



# The foundational role of mycorrhizal networks in self-organization of interior Douglas-fir forests<sup>☆</sup>

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## ABSTRACT

Mycorrhizal fungal networks occur where mycorrhizal fungal mycelia link the roots of multiple plants, including those of different species, sometimes facilitating interplant transfer of carbon, nutrients or water. In this paper, I review recent research on the structure and function of mycorrhizal networks, and how they may serve a foundational role in the self-organization and stability of interior Douglas-fir (*Pseudotsuga menziesii* var. *glauca*) forests through their influences on forest regeneration, stand dynamics and spatial patterns. The stabilizing influence of mycorrhizal networks is particularly important in these forests because they experience an unpredictable and stressful climate; a mixed severity disturbance regime; and episodic seed dispersal with multiple constraints on recruitment. After seed dispersal following gap disturbance, we have found that interior Douglas-fir seedlings are rapidly colonized by ectomycorrhizal (ECM) fungal spores or by the ECM fungal mycelial network formed among residual trees or shrubs, helping the species to regenerate in a patchy pattern. This occurs whether disturbance severity is low or high. In small, shaded gaps of uneven-aged forests, new regeneration also establishes within the extensive mycorrhizal networks of old trees. In open gaps created by variable retention harvesting, establishment of new regeneration is substantially enhanced where seedlings are integrated within the existing network of residual trees, and this is associated with resource transfer through mycorrhizal pathways. As the young trees grow, belowground resource transfer fluctuates with changing source–sink gradients, until the trees eventually gain dominance in stands and become nutrients sources to a new generation of seedlings growing beneath them. Although preliminary, our studies suggest that the degree to which mycorrhizal networks facilitate regeneration establishment increases with disturbance or drought stress, in keeping with the stress-gradient hypothesis of facilitation. The patchy regeneration pattern of Douglas-fir across a climatic gradient can be partly explained by scale-dependent feedbacks involving local facilitation by networks and longer-range competition for resources. The regeneration pattern influenced by mycorrhizal networks may also interact with other organisms, including small mammals. Based on this, I propose that interacting networks function as a hierarchical “meta-network”, where each falls under a network guild and influences other networks to stabilize the forest. Hub trees for mycorrhizal networks are “foundational” because they even out resource availability and create favorable local conditions for tree establishment, which is fundamental to structuring of the whole forest community. Conserving hub trees and mycorrhizal networks during forest management therefore appears important to the conservation, regeneration and restoration of interior Douglas-fir forests.

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## 1. Introduction

The interior Douglas-fir (*Pseudotsuga menziesii* var. *glauca* (Beissn.) Franco) forests of North America are self-organized,

complex, adaptive systems (Levin, 2005). Self-organization involves the interactions and feedbacks through which internal organization of the ecosystems increases in complexity; this is evident in the emergence and continued development of forest structure and pattern following disturbance. Once interior Douglas-fir seed falls and germinates on disturbed seedbeds, internal community order develops through local facilitative and competitive interactions. For example, establishment of germinants in this stressful environment is facilitated through ectomycorrhizal (ECM) colonization by local ECM fungal propagules, allowing seedlings to acquire scarce soil resources. A mycorrhiza, or literally fungus-root, forms when the mycorrhizal propagule

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infects the seedling root, forming a symbiotic (and commonly mutualistic) relationship where the fungus obtains part or all of its carbon from the seedling in exchange for nutrients it takes up through its mycelium from the soil; all forest trees form mycorrhizas, thousands of fungal species are involved, and many tree species share many fungal species whose mycelium connect roots of different plants, leading to formation of mycorrhizal fungus networks (hereafter called “mycorrhizal networks”) (Molina et al., 1992). As the colonized seedlings grow, mortality of smaller individuals results from density-dependent competition for resources over a larger scale. These interactions further impose scale-dependent positive and negative feedbacks on the trees, mycorrhizal fungi, and environment, with the feedbacks serving as important self-organizing forces (Perry, 1995; Levin, 2005; Rietkerk and van de Koppel, 2008). In interior Douglas-fir forests, the multitude of positive and negative interactions, such as mutualisms, competition and herbivory, and the resultant feedbacks across scales, eventually produce patchy, multi-layered forests (Huggard et al., 2005). The ecosystems are adaptive because the interacting organisms adapt and evolve in response to system changes, such as the changing climate, further affecting self-organization (Levin, 2005). This adaptive, self-organization is fundamental to the complexity and stability of these forests (Suding et al., 2004).

The complexity of interior Douglas-fir forests is further compounded by the variability and unpredictability of natural disturbances. Stochastic processes in the mixed fire, insect, pathogen and wind disturbance regimes, for example, leave a suite of biological legacies and potential development pathways (Klenner et al., 2008), resulting in heterogeneous forests characterized by hysteresis (i.e., can exist in several states) and metastability (i.e., in delicate equilibrium and susceptible to small, stochastic changes) (Elmqvist et al., 2003). As an illustration of this, a range of regeneration outcomes can occur in disturbance gaps that vary in size from single tree to whole forests, where the development of the new forest depends precariously on tree species composition, density and distance at the gap edges and the seed rain, seedbed, and seed predator dynamics around the time of disturbance, which are all dependent on local climatic and site quality patterns (Huggard et al., 2005; Vyse et al., 2006). Once established from these initial conditions, the new forest self-organizes through local interactions and adaptation of the composite parts (Perry et al., 1989a; Perry, 1995; Levin, 2005). The Douglas-fir forests that develop from the highly variable post-disturbance conditions – characterized by the abundance and distribution of species and individuals; the spatial and temporal organization of structures and patterns; and the patterns of resource use – range from uneven-aged, tree species-poor, mosaic forests in the drier regions to even-aged, mixed, continuous forests in the moister regions of British Columbia.

The self-organization and stability of interior Douglas-fir forests may be threatened by cumulative human disturbances that, when combined with climate change, appear to increasingly fall outside the natural disturbance regime (Puettmann et al., 2008). For example, removal of the largest, straightest, fittest trees to capitalize on their economic value, and to increase light and water availability to understory trees (Vyse et al., 2006), has almost always taken precedence over conserving genetic diversity and the autocatalytic networks that facilitate energy flow, generate pattern and stabilize ecosystems. A century of high-grading over the entire distribution of interior Douglas-fir forests in British Columbia (Vyse et al., 1991) has likely affected feedbacks across scales, including gene flow, integrity of mycorrhizal networks and hence regeneration success (Aitken et al., 2008). A better understanding of the local interactions that drive ecosystem structure, pattern and processes in these forests may result in better management

practices and help prevent further biodiversity losses and forest degradation.

An important feature that underlies the stability of forest ecosystems is the existence of biological networks (Levin, 2005). Networks are comprised of interacting species through which energy flow, thus maintaining ecological stability across spatial and temporal scales. Mycorrhizal networks are one example of a biological network; the networking mycorrhizal fungus mycelia link trees together in time and space, serving to colonize new seedlings, and shuttle carbon, nutrients or water from older to young trees according to need. There is increasing evidence that mycorrhizal networks are common in boreal, temperate and tropical forests (Kennedy et al., 2003; Booth, 2004; Cline et al., 2005; Southworth et al., 2005; Lian et al., 2006; McGuire, 2007).

The purpose of this paper is to provide evidence for the foundational role of mycorrhizal networks in self-organization of Douglas-fir forests. I start with a review of natural disturbance regimes and forest dynamics because these are important sources of complexity in the Douglas-fir landscape (Franklin et al., 2002). I compare interior Douglas-fir forests across very dry, dry and moist climatic regions. This is followed by reviews of the development and function of mycorrhizal networks in interior Douglas-fir forests, including discussions of how mycorrhizal networks may affect stand dynamics and vegetation patterns. From this basis, I build on the concept of “meta-networks”, which is a series of hierarchical, interacting networks. I then discuss the potential role of networks in forest resilience and what may happen when disturbance thresholds are crossed. I conclude the paper with a discussion of management issues foresters will face when considering maintenance of forest structures in our changing climate.

