

# Early impacts of forest restoration treatments on the ectomycorrhizal fungal community and fine root biomass in a mixed conifer forest

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## Summary

1. The obligate symbiosis formed between ectomycorrhizal fungi (EMF) and roots of tree species in the Pinaceae influences nutrient uptake and surrounding soil structure. Understanding how EMF respond to prescribed fire and thinning will assist forest managers in selecting fuel-reducing restoration treatments that maintain critical soil processes and site productivity.

2. The response of EMF species richness, live fine root biomass and duff levels to various forms and combinations of thinning and burning was investigated in mixed ponderosa pine and Douglas fir stands in the Blue Mountains of Oregon. The below-ground community composition and structure of EMF at the site was characterized using molecular methods.

3. The EMF community consisted of a large number of infrequently detected species. The distribution of a few abundant species (*Cenococcum* sp., *Piloderma* sp., *Rhizopogon salebrosus* and *Wilcoxina rehmii*) in a majority of the treatments both before and after treatment application demonstrates that some EMF species survive or rapidly re-establish after disturbance.

4. EMF species richness, live root biomass and duff levels were reduced significantly by prescribed fire treatments compared to the non-burned treatments.

5. *Synthesis and applications.* These results indicate that prescribed fire results in a short-term reduction in EMF species richness and live root biomass and may influence whether managers can achieve the desired future condition of stands with large-tree retention and low fuel loads. EMF mortality and complete duff reduction after fire have been implicated with poor tree survival and slow stand recovery in forest ecosystems world-wide. The results of this study, along with the recovery potential of a site, and the impending risk of stand-replacing wildfire in stands differing in structure from historic conditions, bear consideration when reintroducing fire.

*Key-words:* ecological restoration, ectomycorrhizae, fine root biomass, prescribed thinning and fire, ponderosa pine

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## Introduction

Low-intensity prescribed fire and mechanical thinning/removal (thinning) are two primary tools applied by

forest managers to reduce the risk of stand-replacing wildfires in forests in the American inland Pacific Northwest. In dry pine-dominated forests in this region, fire suppression, livestock grazing, insect infestations, climate change and logging of the largest trees have resulted in increased stand densities, unusually high fuel loads and changes in plant species composition (Langston

1995; Bachelet *et al.* 2003). Prior to Euro-American settlement in this region, frequent intentional burning of the landscape by Native Americans and lightning strikes promoted open stands dominated by large fire-resistant ponderosa pine *Pinus ponderosa* Dougl. ex Laws. (Biswell 1989; Agee 1993). Historically fires occurred frequently, with an average return interval of c. 10 years (Robbins & Wolf 1994). However, in response to uncontrollable wildfires around the turn of the 20th century the United States Forest Service initiated its fire suppression policy that drastically prolonged the fire return interval and, eventually, placed these ecosystems at high risk of catastrophic wildfire (Biswell 1989; Arno & Allison-Bunnell 2002). In an attempt to restore healthy forest ecosystems, a recent federal fire policy allows for the use of fire to regulate fuels (USDA 2003).

In ponderosa pine-dominated forests within this region, managers now strive to reduce the risk of fire through fuel reduction and thinning of small diameter trees. Perry *et al.* (1989) showed that above-ground ecosystem recovery after timber harvest and site preparation burning is linked directly to the survival of ectomycorrhizal fungi (EMF) that reside mainly in the surface layers of soil and organic matter (Harvey *et al.* 1986; Swezy & Agee 1991). The coevolved symbiosis between EMF and species in the Pinaceae is critical for efficient nutrient acquisition and protection against root pathogens (Smith & Read 1997; Read 1998). Most EMF are able to colonize multiple host genera; a few are specific to a single host genus such as *Pinus* (Molina, Massicotte & Trappe 1992; Horton & Bruns 1998). Knowledge of the below-ground structure and composition and response to prescribed fire and thinning of EMF associated with Pinaceae species in this region is limited.

Numerous studies describe the relationship between recovery of disturbed ecosystems and the EMF community. Byrd *et al.* (2000) noted an overall reduction of EMF species richness and significant changes in species composition after clear-cutting. Changes in EMF species composition after clear-cutting are influenced by the soil environment as well as by loss or change in fungal inoculum (Jones, Durall & Cairney 2003). Dahlberg *et al.* (2001) found a positive correlation among EMF mortality, increased burn intensity and tree mortality. Several studies have shown a short-term reduction in EMF sporocarp production or in numbers of live fine roots after clearcutting and burning (Wright & Tarrant 1958; Harvey, Jurgensen & Larsen 1980; Parke, Linderman & Trappe 1984; Pilz & Perry 1984; Herr *et al.* 1994), thinning and broadcast burning (Waters *et al.* 1994), burning alone (Buchholz & Gallagher 1982; Stendell, Horton & Bruns 1999) or thinning alone (Colgan *et al.* 1999; Gomez, Anthony & Trappe 2003). Results suggest, however, that EMF community composition is not substantially altered by low intensity wildfires (Jonsson *et al.* 1999) or by restoration thinning and burning (Korb, Johnson & Covington 2003) if the organic layer remains relatively undamaged. In contrast, high-intensity natural or prescribed fire that severely burns the mineral

soil (Feller 1998) significantly alters the EMF community (Visser 1995; Baar *et al.* 1999; Grogan, Baar & Bruns 2000; Dahlberg *et al.* 2001).

