Early effects of prescribed fire on the structure of the ectomycorrhizal fungus community in a Sierra Nevada ponderosa pine forest

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The effects of a prescribed fire on the presence of ectomycorrhizal fungi on the root tips of ponderosa pine were investigated one year after a prescribed ground fire. Ectomycorrhizas were sampled within 1 m^2 plots before and one year after the fire, and in nearby control plots that were not burned. The cores were divided into litter/organic, upper mineral, and lower mineral layers. The total ectomycorrhizal biomass in the control plots did not differ between year one and year two samples for any core layer, while in the fire plots the destruction of the litter/organic layer resulted in an eight-fold reduction in total ectomycorrhizal biomass. Mycorrhizal biomass in the two mineral layers was not significantly reduced by the fire. We used molecular tools to identify fungi directly from the ectomycorrhizas. In unburned plots members of the Russulaceae and Thelephoraceae were among the most frequent and abundant ectomycorrhizal types; species of most other taxa were rare. In the control plots these two families were among the dominant species in both years, but patchiness on a fine spatio-temporal scale caused some major changes in ranking of individual species between sample years. *Rhizopogon subcaerulescens* was the most pronounced example; its biomass in the control plot samples was seven times greater in year two than in year one because of an exceptionally large cluster of mycorrhizas encountered in a single core. The effect of fire on individual species was difficult to assess because of this patchiness and because all species were low in abundance after the fire. The most abundant pre-fire species were reduced to undetectable post-fire levels, while several less abundant species, including *R. subcaerulescens*, *Cenococcum geophilum*, and several unknown types were not substantially reduced by the fire. We speculate that the more abundant species, *Martellia* sp., thelephoroid 1, and *Tomentella sublilacina*, were differentially affected because their dominance was most prominent at the litter and organic layers. In any case, a short-term effect of this fire appears to be increased species evenness.

Forest managers use prescribed fire to avoid catastrophic wildfire, maintain forest health, regulate stand composition, and reduce competition. Prescribed fires result in mortality of understorey vegetation, the consumption of litter and the reduction of organic material in the top layer of the soil (Ahlgren & Ahlgren, 1960). The effects of control burns go beyond the above ground portions of the forest ecosystem, affecting soil micro-organisms as well (Ahlgren & Ahlgren, 1965; Pietikainen & Fritz, 1995). After fire, bacteria are stimulated and fungi are depressed in soils (Vázquez, Acea & Carballas, 1993). Ectomycorrhizal fungi are a particularly important component of the soil microbial community, directly providing plant hosts with enhanced water and nutrient uptake, extended root life and protection against root pathogens (Smith & Read, 1997) while influencing successional patterns and overall forest health (Perry *et al*., 1989). Our focus is on the effects of fire on the community structure of ectomycorrhizal fungi.

Since ectomycorrhizas tend to proliferate in the litter and humus layers (Harvey Larsen & Jurgensen, 1976, 1979; Buchholz & Motto, 1981; Buchholz & Gallagher, 1982), consumption of organic materials by fire should decrease ectomycorrhizal root tips. Indeed, Buchholz & Gallagher (1982) reported that active ectomycorrhizal root tips were lower in burned plots than in unburned plots, but this difference was not significant for any soil depth tested (0–7, 7–14, 14–21 cm). Variability in the occurrence of mycorrhizal fungi can be high and Bellgard, Whelan & Mutson (1994) emphasized the need for temporal controls in fire ecology experiments.

In this study we investigated the effects of an early summer prescribed burn on the abundance of ectomycorrhizal root tips on ponderosa pine (*Pinus ponderosa* Laws.) by comparing samples taken before and one year after the fire. We also sampled ectomycorrhizas in unburned control plots for comparison to data from the fire plots. By identifying fungi from the root tips, we were able to provide some insight into how their ectomycorrhizas were distributed in space and time.

MATERIALS AND METHODS

Description of study site

The study site was at 1438 m above sea level in the Sierra National Forest, California (36° 58′ 48″ N, 119° 8′ 13″ W).

