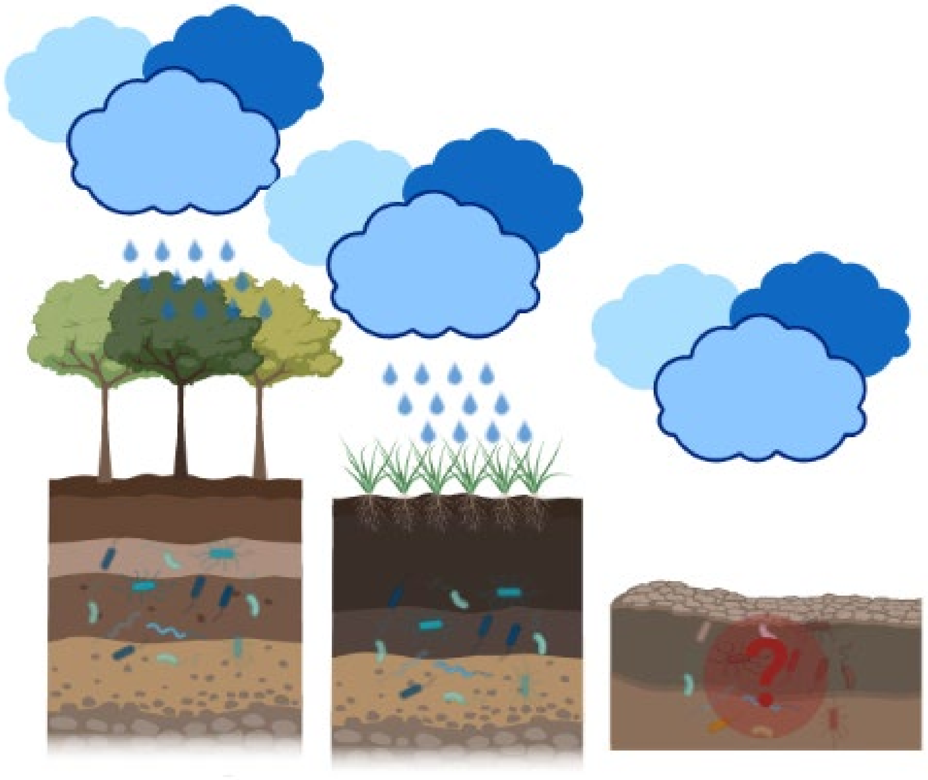
Big roles of microorganisms during drought stress



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Abstract

The soil microbiome is of great importance for ecosystems, as soil microbes provide essential advantages to other organisms in order for them to survive. Currently, ecosystems are facing many anthropogenic challenges. Climate change is one very big challenge that causes extreme weather conditions including drought, which is known to be the key limiting factor for plant growth. However, to be able to understand how drought affects the whole ecosystem and to maintain healthy, sustainable ecosystems, it is important to also understand how drought influences the soil microbiome, and how the soil microbiome affects the ecosystem and its co-occurring organisms under drought conditions in response. In this review, the most recent findings on how drought affects the soil bacterial and fungal biome, with a special focus on arbuscular mycorrhizal fungi, are discussed. Additionally, the effects of the soil microbiome on the ecosystem are discussed in two different aspects: how the soil microbiome affects the soil and how the soil microbiome is of importance for plant growth and health during events of drought. These findings together form a good overview on the current knowledge on how drought influences the soil microbiome and its effect on the ecosystem as a whole in order to improve our understanding on this subject to enable protection of Earth's ecosystems and to ensure sustainable land culturing for the generations to come despite the increase in drought events.

Layman's summary

The Earth has many land ecosystems in which multiple organisms live together, ranging from large organisms living on the surface of the land to microscopic organisms in the soil. They all influence each other and are all affected by the environment and by climate conditions. However, the health and functioning of these ecosystems is highly threatened by several challenges, of which the changing climate is one major challenge. Due to the changing climate, several weather conditions currently occur in more extreme forms and in a higher frequency to ecosystems than before, and a decrease in biodiversity of ecosystems is happening, which ultimately results in lower ecosystem stability. To be able to protect Earth's ecosystems and to enable a sustainable way to culture land for production of food and clothes under the changing climate, it is essential to fully understand how climate change affects the different organisms in the ecosystem and also how these organisms influence each other under these changing conditions.

Increased events of drought are an important effect of climate change that is damaging the land ecosystems severely. For example, in plants, drought is the key limiting factor of growth. Due to the large negative effects of drought on the ecosystem and as it is expected to occur even more intense and more frequently in the near future, drought will be the major focus of this review. As mentioned, drought greatly affects plants, but besides plants, microorganisms living in the soil are also extremely important for the ecosystem stability and functioning. Thousands of bacterial and fungal species for the soil microbiome and perform essential functions for the ecosystem, including chemical and physical structuring of the soil and also providing essential nutrients and other great advantages to plants. To understand what drought is doing to the ecosystem as a whole, it is therefore crucial to gain knowledge on what drought does to the soil microbiome and how the soil microbiome influences the environment during drought. To get a better understanding of this, this review focuses on the newest findings on effects of drought on the different bacterial and fungal organisms in the soil. Then, the review will focus on how these soil microorganisms affect the soil and how they influence plants during drought events. A special focus will be on a specific group of fungi, called the arbuscular mycorrhizal fungi, as these fungi are known to be extremely important to a great majority of land plants and are potentially important in future sustainable agriculture. Together, the results presented in this review give an overview of the most recent findings in the studies on effect of drought on the soil microbiome and contribute to a better understanding of the effect of drought on the land ecosystem.

Introduction

During the Anthropocene, human activities have influenced large fractions of land and their ecosystem tremendously (Geisen et al., 2019). With the increasing world population to 10 billion people in 2050 and the associated increased demand in food, fuel, and fiber, the ecological footprint per capita increases and threatens the natural land that is still left (Dubey et al., 2019; Geisen et al., 2019). Sustainable land management is therefore absolutely necessary to reach the high demand for food, fuel, and fiber while at the same time preventing land degradation in order to be able to provide for future generations and to limit the damage done to existing ecosystems. To enable this, fundamental knowledge on the effects of anthropogenic influences on ecosystems is required, which exists of roughly three aspects: 1) which challenges are ecosystems facing; 2) how are the different organisms in the ecosystems affected by this; and 3) how do these organisms affect ecosystem functioning?

Ecosystems are facing a lot of anthropogenic challenges, ranging from increased nitrogen concentrations (Ackerman et al., 2019) to the changing climate (IPCC Working Group II, 2022). The direct results of climate change are key factors in the challenge ecosystems are facing. In the past decades, atmospheric CO_2 concentrations have increased steadily changing the global climate and increasing the events of extreme weather conditions, which is only predicted to change even more in the years to come (IPCC Working Group II, 2022). These increased extreme weather conditions include increased temperatures, events of extreme rainfall, but one of the most challenging ones for plants, also due to their sessile nature, is the increased events of severe droughts (Sharma et al., 2020). It is said that drought is a key factor in limiting the plant growth, distribution, and productivity, for instance by negatively impacting photosynthesis (Huang et al., 2020). Due to the profound impact of drought and the predicted increased drought in the future, this will be the major focus of this thesis.