This study investigates the response of the EMF community by directly comparing the effects of prescribed fire, mechanical thinning and a combination of fire and thinning with replication at the stand level. Treatments were chosen to represent potential management choices for reducing fuels and accelerating the development of late-successional stand structure in low- to mid-elevation ponderosa pine-dominated forests in north-eastern Oregon. In this study the EMF community is defined as the frequency and abundance of EMF colonizing tree roots. Because other studies have shown variable effects of thinning and burning on EMF community structure depending on disturbance intensity, we predicted the greatest reduction in EMF biomass in the burn treatments. Our objectives were to (i) quantify the effect of restoration thinning and prescribed fire on the EMF community and live fine root biomass; (ii) assess the importance of duff (decaying material) depth as a measure of treatment impact; and (iii) determine whether the number of EMF species and the biomass of live fine roots differ with soil depth in response to restoration treatments.

## Materials and methods

### STUDY AREA

Research was conducted in the Wallowa Valley Ranger District (Wallowa-Whitman NF) between Davis and Crow Creek drainages (45°4'N, 117°3'W), 45 km north of Enterprise, Oregon in the northern extension of the Blue Mountain Range. Stands within the study area are 1300–1600 m elevation and contain a mixture of ponderosa pine and Douglas fir *Pseudotsuga menziesii* (Mirb.) Franco, with snowberry *Symphoricarpos albus* (L.) Blake the dominant shrub in the understorey. The area has been heavily managed since the turn of the 20th century, including fire suppression and logging of most of the larger ponderosa pine throughout the period of 1910–96. Stands are comprised mainly of second-growth trees with stems less than 25 cm diameter at breast height (d.b.h.) and an occasional large 100–200-year-old tree. The d.b.h. of trees range from 10 to 75 cm. Thinning occurred between July and November 1998. Prescribed burning was delayed until September 2000 because weather patterns did not provide safe conditions for the scheduled burn in autumn 1999.

### EXPERIMENTAL DESIGN AND SAMPLING PROCEDURES

The study is a complete randomized design with four replications of each restoration treatment (thinned only, prescribed burn only, thinned and prescribed burned and non-thinned and non-burned control) assigned to c. 10 ha treatment units (stands). A sampling grid, with

c. 2 grid points  $\text{ha}^{-1}$  and grid points at least 50 m from the stand boundary, was established within each stand. A soil core (5 cm diameter  $\times$  10 cm depth) was collected from the vicinity of three randomly selected grid points  $\text{stand}^{-1}$  in June 1998, before the application of restoration treatments, and in June 2001, after the restoration treatments. Post-treatment soil cores were collected within 10–20 cm of the pretreatment soil core locations. Post-treatment sampling in burned stands occurred within burned patches. The ponderosa pine, with d.b.h.  $\geq$  20 cm, closest to each selected grid point stake was marked with an aluminium tag. Soil cores were taken due east of each selected tree at the tree crown edge. All soil cores were separated into two subsamples representing the upper 5 cm and lower 5 cm of the core. Because of rocky soil, coring was restricted from depths deeper than about 10 cm. Duff depth was measured to the nearest 0.5 cm and recorded at each soil core location. The duff layer was removed prior to coring so that a consistent depth was sampled in mineral soil both before and after the restoration treatments. Sporocarps from throughout the Blue Mountains as well as those found on the study site were collected opportunistically to help determine identities of EMF symbionts. Representative voucher collections were accessioned into the Oregon State University Herbarium.

#### SORTING AND PROCESSING OF ECTOMYCORRHIZAS

Soil cores were transported to and stored in the laboratory at 4 °C. Samples were processed within 3 weeks after collection. Soil core samples were soaked in water to loosen debris then rinsed through a soil sieve with a mesh size of 1.0 mm (no. 35 USA standard testing sieve). A stereo dissecting microscope was used to sort ectomycorrhizas into morphological types (morphotypes) based primarily on colour, mantle surface texture, rhizomorph presence or absence and mycorrhiza branching pattern. Viability assessment of the root tips was based on colour and turgidity (Harvey, Larsen & Jurgensen 1976). Some fungi in our study formed a type of mycorrhiza known as ectendomycorrhiza (Smith & Read 1997). This unique type of mycorrhiza was originally described on *Pinus* spp. and defined by intracellular penetration of cortex cells, a weakly defined mantle, and wide hyphae in the Hartig net (Laiho 1965; Mikola 1965). Two root tips from each morphotype within a core sample were placed directly in cetyltrimethyl ammonium bromide (CTAB) buffer and stored at 4 °C. Ectomycorrhizas with slight differences in appearance were separated into several morphotypes and later pooled for data analysis if warranted by identification with molecular techniques. In cases where the two root tips representing a morphotype sample differed, molecular data were obtained for up to 10 additional root tips and the sample biomass apportioned accordingly. Data are presented only for morphotype groups for which molecular data were obtained. Ectomycorrhizas of

