

Impact of abiotic factors on development of the community of arbuscular mycorrhizal fungi in the soil: a Review

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Abstract. Arbuscular mycorrhizal fungi inhabiting soil play an important role for vascular plants. Interaction between arbuscular mycorrhizal fungi, plants and soil microorganisms leads to many mutual advantages. However, the effectiveness of mycorrhizal fungi depends not only on biotic, but also abiotic factors such as physico-chemical properties of the soil, availability of water and biogenic elements, agricultural practices, and climatic conditions. First of all, it is important to adapt the arbuscular mycorrhizal fungi species to changing environmental conditions. The compactness of the soil and its structure have a huge impact on its biological activity. Soil pH reaction has a substantial impact on the mobility of ions in soil dilutions and their uptake by plants and soil microflora. Water excess can be a factor negatively affecting arbuscular mycorrhizal fungi because these microorganisms are sensitive to a lower availability of oxygen. Mechanical cultivation of the soil has a marginal impact on the arbuscular mycorrhizal fungi spores. However, soil translocation can cause changes to the population of the arbuscular mycorrhizal fungi abundance in the soil profile. The geographical location and topographic differentiation of cultivated soils, as well as the variability of climatic factors affect the population of the arbuscular mycorrhizal fungi in the soils and their symbiotic activity.

Key words: mycorrhiza, abiotic factors, dynamics of arbuscular mycorrhizal fungi development

INTRODUCTION

Arbuscular mycorrhiza involve a mutualistic symbiosis of vascular plant roots and fungi belonging to the *Glomeromycota*. The association between mycorrhizal fungi and plant roots was important in the evolution of land plants and currently occurs in at least 80% of all plant spe-

cies (Smith and Read, 2008). Colonization by arbuscular mycorrhizal fungi (AMF) can provide multiple functions, such as increase nutrient uptake and plant growth, as well as provide protection to the plant against pathogen infection (Ronsheim, 2012). Among the most important factors regulating the dynamics of mycorrhizal development are abiotic environmental factors. Also significant are factors such as temperature, soil pH, humidity and the intensity of light as well as the availability of minerals (Bonfante and Perotto, 1995; Miranda and Harris, 1994; Tahat and Sijam, 2012). The production of spores by AMF causes these fungi to survive and propagate in the soil environment despite the absence of a symbiotic plant.

In the soil environment spores can survive longer, preserving their ability to sporulate and colonize roots, even after several years of dormancy (Smith and Read, 2008). AMF spores contain substances such as lipids, proteins and polysaccharides, necessary as energetic substrates in DNA synthesis and in mitotic divisions of chromatin (Bonfante and Perotto, 1995). A proper condition for AMF spores germination is regarded as their survival ability during long periods of dormancy. In field conditions, AMF spores can survive in dormancy over a year (Smith and Read, 2008). The necessary time of dormancy is determined as 4 to 6 months and depends on the genus and species of the AMF fungus (Gazey *et al.*, 1993). To maintain spores' activity for longer (several years) periods it is recommended that they be stored at the temperature of 4-8°C in air-dry soil (Jasper *et al.*, 1993).

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AMF have the ability to achieve limited saprophytic growth; however, without additional signals from the plant, the growth of the fungus is inhibited and contact between the symbionts is not established. The growth of fungal hyphae stops 20-30 days after germination (Giovanetti and Citeresi, 1993; Schreiner and Koide, 1993). The germination of AMF spores depends on numerous factors.

OCCURRENCE OF AMF IN THE SOIL

Arbuscular mycorrhizal fungi are mainly transported by wind and water, soil translocation resulting from erosion as well as heavy rains and plant residues. Endomycorrhizal fungi colonize all types of soil and their number and the variety of AMF species depend on the type of soil (Table 1).

