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Seedlings of *Gaultheria shallon, Pseudotsuga menziesii, Rhododendron macrophyllum* and *Tsuga heterophylla* were grown together in the greenhouse in soils from three young managed Douglas-fir forests in the Oregon Coast Range. The main objectives were 1)to evaluate the ability of ericaceous plants and overstory conifers to share compatible mycorrhizal fungi in order to assess potential mycorrhizal linkages and 2)to determine the influence of edaphic factors on pattems of mycorrhizal colonization. Ericoid mycorrhizal fungi were quantified in the Ericaceae to confirm their assumed presence in soils of the Pacific Northwestern region of the United States. Nine ectomycorrhizal types were recognized on the conifer hosts and two on the Ericaceae. All nine EM types occurred on both conifer species and the two EM types on the ericaceous hosts resembled types associated with the conifer hosts. Ectomycorrhizal fungi occurred on all conifers and 26% of the Ericaceae in the study. Ericoid mycorrhizas developed on all Ericaceae. The influence of edaphic factors and host

specificity on patterns of mycorrhizal colonization are discussed in relation to mycorrhizal associations and plant community dynamics.

Occurrence of Ectomycorrhizae on Ericaceous and Coniferous Seedlings Grown in Soils from the Oregon Coast Range

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Jane E. Smith

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INTRODUCTION

Rhododendron macrophyllum G. Don and *Gaultheria shallon* Pursh often form dense understories in forests of the Pacific Northwestern region of North America. They are considered major competitors for light and nutrients because of their vigorous growth habits and invasive tendencies (Weetman, Fournier & Barker, 1989; Messier & Kimmins, 1990; Dighton & Coleman, 1992; Xiao & Berch, 1992). Like most Ericaceae, they form ericoid mycorrhizae (Harley & Smith, 1983). Ericoid mycorrhizal fungi include a diverse group of soil species including Ascomycetes (*Hymenoscyphus ericae* (Read) Korf & Kernan, *Gymnascella dankalienses* (Castellani) Currah, *Myxotrichum setosum* (Eidam) Orr & Plunkett and *Pseudogymnoascus roseus* Raillo), Hyphomycetes (*Oidiodendron* spp.), dark sterile mycelia (*Mycelia radicis myrtillis* Friesleben), and possibly Basidiomycetes (*Clavaria* spp.) (Seviour, Willing & Chilvers, 1973; Englander & Hull, 1980; Dalpé, 1989). Ericoid mycorrhizal fungi produce abundant proteases that release nitrogen from organic sources (Stribley & Read, 1974,1980; Abuzinadah & Read, 1989; Leake & Read, 1989). Such efficient use of soil nitrogen likely contributes to the competitive success of Ericaceae and also emphasizes their importance in the nitrogen cycle of forest ecosystems.

Some Ericaceae also form ectomycorrhizae (EM). Largent, Sugihara & Wishner (1980) found EM on several Ericaceae in northern California, and Dighton & Coleman (1992) characterized nine EM types associated with *Rhododendron maximum* L. in the southern Appalachian mountains. The

mycorrhizae of Ericaceae have been studied extensively in Europe, yet EM have not been reported. Heathland shrubs in Europe associate exclusively with ericoid mycorrhizal fungi (Allen, 1991) and can antagonize some EM fungi (Dimbleby,1953).

Ecological factors and plant community composition can profoundly influence the ability of plants and fungi to form mycorrhizae (Harley & Smith, 1983; Allen, 1991; Molina, Massicotte & Trappe, 1992). Massicotte, Molina, Luoma & Smith (1993) for example, found that the presence of compatible companion plants influenced the ectomycorrhizal host range of several *Rhizopogon* species. The profound differences in community composition and soil biology between European heathlands and Pacific Northwest forests may influence the range of mycorrhizal fungus associations for Ericaceae. The ability of different plant species to form mycorrhizae with mutually compatible fungi can also influence plant community succession and resiliency (Zak, 1976a,b; Molina & Trappe, 1982a; Borchers & Perry, 1990). For example, in southwestern Oregon many pioneering shrubs and trees, including Ericaceae, can form mycorrhizae with many of the same fungi found with late successional Pinaceae (Zak, 1976a,b; Molina & Trappe, 1982a; Borchers & Perry, 1990). These studies, and the demonstrated sharing of carbohydrates and nutrients between plants linked by mycorrhizal hyphae (Björkman, 1960; Reid & Woods, 1969; Heap & Newman, 1980) led Perry, Amaranthus & Borchers (1989a) to hypothesize that groups of host plants sharing belowground mutualists form "associations for mutual aid and the promotion of common interests." Harley & Smith (1983) termed these functional guilds "social complexes of organisms". Amaranthus & Perry (1989) found that on fire-disturbed sites in southwestern Oregon resprouting

ericaceous hardwoods in the genera *Arctostaphylos* and *Arbutus* retain a reservoir of mycorrhizal fungi that benefit conifer establishment.

Thus, although traditional forestry may view pioneering and understory plants as competitors to tree growth, these plants may also positively affect forest community dynamics through mycorrhizal connections or other belowground factors. Because the dominant forest trees in the Pacific Northwest are ectomycorrhizal, the first objective of this study will evaluate the ability of Ericaceae and overstory conifers to share compatible mycorrhizal fungi in order to assess potential mycorrhizal linkages. This paper describes the type and abundance of EM formed when the Ericaceae *Gaultheria shallon* (salal) and *Rhododendron macrophyllum* (rhododendron) are grown in mixtures with *Pseudotsuga menziesii* (Mirb.) Franco. (Douglas-fir) and *Tsuga heterophylla* (Raf.) Sarg. (western hemlock) in controlled microcosms. The second objective will evaluate the influence of edaphic factors on patterns of mycorrhizal colonization. The relationship between soil chemistry, host specificity and patterns of mycorrhizal colonization are discussed in relation to the nature of mycorrhizal associations and plant community dynamics.

MATERIAL AND METHODS

Sources of soil inocula

Soil was collected on June 12-13, 1990 from three sites in 10-12 year-old Douglas-fir plantations in the Oregon Coast Range. The sites, 60 km west of Eugene, Oregon in the Mapleton District of the Siuslaw National Forest, ranged in elevation from 360 to 410 m. Sites were in T.18S., R.9W; Site 1 was in the $NW^1/_4$Sec.26, Site 2 was in $SE^1/_4$Sec.26, and Site 3 was in the $NW^1/_4$Sec.13. Sites were in the western hemlock zone, with Douglas-fir as the dominant tree species (Franklin & Dyrness, 1984). Relatively open canopies allowed development of abundant understory plants, including rhododendron and salal. The great soil group in the three sites was Haplumbrepts (Western Brown Forest soils) underlain with Tyee Formation, a sandstone parent material (Badura, Legard & Meyer, 1974; Franklin & Dyrness, 1984; Brainerd, 1988). Slopes ranged from 30 to 65%.

Field procedures

Ten soil samples were collected from each site along two randomly selected transects at 20 m intervals. Litter and live plant material were scraped away and soil was excavated to a maximum depth of 30 cm. Soil samples were kept separate so that within site comparisons could be made. Shovels were scrubbed with water and a wire brush to remove adhering soil and rinsed in 95% ethanol to minimize contamination between sample points. Each sample was composited from four randomly selected locations within a 360 degree radius at a distance of 60 cm from the sample point.

