Title: The Understanding of Mycorrhizae Networks: A Historical Approach

Running Title: History of Mycorrhizae

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Abstract

The growth of mycorrhizal fungi into plant roots used to be viewed as a parasitic relationship between plants and fungi, where the fungal symbiont benefits and the plant host is harmed. Current research elucidates a mutualistic relationship. The mycorrhizae network assists the plants by increasing the capabilities for nutrient absorption in the soil. In exchange, the fungi receive carbon supply from the photosynthetic plants for growth. Our scientific understanding of other topics like species specificity, seed germination, and co-evolutionary influence of mycorrhizae and plants has also progressed. Additionally, we now understand that the mycorrhizal mutualism is not limited to the roots of a single plant species and the mycelium associated with it. Mycorrhizae networks have an ecological impact on other species within the community since networks can be developed among roots of multiple plants. Non-photosynthetic plants rely heavily on these interconnected mycorrhizae. In perspective, mycorrhizae influence the relationships between plants and fungi, along with the environmental factors, in the ecosystem. More specifically, the relationships of the plant roots and the fungal mycelium within the soil along with other microorganisms, like bacteria, influences overall productively above and below the soil.

Introduction

Fungi, once considered to be non-photosynthetic plants, are now understood to be heterotrophic organisms that play a large role in decomposition and comprise their own eukaryote kingdom (Cavalier-Smith 1998). From an ecological perspective, fungi play an essential role in nutrient movement, allocation, and cycling throughout the environment, influencing soil fertility, increasing biodiversity, and enhancing overall ecosystem productivity (Finlay 2008). The ecosystem services provided by the fungi extend beyond decomposition. In environmental conservation, fungi can restore landscape habitability by removal of contaminated waste via mycoremediation (Gupta et al. 2017). In pharmaceuticals, fungal metabolites, like mycotoxins, can be used to develop drugs against infectious diseases (Raut 2020). Beyond these contributions, fungi are notable for the mutualistic symbiosis with the roots of plants known as mycorrhizae, in which plant roots and fungal mycelia form physical connections and exchange resources. As much as 90% of land plants form mycorrhizal relationships with fungi (Feijen et al. 2018). Mycorrhizae networks describe a relationship between plants and fungi that connect more than one plant (Simard et al. 2012).

Fungi and plants relationships can be traced back as early as around 360 million years ago when mycorrhizae associations facilitated plant life on land. Fossil records of early nonvascular plants, like *Aglaophyton major,* during the Devonian period show the presence of vesicular arbuscular mycorrhiza (VAM). Preserved anatomical features of fungi associations indicate the presence of fungal endosymbionts that contributed to plant survival on land. The selective co-evolutionary pressures between plants and fungi benefit both species (Remy et al. 1994). Co-evolution is defined as how features of one population of species are affected by another which can in turn influence change in the original population (Janzen 1980). For example, the mycorrhizae can act as roots, absorbing nutrients from the surroundings, for nonvascular plants lacking roots. Rhynie chert fossils of *A. major* show meristematic regions of cells dedicated to VAM infection by fungi. In addition, fungi endophytes may have influenced the beginnings of lignification allowing plants to grow tall. Plants reciprocate by sharing

nutrients with fungi mutualistically (Remy et al. 1994). Therefore, early terrestrial plants with fungi relationships had a selective advantage over those that did not. Survival and reproduction are assisted by the presence of mycorrhizae networks (Malloch et al. 1980; Simard 2018). Strong molecular evidence supports early plant and fungi relationships in fungal species from the Ascomycota, Basidiomycota, and Glomeromycota phyla (Bonfante and Anca 2009). Mycorrhizae networks are generally categorized into two types being either endomycorrhiza, which forms arbuscules, or ectomycorrhiza, which forms Hartig net. The arbuscules form within the interior of root cells where nutrients are shared or exchanged between plants and fungi (Newsham et al. 1995). The Hartig net is a hyphal network surrounding the interior root cells (Martin et al. 2016).

Our understanding of mycorrhizal symbiosis has progressed in the past centuries. Advances in technology, as well as knowledge of plant physiology and the biochemical mechanisms between plants and fungi allow for a better understanding of mycorrhizae, and ultimately the development of applications in global ecology and environmental conservation. In this review, a historical analysis is presented to compare past conclusions to present day understanding of mycorrhizae.