## 2. Drivers of complexity: climate and disturbance regimes of interior Douglas-fir forests

Douglas-fir is a widely distributed native North American tree species, occurring in a broad range of climates (precipitation range 410–3400 mm year<sup>-1</sup>; mean July temperature 7–30 °C; mean January temperature –9 to 3 °C), site qualities (very dry to very moist soil moisture regime; very poor to very rich soil nutrient regime) and forest types (Hermann and Lavender, 1990; Klinka et al., 2000). Its occurrence over the vast and varied landscape reflects its high genetic variability, adaptability, and phenotypic plasticity (St. Clair et al., 2005; Aitken et al., 2008). These characteristics are expressed in high population variability in resource and environmental tolerances (e.g., shade, frost and drought tolerance), reproductive and growth traits, and interaction strengths with other tree species (Hermann and Lavender, 1990; Klinka et al., 2000).

The latitudinal range of the interior variety of Douglas-fir (*P. menziesii* var. *glauca*) stretches from north-central British Columbia (55°N) to northern Mexico (19°N) (Hermann and Lavender, 1990). The elevation distribution of interior Douglas-fir increases from the north (maximum 760 m in north-central British Columbia) to the south (maximum 3260 m in Mexico), closely tracking climatic changes; ergo, establishment is limited by low annual/winter temperatures and high snowfall at high latitudes and elevations, and by low annual precipitation at low latitudes and elevations, such as where the forests interface with scrublands or grasslands (Griesbauer, 2008). Many dendroecological and climate studies verify that Douglas-fir productivity is sensitive to climatic variation (e.g., Nigh et al., 2004; Hamman and Wang, 2006; Griesbauer, 2008), primarily to water deficits but also to snowpack depth/longevity and growing season/winter temperatures and frosts (Zhang and Hebda, 2004; Case and Peterson, 2005; Laroque and Smith, 2005). The variability in composition, structure

and ecophysiology (e.g., shade tolerance) of Douglas-fir forests reflects these sensitivities to climatic and resource limitations (Carter and Klinka, 1992; Drever and Lertzman, 2001). In the very dry to dry climatic regions of interior British Columbia, for example, interior Douglas-fir varieties include a range of shade tolerant races that either form relatively pure, uneven-aged, climatic climax stands or that occur subordinately in mixture with pines, interior spruce (*Picea glauca* (Moench) Voss ssp. *engelmannii* (Parry ex Engelm.) T.M.C. Taylor) or trembling aspen (*Populus tremuloides* Michx) (Meidinger and Pojar, 1991) (Fig. 1a and b). In the wetter, more productive climatic regions of British Columbia, Douglas-fir is considered shade intolerant (Drever and Lertzman, 2001) and grows as an early or mid-seral species in mixture with up to eleven other conifer and broadleaf species on a single site (Fig. 1c); the archetypical mixed seral stands succeed to climatic climax forests dominated by western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) or western redcedar (*Thuja plicata* Don ex. D. Donn) (Meidinger and Pojar, 1991).

Prior to European settlement, natural disturbances in interior Douglas-fir forests were predominantly caused primarily by fire, but also by bark beetles (e.g., *Dendroctonus ponderosae* Hopkins, *D. pseudostugae* Hopkins, *D. brevicomis* LeConte), insect defoliators (e.g., *Choristoneura occidentalis* Freeman, *Orgyia pseudotsuga* McDunnough), and windthrow, with wide variation in disturbance frequency and severity across regional climates (Hadley and Veblen, 1993; Wong, 1999; Campbell et al., 2003; Huggard et al., 2005; Maclauchlan et al., 2007; Heyerdahl et al., 2007; Klenner et al., 2008). In the driest forests in the south and western United States, where interior Douglas-fir is commonly mixed with ponderosa pine (*Pinus ponderosa* Laws), the disturbance regime has generally been dominated by frequent, low severity fires that have left open, multi-aged stands with a vigorous grassy, herbaceous understory (Heyerdahl et al., 2001; Baker et al., 2007) (Fig. 1d). In more northern latitudes and at higher elevations in Canada, where Douglas-fir is mixed with many temperate tree species, including ponderosa pine, lodgepole pine (*Pinus contorta* Douglas ex Loudon var. *latifolia* (Engelm.) Critchfield), western larch (*Larix occidentalis* Nutt.), and paper birch (*Betula papyrifera* Marsh.), the climate is slightly wetter, cooler and considerably more variable, as are frequency of lightning strikes, owing to the complex topography. These forests experience a mixed-severity disturbance regime (i.e., includes low, medium and high severity fires) that is described as diverse, episodic and uncertain at multiple spatial and temporal scales (Wong, 1999; Baker et al., 2007; Klenner et al., 2008). The low to high severity fires leave a wide range of post-fire conditions, often in close proximity with each other, from areas where the trees are mildly scorched and the forest floor is left mostly intact to variable-sized patches where all trees and the forest floor are consumed (Wong, 1999). The variability created by fire is compounded by cyclical insect attacks. Bark beetles kill larger stems as individuals or in extensive groups, whereas defoliators create a range of gap sizes or select against certain tree species, and all insect attacks leave an intact forest floor with a deeper litter layer. The result of this mixed disturbance regime is a complex forest that includes a patchy network of forest and gaps of varying densities, sizes, shapes and age structures (including multi-cohort and single cohort) (Wong, 1999; Klenner et al., 2008) (Fig. 1e). In the wetter, most productive interior Douglas-fir forests east of the Great Basin, where the topography is steep and complex and interior Douglas-fir is mixed with western redcedar, western hemlock and paper birch, the fires are less frequent, more severe and often stand-replacing, resulting in relatively uniform post-fire site conditions and development of single cohort stands (Turner and Franz, 1985; Sanborn et al., 2006; Simard and Vyse, 2006) (Fig. 1f).

Over the past century, the primary disturbance agents in interior Douglas-fir forests have gradually changed from fire and insect attacks to harvesting and more severe insect attacks (Campbell et al., 2003; Maclauchlan et al., 2007; Klenner et al., 2008). The standard harvesting practice in the very dry and dry interior Douglas-fir forests has been to remove the tallest, straightest, largest diameter stems for their economic value, and leave patches of smaller residual trees and advance regeneration to grow and disperse seed into the harvested gaps (Vyse et al., 1991). Where the ground is sufficiently disturbed in the gaps, regeneration is patchy and mortality rates high. Over the past half-century, the density of partially cut stands appears to have increased as a result of fire exclusion and climate patterns (Wong, 1999). Recently, in the upper elevations of both the very dry and dry forests, clearcutting followed by planting has become the most common practice. Provided site preparation is suitable and frost pockets recognized, regeneration of planted Douglas-fir can be successful. Currently, extended droughts and more variable weather conditions, combined with fire suppression and high-grading effects on forest structure, have coincided with larger, more severe fire and insect outbreaks (Flannigan et al., 2005; Maclauchlan et al., 2007; Klenner et al., 2008; Kurz et al., 2008), leading to greater uncertainty in regeneration outcomes. These pressures are profoundly changing the structure of the interior Douglas-fir forests.

### 3. Limits to natural regeneration

Natural regeneration success in gaps created by disturbance is highly variable and depends on seed production and dispersal, seedbed receptivity, competition and herbivory. In most years, either some or no seed is produced, but under favorable climatic conditions for successive years, mast years occur (once or twice every decade; Huggard et al., 2005). The variability in mast seed years results in episodic recruitment over time, leading to a multimodal rather than the classic inverse-J age distribution of multi-aged forests with uniform recruitment (Oliver and Larson, 1997). The fitness of regeneration depends on seed genetics (Aitken et al., 2008), which in turn likely affects community and ecosystem genetics and processes (Kinzig et al., 2001; Whitham et al., 2006). Dispersal to the seedbed is highly dependent on distance from seed-trees and, for long-distance dispersal, local wind patterns (Heineman et al., 2002). Even when Douglas-fir seeds are dispersed to a receptive forest floor, their fate is highly uncertain. A few (<5%) are missed by predators (ants, birds, small mammals) (Janzen, 1971; Sullivan, 1979; Huggard et al., 2005) and others may fail to germinate due to unfavorable environmental conditions (e.g., surface temperature extremes) or insufficient resource availability (Minore and Laacke, 1992; Stark et al., 2006; Barker and Simard, 2008). Receptivity of the forest floor varies with disturbance, but Douglas-fir germination is best on burned, exposed or mixed mineral soil with low levels of herbaceous or grass competition (Klinka et al., 2000). To increase natural regeneration potential, harvested sites are therefore often prepared by exposing mineral soil (Vyse et al., 1991).

