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Review Article

Impact of anthropogenically-disturbed environmental parameters on arbuscular mycorrhizal fungi

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Abstract

Anthropogenic activities in the last century have highly impacted our physical environment in many different ways. Burning of fossil fuels, pollution, deforestation, and production of pesticides and fertilizers have elicited climate change (global warming) and have inadvertently disturbed the ecosystem balance. Arbuscular mycorrhizal fungi (AMF) which are widely distributed in terrestrial ecosystems form a mutualistic interaction known as arbuscular mycorrhiza (AM) with the roots of most land plants. Their contribution to ecosystem functioning by regulating plant function, nutrient uptake, stress resistance, and community interactions is noteworthy. Different studies have suggested that an increase in temperature, carbon dioxide enrichment, and increased nutrient deposition in the ecosystem which is the result of imprudent human activities strongly impact the colonization, diversity, and function of AMF in the terrestrial ecosystems. This review briefly describes the responses of AMF to different climatic factors and their consequences on host plant functioning and productivity. Understanding the dynamics of plant-fungal associations in the context of global climate change will help in designing strategies to alleviate detrimental anthropogenic impacts to protect AMF diversity and consequently ecosystem functioning and its sustainability.

Keywords Anthropogenic, Arbuscular mycorrhizal fungi, Climate change, elevated CO₂ · Temperature

Introduction

The word ‘anthropogenic’ means an effect that arises as a consequence of human activity. The nature of these activities determines neutral, positive, or negative implications on the environment. Presently the biggest challenge for the human race is the global climate change caused by several anthropogenic activities. Pollution from industries, combustion of fossil fuels, deforestation, rapid urbanization, excessive use of fertilizers, habitat destruction, and excessive land use continue to threaten the earth’s environment. All these factors are contributing to an increase in carbon dioxide (CO₂) concentration levels, leading to the greenhouse effect or global warming due to a rise in temperature, formation of various secondary pollutants in the atmosphere like ozone (O₃) and change in precipitation patterns thereby resulting in global climate change. Further, excessive deposition of nitrogen (N) and phosphorus (P) from pollutants in the atmosphere also

disturbs the ecosystem functioning. Anthropogenic driven climate change will ultimately influence the physiological growth, productivity, diversity, and functioning of plants and soil microorganisms. This can potentially lead to the disruption of beneficial interactions between microorganisms and plants (e.g. mycorrhiza) which will subsequently affect the equilibrium in different ecosystems (Reichle, 2020).

The word ‘mycorrhiza’ was introduced by the scientist Albert Bernhard Frank in 1885. It is a symbiotic association between fungi and the roots of plants. It is derived from two words namely ‘myco’ meaning fungi and ‘rhiza’ meaning root. In this beneficial association, the plant provides photosynthates for fungal growth, while fungus in turn facilitates water and nutrient (P, N, sulfur (S), and other micronutrients like zinc and copper) uptake from soil and confers abiotic and biotic stress tolerance (Smith and Read, 2008). These associations are broadly classified into two types viz. endo mycorrhiza and

ectomycorrhiza. Arbuscular mycorrhiza (AM), a type of endomycorrhiza is the most prevalent beneficial association found within the roots of more than 80 % of plant species in nature. It got its name 'arbuscular' from typical dichotomously branched structures named 'arbuscules' formed in the cortical cells of the root and are sites for nutrient exchange (Smith and Read, 2008). AM has three major components: plant roots, fungal structures (amongst and within the host cells), and fungal mycelia in the soil. AM has a significant contribution to plant-microbe-soil interaction that influences the dynamics and sustainability of the ecosystems. The microbial fungi involved in this mutualistic association, called arbuscular mycorrhizal fungi (AMF), significantly influence the ecosystems by facilitating the growth of beneficial microbiota that play a key role in the augmentation of plant health and soil environment. All fungi exhibiting AM belong to the phylum Glomeromycota. They belong to ten out of eleven families present in the phylum Glomeromycota (Giovannini et al., 2020). Currently, there are approximately 343 AMF species (http://www.amf-hylogeny.com/amphylo_species.html; June 2022), and are the most widespread group of fungi interacting with plants. AMF penetrates the cortical cells of roots of almost all the plants except members of Brassicaceae and Chenopodiaceae (Giovannini et al., 2020).