Besides, and also due to these anthropogenic challenges, biodiversity of ecosystems is also threatened, which greatly affects ecosystem functioning. Biodiversity worldwide is declining rapidly with a rate 1000 times larger than before human presence (Joppa et al., 2017; Geisen et al., 2019). Research on the effects of this decline on ecosystem functioning and on ecosystem stability has reached the general consensus that both are influenced in a negative way (Bardgett and van der Putten, 2014). However, these studies have mostly focused on aboveground macroscopic plants and animals. Though the soil biome includes roughly 92 gigatons of biotic carbon, making it the second largest biotic carbon pool on Earth (Geisen et al., 2019), the anthropogenic effects on microscopic and soil organisms have been understudied for a long time. Only recently, studies on the effects of anthropogenic effects on soil biota, and in particular the soil microbiome consisting of thousands of different species of bacteria, fungi, and archaea, gained more attention since their abundance and importance in ecosystem functioning has finally been recognized. It is acknowledged that the soil microbiome is essential for plant health and that soil microbes play key roles in the ecosystem functioning. For example, plant growth promoting (PGP) bacteria in the rhizosphere may play a significant role in plant health and growth, as PGP bacteria can provide nutrients that plants are lacking and in being absent can cause a decrease in plant growth, including phosphorus, fixed nitrogen, and iron. Additionally, PGP bacteria can alter the balance in phytohormones, thereby affecting the plant's growth and response to environmental stresses

(Glick, 2012), and PGP bacteria can increase the resistance against several pathogens by initiating the so-called induced systemic resistance (Pieterse et al., 2014). Another group of organisms in the soil microbiome that is especially well studied and shown to be very advantageous belongs to the fungal kingdom: the group of mycorrhizal fungi (Box 1). Mycorrhizal fungi can be divided into four major groups, of which the group of arbuscular mycorrhizal fungi (AMF) is the most important and most abundant group, as over 80 % of all terrestrial plants are dependent on these fungi by the advantages they experience from living in symbiosis with AMF (Bahadur et al., 2019). However, still much of the impact of climate change on the soil microbiome and the effect of these changes on the ecosystem as a whole is unknown. Acknowledging the importance of the soil microbiome for the ecosystem and gaining understanding in how the soil microbiome is affected by climate change, is essential to maintain healthy and sustainable ecosystems.

Therefore, in this thesis, the most recent findings on the effects of drought on the soil microbiome are described, with a special focus on bacteria and AMF. Due to their abundance and vital role in plant health and growth, and because AMF themselves are also threatened by climate change (García and Mendoza, 2008; Zhang et al., 2016), it is very important to study what the effects of increased drought are on AMF and how this would affect the resistance and resilience of the ecosystem and how it would affect ecosystem multifunctionality. Additionally, effects of the soil microbiome and the drought affected soil microbiome on plant health and ecosystem functioning will be discussed, which will ultimately lead to a better understanding of the effects of climate change on ecosystems and ecosystem functioning. This knowledge is crucial to be able to protect the world's ecosystems and to limit the losses in biodiversity and climate feedback.

Box 1. Mycorrhizal fungi

Since the symbiosis between plants and below-ground mycorrhizal fungi have been first discovered, many studies have been performed to study the organisms and processes involved in this symbiosis. Over the years, it has been established that the great majority of land plants have a symbiotic relationship with mycorrhizal fungi and that mycorrhizal fungi are present in almost all terrestrial ecosystems, where they play a key role in biogeochemical cycles, such as nutrient and carbon cycles, and they influence ecosystem multifunctionality and soil physical and chemical properties, such as the structure. Their importance is illustrated in the numbers as well: the majority of plant nitrogen and phosphorus, up to 80 %, is provided by mycorrhizal fungi and many plants are dependent on their symbiosis with mycorrhizal fungi for their growth and survival. The diversity of relations is large, as there are circa 50,000 fungal species, divided in four groups, which have a symbiotic mycorrhizal association with a total of circa 250,000 plant species (van der Heijden et al., 2015).

Mycorrhizal fungi connect with the host plant with so-called symbiotic interfaces and can develop a hyphal soil network, which connects the colonized plant communities to enable horizontal transfer of, for example, nutrients. Based on how these mycorrhizal fungi colonize the plant roots, they are divided into roughly two major groups: the ectomycorrhizal fungi, where root is only colonized in intercellular spaces by the fungus, or endomycorrhizal fungi, which colonize the plant roots also intracellular (Fig. 1). This latter group is again divided into three different groups: the arbuscular mycorrhizal fungi (AMF), orchid mycorrhizal fungi, and the ericoid mycorrhizal fungi. Different plant species live together in mycorrhizal associations (van der Heijden et al., 2015). Most plant species, approximately 200,000 species in total, host mycorrhizal fungi of the AMF group, belonging to the Glomeromycota. The major groups of plant species associating with these fungi are herbs, grasses, trees, hornworts, and liverworts. EMF belonging to the Basidiomycota and Ascomycota are hosted by circa 6,000 plant species, mostly including Pinaceae and Angiosperms, such as shrubs and trees. Orchid mycorrhizae are hosted by orchid plants solely, but with a range of 20,000 to 35,000 species. Ericoid mycorrhizae are mostly hosted by members of the Ericaceae (van der Heijden et al., 2015). As can be seen in these numbers, AMF are worldwide most abundant; more than 80 % of all land plants live together in symbiosis with members of this mycorrhizal fungi group.

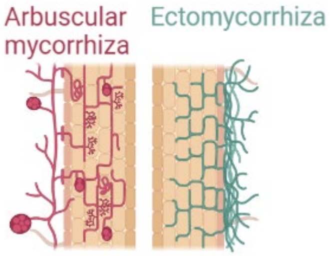

Figure 1. Schematic illustration of root colonization by the endomycorrhizal arbuscular mycorrhiza (red), and ectomycorrhiza (blue).

Additionally, AMF have a known potential as bio-fertilizers. The traditional usage of inorganic fertilizers, herbicides, and fungicides harms the soil health and air- and water systems, and additionally can negatively affect the food quality (Begum et al., 2019). In order to maintain sustainable agriculture and to increase the quality and quantity of the crop yield to provide for the increase in demand, the usage of AMF as bio-fertilizer is studied and highly encouraged by researchers (Begum et al., 2019). Symbiosis with AMF stimulates nutrient uptake by plants and does so in nutrient-deficient soils as well. This can enhance plant growth, as has been shown in several crops including tomatoes and maize (Begum et al., 2019). Additionally, the quality of crops is improved when there is symbiosis with the plant (Begum et al., 2019). This has for example been shown in citrus fruits, where inoculation with AMF leads to an increased fruit size and nutritional quality, including an increased vitamin C concentration (Li et al., 2014). Besides these general advantages of using AMF as bio-fertilizer to improve the crop yield and quality in a sustainable way, inoculation with AMF can also improve the plant's resistance against abiotic stress factors, including drought. Due to its potential as bio-fertilizer in sustainable crop productivity, its abundance in nature, and due to the importance of these fungi in plant health and biogeochemical cycles, this thesis focuses on the effect of drought on AMF.

Drought alters the soil microbiome

The soil microbiome exists of many different organisms, that all influence each other, other organisms in the ecosystem, and which can have a major influence on the abiotic environment as well, for example by affecting the soil chemistry and soil physics, such as the soil structure (Fierer, 2017). The organisms themselves are also affected by the environment surrounding them: ranging from abiotic influences to influences from the organisms living in the same environment. To understand what happens to the soil microbiome during severe drought, this section focuses on the changes in bacterial and fungal communities.

Soil bacterial microbiome altered during drought events

The soil microbiome, including the bacterial communities, are of great importance for plant and soil health (Berendsen et al., 2012). Besides, the bacterial communities play an important role in the chemical processes that occur in soil, including carbon sequestration, nitrogen fixation, nutrient availability, iron sequestration, and remediation of polluted soil (Glick, 2012; Olanrewaju et al., 2017; Niu et al., 2018; Ayangbenro and Babalola, 2021). It is thus important to gain knowledge on how increasing drought events affect the soil bacterial communities and how this will ultimately have its influence on the whole ecosystem.

During events of drought, bacterial communities are in general more affected by the depletion of water factors than fungal communities, because fungi are less susceptible to drought (Naylor and Coleman-Derr, 2018). During events of drought, the bacterial biomass generally decreases (Naylor and Coleman-Derr, 2018). Although drought has little impact on the phylogenetic diversity of the bacterial soil microbiome, the composition of the bacterial soil communities does change, especially when the soil biodiversity is low (Yang et al., 2021). Enrichment of certain species can occur in the soil microbiome and the phylogenetic pattern of this enrichment is often highly conserved (Xu and Coleman-Derr, 2019). Bacterial species can roughly be divided into two categories, monoderms and diderms (Fig. 2), based on their cell membrane and cell wall morphology, which can be visualized using Gram staining (Zerbib, 2017). Under drought conditions, monoderm species are more abundant than diderm species. Due to these differences in their cell walls and cell membranes, monoderms are likely less prone to drought than diderms. Monoderms have one inner membrane covered by a thick peptidoglycan wall, whereas diderms have a thin peptidoglycan layer over their inner membrane, which is again covered by an outer membrane containing lipopolysaccharides (Fig. 2) (Naylor and Coleman-Derr, 2018; Xu and Coleman-Derr, 2019; Megrian et al., 2020). Although the bacterial composition changes upon events of drought, this can fully recover once water depletion is ended (Xu and Coleman-Derr, 2019; Yang et al., 2021).

