Comparison of communities of ectomycorrhizal fungi in old-growth and mature stands of Douglas-fir at two sites on southern Vancouver Island

D.M. Goodman and J.A. Trofymow

Abstract: An old-growth and a mature stand, each of fire origin and similar in drainage, slope, and exposure, were selected at each of two sites. Soil cores were collected in spring and fall for 2 years in each stand. Ectomycorrhizae were separated into types based on detailed examination of morphology and anatomy. All root tips were separated and counted. Sixty-nine morphological types were distinguished. Nineteen accounted for >1% of the 17 500 root tips examined, and 14 types were found in ≥5% of the 120 soil cores. Only three types were found in ≥20% of the cores. Total richness was approximately 100 fungi. Nine codominant mycosymbionts each colonized 2.8–24% of all tips and together colonized 67% of all tips. *Cenococcum geophilum* Fr. was the most abundant, followed by a *Rhizopogon vinicolor* Fr.-like species, an unidentified *Piloderma*-like species, *Lactarius rubrilacteus* Hesler & Smith, *Piloderma fallax* (Libert) Stalpers, and four unidentified species. Old-growth and mature stands had similar richness and diversity of ectomycorrhizal types. There was no evidence that any types were more abundant or frequent in one age-class than in the other.

Résumé : Un vieux peuplement et un peuplement mature, tous les deux issus de feux et dont le drainage, la pente et l'exposition étaient semblables, ont été sélectionnés à chacun des deux sites sous étude. Des carottes de sol ont été prélevées au printemps et à l'automne pendant 2 ans dans chaque peuplement. Les ectomycorhizes ont été classés par type sur la base d'examens morphologique et anatomique détaillés. Tous les apex racinaires ont été séparés et comptés. Soixante-neuf types morphologiques ont été identifiés. Dix-neuf types étaient présents sur >1% des 17 500 apex racinaires examinés, et 14 types furent retrouvés dans ≤5% des 120 carottes de sol. Seulement trois types furent retrouvés dans ≥20% des carottes. La richesse totale était d'environ 100 champignons. Neuf mycosymbiotes colonisaient chacun de 2,8 à 24% des apex et, ensemble, 67% de tous les apex. Le *Cenococcum geophillum* Fr. était le plus abondant, suivi d'une espèce semblable au *Rhizopogon vinicolor* Fr., d'une espèce non identifiée semblable au *Piloderma*, du *Lactarius rubrilacteus* Hesler & Smith, du *Piloderma fallax* (Libert) Stalpers et de quatre espèces non identifiées. La diversité et la richesse des types d'ectomycorhizes étaient semblables dans les vieux peuplements et les peuplements matures. Il n'y avait aucun indice indiquant qu'un type était plus abondant ou fréquent dans une classe d'âge que dans l'autre.
[Traduit par la Rédaction]

Introduction

Of the once extensive old-growth forests of Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) on Vancouver Island, only small fragments remain (British Columbia Ministry of Forests 1991). Many British Columbians are concerned about potential losses of biological diversity as old growth continues to be liquidated. Kellert (1986) described the value of biodiversity as recreational, ecological, moral, scientific, aesthetic, utilitarian, and cultural. Ecologically, one of the most important groups in forest systems are those fungi that form ectomycorrhizae, essential interfaces between soil and trees. Feeder roots of ectomycorrhizal hosts in native forests are usually >90% colonized by ectomycorrhizal fungi (e.g., Visser 1995). Diversity of ectomycorrhizae may be important for the stability of Douglas-fir ecosystems (Perry 1985; Schoenberger and Perry 1982). Long-term productivity (i.e., sustainability) of forests will require maintenance of soil function, which in turn involves a wide range of soil organisms (Franklin et al. 1989; Amaranthus et al. 1989). Ectomycorrhizal fungi are also of value for their sporocarps, which are a recreational, aesthetic, and commercial resource, and a food source for small mammals (Molina et al. 1993; Pilz and Molina 1996).

Hence the need to compare the communities of ectomycorrhizae in mature stands (≈90 years old) of Douglas-fir with those in old-growth stands to determine the importance of old growth for conservation of ectomycorrhizal fungi. This comparison could also indicate whether there is succession of ectomycorrhizal fungi in stands >90 years old. Several observers have noted succession of ectomycorrhizae in stands <40 years old (Gardner and Malajczuk 1985; Marks and Foster 1967; Mason et al. 1982; Visser and Danielson 1990). In stands <12 years old, succession was observed directly whereas in older stands, succession was studied by comparing stands of different ages. Succession appears to be most rapid in young stands, often with almost complete changes in the codominant species

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D.M. Goodman[1] and J.A. Trofymow. Pacific Forestry Centre, Canadian Forest Service, Natural Resources Canada, 506 West Burnside Road, Victoria, BC V8Z 1M5, Canada.