Late 1800s and early 1900s

Mycorrhizae structure

The classification and description of mycorrhizae can be traced back to the early works of Frank (1885) in documenting symbiotic characteristics and observations between plant roots and fungal hyphae. The hyphae are the extensions or branching of the fungi that constitutes the mycelium network. Some of the mycorrhizae were described to be mantle-like in structure and surrounding the plant roots, while others invade within the plant roots. Observations detailed that the initial colonization of the plant with mycorrhizae begins shortly after gemination of the seed when the taproot system beings developing lateral roots. Roots that exhibit slower or ceased growth are heavily branched with hyphae while the longer growing roots, usually the primary central root, are less connected with hyphae.

Nature of mycorrhizal symbiosis

The relationships between fungi and plants through the mycorrhizae networks were originally concluded to be parasitic. The mycelium network grows over the plant roots and some root areas show signs of hypertrophy or growth of fruiting bodies of the mycelium (Frank 1885). The Cupuliferae plant, however, was observed not to be harmed in the symbiosis like in commensalism, where one species benefits, and the other species not affected. Despite this observation, the infective nature of the fungi on the plant roots was ultimately reasoned to be parasitic. Similarly, in other species of plants and fungi, the symbiosis between *Abies firma* and *Cantharellus floccosus* was also concluded to be parasitic since no observable benefit for the plant was noted (Masui 1926). In the root system heavily infected with mycelium, growth of the roots ceased. It was assumed that root growth inhibition is an injury caused by the mycelium infection. In orchid species, the fungi are able to thrive in orchid roots without evidence of the orchid benefiting from the presence of mycorrhizae (Curtis 1939). Orchid rootlets heavily infected with mycorrhizae networks diminishes the growth of the root. A common conclusion

from both studies (Frank 1885 and Masui 1926) are no notable evidence of plant derived benefits in association with fungi. Fungi and plants may associate in a method to benefit from each other's presence as stated in Frank (1885). However, no clear evidence was available in the early studies of mycorrhizae to determine nutrient flow between plants and fungi species to conclude that the symbiosis was not parasitic.

Optimal soil conditions for mycorrhizal growth

How fungi and plants form a relationship is a question proposed in observing the mycorrhizae. Mycorrhizae are exhibited in flood plains, with higher moisture levels, as well as dry environments with less moisture (Frank 1885). Separate experiments to test whether plants can be free of these parasitic-like mycorrhizae were performed by changing the growth medium into a liquid rather than soil (Masui 1926). Mycorrhizae were not able to develop in extreme wet medium or damp environmental conditions since the growth of fungal mycelium was limited. Instead, roots growing in soil are the ideal medium for fungal growth. The depth of the plant roots within the soil is also another factor influencing the growth of mycorrhizae networks. More superficial roots have more hyphae infestation compared to roots that are deeper within the soil. Endophytic mycelia were noted in salt marsh plants like *Armeria maritima* and *Glyceria maritima* (Mason 1928). Physical features observed from endophytic fungi in salt marsh plants including vacuolated cytoplasm and multiple nuclei were considered an indication of plant cell-fungal hyphae union. Fungi can form mycorrhizae networks with plants in different environments, but media without heavy moisture is the ideal condition for fungi relationship between plants.

Mycorrhizae specificity

Mycorrhizal fungi species vary in degree of specificity for forming symbiosis with one versus multiple plant species. Some fungi tend to form mycorrhizae relationships more often with certain plants than others. Such specificity between fungi and plants was observed in the early studies of mycorrhizae. Beech trees (*Fagus* sp.) were observed to be the only species inhabited with fungi even in the presence of other plant species like *Mercurialis perennis*, *Viola canina*, or *Oxalis acetosella* nearby (Frank 1885). The ectomycorrhizal type, *Rhizopogon luteolus,* was similarly observed to form mycorrhizae associations with pine species including *Pinus radiata, P. taeda,* and *P. caribaea.* It was originally concluded that *R. luteolus* is the sole fungus growing symbiotically with *Pinus* until another fungal type, *Boletus granulatus,* was also identified to grow in proximity under the same tree species. Laboratory cultures of different pine seedlings and *R. luteolus* revealed mycorrhizae networks developing from the region of inoculation. No data in laboratory studies involving *B. granulatus* supported a plant partner forming mycorrhizae with multiple fungi species (Young 1937). However, multiple cross studies were performed with different orchid and *Rhizoctonia* species to determine orchid fungal mycorrhizal specificity. It was found that orchid species can harbor many different fungal types and a single fungus can produce mycorrhizae networks in multiple orchid species (Curtis 1939).