each morphotype from a given core sample were placed in individual centrifuge tubes, lyophilized and weighed to the nearest 0.0001 g.

#### MOLECULAR ANALYSES

DNA extraction, polymerase chain reaction (PCR) amplification and restriction fragment length polymorphism (RFLP) protocols followed Gardes & Bruns (1993) with minor modification. DNA was extracted individually from at least two root tips from each morphotype within a core sample and also from small pieces of collected sporocarps. Some EMF morphotype groups did not yield PCR product, even after DNA extraction was attempted from up to 10 root tips. Averaging over both sample times, 87% of the 624 morphotype sample groups yielded PCR product.

Identifications of EMF symbionts were based on PCR amplification of the internal transcribed spacer (ITS) region of the nuclear ribosomal DNA using the fungal specific primer pair ITS-1f and ITS-4 (Gardes & Bruns 1993). The ITS region was characterized by RFLP analysis, which was used to match EMF symbionts to one another and to sporocarps collected from the study site and from throughout the Blue Mountains. Two restriction enzymes (*DpnII*, and *HinfI*) in single enzyme digests were used initially to characterize and match fungal ITS–RFLP patterns. Restriction fragments were subsequently separated on agarose gels (3% agarose) and visualized with ethidium bromide under ultraviolet light. All RFLPs were recorded by AlphaImager™. After visual assessment of the RFLP patterns and comparisons of morphotype descriptions and scores of the two restriction enzymes from all photographed images, samples potentially matching were run in adjacent lanes of the same agarose gel with three restriction enzymes (*AluI*, *DpnI* and *HinfI*) in single enzyme digests. Identical RFLP matches with digests for all three endonucleases determined species-level identification. Restriction fragments resulting from restriction enzyme digest with *AluI* were used to confirm the matching of samples but typically were not scored. There is a general correspondence between ITS–RFLP types and species (Gardes & Bruns 1996; Kårén *et al.* 1997; Horton 2002).

Few morphotype RFLP patterns matched others seen from past surveys carried out by our laboratory (Smith *et al.* 2004). Therefore, taxonomic identifications were attempted for the majority of our RFLP types by sequencing one or two different DNA regions: (i) both spacers of the ITS region of the nuclear ribosomal repeat and the intercalated 5.8S rRNA gene using primer pair ITS1f and ITS4 for amplification; and (ii) an approximately 400 base pairs (bp) fragment of the mitochondrial large subunit rDNA using primer pair ML5 and ML6 for amplification (Bruns *et al.* 1998). PCR products were cleaned using the Qiagen® QIAquick PCR Purification Kit™ or Qbiogene GeneClean®. Samples were sent to the Center for Gene Research and Biotechnology at Oregon State University for sequencing on an

ABI 377 automated sequencer. The resulting sequences were edited in SeqEd (PE Biosystems), and aligned manually using PAUP 3.1 (Swofford 1993) and PAUP\* (Swofford 1999) and a colour font. A sequence similarity search of the National Center for Biotechnology Information (NCBI) database, GenBank, was conducted using the Basic Local Alignment Search Tool (BLAST) 2.0 algorithm.

#### STATISTICAL ANALYSES

A Poisson log-linear regression, suitable for modelling count data (McCullagh & Nelder 1991), was used to analyse count data of EMF species tallied by stand and by core sample depth. Poisson analysis of deviance (ANODEV) tables were derived from the Poisson log-linear models of changes in the number of EMF species explained by stand and core sample depth (Hastie & Pregibon 1992). A  $\chi^2$  test was used to test for the effects of factors and their interactions, using the deviance attributed to the terms and their degrees of freedom (Hastie & Pregibon 1992). EMF root biomass for each stand was summed across core samples, averaged across each restoration treatment and depth (upper, lower), and analysed in an analysis of variance (ANOVA) for each collection year. To assess whether the duff depth differed among treatments, duff depth for each core was averaged within stands for each restoration treatment and analysed in an ANOVA. Even though all 16 stands had similar plant assemblages, one control stand appeared as a potential outlier because of numerous windfallen trees and thick grassy understorey. At the post-treatment sample time, no EMF species were found in the samples from this stand, further suggesting the stand belongs to a population other than the one under investigation. Residual analysis revealed that the stand had standardized residual values exceeding two standard deviations. Removal of the outlier stand produced test results with convincing rather than slight evidence. Results without the outlier are presented. All analyses were carried out with S-Plus version 2000 software (MathSoft 1988–1999). The Sorenson index (SI), designed to equal 1 in cases of complete similarity and 0 if the cases are dissimilar and have no species in common, was used to assess EMF species similarity (Magurran 1988) between all pairs of (i) years, (ii) stands and (iii) year–treatment combinations.

