



British Mycological
Society promoting fungal science

journal homepage: www.elsevier.com/locate/fbr



Review

Mycorrhizal networks: Mechanisms, ecology and modelling

Suzanne W. SIMARD^{a,*}, Kevin J. BEILER^b, Marcus A. BINGHAM^a, Julie R. DESLIPPE^c,
Leanne J. PHILIP^d, François P. TESTE^e

^aDepartment of Forest Sciences, University of British Columbia, 2424 Main Mall, Vancouver, British Columbia, Canada V6T 1Z4

^bBiology Faculty, University of British Columbia Okanagan, 3333 University Way, Kelowna, British Columbia, Canada V1V 1V7

^cEcosystems and Global Change, Landcare Research, Riddet Road, Massey University Campus, Palmerston North 4442, New Zealand

^dBiology/Environmental Studies, Saint Mary's University, Halifax, Nova Scotia, Canada B3H 3C3

^eSchool of Plant Biology, Faculty of Natural and Agricultural Sciences, The University of Western Australia, Crawley WA 6009, Australia

ARTICLE INFO

Article history:

Received 3 November 2011

Received in revised form

22 January 2012

Accepted 31 January 2012

Keywords:

Ascomycota

Basidiomycota

Carbon transfer

Complex adaptive systems

Diversity

Evolution

Glomeromycota

Mycoheterotrophy

Stability

ABSTRACT

Mycorrhizal networks, defined as a common mycorrhizal mycelium linking the roots of at least two plants, occur in all major terrestrial ecosystems. This review discusses the recent progress and challenges in our understanding of the characteristics, functions, ecology and models of mycorrhizal networks, with the goal of encouraging future research to improve our understanding of their ecology, adaptability and evolution. We focus on four themes in the recent literature: (1) the physical, physiological and molecular evidence for the existence of mycorrhizal networks, as well as the genetic characteristics and topology of networks in natural ecosystems; (2) the types, amounts and mechanisms of interplant material transfer (including carbon, nutrients, water, defence signals and allelochemicals) in autotrophic, mycoheterotrophic or partial mycoheterotrophic plants, with particular focus on carbon transfer; (3) the influence of mycorrhizal networks on plant establishment, survival and growth, and the implications for community diversity or stability in response to environmental stress; and (4) insights into emerging methods for modelling the spatial configuration and temporal dynamics of mycorrhizal networks, including the inclusion of mycorrhizal networks in conceptual models of complex adaptive systems. We suggest that mycorrhizal networks are fundamental agents of complex adaptive systems (ecosystems) because they provide avenues for feedbacks and cross-scale interactions that lead to self-organization and emergent properties in ecosystems. We have found that research in the genetics of mycorrhizal networks has accelerated rapidly in the past 5 y with increasing resolution and throughput of molecular tools, but there still remains a large gap between understanding genes and understanding the physiology, ecology and evolution of mycorrhizal networks in our changing environment. There is now enormous and exciting potential for mycorrhizal researchers to address these higher level questions and thus inform ecosystem and evolutionary research more broadly.

© 2012 The British Mycological Society. Published by Elsevier Ltd. All rights reserved.

* Corresponding author. Tel.: +1 604 822 1955; fax: +1 604 822 9102.

E-mail addresses: suzanne.simard@ubc.ca (S. W. Simard), kjbeiler@interchange.ubc.ca (K. J. Beiler), binghm@interchange.ubc.ca (M. A. Bingham), DeslippeJ@landcareresearch.co.nz (J. R. Deslippe), Leanne.Philip@SMU.CA (L. J. Philip), francois.teste@uwa.edu.au (F. P. Teste).

1749-4613/\$ – see front matter © 2012 The British Mycological Society. Published by Elsevier Ltd. All rights reserved.

doi:10.1016/j.fbr.2012.01.001

1. Introduction

Evidence that mycorrhizal fungal mycelia can link plants together in a network, and that this mycorrhizal network (MN) can facilitate fungal colonization or interplant transfer of compounds has intrigued scientists for decades (Leake et al., 2004; Selosse et al., 2006; van der Heijden and Horton, 2009). Through their effects on colonization and interplant transfers, MNs have been shown to facilitate the establishment, growth, survival or defence regulation of individual plants in a wide range of ecosystems (Horton et al., 1999; Dickie et al., 2004; Teste et al., 2009; Song et al., 2010). At the plant community level, MNs have been suggested to influence interplant interactions and plant community diversity (Pietikäinen and Kytöviita, 2007; Deslippe and Simard, 2011). Mycorrhizal networks also appear to affect the composition, interactions and diversity of mycorrhizal fungal communities (Kennedy et al., 2011; Bingham and Simard, 2012). From an ecosystems perspective, it is increasingly recognized that MNs are important in carbon (C), nutrient and water cycling (Eason et al., 1991; Treseder, 2004; Allen, 2007), with the potential for feedbacks to global change (Simard and Austin, 2010; Pickles et al., 2011).

Mycorrhizal networks appear to be ubiquitous in nature, and this raises the possibility that facilitation via networks may be as important as competition in the structuring of plant and fungal communities. It also suggests that MNs play an important role in the functioning of ecosystems as complex adaptive systems (Levin, 2005). Increasing our understanding of the structure and function of MNs in ecosystems may lead to a deeper understanding of ecological stability and evolution, and thus provide new theoretical approaches to improve conservation practices for the management of the Earth's ecosystems (Perry, 1998; Wilkinson, 1998).

This paper reviews the current evidence for the existence of MNs, the mechanisms by which they function, the implications of MNs for the structuring and functioning of ecosystems, and the potential contribution of MNs to modern ecological models. It builds on reviews by Simard and Durall (2004) and Selosse et al. (2006) by focussing largely on literature published after 2006. We begin with a review of the existence of MNs in ecosystems using evidence based on (a) specificity phenomena, (b) physical, physiological and molecular biology, and (c) genet architecture. We then review the mechanisms by which MNs influence plant and fungal communities, starting with the potential pathways through which MNs can influence mycorrhizal colonization and interplant resource transfers. We then discuss the plant and fungal factors that influence C and nutrient transfer, such as source-sink patterns, and the potential physiological mechanisms for these transfers. We end this section with a review of the magnitudes and fates of C transfers that have been measured from ectomycorrhizal (EM) autotrophic plants to full mycoheterotrophic (MH), partial MH and other autotrophic plants.

Our discussion of the ecological implications of MNs addresses evidence at the individual plant, community and ecosystems levels of organization. We start by discussing the significance of MNs to plant establishment and growth, and to fungal biology. We then review evidence for MN effects on plant community dynamics, including our own work in

interior Douglas-fir forests of western North America. We follow this with a review of climatic and disturbance stress effects on MN facilitation, and their potential for influencing feedbacks between ecosystems and climate. We end the paper with ideas to model the spatial and temporal dynamics of MNs, and we discuss how these models may inform an emerging paradigm shift in our understanding of terrestrial ecosystems as complex adaptive systems.

2. Evidence for existence of mycorrhizal networks

Specificity phenomena

Much of the evidence for the existence of MNs stems from the promiscuity of associations between fungi and plants in the mycorrhizal symbiosis. The vast majority of mycorrhizal plants associate with multiple fungal species within a given category of mycorrhizas, but some simultaneously host endo- and ectomycorrhizal fungi (Smith and Read, 2008). Notable exceptions include MH vascular plants (Leake et al., 2004) and nonvascular liverworts, which tend towards very narrow partner specificity (Bidartondo, 2005; Bougoure et al., 2010; Girlanda et al., 2011). Paradoxically, these plants provide the strongest evidence of MN existence because they have been found to exploit networking mycorrhizal fungi to obtain sugars from neighbouring autotrophic plants (Bougoure et al., 2010; Liebel et al., 2010; Courty et al., 2011). Like plants, the host specificity of mycorrhizal fungi has a broad range (Molina et al., 1992). Fungi with intermediate to broad host specificity (those that associate with multiple species of seed plants) have regularly been reported as the most abundant members of mixed species plant communities (Nara, 2006; Twieg et al., 2007).

The general lack of specificity between plants and fungi in the mycorrhizal symbiosis suggests there is a high probability for MN formation with plants and fungi joined in associative guilds (Perry, 1995). Plant species sharing compatible mycorrhizal fungi with other plants have been reported from a wide range of ecosystems including boreal and temperate forests and woodlands (Roy et al., 2008), tropical forests and woodlands (Onguene and Kuyper, 2002; Mangan et al., 2010), Mediterranean and Sclerophyllous woodlands and chaparral (Richard et al., 2005; Tedersoo et al., 2008), woodland savannah (Dickie et al., 2004), grasslands (Gai et al., 2009), and Arctic tundra (Deslippe and Simard, 2011). Moreover, fungal associates are often shared between overstorey and understorey species, suggesting that MNs have the potential to influence plant establishment, resource competition, species diversity and succession within plant communities (Nara, 2006; Tedersoo et al., 2007).

The degree to which fungi and plants form an MN is context dependent. For example, the colonization patterns of networking mycorrhizal fungi are influenced by the availability of an alternate host (Onguene and Kuyper, 2002; Dickie et al., 2004), host plant stress and C allocation patterns (Saito et al., 2004), plant and fungal genotype (Hoeksema, 2010; Bingham and Simard, 2012), interactions with other mycorrhizal species and soil microbes (Wu et al., 1999; Hortal et al., 2008), and soil environmental factors (Teste et al., 2010).

Physical, physiological, & molecular evidence for the existence of networks

There is increasing physical and physiological evidence for the existence of MNs across a wide range of ecosystems, largely owing to advancements in the breadth and availability of molecular techniques for the isolation, identification and analysis of environmental samples (Box 1). These techniques have shed light on the potential for MNs to form among forest trees (Horton *et al.*, 1999) and between overstory and under-story plants (Ogura-Tsujita *et al.*, 2009; Bougoure *et al.*, 2010). In some cases, molecular evidence has uncovered conditional host preferences or cryptic species diversity, leading to more complex patterns of host specificity. For example, at least some species of AM fungi have narrower host specificity than previously appreciated (Sanders, 2003). In other cases, molecular evidence has led to the discovery of fungi simultaneously forming different mycorrhizal anatomical structures (e.g., EM and ericoid (ERM) or arbutoid mycorrhizas (ARM)) in correspondence with different plant lineages, thus broadening the spectrum of plants potentially linked through MNs (Gollotte *et al.*, 2004). In addition, molecular techniques have helped resolve MN functioning, ecology and evolution by identifying potential mechanisms behind material transfers (Hoeksema, 2010; Kiers *et al.*, 2011) and the genes involved (Kemppainen *et al.*, 2009; Martin *et al.*, 2010; Plett *et al.*, 2011).

Genet architecture

One of the primary determinants of MN architecture is the morphology and spatial structure of the fungal mycelia

involved. The extent and continuity of individual fungal genets over space and time is a particularly important life history trait for predicting whether plant roots are 'linked' in an MN (Selosse *et al.*, 2006; Beiler *et al.*, 2010). Although there is a paucity of autecological information available for mycorrhizal species, those described represent an incredibly diverse array of morphologies and physiologies (Hobbie and Agerer, 2010). Likewise, MNs are expected to be multifarious structurally and functionally.

The recent discovery of multi-genomic mycelia (Sanders, 2003; Hijri and Sanders, 2005) and the potential for non-self hyphal fusion (i.e., anastomosis) among some arbuscular mycorrhizal (AM) fungal species present the intriguing possibility that both fungi and plants could be interconnected in compound associative networks (Giovannetti *et al.*, 2005; Croll *et al.*, 2009; Sbrana *et al.*, 2011). In contrast, instances of non-self anastomosis are likely rare among EM fungi where sexual and somatic compatibility is controlled by complex gene regulatory mechanisms.

A morphological feature particularly well suited for extensive MN formation is found among EM fungal species that form highly differentiated hyphal strands, cords or rhizomorphs – literally “root forms” (Heaton *et al.*, 2012). This morphology, represented by such genera as *Boletus*, *Cortinarius*, *Paxillus*, *Piloderma*, *Pisolithus*, *Rhizopogon*, *Suillus* and *Tricholoma*, is typically associated with species forming large, perennial genets (Redecker *et al.*, 2001). Rhizomorphs can span decametres in length with an internal anatomy enabling the efficient transport of water and nutrients through soils (Egerton-Warburton *et al.*, 2007; Agerer, 2001), and rapid colonization of newly establishing seedlings

Box 1. Methods for unearthing mycorrhizal network structure and function.

The first irrefutable evidence of mycelial links between the roots of multiple plants arose from direct visual observations *in situ* and *in vitro* using transparent microcosms and autoradiography (Smith and Read, 2008). The visual representation of MNs afforded by microcosms helped garner interest in research dedicated to exploring the prevalence and ecological significance of MNs. Transparent microcosms and radioactive isotope labelling, in addition to advanced microscopy techniques such as environmental scanning electron microscopy (He *et al.*, 2005), nuclear magnetic resonance imaging (Tuffen *et al.*, 2002) or high-throughput automated image analysis (Heaton *et al.*, 2012), continue to provide means for the physical demonstration of MNs between an increasing number of plant species combinations.

The majority of empirical studies have sought to elucidate the functional significance of MNs to plant population and community ecology using physiological techniques. Radioactive and stable isotope analysis, fluorescent dye tracers, and more recently quantum dots, along with the use of nylon or steel mesh barriers of various pore sizes to isolate MN effects from other soil pathways, have been useful in examining the translocation of water, C, N, P and other nutrients between the roots of the same or differing plant species *via* fungal pathways (He *et al.*, 2005; Egerton-Warburton *et al.*, 2007; Teste *et al.*, 2009). This is discussed in more detail in Section 3.

Perhaps the most significant developments to acquire evidence for the existence of MNs have come from the application of culture-independent DNA-based methods for identifying potential MN participants with high taxonomic resolution. Techniques commonly used to identify mycorrhizal fungi to genus or species for community profiling include combinations of direct sequencing, restriction fragment length polymorphism (RFLP) analysis (Horton and Bruns, 2001), terminal restriction length polymorphism (T-RFLP) analysis (Wolfe *et al.*, 2007), denaturing gradient gel electrophoresis (DGGE) (Jumpponen, 2003), and clone libraries (Deslippe *et al.*, 2011). For studies exploring MN structure, the highest level of resolution is provided by genotype-specific molecular markers such as microsatellite DNA analysis that can be used to concurrently distinguish between individual plants and fungal genets isolated from mycorrhizal root tips (Saari *et al.*, 2005; Lian *et al.*, 2006; Beiler *et al.*, 2010) (Box 5). Other molecular techniques such as amplified fragment length polymorphism (AFLP) and single nucleotide polymorphism (SNP) analysis can distinguish genotypes from environmental samples (Amend *et al.*, 2009), but have not yet been applied concurrently to plants and fungi for the purpose of studying MNs.