Those seeds that germinate remain vulnerable to abiotic and biotic stresses due to their small size (Myers and Katijima, 2007); their survival is limited primarily by moisture availability (Hermann and Lavender, 1990; Newsome et al., 1991), but also by high temperatures (especially on burned soils) (Childs et al., 1985), frost, availability of light, nitrogen and phosphorus (Myers and Katijima, 2007), competition by vegetation (particularly grasses) for water and nutrients (Fleming et al., 1998; Simard et al., 2003), infection by pathogens (e.g., *Rhizina undulata* Fr. following fire; Parker et al., 2006), and herbivory. Prolonged summer drought during seedling establishment is particularly

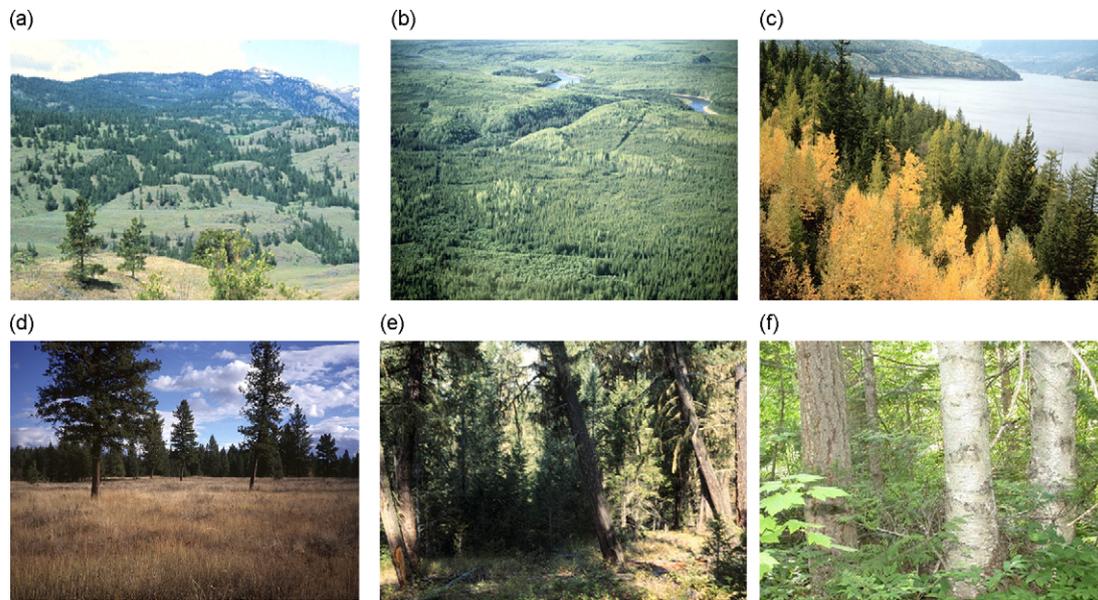


Fig. 1. Landscape and forest interiors of the very dry (a, d), dry (b, e) and moist (c, f) interior Douglas-fir forests.

fateful in the interior Douglas-fir forests, and it is during the first year that colonization by ECM fungi appears important for accessing scarce soil water and nutrients (Berch et al., 1999). Colonization of new germinants depends on availability of appropriate ECM fungal propagules but also on access to an existing mycorrhizal network (Hagerman et al., 2001; Teste et al., 2009, and see below).

Seedlings germinate in clumps in interior Douglas-fir forests, and the strength of the pattern increases with environmental stress, such as regional aridity or disturbance severity (see section on pattern later). This is partly a function of seed dispersal patterns, but also because a neighboring tree or established seedling helps others survive by modifying the local environment. This can involve: (1) greater access to beneficial root symbionts, such as ECM fungi (Simard et al., 1997a; Kranabetter, 1999; Hagerman et al., 2001), (2) buffered air or soil temperatures, (3) greater water availability, (4) greater soil nutrient availability (“island of fertility” phenomenon, Flores and Jurado, 2003), (5) better soil aeration, and (6) protection from herbivores (Brooker et al., 2008). These facilitative effects interact with competition at different spatial scales to generate patterns.

Interior Douglas-fir seedlings that survive into their second year are limited by interspecific competition from the establishing plant community, particularly pinegrass (*Calamagrostis rubescens* Buckl.), fireweed (*Epilobium angustifolium* L.), and seeded domestic grasses (Beyers, 2004; Simard et al., 2003). In regeneration patches in very dry forests, where density of seedlings is high and resource availability is low, intraspecific competition for water can be intense as indicated by prolonged periods of suppression and slow stratification. In the very dry to dry interior Douglas-fir forests, clearcutting has sometimes intensified these constraints to seedling establishment and can lead to insufficient regeneration. Even in partially cut stands, where there is greater seed source and a less abundant understory, regeneration is not taking place as quickly as was assumed (Vyse et al., 1991; Newsome et al., 1991). In the wetter interior Douglas-fir forests, where severe fires result in stand-replacement by multiple species over a shorter time-span, competition for light is more important than competition for soil water, and forest stratification occurs rapidly (Simard and Vyse, 2006). In addition to competition, seedlings are at risk of grazing and trampling by cattle (Newsome et al., 1991), and damage from selective or salvage logging (Donato et al., 2006). In these more

productive ecosystems, where there are fewer constraints on growth, Douglas-fir forests can regenerate naturally in abundance following natural disturbances and harvesting. This has been well documented in areas transitional to coastal climates (Donato et al., 2006; Shatford et al., 2007).

#### 4. Development of mycorrhizal networks following different disturbance severities

Ectomycorrhizal colonization of establishing seedlings occurs through a variety of mechanisms. Ectomycorrhizal inoculum can persist for a short time after a disturbance as chlamydospores, sclerotia, on root tips of surviving trees, and, briefly, as hyphae emanating from dying or recently dead root tips. Without a host, however, the amount and diversity of ECM fungal inoculum decreases rapidly (Dahlberg, 2002; Baar et al., 2002; Jones et al., 2003), with greater declines following more severe disturbances (Bradbury et al., 1998). When the roots of establishing seedlings do encounter viable ECM spore inoculum, their exudates act as stimulatory signals for spore germination (Smith and Read, 1997; Gianinazzi-Pearson et al., 2009). Roots also become colonized by the ECM fungus mycelium or network of an established or dying plant or plant community (Selosse et al., 2006 and references therein). Ectomycorrhizal colonization can occur quickly, with functioning ECMs developing in 8 days (Duplessis et al., 2004). Mycorrhizal networks have been considered the most important method of colonization in forests because most forest disturbances leave some residual plants and forest floor as inoculum (Chapin et al., 2002) and because many ECM fungal species have low host specificity (i.e., colonize many host species) (Molina et al., 1992). Even where ectomycorrhizal fungal mycelia networks are disrupted by soil disturbance (e.g., by soil animals, site preparation equipment, or other disturbances), they retain their inoculum potential as mycelia fragments and can also re-form quickly.

