

# Preface

The overwhelming majority of the world's plant species are associated with mycorrhizal fungi in nature. As the term mycorrhiza implies, the association involves fungal *hyphae* interacting in the *roots* of a plant. Importantly, the hyphae do not penetrate the cell membranes of the root cells, although they may penetrate the cell wall. Further, the plant does not reject the fungus as a parasite or pathogen. The hyphae extend away from the roots into the soil where they take up nutrients and transport them through the mycelium and to colonized roots. Multiple hyphae connect plant hosts into what has become known as a mycorrhizal network. Mycorrhizal networks are below ground and cryptic. As such, plant and ecosystem ecologists in the past had to largely “black-box” the role of mycorrhizal networks in plant community and ecosystem dynamics. Björkman was the first to report field evidence of a mycorrhizal network in his work on the nutritional mode of the mycoheterotrophic plant *Monotropa hypopitys* (Björkman 1960). Newman (1988) provided a thorough review of the structure and function of mycorrhizal networks. Since Newman's initial review there has been an impressive amount of work on the topic using advanced methods such as isotopic labeling and PCR-based identification methodologies and additional reviews have followed (Simard and Durall 2004; Selosse et al. 2006; Horton and Van der Heijden 2008; Peay et al. 2008; Van Der Heijden and Horton 2009; Bahram et al. 2014).

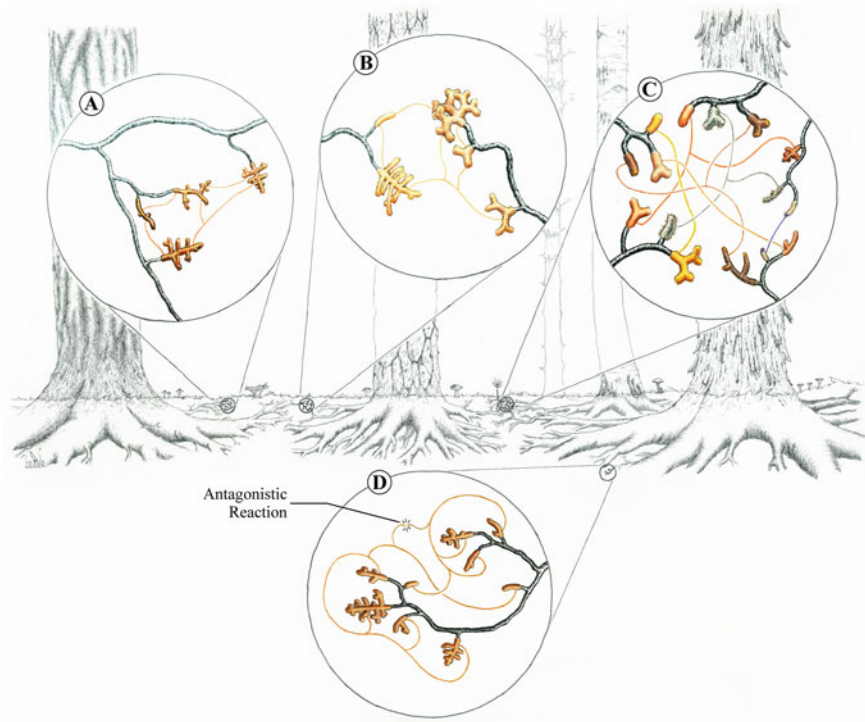
The textbook explanation for the benefit to plants of associating with mycorrhizal fungi is that fungi provide plants with a physical extension of the root system. Importantly, the fungi also produce unique enzymes that give plants access to pools of nutrients with limited availability to the plants alone (e.g., organic nitrogen, phosphorus). However, an individual mycorrhizal plant colonized by a single fungus individual is too simple. The mycorrhizal condition is much more complex and interesting. For example, an ectomycorrhizal tree may support tens of fungus species on its roots and multiple genotypes of each (Bahram et al. 2011). And each genetic entity (genet) may be isolated into multiple independent ramets. Further, this does not address the increasingly recognized role of mycorrhizal fungi in forming intra- and inter-specific plant connections, the mycorrhizal networks.

