

# Mycorrhizal Networks Facilitate Tree Communication, Learning, and Memory



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**Abstract** Mycorrhizal fungal networks linking the roots of trees in forests are increasingly recognized to facilitate inter-tree communication via resource, defense, and kin recognition signaling and thereby influence the sophisticated behavior of neighbors. These tree behaviors have cognitive qualities, including capabilities in perception, learning, and memory, and they influence plant traits indicative of fitness. Here, I present evidence that the topology of mycorrhizal networks is similar to neural networks, with scale-free patterns and small-world properties that are correlated with local and global efficiencies important in intelligence. Moreover, the multiple exploration strategies of interconnecting fungal species have parallels with crystallized and fluid intelligence that are important in memory-based learning. The biochemical signals that transmit between trees through the fungal linkages are thought to provide resource subsidies to receivers, particularly among regenerating seedlings, and some of these signals appear to have similarities with neurotransmitters. I provide examples of neighboring tree behavioral, learning, and memory responses facilitated by communication through mycorrhizal networks, including, respectively, (1) enhanced understory seedling survival, growth, nutrition, and mycorrhization, (2) increased defense chemistry and kin selection, and (3) collective memory-based interactions among trees, fungi, salmon, bears, and people that enhance the health of the whole forest ecosystem. Viewing this evidence through the lens of tree cognition, microbiome collaborations, and forest intelligence may contribute to a more holistic approach to studying ecosystems and a greater human empathy and caring for the health of our forests.

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## 1 Introduction

Today, plants are commonly recognized as microbiomes—where villages of collaborative microbes live in and on their roots, stems, and leaves, forming interaction networks (Faust and Raes 2012; van der Heijden and Hartmann 2016). These microbial networks of fungi, bacteria, archaea, viruses, protists, and algae, as well as nematodes, arthropods, and protozoa (together comprising a soil food web), work together with the plants in complex adaptive systems to drive nature's biogeochemical cycles and influence every aspect of ecosystem structure and function (Ingham et al. 1985; Levin 2005). The interaction networks are highly coevolved and finely attuned, such that the loss of subjects from this village, particularly keystone species, could trigger system shifts to alternative stable states (Scheffer et al. 2001). The interaction among microbiomes and plants is so fundamental to life on earth that it is credited with the chemical weathering of rock and migration of ancient plants from the ocean to land about 360 Mya and the subsequent coevolution of highly specialized gymnosperm and angiosperm trees and ultimately humans (Margulis 1981; Humphreys et al. 2010; Archibald 2011). The rhizosphere (root-soil interface) microbiome is particularly diverse and active, with plants investing 10–90% of their photosynthate belowground to fuel rhizosphere processes involved in the carbon, nutrient, and water cycles, with the smallest proportion allocated belowground in the tropical forest biome and the largest in the grassland and tundra biomes (Poorter et al. 2012). The plant and microbial species that inhabit this rich zone have coevolved sophisticated communication systems to facilitate their multifarious interactions, where information is exchanged among organisms both within and among kingdoms (Baluška and Mancuso 2013).

The microbiome of the rhizosphere includes mycorrhizas (literally “fungus-roots”)—generally mutualistic and obligate symbioses between root-inhabiting fungi and plants, involving 95% of plant families (Trappe 1987). Plants benefit by engaging with the fungus because it is energetically less expensive to invest in hyphal growth than root growth to acquire soil nutrients since complex compounds like cellulose and lignin are not required, and the fungal hyphae grow faster, have smaller diameters for accessing tight soil pores, and branch more profusely. The development of the mycorrhiza involves coevolved communication between the highly active plant root apex (Darwin's “root-brain”; see Baluška et al. 2010; Baluška and Mancuso 2013; more below) and the fungal symbiont, involving bidirectional elicitor signal molecules such as auxins, signal perception, signal transduction, and defense gene activation (Garcia-Garrido and Ocampo 2002). Once the mycorrhizal association is developed, the mycorrhizal fungus exchanges nutrients it forages with its extramatrical mycelium from the soil for photosynthate fixed by the plant. To meet plant nutrient and water demands, the roots and fungal hyphae must explore large volumes of soil to acquire the limiting and patchy resources (Smith and Read 2008), involving cognitive behaviors such as decision-making, search and escape movements, and neighbor recognition (Baluška et al. 2010; Heaton et al. 2012). Without their mycorrhizal fungal partners, the vast majority of plants could not acquire enough soil nutrients and water to grow, survive, and reproduce.

Mycorrhizal fungi can link the roots of different plant hosts, forming mycorrhizal networks (Molina and Horton 2015). Mycorrhizal networks are considered common across biomes because most mycorrhizal symbioses are generic, where a plant species associates with a diverse suite of fungal species or, conversely, a fungal species colonizes many plant species. Some of the associations are highly specialized, however, where some plant and fungal species only associate with a single partner species, with the potential to form exclusive, conspecific networks (Molina et al. 1992). In forests, heterospecific or conspecific networks of ectomycorrhizal fungi (EMF) form among gymnosperm and some angiosperm trees as well as woody shrubs in temperate and boreal forest biomes, whereas networks of the arbuscular mycorrhizal fungi (AMF) form mainly among angiosperm trees along with many herbs and grasses in the tropical forest biome, as well as some conifers (e.g., Cupressaceae and Aceraceae) in temperate forests (Smith and Read 2008). Ectomycorrhizal fungi occur predominantly in the *Basidiomycota* and *Ascomycota* phyla and are characterized by a fungal sheath around the root tip, a Hartig net enveloping the plant host root cell wall, and extramatrical mycelia, whereas the endomycorrhizal AMF occur predominantly in the *Glomeromycota* phylum, and these form arbuscules and sometimes vesicles inside the plant host root cells. Some exceptional plant families and genera are capable of forming viable symbioses with EMF and AMF simultaneously (e.g., *Salicaceae*, *Eucalyptus*) and serve as key hubs linking together ectomycorrhizal and arbuscular mycorrhizal networks (Molina and Horton 2015). Other endomycorrhizal classes include ericoid mycorrhizal fungi on autotrophic plant species in the Ericaceae family, arbutoid mycorrhizas on autotrophic plants in the Ericaceae subfamily Arbutoideae, monotropoid mycorrhizas on heterotrophic and mixotrophic plants in the subfamily Monotropoideae of the Ericaceae, as well as several genera in the Orchidaceae, and orchid mycorrhizas on heterotrophic orchids.

Plants, including trees, are increasingly understood to have cognitive capacity for perceiving, processing, and communicating with other plants, organisms, and the environment and to remember and use this information to learn, adjust their behaviors, and adapt accordingly (Gagliano 2014). In other words, plants are increasingly recognized as having agency that leads to decisions and actions, characteristics of intelligence usually only ascribed to humans or perhaps animals (Brenner et al. 2006). This recognition, that plants have agency and actions, in their capacity to perceive, communicate, remember, learn, and behave, could be transformative for how humans perceive, empathize with, and care for trees and the environment.

Trees are known to perceive and communicate with each other and other plants through root pathways (Baluška et al. 2010; Bierdrzycki et al. 2010) or using airborne signals (Heil and Karban 2009). They can also recognize the identity of neighboring plants and whether they are genetically related through root exudates (Bierdrzycki et al. 2010) or mycorrhizas (Pickles et al. 2016). Baluška and Mancuso (2013) propose that within- and between-plant communication is accomplished primarily via signal transport within and between roots, where compounds such as auxins serve as neurotransmitters across synapses at cell cross-walls within roots, across synapses between the apices of different plant roots, or between plant roots

and symbiotic microbes and fungi in the rhizosphere. Because all trees are mycorrhizal in nature and mycorrhizal networks are considered ubiquitous in forests (Horton 2015), I propose that most belowground communication between trees in nature is mediated by mycorrhizas and that mycorrhizal networks are intimately involved in tree cognition. This follows closely on Baluška and Mancuso's (2013) recognition that communication between plants, and the involvement of cell-to-cell synapses and neurotransmitter-like compounds, has coevolved with microorganisms. Yet, much of the historic research on plant communication and cognition has been conducted on non-mycorrhizal plants grown in the lab or has not reported on the role of mycorrhizal fungi. The present review seeks to help set the stage for more holistic examinations of various aspects of plant cognition by involving their mycorrhizas in nature.

This chapter aims to review the fundamental role of mycorrhizal fungal networks in communication between trees and the functional, ecological, and evolutionary significance of this communication to forest communities in nature. I will review existing experimental evidence for cognition among trees facilitated by mycorrhizas, showcasing examples from the research in my lab. It is my hope that this might lead to an integrated approach to studying plant cognition in natural ecosystems that includes plant microbiomes.