Mycorrhizal effects on seed germination

The mechanisms and timing involving the formation of the mycorrhizae with the plant's root were not completely understood during early research of mycorrhizae. However, the longevity of the mycorrhizae network in the plant root systems correlated to the life duration of the plant organisms (Frank 1885). Since the seed represents the embryonic stage of the plant life cycle, studies of orchids and fungi association demonstrate whether orchids are dependent or independent on mycorrhizae networks for seed germination. Based on observations, Bernard (1904; cited within Curtis 1939) proposed that orchid seed germination is dependent on the presence of endophytic fungi, like *Rhizoctonia*, and that different species of orchid plants will always host the same mycorrhizal fungi species. However, Bernard's hypothesis was disproved by an experiment where plants from the orchid genus *Laeliocattleya* were grown without any fungal symbionts (Knudson 1930; cited within Curtis 1939). In conditions of good soil nutrition for plants, seed germination will occur with or without the presence of mycorrhizae. In contrast, in soil environments where conditions are not favorable, mycorrhizae networks are able to convert essential nutrients like sugars for root uptake, and maintain appropriate acidity levels to improve plant growth. Furthermore, Basidiomycete and Ascomycete mycorrhizal fungi, which are not closely related to the fungal symbionts of orchids, have also been shown capable of influencing seed germination in plants by detoxifying unfavorable soil conditions (Curtis 1939).

Despite decades of work, several topics still needed to be addressed regarding the mycorrhizal association between plants and fungi including: (1) The mycorrhizae structure, (2) the nature of the symbiotic relationship, (3) the fungal influence on seed germination, (4) the specificity of the association between plants species and fungi species, (5) the physiological mechanisms of symbiosis, (6) the environmental tolerances and influences of the fungi, and (7) the ecological interactions between plants and fungi in mycorrhizal associations.

Late 1900s to present day

Mycorrhizae structure

The descriptions of mycorrhizae networks in Frank (1885) describe the structures to be either external or internal to the root cells. These descriptions are now understood in greater detail and correlate to ectomycorrhizae and endomycorrhizae respectively. Endomycorrhizae have hyphae that invade the root interior and form arbuscules within root cortical cells. Ectomycorrhizae have fungal hyphae that also invade the root interior but does not form arbuscules within root cortical cells. Instead, ectomycorrhizae surround the cells within the roots (Malloch et al. 1980). Ectomycorrhizal fungi (EMF) and endomycorrhizal fungi (ENF) are the predominant types of mycorrhizal fungi. EMF, characterized by a Hartig net that surrounds the plant root cells, are generally associated with gymnosperms, inhabiting all *Pinaceae* species, but are also found in some angiosperms. EMF generally belong to the fungal phyla Basidiomycota and Ascomycota. ENF, characterized by the formation of arbuscules within cortical root cells, are generally associated with angiosperms (Marx 1980). ENF and EMF are not restricted to specific plant species (Simard 2018). Fungus and plant root interactions, therefore, are not entirely species specific.

Nature of the mycorrhizal symbiosis

Plants, in addition to being primary producers, are an essential component of ecosystem processes due to the interactions and associations with various organisms. Plant interactions with fungi and bacteria drive biogeochemical cycles within an ecosystem. An example is that disruptions to ecosystem stability due to losing keystone species can be stabilized through networks with fungi or bacteria or both (Simard 2018). The symbiotic relationship between plants and fungi used to be considered a parasitic relationship due to the lack of strong evidence of plant derived benefits (Frank 1885; Masui 1926; Curtis 1939). However, it is now understood from multiple studies (MacDougal and Dufrenoy 1944; Marx 1980; Allen et al. 2003; Simard 2018; Barto et al. 2012; Wyatt et al. 2014; Reinhardt 2007; Deepika and Kothamasi 2015) that the vast majority of mycorrhizal relationships between plants and fungi are mutualistic relationships where both species benefit from the other's presence. Sufficient evidence when examining fungi endophytes, especially in orchid species, show a mutualistic symbiosis between the developing fungal symbionts and the plant roots. Close associations, aided by arbuscules, enable nutrient exchange between plants and fungi. Organic compounds, like sugars, and trace elements, like phosphorous and nitrogen, from the soil are collected by the fungal mycorrhizae and transported to the plant. In exchange, carbon sources from the plant are shared with the fungi (MacDougal and Dufrenoy 1944).