Douglas-fir associates with many host-generalist ECM fungi, with potential to form mycorrhizal networks with plants of different species, but it also associates with several host-specific fungi, including fungal taxa in *Rhizopogon* and *Suillus* (Suilloid clade), with high potential to form networks intraspecifically (Horton et al., 1999, 2005; Kretzer et al., 2003; Twieg et al., 2007). In the interior Douglas-fir forests, we have found that ECM colonization of naturally regenerating seedlings occurs both

through mycorrhizal networks and wind-, soil- or mammal-dispersed inoculum, and which mechanism dominates depends on disturbance severity (Teste et al., 2009; Horton and Bruns, 1998). Colonization occurs by the same mechanisms regardless of whether seedlings establish from seed or planting stock, but for planted seedlings, the native ECM fungi must displace any nursery ECM fungi already colonizing root tips. Notably, interior Douglas-fir nursery stock is generally non-mycorrhizal when it is planted in the field (Berch et al., 1999).

Seedlings colonized by a wide diversity of ECM fungi are considered to have greater functional diversity affecting their productivity (Perry et al., 1989a). This is because ectomycorrhizal fungi vary in their ability to take up nutrients or water and tolerate water stress or temperature extremes (Smith and Read, 1997; Jones et al., 2003 and references therein), and because they partition soil properties (Dickie et al., 2002; Tedersoo et al., 2003; Koide et al., 2005). Research on arbuscular mycorrhizas (AM) also shows that plants colonized by local fungi have a wider and more frequently positive growth response than when they are colonized by exotic fungi (Klironomos, 2003). In the interior Douglas-fir forests, we have found that Douglas-fir seedling productivity is positively correlated with diversity of local colonizing ECM fungi (Simard et al., 1997a).

### 5. High severity disturbance

Where disturbances are so severe that most host plants die, forest floor is consumed and inoculum biomass is reduced, then recolonization by air-, soil-, or mammal-borne spores, or by fungal inoculum found deeper in mineral soil, are of primal importance (Stendell et al., 1999; Dahlberg, 2002). Many studies show that severe fires reduce ECM sporocarp production and result in large losses of ECM fungal tip or mycelial biomass (Dahlberg, 2002 and references therein); in dry forests, however, ECM fungi present on deep tree roots may survive. Following severe wildfire or severe soil disturbance (i.e. where trees and forest floor are consumed) in interior Douglas-fir forests of British Columbia, we have found that *Wilcoxina rehmii* Chin S. Yang & Korf, a weedy ascomycete with low carbon demands and ready dispersal via soil and air, dominates the ECM fungal community of naturally regenerating Douglas-fir seedlings for a few years (Simard et al., 1997b; Hagerman et al., 2001; Barker and Simard, 2008; Teste et al., 2009). Other studies in fire-seral forests have also shown that severe fires favor ascomycetes such as *Wilcoxina* (Visser, 1995; Bradbury et al., 1998; Grogan et al., 2000), and early seral basidiomycetes such as *Thelephora terrestris* Ehrh., over ECM fungi that dominate later seral stages, such as *Rhizopogon*, *Suillus* or *Amanita* species (Baar et al., 2002; Mah et al., 2001; Bruns et al., 2002; Dahlberg, 2002). Barker and Simard (2008) found that establishment and survival of interior Douglas-fir germinants following severe fire was lower and patchier than in moderate disturbances, possibly because slower colonization of the species-poor ECM fungus community left germinants more at risk of desiccation, but perhaps also because of lower seed rain or inhospitable environmental conditions of seedbed patches (e.g., due to temperature extremes, presence of ash or water repellent layers). Of the clumps of seedlings that established in the severe burns, their growth was rapid in response to the post-combustion nutrient flush and high availability of light and water (Barker and Simard, 2008).

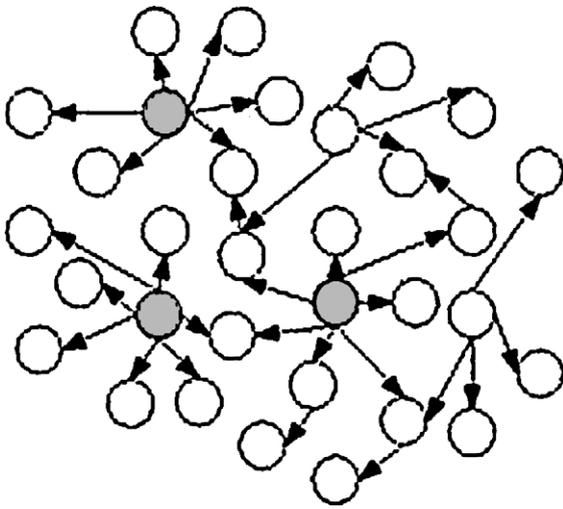
The ruderal, host-generalist ECM fungi colonizing seedlings in severe disturbances likely grow and anastomose quickly, rapidly forming species-poor mycorrhizal networks among the regenerating seedlings (Smith and Read, 1997). With time, the networked seedling clumps may reduce temperature extremes and, by enhancing access to a greater pool of soil resources (e.g. water or nitrogen lost through volatilization or leaching) through uptake

and transfer, enhance resource availability to new recruits, resulting in an “island fertility” effect (Flores and Jurado, 2003). Although not yet tested, it is also possible that tuberculate ECM fungi associated with Douglas-fir increase nitrogen availability through their association with nitrogen fixing bacteria, as shown for lodgepole pine (Paul et al., 2007). The species and structural complexity of these networks is expected to increase over time because, as Douglas-fir grows older, its potential to host a greater diversity of late-seral, carbon-demanding, strand-forming ECM fungi increases (2000 fungal species occur on Douglas-fir; Trappe, 1977) (Twieg et al., 2007; Teste et al., 2009). Because the severe fire patches in Barker's study were small in size (<200 m to an edge), the potential for spore and seed dispersal from the forest edges was also high. In addition to wind dispersal, small mammals are known to disperse ECM fungal spores into clearcuts from forest edges (Maser et al., 2008). Over time, plant invasion, succession, small mammal population increases, and forest floor development would provide additional sources of ECM fungal inoculum, further increasing the complexity of the mycorrhizal network since disturbance, likely enhancing its facilitative effects (Teste et al., in press).

### 6. Low to moderate severity disturbance

In low to moderate severity disturbances where some trees or plants survive, or where the forest edge is nearby, there is greater opportunity for colonization of germinants by existing mycorrhizal networks of live trees. Following most natural disturbances and harvesting practices in the interior Douglas-fir forests of British Columbia, an edge or residual tree is usually not far away (Klenner et al., 2008), and for this reason, colonization by mycorrhizal networks is likely common. (Exceptions are the recent mountain pine beetle salvage clearcuts, where edges are often very far away; Uunila et al., 2006.) In a study examining the effects of distance from mature trees on ECM fungal colonization and seedling establishment in the dry climatic region, Teste et al. (2009) found that interior Douglas-fir seedlings had a more diverse and complex ECM fungus community near mature Douglas-fir trees (sharing over half of the fungal species) than further away (5 m), where a simpler ECM community dominated by *W. rehmii* occurred. Seedlings with access to all sources of inoculum (including mycorrhizal networks, spores and soil propagules), and that were also in close proximity to trees, tended to have the greatest ECM colonization and fungus diversity (Teste et al., 2009). This suggests the mature trees acted as refugia for ECM fungi. However, competition by the mature trees for water and nutrients reduced seedling establishment directly under the canopy dripline, while competition and reduced ECM colonization associated with the pinegrass-dominated plant community reduced performance at further distances, with a peak in seedling performance in an intermediate zone outside the dripline. Seedlings thus established best in a ring around the mature tree, where the positive feedbacks from network colonization outweighed the negative effects of competition.

Linking into the network was much more important for performance of natural regeneration than planted seedlings, probably because they had lower carbohydrates stored in roots and also because relative demand for nutrients was greater. Planted seedlings, by contrast, had older, more nutrient-rich needles (from nursery conditions) and the capacity to recycle foliar nitrogen (Teste and Simard, 2008). Notably, standard reforestation practices recognize that planted seedlings do not suffer establishment nutrient limitations (explaining low responses to presence of mycorrhizal networks) as much as naturally regenerating seedlings, and strive to remove pinegrass and expose mineral soil in patches (thus disrupting the mycorrhizal network) to reduce the



**Fig. 2.** Scale-free network model. Circles represent interior Douglas-fir trees and arrows represent mycorrhizal linkages. Hub trees (shaded circles) are highly connected to neighboring trees (clear circles) via shared colonization by mycorrhizal fungi (image from <http://sangita.us>).

more limiting effects of drought and frost damage in conventional clearcuts (Newsome et al., 1991). This practice is successful for establishment of planted seedlings, even without the nearby presence of refuge trees or plants, illustrating the lower reliance of planted seedlings on presence of mycorrhizal networks for establishment. Even for naturally regenerating seedlings, soil disturbance can improve certain limitations to establishment without reducing the inoculum potential and benefits of the rapidly re-forming mycorrhizal network.