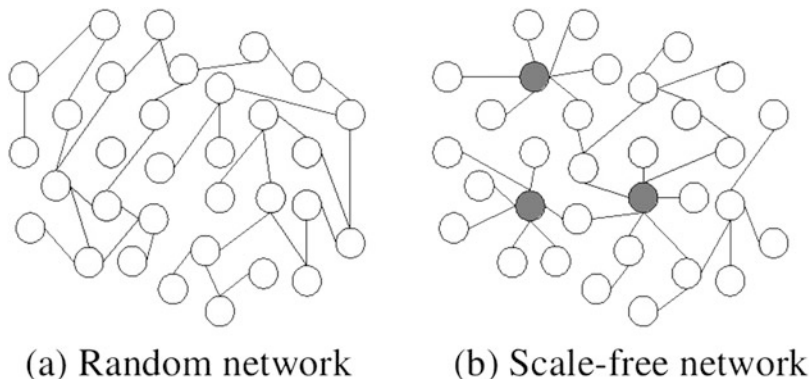
## 2 Evidence for Tree Cognition Facilitated by Mycorrhizas

Cognition of plants, and the complex adaptive behaviors it triggers for enhanced fitness, requires perception, agency, and action (Gagliano 2014). While cognition and intelligence are usually considered exclusively the domain of humans and perhaps animals due to the existence of their central nervous systems, scientists in the field of plant cognition have effectively provided scientific evidence and argued for neuronal aspects in plants. This includes the existence of plant cell cross-walls, plasmodesmata, and synapses at root apices, analogous to neural synapses; signaling molecules that cross these synapses and transmit information via calcium-regulated exocytosis and vesicle recycling to neighboring cells, similar to neurotransmitters; and action potentials that rapidly transmit electrochemical signals to control plant physiology and behaviors, similar to a central nervous system (Baluška et al. 2005). Baluška et al. (2005) extend this concept to include cells of microbes in symbiosis with plants such as fungi and bacteria, where adjacent or interfacing plasma membranes form immunological synapses with plant cell membranes and molecules cross from plant–cell to microbe–cell, as in the trade of carbon and nutrient molecules across the plant–fungal membranes in mycorrhizas. Trees and plants use this neuronal physiology to then perceive the affordances of their environment (Gagliano 2014) through multiple sensory organs, including their leaves, roots, and microbiome (Karban et al. 2014; Bierdrzycki et al. 2010; van der Heijden and Hartmann 2016).

Yet, the absence of a brain, and its vast system of neurons, neurotransmitters, and action potentials organized as nodes and links in a complex modular neural network, now considered fundamental to neural plasticity, flexibility, and hence intelligence, questions the position that plant cognition is sophisticated and intelligent (e.g., good at making decisions, planning, organizing behaviors, solving problems, etc.) (Brenner et al. 2006; Gagliano 2014; Barbey 2017). Charles and Francis Darwin controversially proposed, with their “root-brain” hypothesis, that the root apex, located between the apical meristem and elongation zone of a root tip, acts like a brain-like organ that controls plant behavior, as with animals (Darwin 1880). Baluška et al. (2009) provide support for this hypothesis with the existence of “animal-like sensory-motoric circuits which allow adaptive behavior” such as root crawling and plant tropisms. However, in my view, the “root-brain” hypothesis cannot on its own adequately explain the sophisticated plant behaviors we observe in roots because, by nature of their energy-expensive constitution of cellulose, they lack the degree of flexibility needed to rapidly develop new transient pathways for tackling unique problems. Moreover, the “root-brain” hypothesis does not adequately fit with the new network neuroscience showing that general intelligence (g) arises from the existence of both “crystallized intelligence” (similar to memory) resulting from strong, well-worn overlapping pathways (or bonds) that access easy-to-reach network states, as well as “fluid intelligence” (similar to learning) resulting from weaker, more transient pathways and connections that access difficult-to-reach network states (Barbey 2017). To help complete the picture, I posit that when plants enter into symbioses with mycorrhizal fungi, this provides them with the necessary topology and energetics for sophisticated intelligence. Evidence for this follows.

### 3 Topology of Mycorrhizal Networks

Network topology refers to the arrangement of the various elements (nodes, links) of a communication network. In your brain, nodes and links could be neurons and axons; in a forest, they could be trees and interconnecting mycorrhizal fungal mycelia. Network topology determines how freely nodes interact with each other; how intense, frequent, or efficient their interactions are; and how vulnerable or resilient the network is to loss of specific nodes or groups of nodes (modules) (Bascompte 2009). Research in network neuroscience shows that general intelligence (g) is positively correlated with neural network architecture that is scale-free (the distribution of links per node follows a power-law, where there are a few highly connected nodes (i.e., hubs) and many weakly connected nodes) with small-world properties (cliquish, with frequent and strong links within cliques) (Barbey 2017). The scale-free network topology contrasts with random or regular networks, whose links are distributed more equally among nodes (Fig. 1). This architecture balances local with global efficiencies by having high local clustering (hubs, cliques, modules) and short path lengths (distance between distal nodes or clusters), allowing low-cost short-distance connections as well as shortcuts via hops and skips among distal nodes,



**Fig. 1** (a) Random network and (b) scale-free network models. In forests, the circles (nodes) can represent trees, and the lines (links) can represent interconnecting mycorrhizal fungal genets. The random and scale-free networks differ by the pattern and accessibility of links. In random network models, each tree node is linked to a relatively small number of other nodes that are randomly distributed around the network. These networks can be easily traversed because there are few steps, or degrees of separation, between nodes. Random networks are more resilient to perturbations than scale-free networks. In scale-free models, the degree of links between nodes is variable, where some nodes, or hubs, are highly connected relative to the average (Barabási and Albert 1999). This model is more representative of living networks, such as mycorrhizal networks, which grow by accretion and have a dendritic form. Figure source: Wikipedia. Reproduced with permission from Simard (2012)

modules, or cliques that promote global information processing (Bray 2003). In your brain, you can think of modules or cliques as cortexes and lobes (e.g., frontal, temporal, parietal, etc.). In forests, modules could be clusters of trees, different species, or functional groups of species; or from a fungal perspective, they could be fungal species or functional groups such as exploration types. [Exploration types, including long distance, short distance, and contact, are distinguished based on the amount of emanating hyphae or the presence and differentiation of rhizomorphs and are considered important in accessing the diversity of soil substrates needed to supply trees with adequate nutrition (Agerer 2001)]. They are also important to modes of resource transmission through mycorrhizal networks (Teste et al. 2009; Hobbie and Agerer 2010). In either brains or mycorrhizal networks, modules are interconnected, albeit less frequently than within modules, by axons or mycorrhizal fungi.

In scale-free networks, this modular characteristic allows for specialized information processing while small-world properties allow for global and local efficiency and flexibility in memory-based learning. The presence of strongly connected modules and hubs supports linkage, nestedness, and short path lengths among nodes important in the mobilization of crystallized knowledge (i.e., memory) for learning. On the other hand, they also leave the network vulnerable to loss of key hubs (e.g., local injury to a brain lobe, high-grade logging, or pathological selection of the largest trees in a forest). The presence of weakly linked nodes (e.g., frontoparietal and cingulo-opercular networks or patches of small regenerating trees in forest gaps), by contrast, supports globally efficient small-world topology,

access to difficult-to-reach states, and rapid adaptive behavior in novel situations (i.e., rapid learning) (Barbey 2017). In your brain, weak linkages can develop through rapid growth of synaptic connections between neurons and the myelination of nerve fibers, and these are strengthened via pruning in response to environmental conditions, which represents learning (Craik and Bialystok 2006). In mycorrhizal networks, weak linkages develop rapidly via cell expansion at growing mycelia fronts, where fungal apical tip growth, branching, anastomosis, and colonization of new plants occurs; this is thought to be accomplished predominantly by contact or short-distance explorer ectomycorrhizal fungal species (Agerer 2006; Hobbie and Agerer 2010; Heaton et al. 2012). This mycelium is very active, dynamic, and adaptive to simultaneously grow, prune, and regress in response to the rapidly changing environment, as in learning. It can also develop, via pruning, strong links that involve complex chords, strands, or rhizomorphs, predominantly formed by long-distance explorer fungi (Boddy and Jones 2007). These rhizomorphs not only exploit nutrients over short distances but also grow over long distances to reach disparate resource patches or form connections with distant ectomycorrhizal plants or modules (Agerer 2006; Lilleskov et al. 2011). They are capable of rapid, efficient high-volume resource transfer (Agerer 2006). You can think of the long-distance exploration rhizomorphs as analogous to “crystallized intelligence” and the rapidly expanding mycelial front of short-distance and contact explorers as “fluid intelligence.” According to Barbey (2017), neuroscience research shows that this kind of scale-free network topology provides the greatest flexibility and dynamics that are crucial to learning and intelligence. It also shows that neural networks have the flexibility to transition between topologies, for example, from scale-free toward regular topology that is associated with more specific cognitive abilities and or toward a random topology that is associated with broader, more general abilities. Recent research in forest ecosystems also shows that mycorrhizal networks can transition from scale-free to regular and back to scale-free topology with the harvesting and planting of trees and subsequent stand development (van Dorp 2016). This dynamic flexibility likely underlies the diverse intelligence present among humans and forests.

