

The global distribution patterns of Mycorrhizae

An updated review of its underlying mechanisms.

Bachelor's thesis
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Contents

Abstract	3
Introduction.....	3
The underlying mechanisms of ericoid mycorrhizae	4
Saprotrophic abilities	5
More evidence for saprotrophic abilities	5
The underlying mechanisms of ectomycorrhizae	6
Greater decomposing abilities than previously thought.....	6
Are ectomycorrhizae saprotrophic?	7
The underlying mechanisms of arbuscular mycorrhizae.....	8
Arbuscular saprotrophs?	9
Arbuscular mycorrhizae very able phosphorus scavengers	10
Global patterns of nutrient availability	10
Discussion and conclusion.....	11
Ericoid mycorrhizae.....	11
Ectomycorrhizae.....	12
Arbuscular mycorrhizae.....	12
References.....	13

Abstract

The global distribution pattern of mycorrhizae hypothesized by Read in 1991 described the underlying mechanisms in great detail. In 2003 he reevaluated this hypothesis and provided an review of new evidence for the mechanisms underlying his hypothesis. In this thesis the Read hypothesis will be evaluated once more. Recent studies will be used in a literature study to described the underlying mechanisms for the global distribution pattern into further detail. The literature found, showed that the hypothesis of Read was fairly accurate. Combining biogeographical and plant and fungi physiological evidence were used to create an overview of the distribution of mycorrhizae.

Introduction

In 1885, A.B. Frank was the first to describe a fungi root symbiosis. He studied the possibility of truffle cultivation. Following observations and experience he hypothesized that true truffles establish a connection of the mycelium with living tree roots. Frank found this to be true and named this phenomenon fungus-root.¹ To us fungus-root is known as mycorrhizae, mykós is Greek for fungus and riza is Greek for roots. Back then little was known about the importance of these fungi to the (plant)world. Over a hundred years of research have shown that mycorrhizae do not just provide the beech, hornbeam and oak with nutrients, as described by Frank. They supply most the plants of this planet with nutrients.

In the last hundred years of mycorrhizal research, a lot of comprehensive literature summaries were made.^{2,3} Read (1991) was the first to combine such literature summaries to theorize a global pattern in the distribution of mycorrhiza.⁴ The Read theory describes the global distribution of arbuscular, ericoid and ectomycorrhiza. This distribution is based on the differences of climatic and edaphic conditions around the world. The climatic factors, such as the amount of precipitation and differences in temperature, shape a gradient of decomposition rates and thus of an accumulation of organic matter. The edaphic factors shape the distribution of mycorrhizae on a smaller level. At the local level, quality of soil nutrient resource becomes more important than climate. Ericoid mycorrhiza exist on acidic mor humus soils of high latitudes and altitudes, with high amounts of organic matter. Ectomycorrhiza occur in forest ecosystems of intermediate latitude and altitude, intermediate amounts of organic matter can be found here. Arbuscular mycoorrhiza live in symbiosis with herbaceous and woody plants on mineral soils at lower latitudes (fig. 1).

Even though Bundrett (1991) did not create a similar map of global distribution, he did summarize a extensive amount of data on where mycorrhiza species were found. If these data were to be mapped, it would show a similar picture as fig. 1. Bundrett concluded that back in 1991, there was just a little evidence in favour of the hypothesis that climatic and edaphic factors influence the global distribution of mycorrhizae.

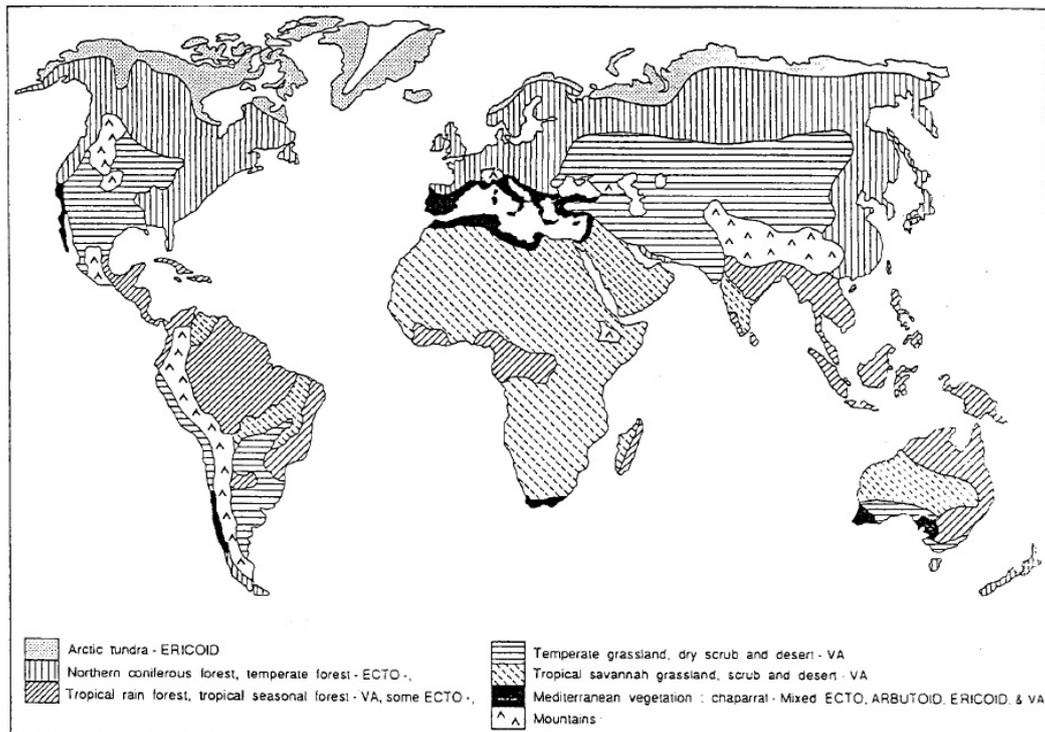


Figure 1. The global distribution of climates, along with their predominant mycorrhiza species.⁴

In this thesis the theory on the global distribution of mycorrhizae will be discussed. This theory is based on the fact that climate has an effect on the speed of decomposition and the therefore dominant form of nutrients, organic or inorganic. Nutrients become increasingly limited for plants when they are present in an organic form. It is favourable for plants to become a host of mycorrhizae, because they have a greater ability to take up organic nutrients. Thus climate has an influence on the distribution of mycorrhizae. The underlying mechanisms of this distribution will be reassessed once again, as already done by Read in 2003,⁵ using new observational and experimental evidence.