AMF play a vital part in ecosystem functioning, and studies related to their response to global climate changes induced by anthropogenic activities have significant implications. AMF plays a very important role in sustaining plant biodiversity and consequently ecosystem functioning by affecting primary production, nitrogen leaching, soil aggregation, and pathogen suppression (Powell and Rillig, 2018). Abiotic stress tolerance of host plants, soil aggregation, carbon sequestration, and augmenting the phytochemicals of host plants are amongst the other benefits to the host provided by AM (Giovannini et al., 2020). AMF has been exploited commercially as a biofertilizer because of the multiple benefits they provide to the plant. Many commercial products of AMF biofertilizers are available in the market today globally suggesting that AMF can substitute chemical fertilizers for improving agricultural productivity and can help plants to adapt to different anthropogenic stresses.

Anthropogenic activities leading to different environmental disparities have been shown to significantly impact the beneficial microorganisms present in the rhizosphere (Zhenget al., 2022). Keeping in view the influence of anthropogenic activities on AMF, this review briefly explores the impact of different human-induced disturbances on environmental parameters like levels of CO₂ and O₃, temperature changes, fertilization regimes for agricultural practices, and precipitation patterns on AMF functioning w.r.t. their colonization, sporulation, community composition and diversity (Fig. 1).

Impact of anthropogenically-disturbed environmental parameters on AMF

CO₂ levels

Rapid deforestation and the burning of fossil fuels like coal and oil have led to a dramatic increase in the concentration of CO₂ in the atmosphere in the last few decades. Most mycorrhizal plants, when exposed to enhanced CO₂ concentration, show better growth as they can fix more CO₂ during photosynthesis, consequently more carbon (C) is allocated to the roots. An increase in the availability of C to roots further improves the colonization of mycorrhizal fungi resulting in better nutrient absorption and hence better plant growth (Pariharet al., 2020). Elevated CO₂ significantly increased the AMF colonization in the roots *Helianthus annuus* (Bellido et al., 2021). In a long-term field experiment (7 years) elevated CO₂ led to an increase in the density and length of extra metrical hypha (EMH) and spore biovolume (Antoninkaet al., 2011), thus indicating a positive effect on AMF growth.

Baslamet al., (2014) showed that elevated CO₂ resulted in better biomass (root, leaf, stem), increased glucose and fructose levels (stem), hemicellulose content, and a decline in the concentration of lignin in leaf cell walls leading to improved forage quality in alfalfa plants colonized by AMF. Cotton et al., (2015) studied the effect of elevated CO₂ on AMF communities present in the roots of *Glycine max*. Elevated CO₂ led to a change in the composition of AMF communities with Glomeraceae members showing more abundance as compared to Gigasporaceae (Cotton et al., 2015).

In another report, elevated CO₂ (400 ppm and 700 ppm) led to enhanced colonization by the AMF, *Rhizophagus irregularis* in *Triticum aestivum*. Plants associated with AMF also displayed increased biomass, C and N uptake, efficient N utilization, and allocation of C and N into the roots (Zhu et al., 2016b). In another report, Ashaet al., (2017) showed elevated CO₂ significantly improved AMF spore count and colonization of groundnut roots. AM plants exposed to elevated CO₂ displayed increased biomass (due to increased photosynthesis) and enhanced nutrient content (N and P). AMF communities of semi-natural grass ecosystems when exposed to elevated CO₂ (long-term exposure; >15 years) showed enhanced AMF richness as revealed by next-generation sequencing (Illumina, HiSeq; Mačeket al., 2019). Most studies support the fact that elevated CO₂ majorly improves AMF colonization, spore density, nutrient uptake, and AMF community structure.