Functions provided by the fungi include: more efficient water and nutrient absorption, increased resilience in the environment, and stimulating plant growth. In exchange, fungi utilize organic compounds produced by the plant, like carbohydrates and amino acids, for growth or reproduction (Marx 1980). Vitamins, minerals, and water collected from the soil by the mycorrhizae networks are transported from the hyphae to the plant roots positively affecting the plants. Additionally, plant communication through hormones like auxin and strigolactone is facilitated through mycorrhizae which are intertwined with multiple plants. Mycorrhizae networks in association with plants can also provide protection against root pathogens or root stress from parasitic nematodes. Therefore, mycorrhizae play a large role not only in plant regulation but also in environmental stability (Garg & Chandel 2011). The topology of the mycorrhizae networks can be seen in Douglas fir species where plant nutrients, defenses, and signaling molecules are transmitted between plant individuals by the means of mycorrhizae. This network enhances inter-plant communication and affects resource allocation, learning, and overall ecosystem productivity (Simard 2018). Therefore, extensive mycorrhizae presence facilities the functionality and growth of the plant with close nutrient exchange.

Formation of mycorrhizae is favorable as mycorrhizae enhances the function of the plant roots by acquiring soil nutrients and growing more numerously in locations where plant roots would not be able to proliferate. As a result, the plants invest less resources into root development and more in establishing mycorrhizal relationships. The carbon sugars that would have been used towards root development are instead traded with the fungi in exchange (Simard 2018). Mycorrhizae networks stimulate species diversity within a community by increasing the productivity of plants with assistance in absorption and cycling of soil nutrients which can influence further plant growth and interspecies interactions.

It is now understood that mycorrhizal relationships can provide mutual advantage to plant and fungal symbionts. However, not all mycorrhizal relationships are mutualistic. Further identification and classification of biodiversity within the vascular plants reveals certain plants that are parasitic with heavy reliance on the mycorrhizae networks. These types of plants, known as mycoheterotrophs, derive nutrition from the mycorrhizae since they do little or no photosynthesis and thus cannot synthesize nutrients on their own. In certain plant families like

Orchidaceae, some species of mycoheterotrophs are further classified as achlorophyllous, meaning they lack chlorophyll and photosynthesis cannot occur (Finlay 2008). From an evolutionary perspective, mycoheterotrophic plants that obtain nutrients from the mycorrhizae networks hold adaptive advantage compared to those that have relationships with other types of fungi. The mycorrhizae are connected within a same network with other autotrophic plants where nutrient flow between species is regulated within the mycorrhizae (Wyatt et al. 2014; Finlay 2018). Carbon supply can be allocated between neighboring connected plants and fungi which can increase the carbon received by the mycoheterotrophic plants by forming multiple mycorrhizae associations (Allen et al. 2003). Isotopes of carbon and nitrogen were used in tracing the path of nutrient flow in mycoheterotrophic plants that are achlorophyllous. Nutrients like carbon are obtained from the mycorrhizae connected with other autotrophic plants. Mycoheterotrophic plants are regarded as parasitic plants in association with fungi. Some Basidiomycetes fungi are associated in particular orchid species that are mycoheterotrophic. (Courty et al. 2011). In extreme cases, with orchid examples like *Corallorhiza,* mycorrhizae function in place of the plant organs needed for nutrient absorption or formation like in the leaves or roots (MacDougal and Dufrenoy 1944). Evidence shows carbon movement within the mycorrhizae networks to mycoheterotrophic plants. Therefore, mycorrhizae have ecological impact beyond fungi and photosynthetic plants.