Mycorrhizal network topology in forest stands, where trees are modeled as nodes and interconnecting fungal hyphae as links, is strikingly similar to the topology of neural networks in our brains (Southworth et al. 2005; Lian et al. 2006; Beiler et al. 2010, 2015; Toju et al. 2014). In Beiler et al. (2010, 2015), we used multi-locus, microsatellite DNA markers to show that most trees in uneven-aged forests of Douglas-fir (*Pseudotsuga menziesii* var. *glauca*) were interconnected by mycorrhizal networks of two ectomycorrhizal fungi, *Rhizopogon vesiculosus* and *R. vinicolor*. These two sister species of *Rhizopogon* share narrow host specificity for Douglas-fir (Kretzer et al. 2003), and they dominate the diverse community of 65 ectomycorrhizal fungal species that occur in all stages of forest stand development (Twieg et al. 2007). The *Rhizopogon* species fruit in truffles belowground and have coralloid or tuberculate structures with fine, dark extramatrical hyphae capable of rapidly growing over short distances and forming highly differentiated rhizomorphs capable of transporting water and dissolved nutrients over long distances (Brownlee et al.

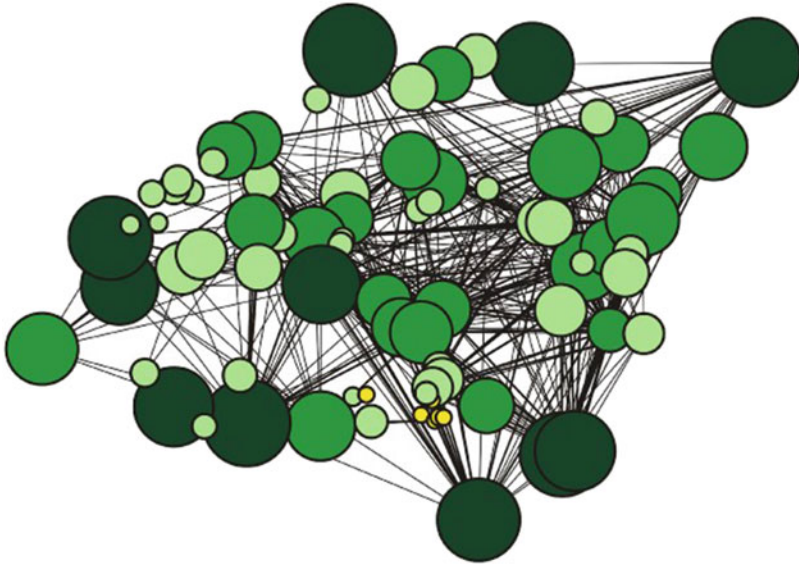


**Fig. 2** *Rhizopogon vinicolor* in a dry interior Douglas-fir forest of British Columbia. (a) Fruiting body (truffle) on forest floor; (b) tubercle with outside rind removed tubercle; (c) tubercle, rhizomorphs, hyphae, and roots in mineral soil profile; and (d) mixed mycorrhizal hyphal network on surface of mineral soil (forest floor peeled off). Photos by Kevin J. Beiler and Hugues Massicotte. Reproduced with permission from Simard (2012)

1983; Molina 2013) (Fig. 2). We found that the short-distance hyphae and long-distance rhizomorphs of *R. vesiculosus* and *R. vinicolor* colonized trees of all sizes and ages, forming spatially continuous, complex networks linking together multiple trees in the forest (Beiler et al. 2012).

The *Rhizopogon*-Douglas-fir mycorrhizal network had a scale-free network structure with small-world properties, where a few large, old hub trees had the greatest number of fungal connections and were linked to many small, young trees that had fewer connections (Beiler et al. 2010, 2015) (Fig. 3). This architecture makes sense given that rooting density and extent, and hence density of mycorrhizal root tips and connection potential, is correlated with the size of a tree. In a  $30 \times 30\text{m}$  patch in one of the stands, a single hub tree was linked to 47 other trees and was estimated to be linked to at least 250 more trees had the larger stand been sampled. The veteran hub trees provided an extensive network into which almost all of the smaller and younger understory seedlings and saplings had established. The high clustering in the network suggested that the old hub trees provided network paths or hyperlinks that bridged





**Fig. 3** Mycorrhizal network topology of Douglas-fir forest showing linkages between interior Douglas-fir trees via shared colonization by *Rhizopogon vesiculosus* and *R. vinicolor* genets. Circles represent tree nodes, sized according to the tree's diameter, and colored with four different shades of yellow or green that increase in darkness with increasing age class. Lines represent the Euclidean distances between trees that are linked. Line width increases with the number of links between tree pairs. Reproduced with permission from Beiler et al. (2010)

cliques (modules) of the densely interconnected younger trees. These pathways allowed the entire network to be easily traversed, which is a small-world property. The high density of fungal links within patches (modules) meant the patches were resilient to random disturbances but also vulnerable to attacks that target hubs. The *R. vinicolor* linkages were smaller and nested within the larger, denser *R. vesiculosus* network, forming a cliquish, nested “meta-network,” and this nestedness increased network resilience. The network density and complexity is undoubtedly vastly more complex than we were able to describe given that we accounted for only two of the 65 ectomycorrhizal species in the forest, and we did not examine the arbuscular, ericoid, arbutoid, or orchidoid subnetworks associated with other tree and understory plant species that would have been nested within the *Rhizopogon* network.

#### 4 Communication Through Mycorrhizal Networks

The scale-free, small-world network topology of the mycorrhizal network is designed for efficiency—for quickly shuttling signals through links among numerous trees, including between old hubs and young nodes, and for minimizing the costs of this information transmission while maximizing the impact on growth and

adaptation of the network (Barbey 2017). Our numerous experiments have found that a multitude of signals—including nitrogen, carbon, water, defense molecules, and kin recognition information—transmit back-and-forth among Douglas-fir trees through ectomycorrhizal networks (for a review, see Simard et al. 2015). Phosphorus (Eason et al. 1991; Finlay and Read 1986; Perry et al. 1989), other defense signals (Song et al. 2010; Babikova et al. 2013), allelochemicals (Barto et al. 2011), nutrient analogues (Meding and Zasoski 2008; Gyuricza et al. 2010), and genetic material (Giovannetti et al. 2004, 2005) have also been shown to transmit through arbuscular networks or among different ectomycorrhizal plants in other studies. These compounds can be large or small and include fungal carbohydrates (e.g., trehalose, mannitol, arabinol, and erythritol, see below), amino acids (e.g., glutamine and glycine), lipids, N ions ( $\text{NH}_4^+$  or  $\text{NO}_3^-$ ), phosphates, and nuclei (Martin et al. 1986; Smith and Smith 1990; Bago et al. 2002; Giovannetti et al. 2005; Nehls et al. 2007). Phytohormones such as auxins and jasmonates, which are signals important in regulating the mycorrhizal symbiosis as well as plant phenotypic plasticity, have also been shown to converge in mycorrhizal hubs (Pozo et al. 2015). Most of these signals shuttle rapidly within and between the plants—within hours or a few days—and they are of sufficient magnitude to influence plant behaviors such as root foraging, nutrient acquisition, growth, or survival (Simard et al. 2012). Even faster and more efficient signaling between plants could occur via sound transmission (Gagliano 2012) through mycorrhizal networks, much like a conversation over the telephone, but this mode of communication has yet to be explored in mycorrhizal networks.

In my view, the transmission of signals or resources or molecules or sounds between plants through mycorrhizal fungal networks constitutes communication. The Latin root of the word communication is *communicat*, or *share*, and it is the transfer or sharing of information through a common system of signals that benefits both the sender and the receiver. As argued by Gagliano (2012), interplant signaling of information is now widely accepted among scientists as a form of communication between plants. Moreover, where signaling is communication, the signals that are communicated constitute language (Gagliano and Grimonprez 2015). Language can include spoken or written words, sounds, signals, or gestures used to communicate and is used by individuals, whether human, animal, or plant, to make sense of and survive in this world. In this sense, the chemistry or sound transmitted between plants is their language, and by analogy, the highly varied compounds or sound waves emitted constitute their vocabulary. This language has emerged from local repeated iterative interactions among plants, fungi, other organisms, and the environment, leading to increased fitness of the species by enhancing their adaptive capacity, learning capabilities, and ultimately coevolution (Gagliano and Grimonprez 2015). It allows plants to plastically adjust to environmental challenges, and this ability is enhanced by their associated microbiota.