The importance of retaining mature trees as refuges for ECM fungal colonization is further illustrated in a detailed examination of two networking ECM fungi (*Rhizopogon vinicolor* and *R. vesiculosus* (Basidiomycota, *Villosuli*-group sensu Kretzer et al., 2003) in an uneven-aged, old-growth, interior Douglas-fir forest in the very dry climatic region (Kevin Beiler, unpublished data). In this study, Beiler uncovered an extensive *Rhizopogon vinicolor/vesiculosus* network that linked trees of all ages, where young Douglas-fir trees were established within the extensive network of veteran trees. Here, the old trees served as hubs for networking fungi, much like the hub of a spoke wheel, where they appeared to play a central role in establishment of seedlings in the forest understory (Fig. 2). Together with experiments showing substantially greater establishment of Douglas-fir germinants when linked into the mycorrhizal networks of larger trees (Teste et al., in press), our findings suggest that the old trees served a foundational role in con-specific regeneration of the forest; it is this sort of self-regeneration that is the defining characteristic of climatic climax forests. Although ECM fungi are best known for their role in seedling establishment (e.g., by increasing resource uptake), it is also well-known that growing saplings and mature trees require colonization by ECM fungi for continued survival and growth (Smith and Read, 1997). Even where the old trees eventually die or are later removed, the established trees would continue to benefit from the colonizing mycorrhizal network, and the role it plays in resource uptake and root protection, inherited from previous generations.

*Rhizopogon vinicolor/vesiculosus* are host specialists to Douglas-fir and have been observed at all stages of succession in studies examining ECM fungi of Douglas-fir forests (e.g., Molina et al., 1999; Luoma et al., 2004, 2006; Horton et al., 2005; Twieg et al., 2007). They are considered strong networking species in Douglas-fir forests and provide an even tighter link within Douglas-fir than

other generalist fungi (Molina et al., 1999). Not only do *Rhizopogon* taxa form strands considered important in inter-tree carbon transfer (Molina et al., 1999), but they have been shown to translocate nutrients and water from soils to host trees (Read and Boyd, 1986), resulting in increased seedling growth and resistance towards drought (Parke et al., 1983; Cairney and Chambers, 1999).

In addition to mature trees, ten abundant shrub species native to interior Douglas-fir forests (*Alnus viridis* subsp. *sinuata* (Regel) Å. Löve & D. Löve, *Arctostaphylos uva-ursi* (L.) Spreng, *Betula papyrifera* Marsh, *Paxisia myrsinites* (Pursh) Raf., *Populus tremuloides* Michx., *Salix commutata* Bebb, *Shepherdia canadensis* (L.) Nutt., and *Spirea betulifolia* Pall. (Dougl.)) have been shown to share 11 ECM fungi (e.g., *Cenococcum*, *Amphinema*, *Wilcoxina*, and *Piloderma* species, and *Mycelium radicans atrovirens* Melin (MRA)) in common with establishing Douglas-fir seedlings, thus potentially providing networks for ECM fungus colonization (Hagerman et al., 2001). In moist, mixed Douglas-fir forests, *B. papyrifera* alone has been shown to share up to 41 ECM fungi with interior Douglas-fir, with the proportion of shared types generally increasing with stand age (from 40% to 80%) (Simard et al., 1997b; Jones et al., 1997; Philip and Simard, 2008; Twieg et al., 2007). With such a rich community of shared fungi, the potential complexity and extent of mycorrhizal networks is likely much greater than in the pure Douglas-fir forests described above. The frequent survival and rapid sprouting of paper birch root stocks following disturbance further ensures a refuge of mycorrhizal networks and is thought to aid in the rapid recovery of these forests from fire or clearcutting (Twieg et al., 2007).

With the high richness and host generality of associated fungi (Molina et al., 1992), there are many other plant species across the extensive distribution of interior Douglas-fir that can serve as refuge plants for ECM fungal colonization of seedlings following disturbance. The potential for plant species to serve as ECM fungal refugia for Douglas-fir was first discovered when ECM fungi isolated from conifer hosts were synthesized as arbutoid mycorrhizas on the ericaceous hosts, *Arbutus menziesii* Pursh. and *Arctostaphylos uva-ursi* (L.) Spreng. (Zak, 1976); later, Molina and Trappe (1982) were able to synthesize a much wider range of ECM fungi from conifers on these two ericaceous hosts. Molina and Trappe (1982) described the potential importance of ericaceous hosts in serving as legacy plants providing ECM fungus inoculum for later colonization of regenerating Pinaceae seedlings, and hence their importance in forest management. In a later study, Horton et al. (1999) found that Douglas-fir seedlings shared 17 ECM fungal species with *Arctostaphylos glandulosa* subsp. *glandulosa* in a chaparral community on the central coast of California. In this community, as in the dry Douglas-fir forests examined by Teste et al. (in press), Douglas-fir seedling survival was improved where they established in close proximity to compatible refuge plants, attributed to colonization by a diverse community of networking ECM fungi. Many studies in montane, tropical and boreal forests also show that seedling survival (Horton et al., 1999; McGuire, 2007), growth (Simard et al., 1997a; Nara and Hogetsu, 2004; Nara, 2006; Teste and Simard, 2008), ECM fungus colonization (Borchers and Perry, 1990; Nara and Hogetsu, 2004; Horton et al., 1999), and ECM fungus diversity (Cline et al., 2005; Teste et al., 2009) are greater where seedlings establish within the mycorrhizal network of mature trees.

Although many trees and understory plants can be incorporated into the ectomycorrhizal network of interior Douglas-fir forests, including some arbutoid and ericoid plants (Horton et al., 1999; Hagerman et al., 2001; Kennedy et al., 2003), AM or non-mycorrhizal plants are usually excluded. Some AM fungi can even inhibit ECM fungus colonization of ECM conifers (Haskins and Gehring, 2004; McHugh and Gehring, 2006); conversely, ECM fungus mats associated with pines can inhibit restoration of AM

plant communities (Theit and Boerner, 2007). For example, the native pinegrass, *Calamagrostis rubescens* Buckl., has been shown to reduce colonization and diversity of ECM fungi colonizing establishing conifer seedlings (Simard et al., 2003; Hagerman et al., 2001). Where regeneration of ECM hosts is delayed or displaced by non- or AM plant invaders following disturbance, re-introduction of native trees can be difficult due to the loss of native inoculum or due to the establishment of exotic mycorrhizal networks. Conversely, conserving native mycorrhizal networks by retaining residual plants and rapid reestablishment of native species may be important barriers to weed invasion in disturbed forests.

### 7. Recovery of the ECM fungal community following mixed severity disturbance in moist forests

Mixed severity fires, which include low, moderate and high severity patches, characterize the natural disturbance regime of moist interior Douglas-fir forests. In a chronosequence study examining recovery of the ECM fungal community on Douglas-fir and paper birch, Twieg et al. (2007) found that the ECM fungal community composition and diversity changed rapidly from 1- to 26 years following mixed severity fire disturbance, after which they stabilized. The ECM fungal community had stabilized near the time of canopy crown closure, congruent with stability patterns in plant community composition and crown cover (Simard and Vyse, 2006). There was little difference in Douglas-fir or paper birch ECM fungal diversity or community structure between clearcut and wildfire origin sites (Twieg et al., 2007), suggesting that clearcutting with forest floor and root retention did well at emulating natural fire disturbance. The ECM fungus composition on root tips from the older forests (Twieg et al., 2007) overlapped with that of ECM sporocarps sampled from 120-year-old fire-origin forests by Durall et al. (2006), suggesting the ECM fungal communities were stable across multiple sites and stayed within the same stability domain following mixed severity fire disturbance.