Biodiversity of AMF is determined with direct (total number, number of spores, microscopic observations) and indirect methods (fungal biomass, enzymatic activities). Changes in genetic diversity that result from various anthropogenic and natural factors can be evaluated using

molecular techniques (*e.g.* ITS PCR, PCR – DGGE, ITS NGS) (Orgiazzi *et al.*, 2013; Schoch *et al.*, 2012). The analysis of a set of genes (genomic DNA) can provide information about the structure and genetic connections of the examined set of AMF (Zholl *et al.*, 2016).

Next Generation Sequencing (NGS) of the hyper alternating regions (ITS Internal Transcribed Spacer) allows one to define the genetic diversity of fungi without cell culture cultivation (Orgiazzi *et al.*, 2013). It consists in the isolation of total DNA from soil sample and the preliminary amplification of hyper alternating regions with the use of specific starters. At next stage, correct adaptors and indexes are attached to amplicons (Lim *et al.*, 2010). Samples concentrations are normalized and then all samples are combined into one cumulative sample designated for sequencing. The use of adequate indexes makes it possible to assign individual amplicons to appropriate samples. Metagenomics analysis is not only aimed at examining the diversity of AMF, but also searching for functional genes – hence the evidence for the occurrence of specific metabolic activities among the members of AMF.

Table 1. A summary of the number of AMF species found in the soils of natural and managed ecosystems

Environment	Region/Contry	Species No.	References
Forest	Słowiński National Park/ Poland	20	Tadych and Błaszowski (2000b)
Forest (<i>Crataegus pontica</i>)	Ilam Province/Iran	13	Mirzaei <i>et al.</i> (2014)
Forest	Tuchola on the Brda river valley/Poland	25	Tadych and Błaszowski (2000a)
Grassland	North Carolina/USA	23	Bever <i>et al.</i> (1996)
Tellgrass prairie	Kansas/USA	14	Bentivenga and Hetrick (1992)
Rupestrian grassland (1 400 m a.s.l.)	Serra do Cipó/Brazil	27	Coutinho <i>et al.</i> (2015)
Rocky outcrop (1 200 m a.s.l.)	Serra do Cipó/Brazil	34	Coutinho <i>et al.</i> (2015)
Rhizosphere soil (990 – 1 845 m a.s.l.)	Tatra Mountains/Poland	20	Zubek <i>et al.</i> (2008)
Sandy soil	Hel/Poland	34	Błaszowski (1994)
Maritime dune	Bornholm/Demmark	26	Błaszowski and Czerniawska (2011)
Desert	Błędowska Desert/Poland	20	Błaszowski <i>et al.</i> (2002)
Conventional agriculture (<i>Zea maydis</i>)	Minessota/USA	13	Kurle and Pflieger (1996)
Conventional agriculture (<i>Sorghum bicolor</i>)	Nebraska/USA	26	Ellis <i>et al.</i> (1992)
Conventional orchard (apple)	Brazil	20	Purin <i>et al.</i> (2006)
Organic orchard (apple)	Brazil	30	Purin <i>et al.</i> (2006)
Cultivated soil	Lubuskie region/Poland	12	Kowalczyk and Błaszowski (2005)
Non cultivated soil	Lubuskie region/Poland	15	Kowalczyk and Błaszowski (2005)

AMF spores were found in both tropical and arctic conditions, in dry and wet lands as well as in natural and artificial conditions (including agroecosystems). A small number or absence of AMF spores is only to be found in chemically treated and physically degraded soils.

Climatic and soil conditions, the plant cover, and the intensity of anthropogenic effect engender substantial diversity in the population and genus composition of AMF spores in various ecosystems (Khalil *et al.*, 1992). Differences can occur between cultivated and non-cultivated soils (fallow and wasteland) as a result of plant rotation and different biochemical and microbiological properties of such soils (Guo *et al.*, 2012; Rillig, 2004).