Signals that are transmitted cell-to-cell and tree-to-tree through mycorrhizal networks can be considered analogous to neurotransmitters in biological neural networks. Some of the amino acids and phytohormones transmitted through mycorrhizal networks are structurally analogous to neurotransmitter transporters that are highly conserved in humans and animals (Wipf et al. 2002; Baluška et al. 2005). Auxin, for

example, is structurally similar to serotonin (Pelagio-Flores et al. 2011; Baluška and Mancuso 2013). Glutamate is the most abundant excitatory neurotransmitter in the central nervous system and accounts for over 90% of synaptic transmissions in the human brain. Glycine is the most common inhibitory neurotransmitter and is highly active in the brain and spinal cord (Bowerly and Smart 2006). Glutamine and glycine are also the primary amino acids through which nitrogen is transferred from EMF to their hosts (Martin et al. 1986; Taylor et al. 2004) and through which nitrogen and carbon are thought to transfer along source-sink gradients through mycorrhizal networks (Martin et al. 1986; Teste et al. 2009, 2010; Deslippe and Simard 2011; Simard et al. 2015; Deslippe et al. 2016).

These signals, the amino acids, hormones, and other compounds that constitute the language of plants, flow symplastically and apoplastically through the interlinking mycorrhizal hyphae and rhizomorphs of the network, crossing plant and fungal synapses and following source-sink gradients among tree and plant nodes (Simard et al. 2015). Leaf photosynthetic activity likely generates nitrogen and carbon source-sink gradients within donor plants that drive the transport of the amino acids into the mycorrhizal roots, followed by their transmission via mass flow through the interconnecting mycelium, and then up into the xylem of the linked receiver sink plants. Glutamine contains five C atoms for every two N atoms, and glycine contains two to one, reflecting the high-energy cost of N assimilation by plants (Martin et al. 1986; Taylor et al. 2004). When glutamine and glycine are delivered in high quantities from the mycelium to the plant (Yang et al. 2010), the plant would receive a significant C subsidy in addition to N, while the fungus would still receive its most limiting resource, C, from the plant. Teste et al. (2009) used dual isotope labeling with  $^{13}\text{C}$  and  $^{15}\text{N}$  to show that nitrogen-rich Douglas-fir saplings simultaneously transferred N and C to N-poor conspecific germinants through mycorrhizal networks and that this corresponded with greater 2-year receiver seedling survival. The relative amounts of N (0.0018%) and C (0.0063% of photo-assimilate) transferred had a stoichiometry of 2N:7C, which is similar to glutamine (2N:5C), alanine, and cysteine (2N:6C), but the transmitted compounds were never identified in that study (Teste et al. 2009). In the central nervous system, some of these amino acids (glutamate, cysteine) activate postsynaptic cells, whereas others (glycine, alanine) depress the activity of postsynaptic cells (Dehaene et al. 2003). In plants, these compounds are involved in basic metabolism, such as regulation of ion transport, modulation of stomatal opening, enzyme and protein synthesis, gene expression, etc. (Rai 2002).

Both the plant nodes and fungal links are involved in the regulation of interplant communication. Resources and signals transmit back-and-forth between plants through the fungal networks according to supply and demand or stress gradients in the plant communities, representing a complex underground trading system. This trading of information is like a conversation, where two or more plants and the fungi exchange information in a local setting. Patterns of transmission of C, N, water, and other information depends on source-sink gradients governed by factors such as physiological, nutrient or water status of the donor and receiver plants, stress gradients within the plant community, degree or dependency of these plants on mycorrhization, the fungal species involved in the network, or nutrient or water status of patchy soil environments. Numerous experiments have shown that differences in

physiological source-sink strength or stress among plants (e.g., in photosynthetic rates, growth rates, nutrient content, age, defoliation by pathogens, insects or drought) influence transmission patterns (Simard and Durall 2004; Leake et al. 2004; Selosse et al. 2006; van der Heijden and Horton 2009; Song et al. 2010). Characteristics of fungal and associated microbial communities also play important roles (Finlay 1989; Rygielwicz and Anderson 1994; Lehto and Zwiasek 2011). The importance of the mycorrhizal fungi to interplant communication has been supported by experiment inoculations with different fungal species (Arnebrant et al. 1993; Ekblad and Huss-Danell 1995; Ek et al. 1996; He et al. 2004, 2005; Egerton-Warburton et al. 2007; Querejeta et al. 2012) and the use of mesh that allows certain fungal exploration types to join the network (Teste et al. 2009; Bingham and Simard 2012).

## 5 Plant Behavioral Responses, Learning, and Memory

Plant behavior responses and learning are actions or changes in plant morphology and physiology to environmental stimuli—these flow from the agents of cognition, which include their senses, mycorrhizal networks and signal transmission, as described above. These agents provide plants with sophisticated mechanisms for perceiving their environment, storing the information in their memory banks such as annual growth rings, seeds, or branching, rooting and network topologies, and using this information for memory-based learning that drives behaviors such as choice, decision-making, defense, and neighbor recognition. Communication between plants through mycorrhizal networks, for example, has been associated with behavioral shifts expressed as changes in rooting patterns, mycorrhizal network development, nutrient uptake, and defense enzyme production. These shifts have resulted in changes in survival, growth, and fitness of the sender and receiver plants. McNickle et al. (2009) define behavior as the expression of plant plasticity that is like a decision point, where each choice involves trade-offs that will affect fitness.

### 5.1 Behaviors

Plant behaviors that have been influenced by interplant signal transmission through mycorrhizal networks include, for example, changes in (1) plant morphology such as rooting depth, height growth, or mycorrhizal network patterns; (2) plant physiology such as photosynthetic rates, stomatal conductance, and nutrient uptake; and (3) plant fitness indicators such as germination, survival, and gene regulation of defense chemistry. These behavioral changes have been well described in previous reviews, including Selosse et al. (2006), Simard et al. (2012, 2013, 2015), Gorzelak et al. (2015), and Horton (2015). Here, I briefly summarize only those that have been associated with interplant transmission of carbon, nitrogen, and water through ectomycorrhizal networks.

Carbon fluxes through ectomycorrhizal networks are substantial and vary with the degree of heterotrophy of the plants; they supply up to 10% of autotrophic, up to 85% of partial mycoheterotrophic, and 100% of fully mycoheterotrophic plant carbon. This carbon supply has been associated with increased survival and growth of autotrophic plants and is essential for the survival of fully mycoheterotrophic plants. For example, in our Douglas-fir forests, seedling establishment success was significantly greater where seedlings had full access to the mycorrhizal networks of older Douglas-fir trees compared to where they did not (Teste et al. 2009; Bingham and Simard 2012). Access to the network of the old trees not only improved conspecific seedling survival, but seedlings were colonized by a more complex fungal community comprising multiple short- and long-distance exploration types. It is because of their ability to nurture the understory seedlings, many of them related (see below), that we have named the old hub trees “mother trees” (Simard 2012). In other plant and tree communities, network-mediated nitrogen fluxes from N<sub>2</sub>-fixing plants have supplied up to 40% of receiver N to non-N<sub>2</sub>-fixing plants, and this has been associated with increased plant productivity (e.g., He et al. 2003, 2005, 2009). Fluxes between non-N<sub>2</sub>-fixing plants have supplied <5% of receiver N (e.g., He et al. 2006; Teste et al. 2009). Ectomycorrhizal networks also facilitate the hydraulic redistribution of soil or plant water following water potential gradients, including Douglas-fir forests, supplying up to 50% of plant water that is essential for plant survival and growth (see Simard et al. 2015).