## Results

#### EMF COMMUNITY RESPONSE TO RESTORATION TREATMENTS

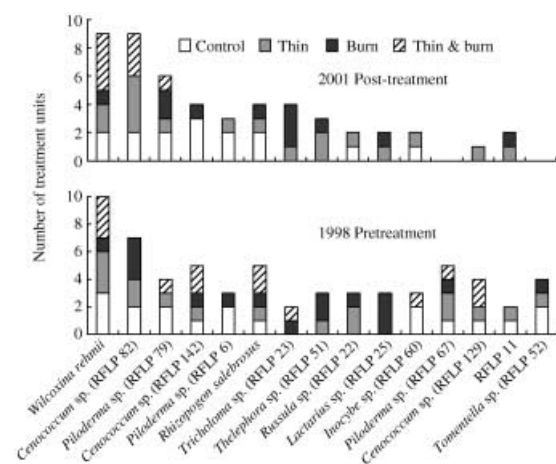
One hundred and seventy-eight RFLP species were distinguished on the roots. Of these, 10 matched to sporocarps based on RFLP patterns or sequences, an additional 47 were identified to family or genus and 26 to class (Table S1; Supplementary material). RFLP species identified beyond class level belonged to the Cortinariaceae (15 species), Thelephoraceae (11 species),

Atheliaceae (seven species) and Russulaceae (six species) (Table S1). One hundred and thirty-eight species (69%) were found in lower core samples, 123 (62%) in upper core samples, 62 species (31%) were found in both soil depths. All but one recurring species detected in four or more cores (19 species in total) were found in both soil depths. The cumulative number of RFLP species increased by 29% at the post-treatment sample time. During the course of the study, most (78%) species were detected in only one stand, 11% were detected in three or more stands. The pre- and post-treatment occurrence of the 15 'frequent' species, those detected in four or more stands, is presented by treatment in Fig. 1. Our results indicate an EMF community consisting of a large number of species scattered at low frequencies across the site before and after the application of restoration treatments.

Prior to treatment application, there were no significant differences in the number of EMF species among treatments ( $\chi^2 = 7.09$ ,  $P = 0.07$ ) or between upper and lower core samples ( $\chi^2 = 0.15$ ,  $P = 0.70$ ; Table 1). After treatment application, the number of RFLP species differed among treatments ( $\chi^2 = 10.65$ ,  $P = 0.01$ ; Table 1). The control and thinned stands had about 68% more EMF species than the burned, and thinned and burned stands (Table 1). The number of EMF species did not differ between the upper and lower soil core depths except in the thinned and burned treatment, where the number of EMF species was less in the upper 5 cm than in the lower 5 cm (depth by treatment interaction  $\chi^2 = 11.91$ ,  $P = 0.01$ ; Table 1).

#### EMF SPECIES SIMILARITY IN SPACE AND TIME

Thirty-two EMF species were common to the pre- and post-treatment years (Sorenson index (SI) = 0.29), indicating persistence of some species through time (Table S1). Most (62%) of the recurring species occurred in neighbouring cores, typically from the control and thinned stands. Species similarity across the landscape



**Fig. 1.** Pre- and post-treatment occurrence within treatment units for the 15 most frequent EMF species. Species are listed in descending order of total frequency.

**Table 1.** Means  $\pm$  standard errors for number of RFLP species and live root biomass ( $n = 15$ ). Values indexed by a different letter are significantly different at the  $P \leq 0.05$  level among treatments and between upper and lower soil core depths

