Nancy C. Johnson interview:

Mycorrhizal ecology, happiness, lessons to students, multilevel selection, and the "mutualism–parasitism continuum"

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Nancy Collins Johnson Ph.D. is a Regents' Professor at the School of Earth & Sustainability (School that she directed for four years), Northern Arizona University, where she has been working since 1997. Nancy has a B.Sc. in Biology and a Ph.D. in Ecology both from the University of Minnesota, and a M.Sc. in Botany from the University of Wisconsin, where her love for the mycorrhizal symbioses started. She has had an impressive career, which among other things, includes two Fulbright research fellowships at Lund University (Sweden) and at the Czech University of Life Sciences, an NSF postdoctoral fellowship, and a Bullard Fellowship at Harvard Forest. She advises or is a fellow of scientific societies like Society for the Protection of Underground Networks, American Association for the Advancement of Science, and Ecological Society of America, among others, and in 2018 she received the Deborah A. Neher Career Award from the Soil Ecology Section of the Ecological Society of America. Nancy usually takes many panels, mentoring, and editorial roles. Through the years she has been invited to dozen of seminars and talks around the world. Her research projects, since 1990, have targeted fundamental questions in mycorrhizal ecology: from pioneer works in the "mutualism–parasitism continuum" and the response of mycorrhizas to a changing, warmer world during the 1990s, effects (of management) and applications of mycorrhizas in agricultural settings, to a

system analysis perspective of the beneficial effects of arbuscular mycorrhizal fungi in sorghum that includes genetics, genomics, imaging, and microbiomics. Nancy`s research goes beyond mycorrhizas and Arizona, extends to fundamental and applied questions in soil ecology, and extends to the Czech Republic, the Serengeti, and around the world.

With more than 100 refereed publications and up to 18 graduate students and postdocs supervised, her impact on mycorrhizal ecology, and on how we think about mycorrhizas, is outstanding. At some point, some of her ideas could have been thought of as "out of the box", but given their strength and continuing supporting evidence, they are now well established in mycorrhizal ecology. In particular, seeing the mycorrhizal

symbiosis as context-dependent (i.e., in soil nutrients; the "mutualism–parasitism continuum") still feeds current debates in our area, and could even affect how we define and characterize a mycorrhiza, for example when non-nutritional mycorrhizal functions are taking into account. Nancy continues to explore new perspectives (i.e., hyphae-bacterial interactions, multilevel selection) and is very approachable, and kind, and all these excellent characteristics are reflected in the people she has supervised. In our new section at the IMS Newsletter, among other things, Nancy shares with us her beginnings in mycorrhizal research, what she considers her biggest achievements, her definition of happiness, advice to Ph.D. students, and how she sees our field in the future.

- Why and when did you start to study the mycorrhizal symbiosis?

I have been interested in soil ecology and plant symbioses since I was a child. In 1983, when I started my MS degree in Botany at the University of Wisconsin, I pondered several options for study systems (Azolla-cyanobacteria, legume-rhizobia, etc.), and when I learned about mycorrhizas, I immediately knew that I wanted to study them. I fortuitously met Tom Hunt, a graduate student in the Restoration Ecology program who had a nicely replicated experiment in a taconite mine not far from Madison. Sampling Tom's experiment provided a wonderful opportunity to study mycorrhizal relationships in early and late successional plants as well as the responses of mycorrhizal fungi to restoration treatments. I collected soil and root samples from the experiment and tried to extract arbuscular mycorrhizal (AM) fungal spores and stain the roots to measure AM colonization based on published protocols. It was very difficult because no one at the university studied mycorrhizas, and I really had no idea what spores and colonization should look like. It was clear that I couldn't accomplish the measurements necessary for my research alone. My advisor Michael Adams suggested that I call Mike Miller at Argonne National Laboratory to ask for help. I'll always remember that Mike Miller said *"you think it is hard to study mycorrhizae? We do too, and we're experts."* Then he invited me to his lab to learn techniques with his postdoc A-C McGraw. I also reached out to Edie and Mike Allen who were doing similar studies in Wyoming. With everyone's help, we discovered many new things and were able to publish three papers from the taconite mine research. I was hooked on mycorrhizas and continued to study them for my PhD with Dave Tilman at the University of Minnesota, and to this day I am still intrigued by mycorrhizal symbioses.