(Richard et al., 2005; Teste and Simard, 2008). However, there are significant C costs associated with the maintenance of such extensive mycelial systems (Nehls et al., 2001). As these fungi encounter and colonize new host roots along their advancing mycelial front, their associated C demands are partitioned among host trees. Thus, the formation of MNs is likely a fundamental life history trait for these mycorrhizal fungi species.

Fungi with relatively limited extraradical mycelial growth, such as AM fungi and short-lived EM fungi, may also connect plant roots within close proximity or for a short duration. These connections may be nested within more extensive networks made by large fungal genets, as demonstrated by Beiler et al. (2010) for co-occurring small and large genets of *Rhizopogon vinicolor* and *R. visiculosus*, respectively. When the physiological diversity characteristic of mycorrhizal fungal communities is superimposed over the structural heterogeneity of their MNs, a highly complex and dynamic system emerges (see Section 5).

3. Functioning of mycorrhizal networks in plant communities

Mycorrhization

Fuelled by C from its host plants, the mycelial front of an MN may quickly encounter the roots of young seedlings, increasing their EM fungal colonization and diversity (Teste and Simard, 2008) (Table 1). For example, the EM fungal community structure of Douglas-fir seedlings changes when growing near mature conspecific trees, which act as refuges for EM fungi (Teste and Simard, 2008; Bingham and Simard, 2012). Likewise, seedling establishment has been aided by older plants with extensively colonized root systems because germinants were able to quickly tap into a larger soil resource pool than they could access on their own (Teste et al., 2009; Bingham and Simard, 2012). The benefits of MNs to seedling colonization can vary in time and space and be influenced by numerous

Table 1 – Summary of mechanisms by which mycorrhizal networks may affect plant and fungal communities, their ecological implications, and some examples of their empirical support.

Mechanism of effect	Ecological implication	Empirical support
Colonization	Primary succession	Nara (2006)
	Secondary succession	Onguene and Kuyper (2002); Twieg et al. (2007)
	Grassland encroachment	Dickie et al. (2004); Dickie et al. (2005)
	Plant-to-plant facilitation under high abiotic stress	Deslippe et al. (2011); Bingham and Simard (2012)
	Fungal community composition and diversity	Teste and Simard (2008); Bingham and Simard (2012)
	Widespread networking by a single fungal genet	Beiler et al. (2010)
	C translocation	Mycoheterotrophy/mixoheterotrophy
Secondary succession		Simard et al. (1997); Lerat et al. (2002); Teste et al. (2009)
Maintenance of diversity		Fitter et al. (1999); Lerat et al. (2002)
Dominance		McGuire (2007); Teste et al. (2009, 2010); Booth and Hoeksema (2010); Deslippe and Simard (2011)
Water translocation (hydraulic redistribution)	Stability of fungal mycelium	Teste and Simard (2008); Deslippe et al. (2011); Kiers et al. (2011)
	Primary succession	None
	Secondary succession	Horton et al. (1999); Schoonmaker et al. (2007)
	Grassland encroachment	None
	Plant-to-plant facilitation under high abiotic stress	Horton et al. (1999); Egerton-Warburton et al. (2007); Bingham and Simard (2011, 2012)
N translocation	Dominance	Schoonmaker et al. (2007); McGuire (2007); Booth and Hoeksema (2010)
	Stability of fungal mycelium	Egerton-Warburton et al. (2007)
	Primary succession	None
P translocation	Secondary succession	Horton et al. (1999); He et al. (2005); Teste et al. (2009)
	Plant-to-plant facilitation under high abiotic stress	None
	Secondary succession	Eason et al. (1991)
	Grassland encroachment	Eason et al. (1991)
Micronutrient translocation	Maintenance of diversity	Eason et al. (1991); Zabinski et al. (2002)
	Dominance	Finlay (1989); Eason et al. (1991); Zabinski et al. (2002)
	Primary succession	None
	Secondary succession	None
Toxin translocation	Plant-to-plant facilitation under high abiotic stress	None
	Allelopathy	Barto et al. (2011)
Enzyme translocation	Pathogen defence induction	Song et al. (2010)

biological and environmental factors (see Section 2). For example, EM fungal colonization of establishing seedlings by an MN of older plants has been most beneficial in their first year of growth, when seedlings are especially susceptible to resource limitations (Jones *et al.*, 2003) (Fig. 1a).

Transfer of C, nutrients and other compounds

Transfer pathways

Perhaps the single most compelling attribute of MNs is their potential to act as belowground avenues for the transfer of C and nutrients among plants within a community. A direct hyphal pathway for resource transfer among plants compartmentalizes valuable resources away from potential disruptions, such as competition with soil microbes, fauna, chemical adsorption of nutrients to soil particles or physical disturbances of the soil structure (Newman, 1988; Philip *et al.*, 2010). Long-distance carbon and nutrient transfer through direct hyphal pathways in MNs appears to occur predominantly by advective mass flow driven by source-sink gradients generated by interplant nutrient differences or by fungal growth, but diffusion or active transport mechanisms may also operate during active cell expansion at growing mycelium fronts (Heaton *et al.*, 2012). Belowground transfer can also occur directly through other pathways, including rhizomes or plant root grafts, or indirectly through uptake of root exudates via the soil solution or via a discontinuous mycelial pathway (Fig. 2). Transfer of C and nutrients through indirect pathways is influenced by soil structure, porosity, organic matter content and immobilisation/mineralisation by soil microorganisms, resulting in more complex and poorly understood transfer mechanisms (Rillig and Mummey, 2006; Philip *et al.*, 2010). Given that plant interactions are influenced differently depending on whether or not they are linked into an MN (Pietikäinen and Kytöviita, 2007) (see Section 4), understanding the relative importance of nutrient transferred through MNs versus other pathways is important for understanding plant community dynamics and diversity.

Ectomycorrhizal fungal species may indirectly influence resource transfer through soil pathways by differentially acquiring C from hosts, influencing rates of root turnover, exudation or death, or by taking up resources from the soil matrix (Rygielwicz and Anderson, 1994; Lehto and Zwiasek, 2011). For example, *Suillus bovinus* colonised *Pinus sylvestris* lateral roots to a greater degree and accumulated more ^{14}C -labelled assimilate from adjacent plants than *Suillus grevillei* or *Boletinus cavipes* (Finlay, 1989). Differences in EM species colonisation rates, physiological activity, metabolite transfer rates to plant hosts, and mycelial morphology and growth rates may also affect transfer (Rygielwicz and Anderson, 1994; Teste *et al.*, 2009; Hobbie and Agerer, 2010). For example, Kiers *et al.* (2011) found that a fungal species delivering more phosphorus to their host in turn received more C from that particular host, and *vice versa*, fungi receiving more C from a particular host provided the host with more phosphorus. While the impact of fungal characteristics on C dynamics has not been well examined, it is likely that the amount of resources moving through different pathways will change with the number and identity of fungal species involved.

Similar to C and nutrients, water can also move through multiple belowground pathways. Brooks *et al.* (2006) observed that deuterated water applied to the soil moved horizontally through the soil matrix in an asymmetric pattern, presumably due to hydraulic redistribution by both plants and fungi. Field experiments have shown that movement of deuterated water applied directly to soil varies horizontally depending on the potential for MNs to form, soil moisture conditions and the functional form of the plants present (Brooks *et al.*, 2006; Schoonmaker *et al.*, 2007). Other studies have shown that water hydraulically lifted via taproots is transferred directly to fungal symbionts and subsequently translocated by the MN independently of soil pathways (Schoonmaker *et al.*, 2007; Egerton-Warburton *et al.*, 2007; Bingham and Simard, 2011). Water can also be shared between plants through root grafts. Thus, water, and any resource that can be carried by water, has the potential to move through multiple pathways, with greatest transfer efficiency through root grafts and MNs.

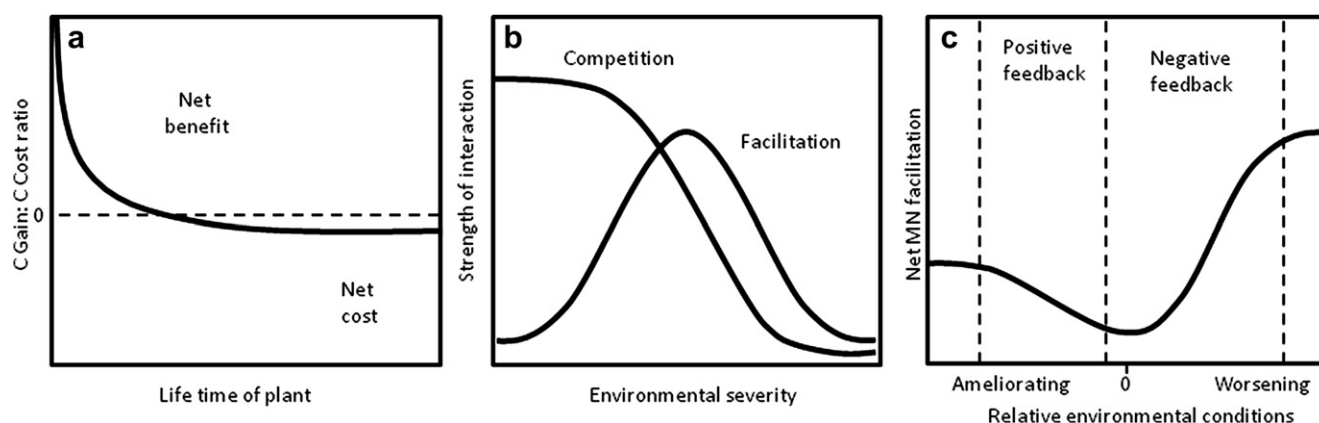


Fig. 1 – Observed or expected relationships for the ecological role of MNs in ecosystems: (a) C gain: cost of being joined in an MN over the lifetime of an EM tree; (b) Relative strength of plant interactions over a gradient of increasing environmental severity; (c) Net effect of MN facilitation as a feedback to higher order state processes over a gradient of improving to worsening environmental conditions. Zero on the x-axis represents the environmental conditions to which the plant is optimally adapted (the *status quo*).

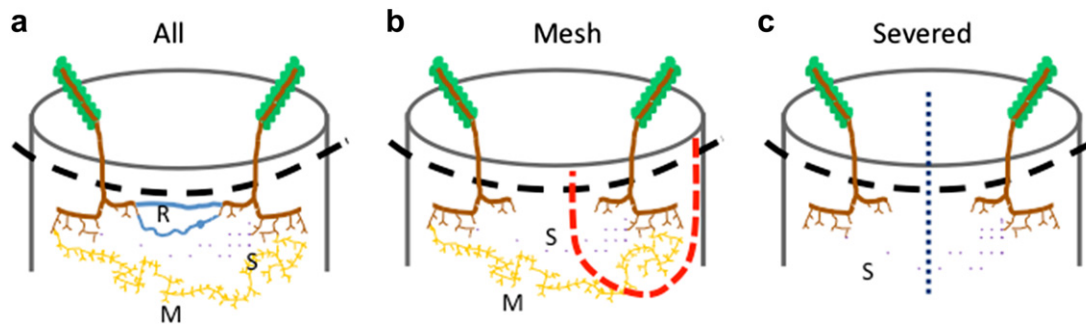


Fig. 2 – Schematic representation of treatments applied to control belowground pathways; R = rhizome and root graft transfer; M = mycorrhizal network transfer; S = soil solution transfer. Total isotope transfer to a receiver plant through rhizome or root grafts would be calculated as the difference between treatments illustrated in (a) and (b); MN transfer would be calculated as the difference between the treatments illustrated in (b) and (c); transfer through the soil solution would be equal to the total isotope transferred in treatment (c). Reproduced, with permission, from [Deslippe and Simard \(2011\)](#).

The facilitative effects of resource transfers through different pathways should vary with plant status. Resource transfer through the soil pathway may be more beneficial to plants able to independently exploit soil resources efficiently, such as ruderal plants with rapid root growth and high nutrient-uptake rates. Transfer through MNs, by contrast, may be of relatively greater benefit to plants with smaller, less active root systems, as observed in MH plants or establishing autotrophic seedlings (see Section 4). In such plants, transfer may be regulated more by plant than fungal or microbial factors.

Resource transfers among autotrophic plants

Most studies examining transfers between plants through MNs have examined C transfer. Interplant C transfer via an MN where one plant receives a net C gain represents a nutritional innovation in plants. Interplant C transfer through MNs has been demonstrated in the field and can affect resource availability to plants ([Selosse et al., 2006](#); [Teste et al., 2009](#); [Deslippe and Simard, 2011](#)). Strong gradients for carbohydrate-C affect C transfer through MNs among forest trees ([Simard and Durall, 2004](#); [Teste et al., 2009](#)), but C transfer is also influenced by other resources, organisms and environmental conditions ([Eason et al., 1991](#); [He et al., 2005](#); [Selosse et al., 2006](#); [Egerton-Warburton et al., 2007](#)). For example, C transfer between *Betula nana* shrubs in Arctic tundra may more strongly reflect the movement of amino acid-C in this highly N-limited ecosystem ([Deslippe and Simard, 2011](#)). Indeed, in many systems, gradients of nutrients in amino acids may be the primary drivers of C transfer.

The transfer of nitrogen and phosphorus through MNs has also been demonstrated. For example, nitrogen transfer between non N_2 -fixing *Eucalyptus maculata* and N_2 -fixing *Casuarina cunninghamiana* linked in an ectomycorrhizal MN was demonstrated using $^{15}NH_4$ and $^{15}NO_3$ tracers ([He et al., 2005](#)). Likewise, phosphorus transfer through networks of both AM and ERM plants has been demonstrated ([Eason et al., 1991](#)). There is also potential for MNs to provide a route for plant hormones and other signalling molecules as demonstrated by [Song et al. \(2010\)](#), who found that MNs facilitated defence signalling between tomato plants (*Lycopersicon esculentum*) linked through the AM fungus, *Glomus mosseae*. This resulted

in increases in disease resistance, corresponding with increases in defence-related gene expression and enzyme activity. Mycorrhizal networks also facilitate transfer of allelochemicals between plants, resulting in increased accumulation of the noxious compounds in soils and reduced growth of the target plants ([Barto et al., 2011](#)).

While the transfer of C, nutrients and other compounds through MNs is well known, the significance of these transfers to interplant interactions and ecosystem dynamics remains a topic of research and debate ([Fitter et al., 1999](#); [van der Heijden and Horton, 2009](#)). Uncertainties regarding the ecological relevance of MN-facilitated resource transfer primarily concern the experimental and isotope methods employed, and the interpretations of data ([Perry, 1998](#); [Wilkinson, 1998](#); [Fitter et al., 1999](#); [Simard and Durall, 2004](#)). With theoretical, experimental and instrumental advances in isotope chemistry, network manipulation and molecular biology, these methods have greatly improved over the past decade.

A principle question to be addressed is why a fungus would give up C to a plant. The answer may lie in the finding that glutamine, which contains five C atoms for every two N atoms, is the primary molecule through which N is transferred from EM fungi to their hosts ([Martin et al., 1986](#)). Thus, if a fungus transfers disproportionately high quantities of glutamine to its host plant relative to the C the plant gives in return, the plant gains a C subsidy in addition to an N subsidy while the fungus still obtains its most limiting resource.