Similar to how the nervous system acts as a network of communication fibers in humans and other animals, mycorrhizae networks are analogous for plant communities (Simard 2018). Chemical signals are the primary method of communication in below-ground networks with other organisms. These signals, termed info-chemicals, include plant hormones or secondary metabolites capable of eliciting a response when mobile in the soil environment. Mycorrhizae act as a passage for cellular signals to travel without interference or degradation within the soil. Since the mycelium is generally not species specific, nutrients and other substances flow among plant individuals through mycorrhizae. Allelopathic chemical movements are also supported within mycorrhizae to other neighboring species, which may result in stronger response than allelopathic chemicals diffusing through the soil (Barto 2012).

Fungi are able to assist plants in other processes besides absorption. Some inorganic compounds, like ammonium, are toxic and cannot be transported to the plant directly. Instead, the mycelium tissue converts ammonium into a nontoxic form, like glutamine, before transportation to the plant (Allen et al. 2003). In addition, fungi influence water regulation in response to evapotranspiration by the shoot system of the plant. An example includes the regulation of the stomata by hormones, like abscisic acid produced by the fungi below the soil, to elicit a response above the soil. Fungi in mutual symbioses exert degrees of control based on nutritional standards met by each partner. This is not limited to just mycorrhizae but is also found in bacterial and plant root nodule relationships. A linear relationship is exhibited in which the amount of resources received is the amount returned between partners (Wyatt et al. 2014). Limited nutrients, like nitrogen or phosphorous, retrieved from the fungi results in less photosynthetic products shared by the plants and vice versa. However, the mechanisms and biological exchange within the mycorrhizae networks is not consistent or fully understood. Cooperation between the symbionts is compared to the concept of the prisoner's dilemma. Natural selection favors mutual cooperation between fungi and plants that contribute equally in terms of resources. Mycorrhizae associations have co-evolved in certain lineages due to the benefits of the symbiosis (Wyatt et al. 2014). Studies agree that the relationship between fungi

and plants is largely mutualistic. The plants supply fungi with sugars and the fungi assist in water and trace element absorption within the soil environment.

Optimal soil conditions for mycorrhizal growth

Mycorrhizae networks found in various biomes vary in density within the soil based on moisture levels (Mason 1928; Masui 1926). These observations still stand in current research on mycorrhizae. In ecosystems like marshes, plants were also observed to develop mycorrhizae. However, the growth of the fungi is limited most likely due to the water-saturated soil (Read et al. 1976). Experiments with *Sorghum vulgare* roots and *Rhizophagus irregularis* tested in control, drought, and flooded condition show differences in phosphorous uptake by the mycorrhizae where 15-20% soil moisture is most optimal. Flooded or wet conditions resulted in the lowest phosphorous absorption compared to control treatments inoculated with the mycorrhizae fungi. Since mycorrhizae fungi grow optimally in aerobic settings, extreme flooding or wet soils can reduce the uptake of oxygen for the fungal symbiont to grow or perform symbiosis with the plants. As a result, a temporary parasitic state can occur in which the fungi receive carbon supplies from the plants without a return in exchange due to the inability of the fungi to perform its function (Deepika and Kothamasi 2015). Soil moisture impacts the relative abundance of mycorrhizae networks.

Mycorrhizae specificity

Mycorrhizae types exhibiting specific host-symbiont relationships include ericoid, arbutoid, monotropoid, and orchid in mutual symbiosis with Ericaceae, along with Ericaceae subfamilies, and Orchidaceae respectively (Simard 2018). Mycorrhizae networks are generally non-species specific, meaning that plants can associate with multiple species of fungi, or a single species of fungus can be a symbiont to multiple plants in a connected ground network (Allen et al. 2003). For example, orchid species do not have a specific mycorrhizae association with a single type of fungus. However, orchid mycorrhizae are generally arbuscular. *Caladenia* orchids tend to associate more frequently with *Sabacina vermifera* while other orchid species, like those of the genus *Diuris*, associate more frequently with *Tulasnella calospora* (Warcup 1971).