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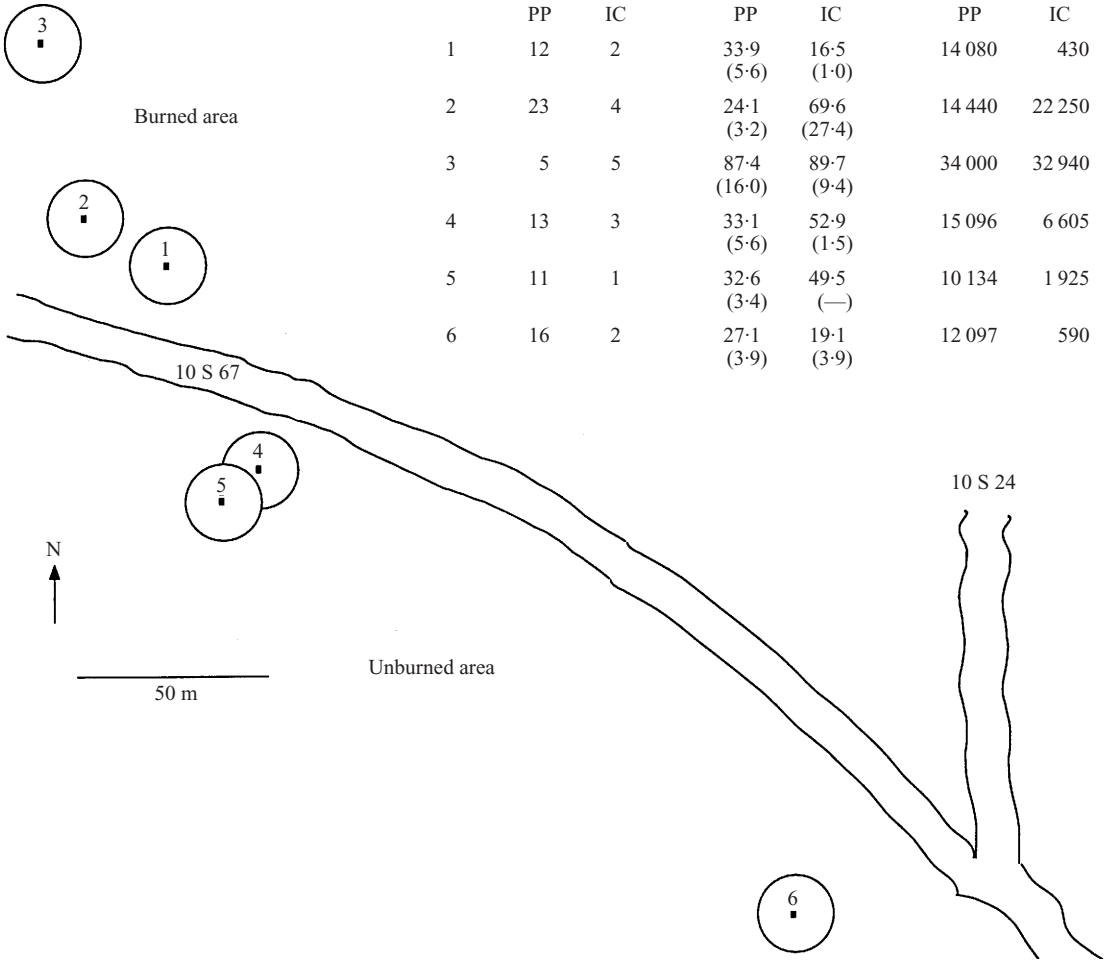


Tree composition in plots

Plot	Number of trees		DBH in cm, mean (S.E.)		Total basal area (cm^2)	
	PP	IC	PP	IC	PP	IC
1	12	2	33·9 (5·6)	16·5 (1·0)	14 080	430
2	23	4	24·1 (3·2)	69·6 (27·4)	14 440	22 250
3	5	5	87·4 (16·0)	89·7 (9·4)	34 000	32 940
4	13	3	33·1 (5·6)	52·9 (1·5)	15 096	6 605
5	11	1	32·6 (3·4)	49·5 (—)	10 134	1 925
6	16	2	27·1 (3·9)	19·1 (3·9)	12 097	590

Fig. 1. Schematic map of research area. Black squares indicate the 1 m^2 plots. Details are given for ponderosa pine (pp) and incense cedar (ic) for the 10 m radii indicated around each plot.