Temperature change

According to Intergovernmental Panel on Climate Change (IPCC) fifth assessment report, more than 95% of the global

warming on earth is due to anthropogenic activities (IPCC, 2013; <https://www.c2es.org/content/ipcc-fifth-assessment-report>). In the last century, rapid industrialization and burning of fossil fuels have resulted in an increase in the levels of CO₂ and other greenhouse gases in the atmosphere, leading to global warming. An increase in the concentration of greenhouse gases leads to more heat retention and consequently a temperature rise. According to the NOAA 2019 Global Climate Summary, since 1880, there is an increase in the average rate of temperature (combined land and ocean) of 0.07°C (0.13°F) per decade, and the average global temperature increase of land and ocean surface for the year 2019 was 0.95°C (1.71°F). World Meteorological Organization (WMO; <https://public.wmo.int/en/media/press-release/wmo-confirms-2019-second-hottest-year-record>) declared 2019 as the second hottest year. This temperature change can dramatically affect the diversity, growth, and development of plants and soil microbes including AMF diversity and functioning. Hence, the study of the impact of elevated temperature on AMF and its influence on ecosystem dynamics is imperative.

Higher temperatures (20 and 26 °C) enhanced AMF colonization of *Populus angustifolia* seedlings (Kilpeläinen et al., 2020). An increase in AMF spore density and root colonization was observed in maize plants exposed to high-temperature stress. Maize plants inoculated with AMF showed better photosynthetic efficiency as compared to control plants suggesting that AMF protected the plants against the damaging effects of high temperature (Mathuret et al., 2021). A general inference obtained from these studies suggests that AMF can develop and effectively function at higher temperatures and the extent of warming can regulate AMF colonization.

Contrary to these reports higher temperature has also been shown to negatively affect AMF colonization. This was demonstrated in an alpine meadow ecosystem, where gradient warming decreased the richness of AMF species (Shi et al., 2017). In a 4-year-old *Cunninghamia lanceolata* plantation, soil warming resulted in a decline in AMF diversity and altered composition of the AMF community (decline in abundance of AMF belonging to Glomeraceae and increase in AMF of families Gigasporaceae, Ambisporaceae, Paraglomeraceae, and Acaulosporaceae) (Cao et al., 2020).

Fertilization regimes

Fertilizers form an indispensable part of agriculture. They are substances containing essential nutrients (mostly N, P, and K) and are added to the soil or sprayed on crops to improve their yield.

In order to increase the productivity of crop plants, humans are making use of fertilizers extensively. Excessive and indiscriminate use of fertilizer can have a negative impact on the environment such as acidification of soil, deterioration of

water quality, and change in soil microbial community composition. Recent investigations have also suggested that fertilizers can alter AMF colonization, abundance, and diversity (Zhu et al., 2016a; Ma et al., 2021; Table 1). In general, the studies suggest that the effect of N and P fertilization on AMF can be positive (Zhenget al., 2014; Wang et al., 2020) or negative (Zhu et al., 2018). Different reports showing the impact of N and P enrichment on AMF have been discussed in the following section.

Table 1. Impact of fertilization regime on various aspects of AMF

Fertilization regime	Impact on AMF	Reference
Nitrogen fertilizer	Positive impact	
	Increased colonization	Weber et al., (2019); Wang et al., (2020)
	Increased AMF diversity	Zheng et al., (2014)
	Negative impact	
	Decreased colonization	Chen et al., (2017)
	Decline in AMF diversity	Williams et al., (2017)
	Decline in spore density	Antoninka et al., (2011)
	Decline in hyphal density	Weber et al., (2019)
	Decline in AMF abundance	Chen et al., (2017); Jiang et al., (2018)
Phosphorus fertilizer	Negative impact	
	Decreased colonization	Ortas and Islam (2018)
	Decline in spore density	Isobe et al., (2008)
	Decline in hyphal density	Chen et al., (2014)
	Decline in AMF abundance	Chen et al., (2014); Maitra et al., (2021)
N-P fertilizer	Positive impact	
	Increased spore abundance	Wang et al., (2018)
	Increased hyphal length	Wang et al., (2018)
	Negative impact	
	Decline in AMF abundance	Liu et al., (2012)
Decline in AMF diversity	Liu et al., (2012)	