Soil samples were stored in plastic bags at 4°C for 1 to 2 days before use in the greenhouse bioassay.

Soil analysis, seedling preparation and growth conditions

A small portion from each soil sample was removed for analysis by the Oregon State University Department of Forest Science Plant and Soils Analysis Laboratory: microkjeldahl digestion for total nitrogen and phosphorus (Thomas, Sheard & Moyer, 1967), high temperature induction for total carbon (Nelson & Sommers, 1982), the ammonium acetate method for extractable cations (Thomas, 1982), and the dilute acid-fluoride method for extractable phosphorus (Olsen & Sommers, 1982). A 1:2 soil to water ratio was used to measure pH. Soil analyses are summarized in Table 1.

Two 7 L pots per soil sample were filled with a 3:1 volume ratio of field soil:perlite to minimize compaction. Perlite has no cation exchange capacity or nutrient value (Fretz, Read & Peele, 1977). Rocks and woody debris were not removed from the samples. Two control pots for each of the three sites were prepared by use of an autoclaved mixture of soil from the 10 sample points on each site to detect ectomycorrhizal contaminants from the greenhouse. A total of 66 pots were set up in the greenhouse at Oregon State University.

Seeds of Douglas-fir and hemlock were surface sterilized in 30% H_2O_2 for 50 min and seeds of rhododendron and salal were surface sterilized in 15% H_2O_2 for 15 min. Seeds were rinsed with distilled water then sown in a soilless mixture of 1:1 vermiculite:perlite in the greenhouse. Most seeds germinated in 10 days. After 8 weeks, four seedlings, one of each species, were transferred and grown together for approximately 1 year in pots of field soil. Each was randomly assigned a position in the pots. A

random sample of each species was examined just prior to transplanting and determined to be free of mycorrhizae.

Seedlings were grown under sodium-vapor lamps with a 16 hr light/8 hr dark period complementing natural light and providing a minimum of 280 $\mu mol.s^{-1}m^{-2}$. Pots were randomly relocated on the greenhouse bench monthly. Air temperature fluctuated between 16 and 25°C. Seedlings were watered once or twice weekly with tapwater in the first 3 months and every 7-10 days in later months. Care was taken not to overwater. Each pot was fertilized three times in the first 8 weeks with 400 ml of Peters fertilizer (N-P-K/473ppm-449ppm-426ppm) amounting to 189 mg N, 180 mg P and 170 mg K. Seedlings grew vigorously and remained healthy throughout the experiment.

Mycorrhiza assessments

Pots were randomly harvested and root systems examined over a 4 month period when the seedlings were 8 to 12 months old. Seedlings were removed from the pots and entwined roots carefully separated to minimize root damage. Root systems were thoroughly washed with tap water and examined for EM types according to the guidelines of Agerer (1987) and Ingleby, Mason, Last (1990). Root squashes and hand sections were examined microscopically to characterize fine details and determine the presence of a Hartig net. Distinguishing features were photographed on Kodachrome 64 film using a Zeiss compound microscope.

Abundance of each EM type present on the coniferous hosts was determined by placing the entire root system over a clear plastic grid with consecutively numbered (2.5 cm^2) squares. A random number table was used to select the grid numbers of short roots to be quantified.

Approximately one hundred short root tips on each seedling were examined and assigned to an EM type. The proportion of short roots colonized by each of the various EM types was calculated for each root system.

Ectomycorrhiza types occurred in trace amounts (less than 1%) on the Ericaceae. Presence or absence, rather than the grid counting method, was used to assess EM development on rhododendron and salal.

Ericaceous roots were examined for the presence of ericoid mycorrhizae. Root samples were randomly selected from root systems that had been washed free of soil in running tapwater and placed in Tissue-Tek plastic capsules (Fisher Scientific Co., Pittsburgh, PA). Root samples were steamed for 20 min in a 10% KOH solution. Samples were rinsed with tapwater, placed in a 1% HCl solution for 20 min and rinsed with tapwater. Cleared samples were left overnight in a staining solution of 0.05% trypan-blue in lactoglycerol, rinsed and stored in tapwater at 4°C until microscopic examination (modified from Phillips & Hayman, 1970). Colonization by ericoid fungi was determined by stereomicroscopy and a modification of a nonsystematic method developed by Kormanik & McGraw (1982). The percentage of roots colonized from the random sample was quantified as follows: (+), 1-25%; (++), 26-50%; (+++), 51-75%;(++++), 76-100%.

Statistical analysis

A randomized block design was used wherein each site represented a block and mycorrhizal host species represented treatments. Random selection of transects within sites insured that collected soil was representative of the site. EM types and soil parameters were compared within and between sites. To evaluate the ability of overstory conifers and Ericaceae to share compatible mycorrhizal fungi, composition of EM types

on conifer seedling roots were compared, and presence of EM types on the Ericaceae were compared. To determine the relation of soil chemical factors on patterns of mycorrhizal colonization, EM types on the conifers and on the Ericaceae were compared between sites. The statistical tests for the analysis are described.

Exploratory plots of the proportions of EM types on conifers indicated that their distributions were not symmetric and variability was not constant. An arcsin square root transformation of the data stabilized the variance and produced symmetric distributions for the analysis (Snedecor & Cochran, 1980). Composition of EM types on conifer seedling roots was compared between conifer species and between sites by a multivariate analysis of covariance (MANOCO). Main effects of conifer species, site and an interaction of these effects on composition of EM type were investigated by MANOCO. Ectomycorrhizal development by the greenhouse contaminant *Thelephora* spp. was used as a covariate to decrease variance between the percentages of colonized root tips for EM types from field-collected soil.

Differences between EM types for site, conifer species and an interaction between site and conifer species were tested using Wilks' Lambda, Pillai and Hotelling-Lawley Multivariate tests (Pillai, 1960; Schatzoff, 1966; Morrison, 1976). Univariate tests were used to examine differences between individual EM type variables for site, tree species and interaction effects. The computer program SYSTAT(1985) was used for the analysis.

Chi Square Tests of Independence were used to compare presence of EM types and percentage of ericoid mycorrhizae on Ericaceae between species and between sites.

Relations between soil chemical factors and percentage mycorrhizae for each EM type were examined by regression analysis; however, linear correlations were not evident. Comparisons of soil parameters between plant species and between sites for EM types were processed using an analysis of variance (ANOVA) and Tukey's test for multiple comparisons (Steel & Torrie, 1960).

RESULTS

Ectomycorrhizal types on conifers

Nine EM types were recognized on the conifer hosts and two on the Ericaceae. All nine EM types associated with both conifer species to varying degrees, and the two EM types on rhododendron and salal resembled types that also occurred on Douglas-fir and hemlock. Distinctive morphological characters allowed for identification to the genus level for most EM types and occasionally to species level. EM types are described below in order of abundance.

