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The Impact of Climate Change on Ectomycorrhizal Fungi

How will the predicted rise in CO_2 concentrations and temperatures affect the symbiotic ectomycorrhizal fungi that dominate forest ecosystems in the northern hemisphere?

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Since the mid-twentieth century, the Earth's climate has been undergoing dramatic change, largely believed to be caused by human activity. According to forecasts, by the end of the twenty-first century, the concentration of carbon dioxide (CO_2) in the atmosphere in some regions of our globe will increase by 200%, to reach 540–970 ppm. Rising concentrations of CO_2 and other greenhouse gases is triggering a phenomenon known as the greenhouse effect, which is manifested as global warming. The Intergovernmental Panel on Climate Change (IPCC) based in Geneva, whose task is to provide objective, scientific information on climate change, reports that over the past 150 years the average temperature has risen by almost 0.8°C globally, and by around 1°C in Europe. According to IPCC estimates, by 2100 the global temperature may rise by another 1.8–4.0°C. Significant changes in precipitation are to be expected, while the frequency of extremely hot days will increase and the number of days with low temperatures will decrease. Droughts and floods will occur more often and will be more intense. It has been determined that in the temperate zone an increase in the average annual temperature by 1°C will shift the average annual isotherm (the line connecting points with the same temperature) northwards by approx. 140 km, and in mountainous areas by 170 m. It is also expected that by 2100, glaciers will shrink by 30–50%, permafrost by 16% and sea levels will rise significantly. In addition, increased nitrogen deposition (i.e. the accumulation of nitrogen in the environment) caused by human activity will double compared to the pre-industrial period and is expected to increase by a factor of 2.5 over the next century. Determining how organisms on Earth will respond to these climate changes is very important and should help us develop strategies to mitigate the negative effects of global warming.

For instance, the species composition and types of forests may undergo significant changes in the coming

A, D–I MARIA RUDAWSKA, B, C TOMASZ LESKI

Fruiting bodies of ectomycorrhizal fungi (A, B, C, D), extramatrical mycelium (E) and ectomycorrhizae of forest trees (F, G, H, I)

years as a result of climate change. This will involve the northward shifting of ecological optima (the most favorable conditions for tree growth) and the rising of the tree line in mountains. However, the soil requirements of different species of trees may pose a problem in adjusting to changes in average temperature and precipitation in new areas. This creates hard to predict problems for forest management.

Ectomycorrhizal fungi

Fungi are crucial to the biological diversity of forest ecosystems. Contemporary systematics treats them as a separate major kingdom of living organisms, next to plants and animals. Fungi occurring in forest ecosystems are very diverse in terms of species and functionality, as is evident in the presence of fungi from various trophic groups, i.e. symbionts, saprotrophs and pathogens.

Most forest trees form, together with symbiotic mycorrhizal fungi, a mutualistic relationship known as ectomycorrhiza, which involves the exchange of nutrients essential for survival.

The plant partner, i.e. the tree, through special structures referred to as ectomycorrhizae, provides its fungi partner with carbohydrates produced during photosynthesis, while the fungi provide trees with water and necessary mineral compounds from the soil, as well as protecting the root system from pathogens and environmental pollution. Mycorrhizal symbiosis provides plants with access to nutrients, helping keep the plant communities of most terrestrial ecosystems alive. Among the various categories of mycorrhizae (arbuscular mycorrhiza, ectomycorrhiza, ectendomycorrhiza, ericaceous and orchidaceous mycorrhizae, etc.), ectomycorrhiza is the most diverse. This diversity is determined by the number of ectomycorrhizal (EM) fungi species within this type of symbiosis. The exact number of EM fungi species is difficult to determine at the present state of knowledge, although it is highly probable that it could be as high as 20,000.