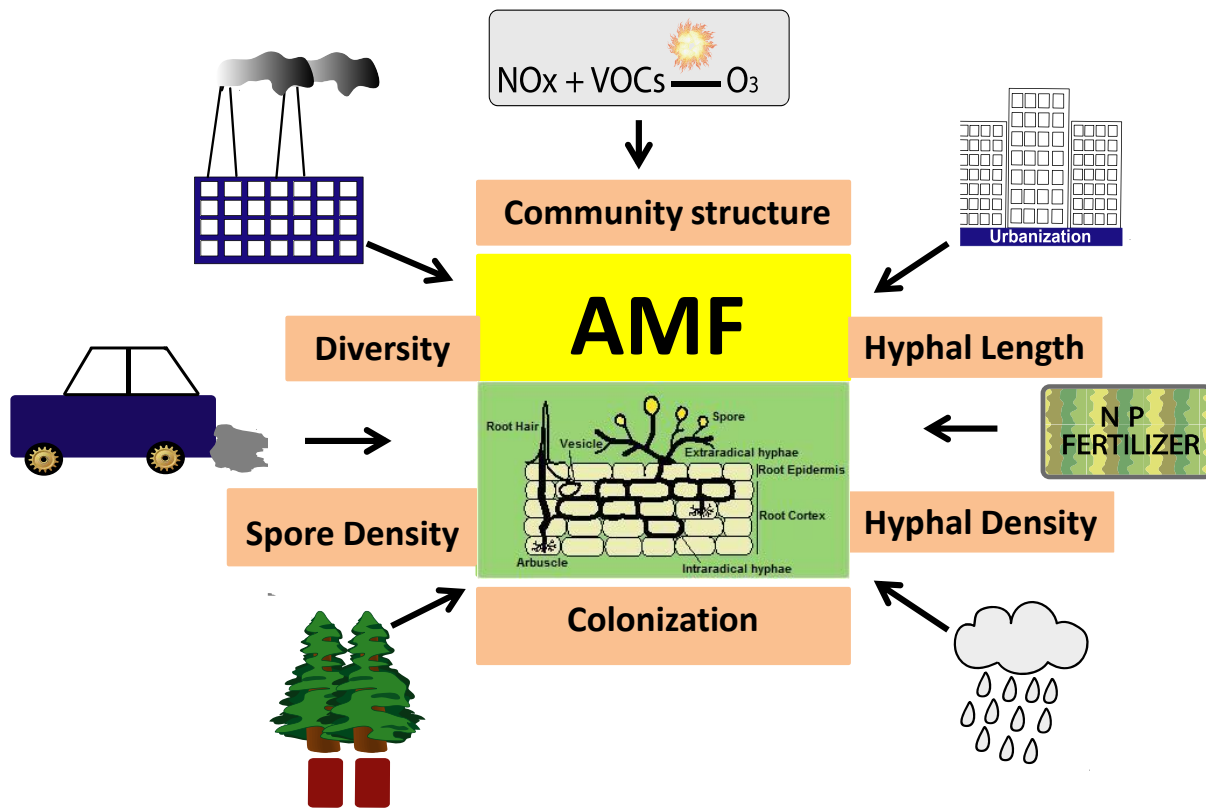


Fig. 1 Impact of different anthropogenic activities on phenotypic traits for hyphal length/density, spore density, colonization of Arbuscular Mycorrhizal Fungi (AMF). VOCs volatile organic compounds; NOx nitrogen oxides.