| Treatment             | Depth (cm) | Pretreatment 1998          | <i>P</i> | Post-treatment 2001        | <i>P</i> |
|-----------------------|------------|----------------------------|----------|----------------------------|----------|
| RFLP species          |            |                            |          |                            |          |
| Control               | 0–10       | 15.0 ± 1.2 <sup>a</sup>    | 0.07     | 12.3 ± 0.9 <sup>a</sup>    | 0.01     |
| Thin                  | 0–10       | 15.3 ± 4.9 <sup>a</sup>    |          | 11.8 ± 3.0 <sup>a,b</sup>  |          |
| Burn                  | 0–10       | 9.5 ± 1.7 <sup>a</sup>     |          | 6.8 ± 2.0 <sup>c</sup>     |          |
| Thin/burn             | 0–10       | 14.8 ± 1.7 <sup>a</sup>    |          | 7.0 ± 2.4 <sup>bc</sup>    |          |
| Upper                 | 0–5        | 8.3 ± 1.0 <sup>a</sup>     | 0.70     | 4.4 ± 0.9 <sup>a</sup>     | 0.01     |
| Lower                 | 5–10       | 7.9 ± 0.9 <sup>a</sup>     |          | 7.1 ± 0.8 <sup>a</sup>     |          |
| Control upper         | 0–5        | 9.3 ± 1.8 <sup>a</sup>     |          | 6.7 ± 0.7 <sup>a</sup>     |          |
| Control lower         | 5–10       | 8.0 ± 1.2 <sup>a</sup>     |          | 8.7 ± 0.9 <sup>a</sup>     |          |
| Thin upper            | 0–5        | 8.5 ± 2.3 <sup>a</sup>     |          | 7.3 ± 2.1 <sup>a</sup>     |          |
| Thin lower            | 5–10       | 9.5 ± 3.2 <sup>a</sup>     |          | 8.0 ± 1.8 <sup>a</sup>     |          |
| Burn upper            | 0–5        | 4.8 ± 1.4 <sup>a</sup>     |          | 3.3 ± 0.9 <sup>a</sup>     |          |
| Burn lower            | 5–10       | 6.3 ± 1.0 <sup>a</sup>     |          | 5.5 ± 1.6 <sup>a</sup>     |          |
| Thin/burn upper       | 0–5        | 11.0 ± 1.7 <sup>a</sup>    |          | 1.0 ± 0.7 <sup>a</sup>     |          |
| Thin/burn lower       | 5–10       | 8.0 ± 0.4 <sup>a</sup>     |          | 6.5 ± 2.1 <sup>b</sup>     |          |
| Live root biomass (g) |            |                            |          |                            |          |
| Control               | 0–10       | 0.102 ± 0.021 <sup>a</sup> | 0.11     | 0.225 ± 0.049 <sup>a</sup> | 0.001    |
| Thin                  | 0–10       | 0.167 ± 0.024 <sup>a</sup> |          | 0.099 ± 0.018 <sup>b</sup> |          |
| Burn                  | 0–10       | 0.059 ± 0.021 <sup>a</sup> |          | 0.037 ± 0.013 <sup>c</sup> |          |
| Thin/burn             | 0–10       | 0.187 ± 0.061 <sup>a</sup> |          | 0.028 ± 0.018 <sup>c</sup> |          |
| Upper                 | 0–5        | 0.055 ± 0.009 <sup>a</sup> | 0.32     | 0.045 ± 0.020 <sup>a</sup> | 0.96     |
| Lower                 | 5–10       | 0.076 ± 0.019 <sup>a</sup> |          | 0.044 ± 0.009 <sup>a</sup> |          |

|          |       |       |       |         |        |        |        |          |
|----------|-------|-------|-------|---------|--------|--------|--------|----------|
| Pre C    | 1.00  | 0.20  | 0.23  | 0.27    | 0.29   | 0.19   | 0.14   | 0.09     |
| Pre T    | 10    | 1.00  | 0.26  | 0.15    | 0.16   | 0.29   | 0.13   | 0.10     |
| Pre B    | 9     | 11    | 1.00  | 0.21    | 0.22   | 0.25   | 0.25   | 0.15     |
| Pre T/B  | 13    | 8     | 9     | 1.00    | 0.14   | 0.13   | 0.21   | 0.18     |
| Post C   | 11    | 7     | 7     | 6       | 1.00   | 0.28   | 0.18   | 0.15     |
| Post T   | 8     | 14    | 9     | 6       | 10     | 1.00   | 0.28   | 0.13     |
| Post B   | 5     | 5     | 7     | 8       | 5      | 9      | 1.00   | 0.21     |
| Post T/B | 3     | 4     | 4     | 7       | 4      | 4      | 5      | 1.00     |
|          | Pre C | Pre T | Pre B | Pre T/B | Post C | Post T | Post B | Post T/B |

**Fig. 2.** Matrix showing EMF species similarity between time and treatment pairs. Boxed, similarity coefficients from the Sorenson index; unboxed, number of species in common. Pre, pretreatment 1998; post, post-treatment 2001; C, control; T, thin; B, burn; T/B, thin and burn.

was evident by most (95%) pairs of stands sharing at least one, and as many as six species ( $SI = 0.03$ – $0.33$ ). Two species, *Cenococcum* sp. (RFLP 82) and *Wilcoxina rehmii* Chin S. Yang & Korf, were each detected in 75% of the stands; *Rhizopogon salebrosus* A.H. Sm. and *Piloderma* sp. (RFLP 79) were each detected in 50% of the stands.

