Symbiosis in the **Serengeti**

Dr Nancy Collins Johnson is presently conducting research into the role of arbuscular mycorrhizal symbioses in Tanzania's Serengeti National Park, the world's largest intact grazing ecosystem. Here, she outlines her work and the relevance it could have on agriculture

To begin with, what are the aims and objectives of this study?

One objective is to gain basic ecological information about the abundance, diversity and species composition of arbuscular mycorrhizal (AM) fungi (*phylum Glomeromycota*) in an intact natural grazing ecosystem.

A second objective is to look for relationships between soil properties, precipitation, grazing, and AM fungi so that we can test hypotheses about the factors that structure *Glomeromycotan* communities and control their mutualistic function.

Could you explain the role of mycorrhizas in the uptake of nitrogen and phosphorus?

Mycorrhizal symbioses increase the surface area through which plants can acquire minerals from the soil because thin fungal hyphae can explore much smaller pores in the soil than roots, or even root hairs. This property of mycorrhizal fungi is important for accessing immobile minerals, particularly phosphorus. Unlike nitrate and potassium that dissolve in water, immobile minerals are held tightly to soil particles and do not move with water in the soil. This means that these minerals are not transported to roots with water that is pulled into roots through the flow generated by transpiration. Instead, immobile nutrients must contact a root, root hair, or fungal hyphae and be actively transported across the cell membrane.

What features of the Serengeti ecosystem afford it a unique position for investigation?

The Serengeti provides a natural laboratory to study how complex interactions among climate, soils, microorganisms, plants and animals can generate a stable ecosystem. Rainfall varies tremendously from year to year, yet the system is resilient to this variation.

Over millennia, interactions among living and non-living components of the Serengeti have generated a complex system of checks and balances. The tight coupling between producers, grazers and scavengers in the Serengeti is remarkable, and differs from anywhere else in the world. For example, despite the millions of grazing animals roaming the Serengeti plains there is surprisingly little dung on the ground because within a few hours dung beetles and other scavengers carry it away and incorporate it into the soil.

How will you investigate the climatic interactions that influence this fauna-plant-fungi relationship?

We are using two approaches. First, we constructed and tested a structural equation model using data collected from a series of grazed and ungrazed (fenced) sites that were selected to create natural gradients of soil fertility and precipitation. This analysis showed that even when all other factors are taken into account, drier sites have a greater abundance of AM hyphae than the wet sites. Now we are conducting controlled experiments to determine if this pattern is caused by slower hyphal decomposition or greater production of new hyphae in dry sites compared to wet sites.

PHOTOS COURTESY OF RICK JOHNSON

What molecular methods have you developed to address the gaps in existing knowledge?

I am currently collaborating with a group of researchers in Estonia who are extracting DNA from the roots of grasses that we collected from the soil fertility and precipitation gradients in the Serengeti and using high-throughput sequencing methods and bioinformatics to analyse the AM fungi inhabiting the dominant grasses.

These new molecular analyses complement our microscopy-based analysis of fungal spore communities. One method shows the fungi that are inside the roots while the other shows the reproductive effort of the fungus. Both are important for understanding the ecology of AM fungi.

Lastly, could you highlight the most significant discoveries you have made in ecosystem dynamics during your career in environmental science?

My colleagues and I have explored the reasons why mycorrhizal symbioses' function varies from mutualism (+/+) to commensalism (+/0) and even parasitism (+/-). A series of studies have helped us elucidate the factors that control whether AM symbioses will help or hinder plant growth. We have discovered that the interaction of soil phosphorous and nitrogen availability often controls mycorrhizal function. Plants grown in soil that is phosphorous-limited, but has ample nitrogen, tend to benefit the most from AMs, while those grown in soils rich in both phosphorus and nitrogen benefit the least from the symbioses.

We believe that fertilisation reduces mycorrhizal benefits because it causes plants to allocate less carbon belowground to roots and mycorrhizas and more aboveground to shoots, leaves, and seeds.

Our most important discovery is that in undisturbed grassland ecosystems, plants and AM fungi adapt to their local environment and each other so that the symbioses that they form maximise mutualistic benefits in phosphorus-limited soils and minimise parasitism in phosphorus-rich soil.

Fungal **fundamentals**

The Serengeti grasslands provide an ideal site to study the ecology of mycorrhizal fungal communities which form nutritional symbioses with plants and comprise a large proportion of the living biomass of soils

ARBUSCULAR MYCORRHIZAL (AM) FUNGI are essential in aiding plant uptake of essential nutrients such as phosphorus. These fungi live symbiotically with plants and form large underground networks of hyphae that are able to acquire immobile minerals from the soil that otherwise would not be accessible to roots or root hairs. Greater knowledge of the processes underlying these exchanges could help to reduce human reliance on inorganic fertilisers, particularly in tropical ecosystems. However, little is currently understood about the effective management of mycorrhizal fungi and how external variables such as climate, soil fertility and herbivore activity affect them.

Dr Nancy Collins Johnson – an expert in soil ecology at Northern Arizona University – is attempting to advance our understanding of these fungal communities, working in collaboration with a team from Syracuse University who are focusing on symbiotic bacteria in legume roots and nitrogen-fixing bacteria on the surfaces of native grasses. Johnson explains the aims of this collaborative project: "We plan to combine our data to test the hypothesis that plants satisfy their nutritional requirements by cultivating complex microbial communities in and around their roots in the same way that animals support communities of gut microorganisms to digest their food".