Factors influencing resource transfers among autotrophs

Resources are shuttled back-and-forth through MNs according to supply and demand in plant communities, representing a complex underground trading system. Differences in physiological source-sink strength among plants (e.g., in photosynthetic rates, growth rates, nutrient content, age, defoliation by pathogens, insects or drought) influence transfer 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, however, also play important roles ([Finlay, 1989](#); [Rygiewicz and Anderson, 1994](#); [Lehto and Zwiazek, 2011](#)). Where resource pools and demands are distributed equitably

among plants in a physiologically uniform community, resource transfer from one plant to another is theoretically balanced by transfer in the opposite direction (i.e., net transfer is zero). However, physiological source-sink gradients among plants are the norm in natural ecosystems, and resources transfer along these gradients, from enriched source plants to rapidly growing sink plants (Simard and Durall, 2004; Selosse et al., 2006; van der Heijden and Horton, 2009). Thus, a sink plant could gain more C than it gives up to its neighbour, at least for a time.

Transfer patterns appear to be governed more by sink strength of receiver plants than by source strength of donors. Teste et al. (2009, 2010) showed that greater C transfer occurred to rapidly growing sink seedlings than to slowly growing ones, and transfer amounts were unrelated to source seedling growth rates. By contrast, studies that have manipulated source strength in seedlings, based on size or elevated CO₂ levels, have found no effect on the amount of C transfer (Fitter et al., 1999; Teste et al., 2009). Thus, larger, more vigorous sink seedlings may outperform smaller seedlings as a result of greater C gains from neighbouring trees (Teste et al., 2009, 2010). In this case, C (and other resources) may move into sink seedlings via xylem driven by transpiration or nutrient demand (Näsholm et al., 1998). Where they establish within the MN of overstory trees, deeply shaded seedlings may depend on transfer of photosynthate from older trees to maintain a positive C balance. Where understory seedlings are released from light limitation by a gap disturbance, source-sink gradients would change as they gain dominance, causing shifts in the pattern of net flux among neighbouring seedlings.

Plants occur in complex mixtures, with many plant and fungal species and individuals, involving more than just pairs of plants connected by the mycelium of a single fungal species. These conditions change as plants germinate, grow, compete, respond to seasons, are consumed and die, resulting in a dynamic flux of resources, which tracks changing strengths and demands among individuals. Thus, not only do the complexity and composition of MNs change over time (Twieg et al., 2007), but belowground fluxes of nutrients change over the growing season with shifts in source-sink gradients among networked plants (Lerat et al., 2002; Philip, 2006; Deslippe and Simard, 2011) (Box 2). Seasonality indirectly affects the magnitude of C transferred not only through shifts in plant but also in fungal physiology. Root turnover, root activity and mycorrhizal colonization dynamics change throughout the growing season (Rygiewicz and Anderson, 1994), and networks are likely disrupted and re-anastomose continuously (Tuffen et al., 2002), shifting the balance between MN and soil pathways for resource transfer. Only a few studies have repeatedly measured C over time; this research indicates a peak in C transfer during leaf expansion or high photosynthetic activity in autotrophic plants (Lerat et al., 2002; Philip, 2006; Deslippe and Simard, 2011). The seasonality of C transfer in MH and partial MH plants remains unknown but likely follows C allocation bursts to nearby autotrophic roots and mycorrhizal fungi. Further research is needed to clarify the effects of temporal and spatial environmental heterogeneity on interplant C transfer through MNs, as well as the roles of different fungal species, fungal exploration types (exploration types are described by Agerer, 2001;

Box 2. Shifting direction of net carbon transfer with season.

Using dual ¹³C/¹⁴C labelling in the field, Philip (2006) found that the direction of net C transfer reversed twice over the growing season: (1) from rapidly growing Douglas-fir to bud-bursting paper birch in spring, (2) then reversing, from nutrient and photosynthate-enriched paper birch to stressed understory Douglas-fir in summer; and (3) reversing yet again, from still-photosynthesizing Douglas-fir to senescent paper birch in the fall. The C moved back-and-forth between paper birch and Douglas-fir through multiple belowground pathways, including MNs, soils and a discontinuous hyphal pathway. Here, there appears to be a dynamic interplay between paper birch, Douglas-fir and the interconnecting fungi, with C and nutrients moving in the direction of greater need over the growing season.

Hobbie and Agerer, 2010) and their effects on fungal biology and fitness.

Soil conditions such as temperature, moisture and nutrient levels, the community of soil organisms, or the degree of soil disturbance are expected to affect the amount of C transferred. Not surprisingly, high levels of nitrogen and phosphorus in soil can affect the magnitude of C transferred (Selosse and Roy, 2009). High temperatures that warm soils can promote extramatrical hyphae growth (Hawkes et al., 2008) and may favour C transfer through MNs (Deslippe and Simard, 2011). Soil disturbance is expected to affect total C transfer, but the size of receiving autotrophic plants is more influential (Teste et al., 2010). There are likely other, yet to be identified factors affecting the magnitude of C transferred in MNs.

Transfers to mycoheterotrophic and partial mycoheterotrophic plants

The greatest dependence on C transfer via MNs appears to occur in MH plants, followed by partial MH plants then autotrophic plants (Leake, 2005; Selosse et al., 2006; Leake and Cameron, 2010). Mycoheterotrophy is a unique nutritional mode where plants are completely dependent on MNs for C and nutrients, and thus their very existence. About 450 MH plant species are known to fully exploit their MNs for C and nutrients (Leake, 2005). The C in MH plants originates from nearby autotrophic plants and delivered through MNs. This strategy has independently evolved at least 40 times, with representative species in the Burmanniaceae, Corsiaceae, Ericaceae, Gentianaceae, Iridaceae, Orchidaceae, Petrosaviaceae, Polygalaceae, Thismiaceae, and Triuridaceae plant families (Merckx et al., 2009). It is suggested that evolutionary radiation and niche expansion took place, for example, in the Orchidaceae and Burmanniaceae, during the Eocene, as increased demand for light-independent C was met by MNs in increasingly shaded conditions in forests (Merckx et al., 2009; Motomura et al., 2010). Cospeciation is also possible, with numerous molecular studies showing high specificity between fully MH plants and narrow-host range EM species

(Hynson and Bruns, 2010). For example, some plants in the divergent genus *Hexalectris* (Orchidaceae) associate exclusively with members of the Thelephoraceae, Russulaceae and Sebaciaceae, showing high specificity for unique associations with narrow clades of mycorrhizal fungi (Kennedy et al., 2011).

Recent studies using stable isotopes and mixed modelling approaches (Tedersoo et al., 2007; Motomura et al., 2010) have demonstrated that numerous plants derive some C from associated fungi while remaining photosynthetically active, thus forming a novel partial MH nutritional strategy. Similar to MH, partial MH plants receive this C from fungi forming MNs with nearby autotrophic plants (Leake et al., 2004; Selosse and Roy, 2009). Approximately 10 % of all plant species appear to be MH or partial MH during all or part of their life (Leake and Cameron, 2010). There are many partial MH pyroloid and orchid species, with potentially more to be discovered in the Gentianaceae, Dioscoreales, Polygalaceae, Iridaceae, Pandanales, and Petrosaviaceae families (Selosse and Roy 2009; Merckx et al., 2009).

Numerous members of the Basidiomycota, Ascomycota and Glomeromycota colonize roots of MH and partial MH plants, as identified with molecular barcoding methods based on fungal rRNA genes (Merckx et al., 2009). These fungi typically form EM or AM fungal structures with autotrophic plants, but occasionally have an altered morphology on the roots of the MH or partial MH plants (Orchidaceae) where intracellular pegs or pelotons are seen (Leake et al., 2004). Most MH plants have specialized associations with single families, genera or even species of fungi (Hynson and Bruns, 2010). The degree of fungal specificity appears to correlate with the proportion of C derived from the fungi in MH and partial MH plants, indicating that efficient MNs have evolved to sustain C transfers. There are reports of novel mycorrhizal formations with litter and wood decaying fungi such as *Gymnopus* and *Mycena* that are 'exploited' by MH and partial MH plants (Ogura-Tsujita et al., 2009; Bougoure et al., 2010).

Magnitude of C transfer in MH and partial MH plants

The magnitude of a net C gain through MNs is closely linked to the degree of mycoheterotrophy or by the N sink in leaves of autotrophic plants. As discussed, this is because source-sink gradients are the primary driver of resource transfer between plants. In MH and partial MH plants, leaflessness, reduced leaf size or number of leaves, variegated leaves and lack (or low levels) of chlorophyll are diagnostic of a dependency on fungi for C (Selosse and Roy, 2009; Merckx et al., 2009). Since MH and partial MH have a reduced photosynthetic machinery (less chlorophyll), a true C sink develops throughout the whole plant where C gained from fungi can be considered as a dependency on MNs to form and channel C from nearby autotrophic plants (Box 3). With autotrophic receiver plants, the opposite appears to hold, where leaf photosynthetic activity generates an N sink that drives C as amino acids (glutamine) into the aboveground tissue via the xylem (Martin et al., 1986; Teste et al., 2010; Deslippe and Simard, 2011).

Fate of transferred carbon

Research is needed to clearly discern the fate of transferred C. Presumably, much of the transferred C is returned to the

atmosphere via respiration within the first hours to days, but these losses have not been measured in MN studies in the field. The peak of C transfer appears to occur within the first 72 h of C fixation by the autotrophic donor plant (Leake et al., 2004). As opposed to AM systems, transferred C is found in the shoots of EM plants (Simard and Durall, 2004; Teste et al., 2009, 2010; Philip et al., 2010; Deslippe and Simard, 2011; Bingham and Simard, 2011). It appears that the demands of the photosynthetic machinery for N are mainly responsible for C allocation to the shoots as C is moved up the xylem as amino acids or low-weight N compounds (Näsholm et al., 1998).

There are few potential mechanisms to explain how C is moved from the fungus to plant (the reverse of the typical movement). Intracellular digestion of fungal hyphae in MH and partial MH orchids occurs (Bougoure et al., 2010), but this process has yet to be documented in autotrophic plants. In MH Monotropeae and Pterosporeae, intracellular hyphal pegs release fungal cytosol by emitting membranaceous sacs. In pyroloids, fungal lysis or other pathways of recovering cellular C probably operate. Nevertheless, it remains conceivable that C can move from fungal to plant tissue as a simple sugar (Bidartondo, 2005). As a sizeable portion of transferred C accumulates in the receiver roots and EM fungal tissue, EM fungi with extensive rhizomorphic structures may accumulate more C (Teste et al., 2009). Future research using stable isotope analysis and mixing models is needed to obtain better estimates of the origin, allocation and fate of transferred C through MNs among different combinations of autotrophic, MH and partial MH (degree of heterotrophy) plants, and to understand how these are affected by environmental heterogeneity.

4. Ecological significance of mycorrhizal networks

Significance of MNs to plant establishment and fungal biology

Effects of MNs on plant survival

Mycorrhizal networks are important to plant establishment and growth. As discussed earlier, the establishment and growth of many MH plants depend on the availability of MNs. Less clear, however, is the importance of MNs to the survival and growth of autotrophic plants. There is a plethora of research showing that EM fungi improve the establishment success of many woody plants (Karst et al., 2008), but studies testing the role of MNs have been sparse.

The first clear evidence that MNs likely affect establishment of autotrophic seedlings was provided by Horton et al. (1999). They showed that *Pseudotsuga menziesii* var. *menziesii* seedlings were only able to establish in EM *Arctostaphylos* spp. patches as opposed to AM *Adenostoma fasciculatum* patches in central California coast chaparral. Seedlings growing in *Arctostaphylos* patches shared 17 species of EM fungi with *Arctostaphylos* spp., while seedlings growing in *A. fasciculatum* were colonized by only two EM species. They found no significant differences between patches in allelopathy, light, temperature, soil N or soil K. The study did not control for the source of mycorrhizal fungal colonization or the potential for MNs to form, however, so it could not be

Box 3. Magnitude of carbon transfer between plants.

By definition, all MH plants gain 100 % of their C from fungi that establish MNs with nearby autotrophic plants. This has been confirmed empirically, *albeit* indirectly, with the analysis of stable isotopes and calculation of fungal-derived C gains with isotope mixing models (Leake *et al.*, 2004; Preiss *et al.*, 2010). As for the partial MH plants, up to 85% C gain appears to have moved through MNs (Selosse and Roy, 2009) (Table 2). Partial MH plants acquiring life-sustaining C from MNs have very low photosynthetic rates compared to autotrophic plants (Cameron *et al.*, 2009). Net C transfer between autotrophic plants has typically been small compared to the C fixed *via* photosynthesis (Deslippe and Simard, 2011; Smith and Read, 2008; Teste *et al.*, 2010; Philip *et al.*, 2010; Simard and Durall, 2004) and compared to the MN-derived C in MH and partial MH plants (Fig. 3).

Total C gains received through MNs are likely underestimated due to respiratory C loss (Girlanda *et al.*, 2011). Furthermore, a proportion of C may be derived from saprotrophic fungi, or EM fungi with saprotrophic ability, without the implication of an MN, but this contribution appears to be small (Bougoure *et al.*, 2010).

Numerous studies have shown that light is an important factor determining the magnitude of C gained from networking fungi (Tedersoo *et al.*, 2007; Motomura *et al.*, 2010; Liebel *et al.*, 2010; Preiss *et al.*, 2010). The amount of C gained from fungi in partial MH plants decreases with increasing light availability (Liebel *et al.*, 2010; Preiss *et al.*, 2010). Net C transferred *via* MNs in autotrophic plants appears to only reach biologically significant levels under shade (Fig. 3) (see Section 3). Future studies are also needed to enhance our understanding of the ecology and evolution of roots forming MNs, and we can use MH and partial MH as model plants. Heterotrophy as seen in partial MH plants, is to some degree, a dynamic adaptation to growing in shaded forests (Preiss *et al.*, 2010). In the case of MH plants, their lack of a well-developed root system and their complete dependency on fungi for C may also represent an adaptation to root competition.

definitively concluded that MNs were the source of inoculation or cause of increased survival.

Key to examining MN effects on seedling survival has been the development of techniques for manipulating MN formation. Some studies have found positive MN effects on autotrophic seedling survival when seedlings are growing near an established conspecific tree (Onguene and Kuyper, 2002; McGuire, 2007; Teste *et al.*, 2009; Booth and Hoeksema, 2010; Bingham and Simard, 2011). Studies that have separated soil, MN and root pathways have usually found that positive effects of MNs are at least partially offset by root competition (Booth, 2004; Booth and Hoeksema, 2010; Bingham and Simard, 2011). However, the likelihood of survival increases significantly where seedlings have the potential to tap into an MN (Teste *et al.*, 2009). Notably, all of these studies have been conducted within the first 3 y of seedling establishment. Thus, it is conceivable that there is a temporal stress threshold at which competitive effects of the established conspecifics outweigh the facilitative effects of the MN, such that mortality increases among seedlings when they approach the age or size of the established conspecific.

