

Ectomycorrhizae and forestry in British Columbia: A summary of current research and conservation strategies

Alan M. Wiensczyk¹, Sharmin Gamiet², Daniel M. Durall³, Melanie D. Jones⁴, and Suzanne W. Simard⁵

Abstract

Ectomycorrhizae are fungus-root associations that comprise the feeder roots of most commercially important conifers in British Columbia. A large body of research has been conducted on ectomycorrhizae as they relate to forestry in the province; however, much of this information is scattered and is generally of a highly technical nature.

This extension note summarizes the latest research on ectomycorrhizae, including information on the role that ectomycorrhizal fungi play in forest ecosystems. The authors discuss several helpful forest management practices that can maintain a diverse community of ectomycorrhizal fungi across the landscape. These include: retaining refuge plants, mature trees, and old-growth forests; retaining the forest floor during harvest and mechanical site preparation; avoiding high-intensity broadcast burns; minimizing the effects of species shifts, particularly following grass seeding; maintaining the edge-to-area ratio of harvested areas within certain limits; planting a mixture of tree species soon after harvest; retaining coarse woody debris; and managing for the fruiting bodies formed by ectomycorrhizal fungi, including edible mushrooms and truffles, fungi species used by wildlife, and rare and endemic species.

Contact Information

- 1 Extension Specialist, FORREX–Forest Research Extension Partnership, 200-640 Borland Street, Williams Lake, BC V2G 4T1. E-mail: alan.wiensczyk@forrex.org
- 2 Mycologist, Mycology Resources, P.O. Box 2603, Clearbrook Station, Abbotsford, BC V2C 6R4. E-mail: sgamiet@dowco.com
- 3 Assistant Professor, Biology Department, Okanagan University College, 3333 College Way, Kelowna, BC V1V 1V7. E-mail: dmdurall@ouc.bc.ca
- 4 Associate Professor, Biology Department, Okanagan University College, 3333 College Way, Kelowna, BC V1V 1V7. E-mail: mjones@ouc.bc.ca
- 5 Associate Professor, Forest Sciences, Faculty of Forestry, University of British Columbia, 2004-2424 Main Mall, Vancouver, BC V6T 1Z4. E-mail: ssimard@interchange.ubc.ca



Introduction

Ectomycorrhizae are fungus-root associations that comprise the feeder roots of most commercially important conifers. Much useful research and management information exists about these tiny “fungus-roots”; however, this information is scattered and is generally of a highly technical nature.

In this extension note, we summarize the latest information on ectomycorrhizae as it applies to forestry in British Columbia¹. We briefly describe ectomycorrhizal fungi and discuss the reasons why forest managers should be concerned about their conservation. We then discuss the functional role these fungi play in tree growth and several important management techniques that can be used to maintain these beneficial plant/fungal associations across the landscape. These include:

- Retaining refuge plants, mature trees, and old-growth forests;
- Retaining the forest floor during harvest and mechanical site preparation;
- Avoiding high-intensity broadcast burns;
- Minimizing the effects of species shifts, particularly following grass seeding;
- Maintaining the edge-to-area ratio of harvested areas within certain limits;
- Planting a mixture of tree species soon after harvest;
- Retaining coarse woody debris; and
- Managing for the fruiting bodies formed by ectomycorrhizal fungi, including edible mushrooms and truffles, fungi species used by wildlife, and rare and endemic species.

With an increased understanding of ectomycorrhizal fungi, beneficial forest practices can be better developed and more extensively applied, while damaging ones may be avoided.

Why the Interest in Ectomycorrhizae?

Mycorrhizal fungi form close physical associations (or symbiotic relationships) with the roots of most vascular plants (Figure 1). The Greek term “mycorrhiza,” which describes the association, literally means “fungus-root.”

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Both fungal and plant partners can benefit from this association (Smith and Read 1997). The fungal partner provides the plant with soil nutrients and water and, in turn, receives photosynthetically derived plant carbohydrate.

Several general types of mycorrhizae exist, of which *ectomycorrhizae* predominate on forest trees of western North America (Molina *et al.* 1992). More than 5000 species of fungi are estimated to form ectomycorrhizae (Molina *et al.* 1992) worldwide, although this number may be low. Most of these fungi produce mushrooms and their allies above-ground, and up to one-quarter form truffles below-ground. Some species of mushrooms and truffles formed by ectomycorrhizal fungi are important food sources for small mammals and some species are harvested commercially.



Michelle Gillespie

FIGURE 1. *Lactarius* mycorrhizae on fine roots of western hemlock.

¹ This extension note contains information on the ecology and management of non-timber forest products. In promoting implementation of this information, the user should recognize the equitable sharing of benefits derived from the management and use of this product (Article 8[j] of the United Nations Convention on the Conservation of Biological Diversity). Where possible, the user should involve the keepers of this knowledge and encourage customary use of biological resources in accordance with traditional cultural practices that are compatible with the conservation and sustainable use requirements (Article 10[c]).



Most of British Columbia's important commercial conifers (e.g., all species of pine, spruce, larch, hemlock, and true fir, as well as both subspecies of Douglas-fir) and some broadleaf trees (aspen and birch species) form ectomycorrhizal associations. Well-known exceptions are cedars and maples, which form other types of mycorrhizal associations, and poplars and alders, which form ectomycorrhizae as well as other types of mycorrhizal associations.

A great deal of research has been conducted on ectomycorrhizae, their functioning in the ecosystem, and the effects of forest management on their abundance and diversity. Forest managers should be concerned about conserving a high diversity of ectomycorrhizal fungi for two main reasons.

1. Different ectomycorrhizal fungi play different roles in tree growth.
2. Different ectomycorrhizal fungal communities associate with differently aged forests across the landscape.

