents which has negative impact on growth of weed in the field. Veiga *et al.* [171] showed that AMF, *G. intraradices* reduced biomass of the weed species significantly.

Knowledge gap and potential developmental field related with plant mycorrhizal interaction

Various techniques and methods are available to study plant mycorrhizal interaction in response to climate change. A multi-omics approach, as well as transcriptome and proteome analysis, have been widely used to investigate plant mycorrhizal interaction. Mycorrhizal colonization causes alteration in gene expression in root of the host plant. Next generation sequencing techniques is effective method to explore the interaction. Differentially expressed genes were observed in the root of sunflower at early and late phase of inoculation with mycorrhiza *R. irregulare* compared with control [172]. Several evidences have been exhibited that mycorrhiza utilize plethora of molecules to combat the biotic

and abiotic stress. There are various primary and secondary metabolites identified after inoculation with mycorrhiza for providing tolerance in host plant [173]. Sugar alcohol or polyol is found in plants. Polyol is involved in osmotic adjustment [174]. Mannitol is one of polyol, found in plant and fungi. Mannitol is also involved in osmotic, salt and oxidative stress tolerance [175]. Research on mannitol formation by inoculation with mycorrhiza and how does it work in response to stress has now opened up a new avenue for plant-mycorrhizal interaction under climate change condition. In this way plant glycobiology will be explored to ameliorate the effect of stress mediated by global climate change.

Micro RNA (miRNA, non-coding RNA) has tremendous effect on gene expression. Prolonged higher level of CO_2 and elevated temperature was found to regulate differentially the expression of miRNA. As a result, growth and development of plant has been affected [176]. What will be the role of mycorrhiza on the expression of climate change induced-miRNA in plants remains unresolved? Investigation may be carried out to unfold the role of mycorrhiza on the expression of climate change induced-miRNA in plants. High temperature stress may have effect on gene regulation [177]. Various abiotic stress like heat, salinity and drought causes changes in chromatin modification like DNA methylation [178-179]. AMF also has impact on DNA methylation in plants. DNA of plant's offspring can be affected by AMF [180]. The involvement of mycorrhiza in epigenetic regulation through DNA methylation in host plant to mitigate the abiotic stress related with climate change has not been unfolded properly. This field holds a very good prospect in future to understand the role of mycorrhiza on epigenetic gene regulation to combat the stress.

Application of nanotechnology is promising field for agricultural development. Mixed type effect was observed with interaction between mycorrhiza and nanoparticles. Nanoparticles may have negative, positive or neutral impact on mycorrhizal colonization [181]. More research on interaction between mycorrhiza and nanoparticle is required to open up this area for betterment of agricultural field. In response to biotic and abiotic stress, plants can take plethora of strategies. One of the such way to mitigate the heat stress is production of heat shock proteins (HSPs). Not only plant HSPs are involved in abiotic and biotic tolerance but also, they may be involved in membrane stabilization and nullifying reactive oxygen species (ROS) [182]. Whether mycorrhiza has a pivotal role in inducing the expression of HSPs is not known to us very clearly. Hence, this area is also open to research.

Climate change has a pivotal role on mycorrhizal structure. According to one report, mycorrhizal structure is affected by alteration of temperature and rainfall, rather than, elevated level of CO_2 [183]. Partially lipophilic, and diffusible signal molecule, 'Myc factor' is essential for colonization of mycorrhiza on roots [184]. Climate change including high temperature, alteration rainfall, drought and water stress may have an impact on formation and function of 'Myc factor'. It may disturb mycorrhizal colonization to the plants. This field remains unexplored till now and is open for future research.

CONCLUSION

Agriculture is the heart of mankind. It is facing a challenge to survive due to global climate change. Biological tools have become essential for the sustainable agriculture in this harsh time. Mycorrhiza is one of the most promising biological tools for this. It is an advanced and eco-friendly option. Mycorrhiza provides resistance to the plant in various ways by providing antioxidant system, secondary metabolites,

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carbohydrates and improving plant defence mechanism. As a result, plants get modified biochemically, morphologically and physiologically to combat the abiotic and biotic stress when inoculated with mycorrhiza. Mycorrhiza also has ability to improve soil quality. Hence, mycorrhiza serve as biofertilizer, bioprotectant and land restoration. Apart from this, several mycorrhizal mediated fields will be explored in the near future for agricultural benefit. The present review was a small attempt to introduce mycorrhiza as a bio-strategy in order to prevent agricultural loss in the future.

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