Six sampling plots were located in small mature stands of ponderosa pine on a south facing slope of approximately 11 degrees on either side of US Forest Service road 10S67. Three plots were established north of the road within an area planned for a control burn; three control plots were established south of the road outside the designated burn area (Fig. 1). The control plots were designed to assess year to year or spatial variation in the ectomycorrhizal community. Ectomycorrhizal community and community structure are defined as the frequency and abundance of ectomycorrhizal fungi colonizing roots of ponderosa pine in our plots. Two of the three control plots were located approximately 30 m south of road 10S67 directly across the road from the fire plots. The third control plot was also south of the road but was approximately 200 m east of the other control plots. These six plots were selected within this area based on the following criteria: (i) large ponderosa pine were present and were the primary ectomycorrhizal host (a few sub-arboreal *Quercus* were present); (ii) understory shrubs and herbs were few; (iii) the soil was deep enough and free enough of gravel to be cored to the depth of a 40 cm; (iv) no two plots were closer than 10 m to each other. The plots chosen were similar for all criteria, but varied somewhat with respect to amount and size of ponderosa pine and incense cedar (*Calocedrus decurrens* (Torrey) Florin) (Fig. 1). Incense cedar is an arbuscular mycorrhizal associate and so was not expected to directly affect the ectomycorrhizal community structure.

Ectomycorrhizas were collected from the study plots in May 1995 (year one) and May 1996 (year two). In late June 1995 the U.S.D.A. Forest Service burned approximately 360 ha north of road 10S67 that included the three fire plots.

Collecting of ectomycorrhizas

Sampling plots were established using a compartmentalized sampling frame (1 m^2). The frame was divided in 25 cm intervals resulting in 16 uniform squares. Eight squares per plot were assigned to each of the two sample years in a chequer-board pattern, such that adjacent squares were assigned to different years. This arrangement maximized spatial sampling within rather than between years. Within each plot, four soil cores were randomly selected from the eight possible positions assigned to a given year. In May 1995 and 1996 soil cores (4 cm diam × 40 cm depth) were collected from each of the six plots and resulting holes were filled with sand to minimize disturbance.

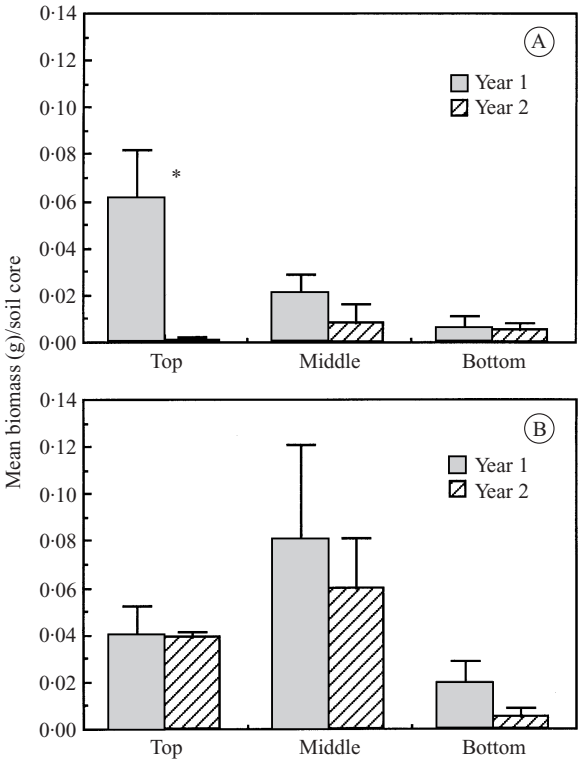


Fig. 2. Ectomycorrhizal biomass in soil cores from fire and control plots: (A), fire plots; (B) control plots. Soil cores were divided into top (litter and organic horizons), middle (upper portion of mineral soil) and bottom (lower portion of mineral soil) layers. Data are the mean ± 1 S.E. of three plots (each year's four cores are pooled for the plot sample). *Denotes means were significantly different, $P = 0{\cdot}05$.