Fungi from the *Glomus* genus are common in cultivated soils. Spores belonging to genera *Gigaspora* and *Sclerocytis* are more frequent in non-cultivated soils. AMF spores from the *Glomus* genus predominate in Poland cultivated soils, which might be related to the pH, fertilization and better structure of these soils (Błaszowski, 1993a,b; Kowalczyk and Błaszowski, 2011). Data concerning the community of AMF in agricultural soils is varied due to the fact that the spore population is largely affected by plant cultivation in the rotation system, the cyclical nature of agrotechnical treatments, and chemical crop protection (Land and Schonbeck, 1991). In consequence, the use of soil for agricultural purposes does not always promote the occurrence of AMF spores. In Polish soils more AMF spores were found in the rhizosphere of cultivated plants as compared to the non-cultivated soil from the rhizosphere of plants growing in the wild (Błaszowski, 1993a,b; Kowalczyk and Błaszowski, 2011). Agrotechnical treatments affect the selection of AMF species and put additional pressure on the adaptation of native AMF to the changing soil conditions (Rillig, 2004).

The studies on the communities of endomycorrhizal fungi revealed that the level of colonization of plant roots was not usually correlated with the population of spores in the soil (Khalil *et al.*, 1992; Oehl *et al.*, 2005). The distribution of mycorrhizal fungi spores in the soil profile depends on the degree of soil penetration by the roots of the host plant. For this reason, the largest populations of spores in cultivated soils were found up to 15 cm of the profile depth, which is a depth characterized by conditions most conducive to soil processes performed by rhizosphere microorganisms.

The population of AMF spores considerably decreases below 30 cm of the soil surface. Generally, no spores of AMF were found at depths below 70 cm (Oehl *et al.*, 2005). However, a number of symbiotic systems between microorganisms and plant roots can appear even deeper, especially in barren and air-drained soils (Guo *et al.*, 1996; Mensah, 2015; Oehl *et al.*, 2005). The topographic field location (e.g. on the slope, in a valley) can also affect the population of AMF spores, which is associated with the nutrient content and the water migration of AMF spores. However,

the correlation between field topography and AMF spore populations has not yet been widely recognized (Khalil and Loynacham, 1994).

PHYSICAL AND CHEMICAL PROPERTIES OF SOIL AFFECTING THE SPREAD OF AMF SPORES

Differentiation of the community of the mycorrhizal fungi largely depends on the content of organic matter, pH of the soil, and water content in the soil. The soil properties have a significant effect on the population of AMF spores in the soil, irrespective of the geographical location, the manner of soil cultivation and the plant density (Khalil and Loynacham, 1994). Negative correlation was observed between the level of root colonization and the content of the organic matter and phosphorus.

The compactness of the soil and its structure have a considerable impact on its biological activity. Loose soils or soils with a poorly formed arable layer are characterized by marginal biological activity and a low population of AMF spores, and low symbiotic activity is usually observed in those soils (Aziz and Sylvia, 1992). Excessive soil cohesion can also be the cause of unfavorable conditions for the growth of plants and symbiosis with AMF and their sporulation (Camel *et al.*, 1991).

Soil pH reaction has a major impact on the mobility of ions in soil dilutions and their uptake by plants and soil microorganisms. A decrease of soil pH in the rhizosphere of mycorrhizal plants can be associated with the fact that AMF hyphae prefer ammonium cations, which at the same time might be a non-specific mechanism of phosphorus mobilization (Bücking and Kafle, 2015). Acid soils create conditions unfavorable to plant growth and AMF activity (Tahat and Sijam, 2012). The soil pH can be a selective factor for the composition of rhizosphere microorganisms in the soil. The soil pH reaction ranging from 4.5 to 7.5 has no impact on the symbiotic activity of AMF in plant roots (Bücking and Kafle, 2015). The direct impact of the pH reaction of the soil environment on AMF is limited to the sporulation stages and the germination of AMF spores in the rhizosphere. Much more spores were found in soils with a neutral pH (pH 6.5) as compared to soils with pH 5.5. In strongly acidic soils (pH below 4.5) a considerable decrease in the number of spores and sometimes their absence was observed (Guo *et al.*, 1996).