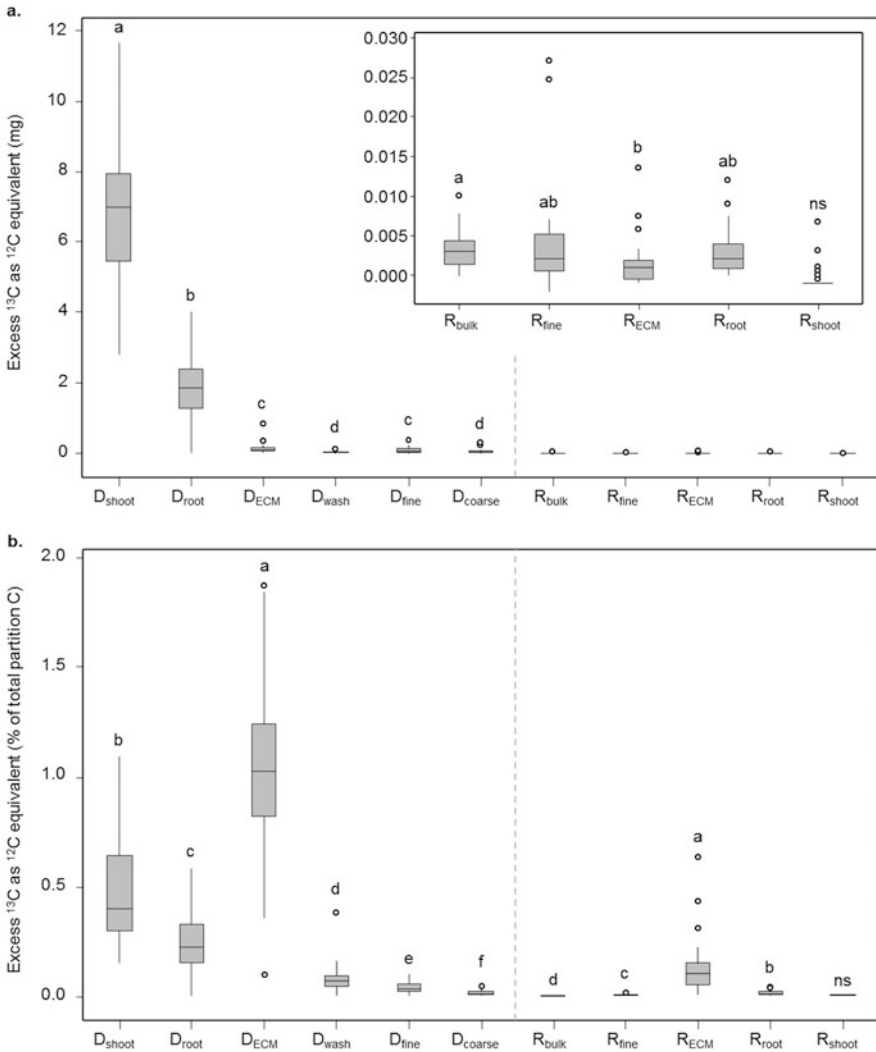
## 5.2 Learning

Learning occurs when plants perceive their environment and use this information to modify their behavior for optimizing environmental resources to increase fitness. It can involve social learning, trial and error, cultural transmission, and epigenetics (Gagliano 2014). Here I provide two examples of mycorrhizal network-mediated social learning and epigenetics in plants involving kin recognition and defense signaling, which we previously described in Gorzelak et al. (2015).

Plants can recognize the degree of relatedness of neighboring plants through a process called kin recognition, change their behavior for optimally interacting with these neighbors, learn to respond to concurrent changes in the behavior of the neighbors, and in so doing increase fitness (Dudley and File 2008; Karban and Shiojiri 2009; Novoplansky 2009; Dudley et al. 2013; Asay 2013; Gorzelak 2017). Kin recognition has been shown in several experiments to be mediated by mycorrhizas or mycorrhizal networks (File et al. 2012a, b; Asay 2013; Pickles et al. 2016; Gorzelak 2017). For example, foliar nutrition in AMF *Ambrosia artemisiifolia* L. improved when it was integrated into a mycorrhizal network with related plants but not conspecific strangers (File et al. 2012a, b). Likewise, in pairs of EMF Douglas-fir seedlings grown in greenhouse conditions, growth attributes and foliar micronutrients were increased in kin compared with strangers grown with older conspecifics (Asay 2013). In both cases, mycorrhizal colonization was elevated in

the related but not stranger neighbors, which led to increased growth and nutrition of both seedlings in the pair (File et al. 2012a, b; Asay 2013). These findings reveal that mycorrhizas and mycorrhizal networks can play an integral role in kin recognition and that learning from increased mycorrhization of kin enhanced the plant morphological and physiological responses. The exact mechanism by which kin recognition occurs, however, is unclear. Nevertheless, there is strong evidence that biochemical signals derived from mycorrhizas or roots are involved (Bierdrzycki et al. 2010; Semchenko et al. 2007). For example, Semchenko et al. (2007) showed that root exudates carried specific information about the genetic relatedness, population origin, and species identity of neighbors, and locally applied exudates triggered different root behavior responses of neighbors. This included increased root density, achieved through changes in morphology rather than biomass allocation, suggesting the plants learned from their neighbors to limit the energetic cost of their behavior. Because the overwhelming majority of plants are predominantly mycorrhizal in situ and because mycorrhizal networks are considered common in nature, any root exudates involved in kin recognition are likely to be filtered through mycorrhizal fungi and mycorrhizal networks. In a recent study using stable-isotope probing, we found that mycorrhizal networks transmitted more carbon from older donor Douglas-fir seedlings to the roots of younger kin receiver seedlings than to stranger receiver seedlings, suggesting a fitness advantage to genetically related neighbors (Fig. 4; Pickles et al. 2016). This may have been facilitated by the greater mycorrhizal colonization of kin than stranger seedlings (Asay 2013), creating a stronger sink in the mycorrhizal network, an effect also noted in the study by File et al. (2012a, b). Gorzelak (2017) later found that herbivory of Douglas-fir induced greater transfer of carbon through mycorrhizal networks to neighboring kin than stranger seedlings.

Defense signals travelling through mycorrhizal networks also result in rapid behavioral responses of recipient plants, and this is evident in sudden changes in foliar defense chemistry (Babikova et al. 2013; Song et al. 2015) and pest resistance (Song et al. 2010, 2014). For instance, broad beans (*Vicia faba*) responded to aphid attack by swiftly transferring defense signals via mycorrhizal networks to neighboring bean plants, which learned from this to produce aphid-repellent chemicals and aphid-predator attractants (Babikova et al. 2013). This learning represents a trophic cascade generated by pest infestation and signal propagation through the mycorrhizal network. In a different study, defoliation of Douglas-fir resulted in a simultaneous transfer of defense signals and carbon to neighboring healthy ponderosa pine through mycorrhizal networks. The ponderosa pine learned from these triggers to increase defense enzyme production and protect itself against the loss of healthy hosts (Song et al. 2015). In earlier studies, Song et al. (2010, 2014) showed that increases in mycorrhizal network-mediated enzyme production flowed from upregulation of defense genes and modification of gene expression, constituting an epigenetic effect. Responses to pest infestations can also lead to larger-scale generational changes in the behavior of plant-symbiont systems. Shifts in ectomycorrhizal community composition caused by a variety of factors, such as host mortality (e.g., pine beetle outbreaks; Kurz et al. 2008), can result in ecological memory effects that



**Fig. 4** Distribution of excess <sup>12</sup>C equivalent (mg) added to each tissue or soil partition in terms of (a) the total mass added and (b) the percentage of partition C comprised of enriched biomass, following labeling and a 6-day chase period for all donor (D) and kin recipient (R) partitions analyzed. Shoot, root, ECM, wash, and fine partitions represent their total biomass, whereas D<sub>coarse</sub> and R<sub>bulk</sub> soil partitions represent a subsampling of the entire soil environment. Inset shows rescaled recipient partitions for comparison. Letters indicate significant differences between partitions compared within D and R compartments. Reproduced with permission from Pickles et al. (2016)

impact future generations of the host species (Karst et al. 2015). For example, in areas of western North America dramatically impacted by the mountain pine beetle-induced dieback of lodgepole pine (*Pinus contorta*), EMF have declined significantly (Treu et al. 2014). Seedlings grown in soils from beetle-attacked pine stands

learned from this decline and then expressed both reduced biomass and reduced production of monoterpenes compared with those grown in soil from undisturbed pine stands. This reveals a transgenerational cascade involving learning, memory, and epigenetics mediated by fungal symbionts (Karst et al. 2015).

### 5.3 *Memory*

Memory is a process by which organisms acquire, encode, store, and retrieve information. This information can then form the basis for experiential learning, where organisms modify their actions for improved fitness. One interesting example of memory-based learning is emerging from our new research in the salmon forests of the Pacific Coast.