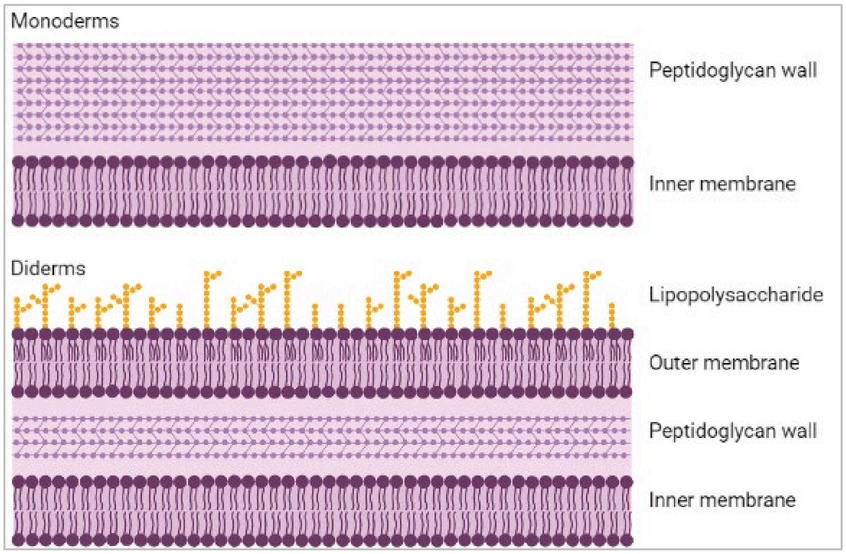

Figure 2. Membrane morphology of monoderm and diderm bacteria.

Besides the direct effects of drought, indirect effects of drought can also alter the soil bacterial communities as water depletion has a significant effect on soil physical and chemical properties (Zhang et al., 2019). For example, the total soil organic carbon concentration decreases significantly upon drought stress (Zhang et al., 2019). However, not only abiotic factors are important for soil microbiome formation, but biotic factors can also greatly affect the composition of the bacterial communities (Xu and Coleman-Derr, 2019). To name one, plants shape their root microbiome by excretion of metabolites, and this can lead to an increased biodiversity in soil where plants have their roots embedded (Naylor and Coleman-Derr, 2018; Xu and Coleman-Derr, 2019; Ayangbenro and Babalola, 2021). This has for example been demonstrated in soil where cotton plant roots are present: the soil biodiversity in soil where cotton roots are present is higher than in bulk soil and additionally, this effect is even increased when the ecosystem is exposed to drought stress (Ullah et al., 2019). Moreover, the secretion of metabolites can be in favor of specific groups of bacteria, such as monoderms. By influencing the rhizosphere, plants also contribute to the enrichment of monoderms. During periods of drought, production reactive oxygen species (ROS) can be increased in plant tissue (Xu and Coleman-Derr, 2019). In the root apoplast of drought-treated maize, the production of ROS was increased (Voothuluru and Sharp, 2013). Simultaneously, the root bacterial microbiome is affected, and it has been demonstrated that monoderm and diderm lineages respond differently to increased ROS levels and that there is a correlation between the cell wall thickness and inactivation of the bacteria (Mai-Prochnow et al., 2016). In monoderms, a thicker cell wall generally leads to decreased inactivation rates. However, a thicker cell wall in diderms does not necessarily increase their ROS resistance when compared to monoderms, indicating that other factors are also likely to be involved in ROS sensitivity, such as the extracellular matrix, cell membrane, DNA, and proteins (Mai-Prochnow et al., 2016). However, in general, monoderms are less prone to ROS than diderms, thus the increased production of ROS by plant roots during drought stress contributes to the enrichment of monoderms. The production of certain amino acids and carbohydrates by plants also improve growth and enrichment of monoderms (Xu and Coleman-Derr, 2019). During drought stress, roots can change their metabolism and increased production of certain carbohydrates, such as xylose and glucose, and of amino acids, including proline, asparagine, and threonine, has been observed (Xu et al., 2018). Amongst the significantly increased produced metabolites in drought-stressed roots of sorghum is glycerol-3-phosphate (G3P), which is a glycolysis intermediate and used by bacteria to produce teichoic acid, which is extremely important for cell wall integrity (Brown et al., 2013). Interestingly, the ATP-binding cassette transporters of G3P are also highly upregulated in drought-stressed monoderms, most likely due to the high demand for G3P by these species due to their thick cell wall (Xu and Coleman-Derr, 2019). Taken together, these results indicate that indirect changes of drought highly impact the composition of soil bacterial communities and make that monoderms have advantages in their growth when compared to diderms.

Besides these metabolic changes, plant root morphology can also affect the composition of the soil microbiome (Naylor and Coleman-Derr, 2018). During drought stress, plants enhance the water uptake by adjusting their root system, especially by increasing their rooting depth and rooting density (Fang and Xiong, 2014). Particularly this increased rooting depth has an impact on the root soil bacterial communities. These communities are significantly differentiated by depth where with increasing depth the relative abundance of *Proteobacteria, Actinobacteria, Planctomycetes*, and *Bacteroidetes* decrease significantly, whereas relative abundance of *Firmicutes* increases. Several factors that change with increasing depth are of importance for these community differences. The different layers in the soil depth profile are characterized by their own chemical and physical properties (Fierer, 2017). For example, changes in microbial community correlate strongly with availability of C and N, which is seen for the decrease in *Proteobacteria* with increasing depth that correlates strongly with the decreasing C availability in the soil. Additionally, with increasing depth, the soil density increases, which also causes a decrease in soil oxygen content (Pandey et al., 2015). Bacteria of the *Planctomycetes* phylum are able to degrade plant saccharides aerobically; their decrease in abundance within deeper layers of soil agrees with this function as well (Zhang et al., 2017). Other factors are also important: the water holding capacity, redox status, and aggregate size also strongly affect the microbial composition of the soil, and these factors vary with increasing depth (Zhang et al., 2017). However, to predict how increasing depth with its changing soil properties influences the soil microbial community composition and its functions is very complicated.

In summary, direct and indirect factors during events of drought have a significant effect on the composition of soil bacterial communities, where in general monoderms have a growth advantage to diderms (Fig. 3). While abiotic factors play a major role in these alterations, the reaction of plants to drought also affects the bacterial soil composition, both by production and secretion of metabolites as due to changes in morphology in their root systems.

Soil fungal microbiome altered during drought events

Although the effects of drought on soil bacterial communities have been studied widely, the effects of drought on the fungal soil biodiversity are still largely unexplored (Carbone et al., 2021). However, it is known that like soil bacterial communities, fungal communities, most importantly mycorrhizal fungi, are very important for several aspects of ecosystem functions, such as nutrient cycling, soil carbon storage, and plant survival (van der Heijden et al., 2015).

Recently, more effort has been done to also uncover how fungal communities are affected by drought stress in order to be able to understand better how the fungal soil communities respond to increased drought and get a complete overview of the response of the soil biodiversity, which is necessary to help in conservation of the soil biodiversity and prediction of the effects of increased drought on ecosystem functioning. Since the group of arbuscular mycorrhizal fungi (AMF) is of immense importance for ecosystem health and functioning and a symbiotic association of plants with AMF helps with an increased drought tolerance (Huang et al., 2011), this group has often been the major focus in studies and will therefore also have the major focus in this section.