[1] Author to whom all correspondence should be addressed. e-mail dgoodman@pfc.forestry.ca

of the ectomycorrhizal community (Danielson and Pruden 1989; Last et al. 1984; Trofymow and van den Driessche 1991). Thereafter, new ectomycorrhizae tend to appear occasionally and the relative abundance of ectomycorrhizae may change. Ectomycorrhizae that dominate in young stands are usually present in low numbers in older stands (e.g., Visser and Danielson 1990). Some successions of ectomycorrhizal fungi might continue through later phases of stand ageing: *Elaphomyces muricatus* Fr. and *Hysterangium crassirachis* Zeller & Dodge were found in abundance in four old-growth stands (200–450 years old), but not in two young stands (69 and 79 years old), during a survey of hypogeous sporocarps of known ectomycorrhizal fungi (Luoma et al. 1991).

Reasons for ectomycorrhizal succession have not been established, although organic layer accumulation (Gardner and Malajczuk 1985; Mason et al. 1982; Visser and Danielson 1990) and changes in nitrogen availability (Abuzinadah et al. 1986; Finlay and Frostegard 1990) may be involved. Many ectomycorrhizal fungi can use peptides, peptones, and proteins as a sole nitrogen source when cultured in vitro, an ability that may allow mycorrhizal plants to access otherwise unavailable nitrogen sources in decomposing litter (Abuzinadah et al. 1986; Abuzinadah and Read 1986, 1989; Finlay et al. 1992). As a forest stand ages, there is usually a depletion of nitrogen in mineral soil and an accumulation of nitrogen in the organic layer (= forest floor), accompanied by a redistribution of fine roots (and ectomycorrhizae) to the organic layer (Gessel et al. 1973; Grier et al. 1981). Forty to 80 years after disturbance by fire or harvesting, the forest floor can recover its predisturbance thickness (Aber et al. 1978; Visser 1995).

Most surveys of fungal sporocarps and ectomycorrhizae in the same area have found many fungi fruiting but not forming ectomycorrhizae, or vice versa (e.g., Chu-Chou 1979; Dahlberg and Stenström 1991; Danielson 1984; Gardes and Bruns 1996; Lamb 1979; Visser and Danielson 1990). Furthermore, there is little correlation between the abundance of ectomycorrhizae and sporocarps for those species that form both. Observation of sporocarps provides limited information about succession and types of ectomycorrhizae present on a site. Similarly, assaying soil for ectomycorrhizae by planting trap-seedlings in a greenhouse is also, by itself, of little value because most late-stage ectomycorrhizal fungi will not form ectomycorrhizae with seedlings under these conditions (Borchers and Perry 1990; Deacon et al. 1983; Parke et al. 1984; Visser and Danielson 1990). However, if trap-seedlings are planted in the forest with minimal soil disturbance, they tend to form mycorrhizae with the dominant ectomycorrhizal fungi (Danielson and Pruden 1990; Fleming 1984; Simard et al. 1997). Surveys of naturally occurring ectomycorrhizae, combined with identification of the ectomycorrhizal fungi by comparing isolates from mycorrhizae and sporocarps, have provided the best evidence of ectomycorrhizal succession (Chu-Chou and Grace 1990; Deacon et al. 1983; Danielson 1984; Visser 1995).

There are several possible sources of inoculum of ectomycorrhizal fungi that colonize mature but not younger stands. A few ectomycorrhizal fungi may be able to form spores, sclerotia, or other resistant structures that survive for decades following clear-cutting or stand-destroying fire (Harley and Smith 1983). Most probably depend on dispersal from mature stands to maturing stands. Ectomycorrhizal fungi are dispersed mainly by wind from epigeous sporocarps (Marx and Kenny 1982) or by mammals from hypogeous sporocarps (Blaschke and Bäumler 1989; Claridge and May 1994; Malajczuk et al. 1987; Maser et al. 1978).