The next section describes some of the basic biology of ectomycorrhizae, their diversity, and the functional role they play in plant growth.

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What Are Ectomycorrhizal Fungi?

Some Biological Basics

Ectomycorrhizal fungi usually form a mantle that encloses the plant rootlet, from which hyphae (i.e., vegetative, non-reproductive, threadlike filaments) radiate outward into the soil, as well as inward between the root cells to form a hyphal network called the "Hartig net." The hyphae of most ectomycorrhizal fungal species proliferate in the duff layer of the forest floor, but some also inhabit mineral soil, and still others prefer decaying wood as a substrate (Goodman and Trofymow 1998). Some ectomycorrhizal fungi require large amounts of carbohydrate, which they acquire from their plant hosts, and so are dependent on mature trees that can meet their carbohydrate demands (Deacon and Fleming 1992). However, these fungi can also colonize



Leonard Hutchison

FIGURE 2. *Hydnellum peckii* (Strawberries and cream, or Bleeding hydnellum) found near Adams Lake, B.C.

seedlings growing in close proximity to roots of mature tree hosts (Simard *et al.* 1997b, Kranabetter and Wylie 1998) via networks of fungal hyphae.

Ectomycorrhizal fungi colonize new roots from several types of inoculum (i.e., material that is the source of fungal cells):

- hyphae;
- spores, produced by sexual structures called sporocarps or fruiting bodies (e.g., mushrooms and their allies as well as truffles; see Figure 2), or spores produced by simple cell division from hyphae; and
- sclerotia, which are little balls of hyphae.

Ectomycorrhizal fungi generally cannot survive in the soil for long periods without a host, so hyphae are typically attached to living roots. The relative importance of these different kinds of inocula in forests is not well understood. However, the total amount and diversity of fungal inoculum usually decreases rapidly following harvesting or burning of host trees (Kranabetter and Wylie 1998; Baar *et al.* 1999; Hagerman *et al.* 1999a, 2001; Kranabetter 1999; Massicotte *et al.* 1999), with greater declines following more severe disturbances (Bradbury *et al.* 1998). The recovery of ectomycorrhizal fungi following a disturbance takes time, usually decades (Visser 1995).

Several studies highlight hyphae attached to living roots as one of the important sources of inoculum in



undisturbed soil. For example, seedlings will form ectomycorrhizae with more species of fungi when they are planted in contact with live roots of mature trees than when a barrier is placed between them (Simard *et al.* 1997b). In addition, seedlings that were originally non-mycorrhizal can become colonized to a greater extent and by more ectomycorrhizal fungi when they are planted near the edges of cutblocks where adjacent forest tree roots extend (Hagerman *et al.* 1999b). In laboratory situations, fungi will form ectomycorrhizae with a wider range of tree species if they colonize from hyphae attached to another seedling rather than from spores (Massicotte *et al.* 1994).

Although all ectomycorrhizal fungi produce spores, only some of these species seem able to colonize from them (Fox 1986a). Nevertheless, spores may be especially important after fire that is severe enough to burn organic soil horizons (Grogan *et al.* 2000). Spores of mushrooms are dispersed by wind and thus can reach the centre of burns and clearcuts (Allen 1987). Spores of truffles are dispersed primarily by small mammals. For instance, mammal species frequenting clearcuts or truffles decomposing underground will leave spores behind (Miller *et al.* 1994), which act as inoculum in the clearcuts.

Once trees are harvested, the ectomycorrhizae remaining in the soil appear to take 1–2 years to die (Harvey *et al.* 1980; Hagerman *et al.* 1999a). Dying ectomycorrhizal roots sometimes support sufficient live hyphae to colonize new roots, depending on the fungal species involved (Bà *et al.* 1991). Thus, they are a possible source of inoculum following clearcut harvesting.

Sclerotia are produced by relatively few ectomycorrhizal fungal species (e.g., *Cenococcum geophilum*). Sclerotia can persist from a few weeks to months, depending on the fungal species, and can be especially abundant following fire (Fox 1986b; Miller *et al.* 1994). Sclerotia contain sufficient hyphae to act as inoculum (Bà *et al.* 1991).

Ectomycorrhizal Fungal Diversity

Ectomycorrhizal fungal species differ in several ways, including:

- their ability to take up various forms and types of nutrients,
- their rate of nutrient uptake,
- their tolerance to water stress and temperature extremes,

Ectomycorrhizal fungi play an important role in tree growth.

- the substrates they inhabit, and
- the parts of the root system (distance from the bole) with which they form the associations (Deacon and Fleming 1992; Smith and Read 1997).

Because of the variability in the characteristics of ectomycorrhizal fungi, trees forming a diverse array of ectomycorrhizae are thought to be better suited to survive and grow in variable soil and climatic conditions than trees forming ectomycorrhizae with only one or a few fungal species (Hagerman *et al.* 1999b). However, testing this hypothesis has yielded ambiguous results (Baxter and Dighton 2001; Jonsson *et al.* 2001), and field experiments under various soil conditions have not yet been conducted. We, therefore, do not yet know how ectomycorrhizal fungal diversity affects tree seedling growth.

The Functional Role of Ectomycorrhizal Fungi

Ectomycorrhizal fungi play an important role in tree growth. They provide numerous benefits to their host plant with different fungal species providing different benefits. These include:

- enhancing the uptake of essential nutrients (mainly phosphorus and nitrogen) and water (Boyd *et al.* 1986; Jones *et al.* 1991);
- protecting against pathogens (Marx 1969; Perrin and Garbaye 1983) and heavy metals (Jones and Hutchinson 1986);
- binding soil particles to create favourable soil structure (Borchers and Perry 1992);
- facilitating below-ground nutrient transfer among plants (Simard *et al.* 1997a); and
- altering the competitive relationships among plants of different species (Perry *et al.* 1989a).