The number of plant partners forming ectomycorrhizae is relatively small because only about 2% of land-based plant species (mainly trees) from 39 different families associate with ectomycorrhizal fungi. However, this relatively small group of ectomycorrhizal plant species is of great ecological and economic importance, because it is a crucial component of forest ecosystems in all climate zones, particularly in temperate and boreal forests of the northern hemispheres. According to estimates, as many as 60% all trees on earth are ectomycorrhizal trees. Ectomycorrhiza occurs primarily in woody plants of the Pine, Beech, Birch, Willow, Linden, and Hazel families. For most of the woody species in which EM fungi have been found, this symbiotic relationship is obligatory. It is assumed that climate change can impact on fungi both directly, by affecting their growth and physiology, but also indirectly by affecting the environment, as well as relationships with other organisms, and lead to changes in their distribution, quantitative and qualitative structure, ecophysiology, life activity, and the frequency and abundance of producing reproductive structures, i.e. fruiting bodies. These changes may have consequences that are difficult to predict, mainly for forest ecosystems.

Ectomycorrhizal trees are a small group of species but have great ecological and economic importance, being a crucial component of forest ecosystems.

Impact of CO_2 on ectomycorrhizae and ectomycorrhizal fungi

The impact of elevated CO_2 concentrations on EM fungal communities is mainly associated with the increased photosynthetic activity of trees, and thus increased transfer of assimilated carbon (sugars) to the roots and EM fungi. In turn, fine roots and ectomycorrhizae may, in the form of exudates, transfer increased amounts of carbon to the soil, thus affecting the composition of microorganisms living in the rhizosphere of various plant species. The consequence of this chain of events is accelerated carbon cycling, which can cause changes to the extent of root colonization by ectomycorrhizal fungi, as well as to the species structure of communities of these fungi.

Experiments carried out in laboratory conditions have shown that the biomass of the mycelium produced by the EM fungus *Hebeloma crustuliniforme*, commonly known as the poisonpie mushroom, in a symbiotic relationship with Scots pine seedlings was three times higher under elevated CO_2 content than on seedlings growing under control conditions. Increased growth of the extramatrical mycelium around Scots pine seedlings, growing in conditions of elevated CO_2 concentration, was also found for such popular EM symbionts of Scots pine as the bovine bolete (*Suillus bovinus*) and the common roll-rim (*Paxillus involutus*). The EM fungus *Pisolithus arhizus* (known as the dead man's foot) in symbiosis with Scots pine seedlings was found to produce three times more highly developed coralloid mycorrhizae in conditions of elevated CO_2 concentration, while the biomass of the external mycelium penetrating the soil around fine roots and ectomycorrhiza doubled. Many other laboratory experiments have also shown that elevated concentration of CO_2 increases the percentage of small root colonization by EM fungi, and also stimulates the development of fine roots on which ectomycorrhizae develop. Due to the crucial role of ectomycorrhizae in tree nutrition, stimulation the development of EM mycelium and ectomycorrhizae should improve the supply of nutrients to trees.

However, the story is a bit more complicated because not all experiments provide the same results. According to some reports, increased ectomycorrhiza formation in conditions of elevated CO_2 is short-lived or does not occur at all. For example, the biomass of mycelium and ectomycorrhizae created by the *Cenococcum geophilium* and fungi from the genus *Suillus* on Scots pine were not found to change due to increased CO_2 concentration. In turn, in an experiment involving the yellow pine and the *Pisolithus arhizus* fungus, no effects of CO_2 were observed after four months, although an increase in ectomycorrhizal colonization was noted a year after the experiment. These results show that under conditions of increased CO_2 concentration, interactions between EM fungi and trees can be quite diverse. Field experiments using special chambers allowing trees to grow in conditions of elevated CO_2 concentration show that the reactions of plants/trees depend on the time of exposure to elevated CO_2 concentration. Many experiments of short duration (days, weeks, months) show only a transient effect, which quickly disappears after the cessation of elevated CO_2 concentration. Longer experiments using poplar, beech, birch, and spruce trees show that these species, growing in conditions of increased CO_2 concentration, exhibit diverse reactions, including increased root biomass, an increased number of fine roots, and changes in the species structure of communities of EM fungi. However, the results obtained regarding the EM communities' structure are not entirely unambiguous and seem to depend on the tree species and their fungal partners. The impact of CO_2 on fruiting bodies seems to be more consistent. In the mentioned field experiments, an increase in the number of emerging sporocarps and their biomass was generally observed, in particular in relation to fungi of late tree development phase, such as *Cortinarius* and *Leccinum* fungi. Ultimately, the effect of increased CO_2 concentration on ectomycorrhizae should be considered in the context of other, also changing environmental factors, because many of them, such as nitrogen deposition, temperature, humidity and other manifestations of climate change, may affect processes in forest ecosystems, and thus the interactions between trees and their symbiotic fungi partners.