Studies comparing the communities of ectomycorrhizal fungi in old-growth and younger mature stands are needed to understand the importance of old-growth forest as habitat for ectomycorrhizal fungi and as refugia from which ectomycorrhizal fungi can disperse into maturing stands. We hypothesized that old growth would have a more diverse ectomycorrhizal community due to a thicker forest floor, more coarse woody debris and larger pieces of coarse woody debris, and lower concentrations of available nutrients. The morphology and anatomy of the ectomycorrhizal types observed in this study have been described in more detail (Goodman 1995).

Methods and materials

Selection and description of study sites

Two sites were selected, each with an old-growth (288 and 441 years) and a mature stand (87 and 89 years) well matched in species composition, soil, slope, aspect, and topography. At each site the stands were roughly 500 m apart. Stand ages were determined from increment cores of eight dominant or codominant trees in each stand. All stands regenerated following stand-destroying fires. The sites have been described in more detail by Goodman (1995).

Both sites were on southeastern Vancouver Island in the Very Dry Maritime subzone of the Coastal Western Hemlock biogeoclimatic zone (CWHxm) (Green and Klinka 1994) within 40 km of Victoria, British Columbia. The first site studied, Koksilah, was several kilometres north of the Koksilah River and is one of the sites studied as a part of the Coastal Forest Chronosequence Project of the Canadian Forest Service (Trofymow et al. 1997). The Koksilah site has an elevation of 580 m and is located at latitude 48°39′20″ and longitude 123°44′50″. The mature stand has a slope of 17° at an aspect of 194°; the old-growth stand has a slope of 13° at an aspect of 133°. Several studies of other groups of organisms and ecological processes have been made using the Koksilah chronosequence (Marshall 1993). The second site, Goldstream, is located in the Greater Victoria Water District, 1 km southeast of Goldstream Lake, elevation 450 m, latitude 48°29′36″, longitude 123°37′48″. The mature stand has a slope of 13° at an aspect of 163° and the old-growth stand a slope of 8° at an aspect of 214°. Each stand was on a well-drained Brunisolic soil. Douglas-fir dominated each stand. Western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) and western redcedar (*Thuja plicata* (Donn ex D. Don)) accounted for <20% of the dominant or codominant trees in each of the four stands. Trees on the mature stands were 76 and 68% as tall (maximum height) as those on the old-growth stands at Koksilah and Goldstream, respectively, and were 39 and 51% as large (maximum diameter at breast height (DBH)). At each stand, there was a patchy distribution of abundant, suppressed Douglas-fir (10–15 cm mean DBH and 8–13 m mean height), especially in the old-growth stands. *Gaultheria shallon* Pursh (salal) dominated the understory vegetation in all stands. None of the stands had been logged.

The understory vegetation indicated a drier soil environment at Koksilah than at Goldstream. *Holodiscus discolor* (Pursh) Maxim., absent from the Goldstream site, was a codominant understory shrub at Koksilah, and western redcedar, western hemlock, and red huckleberry (*Vaccinium parvifolium* Sm.) were less frequent at Koksilah. The Koksilah site was near the top of a slope, steeper, and more exposed to wind and was classified as a poor-quality site (slow growth rate of trees (site index)). The Goldstream site was near the bottom of a slope, <1 km from Goldstream Creek, and was classified as a medium-quality site.

One 60 × 60 m plot was established in each of the four stands.

Table 1. Amount of soil sampled and abundance of ectomycorrhizal root tips and types in the four study plots.

	Site and age-class					
	Koksilah		Goldstream		Both sites	
	Mature (87 ± 6 years)	Old growth (288 ± 45 years)	Mature (89 ± 4 years)	Old growth (441 ± 8 years)	Mature	Old growth
Ectomycorrhizal root tips	5460	5710	2810	3470	8270	9180
Volume of soil sampled (cm^3)	4300	4000	3000	3000	7300	7000
Cores of soil sampled	36	36	24	24	60	60
Ectomycorrhizal types[a]	35	36	35	35	55	53

Note: Stand ages, followed by standard deviations, are based on increment cores from eight dominant or codominant trees in each plot.
[a]Total number of different types.