The underlying mechanisms of ericoid mycorrhizae

Ericoid mycorrhizae occur in the far north and mountainous regions places of the world. The high latitude and altitude give rise to climatic conditions which are very stressful for autotrophs. Low average temperatures, a short growing season, strongly leached and nutrient poor soils⁶ are the characteristics of these ecosystems. Nutrients are not absent in these soils, on the contrary, a lot of nitrogen and phosphorus is present in the humus layer. However, up to 90 to 100% of the total nitrogen in the soil is organic matter⁴. Leaching and the therefore lowering of the pH ensures an inhibition of the mineralization of nitrogen and phosphorus. Plant litter is not broken down and the organic acids, as well as the toxic metals from this litter acidify and toxicify the soil even further. The acidity of the soil slows the growth of plants and thus plant tissues have low nitrogen content. Another consequence of the acid soil is that the plants create high amounts of lignin, polyphenol and organic acids. A low tissue nitrogen content and the plant compounds slow decomposition even further and the organic acids decrease the pH. The plants create a feedback loop in which the stressful conditions are safeguarded. This ensures their ability to outcompete other colonizing plants, that are not adapted to these harsh conditions.

Plants living in the ecosystems of high altitudes and latitudes have adapted to these harsh conditions. Yet, living without their symbiotic fungi would severely decrease their ability to grow on these acidic soils. Ericoid mycorrhizal infections grant access to another source of nitrogen. Ericoid endophytes have the ability to utilize the nitrogen stored in amino acids, peptides and proteins^{7,8,9}. To some extent, ericoid mycorrhizae are capable of degrading chitin, lignin, tannin and organic acids, major components of organic matter in humus layers. The latter two are used by the ericoid endophyte as a carbon source. Metal regulation is one more problem ericoid plants have to deal with. Low soil pH increases the possibility of metal toxicity, but the organic matter can chelate the metal ions, thus making them inaccessible to plants. The mycorrhiza has got a high affinity system for metals if needed. When metals are readily available, this mechanism shuts off.

Saprotrophic abilities

In 1991 Read showed the ability of Ericoid mycorrhizae to degrade certain structural components of dead plant material. In 2003 it had been shown that ericoid endophytes secrete hydrogen peroxide and hydroxyl radicals to degrade some of these components, such as lignin, polyphenols and tannin.⁵ The secretion of hydrogen peroxide and hydroxyl radicals is similar to the manner in which “brown rot” fungi degrade lignin.¹⁰ “Brown rot” fungi being one of the most common decomposers in the world.

Next to dead plant material, the organic matter which makes up the humus layer also consists of a lot of fungal necromass. The fungal necromass originated from the mycorrhizae itself, or “white and brown rot” fungi. An important structural part of the fungal cell wall is chitin. Kerley & Read showed that Ericoid mycorrhizae can break down chitin and can assimilate its subunits. The ericoid endophytes even degrade and assimilate fungal necromass of itself.¹¹

Lastly, Read and Moreno showed experiments with plants that were supplied with necromass (created by Read and Moreno) grow significantly better when infected with ericoid mycorrhizae, than plants that are not infected. The nitrogen in the necromass is almost completely recycled by the ericoid mycorrhizae. The mechanisms described above all are saprotrophic mechanisms which enhance nitrogen availability. Plants infected with ericoid mycorrhizae are able to skip a decomposition step in reclaiming nutrients from organic matter, which is the major nitrogen source in these systems

More evidence for saprotrophic abilities

In the decade after Read and Moreno revised the mechanisms underlying the global distribution of ericoid mycorrhizae, the emphasis is laid on further examination of the saprotrophic abilities of ericoid endophytes.

It was already known that ericoid fungi have some ability to degrade lignin, polyphenols and tannin, using hydrogen peroxide. A recent study has shown that ericoid mycorrhizae are also able to secrete several enzymes such as peroxidase, tyrosinase, laccase and cellulase.¹² Though ericoid mycorrhizal species differ in their capacity to fabricate and secrete these enzymes, all species seem capable to secrete at least some enzymes. In 2011 genetic evidence for the ability to secrete enzymes was found. Gene sequences for multicopper oxidases, or polyphenol oxidases, were found in ericoid mycorrhizae.¹³ Multicopper oxidases are a group of enzymes with very diverse functions, including lignin degradation¹⁴, tissue development and melanin biosynthesis¹⁵. A group of important enzymes of the multicopper oxidases are the laccases. They are thought to be very

important for the decomposition of organic matter in soils and they aid in the release of nutrients.¹⁶

Wurzburger et al. (2011) also found evidence in support of the global distribution pattern by Read. A greater fungal richness was found on roots in organic horizons than in mineral horizons. This suggests that the ericoid mycorrhizae have a preference for organic nutrients.

The underlying mechanisms of ectomycorrhizae

Ectomycorrhizae dominate the forest ecosystems at intermediate latitude and altitude. The vast forests of the northern hemisphere, as well as parts of the tropics and the southern hemisphere are home to the ectomycorrhizae.⁴ Even though the speed of litter decomposition has increased at these latitudes, it is still relatively slow. Organic matter accumulates on these soils. The quality of the organic matter varies from acidic mor humus, through intermediate moder to more alkaline mull humus. The mor soils occur at the higher latitudes and altitudes and organic layer is complemented with an ericoid understory. At lower latitudes and altitudes, the alkaline mull soils are shared with arbuscular mycorrhizae. These soils, as are the ericoid mycorrhizal soils, are not limited in nutrients. However, mineralization of nutrients is inhibited to some extent and because of this a lack of mineral nutrients arises. The rate of nitrogen mineralization is so slow that nitrogen becomes the limiting growth element in these ecosystems.^{17,18} The rate of mineralization in these ecosystems is influenced by acidity of the soil and seasonality of climate with low temperatures and surface drying.