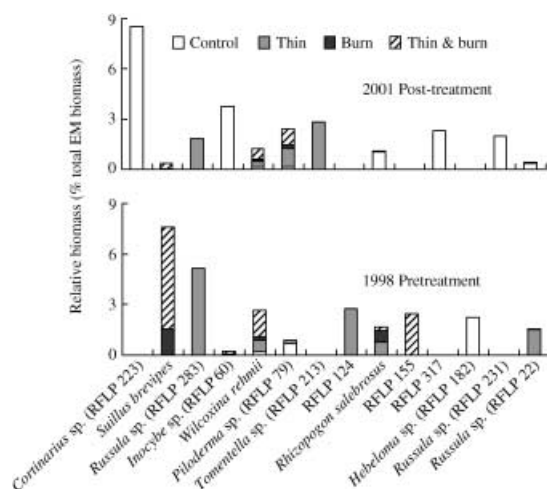
Post-treatment burned, and thinned and burned treatments contained fewer total species (24 and 23 species, respectively) than other time–treatment combinations (31–54 species) and, typically, shared the least number of species (three to nine species,  $SI = 0.09$ – $0.28$ ) with other time–treatment combinations (Fig. 2). Total species refers to the cumulative number of unique RFLP

species found at the replicate sites of each treatment. Relatively high similarity was seen among most pre-treatment comparisons (eight to 13 species,  $SI = 0.15$ – $0.27$ ) and between the post-treatment control and thin comparison (10 species,  $SI = 0.28$ ; Fig. 2). Only one species, *W. rehmii*, was detected in all treatments both before and after treatment application; three species, *Cenococcum* sp. (RFLP 82), *Piloderma* sp. (RFLP 79) and *R. salebrosus*, were detected in at least three treatments both before and after treatment application (Fig. 1).

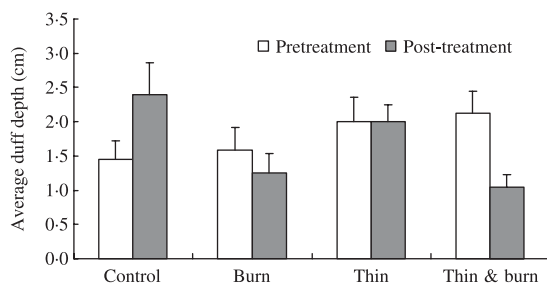
#### EMF ROOT BIOMASS

Fourteen species, each with 2% or more of the total EMF biomass, accounted for 54% of the total EMF biomass. Their pre- and post-treatment abundance is presented by treatment in Fig. 3. An additional 12 species each contributed  $\geq 1\%$  to the total biomass. The distribution within treatments of the 14 biomass dominant species, as well as that of frequent species (Fig. 1), indicated that the EMF community consisted of a few dominant species and a relatively large number of infrequent species. Five of the biomass dominant species, *Inocybe* sp. (RFLP 60), *Piloderma* sp. (RFLP 79), *R. salebrosus*, *Russula* sp. (RFLP 22) and *W. rehmii*, were also among the most frequent species (Figs 1 and 3), indicating some correlation between EMF biomass and frequency. All five species were detected both before and after restoration treatments (Figs 1 and 3).

Prior to treatment application, there were no significant differences in live root biomass among treatments ( $F_{3,11} = 2.51$ ,  $P = 0.11$ ) or between upper and lower core samples ( $F_{1,15} = 1.09$ ,  $P = 0.32$ ; Table 1). After treatment



**Fig. 3.** Pre- and post-treatment biomass of the 14 biomass dominant EMF species within treatments. In certain cases, relative mycorrhizal biomass for a particular RFLP species was so small that it is beyond the resolution of the figure. Species are listed in descending order of total biomass.



**Fig. 4.** Average duff depth before and after restoration treatments ( $n = 15$ ). Bars represent 1 SE at the 95% confidence interval.

application, the live root biomass differed among treatments ( $F_{3,11} = 12.57$ ,  $P < 0.001$ ; Table 1). The control and thinned stands had more live root biomass than the burned, and thinned and burned stands (Table 1). Live root biomass did not differ between the upper and lower soil core depths after treatment application ( $F_{1,12} = 0.002$ ,  $P = 0.96$ ; Table 1).

#### DUFF DEPTH

Prior to treatment application, duff depth did not differ among treatments ( $F_{3,12} = 0.93$ ,  $P = 0.46$ ; Fig. 4). After treatment application, duff depth differed among treatments ( $F_{3,12} = 4.49$ ,  $P = 0.03$ ) and was lower in the thinned and burned stands ( $t_{12} = 3.80$ ,  $P = 0.003$ ) and in the burned stands ( $t_{12} = 3.32$ ,  $P = 0.006$ ) compared to control stands. Duff depth did not differ between the control and thinned stands ( $t_{12} = 1.56$ ,  $P = 0.15$ ) (Fig. 4).