We are studying now, how “mother trees”—the ancient cedars, spruces, and firs of the Pacific Coast—transmit nutrients via their massive fungal networks through the forest, feeding the entire ecosystem. Here is how we think this works. The salmon eggs hatch in the freshwater streams of the coastal forests, and then the fry, swim out to the sea, where the fish spend their adult lives feeding in the open ocean. Every spring and fall, the salmon return to their mother streams to breed and die, carrying with them nutrients from the ocean. The Aboriginal people of the Pacific Coast use the salmon for their livelihoods and have traditionally built tidal stone traps at the mouth of marine spawning rivers to passively catch the fish. Not only people but other predators and scavengers, including grizzlies, wolves, and eagles, also feed on the carcasses. These creatures carry their catch up the riverbanks, settling to feast on the safe, warm, dry benches under the mother trees in the riparian forest. In so doing, they distribute the nutrients in the salmon carcasses and their feces and urine. The bears eat the innards in safety, leaving the carcasses to decay and the nutrients to seep into the soil. The mycorrhizal fungi associated with the roots of the trees and plants acquire the salmon nutrients from the soil and use them to supply 25–90% of the tree and plant nitrogen budgets. Once metabolized in the woody tissues of the trees, the salmon nutrients are stored in tree rings for centuries, providing a memory bank of historical salmon runs for as long as the tree is old. This process contributes to faster tree growth along salmon streams and underlies the great size and unparalleled productivity of these old forests. It has also been shown to shape the diversity and composition of vegetation, insect, and bird communities (Hocking and Reynolds 2011). This process of salmon nutrient uptake by the mycorrhizas, storage in tree rings, and retrieval of the information for tree growth, constitutes a memory embedded in the forest. We are examining now whether these salmon nutrient memories are transmitted from tree to tree and from plant to plant, through their fungal connections, deep into the forest. The spreading of the salmon memory, the telling of the story through their communication networks, allows the trees, fungi, bears, and salmon to collaboratively inform the productivity and health of the ecosystem. These luxurious forests in turn shade and nurture the salmon rivers, modulating the water temperature and transmitting nutrients to the ebb tides through



seepage, thus forming a positive feedback loop that promotes the health and productivity of the fish. The parts of the trees—the bark and roots, made with salmon nitrogen—are harvested by the Aboriginal people to make clothing and art and tools, such as for the harvest of salmon. Mother trees play a crucial role in the closing of this circle. The health of the forest is thus tied to the health of the salmon, and it cycles back to the rivers, the oceans, and the people. The integrity of this circle of life depends on what the Aboriginals call reciprocity—the trade of mutual respect. This is an example of how people are sustainably embedded in this complex adaptive system.

This collective behavior, learning, and memory in the salmon forest may allow the community to solve cognitive problems that go beyond the capacity of a single organism, facilitating altruistic behaviors like kin recognition and more generally promoting cooperation for better ecosystem health.

## 6 Conclusions

This chapter has provided evidence that mycorrhizal networks are crucial agents in tree and plant perceptions of their neighbors and environment, in interplant communication of their strengths, needs and stresses, in the acquisition and storage of memories, and in memory-based learning and adaptive behaviors. The scale-free topology and small-world properties of mycorrhizal networks, along with similarity in transmitted signals to neurotransmitters in vertebrates, provide the necessary biological agency for intelligence in forests. The agency and conveyance of information through the mycorrhizal network provides manifold opportunities for trees to take action for interacting with their neighbors and adapting to the rapidly changing environment. Through sophisticated cognition that is facilitated by their microbiomes, trees and plants are more perceptive, intelligent, and in control of their destiny than humans have ever given them credit for. It is my hope that future research in plant cognition includes the crucial role of plant microbiomes, and mycorrhizal networks in particular.

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## References

- Agerer R (2001) Exploration types of ectomycorrhizal mycelial systems: a proposal to classify mycorrhizal mycelial systems with respect to their ecologically important contact area with the substrate. *Mycorrhiza* 11:107–114
- Agerer R (2006) Fungal relationships and structural identity of their ectomycorrhizae. *Mycol Prog* 5:67–107
- Archibald JM (2011) Origin of eukaryotic cells: 40 years on. *Symbiosis* 54:69–86
- Arnebrant K, Ek H, Finlay RD, Söderström B (1993) Nitrogen translocation between *Alnus glutinosa* (L.) Gaertn. seedlings inoculated with *Frankia* sp. and *Pinus contorta* Dougl. ex Loud seedlings connected by a common ectomycorrhizal mycelium. *New Phytol* 24:231–242
- Asay AK (2013) Mycorrhizal facilitation of kin recognition in interior Douglas-fir (*Pseudotsuga menziesii* var. *glauca*). Master of Science thesis. University of British Columbia, Vancouver, Canada
- Babikova Z, Gilbert L, Bruce TJA, Birkett M, Caulfield JC, Woodcock C, Pickett JA, Johnson D (2013) Underground signals carried through common mycelial networks warn neighbouring plants of aphid attack. *Ecol Lett* 16:835–843
- Bago B, Zipfel W, Williams RM, Jun J, Arreola R, Lammers PJ, Pfeffer PE, Shachar-Hill Y (2002) Translocation and utilization of fungal storage lipid in the arbuscular mycorrhizal symbiosis. *Plant Physiol* 128:109–124
- Baluška F, Mancuso S (2013) Microorganism and filamentous fungi drive evolution of plant synapses. *Front Cell Infect Microbiol* 3:1–9
- Baluška F, Volkmann D, Menzel D (2005) Plant synapses: actin-based domains for cell-to-cell communication. *Trends Plant Sci* 10:106–111
- Baluška F, Mancuso S, Volkmann D, Darwin F (2009) The ‘root-brain’ hypothesis of Charles and Francis Darwin. *Plant Signal Behav* 4:1121–1127
- Baluška F, Mancuso S, Volkmann D, Barlow PW (2010) Root apex transition zone: a signalling-response nexus in the root. *Trends Plant Sci* 15:402–408
- Barabási A-L, Albert R (1999) Emergence of scaling in random networks. *Science* 286:509–512
- Barbey AK (2017) Network neuroscience theory of human intelligence. *Trends Cogn Sci* 22:8–20
- Barto EK, Hilker M, Muller F, Mohney BK, Weidenhamer JD, Rillig MC (2011) The fungal fast lane: common mycorrhizal networks extend bioactive zones of allelochemicals in soils. *PLoS One* 6:e27195
- Bascompte J (2009) Mutualistic networks. *Front Ecol Environ* 7:429e436
- Beiler KJ, Durall DM, Simard SW, Maxwell SA, Kretzer AM (2010) Architecture of the wood-wide web: *Rhizopogon* spp. genets link multiple Douglas-fir cohorts. *New Phytol* 185:543–553
- Beiler KJ, Simard SW, LeMay V, Durall DM (2012) Vertical partitioning between sister species of *Rhizopogon* fungi on mesic and xeric sites in an interior Douglas-fir forest. *Mol Ecol* 21:6163–6174
- Beiler KJ, Simard SW, Durall DM (2015) Topology of tree-mycorrhizal fungus interaction networks in xeric and mesic Douglas-fir forests. *J Ecol* (3):616–628
- Bierdrzycki ML, Jilany TA, Dudley SA, Bais HP (2010) Root exudates mediate kin recognition in plants. *Commun Integr Biol* 3:28–35
- Bingham MA, Simard SW (2012) Ectomycorrhizal networks of old *Pseudotsuga menziesii* var. *glauca* trees facilitate establishment of conspecific seedlings under drought. *Ecosystems* 15:188–199
- Boddy L, Jones TH (2007) Mycelial responses in heterogeneous environments: parallels with macroorganisms. In: Gadd G, Watkinson SC, Dyer P (eds) *Fungi in the environment*. Cambridge University Press, Cambridge, pp 112–158
- Bowery NG, Smart TG (2006) GABA and glycine as neurotransmitters: a brief history. *Br J Pharmacol* 147:S109–S119
- Bray D (2003) Molecular networks: the top-down view. *Science* 301:1864–1865