As with ericoid mycorrhizal infections, plants infected with ectomycorrhizae have the ability to access a nitrogen source other than mineralized nitrogen. Ectomycorrhizal fungi can fabricate polyphenol oxidase¹⁹, cellulase²⁰, phosphatase²¹ and carboxypeptidase. They have proteolytic capabilities, the possibility to obtain the nitrogen stored in protein.²² However, the capability to obtain nitrogen from protein differs between species. Some ectomycorrhizal fungi have a low proteolytic potential and are still dependent upon the mineralization of nitrogen. Having the ability to recycle proteins is very important in these nitrogen limiting soils. Almost 20% of the nitrogen in the organic layer is stored in proteins of fungal necromass.

Although some ectomycorrhizal fungi have proteolytic abilities, in 1991 it was still thought that ectomycorrhizae were incapable of the degradation of more complex structures, such as lignin.

Greater decomposing abilities than previously thought

All the ectomycorrhizal studies up to Read (1991) merely hinted at the decomposing abilities of these fungi. Even though ectomycorrhizae generally demonstrate lower levels of saprotrophic abilities and some ectomycorrhiza show no decomposing activity at all, they have been found able to decompose organic matter, extract the nutrients from them and transport them to their symbiotic hosts.

The fact that DNA sequencing has become more and more available, has enabled scientists to study the genes associated with the saprotrophic abilities of ectomycorrhizae. A 2001 study found that around 68% of the 40 ectomycorrhiza species examined contain at

least one gene which codes for the enzyme lignin peroxidase and several of these also contain genes which code for manganese peroxidase.²³ These enzymes both have a function in the degradation of lignin. In 1991 ectomycorrhiza were thought to be incapable of degrading lignin.

Next to the degradation of lignin, other decomposing capabilities of ectomycorrhizae were brought to light in the decade following Read (1991). Back then it was already known that ectomycorrhizae produced cellulase, an enzyme which degrades cellulose in plant cell walls. Research showed that ectomycorrhizae can also degrade pectin²⁴ and hemicellulose²⁵, other plant cell wall components, as well as cellobiose²⁶, a disaccharide formed in the breakdown of cellulose. Ectomycorrhizae were also found to be able to degrade plant cuticles through the use of fatty acid esterase.²⁷ Observational studies have shown that ectomycorrhizae do not just have the potential to fabricate these enzymes, they have shown that infected soils do have enhanced levels of these enzymes.^{28,29} Ectomycorrhizae are able to degrade organic matter in a similar manner in which conventional decomposers seem to do. However, ectomycorrhizae show far less activity in expression of exoenzymes when compared to actual decomposers.³⁰ It is thought that ectomycorrhiza therefore exploit specific parts of the soil, to avoid competition with specialist decomposers. Other than this very local scale of distribution, the proteolytic abilities of ectomycorrhizae seem to be following a trend on a larger scale. Studies along a transect from north to south through Europe have shown that these abilities are strongly expressed in the mor humus soils in the north and decreases going south, to the mull humus soils.^{31,32} This trend also occurs in more local transects in North America.³³

Besides the ability of ectomycorrhizae to obtain nutrients from proteins and other cellular compounds, they have also been shown to be able to degrade more complex structures, such as pollen³⁴ or necromass.³⁵ The vast temperate and boreal forests of the earth have an annual cycle of pollen production. A very small fraction of this pollen is used in the reproduction of trees. All the pollen that is not used, returns to the ground. The nutrients stored in the pollen are resorbed by the soil. An experimental study by Perez-Moreno and Read hypothesized that pollen could be used as a nitrogen and phosphorus source for ectomycorrhizal plants. The nitrogen and phosphorus contents of pollen supplied to microcosms with mycorrhizal plants was reduced by 75 and 97% after 115 days. For the nutrient contents of pollen supplied to nonmycorrhizal plants this was just 42 and 35%. Therefore, it seems that ectomycorrhizae are able to use pollen as a nutrient source.

As was known in 1991, a lot of nitrogen and other nutrients are stored in necromass. Perez-Moreno and Read tested the ability of ectomycorrhizae to release nutrients from nematode necromass. Again, ectomycorrhizal infections showed a strong reduction in the nitrogen and phosphorus content of this necromass, compared to noninfected microcosms. In 2001 it was suggested that ectomycorrhizae do not only reduce necromass, they also predate on soilfauna directly. It was observed that collembolan death rate increased in the presence of the ectomycorrhizal fungus *Laccaria bicolor*. Observations showed that *Laccaria* immobilized the collembolans before infection, possibly using a paralyzing toxin.³⁶

Are ectomycorrhizae saprotrophic?

All the studies up to ten years ago were keen on describing the saprotrophic abilities of ectomycorrhizae. In the following decade these abilities were critically reassessed. It now seems that there is more to these abilities than previously thought.

The decomposing abilities of ectomycorrhizae were brought to question in an study by Talbot et al. (2008). Talbot et al. came up with the “Coincidental Decomposer Hypothesis”.³⁷ This hypothesis states: “that mycorrhizal fungi decompose soil carbon as a consequence of mining soil for other nutrients.” Experimental evidence is found in favour of this hypothesis.³⁸ The evidence shows that ectomycorrhizae primarily decompose complex organic compounds which hold nitrogen. Of course, these compounds are not composed of merely nitrogen. They also hold other elements such as phosphorus and carbon and thus take these up by “coincidence”.

Although most ectomycorrhizae take up carbon by coincidence, some of them do “knowingly” degrade carbon. Seventeen to 54% of the ectomycorrhizae tested were able to produce enzymes that break down carbon-rich biopolymers, to 83 to 90% of the tested species which could decompose nitrogen containing biopolymers.³⁹ It seems that the decomposition of nitrogen-rich molecules is a more important function than the degradation of carbon-rich biopolymers. The amount of carbon degradation by ectomycorrhizae is still marginal compared to the amount degraded by “true” saprotrophs. Some ectomycorrhizal species have even been shown to be deprived of genes coding for cell wall degrading enzymes, others are severely reduced in the number of genes coding for these enzymes.^{40,41} The saprotrophic capabilities of ectomycorrhizae varies between ectomycorrhiza species. Thus the ability of a mycorrhizal ecosystem to degrade organic matter is dependent on the species composition.