One type of ectomycorrhiza, known as a tuberculate ectomycorrhiza, also harbours nitrogen-fixing bacteria (Li *et al.* 1992; Paul *et al.* 1998).

The next section explains some of the techniques that forest managers can use to conserve ectomycorrhizal fungi, thereby maintaining their diversity and their important role in tree growth in the province.



Forest Management Techniques to Conserve Ectomycorrhizal Fungi

Several important techniques to maintain a diverse community of ectomycorrhizal fungi across the landscape are available to forest managers. This section provides a summary of research information related to nine forest management strategies.

Retain Refuge Plants, Mature Trees, and Old-growth Forests

In their decision making, forest managers should consider the benefits that “refuge plants,” mature trees, and old-growth forests provide a harvested or naturally disturbed forest, including their role in maintaining a diverse community of ectomycorrhizal fungi.

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Refuge Plants

In some situations, ectomycorrhizal plant hosts persist following disturbances such as forest harvesting, and serve as sources of fungal inoculum for regenerating tree species (Perry *et al.* 1989b; Kranabetter 1999). These plants, called “refuge” plants or “reservoir hosts,” include bearberry (*Arctostaphylos uva-ursi*), sitka alder (*Alnus viridis* spp. *sinuata*), willow (*Salix* spp.), paper birch (*Betula papyrifera*), and trembling aspen (*Populus tremuloides*). Research has shown that three years following forest harvesting, bearberry maintained a mycorrhizal fungi community similar to that found on Douglas-fir in the undisturbed forest. Therefore, the bearberry could potentially provide native inoculum for neighbouring Douglas-fir seedlings (Hagerman *et al.* 2001). Some species of refuge plants, particularly trembling aspen and paper birch, are commonly viewed as deleterious because they compete with planted conifer seedlings for light, water, and nutrients (Comeau *et al.* 1999). Because of their competitive abilities, these plants are frequently the targets of vegetation control measures. However, studies show that refuge plants can also facilitate survival or growth of conifer seedlings (e.g., Horton *et al.* 1999).

Mature Trees

The diversity of ectomycorrhizal fungi increases over time up to a certain forest stand age, after which it stabilizes (Visser 1995). As stands age, species are usually added to the fungal community, but they do not necessarily replace the earlier ones (Visser 1995; Bradbury *et al.* 1998). Some fungi, such as *Rhizopogon* spp., may be present throughout the life of a stand (Visser 1995). The change in ectomycorrhizal fungal communities over time is a complex process, which requires further study.

The typically diverse ectomycorrhizal fungal community on mature trees can benefit nearby seedlings. Studies in British Columbia show that significantly greater ectomycorrhizal diversity exists on seedlings planted adjacent to mature trees than on those planted outside of root contact with mature trees (Simard *et al.* 1997b; Hagerman *et al.* 1999b; Kranabetter 1999). This suggests that mature trees can help maintain a diverse ectomycorrhizal fungal community on clearcut sites which include mature tree reserves, and that these trees would be effective sources of inocula. Mature trees may retain these fungal species within the reserves until conditions in the surrounding plantation are favourable for their spread outside the reserves. The importance of green tree retention should increase as the size of the disturbance and distance from the undisturbed forest increases and as the amount of young forest increases across the landscape (Hagerman *et al.* 1999a; Kranabetter 1999).

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Old-growth Forests

Old-growth forests are composed of various tree ages, sizes (including large mature and old trees, and large standing and fallen dead trees), and multiple canopy layers with canopy gaps and understory patchiness (B.C. Ministry of Forests 1991; Franklin and Spies 1991). Old-growth forests have more diverse macro- and microhabitats than young and mature forests and, therefore, are expected to support a more diverse suite of ectomycorrhizal fungi. Therefore, landscape-level plans should include old-growth forest retention areas



and should allow for the recruitment of future old-growth forests.

Some species of ectomycorrhizal fungi fruit exclusively or predominantly in old-growth forests (Ammirati *et al.* 1994; Walker 1995; North and Trappe 1996; Gamiet and Ammirati 1999; O'Dell *et al.* 1999; Smith *et al.* 2000). Studies on the Olympic Peninsula in Washington State reported higher species richness and diversity (see sidebar) of ectomycorrhizal sporocarps in old-growth forests compared with

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mature forests (Walker *et al.* 1994; North and Trappe 1996). In old-growth forests of the northern spotted owl range in the U.S. Pacific Northwest, approximately 235 species of fungi are being considered and rated for site management because they fruit predominantly within these older forests (Forest Ecosystem Management Assessment Team 1993; Ammirati *et al.* 1994). Old-growth forests may be important for maintaining fungal diversity at the landscape level, but further study is required to determine how these areas function “as refugia for fungal diversity and centres of propagule dispersal” (Massicotte *et al.* 1999). While sporocarps are important as a source of food for animals, their abundance is a poor predictor of the abundance of that fungus on root tips underground (Jonsson *et al.* 1999).

Ectomycorrhizal fungi sometimes form dense mats of a single species in forest floor litter and mineral soil. A study in the Cascade Range of Oregon (Griffiths *et al.* 1996) showed that these mats covered a greater area in old forests than in younger forests. Several different genera of fungi form mats and each can differ in the role it plays in nutrient cycling. For instance, some species assist in the nutrient cycle by weathering mineral soils, thereby releasing nutrients (Jongmans *et al.* 1997; Arocena and Glowa 2000; Landeweert *et al.* 2001).

Species Richness and Evenness

Diversity is commonly expressed simply as the total number of species present in a community (species richness), or as an index which includes two components—species *richness* and species *evenness*.