### 8. Mechanisms for mycorrhizal network facilitation in interior Douglas-fir forests

Mycorrhizal networks can mediate distribution of resources among trees or plants and affect plant–plant interactions. In some cases, competition between plants is increased (Kytöviita et al., 2003), but in others there can be a synergistic effect, resulting in a more equitable distribution of resources or greater overall uptake by the community (Grime et al., 1987; Perry et al., 1989b). Some suggest that offspring may be subsidized by resource transfer through the mycorrhizal network of their parents for a more successful head-start (Wilkinson, 1998; Selosse et al., 2006); *sensu* kin selection (Dudley and File, 2007). The facilitative effect of networks on resource availability to seedlings can occur indirectly, by increasing ECM fungal colonization, diversity and hence nutrient uptake. Or it can occur directly by enabling seedlings to survive or by providing a hyphal conduit for transfer of resources between plants. The next section focuses on resource transfer.

### 9. Source–sink gradients as drivers of resource transfer

Plants can shuttle resources back-and-forth through hyphal linkages according to demand, representing a complex underground trading system. It is in this hidden world that resource exchange and competition occur among trees, plants and fungi, helping determine the winners and losers over time in a highly integrated community. The dynamic energy flow through networks, and the resulting feedbacks that occur, may help in the structuring and stability of ecosystems. Recent research suggests

that differences in physiological source–sink strength among plants (e.g., in photosynthetic rates, growth rates or nutrient content) are the major determinants of transfer patterns (Simard and Durall, 2004; Selosse et al., 2006; Teste et al., in press), but characteristics of the fungal and associated microbial communities also likely play important roles (Fitter et al., 1999). Where resource pools and demands are distributed equitably among plants in a physiologically uniform community, then carbon transfer from one plant to another is theoretically balanced by transfer in the opposite direction. However, physiological source–sink gradients among plants are the norm in real ecosystems, and resources have been shown to transfer along these gradients, from enriched source plants to rapidly growing sink plants (Simard and Durall, 2004; He et al., 2006; Selosse et al., 2006 and references therein). Thus, a sink plant could gain more carbon than it gives up to its neighbor, at least for a time (Simard et al., 1997c; Lerat et al., 2002; Philip, 2006; Pietikäinen and Kytöviita, 2007).

Transfer patterns appear to be governed more by sink strength of receiver plants than source strength of donors. As an illustration of this, Teste et al. (in press) found that greater net carbon transfer occurred to seedlings with greater relative sink strength, but that transfer amounts were unrelated to source seedling growth rates. These results suggest that larger, more vigorous seedlings rapidly regenerating in forest gaps may outperform smaller seedlings as a result of relatively greater carbon gains from edge trees. In this case, carbon (and other resources) may move into sink seedlings via xylem cells driven by transpiration or nutrient demand. Where they establish within the network of overstory trees, deeply shaded seedlings may depend on transfer of photosynthate from older trees to maintain a positive carbon balance; here source strength of mature trees may compensate for the weak sink strength of the struggling seedlings (Simard et al., 1997a). Where understory seedlings are released by a gap disturbance, source–sink gradients would change as they gain dominance, causing shifts in the pattern of net flux among neighbors.

### 10. Variation in carbon transfer with changing source–sink gradients

Plants occur in highly complex neighborhoods, with many plant and fungal individuals and species, involving much more than plant pairs interconnected by the mycelium of a single ECM fungal species. These conditions are also continuously changing, as plants germinate, grow, compete, respond to the seasons, are consumed, and eventually die, resulting in a dynamic flux of resources, tracking changing strengths and demands among individuals. In a study examining carbon transfer in mixed Douglas-fir plantations, Simard et al. (1997c) showed that summer shading of Douglas-fir increased its sink strength and net carbon gain from carbon- and nutrient-rich paper birch source trees. The amount Douglas-fir received in deep shade was equivalent to 10% of its total carbon budget, an amount comparable to carbon investments in seed production. In a later study, Philip (2006) showed that shifts in interspecific source–sink relations over the growing season reversed the direction of net transfer in spring and fall; that is, it occurred from Douglas-fir to leafless birch. She also found that the amount of two-way transfer increased over the growing season, when root and ECM fungus development were greatest (Philip, 2006), agreeing with an earlier study in maple forests by Lerat et al. (2002).

In dry Douglas-fir forests, greater establishment of natural regeneration in fully illuminated gaps has been associated with much smaller amounts carbon transferred from nearby residual trees in mid-summer than in the moist, more productive forests (Teste et al., in press). Although the amount of carbon transferred was very low in mid-summer, photosynthetic and transpiration

rates were also very low, as commonly occurs in response to seasonal drought in these dry forests (Fleming et al., 1998). Transfer may have been more important to seedling establishment in the fall, which is when carbon transfer peaks in concert with root and ECM fungus development (Lerat et al., 2002; Philip, 2006). Carbon transfer accumulated over the whole growing season, or at critically important periods, may thus account for the improvement in survival of establishing seedlings (Teste et al., in press). The greater importance of transfer through networks in the fall (Philip, 2006), and in the second than first year of establishment, is supported by the lag in ECM development during the first months of germination (Barker and Simard, 2008) and by measures of increased transfer as seedlings grow older and larger (Simard et al., 1997c). Water stress is also a limitation to carbon fixation in these ecosystems. Schoonmaker et al. (2007) found that water was redistributed belowground from mature trees to nearby seedlings, helping explain their improved water relations.

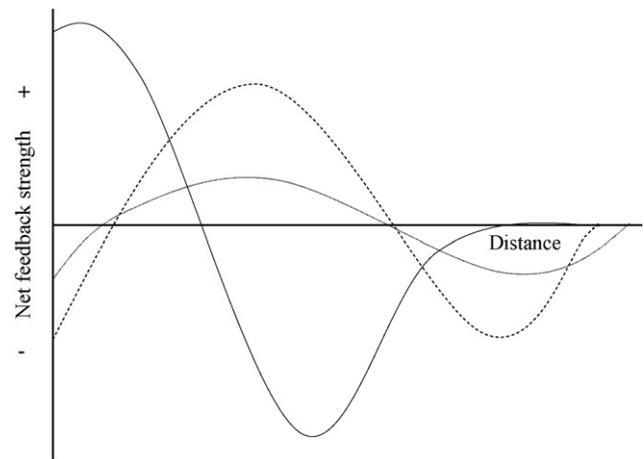
### 11. Variation in network facilitation with regional climate and stand development

Mycorrhizal networks appear to facilitate establishment of new regeneration more so in dry than moist Douglas-fir forests, as predicted by the stress-gradient hypothesis (Maestre et al., 2009). Many other studies show increased facilitation with environmental stress, especially along soil moisture gradients (Brooker et al., 2008 and references therein). Since resource stress affects seedling growth before it affects survival (Wagner et al., 1989), it also follows that mycorrhizal networks benefit tree growth more than survival in productive environments. To that end, we have found that carbon transfer is more important in facilitating growth than survival in the moist, mixed interior Douglas-fir forests, where soil resources are more plentiful and trees compete intensively for light (Simard et al., 1997a). In these forests, seedlings establish in abundance in the moist, rich soils, and then quickly stratify in height based on their ability to compete for light (Simard and Vyse, 2006). Here, linking into a network with fully illuminated overstory trees appears important to growth of shaded, understory saplings (Simard et al., 1997a).

As saplings grow and gain a competitive advantage in forests, it is likely that the benefits of resource transfer through networks diminish. Indeed, trees should change from net sinks to net sources over time, provided they remain in the upper canopy. The carbon and nutrient drain from large trees to establishing seedlings in the understory has been shown as negligible (Simard et al., 1997c). Maintaining fungal networks by large trees is not only necessary for continued uptake of soil resources as they grow, it also provides insurance for regeneration of new seedlings, a stable carbon source for the fungal community, and direct pathways for feedbacks that stabilize the forest community. This is particularly important in the mixed disturbance regime of interior Douglas-fir forests, where mycorrhizal networks can even out resource availability in the unpredictable and variable environment (Perry, 1995).