Seventy-five percent of the soil substrate by area was forest floor (= LFH materials, i.e., litter, fragmented or fermented litter, and humus) over mineral soil. Almost all decayed wood (decay classes 4 and 5 (Sollins 1982)) was covered by LFH materials, and bedrock covered by LFH was present in all plots. Except for coarse woody debris, the frequency of substrate types (proportional to area covered) was similar in old-growth and mature plots within each site. At Goldstream the total forest floor as well as the F and H layers were deeper in the old-growth (50, 20, and 17 mm, respectively) than in the mature plot (34, 12, and 10 mm), but there were no significant differences in LFH depths at Koksilah. At both Koksilah and Goldstream the humus layer in both plots was predominantly humifibrimor, with some moder (Luttmerding et al. 1990). At each site, well-decayed logs (decay classes 5 and 6 (Sollins 1982)) over 16 cm in diameter made up 95% of the volume of coarse woody debris. Logs 40 cm in diameter or larger were common in old-growth and rare in mature plots, and the volume of coarse woody debris in the old-growth plots was twice that in the mature plots.

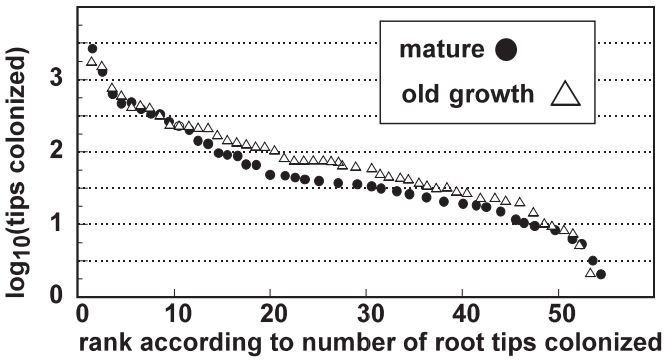
Sampling design

At each site, an identical design with separate randomizations was used for the two plots, mature and old growth. Sampling was stratified according to five broad soil substrate classes (ectomycorrhizal microhabitats): decayed logs, decayed stumps, LFH over bedrock or gravel, LFH and mineral soil at the base of codominant trees, and LFH and mineral soil elsewhere. Stratification permitted comparison of the ectomycorrhizal communities of these substrates. In combination with a survey of the amounts and locations of each of these substrates within each plot, stratification also allowed computation of the variance of ectomycorrhizal parameters for a plot as a whole.

At Koksilah, 72 soil cores were analyzed for numbers and types of ectomycorrhizae, 36 from each plot. At each plot and at each of the three sampling times, three cores were taken from logs, two from stumps, two from near boles, two from rocky areas, and three from the remaining area. Because coarse woody debris is a key contributor to biodiversity in old growth, it was sampled more heavily than other substrates. Cores were collected in May and November 1992 and in May 1993. To randomize and stratify the sampling, a map of each plot was divided into a 60 × 60 m grid of 1-m^2 squares. At each point on the grid the substrate type was determined. For each substrate type the potential sampling points were numbered and used to draw a random sample. All sampling points were separated by 2 m or more.

At Goldstream, a simplified scheme was used. Instead of mapping the substrates, each sampling point was found by starting at a random coordinate and following a random bearing (if necessary) to find suitable substrate. Forty-eight cores were extracted at Goldstream, 24 in November 1993 and 24 in May 1994. Equal numbers of samples were collected from each substrate. From each plot at each sampling time, three cores were collected from each substrate: logs, stumps, near boles, and the remaining area of forest floor and underlying mineral soil. The forest floor on rocky areas was not sampled at Goldstream because there was little of this substrate in the old-growth plot.

Fig. 1. Distribution of abundances of ectomycorrhizal types (equitability curves) for mature and old-growth stands of Douglas-fir: common logarithms of the number of root tips colonized by each ectomycorrhizal type as a function of its rank according to that abundance.



To avoid the influence of sampling time on the comparison of mature and old-growth stands, equal numbers of samples were taken and the same substrates were sampled from each age-class on a sampling day.

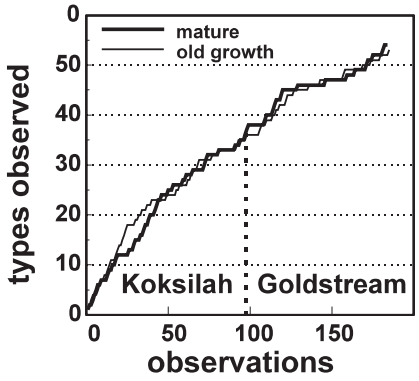
Sampling and storage of soil

The 120 soil cores, each 5 cm in diameter, were extracted to a depth of 15 cm from the surface of the forest floor, or shallower if the tool was blocked by rock or roots. The volume of soil sampled was calculated using measurements of the depth of coring holes. Most ectomycorrhizae in Douglas-fir stands occur in the forest floor and in the uppermost few centimetres of mineral soil (e.g., Fogel 1980; Harvey et al. 1978; McMinn 1963). Soil cores were stored at 2°C for ≤120 days and then cut vertically into halves and examined. Roots were extracted from one half of each core, and the other half was analyzed for nutrients. Forest floor soil was processed separately from mineral soil. Soil was gently washed in a 0.5-mm sieve with distilled water. Clumps of soil and decayed wood or bark were cut or broken into pieces ≤4 cm in diameter before and during washing.