ACCESSIBILITY OF WATER AND BIOGENIC ELEMENTS FOR AMF PLANTS

Water excess can be a factor adversely impacting on AMF because these microorganisms are sensitive to a lower availability of oxygen. Consequently, spores of endomycorrhizal fungi were not usually found in periodically flooded soils (Solaiman and Hirata, 1996). It was proven that with water deficits in the soil, mycorrhizal plants sustained smaller biomass losses than non-mycorrhizal ones. This resulted in an easier uptake of water and mineral

elements by the hyphae of endomycorrhizal fungi (Birhane *et al.*, 2012). In field conditions, a better yielding of mycorrhizal plants (soybean, alfalfa) cultivated with limited access to water or under periodical drought stress was also obtained (Braunberger *et al.*, 1994).

In conditions of water deficiency a higher photosynthetic activity and nitrogen assimilation was simultaneously observed with a double symbiosis (*Rhizobium* sp. + AMF) of papilionaceous plants. More recent research on the vegetation of mycorrhizal and non-mycorrhizal plants in drought conditions revealed the highest effectiveness of plants colonized solely by AMF in the uptake of elements (Sanchez-Diaz *et al.*, 1996). Mycorrhizal plant increases its competitiveness in the speed and scope of absorbing biogenic elements from the soil, especially phosphorus (Olsson *et al.*, 1997). The phosphorus-uptake and storage functions are largely taken over by AMF (Köhl *et al.*, 2016; Schachtman *et al.*, 1998). The phosphorus content in the soil seems to play a substantial regulatory role in the plant's growth processes and the effectiveness of symbiosis as well as in regulating the level of root tissue colonization by AMF hyphae (Kowalska *et al.*, 2015).

Much attention is given in literature to the participation of AMF in the uptake of other elements from the soil, especially those which – in conditions of water deficit or excess in the soil – can have an inhibiting or toxic effect on plants. It was shown that mycorrhizal plants take up less manganese than non-symbiotic plants, which can result from a decrease in the reducing properties (manganese) of root exudates of the mycorrhizal plant and a limited activity of microorganism populations taking part in manganese reduction (Posta *et al.*, 1994).

Fungal hyphae can also be a barrier for the translocation of heavy-metal ions to the plant aboveground parts as these ions are immobilized in the root (Cd, Ti, Ba, B) with the participation of polyphosphates or specific metalloproteins (Nowak and Kunka, 2009; Turnau *et al.*, 1993; Yang *et al.*, 2015). Soil contamination with zinc is also toxic for plants and, at the same time, antagonistic during phosphorus uptake (Ryan and Graham, 2002). AMF, in particular those adapted to higher zinc concentrations in the soil, can limit zinc uptake by plants, while stimulating phosphorus uptake. Therefore, the toxic effect of zinc is reduced in mycorrhizal plants as compared to non-mycorrhizal (Mugabo *et al.*, 2014; Shetty *et al.*, 1995; Tahat and Sijam, 2012). AMF take part in the uptake of iron and zinc by mycorrhizal plants during a deficit of those elements in the soil (Thompson, 1996).

AMF do not only support plants in the uptake of nutritious elements but also produce glomalin, a protein valuable for plants. This glycoprotein commonly occurs in the soil and is a store for carbon whose source is atmospheric CO₂ (Wright *et al.*, 1996). Glomalins constitute nearly 30% of carbon content in the soil and about 2% of the total weight of soil aggregates (Nichols, 2004). The physico-chemical properties of glomalin such as insolubility, viscosity and

hydrophobicity can initiate and protect the appearing soil aggregates and improve the hydrophobic properties of soil particles allowing air permeation and water flow (Gałazka and Gawryjolek, 2015; Wright and Anderson, 2000; Wright *et al.*, 1996). Glycoproteins cover the soil aggregates and protect them from being broken up by forming a characteristic coat on their surface (Wright and Anderson 2000). Glomalins produced by AMF cover the mycelium hyphae, keeping water and nutrients on the way to and from the plant, thus contributing to the better nutrition of plants and to an increased yield (Nichols, 2004; Gałazka and Gawryjolek, 2015).