It has become clear that most mycorrhizal fungi colonize and provide nutrients to multiple plant species. This has important implications for plant competition for soil nutrients, seedling establishment, plant succession, and plant community and ecosystem dynamics. Schimel and Bennett (2004) suggested a paradigm shift was occurring in ecosystem science based on the realization that microbes, including mycorrhizal fungi, acquire organic N through depolymerization of N containing polymers. Plant ecologists have accumulated a rich body of knowledge regarding nutrient acquisition by plants. Much of the work is based on hydroponic systems replete with nutrients and, importantly, without mycorrhizal fungi. However, plants do not typically grow in nutrient-rich soils, or without mycorrhizal fungi. Plant competition for nutrients is not strictly a function of interactions between plants. Rather, mycorrhizal fungi compete for soil nutrients that then become available to multiple plant hosts through mycelial networks. Competition for soil nutrients may therefore involve compatibility interactions between fungi and hosts as much as plant–plant competition. This is a new paradigm for plant ecologists that may be as important as the one highlighted for ecosystem ecologists by Schimel and Bennett (2004).

A mycorrhizal fungus network reduced to its simplest form is a single fungal individual (a thallus) that has colonized multiple root tips of a plant individual (Fig. 1a). The connected mycelium of an individual fungus colonizing roots of multiple plants of the same or different species is a *common mycelial network* (Fig. 1b). Multiple individuals of multiple fungus species colonizing multiple plant species make up a *common mycorrhizal network* (Fig. 1c). The reader should be careful to understand when an author uses CMN to denote a common mycelial network usually with a limited spatial extent versus a common mycorrhizal network that may be much more extensive and involve multiple trees and their fungi.

It is reasonable to assume that an individual plant interacts with a rich assemblage of mycorrhizal fungi as indicated in Bahram et al. (2011) on a single poplar tree, and this level of complexity is ramified by the addition of other local plant hosts. Individual fungi in such a mycorrhizal network have direct and indirect impacts on each other and their hosts through competition for soil resources and compatibility interactions with common hosts. Therefore, a community of mycorrhizal plants and fungi interact not as a superorganism *sensu* Clements (1936) and Phillips (1935) but individually as independent organisms *sensu* Gleason (1926).

Following nutrient dynamics in a mycelial network of a single fungus is daunting, especially in a field setting. Following nutrient dynamics in a complex mycorrhizal network, with many interacting fungal and plant individuals, is all the more difficult. Modeling these interactions is helping to overcome the limitations of an *in vivo* system and is ripe for new research efforts (see Bahram et al. 2014). However, these approaches will only yield accurate results with more and better data on the role each species plays in network dynamics to feed into the models (e.g., the kind and amount of nutrients acquired and transported, compatibility interactions with various hosts, competitive interactions between the fungi, and how plants and fungi recognize and reward good symbionts). It is my hope that the



**Fig. 1** Schematics of mycorrhizal networks. Mycelial connections can vary from one fungus individual connecting root tips of one plant individual (A), to one fungus individual connecting root tips of two plant individuals (B), to multiple fungi interacting on multiple plant species (C). We also highlight an antagonistic interaction between different thalli of the same species (D); the hyphae recognize nonself tissue and reject the attempt to anastomose. Figure drawn by Sam Tourtellot

chapters in this book lay the next foundation for research on mycorrhizal networks and point the way to areas for research needs and opportunities.

The book is organized into three sections: network structure, nutrient dynamics, and the mutualism–parasitism continuum. A necessary requirement for the development of a mycelial network is compatibility between a fungus and a plant. Molina and Horton review specificity of ectomycorrhizal symbionts and its role in plant communities in Chap. 1. A lot of work has been conducted since Molina et al. (1992) provided a comprehensive review of specificity. Chapter 1 includes an updated list of terms and their definitions that should prove useful in communicating about specificity phenomena and mycorrhizal networks. Predictions in the earlier review about the role of specificity phenomena in plant community dynamics have been supported in numerous field studies using molecular techniques. However, difficulties with sampling ectomycorrhizal fungi that are infrequently encountered and belowground continue to be a problem when investigating large-scale patterns of host preference and specificity.