> *"Successful students will be my legacy, and this work is still under construction"*

- What do you consider is your biggest achievement in mycorrhizal research? How do you see your legacy? Or is this work under construction?

Successful students will be my legacy, and this work is still under construction. I have been blessed with some really smart and creative students. I continue to be impressed by their accomplishments, and it is rewarding to think that I may have helped them get started in their professional trajectories.

- Your 1997` "mutualism–parasitism continuum" paper has influenced how many of us think about mycorrhizas, how they work, and their ecology. What is the story behind it, how it came about? What is the main conclusion of that paper? After 25 years, do these conclusions still hold?

The main conclusion of that paper is that the influence of mycorrhizal symbioses on plants is context dependent, and this conclusion has survived the test of time. The International Conference on Mycorrhizas (ICOM) played a key role in that publication. In 1996, in preparation for the First ICOM at the University of California, Berkeley, Randy Molina asked Jim Graham, Andrew Smith and me to organize a session entitled: *'Can mycorrhizal associations be parasitic? Re-addressing our definition of mycorrhiza: structure vs. function.'* At that time, many people felt that by definition mycorrhizas are mutualistic, but this idea was challenged by publications by researchers like Gabe Bethlenfalvay, James Hendrix, Jim Graham, Andrew Smith and myself who had used the word 'parasitism' to describe plant growth depressions caused by mycorrhizal fungi. The workshop was very well attended, with over a hundred mycorrhizal researchers in the audience and I was completely unprepared for the fervor and contentiousness of the controversy about whether mutualistic function should be a defining characteristic of mycorrhizas. In my own work in taconite tailings and grasslands, I observed that mycorrhizal function is context dependent, the same pairs of host plants and fungi could either enhance or depress plant fitness depending on environmental conditions. Other researchers had published similar findings and I was surprised that many people in our audience so adamantly rejected the notion that in some situations, mycorrhizas can have negative effects on plants. The following week I realized that mycorrhizal science could benefit from ecological theories about species interactions, and I outlined the key points of the 1997 paper. I contacted Jim and Andrew to see if they would like to co-author a paper on this subject, and they were both very enthusiastic about the idea. At the time, I was working out of my basement in Santa Fe New Mexico, so I got a babysitter to care for the children and went to St. John's College library to write my parts of the manuscript on a pad of yellow paper (laptops were rare back then). Working with Jim and Andrew was great, and before the end of the year we had a manuscript ready to submit to *New Phytologist*. I am happy that our publication accomplished what we had hoped. Our 1996 ICOM workshop was one of the most uncomfortable events of my life, but in hindsight it was good because it stimulated Jim, Andrew and me to build on the cost-benefit approaches of Alastair Fitter and Roger Koide and propose a theoretical framework of the conditions that are expected to generate mutualistic, commensal or even parasitic mycorrhizal symbioses. This framework has been the basis of much of my own research over the past 30 years.

- How do you define "success" and "happiness" in science? When were you happiest when doing science?

Success is when you make a discovery that advances our understanding of how the world works. My happiest times as a scientist happen when all the pieces of a puzzle line-up and new insights emerge. Major "eureka moments" follow years of work in the field, greenhouse and laboratory, but even mundane tasks – like counting and identifying mycorrhizal fungal spores using a microscope - can be enjoyable, especially if you listen to good music. Science is a systematic process for exploring the unknown - and it is fun.

- What would you recommend to PhD students in general?

When designing your graduate research program always start with a question and then figure out how to answer it using straightforward observations and experiments. Know the literature that is

relevant to your question and be sure to address new aspects that build upon what is already known. Experiments take time and effort so don't waste your time addressing inconsequential questions or questions that have already been sufficiently answered. Strive to address big questions that fit into a larger theoretical framework. Don't be shy to contact other scientists who may be able to help you. Plan a variety of different experiments and be prepared to have many of them fail. Research is the process of searching over-and-over-and-over again, that is why it is called re-search. When things don't work out as expected, learn what you can from the experience and move on. Enjoy the freedom to explore the unknown and be humble when you discover something new.

- What do you do in stressful times?

I go for a long walk in the forest or other natural area, practice some yoga and then try to get a good night sleep.

- What is your favorite conference to attend and why?

