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Till Drought Do Them Part

We can hardly imagine the Earth without majestic trees and omnipresent shrubs. But not all of us realize that these plants owe their success to ubiquitous yet often unnoticeable fungi. What links these two types of organisms together is life-giving water. It is the reason why trees and fungi have been inseparable for hundreds of millions of years. How do droughts affect trees and their evolutionarily ancient symbiosis with fungi?

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The ancient history of life on Earth has long attracted great interest on the part of scholars. The only way to trace the earliest history of living organisms is by studying fossils, which together with modern measurement techniques based on the half-lives of different isotopes allow us to date such prehistoric discoveries. Not so long ago, it was believed that the evolutionary histories of plants and of fungi were closely linked. The fossilized remains of the first plants and the oldest fossils of fungi were dated to the very same period, namely between 450 and 500 million years ago. However, everything changed in 2019, when a discovery was made that greatly impacted on our understanding of the early history of life on Earth.

The great transition to land

Let us imagine the world as it may have existed 500 million years ago, in the geological period referred to as the Cambrian, when there were deserts of bare rocks emerging from boundless oceans. There is no point looking in this Cambrian world for any plants or small animals like those we are familiar with today. But on the other hand, this world is not entirely barren. The surface of the rocks is covered with a thin layer of microorganisms, mainly bacteria but also unicellular algae and fungal hyphae. Today, similar assemblages of many different microbes are referred to as biofilm. It was most probably in such biofilm that plants and fungi first started to cooperate, forming a symbiotic relationship that later enabled plants to colonize land.

But let us get back to modern times, back to 2019 and to the discovery that transformed our understanding of the history of life and evolution on Earth. In that year, a team led by Corentin Loron of the University of Liège presented its discovery to the world. In the rocks of Arctic Canada, the scientists had found fossils of "ur-fungi" (ancient fungi) whose age was estimated at nearly one billion years. The discovery proved clearly that fungi had appeared on land much earlier than previously thought. Thanks to their ability to synthesize many enzymes, they prepared the land for the arrival of plants. For millions of years, they meticulously broke down solid, bare rocks, thus releasing the minerals bound up in them into the environment. We could say that in the very early period of the presence of plants on land fungi actually played the role of roots, which plants did not have. Consequently, plants owe their evolutionary success not only to their ability to use solar energy to bond six molecules of carbon dioxide and six molecules of water together in the process of photosynthesis, but also to their subsequent symbiotic association with fungi, which gave them access to minerals and the possibility of actively absorbing water. On the one hand, cooperation between plants and fungi facilitated a major evolutionary leap by helping plants become independent of the aquatic environment, while on the other it exposed plants to numerous dangers resulting from growth on land. Over millions of years of evolution, the unfavorable and changeable conditions of land environments resulted in the development of many adaptations, both by plants and by fungi, and such adaptions have allowed these organisms to survive until the present day.

Lending a helping hypha

The uninterrupted co-existence of trees and fungi allows both groups of organisms to survive in conditions of water stress. One of the functions of mycorrhiza (as the mutually beneficial symbiotic association between plants and fungi is known) is the protection of tree roots by fungi in adverse conditions such as drought. The mycelium of the mycorrhizal fungus forms a mantle around the small roots of plants, thus protecting them against desiccation. The mycelium connected to the root system stretches for kilometers, thus increasing the roots' absorptive area several thousand times. Unlike plant cells, mycelia are a lot more resistant to desiccation. In extreme drought, hyphae can form sclerotia, or spherical masses that allow them to survive even the worst water shortages. In the conditions of prolonged water stress, we can observe a change in the suite of mycorrhizal fungi colonizing tree roots from drought-sensitive to drought-resistant species, such as *Cenococcum geophilum*, whose mycorrhizae are found on the roots of trees that grow

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Sclerotia – survival structures formed by the fungus *Cenococcum geophilum* in conditions of drought in extremely dry ecosystems. Consequently, the quantitative and qualitative relations in the communities of fungi change, and so does their enzymatic activity, which may result in a change of the ecological function fulfilled by specific fungi in the community.

To the very last drop

In the era of climate change, the greatest danger to many ecosystems is posed by rising temperatures and the accompanying expansion of the areas at risk of drought. We can find out how trees respond to water stress by observing large-seeded species, such as the European beech. Generally the species experiences a mast seeding year (a year characterized by large seed production) once every 5 to 8 years, with the "mass production" of beechnuts by trees across the whole of the continent therefore occurring at the same time. Currently, however, this process has been thrown out of synch. High temperatures, which set new records every year, stimulate trees to produce more seeds. However, the energy that they use to produce seeds is not inexhaustible. Beeches do not have enough time for regeneration, so the number of seeds they produce and their quality go down. This fact is of great significance for forest management – after all, if we lose seeds, in the future we will also lose the forest ecosystems as we know them.

As this example serves to show, rapid changes in abiotic conditions (physical and chemical components of the environment, including atmospheric conditions) affect physiological processes. In response to these changes, trees undergo numerous modifications in terms of their morphology, physiology, and biochemistry. If we look deeper inside cells, we can observe many reactions that plants use as forms of self-defense against the loss of life-giving water. Trees do not remain passive in the face of the danger posed by drought – they fight, and they do so until the last drop of… water. When the level of water in cells decreases, the cell membrane starts to crack and lose its selective permeability, which manifests itself in the wilting of shoots and the wrinkling of leaves. The group of substances that allow plant cells to retain their water potential are called osmolytes; they include proline, mannitol, glucose, and fructose. Special attention should be paid to proline, an amino acid produced and accumulated in conditions of stress – a state of an organism that can be described on a molecular level as involving an upset balance between the production of compounds that damage cells and their detoxification ability. Proline has been shown to facilitate the growth of drought-stressed seedlings, in addition to stabilizing intracellular membranes and membrane proteins, protecting them against oxidative damage. The substance also inhibits stomatal opening, thus reducing transpiration, which is important in situations in which there is insufficient water in the surroundings.