Thelephora type

Thelephora type occurred on 96% of the conifer seedlings, but was more dominant on root systems of hemlock than Douglas-fir (Table 2). On Douglas-fir and hemlock, EM were single to pinnately branched, color variable and darkening with age, creamy-white, golden, reddish-brown, greyish-brown, to dark silvery-grey. The compact mantle was smooth or textured with short extramatrical hyphae. Rhizomorphs, 25-250 μm wide, were abundant and ranged in color from buff to brown. Hyphoid cystidia were common to rare and appeared to be most abundant on young, light-colored mycorrhizas. Cystidia were hyaline, septate, (25)75-150(350) μm long and 3-5 μm wide at the clamped basal septum. Cystidia gradually tapered to a rounded tip and were 1.5-2.0 μm in diameter at the midway point. Indeterminate hyphae were hyaline, 2.5-4.0 μm in diameter with frequent clamp connections.

Young *Thelephora* sp. types were difficult to distinguish from those of *Laccaria* sp.; extramatrical hyphae of *Laccaria* type branched more, tapered less and were more rounded at the tip than those of *Thelephora* type. Clamp connections of *Laccaria* and *Thelephora* types were similar in diameter.

Thelephora terrestris Fr., is a common greenhouse EM fungus because it grows rapidly after germination, produces fruiting bodies midway through the growing season, and disseminates spores through the air (Castellano & Molina, 1989). The presence of *Thelephora* may have supplanted other EM species and lowered proportions of the other EM types. *Thelephora* sporocarps are ubiquitous in our greenhouse and contamination is a continuous problem. Although *Thelephora* does occur in natural environments and could have originated from the field soil, it is not a strong competitor in non-greenhouse conditions and amounts detected in natural environments are generally low. Roth (1990) reports *Thelephora* on roots of outplanted seedlings originating in nurseries where it was prevalent but absent from outplanted seedlings not previously colonized by *Thelephora*.

Replacement of *Thelephora terrestris* by other EM fungi on outplanted seedlings is well known (Trappe, 1977; Bledsoe, Tennyson & Lopushinsky 1982). Displacement of *Thelephora* by *Rhizopogon* on Douglas-fir may explain the greater abundance of *Thelephora* on hemlock than Douglas-fir. Where competition by other EM types was eliminated, as in the control pots, conifer seedlings were colonized with virtually 100% *Thelephora* mycorrhizae.

MRA type

MRA, *Mycelium radicis atrovirens* Melin, colonized 85% of the Douglas-fir and hemlock seedlings but generally occupied less than 5% of the root systems (Table 2). On Douglas-fir and hemlock, EM were single, cylindrical, olive-black to gray-black. The root apex was often uncolonized because it grew through the mantle surface. Extramatrical hyphae were 1.5-2.5(-3.0) µm wide, olive colored, often with papillate ornamentation, septate, without clamps. Squash mounts revealed a mantle configured in a fine jigsaw pattern. MRA type resembles ectomycorrhizas formed by *Cenococcum geophilum* Fr.

Mycelium radicis atrovirens (MRA) mycorrhizae are common both in nursery and field (Danielson, Visser & Parkinson, 1985; Ingleby *et al.*, 1990). Melin (1923) applied the name *Mycelium radicis atrovirens* to a coarse, brown, sterile nonmycorrhizal fungus. Recently, mycorrhizal varieties of sterile fungi with narrow, brown ornamented hyphae have also been termed MRA (Danielson *et al.*, 1985). Pathogenic and mycorrhizal strains are recognized (Summerbell, 1985; Wilcox & Wang, 1987; Danielson & Visser, 1989; Ingleby *et al.*, 1990).

Cenococcum type

Cenococcum geophilum colonized 73% of the Douglas-fir and hemlock seedlings, but typically less than 5% of the root system (Table 2). On Douglas-fir and hemlock, EM were mostly single to occasionally pinnate, black, short (<2.5 mm), cylindrical to club-shaped. Bristly emanating hyphae, 4-6 µm wide, black, thick-walled, septate, without clamps, frequently projected from the mantle surface on young mycorrhizas. Squash mounts

revealed large stellate patterns in the crusty mantle as previously described by Trappe (1971).

C. geophilum occurs in most habitats on a broad range of hosts (Trappe, 1964; Harley & Smith, 1983). Largent *et al.* (1980) observed it on *Rhododendron macrophyllum* and *Gaultheria shallon* as well as on *Arbutus menziesii* Pursh. and several species of *Arctostaphylos* from N. California. It has frequently been observed on *Arctostaphylos uva-ursi* (L.) Spreng. in Oregon and Washington (Trappe, 1964). Dighton & Coleman (1992) observed *Cenococcum* on nursery-grown rhododendron seedlings. *Cenococcum* was not detected on the Ericaceae in this study.

On Douglas-fir and hemlock in this study, *Cenococcum* occurred in approximately equal amounts (Table 2). Schoenberger & Perry (1982) found that *C. geophilum* colonized a greater proportion of hemlock roots than Douglas-fir roots when both hosts were grown in the same soil.

Wilcoxina type

Wilcoxina, formerly termed "E-strain", occurred on 66% of the Douglas-fir and hemlock seedlings (Table 2). Features of *Wilcoxina* type matched those described by Danielson (1982) for E-strain on pine. On Douglas-fir and hemlock they were monopodial, pale to dark brown to deep reddish brown, and possessed a thin glabrous mantle composed of large (4-8 µm in diameter) hyphal cells. Extramatrical hyphae were infrequent, brown, 4-8(-10) µm in diameter.

Wilcoxina mikolae (Yang & Wilcox) Yang & Korf fruited abundantly in several pots, and a spore isolate was obtained from the ascocarps. Douglas-fir seedlings inoculated with this isolate in pure culture synthesis

tubes (Molina & Palmer,1982) developed typical "E-strain" characteristics, thus confirming *Wilcoxina mikolae* as one of our E-strain fungi.

E-strain mycorrhizae are common on a broad range of coniferous and deciduous hosts and are prolific colonizers in nurseries and burned or disturbed forest sites (Laiho, 1965; Mikola, 1965; Wilcox, Neumann & Ganmore, 1974, Wilcox, Yang & Lo-Buglio, 1983; Danielson, 1982; Yang & Wilcox, 1984; Egger & Fortin, 1990). Egger, Danielson & Fortin (1991) employed mitochondrial DNA analysis to separate most E-strain isolates to two taxa, *Wilcoxina mikolae* and *W. rehmii* Yang & Korf. Their work supports the hypothesis of habitat preference for E-strain taxa (Zak, Danielson & Parkinson, 1982; Danielson, Zak & Parkinson, 1984); *W. rehmii* is associated with peaty soils and *W. mikolae* is a common inhabitant of burned sites and mine spoils. Since the field soil in this study was not amended with peat and *W. mikolae* fruiting bodies appeared in the pots, we can conclude that the E-strain encountered in this study originated from the forest sites, which had been clear-cut and burned.

Rhizopogon type

Rhizopogon section *Villosuli* type occurred on 98% of the Douglas-fir seedlings and 25% of the hemlock seedlings (Table 2). On the hemlock seedlings it typically colonized less than 6% of the root system. In five of the 14 pots where it colonized hemlock, *Rhizopogon* type occupied 10-40% of the hemlock root systems. On Douglas-fir, EM were single to pinnate to pinnate-tuberculate; on hemlock, EM were single to pinnate. The felt prosenchymatous mantle appeared crusty and was composed of hyaline, indeterminate hyphae and reddish-brown determinate hyphae. Hyaline hyphae changed to reddish-brown with age. Reddish-brown cystidia were

1.5-2.5(3.0) µm wide, tapered to a point, and were often bent at the midway point with a knee-like appendage. Rhizomorphs, 100-750 µm wide, and mantle hyphae were septate, without clamp connections. A well defined Hartig net was evident between the cortical cells of both hosts.