It has been demonstrated that the soil fungal biodiversity is significantly changed during events of drought when the biodiversity of the soil is moderate to low (Yang et al., 2021). This was tested by diluting fresh soil 10^3 and 10^6 times and a decrease in fungal biodiversity was observed after two months of water depletion. This decrease in biodiversity could fully recover when soil was rewetted with an increase in most fungal species, except for fungi in the phylum of Glomeromycota*,* which include AMF species. These species were significantly reduced or even eliminated during drought stress and were unable to recover when water was again applied to the soil and its microbiome (Yang et al., 2021). Another study however, showed that no significant effects on AMF community structure or diversity indices at operational taxonomical units (OTUs) level, but a decrease in AMF family richness was observed after 4 years of drought treatment (Alguacil et al., 2021). Especially, a decrease in number of *Claroideoglomeraceae*, *Gigasporaceae* and *Diversisporaceae* sequences was observed. This could be due to alterations in carbon allocation by the plant or increased competition amongst AMF taxa and because *Glomeraceae* have a distinct adaptive strategy to avoid and resist drought stress in the soil (Alguacil et al., 2021). One AMF genus from the Glomeraceae family, which has been observed to even increase during events of drought is *Funneliformis*, which makes them remarkably interesting in research for water stress mitigation in agriculture and in order to maintain healthy ecosystems (Carbone et al., 2021).

Since the effect of drought on fungal soil communities has only recently gained interest, a clear general consensus is missing and the working mechanisms behind observed differences need further investigation as well. However, there are indications that the communities are affected by drought, although not as much as bacterial communities (Fig. 3).

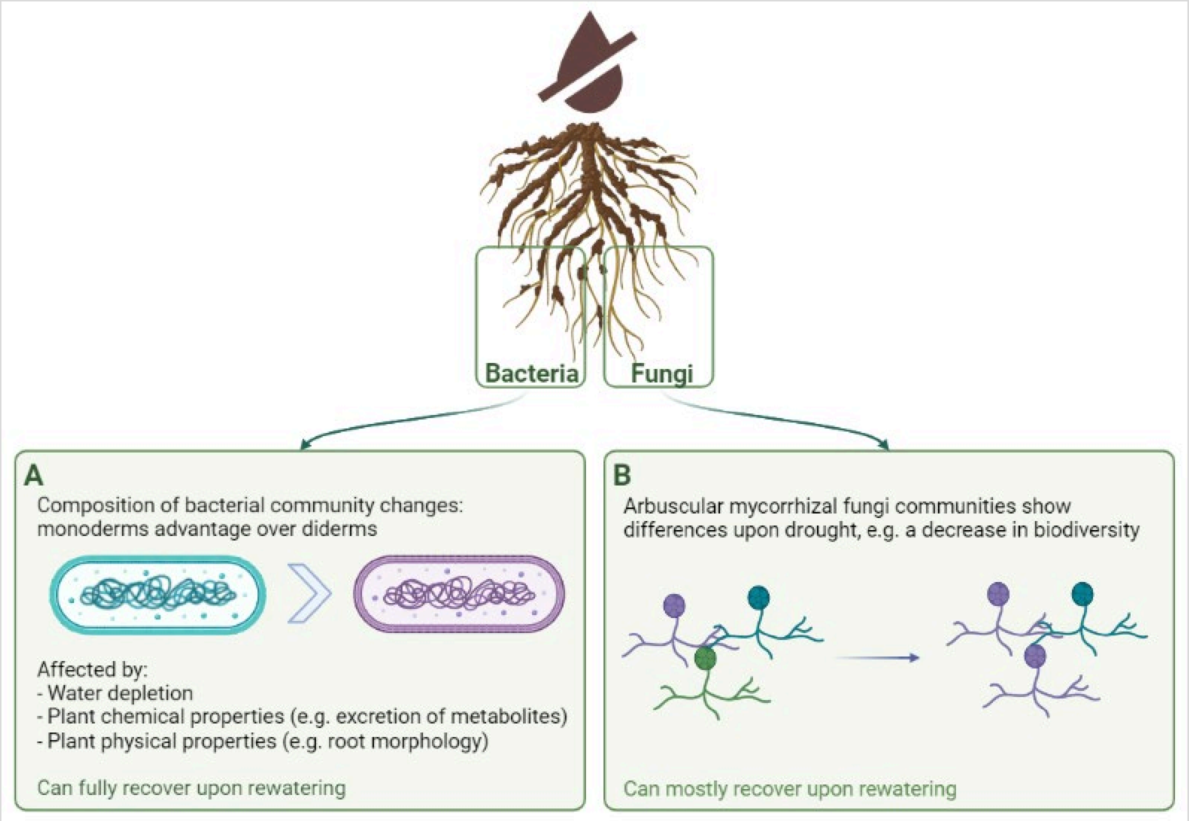

Figure 3. Overview of effects of drought on A) bacterial community composition, and B) arbuscular mycorrhizal fungal community composition.

Effects of soil microbiome on ecosystem during drought

As mentioned before, the soil microbiome plays a significant role in biogeochemical cycles and is of great importance for a healthy soil and stimulation of plant growth and health (Fierer, 2017) (Fig. 4). Growing under drought conditions, plants can recruit microorganisms and in doing so select for organisms in their rhizosphere that have PGP capabilities, and that support plant health and tolerance against drought stress (Soussi et al., 2016). As currently 41% of Earth's surface is covered by drylands and since this is projected to increase in the time to come (Yao et al., 2020), it is important to know what the effects of the soil microbiome on ecosystems are and how this will change upon increased drought to be able to predict changes in ecosystem functioning.

Effects of soil microbiome on soil

For healthy crops to grow, it is extremely important that the soil is of good quality. The quality of the soil is its capacity to operate within an ecosystem and sustain healthy biological productivity and promote plant health and growth (Bünemann et al., 2018). PGP organisms are very important to improve soil health and keep the soil quality high (Ayangbenro and Babalola, 2021). A high soil biodiversity also has a positive impact on soil health, as soils with high biodiversity are able to recover quickly after stress events including drought, and a high biodiversity also increases the protection against soil-borne diseases (Chaparro et al., 2012).

Additionally, the soil microbiome is of great importance when it comes to biogeochemical processes.

One important biogeochemical process that soil microorganisms are involved in, is soil carbon sequestration (Trivedi et al., 2013). Carbon in soil consists of two distinct pools: the soil organic carbon pool (SOC), and the soil inorganic carbon pool (SIC). The SIC pool consists largely of carbonate minerals and elemental C, whereas the SOC pool consists of roughly three origins: 1) residues of plants and animals during decomposition; 2) substances that were produced from the breakdown products; and 3) bodies of living organisms in the soil (Lal, 2008). During carbon sequestration, atmospheric CO_2 is reduced and transferred into long-term soil pools as soil carbon, due to which it is not instantly re-emitted. This process can both happen abiotically and biotically, of which microorganisms play a key role in the latter (Lal, 2008; Trivedi et al., 2013). The composition of the soil microbial community has a major influence on the rate of carbon sequestration (Trivedi et al., 2013). Soil dwelling bacteria can be divided in two ecological functional groups of oligotrophs (*k*-strategists), including members of the phylum Acidobacteria, and copiotrophs (*r*-strategists), including members of the phylum Bacteroidetes and class Betaproteobacteria (Fierer et al., 2007). The abundance of members of these different groups can affect the rate of carbon sequestration. It has for example been postulated that the carbon turnover is lower in oligotrophs and therefore has a lower CO_2 emission and promotes carbon sequestration (Singh et al., 2010). Carbon sequestration has been noticed to be important to improve and stabilize the soil structure and its water holding capacity, thereby enhancing productivity and restoration of degraded soils and ecosystems (Ayangbenro and Babalola, 2021). Aridity greatly influences the capacity to retain carbon in the soil (Ayangbenro and Babalola, 2021). In general, drylands have a lower net primary production and consequently, their capacity to retain carbon is low, as can be seen in dry agricultural lands of Eastern Australia (Rabbi et al., 2015; Ayangbenro and Babalola, 2021). Although carbon sequestration also happens in arid ecosystems, the potential of drylands to function as a carbon sink for atmospheric CO_2 is high, and therefore reclamation of these lands can increase the SOC stock, improve the agricultural outputs, and help to preserve the ecosystem services (Ayangbenro and Babalola, 2021).