Nitrogen fertilization

Nitrogen is the most abundant element present in the atmosphere and is an essential nutrient required for the growth and development of all living organisms. It is predicted that to meet the rising food demands of a rapidly growing population, the manufacturing of N fertilizer needs to be increased. However, mismanaged and excessive use of N-based fertilizers results in N pollution which has detrimental environmental impacts. Excessive nitrogen fertilization leads to an imbalance in the nitrogen cycle, altered biodiversity, soil acidification, and pollution in both terrestrial and aquatic ecosystems. Studies have also shown that N enrichment alters the functioning of forests AMF which, in turn, can affect soil microbial community composition and ecosystem functioning (Lilleskovet al., 2019).

Antoninkaet al., (2011) suggested that N fertilization leads to a decline in the AMF spore abundance. Nitrogen fertilization significantly changed the AMF species composition in both soil and plant roots in the temperate steppe (Chen et al., 2014). A decrease in AMF diversity with an increase in N fertilization was observed in the soils of different sites (with N and P fertilizer) assessed. Using isotope labeling technique, enhanced carbon distribution by barley plants to AMF was observed, while the plant, in turn, received very less amount of P, suggesting a change in nutrient exchange pattern (Williams

et al., 2017). In another report addition of N negatively impacted AMF colonization, abundance, and richness (Chen et al., 2017). Nitrogen fertilization also altered the composition of the AMF community, reduced abundance, and shifted AMF from mutualism to parasitism (Jiang et al., 2018). There are also reports suggesting positive effects of N fertilization on AMF. The optimum level of N, when supplied to the wheat crop, enhanced AMF colonization in the roots (Wang et al., 2020) and increased AMF richness and diversity (Zhenget al., 2014). N fertilization also changes the AMF biomass allocation, enhances colonization in the roots and decreases the density of hyphae (Weber et al., 2019).

P fertilization

Phosphorus is another beneficial element required for optimal development and yield in plants. Fertilizers rich in essential nutrient P are termed P fertilizers. Currently, P fertilizers are also anthropogenically mobilized in the environment for improving plant yield. Excessive mobilization of P in the soil or water can also have detrimental effects like change in microbial diversity, eutrophication, and decline in the bioavailability of essential nutrients like zinc, iron etc. (Bindrabanet al., 2020). Also, fertilization with P has been shown to impact the functioning of AMF in different ways. Studies have indicated that increase in P concentration resulted in decline in spore density and AMF root colonization (Isobeet al., 2008). Application of P in a temperate steppe led

to decline in AMF colonization and hyphal length density (Chen et al., 2014). Study of long-term effect of P fertilization on AMF showed that increased P concentration resulted in reduced C allocation from plant to AMF (Williams et al., 2017). A decline in root colonization by AMF maize (Ortas and Islam, 2018) plants, when crop lands were supplemented with P fertilizer. Further, composition of AMF communities was regulated by P fertilization indicated by a decline in relative abundance of the members of Glomeraceae family in subtropical forests of China (Maitra et al., 2021).

N-P fertilization

N-P fertilizers are also one of the most commonly used fertilizers which make available both nitrogen and phosphorus to plants an alpine meadow, N-P fertilization decreased the diversity of both plant and AMF and also led to a decline in the abundance of AMF belonging to the phylum Glomeromycota (Liu et al., 2012). Chen et al., (2014) studied the effect of N and P enrichment (together) on AMF present in both soil and roots of plants (perennial herbs namely *Artemisia frigida*, *Cleistogenes squarrosa* and *Stipa krylovii*) grown in a temperate steppe and observed change in AMF species composition and abundance. Wang et al., (2018) reported the positive effect of N-P fertilization which resulted in increased spore abundance and density of extra radical hyphal length in the field infested with *Pedicularis kansuensis* (a root hemiparasite)