It would seem that ectomycorrhizae are not true saprotrophs they were thought to be in the previous decade. A lot of evidence found in the decade following Reads hypothesis is based on a few mycorrhiza species which can easily be grown in culture. These abilities still have to be determined for a lot of species.

The underlying mechanisms of arbuscular mycorrhizae

Arbuscular mycorrhizae become increasingly dominant moving towards the equator. The lower latitudes, with increasing mean annual temperatures, are home to this form of mycorrhizae. This is the most abundant mycorrhizal species on earth, up to 80% of all plant species that can form symbiotic relationships with fungi do so with this form of mycorrhizae.⁴² Because of the increasing temperatures and transpiration rates, the leaching of the soil found in higher latitudes tends to decrease and instead of acid, soils of lower latitudes become increasingly alkaline.⁴ The higher pH and higher temperatures are favorable for the soil fauna. Numbers and activity of bacteria increase and so does the decomposition of organic matter. Because of this high rate of decomposition, nitrogen is not limiting anymore. Phosphorus is the limiting nutrient of these ecosystems, because of the high pH of the soil. This reduces the availability of phosphorus, with a pH higher than 7,5, phosphorus forms insoluble compounds with calcium.⁴³ Plants and their symbiotic fungi thriving here would have to be adapted to these conditions.

Plants forming a relationship with arbuscular mycorrhizae have been shown to be dependent upon infection with mycorrhiza for a steady supply of phosphorus.⁴⁴ By determining the phosphorus to nitrogen ratio, it was found that as seed reserves are being depleted and P:N ratio drops. Once the infection has spread, P:N ratio stabilizes. The arbuscular mycelium has a very well developed ability to utilize the available phosphate

resources in the soil.⁴⁵ The less accessible phosphate pools are made available using alkaline phosphatases.⁴⁶

A secondary function of arbuscular mycorrhizae for infected plants is the increased uptake of water. A long time this was thought to be a relic of phosphorus uptake.⁴⁷ However, it had been shown that the increased water uptake has nothing to do with the uptake of phosphorus. Plants of the same size and phosphorus content have been shown to have greater transpiration rates when infected.⁴⁸

Arbuscular mycorrhizae have another very striking feature which sets them apart from the ericoid and the ectomycorrhizae. Using $^{14}\text{CO}_2$, it had been shown that carbon transfers could occur through the hyphae of arbuscular mycorrhizae.⁴⁹ This can also be achieved by the other mycorrhizae. The striking part is that these carbon transfers occurred from one infected plant to another. This study even showed the transportation of carbon to have a preference for shaded plants over illuminated plants. It would seem that natural plant communities are functionally intertwined by their arbuscular mycorrhiza.

Arbuscular saprotrophs?

Arbuscular mycorrhizae seem to function as an extension of the roots. Their abilities being mineral nutrient and water uptake. Apart from these abilities, no other features were found. Research in the 1990's and early 2000's hints at some novel abilities.

Ericoid and ectomycorrhiza have been shown to be able of at least some form of saprotrophic degradation of organic matter. However, there is one example of a arbuscular mycorrhizal specie, *Glomus hoi*, which increases decomposition organic nitrogen.⁵⁰ Using ^{15}N and ^{13}C Hodge et al. showed that the mycorrhiza enhanced the release of ^{13}C and uptake of ^{15}N and the nitrogen gain in the plants could be related to the hyphal density in the organic matter. A analysis of the microbial community in the soils used, showed no qualitative differences between the infected and uninfected soils. It was therefore concluded that *Glomus hoi*, is involved in the decomposition of organic matter.

Read and Perez-Moreno found it very peculiar that the phosphorus scavenging abilities of arbuscular mycorrhizae weren't studied into further detail. As stated, there is at least one known arbuscular mycorrhizal specie has got saprotrophic abilities, it could very well be that there are species which have the ability to mobilize phosphorus from organic matter. The first to show this were Tarafdar and Marschner.⁵¹ They found that arbuscular mycorrhizal contribution, of *Glomus mosseae*, to the total phosphorus uptake by plants (*Triticum aestivum*), was significantly greater when supplied with organic phosphorus compared to inorganic phosphorus. In the latter situation, mycorrhiza contributed for 22-33% of the total phosphorus uptake, to 48-59% when supplied with an organic source. They also showed that arbuscular mycorrhizae produces phosphatases, which can degrade organic phosphorus. However, when repeated by Joner et al. these results were not found.⁵² Though, it should be said that Joner et al. used different mycorrhiza and plant species. In 2000 another arbuscular mycorrhiza, *Glomus intraradices*, was found which has the capability to degrade organic phosphorus sources.⁵³ Jones et al also tested these results and came to the same conclusion, *Glomus intraradices* is possible of degradation and transfer of organic phosphorus.⁵⁴

Even though sound evidence is found for the fact that arbuscular mycorrhizae do have some ability to degrade sources of organic phosphorus, it has only been shown in a couple of species. A lot of species will still have to be examined.

Arbuscular mycorrhizae very able phosphorus scavengers

In the previous decade of research, it was hinted that arbuscular mycorrhizae have got saprotrophic abilities, though a lot of arbuscular mycorrhizal species were still to be examined. This decade a lot of those studies have been performed and new evidence has been found.

A lot of scientific attention had been drawn towards the phosphorus scavenging abilities of arbuscular mycorrhizae this decade. It has been well established that infection with arbuscular mycorrhizae often enhances phosphorus uptake of plant roots and thus improves plant growth.⁵⁵ A significant amount of the phosphorus in soils is unavailable to plants because of the strong adsorption of phosphate to aluminum and iron hydroxides.⁵⁶ Arbuscular mycorrhiza can increase the phosphorus uptake from these insoluble sources.⁵⁷ It seems that arbuscular mycorrhizal plants rely strongly on their symbiotic fungi for the uptake of this plant growth limiting nutrient. Fitter proposed the C-for-P hypothesis.⁵⁸ Plants and mycorrhizae exchanged their “products” at the arbuscular interface. Plants provide the fungi with photosynthates and the mycorrhizae supply plants with phosphorus.