Effects of MNs on plant growth

Studies have also demonstrated an increase in growth when autotrophic seedlings are linked in an MN with older trees (Box 4). Onguene and Kuyper (2002) noted increased biomass for autotrophic EM seedlings growing near EM trees in a tropical rainforest. The effect of EM trees on EM seedling growth was further supported in oak savannah by Dickie *et al.* (2004), who reported a more than tripling of shoot biomass for *Quercus rubra* seedlings growing near EM *Q. montana* trees, versus AM *Acer rubrum* trees. A facilitative effect of *Quercus* rather than simply an inhibitory effect of *Acer* was later confirmed in Dickie *et al.* (2005), where *Q. macrocarpa* seedling growth was maximized at intermediate distances from *Q. ellipsoidalis* trees, in a matrix of AM herbaceous species. These studies suggest that MNs improved autotrophic plant growth, but improvements could simply have been due to increased colonization independent of networks, as the potential to form networks was not manipulated in these experiments. Other experiments have teased apart the effects of the potential to form a network from the benefits of inoculation (Booth, 2004; Nara, 2006; McGuire, 2007; Bingham and Simard, 2011). Booth (2004) utilized trenching and mesh with a 44- μ m pore

Table 2 – Ecological implications of net carbon transfer *via* MNs for the three main nutritional strategies found in forest ecosystems.

Nutritional strategy	Range of net C transfer <i>via</i> MNs under full light and deep shade (%)	Degree of adaptation to shaded environments	Level of development of photosynthetic machinery and root systems	Suggested importance of net C transfer <i>via</i> MNs in complex adaptive ecosystems	Evolutionary implication of MNs under low light environments
Mycoheterotrophic (MH)	95–100	High	Absent to poor	Required for survival	Radiation and cospeciation
Partial MH	0–85	Moderate to high	Poor to excellent (highly flexible)	Required for normal growth and survival	Niche expansion and cospeciation
Autotrophic	0–10	Poor to moderate	Excellent	Seedling survival and growth supplement	Niche expansion

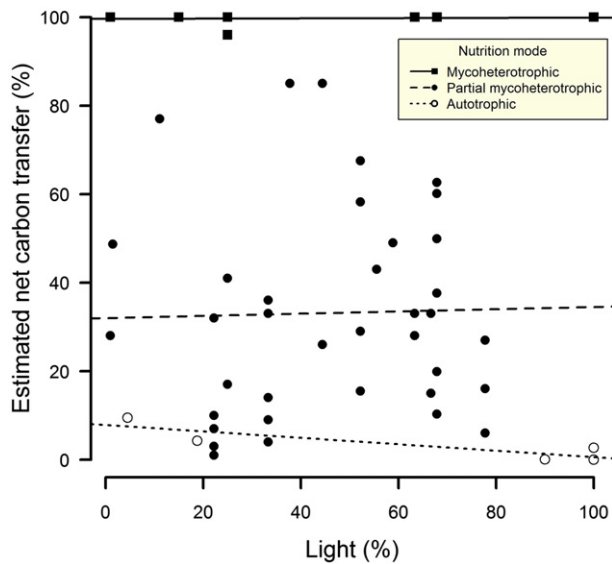


Fig. 3 – Estimated net C gain via MNs in mycoheterotrophic (MH), partial mycoheterotrophic (partial MH), and autotrophic (AU) plants with light intensity. Data consolidated from Bidartondo (2005); Tedersoo et al. (2007); Teste et al. (2010); Simard et al. (1997); Lerat et al. (2002); Motomura et al. (2010), Hynson and Bruns (2010) and others. Included here are field studies with plants associating with EM fungi that estimated net C transfer with dual (^{14}C - ^{13}C) labelling or calculated net C gain via MNs with stable isotope analyses and stable isotope mixing models (Preiss et al., 2010). A notable exception is Lerat et al. (2002), who calculated net C gain between AM plants in the field with ^{14}C . None of the simple linear regressions were statistically significant; MH: $R^2 = 0.01$, $P = 0.66$; partial MH: $R^2 = 0.001$, $P = 0.89$; AU: $R^2 = 0.75$, $P = 0.06$. Net C transfer in partial MH plants as a group (pyroloids, green orchids) is important, reaching in some cases 85 % of all C acquired (Selosse and Roy, 2009); however, this relationship is highly variable. Within the same partial MH genus (e.g., *Cephalanthera* green orchids) a strong relationship does exist between light intensity and the magnitude of C gained from fungi via MNs (Preiss et al., 2010).

size to control for MN formation and found that needle number of *Pinus strobus* seedlings was maximized when they had the opportunity to form MNs in the absence of root competition in a stand dominated by EM trees. Similarly, trenching was used to show that understory Douglas-fir seedlings grew taller and had improved foliar nutrition where they were able to form networks with century-old overstory Douglas-fir and paper birch trees than where they were isolated (Simard and Durall, 2004).

The circumstances under which MNs benefit the growth of autotrophic EM plants are increasingly understood. Both Dickie et al. (2005) and McGuire (2007) found that growth of EM seedlings establishing in an AM plant community matrix was improved when they were located in close proximity to congeneric or conspecific stands of trees. However, Dickie et al. (2005) found that growth peaked at a distance of ~ 12 m, and suggested light competition suppressed growth

at closer distances relative to the grassland matrix environment. In a tropical rainforest, McGuire (2007) observed that autotrophic plant growth was maximized along the stand edge, presumably due to aboveground functional equivalence of conspecifics with AM plant species in the stands. Nara (2006) unambiguously showed that, under primary succession, the growth of an establishing EM plant was improved when networking with an established plant, but that this varied depending on the fungal species involved.

Controlled, small-scale experiments can help to elucidate the mechanisms by which MNs influence survival and growth of establishing plants. In an elegant experiment, Nara (2006) transplanted advanced EM *Salix reinii* seedlings inoculated with differing EM fungal species into biologically depauperate scoria substrate on Mt. Fuji, along with uninoculated *Salix reinii* germinants. He found increased survival of all germinants growing near inoculated advanced seedlings relative to uninoculated controls. Biomass of germinants increased in the inoculation treatments, except in the case of one EM fungal species. This study confirmed that MNs were the mechanism for EM fungal colonization and subsequent facilitation of plant establishment; however, other mechanisms of MN facilitation, such as resource transfer, were not tested. One way to test for resource transfer effects would be to sever the hyphae once seedlings have been colonized by the MN, allowing seedlings to reform MNs in one group while blocking reformation in the other group, using a barrier on the side of the establishing seedling towards the established plant.

Effects of MNs on EM fungal biology

Very few studies have focused on the effects of MNs on EM fungal biology, but those that have, have found a fungal response. Fitter et al. (1999) argue that MNs are primarily relevant in AM systems due to their effects on AM fungal biology. Teste and Simard (2008) used nylon mesh bags of different pore sizes to restrict hyphal, rhizomorph and root growth, and found that most EM fungal taxa decreased in prevalence on interior Douglas-fir seedling root tips with increasing restriction of network potential and distance from an established *P. menziesii* var. *glauca* mature tree. Interestingly, the EM fungi that exhibited the greatest decrease was *Rhizopogon*, the genus most likely to be important in MN formation and water translocation to seedlings due to its ability to form long-distance rhizomorphs and colonize multiple trees within a stand (Beiler et al., 2010). This pattern is congruent with the idea that networking is most advantageous to high-biomass, long-distance exploration-type fungi, since they would be able to colonize establishing plants at long distances, and continue to increase their biomass by tapping into multiple plants in an area. Likewise, EM fungal community similarity between seedlings and tree roots of *P. menziesii* var. *glauca* increased with restriction of network potential and distance, suggesting that long-distance exploration-type fungi tend to quickly dominate seedling root tips when they are able to colonize from adjacent trees (Bingham and Simard, 2012).

In addition to their role in facilitating resource redistribution to establishing plants, MNs may supplement fungi with C and water from neighbouring plants (Querejeta et al., 2003; Brooks et al., 2006; Schoonmaker et al., 2007; Egerton-Warburton et al.,

Box 4. Facilitation by MNs along stress gradients.

Bingham and Simard (2012) hypothesized that MNs are most important to forest regeneration where EM tree seedlings are establishing under high abiotic stress (i.e., at the periphery of their fundamental niche), especially in soils low in EM fungal inoculum, in support of the stress-gradient hypothesis (Maestre et al., 2009). In an experiment using mesh bags with varying pore size to control for hyphal and root growth, Douglas-fir seedlings were planted at varying distances from conspecific mature trees across a climatic moisture gradient, as measured by summer heat:moisture index. The interaction between the potential to form an MN and distance from established congeneric trees reversed along the climatic gradient. Growth of networked seedlings increased most when they were in close proximity to trees in dry climates, after adjusting for total soil N (Bingham and Simard, 2012) (35 μm mesh treatment at 0.5 m (green) shown in right panel in Fig. 4). The inferred mechanism for this is MN facilitation of hydraulic redistribution from the tree to the seedling, based on isotope labelling results from a growth chamber trial (Bingham and Simard, 2011), as well as other field and container studies (Querejeta et al. 2003, Egerton-Warburton et al. 2007, Brooks et al. 2006, Schoonmaker et al. 2007). Under dry conditions, trees generate deeper taproots, enabling them to access water unavailable to establishing seedlings, and this water is then nocturnally redistributed to the EM mycelia and translocated to seedling symbionts. Any benefit of hydraulic redistribution incurred by seedlings establishing on dry sites will be proportionately greater than that incurred by seedlings at wet sites, which also suffer from greater root competition due to higher tree root densities.

2007; Pickles et al., 2010). A greenhouse experiment using dye tracers revealed that oaks accessed water through their taproots and redistributed it to their mycorrhizal symbionts during severe soil drying, thus maintaining the mycelium of both EM and AM fungal partners (Querejeta et al., 2003).

Significance of MNs to plant community dynamics

Very few studies have examined the effects of MNs on plant community dynamics while concurrently demonstrating the existence of a functional MN. Some studies have shown that MNs have the potential to decrease or increase interplant competition (Pietikäinen and Kytöviita, 2007). Competitive dominance may be reduced by the direct flow of C or nutrients from sufficient to deficient plants, resulting in greater growth of

subordinate relative to dominant plants, and greater plant community diversity. On the other hand, there is also evidence that competitive dominance may increase because larger plants acquire more resources from the MN due to their higher nutrient demand (Zabinski et al., 2002; Deslippe and Simard, 2011). In some cases, competitive dominance within plant communities may simply be affected by greater, faster, more diverse or different mycorrhization of plants tapping into the MN, resulting in increased nutrient access for some plant species. To our knowledge, no studies have systematically tested whether the presence of MNs affects the diversity, succession or total productivity of whole plant communities in nature. Moreover, to our knowledge, there have been no studies that have examined whether the characteristics of the MN affect plant community structure. These remain major

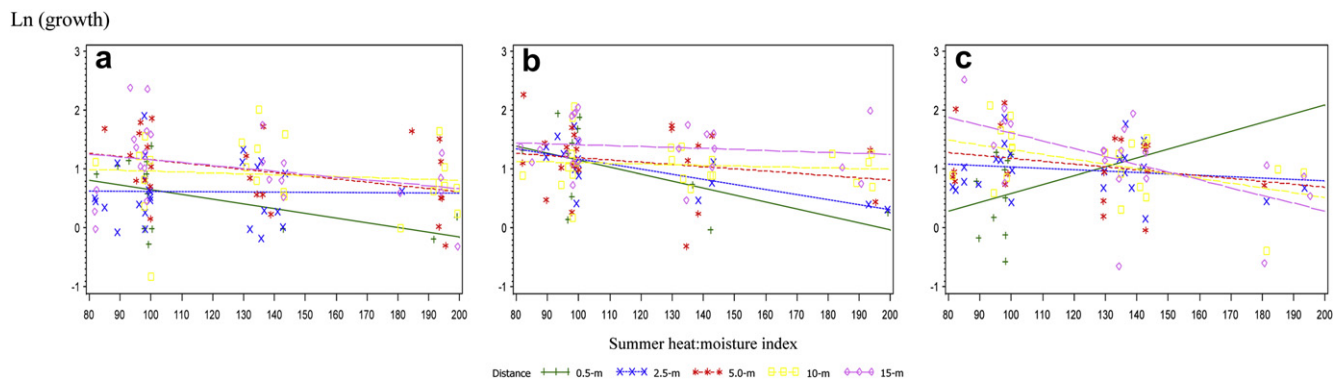


Fig. 4 – Change in growth of Douglas-fir seedlings with drought and distance from congeneric trees among three different treatments controlling for hyphal (MN) and root growth. (a) Growth response of new seedlings to drought where they are able to interact with conspecific mature trees through MN linkages and root competition (seedlings growing directly in soil); (b) Growth response where seedlings are unable to interact with mature trees either through MNs or roots (seedlings growing in 0.5 μm mesh bags); (c) Growth response where seedlings have access to MNs but not roots of mature trees (seedlings growing in 35 μm mesh bags). With kind permission from Springer Science+Business Media: Ecosystems, Ectomycorrhizal Networks of *Pseudotsuga menziesii* var. *glauca* Trees Facilitate Establishment of Conspecific Seedlings Under Drought, 2012, Marcus A. Bingham and Suzanne Simard, Figure 3.

gaps in our understanding of the significance of MNs to plant community dynamics (Box 5).

Significance of network facilitation in a changing climate: feedbacks over multiple scales

MN facilitation and environmental severity gradients

Like competition, facilitation is a powerful force that helps shape the structure and function of terrestrial ecosystems. For example, the formation of plant guilds and the succession of plant communities involve facilitative interactions among plants. Since MNs act as belowground vectors for the transfer of water, C, and nutrients, resource transfer through MNs is likely to be an important mechanism underpinning facilitation between plants. Given the role of sink strength in determining the outcome of MN facilitation, it follows that any factor altering the nutrient status of a networked plant has the potential to alter the intensity and importance of facilitation in a plant community.

Plant communities are optimally adapted to the historic range of environmental conditions where they occur. With our changing climate, many plant communities are being confronted with environmental conditions that exceed their ability to acclimate through physiological mechanisms (Pachauri and Reisinger, 2007). Moreover, current rates of warming are exceeding the migration capacity of many plant species, particularly those that are long-lived. Because plants are sensitive not only to the range of environmental conditions they experience, but also to the temporal variation in this range, the increased variability of environmental conditions with climate change may place additional stress on plants (Aitken et al., 2008). This could ultimately lead to the restructuring of plant communities.