The *Villosuli* group is one of four sections delineated by Smith (1964) for the genus *Rhizopogon* (Trappe, 1975; Molina & Trappe, 1993). *Rhizopogon* section *Villosuli* sporocarps and mycorrhizae are characterized by the presence of a peridial epicutis with brown-walled hyphae.

Rhizopogon species are numerous in coniferous forests of the Pacific Northwest where they are important mycobionts with Pinaceae (Smith & Zeller, 1966). Many, especially members of the *Villosuli* group, are strongly host specific (Molina & Trappe, 1982b, 1993). Douglas-fir, a well-known host of *Rhizopogon* section *Villosuli,* is termed a "primary host" in this study. Other hosts forming this type are termed "secondary hosts". *Rhizopogon* EM have been found in all forest age classes implying an ecological importance throughout conifer life. *Rhizopogon* spores are frequently used to inoculate nursery grown seedlings to enhance growth and outplanting performance (Castellano, 1987; Castellano & Molina, 1989). Benefits derived by the seedlings include increased nutrient uptake (Theodorou & Bowen, 1970; Skinner & Bowen, 1974a,b; Chu-Chou, 1979; Finlay, Odham & Söderström, 1988), tolerance to drought stress (Parke, Linderman & Black, 1983) and resistance to pathogens (Zak, 1971).

Lactarius type

Lactarius type was present on 14% of the Douglas-fir and hemlock seedlings but rarely colonized more than 5% of the root systems (Table 2). EM on Douglas-fir and hemlock were single to sometimes pinnate, swollen, smooth and shiny white to creamy-white. The smooth, multi-layered mantle was 15-25 μm wide and composed of net synenchyma cells. Squash mounts displayed laticiferous hyphae (4.0-5.0 μm wide) through the compact mantle. Emanating hyphae were not observed. Young tips exuded a milky-white juice when pinched with forceps.

Blue green type

Blue green type occurred on approximately 10% of the Douglas-fir and hemlock seedlings in amounts ranging from 1 to 55% (Table 2). On Douglas-fir and hemlock, EM were single, cylindrical structures, with a white, cottony mantle surrounded by a weft of blue-green hyphae. Mantle was composed of net synenchyma, often in geometrical labyrinth patterns. Extramatrical hyphae were pale green in KOH, septate, 3 μm in diameter, frequently branched. Non-septate, curly hyphae as described by Zak(1969) for the blue strain of *Byssoporia terrestris* (DC. ex Fries) Larsen & Zak EM were occasionally present.

This EM type was probably formed by *Byssoporia terrestris* var. *sartoryi*. Zak(1969) described older forms of these EM as consisting of "pinnate fans with surrounding gossamery mycelium and rhizomorphs" with characteristic dark blue spots along elements. Hyphae of older forms are similar to hyphae of the Blue green type encountered in this study in diameter and color.

Mycorrhizae of Douglas-fir + *Byssoporia (Poria) terrestris* var. *sartoryi* are common in Douglas-fir forests of the Oregon Coast Range especially in habitats with large, decayed Douglas-fir stumps (Zak, 1969). Residual stumps from 200+ year old Douglas-fir trees were present on all study sites.

Laccaria type

Laccaria type was detected on 7% of the Douglas-fir and hemlock seedlings in amounts ranging from 1 to 45% (Table 2). On Douglas-fir and hemlock, EM were single to irregularly pinnate with cylindrical branches, 3-15 mm long, tan darkening to a lustrous brown with age, pinkish-purple tones sometimes evident. Loosely structured surface hyphae gave the mantle a cottony appearance. Emanating hyphae were 2.5-4.0 μm wide, frequently branched with abundant clamp connections (4.0-5.0 μm).

Laccaria laccata (Scop. ex Fr.) Berk & Br. fruited in some pots where this type was found. *Laccaria* spp. form EM with a variety of trees and shrubs and commonly fruit in nurseries and forests in the Pacific Northwest (Molina & Trappe, 1982b; Castellano & Molina, 1989). Sporocarps of *Laccaria laccata* encountered in this study probably originated from propagules in the field soil because *Laccaria* EM were not detected on control seedlings grown in autoclaved soil. *Laccaria* type occurred infrequently and may have been replaced by more competitive EM types. Displacement of *Laccaria* after outplanting by other EM types including *Rhizopogon* type has been observed (Bledsoe *et al.*, 1982).

Tuber type

Tuber type was present on 4% of the Douglas-fir and hemlock seedlings and colonized between 2 and 25% of these root systems (Table

2). On Douglas-fir and hemlock, EM were single to irregularly branched, short and robust, brown-yellow to chestnut, with straight bristle-like cystidia projecting from the mantle surface. Cystidia were septate, 3.75-5.0 μm in diameter at the base and 75-150 μm long, tapering to a slightly rounded tip. Mantle was compact, composed of irregular interlocking synenchyma, cells 5-20 μm in diameter. *Tuber californicum* Harkn. is the only species of *Tuber* in this area with bristle-like setae emanating from the peridium (M. Castellano, J. Trappe, personal communication).

Tuber species are hypogeous ascomycetes commonly referred to as truffles. All are mycorrhizal but some are host specific with angiosperms and gymnosperms in forests of the Pacific Northwest.

Statistical comparisons of ectomycorrhizal colonization of conifers

Thelephora EM was a significant covariate ($p<0.001$). Abundance of the six major EM types differed among sites (Table 3). EM types occurring on 11% or fewer of the conifer seedlings provided insufficient data to detect significant variation and were omitted from the analysis. The effect of conifer host was significant on total EM abundance and for four of the six major types: *Thelephora*, MRA, *Wilcoxina*, and *Rhizopogon* (Table 2). There was no interaction between conifer species and site in mean abundance/seedling for the major EM types.

Relation of soil nutrients on ectomycorrhizal colonization of conifers

Rhizopogon type was most abundant in Site 3 soil which was lower in N ($p=0.002$), N:total P ($p=0.021$), Ca ($p=0.005$), Mg ($p=0.002$) and C ($p=0.089$) than Site 1 & 2 soils (Tables 1 & 3). Significantly lower levels of N

(p=0.019), N:total P (p=0.004), and N:ext P (p=0.002) occurred in soils where the *Rhizopogon* type occupied more than 55% of the Douglas-fir root tips.

Thelephora and *Cenococcum* types were more abundant in Site 1 & 2 soils than Site 3 soil (Tables 1 & 3). Although the abundance of *Cenococcum* differed significantly between these sites (p=0.003), the magnitude of the difference was small (Table 3).

Tuber mycorrhizas were obtained only from one soil sample. Soil yielding *Tuber* mycorrhizas was high in Ca with a value of 1635 μg/g compared to a median Ca level of 594 μg/g in all 30 soil samples. Some *Tuber* species have been associated with calcareous soils of Mediterranean climates (Trappe, 1977).