Separation and description of ectomycorrhizal types within a soil sample

To eliminate bias while a core sample was being processed, its identity was not revealed. Ectomycorrhizae were separated into groups based on their morphology as examined at 6–40× magnification under a dissecting scope. Slide mounts of mantles from two or more tips from each group were examined at 1000× with a Leitz Labovert bright-field compound microscope to confirm that the ectomycorrhizal tips within a group were sufficiently similar to be included in the same type. All tips of all types were counted. Fewer slide mounts were made from types that were easily recognized. Root tips with a poorly developed mantle or no mantle were not examined anatomically and

Fig. 2. Progress assessing richness of ectomycorrhizal types in mature and old-growth stands of Douglas-fir at the Koksilah and Goldsteam sites: cumulative number of ectomycorrhizal types observed as a function of cumulative number of observations (an observation is the occurrence of any type in a core sample).



were not counted. The mycorrhizal status of all morphological types with a well-developed mantle was confirmed by presence of a Hartig net.

This study was designed to compare diversity of types of ectomycorrhizae in old-growth and mature stands; therefore, taxonomic identification of ectomycorrhizae was attempted only for the most common or distinctive types. Ectomycorrhizal types were distinguished by morphology, anatomy, reaction to chemical reagents, and autofluorescence (Agerer 1991; Ingleby et al. 1990; Goodman 1995; Goodman et al. 1996). Goodman (1995) described all types and their distribution in microhabitats (substrates).

Estimating richness and equitability of ectomycorrhizal types

To examine the rate at which new ectomycorrhizal types were being found, and to estimate richness of ectomycorrhizal types, number of types found was plotted against number of "observations" of all types. An observation was defined as the occurrence of any type in a sample. For example, if five types were found in a core, then there were five observations. With sufficient sampling, these "progress" curves approach an asymptote equal to the number of types in the area sampled. A rough estimate of richness was made by visually estimating the height of an asymptote. Plots of abundance of types (logarithms of the number of root tips colonized in all cores) versus rank according to abundance were used to compare equitability (the degree to which types are equally abundant) and richness (the total number of types present) (Southwood 1978). If a plot of log(abundance) versus rank is linear, then total richness is the x-intercept. A diversity index α was calculated as the slope of a linear fit to the abundance versus rank plot (Southwood 1978).

Results

Sixty-nine morphological types of ectomycorrhizae were distinguished and described (Goodman 1995). Nineteen types each accounted for more than 1% of the 17 500 ectomycorrhizal root tips examined. More than 97% of live Douglas-fir root tips had a well-developed fungal mantle. Root hairs were not seen. Eighteen types were found in five or more of the 120 soil cores. Each of the six most common ectomycorrhizae accounted for between 3 and 24% of the total number of root tips and occurred in 14–75% of the soil cores. The sigmoid equitability curves of logs of ectomycorrhizal abundance versus rank (Fig. 1) best fit the lognormal distribution or perhaps MacArthur's broken stick model (Southwood 1978). Curves were similar for both sites. The observed distribution was similar to that found for ectomycorrhizae in stands of jack pine (*Pinus banksiana* Lamb.) in Wood Buffalo National Park (Visser 1995), except that the codominant mycosymbionts of Douglas-fir were more clearly dominant than those of jack pine. Linear fits of the curves resulted in lines that approximate the result of log series distributions, with diversity indices of $\alpha = 14$, and a total richness of 90 types. Old-growth and mature stands had very similar richness, equitability, and diversity of types (Tables 1 and 2; Figs. 1 and 2). Considering only the predominant substrate type, i.e., forest floor and underlying mineral soil, 22 types were found in the mature plots compared with 28 in old growth. A plot of the number of types found as a function of the number of observations of ectomycorrhizae (an observation is defined as the occurrence of any type within a soil core) (Fig. 3) shows a decline in the rate at which additional types were encountered and describes and suggests a total richness of about 100 types.