Environmental severity, plant traits and the outcome of plant interactions

Unlike competition, which often declines sigmoidally with increasing environmental severity, facilitation is unimodal across this gradient (Butterfield, 2009). The hump-shaped

distribution stems from the dominance of competitive interactions among species in low-severity environments, and declining effectiveness of facilitation by very tolerant species in extreme environmental stress (Fig. 1b). Declining facilitation effectiveness at very high environmental severities is intimately linked to plant traits. Species that are stress tolerant tend to act as benefactors extending the realized niche of less tolerant beneficiaries and creating facilitative networks in severe environments. In a severely drought-stressed environment, for example, drought-intolerant plants may establish in the MN of more tolerant plants that have deeper roots, and benefit from hydraulic redistribution and reduced evapotranspiration. However, in very severe environments, the temporal variation in environmental severity experienced by a beneficiary tends to increase with proximity to a neighbour. This results in increased temporal variation in plant fitness with neighbours in very extreme environments. Thus, depending on the mean and range of environmental severity relative to the stress tolerance of the benefactor and beneficiary species present, facilitation can either stabilize or destabilize plant community dynamics (Butterfield, 2009).

In all biological networks, negative feedbacks tend to stabilize processes, structures and communities. Conversely, positive feedbacks tend to amplify change and destabilize the status quo. The threshold at which a facilitative plant interaction acts to destabilize a plant community is synchronous with its transition from a negative to a positive feedback. Positive feedbacks tend to enhance change at higher order scales. Positive feedbacks that destabilize plant communities and lead to altered plant community structures can amplify ecosystem change through, for example, cascading effects through food webs (Post et al., 2009) or alterations of an ecosystem's surface albedo (Chapin et al., 2005). These processes are illustrated in Fig. 1c, where the effect of net positive MN facilitation on higher order processes changes along a gradient of improving to worsening environmental conditions. The zero point on the x-axis represents the environmental conditions to which the plant community is

Box 5. Mycorrhizal networks link trees of multiple ages in dry temperate forests.

We can draw inferences about plant community dynamics and resilience to disturbance from studies of MN architecture in forest ecosystems (see Section 2). In Beiler et al. (2010), multi-locus, microsatellite DNA markers were used to show that most trees in an uneven-aged forest of *P. menziesii* var. *glauca* were interconnected by a complex MN of the EM fungi *Rhizopogon vesiculosus* and *R. vinicolor* (Fig. 5). The MN had a scale-free network structure (Box 7), where most of the young trees were linked to large, old hub trees, suggesting the network played a role in facilitating the self-regeneration of these Douglas-fir forests. Likewise, seedling establishment success in this forest type was 26% greater where seedlings had full access to the MN of older Douglas-fir trees compared to where they did not (Teste et al., 2009). Access to the network not only improved seedling survival, but seedlings were colonized by a more complex fungal community comprising multiple long-distance exploration types. The scale-free network structure suggests that these forests are robust against random removals or deaths of individual trees (Albert et al., 2000; Bray, 2003). That tree pairs in Beiler et al. (2010) were also linked repeatedly through contiguous network loops, where a single mycelium linked together multiple roots of the same trees, suggests that the network is reinforced and robust against damage by grazing soil fauna while maintaining high nutrient transfer capacity (Heaton et al., 2012). These loops allow the network to respond to damage by providing an alternative pathway for nutrient transfer and an opportunity to reconnect without losing function. Given that single genets of mycelia have been found to cover hundreds of hectares of forest soil with estimated ages of thousands of years, it is likely that single genets of EM fungi are influencing forest stand dynamics over large areas and many tree generations (Ferguson et al., 2003).

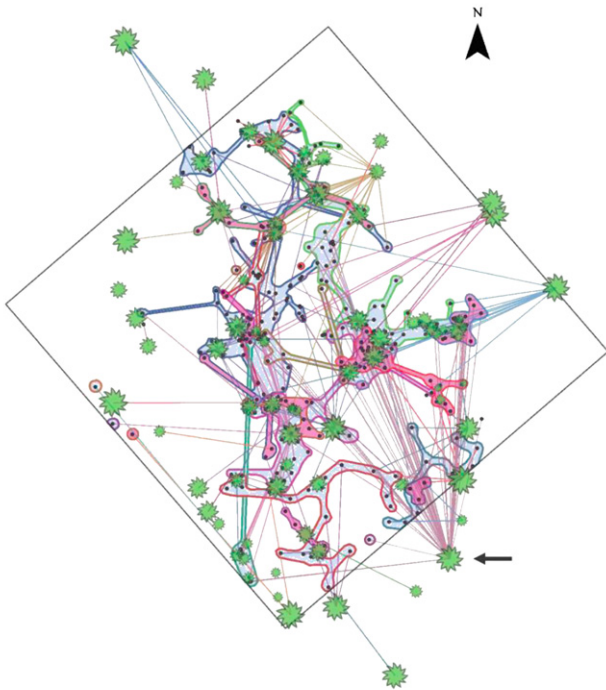


Fig. 5 – Spatial topology of *Rhizopogon* genets and Douglas-fir trees. A 30 × 30 m plot (square outline) contained 67 trees of various ages (green shapes, sized relative to tree diameter). Small black dots mark sampling locations of *Rhizopogon* EM ($n = 401$), 338 of which were associated with a specific tree and fungal genet based on microsatellite DNA analysis. Samples representative of each fungal genet are outlined in colours: *Rhizopogon visiculosus* genets ($n = 14$), blue, and *Rhizopogon vinicolor* genets ($n = 13$), pink. Lines link tree roots encountered by *Rhizopogon* EM with corresponding trees aboveground and are coloured according to tree genotype. The most highly connected tree (arrow) was linked to 47 other trees through eight *R. visiculosus* genets and three *R. vinicolor* genets. Reproduced, with permission, from Beiler et al. (2010).

optimally adapted (the *status quo*). At this position, the range of environmental conditions the plant community experiences, though temporally variable, is not changing directionally. At zero, the net effect of positive MN facilitation is to maintain the current plant community composition and structure, acting as a negative feedback to ecosystem change. As environmental conditions for the plant community worsen, MN facilitation increases (as per the stress-gradient hypothesis) and its feedback to larger scale processes is increasingly negative; that is, the strength of MN facilitation increases as environmental conditions deteriorate, until such a point when environmental conditions are so severe that MN facilitation fails (dashed line at right). Moving left from zero, the plant community experiences ameliorating environmental conditions (e.g., increased precipitation in a previously drought-limited plant community). This plant community is now released from its limitation, yet all above

and belowground characteristics inherent to the community are intact, including plant traits affecting resource acquisition (e.g., leaf area, root surface area). Thus, as the limitation is removed, source-sink gradients that affect MN transfer (e.g., light availability) increase, increasing resource acquisition by networked individuals and enhancing their competitive success relative to non-networked plants. This process changes the structure of the plant community, and acts as a positive feedback to ecosystem change. This process cannot, however, continue indefinitely. As environmental conditions continue to improve, competitive interactions among plants are enhanced until a new stability domain is achieved (dashed line at left).

Climate change is increasing the severity of temporal variation in environments where many plants grow. This will alter the source-sink gradients driving nutrient transfer through MNs, and the balance of competitive and facilitative plant interactions in ecosystems. Where MN facilitation creates negative feedbacks among plants, plant communities will be stabilized. Where MN facilitation creates positive feedbacks between plants, community structure will destabilize, ultimately leading to greater ecosystem change. In the following sections, we consider how nutrient transfer through MNs may act as a negative or positive feedback to ecosystem change (Box 6).

MNs help to maintain ecosystem states through negative feedback

In species-rich ecosystems, MN facilitation among cooperative guilds can help to modulate plant competitive interactions and stabilize plant community dynamics. For example, access to an MN altered the outcome of root competition among over- and understory species in a mixed temperate forest dominated by EM tree species (Booth, 2004). While MN access had negative effects on the survival of the AM species, *Acer rubrum*, it had neutral effects on the survival of three EM species, *B. allegheniensis*, *T. canadensis* and *P. strobus*, and positive effects on the growth of *P. strobus* (Booth, 2004). These results suggest that MN facilitation may promote coexistence of compatible tree species over time, by limiting the effects of size-asymmetric competition, and inhibiting the encroachment of incompatible species in the stand.

Mycorrhizal networks contribute to forest resilience through their role in regeneration following disturbance. In a dry *P. menziesii* var. *glauca* forest that had been partially cut, conspecific seedlings planted within the MN of retained mature trees had greater survival rates and reduced water stress than those that were isolated. Seedling establishment was particularly enhanced at intermediate distances from the mature trees, but suppressed under the crown due to root competition (Teste et al., 2009; Bingham and Simard, 2011). Thus, MN facilitation can enhance seedling establishment in disturbed forests, promoting forest self-regeneration and acting as a negative feedback to ecosystem change.

MNs act to enhance ecosystem change through positive feedbacks

When linking into an MN enhances the performance of networked individuals they are likely to compete successfully with non-networked plants. In this way, MN facilitation may

Box 6. Mycorrhizal networks may act to conserve the state of an ecosystem or to enhance ecosystem change.

(I) MNs act as a negative feedback to ecosystem change in Douglas-fir forests

As predicted by the stress-gradient hypothesis, MNs appear to facilitate establishment of new seedlings more strongly in dry than moist environments (Maestre et al., 2009). Bingham and Simard (2012) found that network facilitation of *P. menziesii* var. *glauca* seedling establishment increased with climatic aridity (see Box 4). Thus, MN facilitation acted to extend the niche breadth of interior Douglas-fir seedlings in the very dry climate. As seedling density increases, competition and density-dependent mortality provide additional negative feedbacks that stabilize the forest community (Simard, 2009). These patterns agree with theoretical models showing that positive or mutualistic interactions dominate in poor habitat qualities and that the fraction of expressed mutualisms decreases at the expense of competition in higher habitat qualities (Filotas et al., 2010). Based on these observations, we expect that facilitation via MNs will become increasingly critical to the stability of ecosystems as climate warming increases the severity and duration of drought in continental regions.

(II) MNs act as a positive feedback to ecosystem change in Arctic tundra

In Alaskan Arctic tundra, where regional rates of warming are the highest globally (IPCC, 2007), environmental conditions that have historically limited plant growth are rapidly ameliorating. These changes are associated with enhanced competition, growth and spread of the rhizomatous EM shrub *Betula nana* (Bret-Harte et al., 2001). Warming alters the physiology of *B. nana* by enhancing its photosynthetic yield and leading to significantly higher leaf C:N ratios as growth becomes increasingly N-limited (Natali et al., 2011). When warmed, *B. nana* reallocates its excess C to EM fungal species with high-biomass growth forms, longer-distance exploration strategies, and enhanced capacities to degrade complex organic matter, thus securing access to limiting N to grow (Deslippe et al., 2011). These fungi are likely to form large MNs connecting multiple *B. nana* individuals. Indeed, enhanced competition by *B. nana* is affected in part by its ability to transfer large quantities of photosynthate belowground through rhizomes and MNs. While interspecific C transfer among plants was not observed, intraspecific C transfer among *B. nana* plants through MNs was more than 4 % of the donor's net photosynthesis (Deslippe and Simard, 2011). C transfer increases with ambient temperature among conspecific *B. nana* pairs, suggesting that warming enhances conspecific facilitation and interspecific competition by *B. nana*. This contributes to ecosystem change in Arctic regions by promoting the conversion of tundra landscapes to shrub-lands as climate warms (Deslippe and Simard, 2011). Shrub-invaded tundra has a lower surface albedo than the tussock tundra vegetation it replaces, and the increased latent heat flux it affects is expected to have further feedbacks to climate, significantly increasing regional summer temperatures (Chapin et al., 2005). Thus, the role of MN facilitation in a plant community can shift over a gradient of environmental severity to enhance competitive plant interactions. In tundra, this appears to create a positive feedback loop that destabilizes the plant community and amplifies ecosystem change through alterations of the surface albedo of the ecosystem.

act to increase competition at the community level. Examples of this arise under good or ameliorating environmental conditions. For example, access to MNs enhanced seedling growth and survival in Guinean tropical forests, and survivorship of wild seedlings was positively associated with proximity to a conspecific adult (McGuire, 2007). These results suggest that MN facilitation acts to enhance competitive ability of networked EM species, which may lead to the competitive exclusion of non-networked species and drive the formation of mono-dominant EM stands in tropical forests (McGuire, 2007). In extreme cases, MN facilitation may be limited to a single plant species, and nutrient transfer through the MN may enhance competitive ability of this species alone (Deslippe and Simard, 2011). Provided it is the dominant feedback mechanism operating, where MN facilitation enhances competition by a single species, it will destabilize plant community structure and act as a positive feedback to ecosystem change.

5. Modelling the spatial structure and temporal dynamics of MNs

Spatial structure

Spatial structure is an intrinsic property of MNs at all levels of organization, from the architecture of plant roots and fungal mycelial systems, to the patterned dispersal of seeds and spores across the landscape. Networking plants and fungi represents a diverse mosaic of forms and functions that overlay heterogeneous biogeoclimatic conditions. The result is a nested, modulated hierarchy of discreet and continuous spatial patterns comprising plants and fungi interacting with each other, other organisms and with their above and below-ground environments across multiple scales. It is important to account for these spatial dependencies when making

predictions or testing hypotheses related to MN patterns and processes, either explicitly in models or by addressing the effects of spatial structure *a priori* (Legendre *et al.*, 2002; Fortin and Dale, 2005). Depending on the research objectives, there are numerous mathematical approaches for detecting and modelling MN spatial patterns, the full range of which is beyond the scope of this review. Likewise, there are a variety of methods for integrating spatial structure into theoretical or analytical models to relate MN spatial patterns to the processes generating them. Additional information on spatial analysis methods relevant to the study of MNs can be found elsewhere (Fortin and Dale, 2005; Zuur *et al.*, 2009).

The spatial topology of MNs is a foundational aspect of their architecture, yet remains largely unknown due to difficulties in sampling and identifying them with adequate resolution. Recent advances in molecular identification techniques have helped to overcome these limitations, especially regarding the use of genotype-specific markers to track networking plants and fungal genets across space (Lian *et al.*, 2006; Beiler *et al.*, 2010; Grelet *et al.*, 2010; Bahram *et al.*, 2011) (see Section 2 and Box 5). Nonetheless, describing MNs typically requires trade-offs between sampling extent and resolution (i.e., grain), which must be addressed *a priori* based on known spatial traits of the system and its components (e.g., size of individual root systems and fungal genets as well as their corresponding population structures) and the research objectives or hypotheses to be tested (Pickles *et al.*, 2010). As a result of sampling limitations, MN studies invariably impose boundaries on otherwise 'open' systems in terms of space, time and complexity (Fortin and Dale, 2005). This warrants careful consideration of sampling strategies to minimize

potential biases or 'edge effects' on spatial measures imposed by the size and shape of sampling plots.

Regardless of the sampling strategy, the structural modelling of MNs typically involves some form of spatial interpolation (point to surface pattern transformations, trend surface analysis, proximity or overlap analysis, inverse distance weighting or kriging techniques) (Fortin and Dale, 2005; Pickles *et al.*, 2010). Examples of spatial measures related to MN components include the three-dimensional spatial coordinates of samples or centroids of sample clusters, geometric area of habitat patches or sample clusters (e.g., based on Delaunay triangulations) or topological and Euclidean distances or least-cost paths between points. These may be mapped directly, included as an explanatory variable in predictive models, or incorporated into the error variance/covariance structure of models to account for sample autocorrelation or confounding effects of spatial non-independence.