Ectomycorrhizal types on Ericaceae

Dark brown type

Dark brown type was encountered on 19% of the rhododendron and salal seedlings but always in trace amounts (Table 4). On rhododendron and salal, EM were monopodal, dark brown to reddish brown with extensive dark brown emanating hyphae. Mycorrhizas were 1-1.5 mm long with a diameter of 0.2-0.3 mm. Mantle surface was composed of net prosenchymatous hyphal cells. Cystidia were 1.5-2.5 μm wide, tapered to a point and often bent at the midway point. Intracellular penetration by the fungal symbiont was observed in squash mounts. Hartig net was present between the outer layer of cortical cells.

Features such as color, presence and appearance of emanating cystidia, and the occurrence of this type in pots where the *Rhizopogon* type

was abundant on Douglas-fir and generally present on hemlock, suggest that the Dark brown type may be attributed to *Rhizopogon* spp.

Hyaline type

Hyaline type was encountered on 7% of the Ericaceae in trace amounts (Table 4). On rhododendron and salal, EM were monopodal, creamish-white, 1-2 mm long and 0.3-0.5 mm in diameter. Mantle surface was composed of net prosenchyma and surrounded by loosely arranged hyaline emergent hyphae, 2.5 μm in diameter, with clamp connections up to 5.0 μm wide. Isolated hyphae penetrated between cortical cells but Hartig net was not typical.

The hyaline hyphae and clamp connections were similar in width to those of *Laccaria* type and *Thelephora* type. The Hyaline type occurred on the Ericaceae in pots where *Thelephora* type but not *Laccaria* type was detected on Douglas-fir and hemlock, so *Thelephora* type is a likely candidate.

Factors influencing ectomycorrhizal colonization of Ericaceae

Ericaceous host influenced the occurrence of the Hyaline type but not the Dark brown type (Table 4). Salal was colonized more often than rhododendron by the Hyaline type ($p=0.03$). However, it must be noted that the Hyaline type occurred on only eight out of 114 Ericaceae. With the exception of one salal seedling, the two EM types occurred on separate seedlings. Colonization of rhododendron or salal by the Dark brown type did not differ.

The occurrence of the Hyaline and Dark brown types on Ericaceae was also influenced by site ($p=0.03$) (Table 5). The Dark brown type

colonized a greater percentage of Ericaceae in Site 3 soil than Site 1 or 2 soils; the Hyaline type was not detected in Site 3 soil. Similarly, *Rhizopogon* type was more abundant on the conifers in Site 3 soil than Site 1 or 2 soils. The possibility of the *Rhizopogon* type occurring on the secondary hosts (hemlock, salal or rhododendron) presents a special case. Factors influencing colonization by the Dark brown type or *Rhizopogon* type will be reported in a separate section and patterns of *Rhizopogon* host specificity will be discussed.

Soils where EM types were encountered on the Ericaceae were higher in extractable P than soils where EM types were absent.(Table 6). Soils where the Hyaline type occurred were higher in N, C, Ca, Mg, C:N, N:total P and lower in pH than soils where the Hyaline type was absent. Soils where the Dark brown type occurred had lower N:ext P ratios than soils where the the Dark brown type was not detected.

Factors influencing colonization of secondary hosts by *Rhizopogon* types

Presence of the *Rhizopogon* type or Dark brown type on the secondary hosts (hemlock, rhododendron, or salal) varied with soil chemistry. *Rhizopogon* type or Dark brown type colonized secondary hosts in soils that averaged lower N:extractable P ($p=0.002$), lower N:total P ($p=0.012$), lower N ($p=0.032$), higher extractable P ($p=0.071$), higher K ($p=0.010$) and lower C ($p=0.096$) (Table 7).

Rhizopogon abundance on Douglas-fir was related to secondary host colonization. Secondary host colonization typically occurred in only one of the paired pots for each soil sample. When percentages of *Rhizopogon*-colonized Douglas-fir roots were compared between these paired pots,

colonization was greater in the paired pot wherein secondary hosts were also colonized by *Rhizopogon* or Dark brown type ($p<0.001$). Colonization of secondary hosts by *Rhizopogon* type or Dark brown type occurred in 28% of the non-control pots. In the 11 pots where both Ericaceae and hemlock were colonized by the Dark brown type or *Rhizopogon* type, 73% of the Douglas-fir root tips were colonized by *Rhizopogon* type. In the six pots where secondary colonization occurred on either the Ericaceae or hemlock but not both, fewer than 55% of the Douglas-fir root tips formed *Rhizopogon* type.

Although not originally intended as a treatment variable, the total number of days to harvest significantly influenced colonization of secondary hosts by *Rhizopogon* or Dark brown type. The number of days to harvest ranged from 230 to 370 and were significantly greater for pots where secondary hosts were colonized by *Rhizopogon* or Dark brown type ($p=0.005$). These results suggest that when nutrient conditions are favorable, longer growing periods lead to the proliferation of *Rhizopogon* and secondary host colonization.

Ericoid mycorrhizal colonization of Ericaceae

Ericoid mycorrhizas developed on all Ericaceae in the study but Seventy-three percent of the salal seedlings and 45% of the rhododendron seedlings had greater than 50% colonization by ericoid mycorrhiza (Table 8). Colonization did not differ between soils from the three sites.

DISCUSSION

Patterns of host specificity of *Rhizopogon* ectomycorrhizal types

Patterns of specificity observed in this study of field soils as inocula sources were similar in some ways and different in others from results obtained by Massicotte *et al.* (1993) on mixtures of host species grown in pasteurized peat and vermiculite in a greenhouse and inoculated with *Rhizopogon* spores. They report that some *Rhizopogon* species colonized secondary hosts, including hemlock, when grown in conjunction with a well-colonized primary host species. Similarly, in our study, secondary hosts colonized by the *Rhizopogon* type or the Dark brown type suggestive of *Rhizopogon* were generally accompanied by a Douglas-fir seedling with at least 55% of its root system occupied by *Rhizopogon* type.

Massicotte *et al.* (1993) found *Rhizopogon vinicolor* A.H. Smith and *R. parksii* A.H. Smith to be strongly specific to Douglas-fir; they observed no colonization of companion hosts even in the presence of a well-colonized primary host. *R. parksii* is in the *Rhizopogon* section *Villosuli* group (Smith & Zeller, 1966). *R. vinicolor,* currently in the *Rhizopogon* section *Fulviglebae*, resembles members of *Rhizopogon* section *Villosuli* in isolate and mycorrhizal characters and host specificity (Molina & Trappe, 1993), and future placement in this taxonomic section is likely (J. Trappe, personal communication). The absence of secondary host colonization by either *R. vinicolor* or *R. parksii* in the study by Massicotte *et al.* (1993) and the repeated occurrence of *Rhizopogon* sect. *Villosuli* type EM on hemlock in this study suggests that factors such as soil chemistry and length of time in

the presence of a well colonized primary host may influence EM colonization of companion plants by host specific fungi.