### 12. Feedbacks with mycorrhizal networks generate forest patterns

Scale-dependent positive and negative feedbacks between disturbance, mycorrhizal networks, regenerating seedlings and the local environment, as well as with other abiotic and biotic factors, may play a role in generating the striking vegetation spatial patterns in the interior Douglas-fir forests. The feedbacks may emerge through short-range facilitation by mycorrhizas and mycorrhizal networks, and short- and long-range competition for resources (Rietkerk and van de Koppel, 2008). Based on previous research, it is likely that the strength of facilitative effects

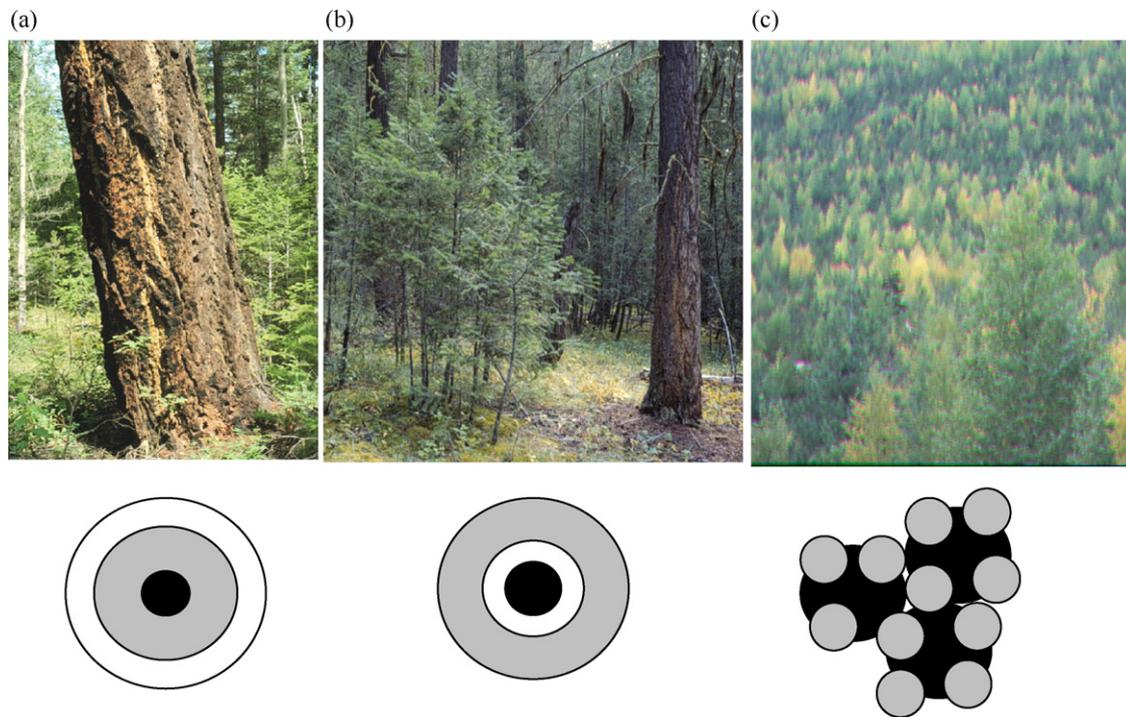


**Fig. 3.** Scale-dependent interactions result in net positive or net negative feedbacks. In very dry forests (solid line), net positive feedback (resulting from mycorrhizal networks and environmental amelioration) occurs at short distances and net negative feedback (due to water competition by hub trees and arbuscular meadow communities) occurs at longer distances, resulting in Douglas-fir regeneration in close proximity to hub trees (0 distance). In dry forests (dashed line), net negative feedback as a result of competition occurs under the dripline of hub trees and at further distances with arbuscular grasses, with a zone of net positive feedback (where mycorrhizal network facilitation exceeds competition) for regeneration in an intermediate zone around the hub tree. In moist forests (dotted line), net negative feedback occurs immediately next to birch trees, but positive feedback due to mycorrhizal networks and protective effects against root disease result in a broad zone suitable for regeneration. Because resources are scarcer in very dry forests, the strength of the positive and negative interactions are stronger than in wetter forests.

by mycorrhizal networks and competition for water increase with climatic aridity, but that the net positive effects in close proximity to hub trees also increase (Fig. 3). Based on the studies presented in this review paper, the following paragraphs present hypotheses about the role mycorrhizal networks may play in generating vegetation patterns in the very dry, dry and moist Douglas-fir forests.

In the very dry forests, regeneration generally occurs in “islands” within a mosaic of grassland meadows, where the facilitative effects of central hub trees may outweigh their competitive effects (Fig. 4a), or where there are patches of high resource availability. In the former case, the mycorrhizal networks of hub trees may supply clumps of germinants establishing on adjacent burned or scarified micro-sites with scarce water and nutrients; these clumps may help more recruits survive by damping temperature extremes and expanding the network frontier for accessing an even larger pool of soil resources. The growing clumps could effectively harvest water beyond their canopies from the surrounding grassy meadow. Thus, there can be positive (facilitative) feedback at short distances within the clumps, but negative (competitive) feedback at longer distances, generating a patchy regeneration pattern in the dry forest/meadow mosaic (Klausmeier, 1999). Similar feedbacks and pattern formation would be expected in severely burned patches.

In the dry forests, forests are more continuous and meadow gaps smaller and less frequent. Here, regeneration success peaks in disturbance gaps outside the dripline of hub trees (Fig. 4b). Because water is more abundant, seedlings do not appear to require the strong facilitative effects immediately next to hub trees, and tree canopy interference for water and light results in a net negative effect immediately adjacent to the tree. Outside the dripline of hub trees, however, our research shows that there can be a zone of enhanced regeneration success, where facilitative effects of networks outweigh the competitive effects of hub trees and the herbaceous plant community (Teste and Simard, 2008). Notably,



**Fig. 4.** Patterns of regeneration in very dry (a), dry (b) and moist (c) interior Douglas-fir forests. Zones of regeneration (shaded circles) organize around hub trees (black circles) in a pattern commensurate with positive and negative feedbacks. In very dry forests (a), there is a net positive effect in close proximity to hub trees and net negative effect in surrounding meadows where islands of trees harvest and compete for resources. In dry forests (b), there is a net positive effect immediately outside the dripline of hub trees, but there is a net negative effect directly under the dripline (due to hub tree interception of resources) and further into the gap (due to competition from arbuscular plants further into the gap). In moist forests, broadleaves provide a net positive effect over a broad zone except immediately under the canopy and outside their root zone.

many dry forests regenerate relatively uniformly in abundance without the presence of hub trees, indicating there can be adequate resource availability for regeneration in disturbed patches.

In the moist forests, regeneration occurs in “gaps” (of varying size) and result not only from local positive and negative interactions but also from disturbance-recovery processes, similar to fire-disturbed forests (Malamud et al., 1998). Gaps created by fire, root disease, or insects regenerate rapidly to intimate mixtures of conifers and broadleaves (paper birch and trembling aspen) (Simard and Vyse, 2006) (Fig. 4c). The roots of the sprouting broadleaves are colonized by a diverse community of late seral ECM fungi surviving from the pre-disturbance forest, which form complex networks with the neighboring conifers (Twieg et al., 2007). The broadleaves shade the new conifers and compete for resources, resulting in long-distance negative feedback, but they also shuttle carbon to them over short distances through the mycorrhizal network, resulting in net carbon gain by nearby individuals (Simard et al., 1997c). The broadleaves also provide the conifers with protection from infection by root diseases (*Armillaria ostoyae* (Romagn.) Herink) (Baleshta et al., 2005) in part by harboring antagonistic fluorescent pseudomonad bacteria in their mycorrhizosphere (DeLong et al., 2002). These complex feedbacks can help explain the mixed species regeneration pattern in disturbance gaps. In all of these forests, pattern is generated by short-distance facilitative effects of networks on conifer regeneration and short- and long-distance negative effects due to competition, and these interact with disturbance-recovery processes; the net effect is a variety of regeneration spatial patterns across climatic regions.