Mycorrhizal influence on seed germination

Seed dormancy is an adaptive response against germination in unfavorable environmental conditions. Sufficient moisture, specific environmental conditions, and the presence of the plant hormones gibberellins, can induce seed germination. Based on the environment, germination may not be favorable, as in deserts during dry periods. Some fungi influence seed germination, especially in *Diurus* species with *Tulasnella* (Warcup 1971). Evidence shows higher seed germination rates in the desert cactus *Opuntia streptacantha* inhabited with fungi species like *Phoma* spp., *Trichoderma koningii*, and *Penicillium chrysogenum* (Delgado-Sánchez et al. 2010). The fungus *Rhizoctonia,* which is common in orchid plant species, was also studied in association with the desert cactus *O. streptacantha.* The results show that germination rates were low, and therefore, *Rhizoctonia* has no influence on seed germination with the cactus plant. Fungi-seed relationships may be species exclusive like in the orchids. Early mycorrhizae formation from these fungi allow efficient germination since the fungi are able to erode the

protective layers of the seed, like the testa and the seed coat, reducing the mechanical strain required to open the seed to initiate germination. As a consequence, mycorrhizae networks have an influence in the early development of the seed plant.

Extensions and mechanics of mycorrhizae

Plant root signals, collectively referred to as the root exudates, influence the formation of mycorrhizae networks. Although the mechanisms of how endophytic fungi develop with the plant's root are still unclear, evidence shows chemical and cellular signaling from the plants guide fungi to locate and form an association with the plant's roots (Reinhardt 2007). The symbiotic relationships between plants and fungi are first initiated through a series of signals between the fungi and the roots. In situations where mutual agreement precedes the formation of an association, the cells of the plant roots and fungi hyphae interact to form a linkage known as an appressorium. Appressorium formation of the fungi in contact with the plant cell stimulates a reorganization within the plant cell's cytosol to form a pre-penetration site where the hyphae will eventually enter through the cell's plasmalemma. These interactions between the host plants and the fungi symbionts further support a mutualistic symbiosis with cellular communication pre-and post-formation of the mycorrhizae. Plants possess degrees of control in allowing the formation of mycorrhizae in response to beneficial exchange between partners. Plants will continue to supply carbon compounds produced in photosynthesis to the fungi in exchange for nutrients absorbed by arbuscular structures. A mutualistic symbiosis is supported between plants and fungi through the formation of these mycorrhizae networks (Garg and Chandel 2011; Reinhardt 2007).

Plants do not only form mutual relationships with fungi as mycorrhizae networks. Plant nodule symbiosis with symbiotic nitrogen-fixing bacteria is also mutualistic (Reinhardt 2007). Furthermore, the plant can form a symbiosis with fungi and bacteria within the soil simultaneously as a tripartite association (Bonfante and Anca 2009). Endobacteria can inhabit the mycelium of the fungi just as the fungi can inhabit the interior of the plant's roots. Therefore, the mycorrhizae can be viewed as a connection between multiple organisms. The tripartite relationships between bacteria, plants, and fungi are ecologically efficient. Chemical signaling and environmental stress resiliency, aided by helper bacteria, improve the growth capabilities of the host plant (Bonfante and Anca 2009). The endobacteria also affect mycelium growth within the soil Chemical signaling and influences on gene expression between plants and fungi play similar roles in the establishment of the rhizosphere. The rhizosphere consists of the plant's roots in symbiosis with bacteria within the soil that affect plant nutrition and growth by assisting in: absorbing soil nutrients, eliciting defense responses both in the shoot and root system, and enabling stress environment resiliency in exchange for carbon supply. A common symbiosis receptor pathway, like the stages of cell signaling, is described where nod factors, which are signaling molecules produced by the bacteria link to receptors on the plant's membrane to elicit a transduction response within the plant cell (Reinhardt 2007). The response, which is the transcription of the plant's symbiosis genes, results in cellular reorganization of the plant's cells to allow an association with either the fungi or bacteria. Formation of the rhizosphere is attributed to plant root exudates, like metabolites, that attract bacterial microbes. (Bakker et al. 2013). Mycorrhizae relationships between plants and fungi extend into the rhizosphere facilitating symbiosis and regulation of overall soil state. The root exudates and strigolactone secreted by the plant influence the initial formation of the network features like appressorium.