Precipitation patterns

Human-induced global warming resulting from the emission of greenhouse gases leads to fluctuation in precipitation regimes. A change in rainfall pattern can drastically influence the growth, development, yield, and biodiversity of plant and microbial communities. A six year study concluded that elevated precipitation irrespective of temperature led to an increase in AMF, ERH, and spore density but a decline in AMF richness in the semiarid steppe (northern China). The combination of elevated temperature and precipitation also resulted in enhanced spore production (Gao et al., 2016) and AMF diversity (Xiao et al., 2021). Altered precipitation (400 to 50 mm) also resulted in different AMF communities at different sites in Tibetan alpine step suggesting that water availability also plays a critical role in shaping the AMF communities (Zhang et al., 2016). An increment in precipitation increased AMF colonization, abundance, and biomass (Chen et al., 2017). Similarly, change in rainfall pattern in Australian grassland resulted in alteration of AMF community composition (Deveautouret et al., 2018; Deveautouret et al., 2020). The subtropical forest of China when exposed to drought conditions (4 years) led to a decline in AMF root colonization, ERH development and spore production (Maitra et al., 2019). Thus, till date the information available suggests that altered precipitation regimes can have negative as well as positive impact on AMF communities.

Ozone concentration

Ozone (O₃) is a gas present mainly in the stratosphere. Due to human activities like the emission of pollutants from industries, cars, power plants, etc. the concentration of O₃ in the form of a secondary pollutants is increasing day by day near the earth's surface. Ozone is produced when two primary pollutants, nitrogen oxides and volatile organic compounds react in the presence of solar radiation. An increase in O₃ concentration in the environment is a threat to humans, plants as well as microbial communities. Elevated O₃ can affect diversity, physiological growth and development, and productivity of different crop species (Ainsworth et al., 2020).

A significant decline in AMF colonization, hyphal length, and arbuscule numbers was observed in AMF associated *Phaseolus vulgaris* plants exposed to elevated O₃ (Wang et al., 2012). Enhanced O₃ concentration decreased the AMF root colonization in *Festuca rubra* and *Leontodon helveticus* (Bassin et al., 2017) and soybean plants (Qiu et al., 2021). Wang et al., (2017) performed meta-analysis to study the effect of elevated O₃ on AMF colonization and function and observed a negative correlation between increased O₃ concentration and AMF root colonization. They also showed that AMF colonization rate was dependent on AMF itself, plant type, duration of O₃ exposure, and any other simultaneous stresses (Wang et al., 2017).

Thus, from the currently available information, it may be inferred that AMF hyphal length is inversely proportional to an increase in O₃ concentration while AMF root colonization can be enhanced or reduced based on plant type and other factors mentioned in the meta-analysis (Wang et al., 2017).

Conclusions

Several studies have indicated a definite influence of anthropogenic activities on various aspects of AMF. This review, summarizes the impact of such activities that apparently elicit a positive, negative and/or neutral response with respect to the development and functional dynamics of AMF. Keeping in view the present trend of human intervention leading to climate change, these anthropogenic activities will certainly lead to further change in the climatic conditions. Hence, it becomes essential to evaluate the response of AMF to those anthropogenic related environmental and climate changes. Responses of AMF to global climate change will subsequently impact the agriculture scenario and functioning of ecosystems. The current research trend shows that it is difficult to have a uniform or consistent model to predict the influence of fluctuating climate on diversity, growth, development, community structure, and functioning of AMF. More research in this area is required to address and understand the roles of anthropogenic activities (influencing the environment) that shape the AMF community. Further investigations will also help in designing strategies to ameliorate the detrimental effects and consequently will assist in conserving the biodiversity of AMF leading to improved plant survival, crop productivity and balanced functioning of the ecosystem.

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Conflicts of interest

The authors have no conflicts of interest to declare that are relevant to the content of this article.

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