- Brenner ED, Stahlberg R, Mancuso S, Vivanco J, Baluška F, Van Volkenburgh E (2006) Plant neurobiology: an integrated view of plant signaling. *Trends Plant Sci* 11:413–419
- Brownlee C, Duddridge J, Malibari A, Read D (1983) The structure and function of mycelial systems of ectomycorrhizal roots with special reference to their role in forming inter-plant connections and providing pathways for assimilate and water transport. *Plant Soil* 71:433–443
- Craik F, Bialystok E (2006) Cognition through the lifespan: mechanisms of change. *Trends Cogn Sci* 10:131–148
- Darwin CR (1880) *The power of movement in plants*. John Murray, London
- Dehaene S, Sergent C, Changeux J-P (2003) A neuronal network model linking subjective reports and objective physiological data during conscious perception. *Proc Natl Acad Sci USA* 100:8520–8525
- Deslippe JR, Simard SW (2011) Below-ground carbon transfer among *Betula nana* may increase with warming in Arctic tundra. *New Phytol* 192:689–698
- Deslippe JR, Hartmann M, Grayston SJ, Simard SW, Mohn WW (2016) Stable isotope probing implicates *Cortinarius collinitus* in carbon transfer through ectomycorrhizal mycelial networks in the field. *New Phytol* 210:383–390
- Dudley SA, File AL (2008) Kin recognition in an annual plant. *Biol Lett* 3:435–438
- Dudley SA, Murphy GP, File AL (2013) Kin recognition and competition in plants. *Funct Ecol* 27:898–906
- Eason WR, Newman EI, Chuba PN (1991) Specificity of interplant cycling of phosphorus: the role of mycorrhizas. *Plant Soil* 137:267–274
- Egerton-Warburton LM, Querejeta JI, Allen MF (2007) Common mycorrhizal networks provide a potential pathway for the transfer of hydraulically lifted water between plants. *J Exp Bot* 58:1473–1483
- Ek H, Andersson S, Söderström B (1996) Carbon and nitrogen flow in silver birch and Norway spruce connected by a common mycorrhizal mycelium. *Mycorrhiza* 6:465–467
- Ekblad A, Huss-Danell K (1995) Nitrogen fixation by *Alnus incana* and nitrogen transfer from *A. incana* to *Pinus sylvestris* influenced by macronutrient and ectomycorrhiza. *New Phytol* 131:453–459
- Faust K, Raes J (2012) Microbial interactions: from networks to models. *Nat Rev Microbiol* 10:538–550
- File AL, Klironomos J, Maherali H, Dudley SA (2012a) Plant kin recognition enhances abundance of symbiotic microbial partner. *PLoS One* 7:e45648
- File AL, Murphy GP, Dudley SA (2012b) Fitness consequences of plants growing with siblings: reconciling kin selection, niche partitioning and competitive ability. *Proc R Soc B* 279:209–218
- Finlay RD (1989) Functional aspects of phosphorus uptake and carbon translocation in incompatible ectomycorrhizal associations between *Pinus sylvestris* and *Suillus grevillei* and *Boletinus cavipes*. *New Phytol* 112:185–192
- Finlay RD, Read DJ (1986) The structure and function of the vegetative mycelium of ectomycorrhizal plants. II. The uptake and distribution of phosphorus by mycelial strands interconnecting host plants. *New Phytol* 103:157–165
- Gagliano M (2012) Green symphonies: a call for studies on acoustic communication in plants. *Behav Ecol* 24:289–296
- Gagliano M (2014) In a green frame of mind: perspectives on the behavioural ecology and cognitive nature of plants. *AoB Plants* 7:plu075
- Gagliano M, Grimonprez M (2015) Breaking the silence – language and the making of meaning in plants. *Ecophys* 7:145–152
- García-Garrido JM, Ocampo JA (2002) Regulation of the plant defence response in arbuscular mycorrhizal symbiosis. *J Exp Bot* 53:1377–1386
- Giovannetti M, Sbrana C, Avio L, Stranil P (2004) Patterns of belowground plant interconnections established by means of arbuscular mycorrhizal networks. *New Phytol* 164:175–181

- Giovannetti M, Avio L, Fortuna P, Pellegrino E, Sbrana C, Strani P (2005) At the root of the Wood Wide Web: self recognition and non-self incompatibility in mycorrhizal networks. *Plant Signal Behav* 1:1–5
- Gozdelak M (2017) Kin selected signal transfer through mycorrhizal networks in Douglas-fir. PhD Dissertation. University of British Columbia, Vancouver, Canada
- Gozdelak M, Asay AK, Pickles BJ, Simard SW (2015) Inter-plant communication through mycorrhizal networks mediates complex adaptive behaviour in plant communities. *AoB Plants* 7: plv050
- Gyuricza V, Thiry Y, Wannijn J, Declerck S, de Boulois HD (2010) Radiocesium transfer between *Medicago truncatula* plants via a common mycorrhizal network. *Environ Microbiol* 12:2180–2189
- He X-H, Critchley C, Bledsoe C (2003) Nitrogen transfer within and between plants through common mycorrhizal networks (CMNs). *Crit Rev Plant Sci* 22:531–567
- He XH, Critchley C, Ng H, Bledsoe C (2004) Reciprocal N ( $^{15}\text{NH}_4^+$  or  $^{15}\text{NO}_3^-$ ) transfer between non- $\text{N}_2$ -fixing *Eucalyptus maculata* and  $\text{N}_2$ -fixing *Casuarina cunninghamiana* linked by the ectomycorrhizal fungus *Pisolithus* sp. *New Phytol* 163:629–640
- He XH, Critchley C, Ng H, Bledsoe C (2005) Nodulated  $\text{N}_2$ -fixing *Casuarina cunninghamiana* is the sink for net N transfer from non- $\text{N}_2$ -fixing *Eucalyptus maculata* via an ectomycorrhizal fungus *Pisolithus* sp. supplied as ammonium nitrate. *New Phytol* 167:897–912
- He XH, Bledsoe CS, Zasoski RJ, Southworth D, Horwath WR (2006) Rapid nitrogen transfer from ectomycorrhizal pines to adjacent ectomycorrhizal and arbuscular mycorrhizal plants in a California oak woodland. *New Phytol* 170:143–151
- He XH, Xu M, Qiu GY, Zhou J (2009) Use of  $^{15}\text{N}$  stable isotope to quantify nitrogen transfer between mycorrhizal plants. *J Plant Ecol* 2:107–118
- Heaton L, Obara B, Grau V, Jones N, Nakagaki T, Boddy L, Fricker MD (2012) Analysis of fungal networks. *Fungal Biol Rev* 26:12e29
- Heil M, Karban R (2009) Explaining evolution of plant communication by airborne signals. *Trends Ecol Evol* 25:137–144
- Hobbie E, Agerer R (2010) Nitrogen isotopes in ectomycorrhizal sporocarps correspond to below-ground exploration types. *Plant Soil* 327:71–83
- Hocking MD, Reynolds JD (2011) Impacts of Salmon on riparian plant diversity. *Science* 331:1609–1612
- Horton TR (ed) (2015) *Mycorrhizal networks. Ecological studies.* Netherlands: Springer, 224
- Humphreys CP, Franks PJ, Rees M, Bidartondo MI, Leake JR, Beerling DJ (2010) Mutualistic mycorrhiza-like symbiosis in the most ancient group of land plants. *Nat Commun* 1:103
- Ingham RE, Trofymow JA, Ingham ER, Coleman DC (1985) Interactions of bacteria, fungi, and their nematode grazers: effects on nutrient cycling and plant growth. *Ecol Monogr* 55:119–140
- Karban R, Shiojiri K (2009) Self-recognition affects plant communication and defense. *Ecol Lett* 12:502–506
- Karban R, Yang LH, Edwards KF (2014) Volatile communication between plants that affects herbivory: a meta-analysis. *Ecol Lett* 17:44–52
- Karst J, Erbilgin N, Pec GJ, Cigan PW, Najar A, Simard SW, Cahill JF Jr (2015) Ectomycorrhizal fungi mediate indirect effects of a bark beetle outbreak on secondary chemistry and establishment of pine seedlings. *New Phytol* 208:904–914
- Kretzer AM, Luoma DL, Molina R, Spatafora JW (2003) Taxonomy of the *Rhizopogon vinicolor* species complex based on analysis of ITS sequences and microsatellite loci. *Mycologia* 95:480–487
- Kurz WA, Dymond CC, Stinson G, Rampley GJ, Neilson ET, Carroll AL, Ebata T, Safranyik L (2008) Mountain pine beetle and forest carbon feedback to climate change. *Nature* 452:987–990
- Leake J, Johnson D, Donnelly D, Muckle G, Boddy L, Read D (2004) Networks of power and influence: the role of mycorrhizal mycelium in controlling plant communities and agroecosystem functioning. *Can J Bot* 82:1016–1045