The ability to produce and store glomalins in fungal hyphae is characteristic exclusively of arbuscular mycorrhizal fungi belonging to order *Glomerales*, accumulating family *Glomeraceae* with genus *Glomus* (Gałazka, 2013; Gałazka and Gawryjolek, 2015). No other fungi except *Glomeromycota* produce glomalins in considerable quantities. Glomalin is mainly localized on the surface of hyphae and spores of AMF and, being hydrophobic, probably covers the mycelium and protects it against degradation from other microorganisms in addition to increasing durability of the structure of the cell walls of those fungi, and facilitating their spread in the soil. The population and symbiotic activity of AMF, and thus a greater production of glomalin, can be increased both by modification of soil conditions promoting the propagation and activity of spores and by introduction of selected microorganisms into the rhizosphere which promote the process of mycorrhiza (Rillig and Steinberg, 2002).

AGROTECHNICAL FACTORS

Farming practices have an impact on AM association, damaging or killing AMF and directly, by creating conditions, either favourable or unfavourable to AMF (Table 2).

Mechanical cultivation of the soil has little impact on the population of AMF spores; however, soil translocation can cause changes in the population of AMF spores in the soil profile. Therefore, a decrease in the infection potential of the soil is possible, which is connected with a more difficult germination of certain AMF spores or propagules in the translocated soil (Duponnois *et al.*, 2001). Frequent cultivation treatments connected with crushing the top soil layer might be the reason for a decreased level of colonization of plant roots by AMF. This is related to an increase of the soil density under the effect of the wheels of machines pressing it. This often affects negatively the growth of roots and creates the risk of destruction of the hyphae or physical damage to AMF spores (Abiala *et al.*, 2013; Oehl *et al.*, 2005). In agricultural soils, considerable differentiation in the composition of AMF was observed. This is connected with the methods of cultivation and the scope of additional agrotechnical treatments (Gosling *et al.*, 2006; Mathimaran *et al.*, 2005; Talukdar and Germida, 1994; Vallini *et al.*, 1993).

Table 2. Organic farm management practices* and their effect on AM association (Gosling *et al.*, 2006)

Practices	Effect
Beneficial practices	
Use of low solubility fertilizers	Low concentration of available nutrients in soil, encourages AMF colonization
Exclusion of most biocides	Toxic effects of some biocides on AMF are avoided
Ley periods	Encourages build up of AMF propagule numbers
Diverse rotations	Encourages a diverse AMF community
Detrimental practices	
Mechanical tillage for weed control	Disrupts mycorrhizal hyphal network
Bare fallows	Lack of host plants results in decline in propagule numbers
Non-mycorrhizal crops	Lack of host plants results in decline in propagule numbers
Use of copper based fungicides	Directly toxic to AMF

*May not be exclusive to organic farming systems.

CLIMATIC FACTORS

The geographical location and topographic differentiation of cultivated soils as well as the variability of climatic factors affect the population of AMF in the soils and their symbiotic activity. The optimum temperatures for the activity of AMF is similar to the optimum range for plant vegetation. However, it was observed that the temperature optimum for development stages of AMF (germination, infectiveness of hyphae, formation of arbuscules and vesicles, sporulation) is differentiated. Moreover, differences between AMF species as regards the values of optimum temperatures of spore germination and hyphae infectiveness were observed. These were connected with the origin of fungi strains from different climatic zones (Lekberg and Koide, 2008).

Extremely low or high temperatures in a given region can considerably reduce the population of AMF in the soil (Addy *et al.*, 1994). It was also found that AMF spores isolated from soils in hot climatic zones (India, Egypt, Florida) are less susceptible to a higher temperature of storage as compared to those isolated from soils in moderate climates (England); this indicated the possibility that AMF adapt themselves to climatic conditions as well (Al-Karaki *et al.*, 2004).