Species evenness refers to the proportional abundance of each species within a community. For example, plant communities 1 and 2 each have four tree species with the following number of stems per hectare (sph):

Community 1	Community 2
Species 1: 110 sph	Species 1: 300 sph
Species 2: 105 sph	Species 2: 10 sph
Species 3: 107 sph	Species 3: 500 sph
Species 4: 100 sph	Species 4: 50 sph

Species richness (the number of species) is the same for each community, which both have four tree species. However, Community 1 has a uniform number of each of the four species and therefore would have a higher species *evenness* value than Community 2. Species evenness values range between 0 and 1, where 1 is uniform or even, and 0 is non-uniform or uneven.

Retain Forest Floor During Harvest and Site Preparation

Both the upper mineral soil and the forest floor, with its organic layers and woody debris, are home to various soil micro-organisms, including the majority of the ectomycorrhizal root tips (Vogt *et al.* 1981; Amaranthus *et al.* 1989; Perry *et al.* 1989b). Removal or loss of the forest floor during site preparation may alter the colonization of seedling roots by ectomycorrhizal fungi (Amaranthus *et al.* 1989; Simard *et al.* 2002a), which in turn can affect seedling survival and growth (Jurgensen *et al.* 1997). Other forest activities, such as timber harvesting, natural and prescribed fires, grazing, and recreation, can also change the character of the forest floor (Graham *et al.* 1999). For example, one unreplicated study has shown that soil compaction and forest floor removal resulted in a 60% decrease in ectomycorrhizal fungal abundance and diversity on



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Douglas-fir seedlings (Amaranthus *et al.* 1996). Ectomycorrhizal fungus diversity on western white pine, by contrast, was not affected by the same treatment. In another study, mechanical removal of pinegrass and the forest floor in 150 × 150-cm patches reduced the diversity and richness of ectomycorrhizal fungi on lodgepole pine seedlings when compared with chemical treatments that left the forest floor intact (Jones *et al.* 1996; Simard *et al.* 2002a). The mechanical treatment also resulted in lower seedling survival and growth. Two years after planting the treatment differences in ectomycorrhizal diversity disappeared probably because the seedling roots had grown outside of the treated patches, but early seedling survival differences continued to persist 9 years after treatment. In northern British Columbia, the diversity of ectomycorrhizal fungi showed no statistically significant change after forest floor removal, but a change in fungal species occurred (Mah *et al.* 2001). Another study (Simard *et al.* 2002a) concluded that removal of forest floor material should be avoided during site preparation because of the short-term negative effects on the ectomycorrhizal community, nutrient availability, and soil physical properties. These results support earlier recommendations (Harvey *et al.* 1987) to minimize massive break-up of the forest floor and to maximize the diversity of microsites following site preparation for regeneration objectives. However, the evidence available at this time does not warrant major changes in forest practices, which already strive to minimize displacement of forest floor materials.

Avoid High-intensity Broadcast Burns

The effects of fire (either natural wildfires or prescribed fires) on ectomycorrhizae are diverse—every fire has unique characteristics as does every plant community and physical environment. Uniformity and depth of burn, heat intensity, and heat penetration into the soil will all vary with the thickness and moisture

content of the forest floor as well as with the type and loading of fuel.

Fire can also have a negative, positive, or negligible effect on ectomycorrhizae depending on the species of fungus involved (Baar *et al.* 1999; Stendell *et al.* 1999; Mah *et al.* 2001). It is not surprising, therefore, that variable effects of fire on ectomycorrhizae are reported in different studies. For example, one found no statistically significant effects of fire on ectomycorrhizal fungus diversity in broadcast-burned clearcuts (Mah *et al.* 2001), whereas others found a decrease in diversity with increasing fire intensity (Dahlberg *et al.* 2001). Severe, hot burns may be more destructive to ectomycorrhizal fungi than physical disturbances such as screefing (Visser and Parkinson 1999). Species evenness, but not species richness, appeared lower in burned stands than in unburned stands in another study (Jonsson *et al.* 1999). Following an under-burn in a mature ponderosa pine forest, a highly statistically significant loss of ectomycorrhizal biomass in the forest floor occurred, but no statistically significant change occurred in the upper mineral soil layers (Stendell *et al.* 1999). However, in another mature ponderosa pine forest where the forest floor was moist at the time of under-burning, the microbiological and nutrient properties of the organic layer were preserved (Graham *et al.* 1999).

The use of low-intensity fire as a site preparation treatment may be useful since it facilitates seedling establishment and limits the effects on ectomycorrhizal fungal diversity (Figure 3). At the same time, variability in fire characteristics can help to maintain variability in forest types across the landscape. Where landscape-level



Alan Vyse

FIGURE 3. A prescribed burn at the Sicamous Creek Silviculture Systems Trial, Sicamous, B.C.



management plans include higher-intensity fires in localized areas, forest managers should ensure that sources of fungal inocula for regenerating stands are in close proximity.

Minimize Grass Seeding and Avoid Species Shifts

Invasion or dominance by non-mycorrhizal or other types of mycorrhizal plants can suppress the growth of ectomycorrhizal plants, especially if the site has been altered substantially during or after harvest. Survival and growth of ectomycorrhizal tree species can decrease dramatically when domestic grasses seeded to the site out-compete the native shrub-dominated plant community (Amaranthus and Perry 1994; Simard *et al.* 2002b). Such declines in tree performance were attributed to reduced levels of ectomycorrhizal inoculum, and direct competition with grasses for soil water (Simard *et al.* 2002b). However, where native plants still dominate the community, low rates of grass seeding likely have little effect on the ectomycorrhizal community (Simard *et al.* 2002b).