Water stress may also leave its mark at the level of genetics. The most recent studies carried out in the forests of Spain, France, Italy, Germany, and Sweden confirm that changing conditions such as drought or higher temperatures increase the genetic diversity of forest trees (even among those growing next to one another), which allows them to adapt more rapidly to climate change. Scientists identified the tree genes responsible for the growth of leaves in springtime, flowering periods, and resistance to drought and then demonstrated that the variability of these genes was related not to the origin of the population but to environmental conditions.

In periods of drought, another factor conducive to the retention of water by organisms is increased production of phytohormones. These substances stimulate such physiological reactions as the appearance of evaporation-reducing trichomes or waxy layers on the epidermis, the inhibition of the growth of shoots and simultaneous stimulation of the growth of roots, which facilitates faster access to water resources in deeper soil layers. An interesting strategy called cladoptosis has been developed by different oak species. The development of a cleavage zone at the base of shoots causes the narrowing of the lumen of the vessel elements in the xylem. If the level of water in soil drops significantly, the shoots fall off. This leads to the reduction of the amount of metabolically active water-consuming tissue, and the main route of water loss through transpiration is then cut off.

Trees are also assisted in their adaptation to drought by the fungi that live together with them. Several decades ago, researchers noticed that plants with roots colonized by symbiotic fungi were more resistant than plants without mycorrhizal fungi. However, the mechanisms that help plants survive periods of water stress have only been discovered in recent years.


MARIOLA MATELSKA

Ectomycorrhizae formed by fungi of the *Tulasnella* genus in the roots of a pine tree growing in the extremely dry conditions of a lichen Scots pine forest


KATARZYNA BRONIEWSKA

A bald cypress forming aerial roots, known as pneumatophores

Trees that grow in forest ecosystems are connected up to what could be called a kind of "water pipeline system" created by networks of fungal hyphae, which can transport water across considerable distances. Tree roots colonized by fungi are also characterized by substantially better hydraulic conductivity that the roots that are not colonized. Fungi stimulate plants to produce phytohormones such as jasmonic acid and abscisic acid, which increase hydraulic conductivity in plant tissues. They can also interfere in the processes in tree roots to a greater extent. One example is the well-known fly agaric, which wraps around the small roots of trees and may in this way affect the production of aquaporins, which are proteins responsible for forming small channels in semipermeable membranes, which facilitate the transport of water between cells. The presence of fly agaric hyphae inside the roots significantly increases the expression of three out of seven genes responsible for the synthesis of aquaporins. And so, the colonization of roots by a fungus improves the possibility of the transport of water in such roots.

Adapting to survive

Over the course of evolution, trees have developed many amazing forms of adaptation allowing them to survive droughts, including morphological mechanisms. One popular example is the baobab. Its barrel-shaped trunk is built of parenchyma and can store around 100,000 liters of water. Acacias that grow on African savannahs have strongly reduced leaves and use flat petioles for photosynthesis. The impulses for the development of such interesting adaptations include not only shortages of water but also… its overabundance. If the roots of many plants are waterlogged as a result of flooding or springtime snowmelt, they lose their ability to breathe, and so they rot. However, this does not apply to the bald cypress, which copes well in waterlogged areas thanks to its pneumatophores, which stick up out of the soil above the level of stagnant water, allowing air to pass to the roots of the tree. Similar solutions apply to species found in coastal mangroves almost in the entire subtropics, where the level of water changes with the rise and fall of sea levels. Being surrounded by water is not always a hindrance – some trees can use this situation to their advantage. Examples include alders and birches. The seeds of these trees have small and thin "wings" whose surface is poorly permeable for water. These "wings" are used as a mode of seed transport. This phenomenon, referred to as hydrochory, may nonetheless disappear if water disappears. Even if birches and alders themselves can then use wind for the purpose of expanding elsewhere, the problem still remains. We must remember that we owe the water stored in soil to trees. If areas become deprived of these beautiful, long-living organisms, water runs off into rivers and then seas, instead of replenishing groundwaters, which are sorely needed in periods of drought.

When water goes short

Five hundred million years of co-existence have allowed plants and their fungal partners to achieve great evolutionary success. By living in symbiosis, they have colonized most land areas and brought about great biodiversity on Earth. Symbiotic fungi, which act as a buffer improving the resistance of woody plants to adverse conditions, help them adapt to new surroundings. The migration of tree species related to climate change may be largely dependent on the spread of suitable species of mycorrhizal fungi. Fungi are older in terms of evolution and therefore appear more resistant to changing conditions. The wide diversity of fungal species and the possibility of very fast genetic recombination allow fungi to respond very quickly to ongoing changes in the environment. However, the survival of all symbiotic fungi depends on the presence of the plants with which they form symbiotic relationships. Consequently, both plants and fungi may be jeopardized by the negative consequences of global climate change, in particular long-term droughts in the growing season. Fungi may reduce to some extent the negative impact that water stress has on plants, but the massive dying off of trees observed in recent years shows the magnitude of the threat that climate change may pose to them. The cascade of events triggered by the dying of forests will have catastrophic consequences for fungi and for the protection of biodiversity on Earth. This is why the fight for every drop of water retained in the forest ecosystem is so important.