Network models provide a comprehensive framework for the visualization and analysis of MN spatial dynamics, for elucidating the relationships between MN structure and functioning, or for incorporation of MN spatial dynamics into other models (Fortin and Dale, 2005) [Box 7]. For example, the degree of connectivity between two networking plants or fungal nodes and the spatial and physical attributes of links can be used to measure the type, volume, direction or rate of material flow between the nodes. Nodes are points (trees or mycelia) joined by a physical, functional, or physiological link or pathway. Links can be fungal mycelia and rhizomorphs, or trees, respectively. Material flows between nodes can be examined directly within the network analytical framework

Box 7. Mycorrhizal networks as spatial graphs.

Network analysis, based on the principles of graph theory, provides a template for cataloguing the complex patterns and processes associated with MNs. Here, individuals, species or species guilds can be modelled as nodes linked through their ecological associations (Bascompte, 2009; Beiler *et al.*, 2010) (see Sections 2 and 4).

Most biological networks have regular, random or scale-free structures depending on the density and distribution of links among nodes. In both regular and random networks, links tend to distribute equally among nodes, but the topology of regular networks is generally more cliquish and harder to traverse than random networks. In scale-free networks, some nodes (i.e., hubs) are highly linked and more central to the network, resulting in a skewed or power law node degree distribution (Albert *et al.*, 2000; Bray, 2003; Selosse *et al.*, 2006). Scale-free networks are both cliquish and easily traversed, and tend to be more robust to perturbations than regular or random networks. For example, the random deletion of a node would have little effect on the overall connectivity of the network, unless hubs were specifically targeted for removal (Albert *et al.*, 2000; Bray, 2003). Weighted scale-free networks, where links are weighted according to the frequency of loops, have been modelled to be the functionally most efficient network structure in resource transfer behaviour (Heaton *et al.*, 2012).

The diversity of autecological traits among networking plants and fungi collectively leads to complex, hierarchically structured MNs at the community level. This complexity may be analytically deconstructed based on the spatial properties of and relationships between nodes or by the attributes of links between nodes (Beiler *et al.*, 2010). In this regard, network models provide a means for studying the structure and function of MNs as part of complex adaptive systems (Parrott, 2010).

One of the principle advantages of network models is their flexibility to accommodate differing perspectives and levels of complexity within the same analytical template. An incidence matrix with plants on one axis and fungi on another can be used to model their pairwise associations as a simple undirected network, with spatial coordinates included as vectors to produce spatially explicit or implicit models. This basic template is equally applicable whether the units of interest are a single plant and fungal genet, or networking plant and fungal populations, communities, meta-populations or meta-communities.

or by incorporating these measures into corresponding functional models (cost-benefit analysis, economic market models, profile analysis, competition-facilitation and other feedback models, reaction-diffusion equations, trophic networks or other matrix models). In addition, reduced network models can be directly nested within more inclusive network constructs (Urban et al., 2009). For example, a guild of networking plants and fungi may be represented by a single node in a meta-community, trophic network or meta-network.

MNs can be modelled from the 'phytcentric' or 'myco-centric' perspective (with either plants or fungi as nodes, respectively), or with both plants and fungi as nodes linked through their affiliations in a bipartite network model (Selosse et al., 2006). In each of these perspectives qualitative or quantitative features such as taxonomic affiliation, age, longevity, body size or growth rate may be assigned to nodes for marked process network analysis. This may be particularly useful for determining substructures within MNs (e.g., critical elements or processes generating the structure) or classifying nodes based on their affiliations (e.g., delineating population and community boundaries, functional groups, etc.). This approach can also be used to accommodate special circumstances such as direct root grafting between plants or non-self anastomosis among AM mycelia systems. Network links are also qualitatively and quantitatively amenable. They can be given weights or direction, and their topology may be spatially explicit (e.g., the actual route traversed between nodes), implicit (e.g., Euclidean distances between spatially fixed nodes) or aspatial (e.g., representing affiliations or flow between individuals, groups or landscape patches).

Although we emphasize the applicability of network analysis for modelling MN spatial dynamics, it is far from being the only approach available. Techniques such as autoradiography (Wu et al., 1999), environmental scanning electron microscopy (He et al., 2005) or high-throughput image analysis (Heaton et al., 2012) may be used to visualize MNs in experimental microcosms (see Sections 2 and 3), while enzymatic imprinting (Dong et al., 2007), quantum dot imaging (Whiteside et al., 2009), 'micromapping' or contiguously sampled lattice designs (Zhou and Hogetsu, 2002) can be used to explicitly map MN topologies in natural conditions. The spatial dynamics of MNs can be studied using trend surface analysis, cluster analysis, point- or polygon-based proximity and overlap statistics, or dynamic growth and cellular automata models (Fortin and Dale, 2005; Pickles et al., 2010). These represent only a small sample of methods that can be applied to empirical studies of MN spatial structure. Regardless of the methods used, valuable insights may be gained from the study of MN spatial structure and from the incorporation of these patterns into theoretical and analytical models of MN ecology and evolution.

Temporal dynamics

Mechanistic modelling

Mathematical modelling can pinpoint which of the various processes operating in belowground C and nutrient transfers

are important. Very little temporal modelling of C and nutrient exchanges via MNs has been attempted. However, some currently used models, primarily the "Mycorrhizal Status, C and Nutrient Cycling" (MySCaN) model could form the basis of an MN nutrient exchange model (Orwin et al., 2011). The MySCaN simulates C and nutrient cycling through various pools on a daily basis and could include the cycling through MNs. Co-varying effects of factors (soil fertility, soil biota composition) can potentially be disentangled by MySCaN and provide better insights into ecosystem functioning (Orwin et al., 2011). There is a suite of relevant models that could also be modified to study the role of MNs in transfer of nutrients through time, such as the mechanistic system dynamics models (Brennan and Shelley, 1999), pulse-reserve models where episodic precipitation events stimulate biological activity, a Threshold-Delay Nutrient Dynamics (TDND) model (Collins et al., 2008), and nutrient-uptake models developed for mycorrhizal fungi (Deressa and Schenk, 2008).

Mycorrhizal network-derived C and nutrients depend on multiple interacting factors (plant, fungal and soil processes). Many of these factors have not been studied; hence a mechanistic model (one that simulates the effects of plant, fungi and soil processes on C gain via MNs) is not expected to make accurate predictions (Jones et al., 2009). A basic model could, however, provide a better understanding of temporal nutrient exchange concentrations and rates (Darrach et al., 2006). Mechanistic models for providing information about key processes expressed as mathematical equations at various time intervals. A simplified mathematical model with the use of quasi-steady-state approximations could be used to provide biologically plausible processes involved in MN growth over time (Jeger et al., 2008). Furthermore, important questions related to the ecology of MNs could be addressed with the theoretical framework of mathematical models. For example, dynamic models could answer questions related to MN re-establishment after perturbation, C flux and growth of MNs in C-limited systems. Mathematical modelling of MN growth can also be an insightful addition to experimental studies, as more focus can be placed on the fundamental properties of MN growth and expansion, ultimately generating testable hypotheses.

Statistical modelling

Carbon availability in plants connected by an MN is expected to be temporally heterogeneous as it is ultimately driven by the dynamic nature of photosynthesis and C allocation to roots. More realistic microcosm and field experiments investigating the synergy between multiple factors (including seasonality) set up as multi-factorial designs conducive for structural equation modelling (SEM) are needed (Klironomos et al., 2011). Structural equation modelling was used to determine the seasonal changes in environmental factors that affect rhizomorph production (Hasselquist et al., 2010) and we suggest a similar approach to better understand MN expansion through time. For example, SEM could be used for analysing field experiments where EM plant species are added sequentially through time (i.e., plant establishment order) (Hausmann and Hawkes, 2010) to determine if more complex MNs arise and whether this influences C transfer magnitude in the presence of multiple environmental factors.

Information theoretics (model selection and multimodel inference) is another statistical approach that could be applied with similar intentions as SEM (Anderson, 2008). With a candidate set of models constructed *a priori*, time can be included as a leading factor with the most relevant abiotic and biotic factors regulating MN-facilitated nutrient transfer. Such an approach would highlight the relative importance of time and produce a list of ranked models that could be used for making simple temporal predictions of MN functioning.

Mycorrhizal networks as agents of complex adaptive systems

Ecological theory that ecosystems can be represented by energy and material flows through interacting parts provides a conceptual model for MNs compatible with complex adaptive systems (CAS) theory (Levin, 2005). In CAS, ecosystems are modelled as adaptive dynamic networks of interacting parts where feedbacks and cross-scale interactions lead to self-organization and emergent properties (Bascompte, 2009; Parrott, 2010). The spatial and temporal patterns in ecosystems have commonly been modelled as networks, and usually have been characterized as complex with small-world properties using graph theory (see Section 5). In CAS theory, non-linear, scale-free (or power law) topology and behaviour, where there are many small nodes and a few large hubs, is a fundamental characteristic of self-organization (Sole *et al.*, 2002); this is because most systems evolve towards this critical fractal structure that is resilient and self-reinforcing (Perry *et al.*, 2011). The scale-free topology of MNs (Beiler *et al.*, 2010) (see Sections 2 and 5) and fractal structure of the interconnecting mycelia (Heaton *et al.*, 2012) are, thus, consistent with self-organization in CAS, where mycorrhizal colonization and nutrient fluxes through the MN provide feedbacks (positive or negative) to plants that can influence the stability of the ecosystem (see Section 4). Mycorrhizal networks can thus be considered fundamental agents of self-organization in ecosystems because they provide direct avenues through which cross-scale interactions and feedbacks are played out (Simard, 2009). They can be considered central to the organization of most terrestrial ecosystems because of their critical, obligate role in the establishment of most plants, which themselves are foundational. A meta-modelling approach can be used to model the cross-scale interactions between MNs and other networks in ecosystems (e.g., food webs, nest webs, riparian networks, landscape patterns), to improve our understanding of internal organization, outside influences, feedbacks and non-linear dynamics that are characteristics of CAS.

A fundamental property of MNs as agents of CAS is that the parts (e.g., plant and fungal species) are subject to selective pressures through localized interactions with each other, other parts and processes, leading to local adaptation and influence on the functioning of the network (Sole *et al.*, 2002). The local, bottom-up, iterative development of nodes and links through differential growth, strengthening and weakening (e.g., self-thinning or pruning of trees or fungi) that is characteristic of MNs (Heaton *et al.*, 2012) is also a fundamental feature of CAS. These behaviours and interactions of the network parts influence the whole MN. Thus,

modelling the dynamic interactions and selection pressures in networks will help us understand the dynamics and resilience of ecosystems under changing environments, such as global change. Analysis and modelling the spatial configuration and temporal dynamics of networks within the framework of CAS theory can thus be useful for conservation management if the long-term objectives are to maintain resilient ecosystems or assist in re-organization of novel ones that are productive, adaptive and resilient. For example, identification of hubs (individuals or species of plants or fungi), the connective links or overlapping components in the MN, and the critical rates, inflections, or processes (e.g., thresholds of colonization or nutrient flow for plant establishment) are important in models for ecosystem dynamics and in developing criteria for conservation management decisions.

6. Conclusions

1. The existence of MNs was originally based primarily on specificity phenomena estimated from mycorrhizal morphotypes, but it is now supported by physical, physiological and molecular evidence for a wide range of ecosystems. High resolution models of MN topology are now being developed based on genotype-specific markers and network analysis. Carbon, nutrients, water, defence signal and allelochemical fluxes have also been examined using isotope, dye and model chemical tracers, quantum dots, mesh and metal barriers, high resolution imaging and gene expression.
2. The occurrence of mycoheterotrophy indicates that MNs can sustain the life of some plant species. Mycoheterotrophic plants acquire all their C from MNs and partial MH plants can gain up to 85 %. Autotrophic plants appear to gain much less (up to 9.5 %). Light appears to be an important driver of C transfer along source-sink gradients in autotrophic plants but also in partial MH plants within the same ecosystem.
3. Facilitation of mycorrhizal colonization and establishment or growth of autotrophic plants by MNs have been demonstrated in a wide range of ecosystems, including forest, woodland and grassland. MNs facilitate transfer of C, nutrients, water, defence signals and allelochemicals, but how these affect autotrophic plant establishment, growth, health or fitness is not well understood.
4. Mycorrhizal networks have been shown in some cases to influence plant interactions (facilitation and competition), forest regeneration or plant dominance; however, their net effects on ecosystem diversity, productivity or stability are poorly understood. In some systems, MNs appear to play important roles in facilitation and competition processes that stabilize ecosystems, but in others they can provide avenues for positive feedbacks that may destabilize ecosystems.
5. Network analysis using graph theory is a good approach for modelling the spatial topology of MNs, and can be used to understand interactions, feedbacks and system stability. Temporal modelling of MNs and their effects

on ecosystem processes is at its infancy but the mechanistic model MySCaN is a good starting point. The spatial and temporal patterns of MNs are consistent with CAS theory, and MNs can thus be included in larger CAS models for modelling ecosystem behaviour under changing environmental conditions.



Acknowledgements

Much of our own research discussed in this paper was conducted as PhD dissertation research in the Forest Sciences Department at The University of British Columbia. We thank the many assistants and countless others who provided support for our research. We are particularly grateful for many discussions held in committee meetings or in the field or lab with Daniel Durall, Melanie Jones, Robert Guy, Shannon Berch, Marty Kranabetter, Brendan Twieg, Jason Barker, Shannon Guichon, Bill Mohn, Valerie LeMay, Sally Aitken, Sue Grayston, John Hobbie and Gaius Shaver. We also very much appreciate the insightful suggestions for improving the manuscript by the Executive Editor, Lynne Boddy. This work was supported by the Natural Sciences and Engineering Research Council of Canada (NSERC).

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.
- Aitken, S.N., Yeaman, S., Holliday, J.A., Wang, T., Curtis-McLane, S., 2008. Adaptation, migration or extirpation: climate change outcomes for tree populations. *Evol. Appl.* 1, 95–111.
- Albert, R., Hawoong, J., Barabasi, A.-L., 2000. Error and attack tolerance of complex networks. *Nature* 406, 542.
- Allen, M.F., 2007. Mycorrhizal fungi: highways for water and nutrients in arid soils. *Vadose Zone J.* 6, 291–297.