Duddridge & Read (1984) and Duddridge (1986a,b) reported that high glucose levels enhance EM syntheses in controlled environments. Laboratory studies using single host-single fungus systems with vegetative inocula in pure culture synthesis tubes illustrated that EM thought to be host specific could form infrequent or poorly developed mycorrhizal associations with unexpected hosts (Zak, 1976a,b; Molina & Trappe, 1982b). Molina & Trappe (1982b) found that *R. vinicolor* formed abundant EM with Douglas-fir seedlings but only weakly colonized western hemlock when grown in aseptic conditions. Zak (1976a,b) and Molina & Trappe (1982a) demonstrated that the Ericaceae *Arbutus menziesii* and *Arctostaphylos uva-ursi* were mycorrhizal generalists and sometimes formed well-developed associations with EM previously thought to be host specific, including *R. vinicolor.*

Nutrient relationships to ectomycorrhizal colonization

In our study, *Rhizopogon* type was most abundant in soils where N levels were lowest. This is consistent with Brainerd's (1988) results that numbers of *Rhizopogon* sp. tips on Douglas-fir negatively correlated with the ratio of N to P in soils collected from the same sites that we sampled in this study. Litter leachates have been shown to inhibit *Rhizopogon* (Schoenberger & Perry, 1982; Rose, Perry & Pilz, 1983). Marx *et al.* (1977) found negative correlations between high levels of N and P in soils and EM colonization of *Pinus taeda* L. (loblolly pine) by *Pisolithus tinctorius* (Pers.) Coker & Couch and between high levels of N and P and the sucrose content of short roots. Marx *et al.* (1977) concluded that high concentrations of

carbohydrate in the root tissue stimulated EM colonization. When N limits the photosynthetic process, canopy development slows and an increased proportion of carbohydrate moves toward the roots (Waring & Schlesinger, 1985). In our study, the availability of more C belowground may have favored *Rhizopogon* colonization of Douglas-fir, hence, increased the probability of *Rhizopogon* colonizing associated plants.

In general, high nutrient levels inhibit mycorrhiza formation (Slankis, 1974; Marx, Hatch & Mendicino, 1977; Wallander & Nylund, 1991, 1992). However, in this study, *Thelephora* EM developed most abundantly in soils high in N, N:total P, C, Ca and Mg. Miller, Koo & Molina (1993) observed higher percentages of *Thelephora* on Douglas-fir seedlings grown in soils from an 18-year old conifer plantation than from a conifer clearcut or stands of rotation-aged conifer, old growth conifer or alder. Consistent with our results, soils from the conifer plantation in the study by Miller *et al.* (1993) were higher in total N and C than soils from the clearcut or other conifer stands and higher in Ca than the clearcut or rotation-aged conifer stand. Our study and the study by Miller *et al.* (1993) suggest that high levels of soil N favor colonization by the greenhouse fungus, *Thelephora*.

Ecological consideration of potential inter-plant linkages

Inter-plant connections by fungal hyphae resulting in an exchange of C and nutrients have been demonstrated between plants of the same and different species (Björkman, 1960; Read,1984; Read *et al.*, 1985; Finlay & Read, 1986a,b; Finlay, 1989). Association with a diversity of mycorrhizal fungi is likely to benefit hosts because the fungi differ in the benefits they offer and the environmental conditions under which they operate (Perry *et al.*, 1987). Mycorrhizal fungi may benefit from having diverse hosts for much

the same reasons; fluctuations in their C supply are reduced (Perry *et al.*, 1992). The fact that most EM fungi associate with more than one plant species suggests the probability of linkages in natural settings. Mycorrhizal links between plants are believed to be common although few field studies support this hypothesis (Newman, 1988). In a greenhouse experiment, Perry *et al.* (1989b) found that *Laccaria laccata* mediated a redistribution of foliar N between Douglas-fir and *Pinus ponderosa* Laws. (ponderosa pine) seedlings and hypothesized that shared mycorrhizal fungi more evenly distribute nutrients between plants of different species (Perry *et al.*, 1992).

Hyphal linkages between Pinaceae and Monotropoideae, a subfamily of the Ericaceae, have been documented. Ectomycorrhizal fungi that form monotropoid mycorrhizae enter into a source-sink relationship where the achlorophyllous plant receives carbohydrates via the fungus which is linked to a member of the Pinaceae (Björkman, 1960; Furman & Trappe, 1971; Trappe & Luoma, 1992). Reasons why the fungus facilitates nutrient transfer are unclear (Trappe & Luoma, 1992). Castellano & Trappe (1985) observed *Rhizopogon* sp. mycorrhizae on several species of achlorophyllous hosts in the Monotropoideae. DNA analyses have confirmed the presence of *Rhizopogon* sp. mycorrhizas on *Monotropa*, *Pterospora* and *Sarcodes* (T. Bruns, personal communication).

Formation of the *Rhizopogon*-like Dark brown type EM on the Ericaceae in our soil with the lowest N levels and where the *Rhizopogon* type was encountered on hemlock and Douglas-fir suggests the possibility of *Rhizopogon* links between conifers and Ericaceae. Ultrastructural (Bonfante-Fasolo, 1980; Peterson, Mueller & Englander, 1980), physiological (Englander & Hull, 1980) and observational studies (Largent

et al., 1980; Dighton & Coleman,1992) suggest that basidiomycetes may be symbionts with *Rhododendron*. The ability of *Rhizopogon* to form mycorrhizas with arbutoid and monotropoid members of the Ericaceae indicates its potential to associate with ericoid mycorrhizal species as well. However, it is possible that the Dark brown type was not *Rhizopogon* but some other EM that colonized the Ericaceae under similar edaphic conditions. Developing DNA "fingerprints" of these EM types could yield valuable data on this hypothesis.

The low levels of EM colonization detected on the Ericaceae in this study must be considered. Since EM colonization of naturally occurring Ericaceae has not been quantitatively assessed, it is not known whether amounts found in our experiment represent Ericaceae in the Pacific Northwest. Short term pot studies may underestimate EM colonization of Ericaceae in the field where the potential for interaction with other EM hosts would be longer. It is also not known if these amounts benefit the Ericaceae or facilitate nutrient transfer between members of the Pinaceae and Ericaceae. Dighton & Coleman (1992) found that rhododendron roots colonized by EM produced more surface phosphatase than ericoid or VA mycorrhizae colonized roots. They concluded that the EM root system may be better able to obtain phosphorus from organic complexes in soil than the other mycorrhizal root types associated with rhododendron.

Ecological significance of ericoid mycorrhizas to Ericaceae

Ericoid mycorrhizal fungi degrade complex organic substrates, thus providing Ericaceae with an N source that would otherwise be unavailable (Stribley & Read, 1974,1980; Read, 1983; Abuzinadah & Read, 1989; Leake & Read, 1989). Because such a mechanism contributes to the adaptation of Ericaceae to nutrient-poor soils, we hypothesize that it also contributes to their successful growth in heavily organic soils with slow nutrient cycling. Soils in this study were rich in N. Nutrient-poor, acid soils typically have low rates of mineralization, so the ability of the ericoid mycorrhizae to assimilate organic compounds containing N and transfer this N to the host plant may be essential to plant survival (Harley & Smith, 1983).

In this study, no difference in percentage colonization of ericoid mycorrhiza was observed between Ericaceae grown in soils from the three sites, although mean total N levels differed between sites. Stribley & Read (1976) found no difference between degrees of ericoid mycorrhizal colonization in *Vaccinium macrocarpon* Ait. (cranberry) when organic N in the form of $(NH_4)_2SO_4$ was supplied at a rate of 1.0 to 7.5 mg l^{-1}, but observed a decrease in colonization at 20.5 mg l^{-1}. Studies are needed to examine the presence and benefits of ericoid mycorrhizal colonization over the range of organic N levels found in Pacific Northwestern soils.