Fungi along with other soil microorganisms are important influences in environmental ecology and overall plant productivity. Fungi and bacteria can decompose, recycle, and acquire resources, in exchange for sugar (Finlay 2008; Bonfante and Anca 2009). In an ecological view, mycorrhizal fungi and bacteria within the rhizosphere can compete for plants that supply carbon photosynthates. Conditions experienced by plants can increase participation in mycorrhizal mutualisms. For example, seedlings of grass species like *Festuca ovina* or *Deschampsia flexuosa* growing in nutrient deficient environments tend to exhibit extensive mycorrhizae networks (Read et al. 1976). Furthermore, strong competition between neighboring plants also stimulates increase in mycorrhizae networks as the symbiont mycelium functions to increase surface area for nutrient absorption. Even plant Families that have not been widely observed to associate with mycorrhizae, like Juncaceae and Cyperaceae, will develop mycorrhizae networks in times of nutrient stress, which may aid in competition against other plant species.

Discussion

A comparison between historical and contemporary studies of mycorrhizae networks is presented. The understanding of mycorrhizae has changed since the late 19th and early 20th century. Early work describing the morphological and physiological aspects of mycorrhizae provided the fundamentals upon which newer elucidations of mycorrhizae were based. Common conclusions from early studies regarding mycorrhizae included: the relationships between fungi and plants were thought to be parasitic; fungi are present throughout the life of the plants starting early in seed germination, although the extent of whether the mycorrhizae influence seed germination is unclear; mycorrhizal fungi can be found in multiple environmental conditions; and some fungi exhibit species specific associations with certain plant species, while other fungi in mycorrhizal associations are generalists. Research in the 21st century showed mycorrhizae networks to be fundamental ecological features of plants and other microorganisms in the soil. This intensive below ground network of plant roots, fungi, and other microorganisms like bacteria, facilitates a system of underground communication between multiple organisms and species. Figure 1 depicts a general timeline of the progress that has been made in the understanding of mycorrhizae networks.

To summarize our current understanding of mycorrhizae, the relationship between mycorrhizal fungi and plants are primarily mutualistic, with mycoheterotrophic plants as an exception. These associations can be traced back to the early vascular plants where plant life on land was facilitated by mycorrhizae networks. Mycorrhizae networks can extend into other neighboring plant roots and facilitate the movement of resources in multiple interconnected paths impacting the overall community or ecosystem in nutrient cycling and flow (Allen 2003). Conclusions that fungi do not have influences on seed germination (e.g. Curtis 1939) are instead corrected in a study by Delgado-Sánchez et al. (2011) where seed germination of the desert cactus, *Opuntia streptacantha,* was influenced by the fungus. Therefore, mycorrhizae can develop and influence the early stages of seed germination. The majority of plants and fungi species are not limited to species-specific interactions. Instead, a plant host can accommodate multiple fungi species, and a single fungus species can be a symbiont of multiple plants. In certain plant taxa, like Orchidaceae and Ericales, arbuscular mycorrhizae are generally specific to those plant types. Mycorrhizae networks are intertwined with other networks associated with different plant roots forming a pathway for nutrient movement between fungi and plants (Bonfante & Anca 2009). Depending on the relationship, different mycorrhizae networks can be

developed in an endophytic fashion, which is common in the fungal phylum Glomeromycetes, in Ericoid fashion in the Ericales plant order, or in an ectophytic fashion. Plant root exudates and hormones are important factors in signaling, communication, and establishment of mycorrhizae networks. These effects extend to bacteria of the rhizosphere by root nodule symbiosis (Reinhardt 2007). Mycorrhizae networks enhance plant nutrition in addition to their role as natural decomposers. Nutrient cycling within the soil impacts ecological interactions of organisms in the community and increases productivity.