Networks of mycorrhizal fungi involve interactions between symbionts but also interactions between fungal individuals, a topic explored by Giovannetti et al. in Chap. 2. When hyphae from the same genotype come into contact, they can anastomose, or fuse, into a continuous thallus even if the two hyphae were from different ramets of the same genet. Ectomycorrhizal fungi in the Basidiomycota and the Ascomycota have genetic systems for recognizing and rejecting nonself tissue, preventing anastomosis between different genotypes in a mycorrhizal network (Fig. 1d). This so-called vegetative incompatibility system is analogous to our own immune system. The vegetative incompatibility system in ectomycorrhizal fungi is why I suggested above that a community of mycorrhizal fungi functions individually rather than as a superorganism. However, as Giovannetti et al. review in Chap. 2, interactions between arbuscular mycorrhizal fungi may be different. These fungi are thought to be strictly clonal over the course of their greater-than-400-million-year history, yet there is evidence for recombination in the group. Thalli of Glomeromycota have few septae, making a mycelial network essentially a single cell with hundreds and even thousands of nuclei. Germinants of single spores contain multiple genotypes but whether the genetic diversity occurs within the nucleus that is mitotically propagated and packaged into new spores (homokaryosis model; Pawlowska and Taylor 2004) or across multiple genetically distinct nuclei, each with their own mitotic fate and possibility for packaging into new spores (heterokaryosis model; Sanders et al. 1995) is hotly debated. The vegetative incompatibility system may not be as active in the arbuscular mycorrhizal fungi as it is in the ectomycorrhizal fungi and anastomosis between thalli derived from different genets may be a way of generating and maintaining a mosaic of genetic types in a thallus. Interestingly, Tisserant et al. (2012) report finding meiosis-specific genes in the transcriptome of *Glomus interradices* (now *Rhizophagus irregularis*) raising the possibility for some mechanism supporting recombination in the group other than heterothallic anastomosis. This is an exciting area with great potential for additional lessons about the unique genetic system in Glomeromycota and interactions between symbionts in mycorrhizal networks.

The second section of the book focuses on nutrients and their movement through networks. Wallander and Ekblad begin the section with Chap. 3 and their coverage of extramatrical mycelium in ectomycorrhizal fungi (extramatrical being mycelia beyond the root tips). They focus on carbon and nitrogen. Plants allocate an estimated 15–20 % of the carbon they fix to their mycorrhizal fungi (Hobbie and Hobbie 2006). The fungi use this carbon in part to produce mycelial networks in soils to gain access to limiting resources. It is well known that fertilized plants allocate fewer resources belowground and as a result, fewer resources to mycorrhizal fungi. Conversely, if a plant is growing under nutrient limitation, more carbon is allocated belowground, supporting mycelia of fungi that provide access to the limiting nutrient (Werner and Kiers 2015). Network production is then a function of both carbon availability and nutrient availability. It is still hard to quantify the rate of extramatrical mycelium turnover, but Clemmensen et al. (2015) have shown that dark septate root endophytes may support long-term sequestration of host carbon in boreal forests. As Wallander and Ekblad suggest,

there is increasing evidence that ectomycorrhizal fungus networks should be included in soil carbon models.

In Chap. 4, Jakobsen and Hammer review the influence of mycorrhizal networks on outcomes of plant competition in arbuscular mycorrhizal plant communities. Observations that plants do not always benefit from associating with mycorrhizal fungi have led to the idea that the symbiosis exists on a mutualism–parasitism continuum (Johnson et al. 1997), a topic that will be explored further in Section 3 of this book. Clearly, plant hosts allocate carbon to their symbionts, and this allocation reduces the carbon available for their own growth. This reduced growth may, in situations of high nutrient availability or intense competition, reduce the competitive outcome and fitness of the host. Jakobsen and Hammer suggest that nutrient movement in networks moves toward carbon sources and larger plants. As a result, these authors suggest mycorrhizal networks accentuate competitive outcomes rather than relaxing them. While it is known that seedlings can experience reduced growth when connected to mycorrhizal networks, the negative effect of mycorrhizal networks on seedling establishment may be temporary, especially when larger hosts become less significant carbon sources through senescence. Still, Jakobsen and Hammer predict that mycorrhizal networks help plants that are already larger than others in the network.