Changes in the mycorrhizal and microbial communities following herbicide treatment and grass invasion were also studied at a high-elevation site in the Pacific Northwest (Perry *et al.* 1989b). These treatments resulted in a shift in the plant community to one dominated by other non-ectomycorrhizal plants. This may be partially responsible for the failure (after four attempts) to regenerate this once-productive white fir (*Abies concolor*) site to native ectomycorrhizal tree species.

Non-mycorrhizal plants can also replace the natural, mycorrhizal species as a result of overgrazing and cultivation (Perry *et al.* 1989b). Dramatic changes in plant community composition, such as can occur with heavy grass seeding, overgrazing, or invasion by exotic weeds, may weaken the ectomycorrhizal linkages between old and new stands (Amaranthus and Perry 1994) and reduce ecosystem productivity.

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Harvesting of forest stands reduces one of the major sources of inoculum—the hyphae attached to living roots.

Plant Soon After Harvest

Harvesting of forest stands reduces one of the major sources of inoculum—the hyphae attached to living roots. Dying ectomycorrhizae may act as an inoculum source, but most ectomycorrhizal roots typically die and disappear within two years following clearcut logging (Harvey *et al.* 1980; Bradbury 1998; Visser *et al.* 1998; Hagerman *et al.* 1999a; Byrd *et al.* 2000). For example, in Douglas-fir, western larch, subalpine fir, and Engelmann spruce stands in western Montana, the numbers of active ectomycorrhizal roots decreased considerably by the first July following October logging (Harvey *et al.* 1980). In a subalpine fir and Engelmann spruce stand in the Southern Interior of British Columbia, numbers and diversity of ectomycorrhizae 16 m and greater from the forest edge remained unchanged for the first summer after winter logging, but declined dramatically by the second summer (Hagerman *et al.* 1999a).

Other sources of ectomycorrhizal fungal inoculum that remain on a site after clearcut logging include sclerotia and spores. These can be highly effective sources of inoculum for germinants that appear immediately after a stand-destroying fire (Baar *et al.* 1999; Grogan *et al.* 2000) and the same is likely true on clearcuts. Unfortunately, we do not know how long spores or sclerotia remain viable in soils; consequently, we do not know how soon to plant after harvest in order to retain high inoculum levels. For instance, when Douglas-fir and ponderosa pine were grown in a greenhouse in soils from clearcuts 1–22 years old, no correlation existed between time since clearcut harvesting and ectomycorrhiza formation (Parke *et al.* 1984). However, these soils were all collected from clearcuts classified as “difficult to regenerate.” In contrast, seedlings planted in clearcuts that had no living ectomycorrhizal hosts for 5 years or more showed reduced colonization (Amaranthus *et al.* 1990; Borchers and Perry 1990). To take advantage of ectomycorrhizae inoculum from the previous stand (and therefore the widest range of inoculum), seedlings should be planted within the first growing season after clearcut logging. If planted more than 5 years after harvest, total inoculum levels



will more likely be below the threshold for complete colonization.

Plant a Mixture of Tree Species

Regenerating mixed species stands is a valuable ectomycorrhizae management strategy for two reasons.

1. Some evidence suggests that trees are able to associate with a wider range of ectomycorrhizal fungi when they are grown adjacent to trees of other species (Massicotte *et al.* 1999). For example, when Douglas-fir is grown together with paper birch, the number of fungi shared by the two species appears to increase compared to when they are grown separately (Simard *et al.* 1997c). In the field, ectomycorrhiza species evenness increased slightly for Douglas-fir when grown in plots with paper birch (Jones *et al.* 1997).
2. Mixed stands help sustain a higher species diversity of ectomycorrhizal fungi on a site because they contain more hosts for fungi with narrow host ranges as well as for fungi with broad host ranges². A recent study of mixed stands in the Canadian boreal forest (Kernaghan *et al.* 2001) showed a clear, positive relationship between the diversity of overstorey trees and the diversity of ectomycorrhizae present in the soil. Higher fungal diversity is probably important for tree growth because different species exhibit different characteristics and provide different benefits to the host tree. Fungi with narrow host ranges will disappear from a harvested site unless their particular host is retained or included in the regenerated mixture of tree species.

Maintain Edge-to-Area Ratio Within Certain Limits

After clearcut harvesting, there are two sources of ectomycorrhizal hyphae on living roots. The first source is living ectomycorrhizal hosts in the cutblock, such as:

- residual conifer stems,
- advance regeneration,
- broad-leaved trees such as aspen or birch, or
- woody shrubs such as bearberry, sitka alder, and willow (see section on *Refuge Plants*).

The second source is the roots of trees in the surrounding forest, which are likely to extend 8–13 m into the harvested area (Stone and Kalisz 1991; Parsons *et al.* 1994). Levels of ectomycorrhizal fungal inoculum are therefore expected to be greatest in the periphery of the cutblock (Harvey *et al.* 1980). For instance, research has shown that young, non-mycorrhizal Engelmann spruce seedlings planted 2 or 3 m from the forest edge were colonized at twice the rate as seedlings planted 16 m or more from the edge (Hagerman *et al.* 1999b). These seedlings were also colonized by 50% more types of ectomycorrhizal fungi (Figure 4). Similar reductions in ectomycorrhizal fungal diversity with increasing distance from the forest edge were observed for naturally regenerating western hemlock seedlings (Kranabetter and Wylie 1998).

Interestingly, reduced colonization or decreased ectomycorrhizal diversity with distance from the edge was less apparent for seedlings grown in nurseries than for naturally regenerated seedlings (Durall *et al.* 1999; Jones *et al.* 2002). This may mean that high edge-to-area ratios are more important in naturally generated clearcuts than in planted clearcuts. Containerized seedlings frequently become mycorrhizal in the nursery, either from air-borne spores of ectomycorrhizal fungi or as a result of inoculation with a commercial product. Edge-effect patterns are probably masked in these cases



FIGURE 4. A 1-ha harvested patch in the Sicamous Creek Silviculture Systems Trial, Sicamous, B.C.