Table 2. Frequency and abundance of codominant ectomycorrhizae in two old-growth and two mature stands.

	Abundance[b]		Frequency[c]	
Ectomycorrhizal type[a]	Old growth	Mature	Old growth	Mature
Cenococcum geophilum	14.1	21.4	29.2	33.3
Piloderma?	3.5	10.3	10.8	20.0
Rhizopogon vinicolor?	12.0	3.0	11.7	9.2
Piloderma fallax	2.6	2.6	9.2	8.3
Lactarius rubrilacteus Hesler & Smith	4.7	3.7	5.0	10.0
Type 27, unidentified	1.8	2.5	5.8	5.8
All types combined	140.4	117.6	71.7	78.3

[a]See Table 3.
[b]Mean number of ectomycorrhizal root tips per soil core ($n = 120$).
[c]Percent of soil cores containing the type ($n = 120$).

In several cases, mycosymbionts were recognizable, or were similar to previously described ectomycorrhizae (Table 3). *Lactarius rubrilacteus* Hesler & Smith was identified by the presence of laticiferous hyphae containing orange latex, green colour reaction to age or bruising, and association with sporocarps.

Discussion

Mature second-growth stands of fire origin can provide habitat for the most common ectomycorrhizae found in old growth. Luoma et al. (1991) also found that old-growth and mature stands of Douglas-fir had similar ectomycorrhizal communities. It is perhaps not surprising that the ectomycorrhizal communities of old-growth and mature stands were similar, considering their proximity and the similarity of their vegetation and soil. Many ectomycorrhizal fungi do not survive clear-cutting (Amaranthus 1991; Borchers and Perry 1990), and therefore depend on dispersal from older stands to colonize younger stands. Proximity of old-growth stands to maturing ones may be especially important for hypogeously fruiting species, which are dispersed mainly by small mammals. The recovery of the ectomycorrhizal community in the mature plots may have been due to the proximity of old-growth stands and individual old trees and the presence of some old-growth legacy of large stumps and logs. The weighting of sampling

Fig. 3. Progress assessing richness of ectomycorrhizal types in stands of Douglas-fir at the Koksilah and Goldstream sites: cumulative number of ectomycorrhizal types observed as a function of cumulative number of observations (an observation is the occurrence of any type in a core sample). The five sampling times (month/year) are indicated above the curve.

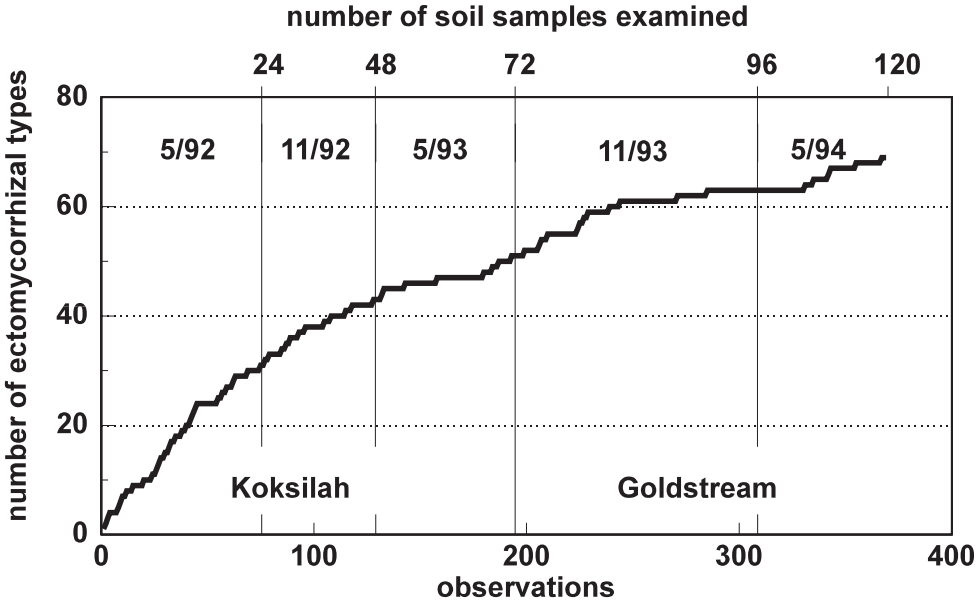


Table 3. Mycosymbionts in soil cores from two old-growth and two mature stands at two sites on southeastern Vancouver Island.