Additionally, microorganisms play a key role in improving the soil fertility by facilitating the bioavailability of nutrients for plants (Ayangbenro and Babalola, 2021). Since many nutrients are limited in dryland soils that are required by plants (Ayangbenro and Babalola, 2021), it is not surprising that they are of great importance to create a habitable soil and help in the accessibility of these scarce nutrients. In arid soils, nitrogen, which is a key component of amino acids, is the second most crucial factor to limit bioactivity and biomass production, after water (Delgado-Baquerizo et al., 2013). Additionally, since arid soils have a decreased fertility, water holding capacity and phosphorus concentration, fixation of nitrogen is reduced in these ecosystems as nitrogenase enzymes are lowered in their activity in nitrogen fixing organisms, rendering the soil in nitrogen stress (Ayangbenro and Babalola, 2021). As certain microbes can convert atmospheric nitrogen to nitrogen forms that can be used by plants to mediate biological nitrogen fixation, the soil microbiome and its composition are very important to manage the soil nitrogen stress under water deprived conditions (Ahemad and Kibret, 2014; Ayangbenro and Babalola, 2021). Furthermore, soil microbes are essential in the mobilization and availability of two other important nutrients, namely phosphorus and potassium, which are also important for soil fertility and plant growth (Ayangbenro and Babalola, 2021). Other nutrients, such as copper, manganese, and zinc are also increased in availability by different processes of the soil microbiome (Ayangbenro and Babalola, 2021). Under drought conditions, iron is especially depleted, which can have adverse effects on plant growth since it is a very important micronutrient. This depletion is also reduced by organisms in the soil microbiome: siderophores, produced by PGP strains, have a high affinity for iron ions, which enables them to improve the iron availability and uptake in plants. The bacterial siderophore-bound iron ions can combine with phytosiderophores, facilitated by ligand exchange reactions, which can then be absorbed by plants (Etesami and Maheshwari, 2018).

Besides facilitating the availability of many essential nutrients, some soil microorganisms are also able to very efficiently decontaminate polluted soil (Vimal et al., 2017). Due to anthropogenic activities, drylands often are polluted and therefore bioremediation of this pollution is needed to restore this contaminated soil and to allow for sustainable development. Microorganisms are essential in this remediation and in the removal of organic and inorganic pollutants. For example, some mycorrhizal fungi are able to take metal pollutant up and in doing so decrease metal pollution (Vimal et al., 2017) (Ayangbenro and Babalola, 2021). Additionally, some PGP rhizobacteria are able to sequester toxic metals, which also efficiently removes the metal pollution from the rhizosphere. PGP rhizobacteria that are tolerant to heavy metals can for example change the bioavailable forms of toxic metals to non-bioavailable forms, thereby increasing the quality of the soil for plants, as this transformation decreases the uptake of these metals by plants (Etesami and Maheshwari, 2018).

Besides having their impact on these chemical properties, the soil microbiome also greatly influences soil physical properties (Ayangbenro and Babalola, 2021). Soil aggregate and pore formation is promoted by these organisms and additionally, they can secrete exopolysaccharides (EPS) (Ayangbenro and Babalola, 2021). The formation of micro-network aggregates is facilitated by EPS: organo-mineral complexes are formed by EPS, which help soil particles to adhere and in doing so, form the micro-network aggregates. These micro-network aggregates promote plant nutrient uptake, protect microbes from alterations in water potential, and help organisms in the rhizosphere to adhere to plant roots (Ayangbenro and Babalola, 2021). This last finding has been confirmed by experiments that show that plants under drought conditions that were treated with EPS producing strains had an increased biomass in the root adhering soil (Daffonchio et al., 2015). Besides forming micro-network aggregates, EPS also facilitate regulation of hydraulic conductivity, which results in an enhanced water-holding capacity and increased water content when water potential declines (Ayangbenro and Babalola, 2021).

These combined studies show that the soil microbiome is essential for a healthy soil environment, both influencing chemical and physical properties of the soil.

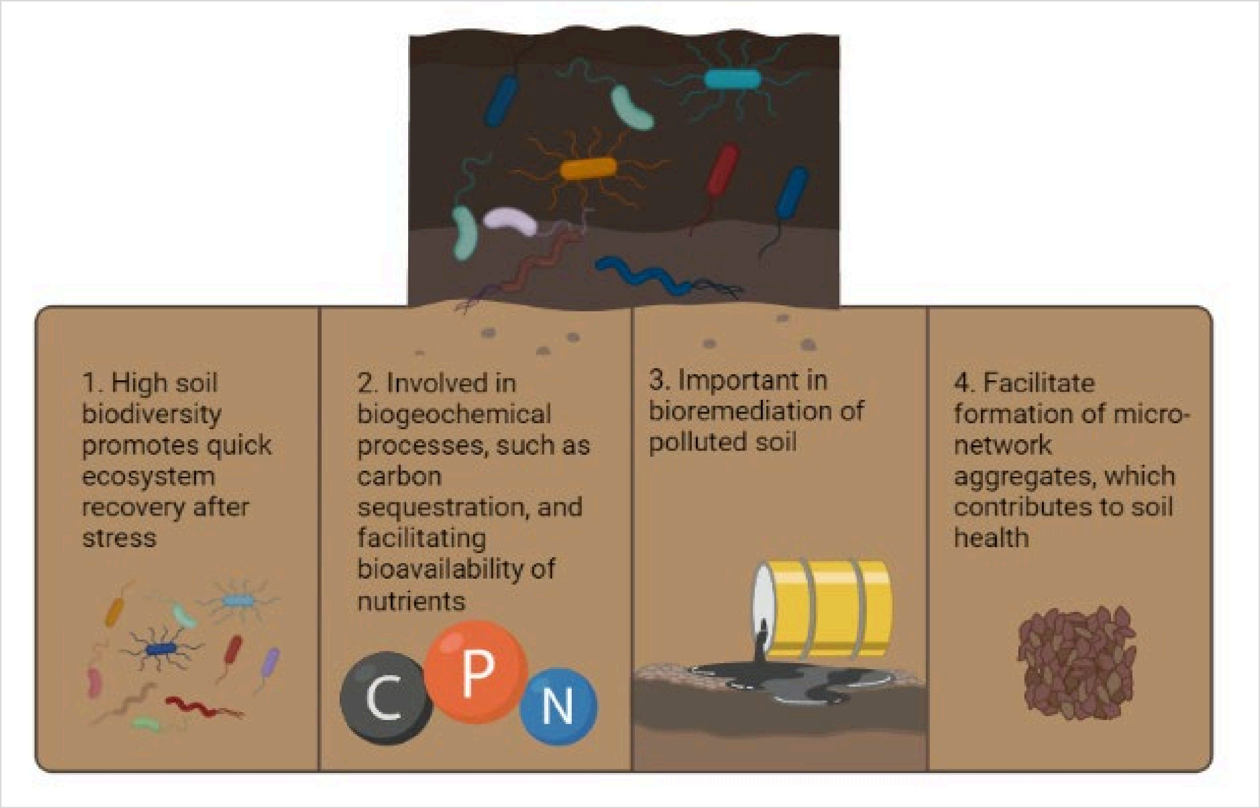

Figure 4. Overview of effects of soil microbiome on soil.

Effects of soil microbiome on plant health

Besides their positive impact on plants by maintaining soil health and fertility, and the inhibition of soil borne pathogens, soil microbes can also promote plant growth and plant health directly (Ayangbenro and Babalola, 2021) (Fig. 5). A high soil biodiversity has shown to have many positive effects on the ecosystem and plant diversity (Wagg et al., 2014). Additionally, a high soil biodiversity can promote a full recovery after periods of stress (Yang et al., 2021). In this section, the effects on plant health and plant growth of bacterial and fungal communities, and in more detail arbuscular mycorrhizal fungi, are discussed.

Bacterial effects on plant health

PGP bacteria can promote plant health and growth under normal conditions. When plants are exposed to drought stress, PGP bacteria are also involved in numerous processes that help the plant increase its drought tolerance and survive the stress (Naylor and Coleman-Derr, 2018).