#### Discussion

In this study, both burning treatments significantly reduced EMF species richness, live root biomass and

duff depth compared to the non-thinned and non-burned treatment. The effect of thinning alone on these response variables was generally similar to that of the non-thinned and non-burned treatment. Thinning occurred 2 years before burning and the longer recovery time of the thinned stands compared to the burned stands may have contributed to the similarity in measured responses between the non-burned treatments. The effects of the unavoidable difference in time between thinning and burning treatments on root turnover are unknown. Post-treatment results were compared to those of the non-thinned and non-burned treatment within the same year. Both treatments with burning reduced EMF species richness by about a third compared to the non-burned treatments. However, while not significantly different, the average species richness prior to treatment in the stands assigned for burning was lower than in stands assigned to the other treatments. This suggestive evidence of a difference combined with an overall decrease in average species richness in treatments between the pre- and post-treatment years suggests that burning alone may have impacted EMF species richness less than did the thinning and burning treatment. Indeed, the thinned and burned treatment greatly reduced (by about 60%) the number of frequently occurring species in samples from stands receiving this treatment (Fig. 1). After the removal of merchantable timber (thinning), small diameter fuels (branches and needles) left on the ground probably contributed to greater localized fire intensity than in the burned-only treatment (Sandberg, Ottmar & Cushon 2001).

Greater reduction of EMF species richness in the upper soil level compared to the lower in the thinned and burned treatment-only also suggests greater localized fire intensity at the sample points in this treatment compared to those in the other treatments. Burn treatments resulting in the complete consumption of duff and exposure of mineral soil can lead to old-growth pine mortality (Harrington 1987; Swezy & Agee 1991; Scott 2002) and fail to achieve the desired future condition of large-tree pine retention with low fuel loads (Scott 2002). However, most prescribed burns, including those in this study, are spatially heterogeneous, leaving unburned patches and low-intensity burned areas within most sites. EMF surviving within these areas may facilitate re-establishment by propagules (Mah *et al.* 2001). Propagules of EMF species have been shown to persist in forest soils (Pilz & Perry 1984; Danielson 1991; Miller, Torres & McLean 1993, 1994; Massicotte *et al.* 1999; Kjoller & Bruns 2003) even after fire (Danielson 1982; Visser 1995; Torres & Honrubia 1997; Horton *et al.* 1998; Baar *et al.* 1999; Grogan *et al.* 2000). Indeed, 18% of the RFLP species in our study were common to the pre- and post-treatment years after 3 years of root turnover. Colonization from lightly burned and EMF persistence in deeper soil layers of intensely burned patches may mitigate short-term declines in EMF species richness and spur recovery at the stand level.

In northern Arizona, in a study of ponderosa pine restoration treatments mirroring those in this study, Korb *et al.* (2003) report no difference among the treatments in the proportion of ponderosa pine roots colonized by EMF. Korb *et al.* (2003) suggest that a largely undamaged organic layer may account for the lack of detected differences among treatments in their study. Indeed, Jonsson *et al.* (1999) report little change in EMF species richness after low-intensity wildfires that did not completely remove the litter layer while Stendell *et al.* (1999) report that abundant species were reduced to undetectable levels following a high intensity prescribed fire in which the litter layer was completely removed.

The divergent findings between this study and the study by Korb *et al.* (2003) may also be attributed to differences in methodology. In this study EMF species were identified and quantified directly from tree roots collected on site, whereas Korb *et al.* (2003) assessed EMF propagule density on seedlings grown in a greenhouse in field soil. One or several frequently encountered EMF species may have flourished in the greenhouse environment, colonizing all seedlings, regardless of treatment, in approximately equal proportions. Indeed, Korb *et al.* (2003) report a dominant EMF morphotype on seedlings grown in soil from all stands. Some EMF, particularly *Thelephora* spp., commonly persist in greenhouse environments and abundantly colonize greenhouse-grown tree seedlings (Castellano & Molina 1989), even when grown in field soil (Smith, Molina & Perry 1995). *Rhizopogon* is commonly detected on Pinaceae seedlings grown in a greenhouse in field soil (Smith *et al.* 1995; Baar *et al.* 1999; Massicotte *et al.* 1999). The widespread and uniform presence of certain EMF species, particularly species of *Rhizopogon*, is well documented in other studies both before and after fire (Horton, Cázares & Bruns 1998; Baar *et al.* 1999; Stendell *et al.* 1999; Taylor & Bruns 1999; Grogan *et al.* 2000; Kjeller & Bruns 2003; Smith *et al.* 2004).