      Increasing human population increases demands for food production. However, current agricultural methods do not meet the recommended requirements of a balanced diet. Consumption of meats require large area of land dedicated to raising livestock which not only depletes the land available for crops, but also increases greenhouse gas emissions into the atmosphere. Instead, a shift to plant-derived foods as sources of protein can not only reduce greenhouse gas emissions, but also promote environmental sustainability and human health (Bahadur et al. 2018). Fungi and microorganisms form symbiotic associations with plants which increase plant productivity, while performing other functions like soil detoxification and nutrient cycling between organisms. (Garg & Chandel 2011). Utilizing these interactions between fungi and plants in agricultural practices can increase crop production based on resource allocation from above and belowground exchange (Wyatt 2014). These can be solutions when addressing human population growth. Despite the progress made in understanding mycorrhizae and how it can benefit humans, more research is needed in elucidating the mechanism involved with mycorrhizae formation and how nutrient movement are allocated between species.
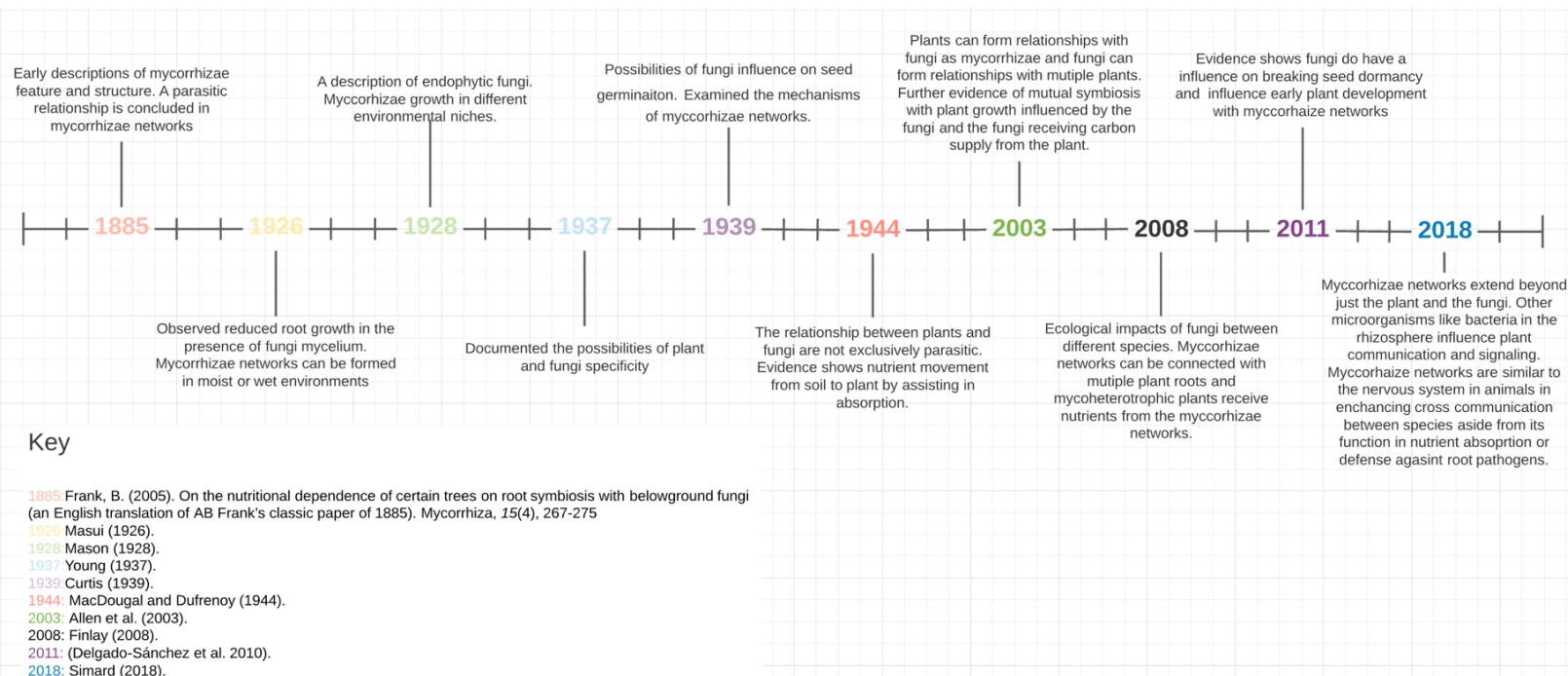

Figure 1. The timeline depicts how understanding of mycorrhizae has changed and progressed. The years shown (not to scale) correspond to the works of the authors in the colored key respectively. This timeline does not include every research work of mycorrhizae, but instead

highlights manuscripts cited in this review that represent major developments in the science of mycorrhizae.

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