Sorting and processing of ectomycorrhizas

Soil cores were stored at 4 °C after returning to the laboratory. The cores were divided into three layers: the litter and organic soil layer comprised the top section, while the mineral soil was divided into two equal middle and bottom sections. The soil sections were filtered through a series of metal screens by washing with cold tap water. The final screen size was 0·5 mm (No. 35 U.S.A. standard testing sieve). Washed roots were collected and stored at 4° in water for up to 7 d until further sorting. Final separation of root material from soil was conducted under a dissecting microscope.

All viable lateral short roots covered by a fungal mantle were classified as ectomycorrhizal. Viability of the root tips was based on colour and turgidity (Harvey *et al.*, 1976). Ectomycorrhizas were sorted into morphological types (morphotypes) based on colour, size and type of ramification as described in Agerer (1994). Representative samples from each morphotype were sectioned to determine the presence of a Hartig net. We examined and sorted ectomycorrhizas from each layer of each core separately. Ectomycorrhizas of a single morphotype from a given core section were placed in individual plastic centrifuge tubes (1·5 ml), quick frozen in liquid nitrogen and immediately lyophilized. After lyophilization, the samples were weighed and stored at −20°. The entire process, from collection to lyophilization, was performed within 3 wk. We made no attempt to relate morphotypes between cores or layers until molecular analysis was complete.

Molecular techniques

Fungal identification. DNA was extracted individually from one to three root tips as described in Gardes & Bruns (1993). Several tips were extracted together only when part of a single morphologically uniform clump. When available, replicates from each morphotype were extracted. DNA was also extracted from small pieces of voucher sporocarps by the same method.

The reagents, protocols, and cycling parameters used in PCR followed Gardes & Bruns (1993). Identifications of ectomycorrhizal fungal symbionts were based on PCR amplification of the ITS region using ITS1-F and ITS4-B, or ITS1-F and ITS-4 as primer pairs (White *et al.*, 1990; Gardes & Bruns, 1993). Both primer pairs preferentially amplify specific fragments of fungal DNA from mixtures of plant and fungal DNA. The ITS region was characterized by RFLP analysis, which was used to match ectomycorrhizas to one another and to sporocarps of voucher collections. Species-level identification was determined by identical RFLP matches with digests of two enzymes, *Alu* I, and *Hinf* I.

Basidiomycete family placement was conducted using the mitochondrial large subunit rRNA gene database (Bruns *et al.*, 1998). PCR amplification was done with primer pair ML-5 and ML-6. Determination of the fungal division (Ascomycota or Basidiomycota) was accomplished with a database of the 5.8S nuclear rRNA gene (Cullings & Vogler, 1998). Sequencing was done with the same primer pair by the cyclic reaction termination method using fluorescence labelled dideoxyribonucleotide triphosphates. The processing of templates for sequencing were performed following the instructions for the sequencing kit (PRISM Ready Reaction Diedioxy Terminator Cycle sequencing Kit, Perkin-Elmer Corporation). Electrophoresis and data collection were done on an ABI Model 377 DNA sequencer (Perkin-Elmer Corporation). DNA sequencing Analysis (version 2.01) and Sequence Navigator software were used to process the raw data. Sequences were aligned by visual estimation using a matrix created in PAUP 3.1.1 (Swofford, 1993). Identification was based on phylogenetic analysis with PAUP 3.1.1 (Swofford, 1993) and the heuristic search option or with the test version of PAUP 4.053 using the neighbour joining option. If no ITS-RFLP match was found for basidiomycetes identified to family, we labelled the fungus by its family group name, replacing the ending with -oid followed by a number for that group (i.e. the first unknown ITS-RFLP pattern in the Russulaceae becomes russuloid 1, the fifth unknown member of the Thelephoraceae becomes thelephoroid 5). Agaricoid refers to fungal sequences whose placement in the database was in an unresolved region that includes members of the Cortinariaceae, Tricholomataceae, Entolomataceae and Strophariaceae.

DNA could not be amplified from a small number of morphotypes. The biomass of these samples was grouped for the purposes of graphical presentation. The biomass of unique types whose individual biomass was less than 1 mg was also grouped for graphical presentation.