Only a few ericoid endophytes have been identified, and their presence in Pacific Northwestern soils remains largely unknown. In this study, ericoid mycorrhizal colonization of all Ericaceae grown in field-collected soils illustrates the widespread occurrence of ericoid mycorrhizal fungi in young managed Douglas-fir stands. Pearson &

Read (1973) demonstrated the ubiquity of ericoid mycorrhizal fungi in the United Kingdom by obtaining isolates from ericoid mycorrhizae and from soils where Ericaceae were present as well as where they were absent.

Ericoid mycorrhizal fungi are thought to be restricted to Ericaceae but are broad-host-ranging among them. For example, *Oidiodendron griseum* Robak has been isolated from *Vaccinium* spp. (Couture, Fortin & Dalpé, 1983) and *Gaultheria shallon* (Xiao & Berch, 1992). Studies exploring the biochemical affinities, diversity, specificity with Ericaceae and ubiquitous nature of ericoid mycorrhizal fungi are needed to understand their ecosystem function in the Pacific Northwest.

CONCLUSIONS

A greenhouse soil bioassay proved to be a successful method of inoculating mixtures of coniferous and ericaceous seedlings with EM fungi from the field. It is not known whether spores or hyphal fragments were responsible for colonization. Nine EM fungal types were detected on Douglas-fir and hemlock and two EM fungal types on rhododendron and salal. These observations support those of Dighton & Coleman (1992) that rhododendrons form EM and confirm reports by Largent *et al.* (1980) that Ericaceae in the Pacific Northwest can form EM.

Soil chemical factors appear related to EM associations with Ericaceae as hypothesized by Largent *et al.* (1980). Field studies are needed to elucidate the relationships between edaphic conditions, mycorrhizal symbionts, and connections between plant species in order to better understand plant community dynamics.

Plant communities have been traditionally viewed as being structured primarily by competition. Dense coverage of rhododendron and salal have been shown to inhibit regrowth of commercial tree species (Long, 1977; Bunnell, 1990; Dighton and Coleman, 1992) by competing for moisture and possibly nutrients (Black, Tan & Nnyamah, 1980; Price, Black & Kelliher, 1986; Vihnanek & Ballard, 1988; Weetman *et al.*, 1990). Current forest management strategies for controlling the growth of salal and other Ericaceae are discussed by Bunnell (1990). However, the influence of rhizosphere organisms on plant growth, nutrient cycling and competition is absent from these management strategies. Since plant competition can be altered by mycorrhizal fungi, understanding interactions between plants,

mycorrhizal fungi and soil chemistry is essential to future forest management.

Formation of like mycorrhizae by the conifers and Ericaceae in this study indicates the potential for hyphal linkages and suggests a positive interaction between overstory conifers and Ericaceae. Hyphal connections between plants illustrate the complexity of the belowground structure of forest ecosystems and may result in significant ecological consequences. It can be hypothesized that conifers obtain N through hyphal linkages with the Ericaceae. Ericaceae may obtain fixed C from the overstory conifers through fungal connections. These hypotheses add another dimension to the role of EM in mediating interaction among different plant species.

Table 1. Soil chemical properties of three young, managed Douglas-fir stands in the Coast Range of Oregon.

Location	Total N (%)	Total P (mg/kg)	Extractable P (mg/kg)	Total C (%)	N:total P	N:ext.P	C:N	K (µg/g)	Ca (µg/g)	Mg (µg/g)	pH
Site 1	0.439a[1] (0.059)[2]	525a (41.121)	11.743a (2.364)	14.126a (4.539)	8.99a (1.85)	420.8a (67.9)	29.066a (5.732)	266.3a (23.46)	834.1a (140.106)	313.6a (36.196)	4.907a (0.098)
Site 2	0.476a (0.056)	481.7a (45.382)	8.849a (2.884)	14.02a (2.415)	9.99a (1.07)	807.9b (109.5)	28.671a (2.051)	206.2a (25.649)	1002.1a (184.959)	329.2a (54.822)	4.95a (0.075)
Site 3	0.223b (0.018)	451.2a (21.142)	10.378a (1.869)	5.625a (0.7)	4.90b (0.20)	273.8a (45.3)	25.404a (2.830)	226.6a (16.476)	320.2b (62.112)	126.5b (22.15)	5.205b (0.057)
	p=0.002[3]	p=0.387	p=0.700	p=0.089	p=0.021	p<0.001	p=0.773	p=0.170	p=0.005	p=0.002	p=0.026

[1]For the sites, means in the same column followed by different letters are significantly different at the 5% level.

[2]Numbers in parentheses are standard errors.

[3]p-value is from the ANOVA for comparison of soil chemical properties between sites.

Table 2. Abundance of ectomycorrhiza types on Douglas-fir and western hemlock grown in potted soil from three sites of young, managed Douglas-fir stands in the Coast Range of Oregon.

Ectomycorrhiza type[1]	Host	No. of Seedlings Colonized (-Controls)	No. of Colonized Seedlings with <5% of the Root System Colonized by the EM type	Mean abundance[2] of EM type on Conifer Host[3]
Thelephora type	Douglas-fir	56/57 (98%)	12/56 (21%)	0.394 (0.042)[4]a[5]
	Hemlock	54/57 (95%)	4/54 (7%)	0.575 (0.044)b
	Pinaceae Host Total	110/114 (96%)	16/110 (15%)	p=0.008
MRA type	Douglas-fir	47/57 (82%)	32/47 (68%)	0.047 (0.009)a
	Hemlock	50/57 (88%)	27/50 (54%)	0.095 (0.017)b
	Pinaceae Host Total	97/114 (85%)	59/97 (61%)	p<0.001
Cenococcum type	Douglas-fir	44/57 (77%)	36/44 (82%)	0.020 (0.003)a
	Hemlock	39/57 (68%)	31/39 (79%)	0.022 (0.003)b
	Pinaceae Host Total	83/114 (73%)	67/83 (81%)	p=0.514
Wilcoxina type	Douglas-fir	38/57 (67%)	9/38 (24%)	0.147 (0.026)a
	Hemlock	37/57 (65%)	6/37 (16%)	0.236 (0.038)b
	Pinaceae Host Total	75/114 (66%)	15/75 (20%)	p<0.001
Rhizopogon type	Douglas-fir	56/57 (98%)	2/56 (4%)	0.355 (0.032)a
	Hemlock	14/57 (25%)	8/14 (57%)	0.021 (0.008)b
	Pinaceae Host Total	70/114 (61%)	10/70 (14%)	p<0.001
Lactarius type	Douglas-fir	8/57 (14%)	6/8 (75%)	0.008 (0.004)a
	Hemlock	8/57 (14%)	6/8 (75%)	0.007 (0.004)a
	Pinaceae Host Total	16/114 (14%)	12/16 (75%)	p=0.735
Blue-green type	Douglas-fir	7/57 (12%)	3/7 (43%)	0.013 (0.007)a
	Hemlock	6/57 (11%)	2/6 (33%)	0.025 (0.013)a
	Pinaceae Host Total	13/114 (11%)	5/13 (38%)	p=0.318
Laccaria type	Douglas-fir	4/57 (7%)	3/4 (75%)	0.009 (0.007)a
	Hemlock	4/57 (7%)	1/4 (25%)	0.015 (0.009)a
	Pinaceae Host Total	8/114 (7%)	4/8 (50%)	p=0.309
Tuber type	Douglas-fir	2/57 (4%)	0/2 (0%)	0.003 (0.002)a
	Hemlock	2/57 (4%)	1/2 (50%)	0.004 (0.004)a
	Pinaceae Host Total	4/114 (4%)	1/4 (25%)	p=0.298

[1]EM types in descending order of abundance.