It was already known that at least some arbuscular mycorrhizae are able of the capture of organic nitrogen compounds.⁵⁰ This decade, more studies have shown arbuscular mycorrhizal abilities to mobilize nitrogen from organic sources.^{59,60} However the same problem arises as in the last decade, the studies showing these results are mostly based on one family of fungi, namely the Glomeraceae. When tested in the fungal family of the Gigasporaceae, these abilities were not found.⁶¹ Though some arbuscular mycorrhizae are capable of the capture of organic nitrogen, they do not have direct saprotrophic abilities. **Fout! Bladwijzer niet gedefinieerd.** It is possible that these mycorrhizae affect the degradation of organic matter indirectly, through modification of the microbial community.⁶² Some arbuscular mycorrhizae, as those in the family of the Gigasporaceae, remain dependent on saprotrophic microorganisms for the decomposition of organic matter and release of inorganic nitrogen ions. It has been shown that arbuscular mycorrhizae obtain nitrogen from the soil and transfer a substantial part of it to the roots of the host plant. However studies trying to show the direct benefits for plants of mycorrhizal nitrogen uptake find little evidence for these benefits. Plants infected with arbuscular mycorrhizae showed no increase of nitrogen gain or plant biomass.⁶³

Arbuscular mycorrhizae have evolved to be very effective phosphorus scavengers and can take up this nutrient in numerous forms. They also have the ability to take up nitrogen. Though for the decomposition of organic matter, still rely on saprotrophic microorganisms.

Global patterns of nutrient availability

As described, rates of decomposition and nutrient limitation are very important in determining the species of mycorrhizae. These factors have forced the mycorrhizae to evolve specific means of nutrients absorption and potential saprotrophic abilities.

Studies using global data sets of leaf nitrogen and phosphorus have shown that nitrogen phosphorus ratio decreases with an increase in latitude and the N:P ratio increases with increasing mean annual temperature.^{64,65} This shows that phosphorus is indeed limiting in the tropics, probably because the tropic soils are very old.⁶⁶ Nitrogen becomes more and more limiting as one progresses towards the poles. The limitations of nitrogen and phosphorus have an effect on the nutrient resorption in leaves. When nutrients are limiting,

plants minimize nutrient losses by resorption of nutrients from senescent leaves. Yuan and Chen showed that the nitrogen resorption efficiency (the percentage difference in nitrogen concentration between green and senescent leaves) increases with latitude. The phosphorus resorption efficiency decreases with latitude.⁶⁷ Nutrient resorption by leaves has its effect on litter. The quality of the litter decreases, because of the resorption of nutrients. The quality of litter, along with a few other factors, such as mean annual temperature and total nutrient elements determines the rate of decomposition.⁶⁸ Though the quality of the litter is the most important factor. The rate of decomposition decreases with latitude.

Discussion and conclusion

The cycling of nutrients has been thought to be a relatively simple system of producers, consumers and decomposers. Symbiotic fungi such as mycorrhizae were thought to enhance the capability of producers to obtain nutrients. These nutrients were provided by the decomposers, saprotrophic microorganisms. Evidence found over the last twenty years seems to point in a different direction. Nutrient cycling is not as simple as previously thought. Symbiotic fungi, as the arbuscular mycorrhizae, have been shown to be able to direct the saprotrophic microorganisms involved in the decomposition of organic matter. Others, ericoid and ectomycorrhizae, are able of these decomposing capabilities themselves. The mycorrhizae are well adapted to their environment. Because of slow decomposition rates in the high and intermediate latitudes, ericoid and ectomycorrhizae must degrade the organic matter, to obtain nutrient. Arbuscular mycorrhizae do not have these abilities, their environment is one of a fast rate of decomposition.

Nutrient limitation has had similar selective effects on the symbiotic relationship of plant and mycorrhizae. Evidence shows that mycorrhizae are specialized in the uptake of the nutrient which is limiting in its habit. Mycorrhizae are adapted to their habit in such a way that they utilize it to the fullest. Ectomycorrhizae growing in the vast boreal and temperal forests utilize the nutrients stored in the pollen which is produced annually in very large quantities. Arbuscular mycorrhizae have the ability to create a hyphal network connecting different plants with one another. This provide an extra dimension to the already complex nutrient cycle in the tropics.

The global distribution of mycorrhizae and the underlying mechanisms by which this distribution is created, has received a lot of support from evidence found over the last two decades. The plant and fungal physiological capabilities of this symbiosis have been charted more and more.

Ericoid mycorrhizae

The ericoid mycorrhizae are most important to plants in their ability to take up nitrogen. They are saprotrophic, they have a variety of enzymes to degrade complex plant and fungal necromass. Because of their saprotrophic nature, they have a preference for the availability of organic nutrients. The ericoid mycorrhizae are well adapted to their environment. The high latitudes at which they exist are home to slow rates of decomposition and these latitudes are nitrogen limiting. The slow rate of decomposition ensures an accumulation of organic matter, which can readily be degraded by the ericoid mycorrhizae. The limitation of nitrogen has made these fungal symbionts almost indispensable to plants.

Ectomycorrhizae

As with ericoid mycorrhizae, the main nutrient to be supply to plants by ectomycorrhizae is nitrogen. Ectomycorrhizae are also saprotrophic, though the saprotrophic abilities vary widely. A north to south decline is found in these abilities. Ectomycorrhizae are able to degrade plant and fungal necromass, such as pollen, as well as faunal necromass. At the intermediate latitudes, nitrogen is the limiting plant nutrient, though nitrogen becomes less limiting towards the lower latitudes. This is also seen in the north south gradient of saprotrophic capabilities of ectomycorrhizae. The ability of ectomycorrhizae to degrade necromass as pollen is an neat attribute in forest ecosystems where a lot of pollen is produced annually.