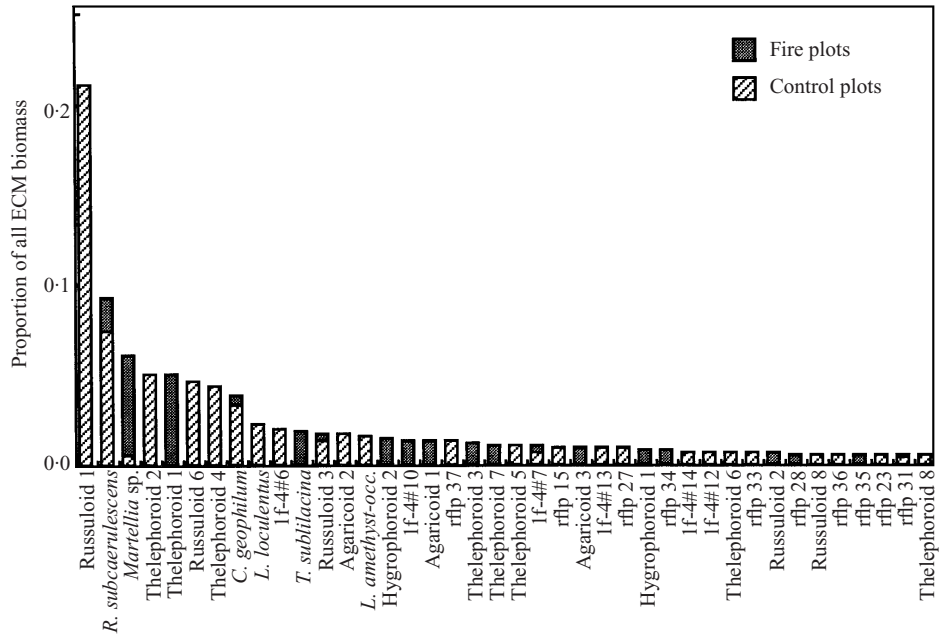


Fig. 3. Proportion of ectomycorrhizal biomass for all unburned plots in both years for the 40 most abundant taxa. In addition to those shown, 1f-4 # 12, *Russula murrillii*, russuloid 4 and 1f-4 # 11 were found in both control and fire plots. Forty-seven other taxa, with a relative abundance less than that of thelephoroid 8, also occurred. See Table 1 for an expansion of abbreviated names.

Host tree verification. Although ponderosa pine was the dominant ectomycorrhizal host in our study area, a few *Quercus* were also present. To confirm the ectomycorrhizas were ponderosa pine, we used a region of the nuclear large subunit using the plant specific primer pair 28KJ and TW14 (Cullings, 1992). We used single digests from one restriction enzyme, *Dpn* II, to produce RFLPs from DNA amplified from ectomycorrhizas and plant leaves. These analyses confirmed that ponderosa pine was the host in all collected ectomycorrhizas.

Assessment of fire intensity

We attempted to quantify the effects of fire on soil temperature. OMEGALAQ temperature sensitive paints ranging from 41 to 804° (melting point) were applied on metal razor blades and glass slides. At the time of field placement, the litter layer was very wet. The razor blades and glass slides were positioned from the middle of the litter layer to the interface of the organic layer and mineral soil. The control burn was, however, delayed for several weeks, allowing the litter and organic soil layers to dry. The fire consumed all organic material from the litter and organic soil layers. Several large logs were greatly reduced in size and scorch marks on the surviving trees extended 1–2 m up the trunks. All the temperature sensitive paints were damaged in the fire and we were not able to obtain any data from this method.

Statistical analysis

The Mann-Whitney statistic was calculated to test for the effects of fire on the abundance of ectomycorrhizal roots in each of the three layers. We pooled data from the four cores taken from each plot in a given year into one sample, resulting in a sample size of three, the number of plots in each of the experimental treatments.

RESULTS

In the fire plots, there was an eight-fold reduction of ectomycorrhizal biomass between year one and year two samples. Significantly less ectomycorrhizal biomass was observed, however, only in the top layer (litter and organic horizons) of the soil cores (Fig. 2A, one tailed Mann-Whitney test, $P = 0{\cdot}05$) after the fire; no significant differences were detected for the middle and bottom layers of the fire plot cores. In the control plots we found no significant change in ectomycorrhizal biomass between years for any core layer (Fig. 2B).