Simard and colleagues have used labeled isotopes to follow transfer of resources between plants through ectomycorrhizal fungus networks. In Chap. 5, Simard et al. review the literature on nutrient movement between plants through networks with a focus on the magnitude, fate, and importance of mycorrhiza-derived nutrients in ectomycorrhizal plants. It is clear that many mycoheterotrophic hosts are dependent on network fungi to supply carbon, and that carbon comes from autotrophic hosts in the network. While there are data showing a low level of carbon can be transported to autotrophic hosts, it remains controversial whether the amounts are ecologically significant. Other nutrients such as nitrogen and water are transported through networks and contribute to plant survival. Phosphorus transport remains difficult to trace. In summary, resource fluxes through ectomycorrhizal networks can contribute to plant establishment and survival, but the level of the effect is context dependent.

Section three focuses on studies that investigate mycorrhizal fungi as mutualists or parasites and the implications of those two symbiotic types for plant community dynamics. Nara opens this section with Chap. 6 and a review of his work on the role of ectomycorrhizal networks on seedling establishment in a primary successional habitat. Networks of ectomycorrhizal fungi associated with pioneer *Salix* support establishment of conspecific *Salix* seedlings, but also seedlings of successional hosts such as *Picea* and *Betula*. Plant hosts planted away from *Salix* patches are not colonized by ectomycorrhizal fungi, suggesting spores are not functioning as inocula as much as *Salix*-associated mycelial networks. Using microsatellite markers, Nara shows that some species such as *Laccaria* produce small thalli generally less than a meter in extent and short lived. However, other species produce longer-lived thalli that are up to 10 m in extent. These data are consistent with other studies from a variety of successional settings suggesting most individuals of

ectomycorrhizal species are typically less than 3 m in extent, but some individuals of some species can be much larger (Douhan et al. 2011). Although the degree of benefit to the plant host varied by fungus species, ectomycorrhizal fungus networks are important for facilitating seedling establishment in this system.

Wagg and colleagues focus Chap. 7 on facilitation and antagonism in arbuscular mycorrhizal networks. They suggest arbuscular fungal communities might contribute to greater plant performance through functional complementarity or niche specialization. They argue that allocation of resources through mycorrhizal networks alters competitive outcomes among the plant species, an idea that follows a model proposed by Bever (2003). By considering antagonistic as well as facilitation in the mycorrhizal mutualism, the authors give a more complete framework for understanding how networks function in plant community dynamics.

Kennedy et al. explore the unique networking dynamic of *Alnus* in Chap. 8. Most ectomycorrhizal plant hosts are known to associate with multiple fungal species and vice versa, resulting in a high potential for complex ectomycorrhizal networks in a forest setting. However, exceptions to this pattern are known, with *Alnus* being the most commonly cited exception. *Alnus* forms isolated networks with little direct connections to networks of other host species in a forest. This seems to put both the fungus and plant at a disadvantage given the fungus has fewer sources of carbon and the plant has less access to nutrients than if they were generalist symbionts. In addition to reviewing the literature on the specificity observed in *Alnus*, the authors discuss why having isolated networks is an advantage, and how the high specificity in the genus is maintained.

It should be clear from the coverage of these chapters that nutrient transfer between plants via mycorrhizal networks and its effects on plant community dynamics remains controversial or at least context dependent. Hoeksema argues in Chap. 9 that most experiments have not adequately tested the role of mycorrhizal networks on plant community dynamics. He suggests more tests should be conducted to rule out alternative hypotheses to carbon movement between plants, especially those that include experimental manipulations of the mycorrhizal networks. This is obviously not a trivial request considering the fact that mycorrhizal networks function largely belowground and are difficult to observe. However, Hoeksema's recommendations for future studies (and those of the authors of all the chapters) point to the exciting possibilities for additional research on mycorrhizal networks.

I close with my acknowledgements to all the people that have helped make this book possible. First and foremost are my coauthors who accepted the invitation to write a review chapter focused on their research. A book on a topic such as mycorrhizal networks will already seem rather narrowly focused to some, yet as each chapter shows, the topic can be broken down even further. I have learned a lot from these authors in the past and even more from this project. I thank all the authors for their patience with the delays in my completing the book. I also thank the anonymous reviewers who helped make the book stronger with their constructive comments and edits. I thank Valeria Rinaudo for her interest and enthusiasm for a book on mycorrhizal networks and shepherding the proposal through

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