² Some species of ectomycorrhizal fungi will only colonize the roots of a few specific plant species (Molina *et al.* 1992). These fungi are said to have narrow host ranges. Other species of ectomycorrhizal fungi will colonize the roots of many different plant species and thus are said to have broad host ranges.



as nursery fungi may slow the rate of colonization by indigenous fungi following planting (McAfee and Fortin 1987), although indigenous fungi will eventually replace nursery fungi.

On sites where conifers, broadleaves, or other refuge plants are not retained, ectomycorrhizal inoculum is maximized when harvested areas are designed with a reasonably high edge-to-area ratio or with reserves. Ectomycorrhizal colonization of trees is highest when both light and inoculum levels are adequate, such as along forest edges of clearcuts (Hagerman *et al.* 1999b), or in thinned stands (Zhou and Sharik 1997). Partially cut forests also retain a diversity of ectomycorrhizal fungi (Durall *et al.* 1999; Kranabetter and Kroeger 2001). Some component of partial cutting on a landscape allows timber removal, while maintaining the mature forest and fungal communities. These forests could be an important source of inocula, along with old-growth reserves, thereby facilitating the succession of ectomycorrhizal fungi into clearcuts.

Retain Coarse Woody Debris

Different species of ectomycorrhizal fungi colonize different substrates, including various types of organic substrates. Studies in Idaho and Oregon and on Vancouver Island showed that some fungi preferentially colonize rotten wood, while others colonize mineral or organic soil horizons (Kropp 1982; Harvey *et al.* 1997; Goodman and Trofymow 1998). Maintaining a diverse mix of mineral and organic patches in clearcuts will therefore encourage a varied ectomycorrhizal fungal community.

The highest number of ectomycorrhizal roots are generally found in organic substrates, particularly in decayed wood or soil mixtures containing decayed wood and organic matter, and comparably fewer numbers are found in mineral substrates (Harvey *et al.* 1997; Goodman and Trofymow 1998). On extremely dry, harsh sites, coarse woody debris and decayed wood are particularly important because these substrates hold moisture during summer drought periods (Harvey *et al.* 1986; Amaranthus *et al.* 1994). Logs appear more productive than stumps, containing a greater number of ectomycorrhizae as well as more types of ectomycorrhizal fungi (Goodman and Trofymow 1998).

In lodgepole pine forests of central British Columbia, coarse woody debris is an important substrate for tuberculate mycorrhizae and associated nitrogen-fixing

Maintaining a diverse mix of mineral and organic patches in clearcuts will encourage a varied ectomycorrhizal fungal community.

bacteria (Paul *et al.* 1998). It is also exceedingly important as a habitat for the production of both below-ground (truffles) and above-ground (mushrooms) fruiting bodies of ectomycorrhizal fungi.

At Douglas-fir forest sites in Oregon, eight of the 21 truffle species occurred only in coarse woody debris (Amaranthus *et al.* 1994) and the dry weight of truffles was ten times higher in coarse woody debris than in soil in the mature forest. Although this great a difference was not observed in any of the nearby plantations, it suggests that coarse woody debris is required for some ectomycorrhizal fungi to fruit. This study highlights the importance of forest management practices that retain coarse woody debris in helping to conserve the abundance and diversity of truffles, as well as the small mammals that depend on them (Amaranthus *et al.* 1994). Coarse woody debris management recommendations are available for several Montana, Arizona, and Idaho ecosystems (Graham *et al.* 1994), some of which are similar to ecosystems in the Nelson Forest Region.

Manage for Fruiting Bodies Formed by Ectomycorrhizal Fungi

The ectomycorrhizal association is part of the vegetative stage of a fungus. When environmental conditions are appropriate, many ectomycorrhizal fungi also produce reproductive structures, or fruiting bodies, either above- or below-ground (Figure 5). Fruiting bodies come in a variety of shapes, sizes, colours, and odours. Their importance to humans varies—some are poisonous or unpalatable, while others are delectable and are harvested commercially or for personal consumption. They are also important to several species of mammals and invertebrates, such as northern flying squirrels (*Glaucomys sabrinus*), California red-backed voles (*Clethrionomys californicus*), kangaroo rats, deer, springtails, and beetles. The fruiting bodies of some ectomycorrhizal fungi are also classified as “rare.” Various forest management activities can have either





FIGURE 5. *Boletus edulis* (King bolete): a deliciously edible ectomycorrhizal fruiting body.

beneficial or negative effects on the production of ectomycorrhizal fungal fruiting bodies. Resource managers need to be aware of these effects so that management practices can be designed accordingly. This may be critical for those ectomycorrhizal fungi that rarely fruit.

Edible Mushrooms

British Columbia's wild edible mushroom harvest generates millions of dollars each year and consists largely of ectomycorrhizal fungi, such as pine mushrooms (*Tricholoma magnivelare*), chanterelles (*Cantharellus formosus* and *C. subalbidus*), and boletes (*Boletus edulis*). Pine mushrooms are the most commercially important wild forest mushroom in the province and are exported exclusively to Japan (de Geus 1995), while chanterelles, boletes, and others are primarily exported to parts of North America and Europe (de Geus 1995). Known commercial mushroom sites are located across all regions of the province (de Geus 1995; Freeman 1997; Trowbridge and Macadam 1999; Ehlers and Frederickson 2000; Berch and Wiensczyk 2001; Kranabetter *et al.* 2002) in forests from 20 to more than 200 years old (Hosford and Ohara 1995; Norvell 1995; Redhead 1997a; Pilz *et al.* 1998).