We distinguished over 50 taxa of ectomycorrhizal fungi on the roots (Fig. 3, Table 1). Six ectomycorrhizal types were matched to sporocarps. Twenty-three unmatched ectomycorrhizal types were identified to the family group level. Eleven species were found in both the control and fire plots. In general, a few ectomycorrhizal fungi were abundant while most species occurred in low abundance.

Prior to the fire, members of the Thelephoraceae and Russulaceae were among the most dominant species in both the fire and control plots. Within the fire plots *Martellia* sp. (Russulaceae) and thelephoroid 1 accounted for 21% and 19% of the ectomycorrhizal biomass, respectively (Fig. 4). The next most common type was *Tomentella sublilacina* (Ellis & Holw.) Wakef. (7%). In the control plots, russuloid 1 accounted for 40% of the biomass; the next most common species were russuloid 6 and thelephoroid 4, which accounted for 12 and 11% of the biomass, respectively (Fig. 5).

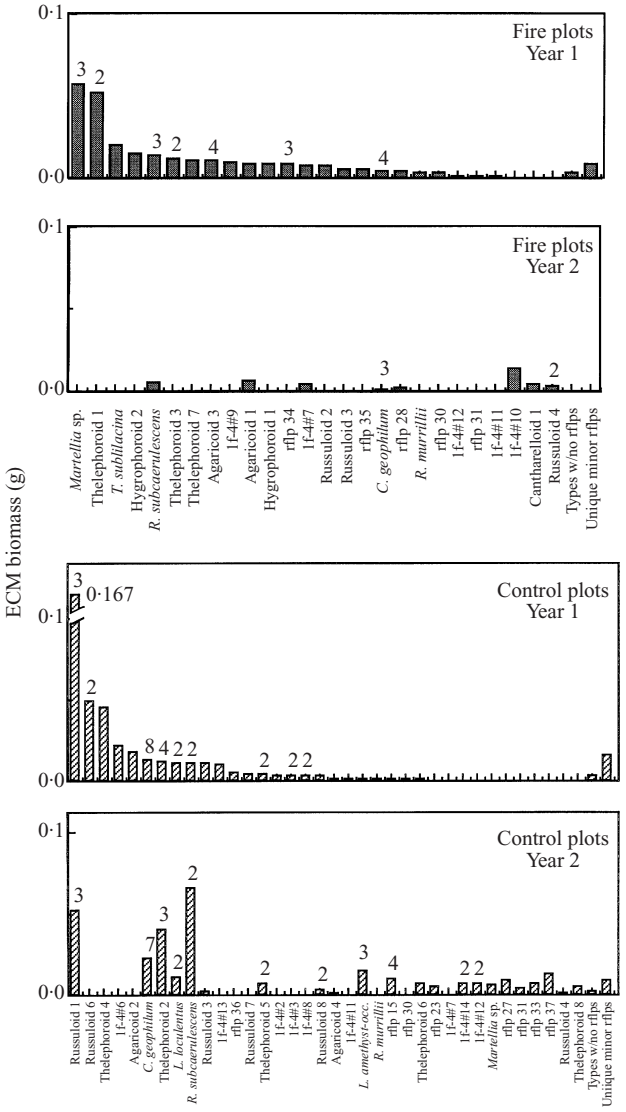
In the second year control plots russuloid 1 and thelephoroid 2 were the second and third most abundant types, accounting

Table 1. Restriction fragment band sizes (in base pairs) for ectomycorrhizal morphotypes. Fungal DNA was amplified with the primer pair ITS-1f and ITS-4b or with ITS-1f and ITS-4 (indicated with a superscript *a*). Voucher collection codes given are for sporocarps that matched fungi from mycorrhizas. Band sizes in parenthesis are submolar. Species are listed according to abundances shown in Fig. 3.