Light is a factor which affects mycorrhizas indirectly. It regulates the activity of symbioses mainly through the products of photosynthesis, *i.e.* carbohydrates transported to the roots (Saia *et al.*, 2015). High light intensity increases root colonization and AMF spore production. On the other hand, shortage of light might cause disturbances in the nutritious balance of symbionts and reduce the level of colonization of plant roots. The prevalence of the daytime period (more than 12 h) in the photoperiod cycle also stimulates the process of mycorrhiza and the development of AMF (Lahrman *et al.*, 2013).

Due to fungi ability to adapt to different environmental conditions, such as temperature, light and humidity, AMF are practically present in the soils of different climatic

zones. The effect of adaptation to a definite climate is the ecotypic differentiation of AMF. It is for example expressed in differences in the physiological activity of AMF from various climatic zones despite the morphological affiliation within one species (Hamel *et al.*, 1994). The seasonal character of climatic changes in a given region determines the indirect impact (through a plant) of climatic factors on AMF. This is connected with nutritious relations between endomycorrhizal fungi and plants. Those relations are visible especially in the cultivation of annual or winter plants and they are reflected in the adaptation of the stages of the development of AMF to the seasonably changing plant vegetation (Al-Karaki *et al.*, 2004).

SUMMARY

The most important abiotic factors affecting the efficiency of arbuscular mycorrhiza include the physico-chemical properties of soil, the availability of water and biogenic elements, agricultural practices, and weather conditions. As regards physico-chemical properties, the following are important: pH, correlation between water and air, and water and sorption capacities of the soil.

The pH of the soil plays an important role in the mobility of ions in aqueous solutions and their uptake by plants and microorganisms. Generally, a low pH adversely affects plant growth and development and the growth and activity of AMF. This is probably related to the inhibitory effect of aluminium ions. The excess of water can adversely affect the development of mycorrhiza, because AMF are microorganisms sensitive to reduced oxygen availability. The resistance of mycorrhizal plants to drought depends on the AMF species colonizing plant roots. It is assumed that mycorrhizal fungi can modify the growth of the aerial parts of plants under conditions of drought stress by affecting the plant complex mechanisms of response to water deficit, associated with the uptake of P and K, the root respiration, photosynthesis, transpiration, and the osmotic potential of leaves.

One of the most important agricultural treatments is the mechanical cultivation of soil, which has a slight effect on the number of AMF spores; however, the movement of soil can lead to changes in the number of spores in the soil profile. It may cause a decrease in the infection potential of the soil due to the difficulties in the germination of AMF spores in the displaced soil. The geographic and topographic diversity of soils and the variability of climatic factors affect the growth of plants and the quantity of AMF and their symbiotic activity. This applies particularly to temperature, precipitation, photoperiod and light intensity, which change daily and seasonally. The optimum temperature for the AMF activity is similar to temperature for plant growth. However, it was observed that optimum temperature for the different stages of AMF development is varied. The differences in the values of optimum temperature for spores germination and hyphae infectivity between AMF species were also observed. Extremely low or high temperatures can significantly reduce the number of AMF propagules in the soil. The ability of AMF to adapt to climatic conditions was observed.

Light is an indirect factor affecting AMF and one which regulates the activity of symbiosis mainly by transporting assimilates to the roots.

The high intensity of light increases the level of colonization of roots and production of AMF spores, while the deficiency of light energy can cause nutritional disorders in symbionts and decrease the colonization of plant roots. The adaptability of AMF to changing environmental conditions means that these fungi are found in all types of soils in different climate zones. The ecotype variety of AMF is the result of fungi adaptation to changing environmental conditions. This is expressed by the varied physiological activity of AMF coming from different climatic zones. Seasonality of climate changes in the region affects the AMF indirectly. This is due to the discussed developmental and nutritional relationships between endomycorrhizal fungi and plants. These relationships are especially noticeable in the case of annual or winter crops, and expressed through the adaptation of the development stages of AMF to changing seasonal vegetation.

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