Forest practices, such as logging, site preparation, tree selection, fire, fertilization, pesticide use, brushing and spacing, and grazing, will influence mushroom presence, reproduction, and productivity. Ectomycorrhizal fungi require living roots, and therefore living

trees to survive. As a result, timber harvesting, particularly clearcutting, profoundly reduces mushroom production (Durall, Gamiet, and Simard [unpublished]); Smith *et al.* 2002) until the mature forest becomes re-established. Local pickers in the Anaheim Lake area (Chilcotin Region, B.C.) report, however, that pine mushrooms are still produced in any island remnants retained within a cutblock. These island remnants apparently provide appropriate inoculum levels and environmental conditions, and a carbon source for some level of mushroom production (Bill Chapman, B.C. Ministry of Forests, pers. comm., March 2001); however, for how long and at what level is unknown. In the Date Creek area of the Prince Rupert Forest Region, gap area size significantly affected the production of fruiting bodies in forests (Durall *et al.* 1999). In this study area, sporocarp diversity declined significantly in gaps larger than 900 m². Soil compaction from machinery and trampling can damage the mycelium (a mat-like mass of fungal hyphal), and reduce mushroom productivity (Colgan *et al.* 1999; Bill Chapman, B.C. Ministry of Forests, pers. comm., March 2001).

Forest management techniques that promote mushroom production have been studied in other countries. To encourage matsutake mushroom (*Tricholoma matsutake*, a close relative of the pine mushroom) production in Japanese forests, for example, various silviculture treatments have been applied. Overstorey trees are thinned, tree species composition is altered, non-host understorey shrubs and herbs are cut, and organic litter is removed from the forest floor (Hosford *et al.* 1997). In North America, such intense management of forests for pine mushroom production does not occur. Studies in Europe show that nitrogen deposits from air pollution (Arnolds 1991) and applications of nitrogen fertilizers (Termorshuizen 1993) reduce the productivity of edible ectomycorrhizal fungi. Information on the effects of pesticide application or grazing on edible mushrooms is currently not available for British Columbia. More research is required to determine how silviculture techniques could be used to promote the fruiting of economically important fungi in North American forests.

Ectomycorrhizal Fruiting Bodies and Wildlife

A highly evolved, beneficial relationship exists between ectomycorrhizal fruiting bodies, host trees, and wildlife. Fruiting bodies of ectomycorrhizal fungi are an important food source for many temperate forest mammals and invertebrates (North and Trappe 1996; Janos and Sahley 1995; Cazares and Trappe 1994; Johnson 1994;

Lawrence 1989; Bruns 1984; Fogel and Trappe 1978; Fogel 1975). In the process of consuming the fruiting body, fungal inoculum is dispersed throughout the animal's range, thereby exposing the ectomycorrhizal host trees to a higher diversity of inocula. Above-ground sporocarps generally disperse their spores through the forest by means of air and water currents. Below-ground fruiting bodies, by contrast, depend on animals for spore dispersal. Animals are attracted to the aromatic compounds produced by truffles and false-truffles (i.e., true truffles belong to the class Ascomycete; false-truffles belong to the class Basidiomycete), which lead them to excavate and consume these fungi. The spores in the fruiting bodies ingested by the animal pass through the gut and are deposited with fecal pellets (Cazares and Trappe 1994; Johnson 1994; Currah *et al.* 2000).

Some small mammals, such as the northern flying squirrel and the California red-backed vole use truffles as their primary food source (Amaranthus *et al.* 1994). These mammals, in turn, are important prey for other species of animals such as the threatened northern spotted owl (Forsman *et al.* 1984). Cavities in downed and standing dead wood are commonly used by small mammals to store food when foraging (Bunnell *et al.* 1999), and are therefore important not only for wildlife survival, but also as sources of ectomycorrhizal fungal inocula for the surrounding forest. Retaining standing and downed coarse woody debris is thus important for the dispersal of spores from both above- and below-ground ectomycorrhizal fruiting bodies.

Managers should practise forestry that encourages long-term, sustainable productivity of ectomycorrhizal fruiting bodies used by small mammals and invertebrates. A study in the U.S. Pacific Northwest showed that thinning Douglas-fir forests resulted in a shift in truffle species dominance. For example, some truffle species occurred only in thinned stands and not in the uncut controls, while other species declined significantly in thinned stands (Colgan *et al.* 1999). Another study showed that truffle density tends to be lower in young stands until the canopy closes, after which diversity increases over time (Amaranthus *et al.* 1994). Similar results were observed in high-elevation Engelmann spruce–subalpine fir forests in British Columbia where

Fruiting bodies of ectomycorrhizal fungi are an important food source for many temperate forest mammals and invertebrates.

no truffles were collected in 0.1-, 1-, and 10-ha cutblocks four years following harvesting (Durall, unpublished).

In young (4–27 year old) Douglas-fir plantations, few truffles were produced on coarse woody debris because the trees in this study had not yet developed root systems and mycorrhizae within this substrate (Amaranthus *et al.* 1994). Many above- and below-ground ectomycorrhizal fungi fruit predominantly in coarse woody debris, therefore its retention following silvicultural and logging practices encourages fruiting of these fungi.