	Hinf I	*Alu* I
russuloid 1	409/372/98	490/(360)/260
Rhizopogon subcaerulescens, tdb 1039	252/133/75	471/(423)/334/87
Martellia species, snf 273	379/114	508/265/90
thelephoroid 2	400/225/130/125	795/88
thelephoroid 1	366/223/126/107	165/145/111/86
[a]russuloid 6	391/219/158	541/233
thelephoroid 4	350/211/143/117	363/106/84
[a]*Cenococcum geophilum*	161/118/110/92	395/187
Lactarius loculentis Burl., trh 163	434/280/133/120	521/(363)/283/83
thelephoroid 6	381/222/112/92	550/188/90
[a]1f-4 #6	200/(120)/110	553/94
Tomentella sublilacina, tdb 2015	366/223/126/107	458/(145)/111/86
russuloid 3	(350)/180/170/100	600/90
agaricoid 2	412/337/117	533/(220/143
Laccaria amethysteo-occidentalis G. M. Muell., trh 250	379/353/120	364/(288)/145/91
hygrophoroid 2	350/150/100	500/190/150/90
[a]1f-4 #10	270/192/107	247/203
agaricoid 1	368/337/120	758/87
rflp 37	360/230/120	500/120/90
thelephoroid 3	212/176/142/117	451/105/86
thelephoroid 7	374/120	313/194/169/94
thelephoroid 5	397/324/126	739/80
[a]1f-4 #7	355/321	(622)/540/122
rflp 15	400/205/90	379/243/100
agaricoid 3	368/337/120	758/87
[a]1f-4 #13	330	520/100
rflp 27	442/229/136	449/326/107/98
hygrophoroid 1	350/120/100	750/(520)/190/90
rflp 34	250/110/100	850
[a]1f-4 #14	350/200/160	690
[a]1f-4 #12	386/218/101	503/203
thelephoroid 6	381/222/112/92	550/188/90
rflp 33	381	352/265/196/118
russuloid 2	353/253/192/170/118	519/320/292/83
rflp 28	353/222/183/130/100	393/249/214
russuloid 8	402/358/125	376/(240)/172/150/95
rflp 36	340/300/115	550/(420)/130
rflp 35	320/300/90	400/250
rflp 23	(385)/353/251/117	282/(254)/239/207
rflp 31	340/290	590/200/90
thelephoroid 8	354/206/139/120	240/152/95
cantherelloid 1	290/170/120/105	510/(260)/140/120/90
agaricoid 5	350/300/125	725
Russula murrillii Burl., snf 28	410/350/110	333/265/90
russuloid 4	395/348/119	490(390)/286/85
rflp 30	369/229/115/89	735/90
[a]russuloid 7	390/225/160	670/430/150
[a]1f-4 #3	372/179/151	573/89
[a]1f-4 #8	370/230/(210)	375/210/90
[a]1f-4 #2	366/121/98	464/(307)/179
[a]1f-4 #9	172/157	520/114
agaricoid 4	333/286/110/90	620/144/99
[a]1f-4 #1	377/364	504/157

for 17 and 13% of the ectomycorrhizal biomass, respectively (Fig. 5). *Rhizopogon subcaerulescens* A. H. Sm., however, was the most abundant type accounting for 21% of the biomass; this contrasts with its low abundance (3%) in the previous year from the same untreated plots. The difference was caused by a large coralloid mycorrhiza sampled in the second year. This cluster of rootlets was over 1 cm diam. and weighed 65 mg D.W. This contrasts with single rootlets or small open clusters of other species that typically weighed 2–6 mg.

Data from the control plots show a high level of spatio-temporal variation in the occurrence and abundance of many fungal species. Although many cores were within 25 cm of each other, many species/RFLP types were sampled only once during the study. In the control plot samples, 42% of the



Figs 4–5. Ectomycorrhizal biomass from fire plots (**Fig. 4**) and control plots (**Fig. 5**). Numbers above each bar are the no. of cores in which a fungus occurred if > 1. Species sorted by year 1 abundance.

species/RFLP types were found in only one core, and only twelve of the 25 morphotypes found in year one were found in year two, while 11 morphotypes were unique to the second year (Fig. 5). These numbers do not include types with no RFLPs or minor types (unique morphotypes that were $\leqslant 1$ mg D.W.). In addition, species that were relatively frequent (occurred in multiple cores) showed an uneven distribution. For instance, russuloid 1 was the most abundant fungus sampled in the study, but it occurred in cores from only one of the six 1 m² plots. *Rhizopogon subcaerulescens* occurred frequently but in low abundance (ectomycorrhizal biomass) except for the single coralloid ectomycorrhiza discussed above that contributed over 50% of its total biomass in the study. Only mycorrhizae of *Cenococcum geophilum* Fr. had a relatively even distribution.