One of the mechanisms activated under drought stress in PGP bacteria is the production of plant hormones that can disrupt the synthesis of other plant hormones (Daffonchio et al., 2015). One such hormone is 1-aminocyclopropane-1-carboxylate (ACC) deaminase. During periods of stress, such as drought, the expression of several plant stress hormones is increased. One of these increased plant stress hormones is ethylene. An increased ethylene concentration inhibits root growth, which may affect the growth of the plant as a whole. However, ACC can disrupt the synthesis of ethylene by hydrolysis of the ethylene precursor ACC (Daffonchio et al., 2015). This ultimately reduces the ethylene levels in plants, which confers drought tolerance as the plant, as it can improve the root and shoot biomass (Saleem et al., 2007; Ayangbenro and Babalola, 2021).

That the soil bacterial microbiome can improve drought tolerance, was also shown in cotton plants (Ullah et al., 2019). Analysis of the cotton root soil microbiome compared to the bulk soil showed that certain phyla were more abundant in the root soil microbiome. Amongst these are species of the phyla Proteobacteria, Actinobacteria, Gemmatimonadetes, Chloroflexi, Cyanobacteria, and Acidobacteria. Especially Chloroflexi and Gemmatimonadetes were highly abundant in drought-treated rhizosphere, indicating that these are associated with drought stress and can help the cotton plants to increase the drought tolerance (Ullah et al., 2019). Additionally, Sphingomonas, Streptomyces, Gemmatimonas, Sphingopyxis, Acidothermus, and Jatrophihabitans were also more abundant in the rhizosphere than in bulk soil. Besides being known to have antifungal and antibiotic activities (Sousa and Olivares, 2016), bacteria from the phylum of Streptomyces also can promote plant growth, also during periods of water depletion, and increase tolerance to water depletion (Yandigeri et al., 2012). Certain amino acids, such as glutamine, proline, and glycine betaine, and certain carbohydrates, such as trehalose, and raffinose enhance drought tolerance in plants (Santana-Vieira et al., 2016). In the rhizobia the metabolic pathways involved in the synthesis of these compounds are high and expected to contribute to tolerance to drought in plants (Ullah et al., 2019).

Fungal effects on plant health: arbuscular mycorrhizal fungi

Most terrestrial plant species have a symbiotic relationship with mycorrhizal fungi. AMF provide up to 80% of plant nitrogen (N) and phosphor (P) and many plant species are dependent on these organisms for growth and survival, which causes them to play a key role in ecosystem functionality (van der Heijden et al., 2015). Besides contributing to the carbon and nutrient cycling, the mutualism between AMF and plants plays a vital role in the productivity, diversity, and enhancement of stress resistance of the plant communities. Moreover, the AMF species are keystone taxa in the plant-associated microbiomes (Jia et al., 2021). In general, plants that live in symbiosis with AMF show a better nutrient uptake and an increased drought resistance. To understand what increased drought events will have for effect on plants and ecosystems, it is important to have a better understanding of the mechanisms that work behind this increased drought resistance.

To start with, AMF facilitate water management between plants with deep and shallow roots by forming a common mycorrhizal network (CMN) between the plants and promoting the hydraulic lift (HL). During HL, water from deeper soil flows passively to dry, shallow soil through roots of plants (Singh et al., 2019). However, the transfer between plants with deep roots and plants with shallow roots remains an issue. This transfer of water is particularly important for the yield of shallow-rooted crops, especially in dry regions and during periods of drought, as it contributes to better water availability for plants with their roots in shallow soils (Singh et al., 2019). In an experiment with the pigeon pea (*Cajanu cajan*), a drought tolerant crop with deep roots, and Indian goosegrass (*Eleusine coracana*), a shallow-rooted crop, this was nicely illustrated using deuterium labeled water in the bottom of the pot to be able to track the hydraulic lifted water (HLW). This experiment revealed that water content containing deuterium in the topsoil layer of *E. coracana* was significantly higher when there was a CMN and when there was intercropping with *C. cajan*. Additionally, it was observed that in general, there was no deuterium seen in the root crown of *E. coracana*. However, when intercropped with *C. cajan* and inoculated with AMF which formed a CMN, a significant amount of deuterium was also observed in the root crown, which is the part of the root system where the stem begins (Singh et al., 2019). Moreover, an increase in deuterium was also observed in the root crown of *C. cajan* when AMF was present, also when *E. coracana* was absent. These results show that AMF stimulates HL in deep-rooter crops and that the transfer of this HLW between deep-rooted crops and shallow-rooted crops is facilitated by AMF (Singh et al., 2019). Additional studies have also shown that shallow-rooted crops also benefit from HL when growing nearby deep-rooted plants (Bogie et al., 2018; Singh et al., 2019).

Furthermore, photosynthesis is greatly affected in plants when they are subjected to abiotic stress factors, including drought (Singh and Thakur, 2018). Photosynthesis is extremely important in plants, as it forms the basis for all other metabolic processes in plants (Yang et al., 2014). During drought stress, the photosynthetic capacity of plants is greatly reduced (Singh and Thakur, 2018). Inoculation and symbiosis with AMF can alleviate these effects. The net photosynthesis rate (Pn) is significantly reduced when plants without AMF are subjected to drought (Huang et al., 2011, 2020; Mo et al., 2016). Although inoculation with AMF cannot prevent the Pn to decrease, it can cause the reduction to be less dramatic and thereby help the plant during periods of drought to be able to successfully photosynthesize

(Huang et al., 2020). Additionally, the stomatal openings are closing when plants experience drought stress, which ultimately translates to a decreased stomatal conductance and transpiration rate, leading to a decreased photosynthesis as well (Huang et al., 2020; Sharma et al., 2020). Symbiosis with AMF can decrease the reduction of the transpiration rate (Huang et al., 2020). However, the effect of AMF on stomatal conductance (Gs) is not always consistent. For example, in apple species *Malus hupehensis*, there is no significant difference between the plants with or without AMF symbiosis under drought stress (Huang et al., 2020). However, shallow-rooted plant *E. coracana* showed a decrease under certain conditions. Although stomatal conditions did not differ in *E. coracana* between conditions with and without AMF or in monocrop or intercrop conditions when water was abundant, after a progressive drought, all Gs values, except for the split-root intercrop with AMF, reduced to zero (Singh et al., 2019). In the split-root intercrop, the Gs was constant throughout progressive drought (Singh et al., 2019), indicating that the HL and transfer from HLW between the plants facilitated by AMF has a positive influence on the Gs and overall survival of the shallow-rooted plants during drought.

Besides the ability to increase water availability, AMF can also improve water uptake: their hyphal network is of great importance for this. The plant root system has an absorption surface area that can be increased by AMF hyphae by two orders of magnitude, because absorbing hyphae can absorb water to up to 10 cm away from the roots and by doing so, positively affect the plant in its water uptake (Püschel et al., 2020). Absorbing hyphae start with one single, large hypha that extends and branches into two smaller hyphae, which branch again into two smaller hyphae, to an eight-order branching unit. The tips of these last branches hyphae are not bigger than 2 µm in diameter. This small diameter can help plants in receiving water during events of drought, as they are much smaller than the diameters of roots and root hairs. Roots are often able to penetrate soil macropores, which are bigger than 80 µm. Root hairs can penetrate smaller pores, such as mesopores, which are bigger than 30 µm. The smallest root hairs of grass are even able to penetrate micropores. However, roots and root hairs are not able to retrieve water from pores smaller than this. During conditions where water is abundant, this is not an issue, as macrospores and mesopores are filled with water, and AMF hyphae are not necessary to comply the plant's need for water. However, when soil dries, water retreats into soil pores where roots and root hairs cannot reach, leaving the plant's need for water unfulfilled and leaving the plant in drought stress. AMF hyphae can alleviate this stress, as they are able to penetrate ultramicropores with their smallest hyphae. Since 1 mm of root can already suffice for at least 128 hyphal tips with a diameter of 2 µm, this can positively regulate the water management of the plant (Allen, 2007). Furthermore, AMF hyphae have been shown to be able to penetrate rocks, such as limestone and granite, unlike plant roots (Allen, 2007; Schwinning, 2020). Since the rocks are a resource of water, but low on resources of C and other nutrients, it is thought that hyphae are necessary for tapping water from resources plant roots cannot reach, which provides them with more water during events of drought (Allen, 2007).