- Lehto T, Zwiazek JJ (2011) Ectomycorrhizas and water relations of trees: a review. *Mycorrhiza* 21:71–90
- Levin SA (2005) Self-organization and the emergence of complexity in ecological systems. *Bioscience* 55:1075
- Lian C, Narimatsu M, Nara K, Hogetsu T (2006) *Tricholoma matsutake* in a natural *Pinus densiflora* forest: correspondence between above- and below- ground genets, association with multiple host trees and alteration of existing ectomycorrhizal communities. *New Phytol* 171:825–836
- Lilleskov EA, Hobbie EA, Horton TR (2011) Conservation of ectomycorrhizal fungi: exploring the linkages between functional and taxonomic responses to anthropogenic N deposition. *Fungal Ecol* 4:174–183
- Margulis L (1981) Symbiosis in cell evolution. WH Freeman Company, San Francisco
- Martin F, Stewart GR, Genetet I, Le Tacon F (1986) Assimilation of  $^{15}\text{NH}_4$  by beech (*Fagus sylvatica* L.) ectomycorrhizas. *New Phytol* 102:85–94
- McNickle GG, St. Clair CC, Cahill JF Jr (2009) Focusing the metaphor: plant root foraging behavior. *Trends Ecol Evol* 24:419–426
- Meding SM, Zasoski RJ (2008) Hyphal-mediated transfer of nitrate, arsenic, cesium, rubidium, and strontium between arbuscular mycorrhizal forbs and grasses from a California oak woodland. *Soil Biol Biochem* 40:126–134
- Molina R (2013) Rhizopogon. In: Cairney JWG, Chamber SM (eds) Ectomycorrhizal fungi: key Genera in profile. Springer Verlag, Berlin, pp 129–152
- Molina R, Horton TR (2015) Mycorrhiza specificity: its role in the development and function of common mycelial networks. In: Horton TR (ed) Mycorrhizal networks, Ecological studies, vol 224. Springer, Netherlands, pp 1–39
- Molina R, Massicotte H, Trappe J (1992) Specificity phenomena in mycorrhizal symbioses: community-ecological consequences and practical implications. In: Allen MF (ed) Mycorrhizal functioning: an integrative plant–fungal process. Chapman and Hall, New York, pp 357–423
- Nehls U, Grunze B, Willmann M, Reich M, Küster H (2007) Sugar for my honey: carbohydrate partitioning in ectomycorrhizal symbiosis. *Phytochemistry* 68:82–91
- Novoplansky A (2009) Picking battles wisely: plant behaviour under competition. *Plant Cell Environ* 32:726–741
- Pelagio-Flores R, Ortíz-Castro R, Méndez-Bravo A, Macías-Rodríguez L, López-Bucio J (2011) Serotonin, a tryptophan-derived signal conserved in plants and animals, regulates root system architecture probably acting as a natural auxin inhibitor in *Arabidopsis thaliana*. *Plant Cell Physiol* 52:490–508
- Perry DA, Margolis H, Choquette C, Molina R, Trappe JM (1989) Ectomycorrhizal mediation of competition between coniferous tree species. *New Phytol* 112:501–511
- Pickles BJ, Wilhelm R, Asay AK, Hahn A, Simard SW, Mohn WW (2016) Transfer of  $^{13}\text{C}$  between paired Douglas-fir seedlings reveals plant kinship effects and uptake of exudates by ectomycorrhizas. *New Phytol* 214:400–411
- Poorter H, Niklas KJ, Reich PB, Oleksy J, Poot P, Mommer L (2012) Biomass allocation to leaves, stems and roots: meta-analyses of interspecific variation and environmental control. *New Phytol* 193:30–50
- Pozo MJ, López-Ráez JA, Azcón-Aguilar C, García-Garrido JM (2015) Phytohormones as integrators of environmental signals in the regulation of mycorrhizal symbioses. *New Phytol* 205:1431–1436
- Querejeta JI, Egerton-Warburton LM, Prieto I, Vargas R, Allen MF (2012) Changes in soil hyphal abundance and viability can alter the patterns of hydraulic redistribution by plant roots. *Plant Soil* 355:63–73
- Rai V (2002) Role of amino acids in plant responses to stresses. *Biol Plant* 45:481–487
- Rygiewicz PT, Anderson CP (1994) Mycorrhizae alter quality and quantity of carbon allocated below ground. *Nature* 369:58–60

- Scheffer M, Carpenter S, Foley JA, Folke C, Walker B (2001) Catastrophic shifts in ecosystems. *Nat Rev* 413:591–596
- Selosse M-A, Richard F, He X, Simard SW (2006) Mycorrhizal network: des liaisons dangereuses? *Trends Ecol Evol* 21:621–628
- Semchenko M, John EA, Hutchings MJ (2007) Effects of physical connection and genetic identity of neighbouring ramets on root-placement patterns in two clonal species. *New Phytol* 176:644–654
- Simard SW (2012) Mycorrhizal networks and seedling establishment in Douglas-fir forests (Chapter 4). In: Southworth D (ed) *Biocomplexity of plant–fungal interactions*, 1st edn. Wiley, Chichester, pp 85–107. isbn-10:0813815940 | isbn-13:978-0813815947
- Simard SW, Durall DM (2004) Mycorrhizal networks: a review of their extent, function, and importance. *Can J Bot* 82:1140–1165
- Simard SW, Beiler KJ, Bingham MA, Deslippe JR, Philip LJ, Teste FP (2012) Mycorrhizal networks: mechanisms, ecology and modelling. *Fungal Biol Rev* 26:39–60
- Simard SW, Martin K, Vyse A, Larson B (2013) Meta-networks of fungi, fauna and flora as agents of complex adaptive systems. In: Puettmann K, Messier C, Coates KD (eds) *Managing world forests as complex adaptive systems: building resilience to the challenge of global change*, vol 7. Routledge, New York, pp 133–164
- Simard SW, Asay AK, Beiler KJ, Bingham MA, Deslippe JR, He X, Philip LJ, Song Y, Teste FP (2015) Resource transfer between plants through ectomycorrhizal networks. In: Horton TR (ed) *Mycorrhizal networks, Ecological studies*, vol 224. Springer, Netherlands, pp 133–176
- Smith S, Read D (2008) *Mycorrhizal symbiosis*. Academic, London
- Smith SE, Smith FA (1990) Structure and function of the interfaces in biotrophic symbioses as they relate to nutrient transport. *New Phytol* 114:1–38
- Song YY, Zeng RS, Xu JF, Li J, Shen X, Yihdego WG (2010) Interplant communication of tomato plants through underground common mycorrhizal networks. *PLoS One* 5:e13324
- Song YY, Ye M, Li C, He X, Zhu-Salzman K, Wang RL, Su YJ, Luo SM, Zheng RS (2014) Hijacking common mycorrhizal networks for herbivore-induced defence signal transfer between tomato plants. *Sci Rep* 4:3915
- Song YY, Simard SW, Carroll A, Mohn WW, Zheng RS (2015) Defoliation of interior Douglas-fir elicits carbon transfer and defense signalling to ponderosa pine neighbors through ectomycorrhizal networks. *Sci Rep* 5:8495
- Southworth D, He X-H, Swenson W, Bledsoe CS (2005) Application of network theory to potential mycorrhizal networks. *Mycorrhiza* 15:589–595
- Taylor AFS, Gebauer G, Read DJ (2004) Uptake of nitrogen and carbon from double-labelled (<sup>15</sup>N and <sup>13</sup>C) glycine by mycorrhizal pine seedlings. *New Phytol* 164:383–388
- Teste FP, Simard SW, Durall DM, Guy RD, Jones MD (2009) Access to mycorrhizal networks and roots of trees: importance for seedling survival and resource transfer. *Ecology* 90:2808–2822
- Teste FP, Simard SW, Durall DM, Guy RD, Berch SM (2010) Net carbon transfer between *Pseudotsuga menziesii* var. *glauca* seedlings in the field is influenced by soil disturbance. *J Ecol* 98:429–439
- Toju H, Sato H, Tanabe AS (2014) Diversity and spatial structure of belowground plant– fungal symbiosis in a mixed subtropical forest of ectomycorrhizal and arbuscular mycorrhizal plants. *PLoS One*:e86566
- Trappe JM (1987) Phylogenetic and ecologic aspects of mycotrophy in the angiosperms from an evolutionary standpoint. In: Safir GR (ed) *Ecophysiology of VA mycorrhizal plants*. CRC Press, Florida
- Treu R, Karst J, Randall M, Pec GJ, Cigan P, Simard SW, Cooke J, Erbilgin N, Cahill JF Jr (2014) Decline of ectomycorrhizal fungi following mountain pine beetle infestation. *Ecology* 95:1096–1103
- Twieg B, Durall DM, Simard SW (2007) Ectomycorrhizal fungal succession in mixed temperate forests. *New Phytol* 176:437–447

- Van der Heijden MGA, Hartmann M (2016) Networking in the plant microbiome. *PLoS Biol* 14: e1002378
- Van der Heijden MGA, Horton TR (2009) Socialism in soil? The importance of mycorrhizal fungal networks for facilitation in natural ecosystems. *J Ecol* 97:1139–1150
- Van Dorp C (2016) *Rhizopogon* mycorrhizal networks with interior douglas-fir in selectively harvested and non-harvested forests. Master of Science Thesis, University of British Columbia
- Wipf D, Ludewig U, Tegeder M, Rentsch D, Koch W, Frommer WB (2002) Conservation of amino acid transporters in fungi, plants and animals. *Trends Biochem Sci* 27:139–147
- Yang H, Bognor M, Steinhoff Y-D, Ludewig U (2010) H<sup>+</sup>-independent glutamine transport in plant root tips. *PLoS One* 5:e8917