The impact of temperature

Although fungi are known to tolerate a very wide range of temperatures (from −17.5 to +40°C), we cannot rule out the possibility that rising soil temperatures will affect the development of the hyphae network forming the extramatrical mycelium. In addition, dehydrated soil may increase the death of fine roots on which ectomycorrhizae form, thereby reducing the extent of mycorrhizal colonization.

Global warming seems to primarily affect EM symbiosis indirectly by affecting the functioning of the plant partner, i.e. the tree. Experiments involving heating the soil have been conducted in recent years in both Europe and North America to determine how the qualitative and quantitative structure of EM fungi communities changes under such conditions. The results obtained have been inconclusive: some studies indicate a significant decrease in the species diversity of EM fungi on heated plots, while other experiments give quite opposite results. One positive effect of soil heating on the variety of EM fungi, especially without additional fertilization, was obtained in an experiment involving dwarf birch seedlings in Alaska. In addition, an interesting change to the ectomycorrhizae structure was observed involving an increase in the number of *Cortinarius* fungi, which can break down proteins, and a decrease in other fungi, mainly of the *Russula* genus, which prefers inorganic nitrogen. This indicates that heating the soil affects the structure of ectomycorrhizae by changing the element turnover, and thus facilitates the expansion of dwarf birch in tundra conditions. Other studies have shown that as a result of simultaneous heating and drying of the soil, there is an increase in the abundance of ascomycetes fungi and a decrease in the abundance of basidiomycetes fungi. Presumably, this is largely caused by decreased water availability. Similarly, a three-year experiment conducted on the European larch and mountain pine on the tree-line in the Alps showed a significant effect of substrate heating on the structure of the EM fungi community. However, an experiment carried out in Tyrol, Austria, in spruce forests, where the soil surface was heated for three years during periods of no snow cover, did not show the effect of heating on the structure of microorganism communities, including EM fungi.

At the same time, some experiments showed a decrease in the richness of EM species on heated plots. This was in an 18-year experiment in damp tundra in Alaska, where the temperature was raised by 2°C during two summer months. Significant reorganization of the EM fungi community has been found on dwarf birch seedlings. The species richness of EM fungi of the basidiomycetes genus deteriorated and shifted, as in the aforementioned experiment, towards the *Cortinarius* genus, forming ectomycorrhizae with a less extensive network of external mycelium. These results show that *Cortinarius* fungi in humid tundra conditions are probably more resistant and better adapted to conditions caused by warming than other fungi. However, there is still not enough experimental data to make a reliable prediction on the impact of global warming on specific groups of EM fungi.

Global warming seems to primarily affect ectomycorrhizal symbiosis by affecting the functioning of the plant partner, i.e. the tree.

Conclusion

Climate change may affect the relationship between EM fungi and their plant partners, mainly trees, in various ways. The effects of these interactions depend on the factor driving the climate change (increased CO_2 concentrations, rising temperatures, etc.), as well as on the tree species, the taxonomic position of fungi, the type of ecosystem, and type of soil, etc.