Besides the direct results of shortage of water and increased closed stomata, plants also have their chemical reactions to stress. For example, the production of ROS increases as well, which affects the photosynthesis apparatus (Gururani et al., 2015). In oxygenic photosynthesis, two photosystems (PS; PSI and PSII) together lead to oxidation of water and NADP reduction (Hamdani et al., 2019). The processes happening in PSII, such as light-harvesting, excitation transfer, charge separation, and electron transfer, are essential for successful photosynthesis and therefore PSII efficiency is determinative for the total photosynthesis efficiency (Sperdouli et al., 2021). Under environmental stress, the photosynthetic apparatus is exposed to damaging components due to the increased ROS levels, which also inactivate the repair mechanism of the photosynthetic apparatus (Gururani et al., 2015; Singh and Thakur, 2018). PSII is especially exposed to damage (Sperdouli et al., 2021) (Box 2), which ultimately lowers the photosynthetic yield (Huang et al., 2020; Sperdouli et al., 2021). This was confirmed during several experiments, where plants exposed to drought stress had a significantly lowered maximum fluorescence efficiency, actual photochemical efficiency of PSII, electron transfer rate and photochemical quenching coefficient. However, inoculation with AMF could significantly alleviate these negative drought effects on the photosynthesis apparatus efficiency, although not always to the well-watered rate (Mo et al., 2016; Wang et al., 2018; Mathur et al., 2019; Huang et al., 2020). Amongst others, AMF can stimulate expression of enzymatic antioxidants, which besides scavenging ROS also trigger other signaling events to keep the ROS levels under control (Bahadur et al., 2019). For example, members of this ROS scavenging enzyme system include the antioxidant enzymes catalase (CAT), peroxidase (POD), and superoxide dismutase (SOD). It was shown that SOD and POD activity significantly increased, especially during drought stress, and the ROS concentrations were lower when plants were inoculated with AMF (Huang et al., 2020). The accumulation of ROS therefore stays at a relatively low level when plants that experience drought stress are inoculated with AMF compared to non-mycorrhizal plants. The lowered ROS concentration as a result of symbiosis with AMF therefore increases the drought tolerance of plants and prevents severe damaging of the photosynthetic apparatus due to ROS.

Besides the increased production of antioxidant enzymes, apple and sweet potato plants inoculated with AMF also have been shown to accumulate sugars that are known to enhance their drought tolerance, such as proline and soluble sugars (Yooyongwech et al., 2016; Huang et al., 2020). Although during drought stress non-mycorrhizal plants also show an increase in proline and soluble sugars accumulation in their leaves, this increase is significantly higher when plants are inoculated with AMF (Huang et al., 2020). That not only the accumulation of proline is elevated, but also the production is confirmed by measuring the concentration of P5CS, which is a key-enzyme in the synthesis of proline (Huang et al., 2020). The increase in proline in leaves is however not consistent in all plants when they are inoculated with AMF. For example, in trifoliate oranges the production of P5CS and P5CR, another proline synthesizing enzyme, and consequently the proline concentration is significantly lower in AMF-plants than in non-mycorrhizal plants (Wu et al., 2017). However, the soluble sugar concentration is also increased when plants are inoculated with AMF, confirming findings of other studies.

Box 2. Increased reactive oxygen species production damages photosynthetic apparatus during drought stress.

During photosynthesis, light, CO_2, and water are converted into carbohydrates that serve as the primary source as energy for both plants and heterotrophic organisms. This process is led by the photosynthetic apparatus, which consists of several components, including photosynthetic pigments and photosystems I and II (PSI and PSII). Photosynthetic pigments, such as chlorophyll a, chlorophyll b, pheophytins, and carotenoids, are responsible for absorption of light to harvest energy for photosynthesis. All plants have chlorophyll a, which resides in the reaction centers of PSI and PSII. Chlorophyll b and carotenoids are accessory light-absorbing pigments, which can absorb light at a different wavelength and transfer the light energy to chlorophyll for photosynthesis. Additionally, carotenoids are important to protect plants from damage caused by high light intensities by quenching triplet chlorophylls and the ROS singlet oxygen ($^1O_2$) they can produce. Pheophytins are derivatives of chlorophyll, without MG^{2+} in their center, which serve as the primary electron acceptor in PSII, due to their high reduction potential. The two photosystems are the major drivers in photosynthesis, residing in the thylakoid membranes within the chloroplasts. They both consist of multiple proteins and light-absorbing pigments and are responsible for the production of NADPH, O_2, and ATP. CO_2 is fixed as carbohydrates in the Calvin cycle, where NADPH acts as a reducing agent and is reduced to $NADP^+$, which in its turn can again accept electrons from the electron transport chain which takes place in the thylakoid membrane.

However, during drought stress, several mechanisms, including a misfunctioning photosynthetic apparatus, may lead to the increased production of ROS, such as superoxide ($O_2^{\bullet}$–), $^1O_2$, hydroxyl radicals ($HO^{\bullet}$), and hydrogen peroxide (H_2O_2). These ROS cause oxidative stress in plants and ultimately damage the photosynthetic apparatus as well. Because of the closure of stomata in the plant’s reaction to drought stress to reduce the loss of water, the CO_2 concentration in the chloroplasts drops. This results in a reduction of fixed CO_2, and consequently in reduced $NADP^+$ concentrations. As a result, the electrons from the electron transport chain will not be accepted by $NADP^+$, but will be channeled to O_2, thereby producing the ROS $O_2^{\bullet}$–, which is converted further into H_2O_2. Additionally, the production of H_2O_2 is increased by photorespiration, which is stimulated by the low CO_2 concentration as well. Furthermore, $^1O_2$ is likely to be more produced in PSII during drought stress. These produced ROS will ultimately decrease the photosynthetic rate both by disrupting and damaging the photosynthetic apparatus and by inhibiting the restoration of it. For example, ROS can damage the thylakoid membrane, chlorophyll pigments, and two proteins (D1 and D2) that are in the center of PSII, thereby disrupting PSII, and they inhibit the translation of D1 and D2. This causes a significant loss in photosynthesis during drought stress, which causes a great loss in growth.

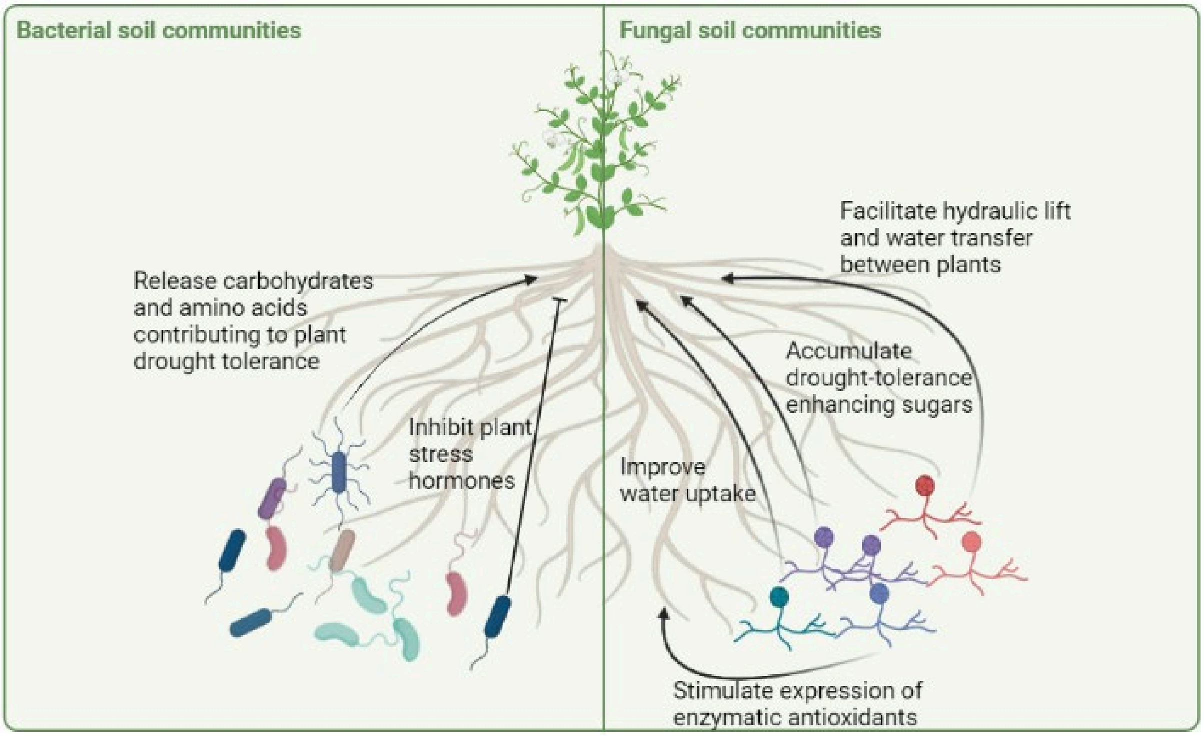

Figure 5. Overview of bacterial and fungal effects on plant health and growth during drought stress.