My favorite conference is ICOM because it is a small and focused meeting that allows me to travel to interesting places, make new friends and meet up with old ones. It is the only conference where everyone is a mycorrhizal geek.

- What is your favorite mycorrhizal fungal species?

Gigaspora margarita is my favorite mycorrhizal fungal species because its beautiful, big, fat, pearly white spores are so easy to see – even without a microscope!

- How to integrate bacteria and other organisms interacting with mycorrhizal hyphae into understanding the (multi)functionality of this symbiosis? How to account for those interactions?

This is a great question, and something that

Gigaspora margarita. Photo by: Vasilis Kokkoris

we think about a lot in my research lab. The first step is to characterize the composition of microbial communities associated with mycorrhizal fungi and discover any patterns that may occur. The advent of high-throughput genetic analyses has made it possible to begin to elucidate the complex microbial communities associated with mycorrhizal fungi. The next step is to look for causal linkages between the structure of the mycorrhizal microbiome and the function of mycorrhizal symbiosis. This will require many creative experiments using both reductionist and holistic methods. It will also require collaborations with a diversity of researchers including bacteriologists, soil scientists, ecologists, plant physiologists, geneticists and biochemists. This is an exciting time to be a mycorrhizal researcher because new analytical and computational methods make it possible to observe and measure microbes like never before.

- A favorite topic of mine is multilevel selection (natural selection, ie. phenotypic variability, differential fitness, and heritability, occurring at least in two levels of the biological hierarchy). You have written about this regarding mycorrhizas. Do you think a multilevel selection perspective would lead to a better

understanding of the mycorrhizal symbiosis? If so, how?

Yes, I believe that the concept of multilevel selection will help generate new insights about mycorrhizas because this perspective accounts for the emergent properties that arise in mycorrhizal systems (i.e. the sum of plant-fungus-microbe-environment interactions). The traditional view of natural selection as a solely population scale phenomenon does not accommodate horizonal gene transfer, nor can it explain how mycorrhizal symbioses between plant genotypes and their associated team of microbes become adapted to local environmental conditions. In contrast, multilevel selection recognizes that variation and heritability can occur at both population and community scales and opens the possibility that groups of plants, fungi and microbes may be selected as a team based on their cumulative success in their particular environment. Group Selection Theory has been around a long time and it is finally gaining more main-stream acceptance. I believe that the next innovation in evolution science will build on group selection to develop *Team Selection Theory*, and mycorrhizal systems may be the perfect system to develop and test this theory.

- There are inevitable biases when studying mycorrhizas. Besides general geographical biases (ie. towards the Northern hemisphere), also more specific biases, for example, in certain regions towards the dominant mycorrhizal types (ie. arbuscular mycorrhizal fungi in the tropics), or towards the effects of mycorhizas on plant growth and nutrition, while other functions as soil aggregation, chemical defense, and drought and disease resistance are less studied. Do you think these biases have an effect on how we understand the mycorrhizal symbiosis? And if so, how to counteract such biases?

I agree, historical variation in scientific literature about mycorrhizas creates biases in our understanding of the symbiosis. In my opinion, the best way to counteract this problem is to increase the diversity of mycorrhizal research endeavors. One way to accomplish this goal is to encourage funding agencies to provide additional support for research in understudied parts of the world and to encourage more cross-cutting collaborations among mycorrhizal researchers and scientists in diverse applied fields such as soil science, entomology, plant pathology, agronomy and forestry as well as basic sciences such as chemistry, physics and genetics. These collaborations are likely to reveal new and exciting discoveries about the contributions of mycorrhizal symbioses to our world.

- Finally, what ecological questions do you think mycorrhizal researchers should address in the following decades? How do you see our research area developing?

Your previous question helps answer this. In my opinion, future research should strive to examine mycorrhizas in understudied ecosystems and expand the breadth of knowledge about the mechanisms that control the function of mycorrhizal symbioses in the world outside of the greenhouse and laboratory. Better understanding of the genetic mechanisms that control mycorrhizal symbiosis along with the chemical signaling among symbionts are sure to advance our field. We should expect many surprises as we expand the scope of our inferences to include the complex interactions among biotic and abiotic components of ecosystems. This expansion will meld our science with other fields of study and ultimately provide a better understanding of the world that we live in.