- Amend, A., Keeley, S., Garbelotto, M., 2009. Forest age correlates with fine-scale spatial structure of Matsutake mycorrhizas. *Mycol. Res.* 113, 541–551.
- Anderson, D.R., 2008. *Model Based Inference in the Life Sciences: A Primer on Evidence*. Springer, New York.
- Bahram, M., Pölme, S., Köljalg, U., Tedersoo, L., 2011. A single European aspen (*Populus tremula*) tree individual may potentially harbour dozens of *Cenococcum geophilum* ITS genotypes and hundreds of species of ectomycorrhizal fungi. *FEMS Microbiol. Ecol.* 75, 313–332.
- Barto, E.K., Hilker, M., Muller, F., Mohney, B.K., Weidenhamer, J.D., Rillig, M.C., 2011. The fungal fast land: common mycorrhizal networks extend bioactive zones of allelochemicals in soils. *PLoS ONE* 6, e27195.
- Bascompte, J., 2009. Mutualistic networks. *Front. Ecol. Environ.* 7, 429–436.
- Beiler, K.J., Durall, D.M., Simard, S.W., Maxwell, S.A., Kretzer, A.M., 2010. Architecture of the wood-wide web: *Rhizopogon* spp. genets link multiple Douglas-fir cohorts. *New Phytol.* 185, 543–553.
- Bidartondo, M.I., 2005. The evolutionary ecology of myco-heterotrophy. *New Phytol.* 167, 335–352.
- Bingham, M.A., Simard, S.W., 2012. Mycorrhizal networks affect ectomycorrhizal fungal community similarity between conspecific trees and seedlings. *Mycorrhiza*. doi: 10.1007/s00572-011-0406-y.
- Bingham, M.A., Simard, S.W., 2011. Do mycorrhizal network benefits to survival and growth of interior Douglas-fir seedlings increase with soil moisture stress? *Ecol. Evol.* 1, 306–316.
- Bingham, M.A., Simard, S.W., 2012. Ectomycorrhizal networks of old *Pseudotsuga menziesii* var. *glauca* trees facilitate establishment of conspecific seedlings under drought. *Ecosystems* 15, 188–199.
- Booth, M.G., Hoeksema, J.D., 2010. Ectomycorrhizal networks counteract competitive effects of canopy trees on seedling survival. *Ecology* 91, 2294–2302.
- Booth, M.G., 2004. Mycorrhizal networks mediate overstorey–understorey competition in a temperate forest. *Ecol. Lett.* 7, 538–546.
- Bougoure, J.J., Brundrett, M.C., Grierson, P.F., 2010. Carbon and nitrogen supply to the underground orchid, *Rhizanthella gardneri*. *New Phytol.* 186, 947–956.
- Bray, D., 2003. Molecular networks: the top-down view. *Science* 301, 1864–1865.
- Brennan, M.A., Shelley, M.L., 1999. A model of the uptake, translocation, and accumulation of lead (Pb) by maize for the purpose of phytoextraction. *Ecol. Eng.* 12, 271–297.
- Bret-Harte, M.S., Shaver, G.R., Zoerner, J.P., Johnstone, J.F., Wagner, J.L., Chavez, A.S., Gunkelman IV, R.F., Lippert, S.C., Laundre, J.A., 2001. Developmental plasticity allows *Betula nana* to dominate tundra subjected to an altered environment. *Ecology* 82, 18–32.
- Brooks, R., Meinzer, F.C., Warren, J.M., Domec, J.-C., Coulombe, R., 2006. Hydraulic redistribution in a Douglas-fir forest: lessons from system manipulations. *Plant Cell Environ.* 29, 138–150.
- Butterfield, B.J., 2009. Effects of facilitation on community stability and dynamics: synthesis and future directions. *J. Ecol.* 97, 1192–1201.
- Cameron, D.D., Preiss, K., Gebauer, G., Read, D.J., 2009. The chlorophyll-containing orchid *Corallorhiza trifida* derives little carbon through photosynthesis. *New Phytol.* 183, 358–364.
- Chapin III, F.S., Sturm, M., Serreze, M.C., McFadden, J.P., 2005. Role of land-surface changes in Arctic summer warming. *Science* 310, 657–660.
- Collins, S.L., Sinsabaugh, R.L., Crenshaw, C., Green, L., Porras-Alfaro, A., Stursova, M., Zeglin, L.H., 2008. Pulse dynamics and microbial processes in aridland ecosystems. *J. Ecol.* 96, 413–420.
- Courty, P.-E., Walder, F., Boller, T., Ineichen, K., Wiemken, A., Rousteau, A., Selosse, M.-A., 2011. Carbon and nitrogen metabolism in mycorrhizal networks and mycoheterotrophic plants of tropical forests: a stable isotope analysis. *Plant Physiol.* 156, 952–961.
- Croll, D., Giovannetti, M., Koch, A.M., Sbrana, C., Ehinger, M., Lammers, P.J., Sanders, I.R., 2009. Nonself vegetative fusion and genetic exchange in the arbuscular mycorrhizal fungus *Glomus intraradices*. *New Phytol.* 181, 924–937.
- Darrah, P.R., Jones, D.L., Kirk, G.J.D., Roose, T., 2006. Modelling the rhizosphere: a review of methods for ‘upscaling’ to the whole-plant scale. *Eur. J. Soil Sci.* 7, 13–25.
- Deressa, T.G., Schenk, M.K., 2008. Contribution of roots and hyphae to phosphorus uptake of mycorrhizal onion (*Allium cepa* L.)—A mechanistic modeling approach. *J. Plant Nutr. Soil Sci.* 17, 810–820.
- Deslippe, J.R., Hartmann, M., Mohn, W.W., Simard, S.W., 2011. Long-term experimental manipulation of climate alters the ectomycorrhizal community of *Betula nana* in Arctic tundra. *Glob. Change Biol.* 17, 1625–1636.
- Deslippe, J.R., Simard, S.W., 2011. Below-ground carbon transfer among *Betula nana* may increase with warming in Arctic tundra. *New Phytol.* 192, 689–698.
- Dickie, I.A., Guza, R.C., Krazewski, S.E., Reich, P.B., 2004. Shared ectomycorrhizal fungi between a herbaceous perennial (*Helianthemum bicknellii*) and oak (*Quercus*) seedlings. *New Phytol.* 164, 375–382.
- Dickie, I.A., Schnitzer, S.A., Reich, P.B., Hobbie, S.E., 2005. Spatially disjunct effects of co-occurring competition and facilitation. *Ecol. Lett.* 8, 1191–1200.
- Dong, S., Brooks, D., Jones, M.D., Grayston, S.J., 2007. A method for linking in situ activities of hydrolytic enzymes to associated organisms in forest soils. *Soil Biol. Biochem.* 39, 2414–2419.
- Eason, W.R., Newman, E.I., Chuba, P.N., 1991. Specificity of interplant cycling of phosphorus: the role of mycorrhizas. *Plant Soil* 137, 267–274.
- Egerton-Warburton, L.M., Querejeta, J.I., Allen, M.F., 2007. Common mycorrhizal networks provide a potential pathway for the transfer of hydraulically lifted water between plants. *J. Exp. Bot.* 58, 1473–1483.
- Ferguson, B.A., Dreisbach, T.A., Parks, C.G., Filip, G.M., Schmitt, C.L., 2003. Coarse-scale population structure of pathogenic *Armillaria* species in a mixed-conifer forest in the Blue Mountains of northeast Oregon. *Can. J. For. Res.* 33, 612–623.
- Filotas, E., Grant, M., Parrott, L., Rivkold, P.A., 2010. The effect of positive interactions on community structure in a multi-species metacommunity model along an environmental gradient. *Ecol. Modell.* 221, 885–894.
- Finlay, R.D., 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.
- Fitter, A.H., Hodge, A., Daniell, T.J., Robinson, D., 1999. Resource sharing in plant–fungus communities: did the carbon move for you? *Trends Ecol. Evol.* 14, 70–71.
- Fortin, M., Dale, M.R.T., 2005. *Spatial Analysis: A Guide for Ecologists*. Cambridge University Press, Cambridge, UK.
- Gai, J., Christie, P., Cai, X., Fan, J., Zhang, J., Feng, G., Li, X., 2009. Occurrence and distribution of arbuscular mycorrhizal fungal species in three types of grassland community of the Tibetan Plateau. *Ecol. Res.* 24, 1345–1350.
- 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.
- Girlanda, M., Segreto, R., Cafasso, D., Liebel, H.T., Rodda, M., Ercole, E., Perotto, S., 2011. Photosynthetic Mediterranean

- meadow orchids feature partial mycoheterotrophy and specific mycorrhizal associations. *Am. J. Bot.* 98, 1148–1163.
- Golotte, A., van Tuinen, D., Atkinson, D., 2004. Diversity of arbuscular mycorrhizal fungi colonising roots of the grass species *Agrostis capillaris* and *Lolium perenne* in a field experiment. *Mycorrhiza* 14, 111–117.
- Grelet, G.-A., Johnson, D., Vrålstad, T., Alexander, I.J., Anderson, I.C., 2010. New insights into the mycorrhizal *Rhizoscypha ericae* aggregate: spatial structure and co-colonization of ectomycorrhizal and ericoid roots. *New Phytol.* 188, 210–222.
- Hasselquist, N.J., Vargas, R., Allen, M.F., 2010. Using soil sensing technology to examine interactions and controls between ectomycorrhizal growth and environmental factors on soil CO₂ dynamics. *Plant Soil* 331, 17–29.
- Hausmann, N.T., Hawkes, C.V., 2010. Order of plant host establishment alters the composition of arbuscular mycorrhizal communities. *Ecology* 91, 2333–2343.
- Hawkes, C., Hartley, I.P., Ineson, P., Fitter, A.H., 2008. Soil temperature affects carbon allocation within arbuscular mycorrhizal networks and carbon transport from plant to fungus. *Glob. Change Biol.* 14, 1181–1190.
- He, X., Critchley, C., Ng, H., Bledsoe, C., 2005. Nodulated N₂-fixing *Casuarina cunninghamiana* is the sink for net N transfer from non-N₂-fixing *Eucalyptus maculata* via an ectomycorrhizal fungus *Pisolithus* sp. using ¹⁵NH₄⁺ or ¹⁵NO₃⁻ supplied as ammonium nitrate. *New Phytol.* 167, 897–912.
- Heaton, L., Obara, B., Grau, V., Jones, N., Nakagaki, T., Boddy, L., Fricker, M.D., 2012. Analysis of fungal networks. *Fungal Biology Reviews* 26, 12–29.
- Hijri, M., Sanders, I.R., 2005. Low gene copy number shows that arbuscular mycorrhizal fungi inherit genetically different nuclei. *Nature* 433, 160–163.
- Hobbie, E., Agerer, R., 2010. Nitrogen isotopes in ectomycorrhizal sporocarps correspond to belowground exploration types. *Plant Soil* 327, 71–83.
- Hoeksema, J.D., 2010. Ongoing coevolution in mycorrhizal interactions. *New Phytol.* 187, 286–300.
- Hortal, S., Pera, J., Parladé, J., 2008. Tracking mycorrhizas and extraradical mycelium of the edible fungus *Lactarius deliciosus* under field competition with *Rhizopogon* spp. *Mycorrhiza* 18, 69–77.
- Horton, T.R., Bruns, T.D., 2001. The molecular revolution in ectomycorrhizal ecology: peeking into the black-box. *Mol. Ecol.* 10, 1855–1871.
- Horton, T.R., Bruns, T.D., Parker, V.T., 1999. Ectomycorrhizal fungi associated with *Arctostaphylos* contribute to *Pseudotsuga menziesii* establishment. *Can. J. Bot.* 77, 93–102.
- Hynson, N.A., Bruns, T.D., 2010. Fungal hosts for mycoheterotrophic plants: a nonexclusive, but highly selective club. *New Phytol.* 185, 598–601.
- IPCC, 2007. Synthesis report. In: Pachauri, R.K., Reisinger, A. (Eds.), Contribution of Working Groups I, II and III to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change Core Writing Team. IPCC, Geneva, Switzerland, p. 104.
- Jeger, M.J., Lamour, A., Gilligan, C.A., Otten, W., 2008. A fungal growth model fitted to carbon-limited dynamics of *Rhizoctonia solani*. *New Phytol.* 178, 625–633.
- Jones, M.D., Durall, D.M., Cairney, J.W.G., 2003. Tansley review: ectomycorrhizal fungal communities in young stands regenerating after clearcut logging. *New Phytol.* 157, 399–422.
- Jones, D.L., Nguyen, C., Finlay, R.D., 2009. Carbon flow in the rhizosphere: carbon trading at the soil-root interface. *Plant Soil* 321, 5–33.
- Jumpponen, A., 2003. Soil fungal community assembly in a primary successional glacier forefront ecosystem as inferred from rDNA sequence analyses. *New Phytol.* 158, 569–578.
- Karst, J., Marzcek, L., Jones, M.D., Turkington, R., 2008. The mutualism-parasitism continuum in ectomycorrhizas: a quantitative assessment using meta-analysis. *Ecology* 89, 1032–1042.
- Kemppainen, M., Duplessis, S., Martin, F., Pardo, A.G., 2009. RNA silencing in the model mycorrhizal fungus *Laccaria bicolor*: gene knock-down of nitrate reductase results in inhibition of symbiosis with *Populus*. *Environ. Microbiol.* 11, 1878–1896.
- Kennedy, A.H., Taylor, D.L., Watson, L.E., 2011. Mycorrhizal specificity in the fully mycoheterotrophic *Hexaletris* Raf. (Orchidaceae: Epidendroideae). *Mol. Ecol.* 20, 1303–1316.
- Kiers, E.T., Duhamel, M., Beesetty, Y., Mensah, J.A., Franken, O., Verbruggen, E., Fellbaum, C.R., Kowalchuk, G.A., Hart, M.M., Bago, A., Palmer, T.M., West, S.A., Vandenkoornhuys, P., Jansa, J., Bücking, H., 2011. Reciprocal rewards stabilize cooperation in the mycorrhizal symbiosis. *Science* 330, 880–882.
- Klironomos, J., Zobel, M., Tibbett, M., Stock, W.D., Rillig, M.C., Parrent, J.L., Moora, M., Koch, A.M., Facelli, J.M., Facelli, E., Dickie, I.A., Bever, J.D., 2011. Forces that structure plant communities: quantifying the importance of the mycorrhizal symbiosis. *New Phytol.* 189, 366–370.
- Leake, J.R., Cameron, D.D., 2010. Physiological ecology of mycoheterotrophy. *New Phytol.* 185, 601–605.
- Leake, J.R., 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.
- Leake, J.R., 2005. Plants parasitic on fungi: unearthing the fungi in myco-heterotrophs and debunking the ‘saprophytic’ plant myth. *Mycologist* 19, 113–122.
- Legendre, P., Dale, M.R.T., Fortin, M.-J., Gurevitch, J., Hohn, M., Myers, D., 2002. The consequences of spatial structure for the design and analysis of ecological field surveys. *Ecography* 25, 601–615.
- Lehto, T., Zwiazek, J.J., 2011. Ectomycorrhizas and water relations of trees: a review. *Mycorrhiza* 21, 71–90.
- Lerat, S., Gauci, R., Catford, J., Vierheilig, H., Piché, Y., Lapointe, L., 2002. ¹⁴C transfer between the spring ephemeral *Erythronium americanum* and sugar maple saplings via arbuscular mycorrhizal fungi in natural stands. *Oecologia* 132, 181–187.
- Levin, S.A., 2005. Self-organization and the emergence of complexity in ecological systems. *BioScience* 55, 1075–1079.
- Lian, C.L., 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.
- Liebel, H.T., Bidartondo, M.I., Preiss, K., Segreto, R., Stöckel, M., Rodda, M., Gebauer, G., 2010. Carbon balance and allocation of assimilated CO₂ in Scots pine, Norway spruce, and Silver birch seedlings determined with gas exchange measurements and ¹⁴C pulse labelling. *Am. J. Bot.* 97, 903–912.
- Maestre, F.T., Callaway, R.M., Valladares, F., Lortie, C.J., 2009. Refining the stress-gradient hypothesis for competition and facilitation in plant communities. *J. Ecol.* 97, 199–205.
- Mangan, S.A., Herre, E.A., Bever, J.D., 2010. Specificity between Neotropical tree seedlings and their fungal mutualists leads to plant–soil feedback. *Ecology* 91, 2594–2603.
- Martin, F., Kohler, A., Murat, C., Balestrini, R., Coutinho, P.M., Jaillon, O., Wincker, P., 2010. Perigord black truffle genome uncovers evolutionary origins and mechanisms of symbiosis. *Nature* 464, 1033–1038.
- Martin, F., Stewart, G.R., Genetet, I., Le Tacon, F., 1986. Assimilation of ¹⁵NH₄ by beech (*Fagus sylvatica* L.) ectomycorrhizas. *New Phytol.* 102, 85–94.
- McGuire, K.L., 2007. Common ectomycorrhizal networks may maintain mono-dominance in a tropical rain forest. *Ecology* 88, 567–574.