### 13. Meta-networks in interior Douglas-fir forests

Mycorrhizal networks likely interact with and stabilize other biological networks in forests. In the dry interior Douglas-fir

forests, clusters of trees establishing within mycorrhizal networks are commonly centered on older, hub trees, and these tree clusters are interwoven with meadows dominated by AM grasses and herbs. This pattern is expressed at a higher spatial scale as a plant community network. In the meadow gaps, tree establishment is limited by low resource availability (due to harvesting of resources by trees in the clump, but also due to competition from the herbaceous and graminoid plant community) and the paucity of compatible ECM fungus inoculum (Haskins and Gehring, 2004). Small mammals interact with this plant community network by living in the cavities or canopies of large, old and sometimes senescing trees (which are also mycorrhizal hub trees); they share these nest sites in hierarchical nest network, forming a complex, strongly structured wildlife community (Martin and Eadie, 1999; Martin et al., 2008). The interactions among these three networks: mycorrhizal, plant community, and nest networks; reinforce each other. For example, flying squirrels reside in old ECM tree canopies (including Douglas-fir) but forage on the forest floor for ECM truffles, a main part of their diet (Maser et al., 2008). The squirrels consume and disperse the ECM truffles, spreading spores that colonize new seedlings. The ECM fungi benefit seedling nutrition in exchange for fixed carbon, thus facilitating establishment of new trees that eventually become a nest resource for future generations of flying squirrels and other small mammals. This very tight fungi-tree-wildlife interdependency is played out throughout western North American conifer forests (Maser et al., 2008). I propose that these three networks function as a hierarchical “meta-network”, where (a) each network is classified as a network guild according to the manner in which it acquires limiting resources (i.e., fixed carbon for ECM fungi, soil water and nutrients for establishing trees, and canopies and cavities for small mammals) (after Martin and Eadie, 1999), and (b) the networks interact with and stabilize each other, from which emerges complex structures and functions that stabilize the whole forest.

Hub trees that serve as the center of mycorrhizal networks are foundational in these ecosystems because they stabilize resource availability and create favorable local conditions for tree establishment, and thus are fundamentally important in structuring the whole forest community (Ellison et al., 2005; Whitham et al., 2006). Ellison et al. (2005) considers Douglas-fir a foundational species in Douglas-fir forests. This is because it defines forest structure and function, and its gradual or rapid loss would affect key factors (e.g., mast production; mycorrhizal network facilitation; nest centers) that would cascade through complex indirect relationships, resulting in threshold transitions.

#### 14. Crossing thresholds that destabilize ecosystems

The emergent patchy patterns of interior Douglas-fir forests make them resilient to disturbance and climate change (Rietkerk and van de Koppel, 2008). In the dry forests, networked seedling patches concentrate resources in their local environment, allowing them to persist when mean soil moisture levels are too low for their survival. This has positive consequences for forest productivity and biodiversity (Huggard et al., 2005). In the moist forests, broadleaves help enable conifers to grow when pathogens and insects persist or light levels are low (Simard et al., 2005).

Changes in the natural patterns in these forests, by contrast, may signal a loss of resilience in the ecosystem. Where forests are severely disturbed with refuge plants killed over extensive areas, and where there are additional stresses, such as invasion by exotic weeds or extreme climatic events, threshold transitions can occur where ecosystems shift from one steady state to another (e.g., from forest to grassland or weed fields). Changes in the ECM fungus community have been implicated in these transitions in the interior Douglas-fir forests (Simard, 2009), as well as other montane and tropical forests (Perry, 1995; Haskins and Gehring, 2004). In a moist interior Douglas-fir forest that had been clearcut, destumped (a severe disturbance that removes stumps and roots and displaces forest floor) to reduce *A. ostoyae* root disease, and seeded to domestic AM grasses to increase cattle forage (all common silvicultural practices in western Canada), establishment of a Douglas-fir plantation subsequently failed (Simard, 2009). Research revealed that, relative to adjacent forest soils, roots of seedlings in the clearcut failed to form a diverse ECM fungal community, and were infected by AM fungi over 22–26% of their length and by the root endophytic pathogen, *Olpidium*. These changes in the rhizosphere community of Douglas-fir, combined with the high competitive abilities of the grasses, reduced water and nutrient uptake and caused seedling mortality. Similar to studies by Perry et al. (1989b), transfer of soils from beneath hub trees of adjacent intact forest to the planting holes increased colonization of a diverse ECM fungal community and enhanced seedling survival and growth.

These results indicate that displacement of the native ECM fungal inoculum with destumping, and introduction of AM fungi with grass-seeding disrupted the belowground foodweb, leading to a breakdown of resource uptake and other biochemical feedbacks. Other stresses, such as summer drought, soil compaction, and infection by *A. ostoyae*, likely interacted with the ECM fungi to degrade the site. The annual grasses that are commonly seeded for cattle forage and erosion control following clearcutting or wildfire in British Columbia (Stark et al., 2006), and the exotic weeds that are invading forests with increasing frequency (Liebhold et al., 1995), are either AM or non-mycorrhizal. With introduction and invasion of these plants, the resulting shift away from the native ECM fungus community could lead to more wide-spread degradation of interior Douglas-fir forests. Similar shifts in native ECM fungus communities have been documented with severe or

frequent disturbance and weed invasion in tropical forest, boreal forest and native rangeland (Perry, 1995 and references therein).

#### 15. Managing to maintain forest ecosystems in a changing climate

The natural patterns and processes in native forests provide an intuitive strategy for their protection or, where they are disturbed or damaged, for reforestation or restoration. The successful establishment of seedlings and mycorrhizal networks across a range of disturbance severities suggests that these ecosystems are resilient to the natural mixed severity disturbance regimes. Provided disturbances are not unusually extensive, and that residual trees and plants are retained nearby, the native inoculum will recover quickly, even in small, severely disturbed patches. Great care is needed in mountain pine beetle salvage programs to ensure residual trees and plants are well distributed through openings, and that sites are reforested rapidly to capture the ECM fungal legacy from the previous forest. Otherwise, variable retention harvesting that includes a variety of opening sizes across the landscape appears to do well at emulating natural disturbance effects on the ECM fungal community.

For protecting forest stability, it is obvious that harvesting practices should not high-grade the largest, fittest trees from the landscape. Instead, these trees should be conserved in patches, where neighbors protect them against abiotic and biotic damaging agents and serve as future recruits when the central hub tree dies. Likewise, broadleaves should be maintained for their facilitative and protective effects rather than removed because they compete with commercial conifers, as is current practice in Canada (Liefers et al., 2007). Conserving these key trees will not only conserve genetically diverse tree populations and mycorrhizal networks, thus facilitating natural regeneration of genetically diverse tree communities with high adaptive capacity (*sensu* Whitham et al., 2006), but they will also serve to modify the abiotic and biotic environment for regeneration, and provide future nesting sites for birds and small mammals. Equally important is retention of forest floor materials on site for their ECM fungal inoculum and other ecosystem services, even if they are disturbed and redistributed within sites (Graham et al., 1994).

For reforestation of disturbed sites, native genotypes should be seeded or planted as quickly after disturbance as possible in clumps centered on old conifers or broadleaves. Natural regeneration (seeded or naturally dispersed) should be favored over plantings and in subsequent silvicultural treatments for its local adaptation. Planting should also take advantage of spatial patterns in high resource availability and native soil inoculum should be replaced where necessary. Seeding with exotic grasses should be avoided as much as possible since most are non-mycorrhizal increasers and native plants generally regenerate quickly, even on severely disturbed sites (Stark et al., 2006). Finally, trees should be allowed to grow to an old age so they can provide valuable feedback to regenerating seedlings, thus stabilizing the whole forest community.

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