These communities can best be observed in undisturbed ecosystems, and Johnson's team has had the good fortune of conducting fieldwork in Tanzania's Serengeti National Park, the world's largest intact grazing ecosystem. Prior work on mycorrhizas has generally concentrated on grasslands in temperate regions, particularly in North America, but very little work has been done in tropical grasslands where mycorrhizal symbioses are believed to play key roles in nutrient cycling and plant nutrition. The Serengeti is also an ideal location to study complex interactions among grazing animals, the plants they consume and underground fungal communities.

REFINING EXISTING MODELS

The researchers are using natural gradients in precipitation, soil texture, soil nutrients and organic matter within the Serengeti to measure the impacts these have on the abundance and community composition of AM fungi at eight different sites. Replicated plots at each site were fenced off in order to create a long-term grazer removal treatment so the influence of herbivorous animals can be measured. In addition, Johnson and her colleagues are studying mycorrhizal responses to watering and phosphorus fertilisation treatments in field plots in the Serengeti. Combining insights from studies of natural gradients with the findings from the manipulative experiments will help uncouple the complex interactions among factors controlling mycorrhizal symbioses in the Serengeti.

This research draws on a number of existing models that predict the structure and function of AM fungal communities. The functional equilibrium model suggests that plants will benefit most from mycorrhizas and support more AM fungi when soil resources such as phosphorus are scarcer than photosynthate. This is because the symbiotic relationship supplies carbon to the fungi in the form of sugars in return for the immobile minerals accessed by the hyphae on behalf of the plant. The model predicts that the abundance of AM fungi should be inversely related to the availability of essential soil resources.

To a large extent, this expectation has been borne out by Johnson's earlier research; however, the Serengeti studies have revealed important interactions with precipitation and soil type, and also differences among fungal families. During the most recent fieldwork, Johnson discovered that certain families of AM fungi survive better in coarse textured sandy soil, whereas others prefer fine-textured clay soil.

A further significant finding from the study, derived from the long-term grazing removal experiment, is that grazing has surprisingly little effect on the biomass of roots and AM fungi. However, analysis of communities of AM fungal spores suggests that removal of grazing may cause a shift in the community composition of AM fungi. Ongoing studies of fungal DNA inside roots will help determine the extent of divergence of fungal communities in grazed and un-grazed vegetation. Combining these analyses with structural equation modelling represents an important advance in understanding fauna-plant-fungi relationships at an ecosystem scale.

Previous studies in North American grasslands by Johnson and her colleagues supports the co-

adaptation model, which posits that in natural ecosystems plants and indigenous fungal communities adapt to their surroundings and to each other in order to maximise mutualism and minimise parasitism. This result was derived by comparing the symbiotic functioning of 'home' and 'away' communities of AM fungi, by placing the spores in soil types different to those in which they had evolved. When transplanted to 'away' soils the fungi were significantly less beneficial to plant growth, thus demonstrating that AM fungal communities function best in the soil type that they are adapted to. This has important ramifications for ecosystem management, suggesting that non-native fungal communities may not function the same if they are introduced into soils to which they are not adapted.

FIRST PRINCIPLES

While Johnson recognises that the Serengeti is an ecosystem unlike any other in the world due to its complex system of natural checks and balances, she believes that findings from the Serengeti research will help develop hypotheses that can be tested anywhere in the world. "Our ultimate goal is to develop first principles that can be used to make ecology a more predictive science," she explains.

A handful of soil contains many kilometers of AM fungal hyphae. Photo shows hyphae magnified 400X. Image courtesy of Julie Wolf.

"Insights gained from this work and from our studies elsewhere will help us develop ecological principles that are applicable to any ecosystem."

Gaining a deeper understanding of the functioning of mycorrhizas will also have practical benefits beyond the Serengeti, particularly in the development of more sustainable agricultural practices: "There is a great interest in reducing the need for inorganic fertilisers in agriculture. Proper management of AM symbioses may help achieve this goal," Johnson suggests. The insights derived from studying which fungal families are suited to different soil types and climatic conditions in the Serengeti and in other systems around the world will help farmers to manage their crops in order to maximise the mycorrhizal benefits. Selecting crops that are adapted to a particular soil type and have known benefits from mycorrhizal symbiosis could be more efficient than selecting cultivars that maximise yield but require high inputs of chemical fertilisers.

CARBON SEQUESTRATION

Because of the extensive biomass of mycorrhizas in the soil, there is also great interest in managing them to maximise their potential to sequester carbon underground. Johnson explains precisely why her recent research is so important in understanding these possibilities: "AM hyphae are potentially a sizable sink for carbon in the soil but it is necessary to understand the extent to which this carbon-sink changes with precipitation and across the season before we can fully understand the levels of carbon sequestered in AM hyphal networks". Managing mycorrhizal communities effectively to encourage sequestration of carbon belowground could have a significant impact on levels of atmospheric carbon, while encouraging symbiosis with fungal communities as opposed to inorganic fertilisers could also help to limit the impact of agriculture on the environment.

INTELLIGENCE

EFFECTS OF HERBIVORES AND MYCORRHIZAS ON N-FIXERS ACROSS SOIL AND CLIMATE GRADIENTS IN THE SERENGETI

OBJECTIVES

To provide the scientific basis for developing management strategies to maximise the benefits of mycorrhizal fungi for sustainable production of food and fibre in semi-arid grasslands, savannas and other tropical ecosystems.

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FUNDING

US National Science Foundation (NSF) – award no. 0842327

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