Taxon or artificial name		CDE[a]	Type[b]	Reference(s)
Cenococcum	*geophilum*	CDE10	1	Harniman and Durall 1996
Piloderma?[c]			2	Goodman 1995
"Pseudotsugarhiza"[d]	"baculifera"			Müller and Agerer 1996
Piloderma	*fallax*	CDE1	3	Goodman and Trofymow 1996
Byssoporia?	*terrestris*?		5	Goodman 1995
Rhizopogon	*vinicolor*?	CDE7	7	Goodman 1996*a*
Lactarius	*rubrilacteus*		13	Goodman 1995
Tomentella?		CDE2	14	Goodman 1996*b*
"Fagirhiza"[e]	"spinulosa"		28	Brand 1991
"Piceirhiza"[e]	"bicolorata"		41	Brand et al. 1992
Tuber?			44	Goodman 1995
Russula	*aeruginea*?		62	Taylor and Alexander 1989
Hydnellum?	*peckii*?		68	Agerer 1993
Unidentified	Unidentified		All others	Goodman 1995, 1996*c*, 1996*d*, 1996*e*, 1996*f*

[a]Serial number of description in Goodman et al. (1996).
[b]Serial number of description in Goodman (1995).
[c]Question marks indicate a tentative identification.
[d]Names in quotes are not scientific names of fungi, but are artificial names of ectomycorrhizae (Agerer 1996).
[e]Although these are ectomycorrhizae of hosts other than Douglas-fir, they closely resembled types 28 and 41.

towards coarse woody debris (nonproportional stratified sampling), which was twice as abundant in the old-growth plots as in the mature plots, may have increased the number of types observed in the mature plots. The actual richness of types in the mature plots may have been about 20% less than in the old growth, similar to the observed ratio in the predominant substrate type, the forest floor and underlying mineral soil.

The observed differences in abundance and frequency of ectomycorrhizal types between age-classes (Table 2) could not be analyzed statistically due to insufficient replication. However, these differences may prove significant in combination with the results of future research. Our data do not include the distribution of rarer ectomycorrhizal fungi, which can only be ascertained by more intensive surveys of ectomycorrhizae or sporocarps. Surveys of sporocarps have provided complementary information used to set guidelines for the conservation of old-growth-dependent fungi, such as those of the Northwest Forest Plan (Anonymous 1994). Studies of sporocarps have recently been initiated on the Koksilah plots and at other sites on southern Vancouver Island as a part of the Coastal Forest Chronosequence Project (Trofymow et al. 1997).

Our estimated richness of 100 ectomycorrhizal types was similar to other reports for conifers in western North America (Luoma et al. 1991, 1996, 1997; Miller 1983; Visser 1995). Miller

(1983) found 78 species of ectomycorrhizal fungi fruiting in an old-growth stand of western white pine (*Pinus monticola* Dougl. ex D. Don), Luoma et al. (1991) found 47 species of truffle-forming ectomycorrhizal fungi fruiting in Douglas-fir stands, and Visser (1995) found 50 ectomycorrhizal fungi fruiting in four jack pine stands. Note that we have estimated richness in four 0.36-ha plots. Richness in the entire stand would be greater.

Disturbance of an ecosystem by fire is similar in many ways to that caused by clear-cutting and slash burning (Kimmins 1987). Therefore the results of this study may be applicable to some logged sites. However, if clear-cutting is accompanied by severe soil disturbance or compaction, or abundant slash is left unburned, or if most of the coarse woody debris is removed for utilization, then there may be important effects on mycorrhizae that would not be seen in most stands of fire origin. Ectomycorrhizal communities in mature forests may be impoverished where there is a history of frequent or severe disturbance, a lack of old-growth legacies, or a lack of old-growth stands from which fungi can disperse. Future comparisons of old-growth and mature plots might best include intensive sampling of large stumps and logs, which are absent from most mature stands. In a commercial forest with even-aged stands that are cut upon maturity, mature stands will cover only a small percentage of the land area. In such cases, it is necessary to study immature stands to determine if diversity of ectomycorrhizae can be maintained. In the long term (e.g. more than four rotations), soil conditions may gradually change in forests kept at ages <100 years by repeated harvesting. Additional research is needed to determine how losses of natural stands >250 years old (old growth) affect ectomycorrhizal diversity.

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