[2]Mean abundance is the average percentage of root tips colonized.

[3]Statistical differences determined on transformed data (arcsine square root of % mycorrhizal tips). Values in table are not transformed.

[4]Numbers in parentheses are standard errors.

[5]Data are expressed as average values per host. Values followed by the same letter are not significantly different at the 5% level.

Table 3. Mean proportion of root tips colonized by the major ectomycorrhizal types on conifers grown in potted soil from three sites of young, managed Douglas-fir stands in the Coast Range of Oregon.

Location	Thelephora type	MRA type	Cenococcum type	E-strain type	Rhizopogon type	Lactarius type
Site 1	0.519a[1] (0.054)[2]	0.039a (0.008)	0.020a (0.004)	0.227a (0.040)	0.183a (0.037)	0.001a (0.001)
Site 2	0.560a (0.049)	0.086b (0.020)	0.029a (0.004)	0.133b (0.033)	0.130a (0.028)	0.017b (0.002)
Site 3	0.361b (0.058)	0.088b (0.021)	0.014b (0.003)	0.219a (0.047)	0.264b (0.049)	0.004a (0.002)
	p=0.024[3]	p=0.053	p=0.003	p=0.027	p=0.038	p=0.049

[1]For the EM types, means in the same column followed by different letters are significantly different at the 5% level.

[2]Numbers in parentheses are standard errors.

[3]Statistical differences determined on transformed data (arcsine square root of % mycorrhizal tips). Values in table are not transformed. The p-value is from the ANOVA for treatment effects.

Table 4. Ectomycorrhiza types and frequency of occurrence on rhododendron and salal seedlings grown in potted soil from three sites of young, managed Douglas-fir stands in the Coast Range of Oregon.

Ectomycorrhiza type	Host	Number of Seedlings Colonized (-Controls)
Dark brown type	Rhododendron	10/54 (19%)a[1]
	Salal	12/60 (20%)a
	Ericaceae Host Total	22/114 (19%)
Hyaline type	Rhododendron	1/54 (2%)a
	Salal	7/60 (12%)b
	Ericaceae Host Total	8/114 (7%)

[1]Data are expressed as percent of seedlings colonized by EM type. Values followed by the same letter are not significantly different (p=0.05) using Chi Squrare Tests of Independence.

Table 5. Ectomycorrhizal colonization of Ericaceae grown in potted soil from three sites of young, managed Douglas-fir stands in the Coast Range of Oregon.

Location	Ericaceous seedlings colonized by Hyaline type	Ericaceous seedlings colonized by Dark brown type
Site 1	5/38 (13%)[1]	7/38 (18%)
Site 2	3/38 (9%)	3/38 (9%)
Site 3	0/38 (0%)	12/38 (32%)
	p=0.03[2]	p=0.03

[1]Data are expressed as percent of seedlings colonized by EM type.

[2]Levels of significance were determined using Chi Square Tests of Independence.

Table 6. Comparison of soil chemical properties of soils from three sites of young, managed Douglas-fir stands in the Coast Range of Oregon when Ericaceae are colonized by Dark brown type, Hyaline type or no ectomycorrhizal types.

EM Colonization of Ericaceous Host	Total N (%)	Total P (mg/kg)	Extractable P (mg/kg)	Total C (%)	N:total P	N:ext.P	C:N	K (µg/g)	Ca (µg/g)	Mg (µg/g)	pH
Dark brown type	0.336a[1] (0.051)[2]	508.428a (32.104)	13.546a (2.293)	9.354a (1.754)	6.27a (0.62)	305.5a (46.6)	27.924a (2.975)	261.714a (20.103)	710.857a (151.825)	261.000a (51.602)	5.13a (0.06)
Hyaline type	0.624b (0.075)	470.714a (63.498)	13.216a (3.116)	30.026b (6.275)	14.99b (2.86)	607.6b (113.6)	46.953b (8.539)	235.714a (18.326)	1462.429b (90.760)	436.429b (25.341)	4.68b (0.09)
No EM Colonization	0.356a (0.023)	481.625a (16.896)	8.647b (0.993)	8.910a (0.788)	7.39a (1.58)	554.3b (55.2)	24.567a (0.693)	223.800a (11.426)	617.425a (70.211)	229.725a (20.757)	5.04a (0.04)
	p<0.001[3]	p=0.713	p=0.050	p<0.001	p<0.001	p=0.031	p<0.001	p=0.235	p<0.001	p<0.001	p<0.001

[1]For the EM types, means in the same column followed by different letters are significantly different at the 5% level based on Tukey's Honestly Significant Difference Test.

[2]Numbers in parentheses are standard errors.

[3]p-value is from the ANOVA for treatment effects.

Table 7. Comparison of soil chemical properties of soils from three sites of young, managed Douglas-fir stands in the Coast Range of Oregon when secondary hosts (hemlock, rhododendron, salal) were colonized and uncolonized by *Rhizopogon* or Dark brown type.

Colonization Status of Secondary Hosts by *Rhizopogon* or brown type	Total N (%)	Total P (mg/kg)	Extractable P (mg/kg)	Total C (%)	N:total P	N:extP	C:N	K (µg/g)	Ca (µg/g)	Mg (µg/g)	pH
hemlock, rhododendron, salal Colonized n=15	0.332a[1] (0.048)[2]	512a (29.435)	12.397a (2.232)	8.771a (1.665)	6.181a (0.59)	331.4a (42.7)	25.779a (2.279)	263.667a (19.404)	679.467a (144.821)	255.133a (48.909)	5.097a (0.055)
hemlock, rhododendron, salal Uncolonized n=15	0.427b (0.046)	459a (30.984)	8.249a (1.435)	13.741a (3.186)	9.742b (1.37)	670.3b (96.5)	29.648a (7.610)	201.867b (14.468)	758.133a (124.716)	257.733a (29.651)	5.011a (0.085)
	p=0.032	p=0.121	p=0.071	p=0.096	p=0.012	p=0.002	p=0.201	p=0.010	p=0.347	p=0.493	p=0.209

[1]For the colonization status of the alternate hosts, means in the same column followed by different letters are significantly different at the 5% level by Student's t-test.

[2]Numbers in parentheses are standard errors.

Table 8. Occurrence of ericoid mycorrhizae in rhododendron and salal grown in potted soil from three sites of young, managed Douglas-fir stands in the Coast Range of Oregon.

	Colonization by ericoid mycorrhizae			
Ericaceous host	(+)[1]	(++)	(+++)	(++++)
rhododendron	3%[2] (2/60)	52% (31/60)	43% (26/60)	2% (1/60)
salal	5% (3/66)	23% (15/66)	61% (40/66)	12% (8/66)

[1]Percent colonization: (+), 1-25%; (++); 26-50%; (+++), 51-75%; (++++), 76-100%.

[2]Percentage is number of seedlings colonized by the indicated percent colonization.

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