Rare and Endemic Ectomycorrhizal Fungi

Some species of ectomycorrhizal fungi fruit infrequently and thus are considered rare. In the Netherlands, approximately 944 fungi are “red-listed,” of which 182 are threatened with extirpation and 91 are considered extinct (Arnolds 1991, 1992; Redhead 1997b). In the American Pacific Northwest, the U.S. Department of Agriculture’s Forest Ecosystem Management Assessment Team has compiled a list of rare and uncommon mycorrhizal, saprophytic, and pathogenic fungi associated with old-growth forests (Forest Ecosystem Management Assessment Team 1993). In British Columbia, the list of uncommon, rare, and endangered species is limited because many ecosystems are not yet inventoried, or specimens of various species are not adequately documented and preserved in herbariums. Using Conservation Data Centre criteria³, only two ectomycorrhizal species (*Albatrellus caeruleoporus* and *Suillus pseudobrevipes*) are considered rare for the central and southern interior regions of the province (Redhead 1997b), while approximately 20 are tentatively identified as uncommon or rare (Ginns *et al.* 1998). However, a species that might appear rare because it is reported only once or twice might be found more commonly if the province was extensively inventoried.

³ The British Columbia Conservation Data Centre (CDC) (<http://srmwww.gov.bc.ca/cdc>) is a provincial government organization that, in conjunction with the Nature Trust of BC, the Nature Conservancy of Canada, and the Nature Conservancy (US), documents and maintains a database of rare and endangered plants, animals, and plant communities in the province. The status of each species is determined using CDC criteria on the nature of occurrence (global or provincial) and the number of still surviving occurrences (from extremely rare to common) (Redhead 1997b).



Another threat to specific mycorrhizal fungi is the reduction in habitat and host ranges. Some native, or endemic, ectomycorrhizal fungi associate exclusively with birch, pine, Douglas-fir, or larch species (Molina *et al.* 1992). While pine, Douglas-fir, and birch species occur extensively in the interior of the province, larch are more restricted in their range. As at least nine ectomycorrhizal fungi are associated exclusively with larch species (Molina *et al.* 1992), threats to larch habitats are also threats to these fungi. Young, pure stands of birch are also decreasing because of fire suppression, silviculture treatments in young stands, and forest type conversions, which could all affect the availability of old birch stands in the future. Other species with limited distribution in interior British Columbia that could be threatened by habitat loss or climate change include: Pacific yew (*Taxus brevifolia*), whitebark pine (*Pinus albicaulus*), tamarack (*Larix lyallii*), grand fir (*Abies grandis*), Alaska yellow-cedar (*Chamaecyparis nootkatensis*), and mountain hemlock (*Tsuga mertensiana*).

Forest management strategies for the conservation of rare and endemic fungi are similar to those suggested for sustainable wild edible mushroom harvests. Recommendations for managing rare, endemic, and endangered fungal species are also available (see Ginns *et al.* 1998). Compiling baseline species lists from existing literature and collecting from specific habitats is a first step. Samples of any suspected rare, endemic, or endangered species should be collected, evaluated by trained taxonomists, and preserved for future reference in herbariums. Then, habitats supporting these species should be inventoried, mapped (Trappe and Castellano 1996), and monitored over the long term for changes.

Recommendations

Several existing forest management practices can help to maintain a diverse community of ectomycorrhizal fungi across the landscape. Table 1 provides a summary of the forest management strategies recommended in this extension note.

TABLE 1. Summary of forest management strategies to maintain ectomycorrhizal fungi diversity

Strategy	Management Practice
PROVIDE SOURCE OF ECTOMYCORRHIZAL FUNGAL INOCULUM	<ul style="list-style-type: none"> Retain refuge plants (e.g., bearberry, aspen, birch, willow) in harvested areas Retain green trees (single trees and patches) Retain areas of old-growth forest across the landscape Conduct partial harvesting in some areas Maintain high edge-to-area ratio by keeping harvested areas small or by including green tree retention areas
PROVIDE VARIOUS HABITATS OR MICROSITES TO ENCOURAGE A DIVERSE ECTOMYCORRHIZAL FUNGAL COMMUNITY	<ul style="list-style-type: none"> Avoid high-intensity broadcast burns as much as possible; where broadcast burning is required, use mainly low-intensity burns Minimize disturbance to forest floor during harvesting and site preparation Retain standing and downed coarse woody debris
MAINTAIN A DIVERSE ECTOMYCORRHIZAL FUNGAL POPULATION	<ul style="list-style-type: none"> Use low seeding rates where grass seeding is required, and ensure native plant species still dominate the community Plant soon after harvest: within first season after harvest is best; maximum limit is within 5 years Plant or encourage regeneration of a mixture of tree species
CONSERVE ECTOMYCORRHIZAL FRUITING BODY PRODUCTION FOR: <ul style="list-style-type: none"> HUMAN USE (COMMERCIAL AND PERSONAL CONSUMPTION) WILDLIFE RARE AND ENDEMIC FUNGAL SPECIES 	<ul style="list-style-type: none"> Minimize soil compaction from heavy machinery and trampling Minimize disturbance to forest floor when harvesting mushrooms and truffles Maintain green tree retention areas Retain standing and downed coarse woody debris Keep logged areas small (i.e., < 900m²) Maintain populations of host species (e.g., birch) Be aware of cultural and social differences amongst mushroom harvesters Watch for potential conflicts with mushroom and truffle harvesting and archaeological sites



Our understanding of ectomycorrhizal fungal ecology is improving every year. In the future, we should have more information about many important topics, including:

- the effects of fungal diversity on stand growth and health;
- the significance of hyphal linkages in reducing competition between trees;
- the suspected occurrence of “keystone” fungal species in certain habitats;
- the time needed for ectomycorrhizal fungal species to recover after disturbance in different forest types and tree species; and
- the indicator mushroom species for mature forest habitat.

Further research is also required on the taxonomy, biology, and ecology of specific mushrooms and truffles, on productivity levels of ectomycorrhizal fungal species in different habitats, including mapping these habitats at local and landscape levels, and on the effects of various silviculture systems and techniques on fruiting body production.

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