Arbuscular mycorrhizae

Phosphorus uptake is the main characteristic of arbuscular mycorrhizae, when compared to the other two mycorrhizae. Arbuscular mycorrhizae are very capable of the uptake of phosphorus, even in insoluble forms. Though they themselves do not possess saprotrophic capabilities, they are able to stimulate saprotrophic microorganisms to degrade the organic matter. The outstanding ability of arbuscular mycorrhizae to take up phosphorus is of great importance in the phosphorus limiting ecosystems of the earth. The fact that arbuscular mycorrhizae have not evolved saprotrophic abilities, is the consequence of the fast turnover rate of these latitudes.

It seems that the evidence over the last twenty years has piled up in favour of Reads hypothesis. When linked to biogeographical evidence, the global distribution pattern described by Read in 1991 becomes apparent (fig. 2).

	← Increasing latitude		
Main ecosystem	 Tundra	 Temperate and boreal forests	 Tropics
Soil	Organic	Organic, increasingly mineral	Mineral
Limiting nutrient	Nitrogen	Nitrogen	Phosphorus
Mycorrhizae Specialized in	Ericoid -Nitrogen uptake -Saprotrophic	Ecto- -Nitrogen uptake -Saprotrophic, north-south gradient -Pollen degradation	Arbuscular -Phosphorus uptake -Indirect effects on saprotrophic microorganisms
	→ Increasing decomposition rate and N:P ratio		

Figure 2. The patterns of nutrient availability and underlying mechanisms of mycorrhizae summarized.

References

- ¹Frank, B. (2005). On the nutritional dependence of certain trees on root symbiosis with belowground fungi (an English translation of AB Frank's classic paper of 1885). *Mycorrhiza*, 15(4), 267-275.
- ²Newman, E. I., & Reddell, P. (1987). The distribution of mycorrhizas among families of vascular plants. *New Phytologist*, 106(4), 745-751.
- ³Trappe, JM. (1987). Phylogenetic and ecologic aspects of mycotrophy in the angiosperms from an evolutionary standpoint. *Ecophysiology of VA mycorrhizal plants* 5–25
- ⁴Read, D. J. (1991). Mycorrhizas in ecosystems. *Experientia*, 47(4), 376-391.
- ⁵Read, D. J., & Perez-Moreno, J. (2003). Mycorrhizas and nutrient cycling in ecosystems—a journey towards relevance?. *New Phytologist*, 157(3), 475-492.
- ⁶Specht, R. L., & Moll, E. J. (1983). Mediterranean-type heathlands and sclerophyllous shrublands of the world: an overview. *Mediterranean-type Ecosystems* (pp. 41-65).
- ⁷Stribley D.P. & Read D.J. (1980) The biology of mycorrhiza in the Ericaceae. VII. The relationship between mycorrhizal infection and the capacity to utilize simple and complex organic nitrogen sources. *New Phytologist* 86: 365-371
- ⁸Bajwa, R., & Read, D. J. (1985). The biology of mycorrhiza in the Ericaceae. IX. Peptides as nitrogen sources for the ericoid endophyte and for mycorrhizal and non-mycorrhizal plants. *New Phytologist*, 459-467.
- ⁹Bajwa, R., Abuarghub, S. & Read D. J. (1985) The biology of mycorrhiza in the Ericaceae. X. The utilization of proteins and the production of proteolytic enzymes by the mycorrhizal endophyte and by mycorrhizal plants. *New Phytologist* 101: 469-486
- ¹⁰Cairney, J. W. G., & Burke, R. M. (1994). Fungal enzymes degrading plant cell walls: their possible significance in the ectomycorrhizal symbiosis. *Mycological Research*, 98(12), 1345-1356.
- ¹¹Kerley S. J. & Read D. J. (1997) The biology of mycorrhiza in the Ericaceae XIX. Fungal mycelium as a nitrogen source for the ericoid mycorrhizal fungi *Hymenoscyphus ericae*. *New Phytologist* 136, 691–701
- ¹²Lin, L. C., Lee, M. J., & Chen, J. L. (2011). Decomposition of organic matter by the ericoid mycorrhizal endophytes of Formosan rhododendron (*Rhododendron formosanum* Hemsl.). *Mycorrhiza*, 21(5), 331-339.
- ¹³Wurzburger, N., Higgins, B. P., & Hendrick, R. L. (2012). Ericoid mycorrhizal root fungi and their multicopper oxidases from a temperate forest shrub. *Ecology and evolution*, 2(1), 65-79.
- ¹⁴Leonowicz, A., Cho, N. S., Luterek, J., Wilkolazka, A., Wojtas-Wasilewska, M., Matuszewska, A., Hofricheter, M., Wesenberg, D. & Rogalski, J. (2001) Fungal laccase: properties and activity on lignin. *Basic Microbiology* 41, 185–227.
- ¹⁵Hoegger, P. J., Kilaru, S., James, T. Y., Thacker, J. R., & Kües, U. (2006). Phylogenetic comparison and classification of laccase and related multicopper oxidase protein sequences. *Febs Journal*, 273(10), 2308-2326.
- ¹⁶Kellner, H., Luis, P., & Buscot, F. (2007). Diversity of laccase-like multicopper oxidase genes in Morchellaceae: identification of genes potentially involved in extracellular activities related to plant litter decay. *FEMS microbiology ecology*, 61(1), 153-163.
- ¹⁷Baath, E. & Söderström, B. (1979) Fungal biomass and fungal immobilization of plant nutrients in Swedish coniferous forest soils. *Reviews in Ecology and Biology of Soil* 16, 477-489.
- ¹⁸Ellenberg, H. (1988) *Vegetation Ecology of Central Europe*. Book by Cambridge University Press, London
- ¹⁹Giltrap, N. J. (1982). Production of polyphenol oxidases by ectomycorrhizal fungi with special reference to *Lactarius* spp. *Transactions of the British Mycological Society*, 78(1), 75-81.
- ²⁰Linkins, A.E. & Antibus, R.K. (1981) Mycorrhizae of *Salix rotundifolia* in coastal arctic tundra. *Arctic and Alpine Mycology* 509-531
- ²¹Bartlett, E. M., & Lewis, D. H. (1973). Surface phosphatase activity of mycorrhizal roots of beech. *Soil Biology and Biochemistry*, 5(2), 249-257.
- ²²Abuzinadah, R.A. & Read, D.J. (1986) The role of proteins in the nitrogen nutrition of ectomycorrhizal plants. I. Utilization of peptides and proteins by ectomycorrhizal fungi. *New Phytologist* 103, 481-493.
- ²³Chen, D. M., Taylor, A. F., Burke, R. M., & Cairney, J. W. (2001). Identification of genes for lignin peroxidases and manganese peroxidases in ectomycorrhizal fungi. *New Phytologist*, 152(1), 151-158.
- ²⁴Hutchison, L. J. (1990). Studies on the systematics of ectomycorrhizal fungi in axenic culture. II. The enzymatic degradation of selected carbon and nitrogen compounds. *Canadian Journal of Botany*, 68(7), 1522-1530.
- ²⁵Cairney, J. W. G. & Burke, R. M. (1996). Plant cell wall-degrading enzymes in ericoid and ectomycorrhizal fungi. *Mycorrhizas in integrated systems* 218–221.
- ²⁶Burke, R. M., & Cairney, J. W. G. (1998). Carbohydrate oxidases in ericoid and ectomycorrhizal fungi: a possible source of Fenton radicals during the degradation of lignocellulose. *New Phytologist*, 139(4), 637-645.
- ²⁷Caldwell, B. A., Castellano, M. A., & Griffiths, R. P. (1991). Fatty acid esterase production by ectomycorrhizal fungi. *Mycologia*, 83(2), 233-236.
- ²⁸Griffiths, R. P., Castellano, M. A. & Caldwell, B. A. (1991) Ectomycorrhizal mats formed by *Gautieria monticola* and *Hysterangium setchellii* and their association with Douglas-fir seedlings, a case study. *Plant and Soil* 134: 255–259.
- ²⁹Bending, G. D. & Read, D. J. (1995). The structure and function of the vegetative mycelium of ectomycorrhizal plants. VI. Activities of nutrient mobilizing enzymes in birch litter colonised by *Paxillus involutus*. *New Phytologist*, 130: 411–417.
- ³⁰Colpaert, J. V., & van Tichelen, K. K. (1996). Decomposition, nitrogen and phosphorus mineralization from beech leaf litter colonized by ectomycorrhizal or litter-decomposing basidiomycetes. *New Phytologist*, 123-132.