Similarity in the EMF community was evident between the northern and southernmost extension of the Blue Mountain Range, a distance of about 250 km. The majority of identified species belonged to the Cortinariaceae and Thelephoraceae in both this study in a mixed conifer forest and in a ponderosa pine forest to the south (Smith *et al.* 2004). Numerous studies in coniferous ecosystems have shown Thelephoraceae, non-thelephoroid resupinates (e.g. *Piloderma*) and Russulaceae among the most abundant and frequent EMF symbionts on roots (see reviews by Dahlberg 2001; Horton & Bruns 2001). In this study, a frequent occurrence across the landscape was noted for EMF species within the genera of *Wilcoxina*, *Cenococcum* and *Piloderma*, and to a somewhat lesser extent *Rhizopogon*, *Tricholoma* and *Thelephora*. *W. rehmii* and *R. salebrosus* were broadly distributed in the northern and southern extension of the Blue Mountains, both before and after restoration treatments, and were among the most frequent and biomass-dominant species. In contrast, EMF colonization by species of *Wilcoxina* and *Rhizopogon* were frequent

only after fire in a bishop pine *P. muricata* D. Don forest (Taylor & Bruns 1999). An increase in the frequency of *Wilcoxina* on seedlings after burns appears common (Torres & Honrubia 1997; Horton *et al.* 1998; Baar *et al.* 1999; Grogan *et al.* 2000). *W. rehmii*, typically reported fruiting on unburned soil and coniferous litter (Yang & Korf 1985), was the most frequently encountered mycorrhizal ascomycete after fire in a mature ponderosa pine forest in the Blue Mountains of Oregon (Fujimura *et al.* 2005).

Regional climate control of spatial variation in historical fire regimes probably contributes to differences in the EMF community across the range of the Blue Mountains. Ponderosa pine stands in the southern extension of the Blue Mountains have longer and drier fire seasons and historically burned twice as frequently as ponderosa pine-dominated stands in the north (Heyerdahl, Brubaker & Agee 2001). About 25% more EMF species were detected, with similar number of samples over fewer years, in this study in the northern mixed ponderosa pine and Douglas fir forest, compared to the pure ponderosa pine forest in the south (Smith *et al.* 2004). Greater EMF species richness, including a greater number of *Piloderma* and *Russula* species, in the northern forest site compared to the southern forest site may be due to the increased number of tree host genera, less harsh growing conditions or differences in available microhabitat. *Piloderma* and *Russula* species are typically abundant in mature and late-successional stands of temperate forests where large down wood in advanced stages of decay is common (Goodman & Trofymow 1998; Smith *et al.* 2000, 2002; Bergemann & Miller 2002). Although amounts of large down wood were not measured in this study or in the study by Smith *et al.* (2004) in the southern extension of the Blue Mountains, a paucity of down wood was noted in the ponderosa pine forest in the south. Historically, more frequent fires in the southern extension of the Blue Mountains compared to the north probably reduced this structural component, and the suppression of fire in the last century may have promoted greater non-historic amounts of down wood in the densely wooded northern forest.

It must be emphasized that the current structure of the stands in this study, as well as in forests throughout the inland Pacific North-west, differs substantially from historic conditions and is at risk of high intensity wildfire (Agee 1993; Brown 2000). The EMF community structure in non-thinned and non-burned stands in our study served as a comparison to that in stands receiving fuel-reducing restoration treatments, but probably does not represent the historic condition or what would occur under desired stand conditions. A relatively high similarity of EMF species was seen in the comparison between the non-disturbed and thinned-only stands; however, thinning alone increases small diameter fuels on the ground, thereby increasing the risk for high intensity wildfire. Disposal of small diameter fuels after thinning poses a dilemma for forest

managers. Piling and burning of such fuels generates severely burned areas that often remain unvegetated (Covington, DeBano & Huntsberger 1991) or are susceptible to invasion by exotic plant species (Haskins & Gehring 2004; Korb, Johnson & Covington 2004). Even though fire historically played an important role in structuring forests and the EMF community in the Blue Mountains, the complexity of the historical condition, previous disturbances and the recovery potential of the site must be considered in plans to achieve the desired future condition (Neary *et al.* 1999; Cromack *et al.* 2000; Heyerdahl *et al.* 2001).

Management prescriptions resulting in complete duff reduction lead to the mortality of large old-growth pine and fail to achieve the desired future condition of large-tree retention with low fuel loads (Kaufman & Covington 2001; Scott 2002). The reintroduction of fire at times of the year when fuels are less combustible may reduce duff accumulations around large trees without tree mortality and allow the return to a fire regimen on the historic fire return frequency and season with favourable outcome (Scott 2002). Restoration treatments using combinations of seasonal prescribed burning and thinning seem reasonable given the findings of this and other studies (Scott 2002; Smith *et al.* 2004), but the impact of such temporal and fuel-reduction combinations on fine root survival and the EMF community are as yet untested.

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### Supplementary material

The following supplementary material is available for this article online.

**Table S1.** Annual occurrence within treatment units of ectomycorrhizal RFLP species identified by PCR-RFLP or by nucleotide sequencing.

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