Besides being a key player in individual plant health and growth, AMF can also greatly influence the ecosystem and its drought resistance and resilience, and ecosystem multifunctioning. Up until 2021, this area was largely unexplored, but recently, studies have started to study empirically what the role of AMF is in resistance and resilience of ecosystems and how ecosystem multifunctionality is affected by AMF, under drought conditions and during elevated N deposition (Jia et al., 2021). As N deposition is not in scope of this thesis, only the effects of AMF during drought stress will be discussed. Before drought stress is induced, presence of AMF increases the plant community biomass, the Shannon-Wiener diversity, and total N uptake. The peak of N_2O flux, cumulative N_2O emission and N leachate are reduced in the grassland ecosystem when roots are colonized by AMF (Jia et al., 2021). During drought stress, the total community biomass, peak of N_2O flux, cumulative N_2O emission, and total N uptake were significantly reduced, while leachate of N after rainfall, after the period of drought, increased. Although the plant community biomass and total N uptake were lower under drought conditions, the presence of AMF still caused these properties to be higher than when AMF is absent. Additionally, the N leachate and peak in N_2O emissions were also decreased when AMF was present under drought conditions. However, the cumulative N_2O emissions were not affected by AMF under ambient watering conditions. During the recovery period, there were no significant differences between the plants that experienced drought stress and the plants that were held under ambient water conditions for the total biomass cumulative N_2O emissions, and leachate N. The Shannon-Wiener diversity and total N uptake were higher in the samples that were grown under drought conditions and the presence of AMF strengthened this increase even more. Additionally, when AMF was present, ecosystem multifunctionality was increased on average during events of drought and drought recovery, but also under ambient conditions. Most notably, ecosystem multifunctioning was significantly decreased under drought conditions in absence of AMF, whereas presence of AMF caused the difference to disappear (Jia et al., 2021). These results were linked to drought resistance. The drought resistance of the plant community biomass, N uptake, and leachate N were lower than 0 both is presence and absence of AMF, while only cumulative N_2O was lower than 0 when AMF were present. Additionally, the effect of drought on ecosystem multifunctionality was decreased when AMF was present. This leads to the conclusion that AMF increases the drought resistance of ecosystem multifunctionality.

Discussion

Due to anthropogenic challenges, ecosystems experience a lot of stress: increased exposure to pollutants, introduction of exotic species, and various abiotic factors initiated by climate change have major effects on the organisms that are part of the ecosystem and ultimately affect ecosystem functioning (Geisen et al., 2019). To be able to maintain healthy ecosystems and to ensure sustainable culturing of land for future generations, fundamental knowledge is key to advice policymakers and governments. In this review, the most recent findings of the effect of drought on the soil microbiome, with focus on bacteria and fungi, have been discussed, as the increase of events of drought is a global issue as an effect of climate change.

The most recent studies have shown that the microbiome is severely affected during droughts. Especially bacteria are prone to dehydration, with the abundance of monoderms mostly decreasing during drought. Fungi, on the other hand, are less susceptible to drought, likely because of their fungal networks that can provide access to the smallest pores in the soil containing water and nutrients (Jansson and Hofmockel, 2020). Even though fungi are less susceptible to drought, their community composition also differs during droughts (Yang et al., 2021). The changes in the composition of these microbial communities also have their influence on the vegetation in the ecosystem (Chaparro et al., 2012), which emphasizes the need to understand these changes. Although the studies currently available and largely discussed in this review gain a lot of information on the observed trends, there are still knowledge gaps that need attention to understand how drought affects ecosystems on earth.

First and foremost, many studies performed have gained their results and thus their conclusions under controlled experimental conditions, limiting only water. However, the conclusions based on these results may be spurious, as drought events have their own characteristics in nature. Drought itself already has differences in duration, intensity, recurrence interval, and peak intensity, which all affect the influence of the drought event on its environment (Mukherjee et al., 2018). Besides, many more factors than only water shortage may be altered during drought. For example, increased temperatures and extreme heatwaves are also associated with increased aridity, and additional factors like wind can also increase land degradation, ultimately influencing the organisms (Hermans et al., 2021). Although studying multiple factors makes it unclear what the real effect of the specific factors of climate change are on ecosystems, taking these additional factors into account is required for a complete overview of how climate change affects the global ecosystems and helps to enable us to maintain healthy ecosystems.

Besides the multiple abiotic factors that may be of influence on the organisms living in the ecosystems, organisms also greatly influence each other. As mentioned before, during drought stress, plants synthesize several compounds, including ROS, which influence the soil microbiome communities. Furthermore, plants are able to recruit beneficial microorganisms in the soil by excretion of secondary metabolites and additionally, the physiological form and location of the root system also influences the soil microbiome (Fang and Xiong, 2014; Soussi et al., 2016; Zhang et al., 2017; Naylor and Coleman-Derr, 2018). The other way around, rhizobia and fungi living in the soil microbiome also greatly affect plants: PGP rhizobacteria can for example initiate induced systemic resistance and rhizobacteria and fungi, under which

AMF, may be essential for plants to live and may even increase their tolerance and resilience to drought (Pieterse et al., 2014; van der Heijden et al., 2015; Mathur et al., 2019; Huang et al., 2020). However, still much is unknown about these species' interactions, co-occurrence patterns, and which factors influences the soil microbiome and what the effects of each specific species in the soil microbiome has on the ecosystem. It is important to understand the soil biodiversity, role of the specific present species, and the interactions between species to a detailed level in order to make good predictions on what soil biodiversity and changes in soil biodiversity may contribute to and change in the ecosystem and ecosystem functioning. If the contribution of specific species is fully understood, this knowledge could even be applied in agricultural practices, where inoculation with specific species or novel discovered natural products may help in sustainable land management. This idea is already widely used in agricultural settings. For example, in agriculture, several entomopathogenic fungi are already used as a biopesticide to protect the crops from the most severe insect pests, and some entomopathogenic fungi are even focused on in order to develop a biological control management system to control insect pests that also influence the human medicinal world, such as the increased abundance of ticks (Punya et al., 2015; Sullivan et al., 2022). Knowing the functioning of species, their transcriptomics, and their metabolomic and how these factors affect the ecosystem and how they affect organisms that are prone to drought, or other climate change-induced factors, might provide information that would help in the development of biological treatments or treatments with natural products in agriculture and will ultimately help us to maintain healthy ecosystems under the changing climate. However, development of these techniques and studying of the roles of specific organisms might be quite challenging, as it is difficult to make a general prediction on how microbiomes react on drought in different ecosystems. For example, in deserts, the annual rainfall is extremely low and organisms living in these areas are adapted to these circumstances. This results in the formation of biocrusts in dryland areas, which can also fulfill functions that are performed in soil microbiomes where water is not limited, such as the fixation of carbon and nitrogen, and soil stabilization (Chung et al., 2019). Therefore, in future studies, it is very important to use multiple different ecosystems and focus on one ecosystem per study, in order to create a realistic image, of which the combined found results could provide additional knowledge to the general idea on what the roles of specific species are and under which conditions they thrive. In studying this, novel keystone taxa might be uncovered as well, as many keystone taxa from different ecosystems are still lacking information or are yet to be discovered (Banerjee et al., 2018). If these discussed aspects are taken into account, this would all help in our complete understanding of the impact of climate change on the soil microbiome and on the ecosystem as a whole.

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