- Merckx, V., Bidartondo, M.I., Hynson, N.A., 2009. Myco-heterotrophy: when fungi host plants. *Ann. Bot.* 104, 1255–1261.
- Molina, R., Massicotte, H., Trappe, J.M., 1992. Specificity phenomena in mycorrhizal symbioses: community-ecological consequences and practical implications. In: Allen, M.F. (Ed.), *Mycorrhizal Functioning: An Integrative Plant-fungal Process*. Chapman and Hall, London, pp. 357–422.
- Motomura, H., Selosse, M.-A., Martos, F., Kagawa, A., Yukawa, T., 2010. Mycoheterotrophy evolved from mixotrophic ancestors: evidence in *Cymbidium* (Orchidaceae). *Ann. Bot.* 106, 573–581.
- Nara, K., 2006. Ectomycorrhizal networks and seedling establishment during early primary succession. *New Phytol.* 169, 169–178.
- Näsholm, T., Ekblad, A., Nordin, A., Giesler, R., Högberg, M., Högberg, P., 1998. Boreal forest plants take up organic nitrogen. *Nature* 392, 914–916.
- Natali, S.M., Schuur, E.A.G., Trucco, C., Hicks Pries, C.E., Crummer, K.G., Baron Lopez, A.F., 2011. Effects of experimental warming of air, soil and permafrost on carbon balance in Alaskan tundra. *Glob. Change Biol.* 17, 1394–1407.
- Nehls, U., Mikolajewski, S., Magel, E., Hampp, R., 2001. Carbohydrate metabolism in ectomycorrhizas: gene expression, monosaccharide transport and metabolic control. *New Phytol.* 150, 533–541.
- Newman, E.I., 1988. Mycorrhizal links between plants: their functioning and ecological significance. *Adv. Ecol. Res.* 18, 243–270.
- Ogura-Tsujita, Y., Gebauer, G., Hashimoto, T., Umata, H., Yukawa, T., 2009. Evidence for novel and specialized mycorrhizal parasitism: the orchid *Gastrodia confusa* gains carbon from saprotrophic *Mycena*. *Proc. R. Soc. London, Ser. B* 276, 761–767.
- Onguene, N.A., Kuyper, T.W., 2002. Importance of the ectomycorrhizal network for seedling survival and ectomycorrhiza formation in rain forests of south Cameroon. *Mycorrhiza* 12, 13–17.
- Orwin, K.H., Kirschbaum, M.U.F., St John, M.G., Dickie, I.A., 2011. Organic nutrient uptake by mycorrhizal fungi enhances ecosystem carbon storage: a model-based assessment. *Ecol. Lett.* 14, 493–502.
- Parrott, L., 2010. Measuring ecological complexity. *Ecol. Indicat.* 10, 1069–1076.
- Perry, D.A., Hessburg, P.F., Skinner, C.N., Spies, T.A., Stephens, S.L., Taylor, A.H., Franklin, J.F., McComb, B., Riegel, G., 2011. The ecology of mixed severity fire regimes in Washington, Oregon, and Northern California. *For. Ecol. Manage.* 262, 703–717.
- Perry, D.A., 1995. Self-organizing systems across scales. *Trends Ecol. Evol.* 19, 241–244.
- Perry, D.A., 1998. A moveable feast: the evolution of resource sharing in plant-fungus communities. *Trends Ecol. Evol.* 13, 432–434.
- Philip, L.J., Simard, S.W., Jones, M.D., 2010. Pathways for below-ground carbon transfer between paper birch and Douglas-fir seedlings. *Plant Ecol. Divers.* 3, 221–233.
- Philip, L.J., 2006. Carbon Transfer between Ectomycorrhizal Paper Birch (*Betula papyrifera*) and Douglas-fir (*Pseudotsuga menziesii*). PhD thesis, UBC, Vancouver, Canada.
- Pickles, B.J., Genny, D.R., Potts, J.M., Lennon, J.J., Anderson, I.C., Alexander, I.J., 2010. Spatial and temporal ecology of Scots pine ectomycorrhizas. *New Phytol.* 186, 755–768.
- Pickles, B.J., Egger, K.N., Massicotte, H.B., Green, S.G., 2011. Mycorrhizas and climate change. *Fungal Ecol.* 5, 75–83.
- Pietikäinen, A., Kytöviita, M.-M., 2007. Defoliation changes mycorrhizal benefit and competitive interactions between seedlings and adult plants. *J. Ecol.* 95, 639–647.
- Plett, J.M., Kemppainen, M., Kale, S.D., Kohler, A., Legué, V., Brun, A., Tyler, B.M., Pardo, A.G., Martin, F., 2011. A secreted effector protein of *Laccaria bicolor* is required for symbiosis development. *Curr. Biol.* 21, 1197–1203.
- Post, E., Forchhammer, M.C., Bret-Harte, M.S., Callaghan, T.V., Christensen, T.R., Elberling, B., Fox, A.D., et al., 2009. Ecological dynamics across the Arctic associated with recent climate change. *Science* 325, 1355–1358.
- Preiss, K., Adam, I.K.U., Gebauer, G., 2010. Irradiance governs exploitation of fungi: fine-tuning of carbon gain by two partially myco-heterotrophic orchids. *Proc. R. Soc. B* 277, 1333–1336.
- Quejeta, J.F., Egerton-Warburton, L.M., Allen, M.F., 2003. Direct nocturnal water transfer from oaks to their mycorrhizal symbionts during severe soil drying. *Oecologia* 134, 55–64.
- Redecker, D., Szaro, T.M., Bowman, R.J., Bruns, T.D., 2001. Small genets of *Lactarius xanthogalactus*, *Russula cremoricolor* and *Amanita francheti* in late-stage ectomycorrhizal successions. *Mol. Ecol.* 10, 1025–1034.
- Richard, F., Millot, S., Gardes, M., Selosse, M.A., 2005. Diversity and specificity of ectomycorrhizal fungi retrieved from an old-growth Mediterranean forest dominated by *Quercus ilex*. *New Phytol.* 166, 1011–1023.
- Rillig, M.C., Mummey, D.L., 2006. Tansley review: Mycorrhizas and soil structure. *New Phytol.* 171, 41–53.
- Roy, M., Dubois, M.-P., Proffit, M., Vincenot, L., Desmarais, E., Selosse, M.-A., 2008. Evidence from population genetics that the ectomycorrhizal basidiomycete *Laccaria amethystina* is an actual multihost symbiont. *Mol. Ecol.* 17, 2825–2838.
- Rygielwicz, P.T., Anderson, C.P., 1994. Mycorrhizae alter quality and quantity of carbon allocated below ground. *Nature* 369, 58–60.
- Saari, S.K., Campbell, C.D., Russell, J., Alexander, I.J., Anderson, I.C., 2005. Pine microsatellite markers allow roots and ectomycorrhizas to be linked to individual trees. *New Phytol.* 165, 295–304.
- Saito, K., Suyama, Y., Sato, S., Sugawara, K., 2004. Defoliation effects on the community structure of arbuscular mycorrhizal fungi based on 18S rDNA sequences. *Mycorrhiza* 14, 363–373.
- Sanders, I.R., 2003. Preference, specificity and cheating in the arbuscular mycorrhizal symbiosis. *Trends Plant Sci.* 8, 143–145.
- Sbrana, C., Fortuna, P., Giovanetti, M., 2011. Plugging into the network: belowground connections between germlings and extraradical mycelium of arbuscular mycorrhizal fungi. *Mycologia* 103, 307–316.
- Schoonmaker, A.L., Teste, F.P., Simard, S.W., Guy, R.D., 2007. Tree proximity, soil pathways and common mycorrhizal networks: their influence on utilization of redistributed water by understory seedlings. *Oecologia* 154, 455–466.
- Selosse, M.-A., Richard, F., He, X., Simard, S.W., 2006. Mycorrhizal networks: *des liaisons dangereuses?* *Trends Ecol. Evol.* 21, 621–628.
- Selosse, M.-A., Roy, M., 2009. Green plants that feed on fungi: facts and questions about mixotrophy. *Trends Plant Sci.* 14, 64–70.
- Simard, S.W., Perry, D.A., Jones, M.D., Myrold, D.D., Durall, D.M., Molina, R., 1997. Net transfer of carbon between tree species with shared ectomycorrhizal fungi. *Nature* 388, 579–582.
- Simard, S.W., Austin, M.E., 2010. The role of mycorrhizas in forest soil stability with climate change. In: Simard, S.W. (Ed.), *Climate Change and Variability*. InTech, pp. 275–302. Chapter 15.
- Simard, S.W., Durall, D.M., 2004. Mycorrhizal networks: a review of their extent, function and importance. *Can. J. Bot.* 82, 1140–1165.
- Simard, S.W., 2009. The foundational role of mycorrhizal networks in the self-organization of interior Douglas-fir forests. *For. Ecol. Manage.* 258S, S95–S107.
- Smith, S.E., Read, D.J., 2008. *Mycorrhizal Symbiosis*, third ed. Academic Press, London.

- Sole, R.V., Ferrer-Cancho, R., Montoya, J.M., Valverde, S., 2002. Selection, tinkering and emergence in complex networks. *Complexity* 8, 20–33.
- Song, Y.Y., Zeng, R.S., Xu, J.F., Li, J., Shen, X., Yihdego, W.G., 2010. Interplant communication of tomato plants through underground common mycorrhizal networks. *PLoS ONE* 5, e13324.
- Tedersoo, L., Jairus, T., Horton, B.M., Abarenkov, K., Suvi, T., Saar, I., Kõljalg, U., 2008. Strong host preference of ectomycorrhizal fungi in a Tasmanian wet sclerophyll forest as revealed by DNA barcoding and taxon-specific primers. *New Phytol.* 180, 479–490.
- Tedersoo, L., Suvi, T., Beaver, K., Kõljalg, U., 2007. Ectomycorrhizal fungi of the Seychelles: diversity patterns and host shifts from the native *Vateriopsis seychellarum* (Dipterocarpaceae) and *Intsia bijuga* (Caesalpiniaceae) to the introduced *Eucalyptus robusta* (Myrtaceae), but not *Pinus caribea* (Pinaceae). *New Phytol.* 175, 321–333.
- Teste, F.P., Simard, S.W., Durall, D.M., Guy, R.D., Berch, S.M., 2010. Net carbon transfer between *Pseudotsuga menziesii* var. *glauca* seedlings in the field is influenced by soil disturbance. *J. Ecol.* 98, 429–439.
- Teste, F.P., Simard, S.W., Durall, D.M., Guy, R.D., Jones, M.D., Schoonmaker, A.L., 2009. Access to mycorrhizal networks and tree roots: importance for seedling survival and resource transfer. *Ecology* 90, 2808–2822.
- Teste, F.P., Simard, S.W., 2008. Mycorrhizal networks and distance from mature trees alter patterns of competition and facilitation in dry Douglas-fir forests. *Oecologia* 158, 193–203.
- Treseder, K.K., 2004. A meta-analysis of mycorrhizal responses to nitrogen, phosphorus, and atmospheric CO₂ in field studies. *New Phytol.* 164, 347–355.
- Tuffen, F., Eason, W.R., Scullion, J., 2002. The effect of earthworms and arbuscular mycorrhizal fungi on growth of and ³²P transfer between *Allium porrum* plants. *Soil Biol. Biochem.* 34, 1027–1036.
- Twieg, B.D., Durall, D.M., Simard, S.W., 2007. Ectomycorrhizal fungal succession in mixed temperate forests. *New Phytol.* 176, 437–447.
- Urban, D.L., Minor, E.S., Trembl, E.A., Schick, R.S., 2009. Graph models of habitat mosaics. *Ecol. Lett.* 12, 260–273.
- van der Heijden, M.G.A., Horton, T.R., 2009. Socialism in soil? The importance of mycorrhizal fungal networks for facilitation in natural ecosystems. *J. Ecol.* 97, 1139–1150.
- Whiteside, M.D., Treseder, K.K., Atsatt, P.R., 2009. The brighter side of soils: quantum dots track organic nitrogen through fungi and plants. *Ecology* 90, 100–108.
- Wilkinson, D.M., 1998. The evolutionary ecology of mycorrhizal networks. *Oikos* 82, 407–410.
- Wolfe, B., Mummey, D., Rillig, M., Klironomos, J., 2007. Small-scale spatial heterogeneity of arbuscular mycorrhizal fungal abundance and community composition in a wetland plant community. *Mycorrhiza* 17, 175–183.
- Wu, B., Nara, K., Hogetsu, T., 1999. Competition between ectomycorrhizal fungi colonizing *Pinus densiflora*. *Mycorrhiza* 9, 151–159.
- Zabinski, C.A., Quinn, L., Callaway, R.M., 2002. Phosphorus uptake, not carbon transfer, explains arbuscular mycorrhizal enhancement of *Centaurea maculosa* in the presence of native grassland species. *Funct. Ecol.* 16, 758–765.
- Zhou, Z., Hogetsu, T., 2002. Subterranean community structure of ectomycorrhizal fungi under *Suillus grevillei* sporocarps in a *Larix kaempferi* forest. *New Phytol.* 154, 529–539.
- Zuur, A.F., Ieno, E.N., Walker, N.J., Saveliev, A., Smith, G.M., 2009. *Mixed Effects Models and Extensions in Ecology with R*. Springer, New York.