-
- ³¹ Schulze, E. D., Högberg, P., Van Oene, H., Persson, T., Harrison, A. F., Read, D. J., Kjølter, A. & Matteucci, G. (2000). Interactions between the carbon and nitrogen cycles and the role of biodiversity: A synopsis of a study along a north-south transect through Europe. *Ecological Studies* 142, 468-491.
- ³² Taylor, A. F. S., Martin, F., & Read, D. J. (2000). 16 Fungal Diversity in Ectomycorrhizal Communities of Norway Spruce (*Picea abies* (L.) Karst.) and Beech (*Fagus sylvatica* L.) Along North-South Transects in Europe. *Ecological Studies* 142, 343-365.
- ³³ Lilleskov, E. A., Fahey, T. J., Horton, T. R., & Lovett, G. M. (2002). Belowground ectomycorrhizal fungal community change over a nitrogen deposition gradient in Alaska. *Ecology*, 83(1), 104-115.
- ³⁴ Perez-Moreno, J., & Read, D. J. (2001). Exploitation of pollen by mycorrhizal mycelial systems with special reference to nutrient recycling in boreal forests. *Biological Sciences*, 268(1474), 1329-1335.
- ³⁵ Perez-Moreno, J., & Read, D. J. (2001). Nutrient transfer from soil nematodes to plants: a direct pathway provided by the mycorrhizal mycelial network. *Plant, Cell & Environment*, 24(11), 1219-1226.
- ³⁶ Klironomos, J. N., & Hart, M. M. (2001). Food-web dynamics: Animal nitrogen swap for plant carbon. *Nature*, 410(6829), 651-652.
- ³⁷ Talbot, J. M., Allison, S. D., & Treseder, K. K. (2008). Decomposers in disguise: mycorrhizal fungi as regulators of soil C dynamics in ecosystems under global change. *Functional Ecology*, 22(6), 955-963.
- ³⁸ Talbot, J. M., Bruns, T. D., Smith, D. P., Branco, S., Glassman, S. I., Erlandson, S., Vilgalys, R., & Peay, K. G. (2012). Independent roles of ectomycorrhizal and saprotrophic communities in soil organic matter decomposition. *Soil Biology and Biochemistry* 57, 282-291
- ³⁹ Talbot, J. M., & Treseder, K. K. (2010). Controls over mycorrhizal uptake of organic nitrogen. *Pedobiologia*, 53(3), 169-179.
- ⁴⁰ Courty, P. E., Hoegger, P. J., Kilaru, S., Kohler, A., Buée, M., Garbaye, J., ... & Kües, U. (2009). Phylogenetic analysis, genomic organization, and expression analysis of multi-copper oxidases in the ectomycorrhizal basidiomycete *Laccaria bicolor*. *New Phytologist*, 182(3), 736-750
- ⁴¹ Nagendran, S., & Hallen-Adams, H. E. Paper JM, Aslam N, Walton JD (2009) Reduced genomic potential for secreted plant cell-wall-degrading enzymes in the ectomycorrhizal fungus *Amanita bisporigera*, based on the secretome of *Trichoderma reesei*. *Fungal Genet Biol*, 46(5), 427-435.
- ⁴² Schüßler, A., Schwarzott, D., & Walker, C. (2001). A new fungal phylum, the Glomeromycota: phylogeny and evolution. *Mycological research*, 105(12), 1413-1421.
- ⁴³ Smith, S. E., & Smith, F. A. (2011). Roles of arbuscular mycorrhizas in plant nutrition and growth: new paradigms from cellular to ecosystem scales. *Annual review of plant biology*, 62, 227-250.
- ⁴⁴ Read, D. J., & Birch, C. P. D. (1988). The effects and implications of disturbance of mycorrhizal mycelial systems. *Proceedings of the Royal Society of Edinburgh* 94, 13-24.
- ⁴⁵ Sanders, F. E., and Tinker, P. B., (1971). Mechanism of absorption of phosphate from soil by endogene mycorrhizas. *Nature*, 233, 278-279.
- ⁴⁶ Gianinazzi-Pearson, V., & Gianinazzi, S. (1983). The physiology of vesicular-arbuscular mycorrhizal roots. *Plant and Soil*, 71(1-3), 197-209.
- ⁴⁷ Nelsen, C. E., & Safir, G. (1982). Increased drought tolerance of mycorrhizal onion plants caused by improved phosphorus nutrition. *Planta*, 154(5), 407-413.
- ⁴⁸ Augé, R. M., Schekel, K. A., & Wample, R. L. (1986). Greater leaf conductance of well-watered VA mycorrhizal rose plants is not related to phosphorus nutrition. *New Phytologist*, 103(1), 107-116.
- ⁴⁹ Read, D. J., Francis, R., & Finlay, R. D. (1985). Mycorrhizal mycelia and nutrient cycling in plant communities. *Special publication of the British Ecological Society*, (4), 193-217.
- ⁵⁰ Hodge, A., Campbell, C. D., & Fitter, A. H. (2001). An arbuscular mycorrhizal fungus accelerates decomposition and acquires nitrogen directly from organic material. *Nature*, 413(6853), 297-299.
- ⁵¹ Tarafdar, J. C., & Marschner, H. (1994). Phosphatase activity in the rhizosphere and hyphosphere of VA mycorrhizal wheat supplied with inorganic and organic phosphorus. *Soil Biology and Biochemistry*, 26(3), 387-395.
- ⁵² Joner, E. J., Magid, J., Gahoonia, T. S., & Jakobsen, I. (1995). P depletion and activity of phosphatases in the rhizosphere of mycorrhizal and non-mycorrhizal cucumber (*cucumis sativus* L.). *Soil Biology and Biochemistry*, 27(9), 1145-1151.
- ⁵³ Koide, R. T., & Kabir, Z. (2000). Extraradical hyphae of the mycorrhizal fungus *Glomus intraradices* can hydrolyse organic phosphate. *New Phytologist*, 148(3), 511-517.
- ⁵⁴ Joner, E. J., Ravnskov, S., & Jakobsen, I. (2000). Arbuscular mycorrhizal phosphate transport under monoxenic conditions using radio-labelled inorganic and organic phosphate. *Biotechnology Letters*, 22(21), 1705-1708.
- ⁵⁵ Medina, A., Jakobsen, I., Vassilev, N., Azcón, R., & Larsen, J. (2007). Fermentation of sugar beet waste by *Aspergillus niger* facilitates growth and P uptake of external mycelium of mixed populations of arbuscular mycorrhizal fungi. *Soil Biology and Biochemistry*, 39(2), 485-492.
- ⁵⁶ Cardoso, I. M., & Kuyper, T. W. (2006). Mycorrhizas and tropical soil fertility. *Agriculture, ecosystems & environment*, 116(1), 72-84.
- ⁵⁷ Shibata, R., & Yano, K. (2003). Phosphorus acquisition from non-labile sources in peanut and pigeonpea with mycorrhizal interaction. *Applied Soil Ecology*, 24(2), 133-141.
- ⁵⁸ Fitter, A. H. (2006). What is the link between carbon and phosphorus fluxes in arbuscular mycorrhizas? A null hypothesis for symbiotic function. *New Phytologist*, 172(1), 3-6.
- ⁵⁹ Atul-Nayyar, A., Hamel, C., Hanson, K., & Germida, J. (2009). The arbuscular mycorrhizal symbiosis links N mineralization to plant demand. *Mycorrhiza*, 19(4), 239-246.
- ⁶⁰ Hodge, A., & Fitter, A. H. (2010). Substantial nitrogen acquisition by arbuscular mycorrhizal fungi from organic material has implications for N cycling. *Proceedings of the National Academy of Sciences*, 107(31), 13754-13759.