In the fire plots, at least 18 species found in year one were absent from year two samples (this does not include types with no RFLPs or unique minor RFLPs in Fig. 4). *R. subcaerulescens*, *C. geophilum*, and three unidentified types were sampled as active ectomycorrhizae before and after the fire (Fig. 5). Three other types (1f-4 number 10, cantherelloid 1 and russuloid 4) were sampled in year two, but not in year one.

DISCUSSION

The general structure of the unburned fungal ectomycorrhizal community in this Sierra Nevada *Pinus ponderosa* forest is strikingly similar to those studied in coastal forests dominated by (i) *Pinus muricata* (Gardes & Bruns, 1996), (ii) a mixture of *P. muricata* and *Pseudotsuga menziesii* (Horton & Bruns, 1998) or (iii) *Arctostaphylos glandulosa* with *P. menziesii* (Horton, Bruns & Parker, in press). All four communities were composed of many species, but had a set of three to four species that accounted for more than 50% of the biomass; other species were either rare, or low in abundance, or both. Dominance by a few species and rarity of most others is the common pattern seen in communities of any taxonomic group (Putnam, 1994); thus, it is expected in ectomycorrhizal fungus communities. What was not expected was that members of the Russulaceae and Thelephoraceae would constitute the primary dominants in all four communities. *Abies* communities in northern Europe, which have *Tylospora fibrillosa* (Thelephoraceae) as a dominant, provide another example (Taylor & Alexander, 1990; Erland, 1995). We suggest that dominance by these two families may constitute a widespread pattern, at least in relatively young (< 100 y) Pineaceae-dominated ecosystems.

The spatio-temporal variation of ectomycorrhizal fungi on root tips is clearly very high. Most species show a clumped distribution. Russuloid 1 occurred in a single 1 m² plot while *R. subcaerulescens* was not particularly abundant except for a single coralloid ectomycorrhiza. Clumpy distributions have been observed with *Tomentella sublilacina* and an unknown thelephoroid species (Horton & Bruns, 1998). Most species in our samples occurred in three or fewer cores, typically within single plots. Thus, we can not determine whether infrequent species unique to a single sample year were missed due to spatial rarity or absent due to differences between years.

The clearest effect of the fire was the significant loss of ectomycorrhizal biomass in the litter and organic soil horizons (Fig. 2). This distribution was expected since many ectomycorrhizal root tips occur in the litter and organic horizons (Harvey *et al.*, 1976, 1979). Survival at greater depth was also expected because soil is a relatively good insulator and heat from a forest fire typically penetrates only a few centimetres (Barbour Burk & Pitts, 1987). The indirect effects from ash leaching could potentially affect mycorrhizal fungi via pH and nutrient shifts, but the impact might be expected to be more subtle.

The high degree of variation evident in the control plots means that we were unable to assess the effects of fire on most individual species with these samples. It is interesting, however, that none of the fungi that occurred after the fire were particularly abundant prior to the fire, suggesting abundance is a poor indicator of persistence after fire. We speculate that this observation may be caused by depth patterning of mycorrhizas at this site, coupled with the destruction of the upper layer by the fire. The top layer

accounted for 73% of mycorrhizal biomass prior to the fire, while post-fire it was reduced to nearly undetectable levels (Fig. 2). The three most dominant species in the fire plots, *Martellia* sp., thelephoroid 1, and *T. sublilacina* had 90%, 72% and 54% of their biomass in the top layer, respectively; thus the upper layer was the main component of their dominance. When this layer was destroyed by the fire it effectively flattened the abundance curve, dropping most species, including the three previously dominant ones, to low or undetectable levels. If the dominant species are impacted more heavily this may result in at least temporary increase in species evenness.

We thank Bernadette Lato for her help with the first year samples. We are also indebted to Dave McCandliss for helping us select the site for our fire study and for executing the prescribed burn. We thank Jerry Verner and George Steger of the U.S.D.A. Forest Service for logistical support at the Dinkey Creek Work station. Financial support was provided in part by a cooperative agreement with the U.S.D.A. Southwest Experiment Station and NSF grant DEB 9628852.

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