-
- ⁶¹ Veresoglou, S. D., Shaw, L. J., & Sen, R. (2011). Glomus intraradices and Gigaspora margarita arbuscular mycorrhizal associations differentially affect nitrogen and potassium nutrition of Plantago lanceolata in a low fertility dune soil. *Plant and soil*, 340(1-2), 481-490.
- ⁶² Liebich, J., Schloter, M., Schäffer, A., Vereecken, H., & Buraue, P. (2007). Degradation and humification of maize straw in soil microcosms inoculated with simple and complex microbial communities. *European journal of soil science*, 58(1), 141-151.
- ⁶³ Reynolds, H. L., Hartley, A. E., Vogelsang, K. M., Bever, J. D., & Schultz, P. A. (2005). Arbuscular mycorrhizal fungi do not enhance nitrogen acquisition and growth of old-field perennials under low nitrogen supply in glasshouse culture. *New Phytologist*, 167(3), 869-880.
- ⁶⁴ Reich, P. B., & Oleksyn, J. (2004). Global patterns of plant leaf N and P in relation to temperature and latitude. *Proceedings of the National Academy of Sciences of the United States of America*, 101(30), 11001-11006.
- ⁶⁵ Kang, H., Xin, Z., Berg, B., Burgess, P. J., Liu, Q., Liu, Z., Li, Z., & Liu, C. (2010). Global pattern of leaf litter nitrogen and phosphorus in woody plants. *Annals of forest science*, 67(8), 811.
- ⁶⁶ Chadwick, O. A., Derry, L. A., Vitousek, P. M., Huebert, B. J., & Hedin, L. O. (1999). Changing sources of nutrients during four million years of ecosystem development. *Nature*, 397(6719), 491-497.
- ⁶⁷ Yuan, Z. Y., & Chen, H. Y. (2009). Global-scale patterns of nutrient resorption associated with latitude, temperature and precipitation. *Global Ecology and Biogeography*, 18(1), 11-18.
- ⁶⁸ Zhang, D., Hui, D., Luo, Y., & Zhou, G. (2008). Rates of litter decomposition in terrestrial ecosystems: global patterns and controlling factors. *Journal of Plant Ecology*, 1(2), 85-93.