

The influence of clear-cutting on ectomycorrhizal fungus diversity in a lodgepole pine (*Pinus contorta*) stand, Yellowstone National Park, Wyoming, and Gallatin National Forest, Montana

Kristin B. Byrd, V. Thomas Parker, Detlev R. Vogler, and Ken W. Cullings

Abstract: Effects of clear-cutting on the ectomycorrhizal (EM) fungus community in a *Pinus contorta* Dougl. ex Loud. forest near Yellowstone National Park, Wyoming, U.S.A., were assessed using molecular techniques. Samples were taken by soil core in both undisturbed and clear-cut sites by randomized block design. Species overlap was compared between clear-cut and undisturbed sites and ascomycete–basidiomycete ratio was determined, using PCR–RFLP methods. Fifty species of EM fungi were detected in the clear-cut sites, the most common being *Cenococcum geophilum* Fr., *Suillus* sp., a member of the suilloid group, a Russulaceae species, and a Thelephoraceae species. Sixty-six species were detected in the undisturbed sites, which were dominated by a Suilloid species, a Tricholomataceae species, *Cortinarius* sp., and *Cenococcum geophilum*. Species composition in the clear-cut sites differed significantly from that in the undisturbed sites ($P = 0.0001$). However, 9 of the 14 species most commonly found in the clear-cut sites were also found in the undisturbed sites, but in much lower abundance, while species rank curves of both stand types mirrored each other. There were no significant differences in species richness, root-tip abundance, or ascomycete–basidiomycete ratio between the clear-cut and undisturbed sites. However, species richness was lower in the clear-cut sites than in the undisturbed sites. An overall loss of species richness after clear-cutting and significant changes in species composition indicate that clear-cutting can negatively alter the EM fungal community, and this may have profound effects on ecosystem function.

Key words: ectomycorrhizae, community structure, clear-cutting, molecular techniques.

Résumé : À l'aide de techniques moléculaires, les auteurs ont évalué les effets de la coupe à blanc sur la communauté fongique ectomycorhizienne (EM) d'une forêt de *Pinus contorta* Dougl. ex Loud. près le parc Yellowstone, au Wyoming, U.S.A. Ils ont récolté des échantillons par carottage dans des sites coupés à blanc et dans des sites non-perturbés, selon un dispositif en blocs aléatoires. Ils ont comparé les recouvrements d'espèces entre les sites coupés à blanc et les sites non-perturbés et ils ont déterminé les rapports ascomycètes–basidiomycètes par des méthodes PCR–RFLP. Ils ont décelé 50 espèces de champignons EM dans les sites coupés à blanc, les plus communes étant le *Cenococcum geophilum* Fr., des *Suillus* sp., un membre du groupe Suilloïde, une espèce de Russulaceae, et une espèce de Thelephoraceae. Dans les sites non-perturbés, ils ont trouvé 66 espèces, dominées par une espèce suilloïde, une espèce de Tricholomataceae, un *Cortinarius* sp., et le *Cenococcum geophilum*. La composition en espèces dans les sites coupés à blanc diffère significativement de celle des sites non-perturbés ($P = 0.0001$). Cependant, 9 des 14 espèces les plus communes dans les sites coupés à blanc se retrouvent également dans les sites non-perturbés, mais en beaucoup plus faible abondance, alors que les courbes d'importance des espèces des deux types de site sont l'image virtuelle l'une de l'autre. Il n'y a pas de différence dans la richesse en espèces, l'abondance des apex racinaires, ou les rapports ascomycètes–basidiomycètes, entre les sites coupés à blanc et les sites non-perturbés. Cependant la richesse en espèces est plus faible dans les sites coupés à blanc, comparativement aux sites non-perturbés. Une diminution globale de la richesse en espèces, après coupe à blanc, et un changement significatif de la composition en espèces indiquent que la coupe à blanc peu altérer négativement la communauté fongique ectomycorhizienne, et que ceci pourrait avoir des effets marqués sur le fonctionnement de l'écosystème.

Mots clés : ectomycorhizes, structure des communautés, coupe à blanc, techniques moléculaires.

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K.B. Byrd¹ and V.T. Parker. Department of Biology, San Francisco State University, San Francisco, CA 94132, U.S.A.

D.R. Vogler. Search for Extra-terrestrial Intelligence Institute, 2035 Landings Drive, Mountain View, CA 94043, U.S.A.

K.W. Cullings. National Aeronautics and Space Administration, Ames Research Center, MS 239-4, Moffett Field, CA 94035-1000, U.S.A.

¹Author to whom all correspondence should be sent at the following address: URS Greiner Woodward Clyde, 500 12th Street, Suite 200, Oakland, CA 94607, U.S.A. (e-mail: kristin_byrd@urscorp.com).

Introduction

Mycorrhizal fungi are integral to forest ecosystems. They are instrumental in the uptake of water and nutrients by plant roots, increase the survival of seedlings, and protect against root pathogens (Miller 1995). Despite their importance, little is known about mycorrhizal-community structure and composition. Consequently, little is known about the link between the mycorrhizal community and forests and how changes in forest systems affect the fungal community.

A high diversity of fungi may be necessary to maintain the stability of the forest ecosystem; in changing environments, fungal species with different environmental tolerances may shift in abundance on a plant host. Ecosystem stability and resilience to disturbance may be increased by high fungal species diversity (Perry et al. 1989). With many species in the system, maintenance of mycorrhizal associations is ensured, despite changes in the environment and in fungal composition.

Because of the role of fungal diversity in ecosystem function, studies of ectomycorrhizal (EM) community structure are important (Gardes and Bruns 1996; Visser 1995; Dahlberg et al. 1997; Horton and Bruns 1998). An impetus for these studies is the need to understand how EM-community structure is altered by human disturbances such as clear-cutting. Clear-cutting reduces EM abundance through increased soil evaporation and degradation of the fine roots of cut trees (Perry et al. 1987, 1990; Pietikäinen and Fritze 1995). Other detrimental effects of clear-cutting include increased variation in soil temperature and moisture (Bååth 1980; Entry et al. 1986) and a loss of organic matter and soil aggregation (Perry et al. 1989). However, while these environmental changes directly affect EM abundance, the major cause of their reduction is the removal of the fungi's energy source—carbohydrates from trees (Perry et al. 1989).

Forest disturbance not only affects mycorrhizal abundance but also species composition. A change in mycorrhizal community structure or species composition can be an indicator of how a disturbance, such as clear-cutting, impacts the forest ecosystem. For example, in relation to basidiomycetes, ascomycetes become more dominant after fire (Wicklow and Hirschfield 1979; Wicklow 1988). Despite this research, little is known about the effects of disturbance on ascomycete–basidiomycete ratios and EM community structure and species diversity. Assessment of fungal diversity has been difficult, because of an incomplete understanding of fungal taxonomy and a lack of resolution by morphotyping (Miller 1995). Molecular techniques, however, have greatly advanced the opportunities to study fungal diversity (Gardes and Bruns 1993) and can increase the potential of identifying and quantifying mycorrhizal species.

In this study, we determined the effects of clear-cutting on species richness, species composition, and relative abundance of EM fungi in a *Pinus contorta* var. *latifolia* Engelm. forest. Impacts were determined by comparing the mycorrhizal community of clear-cut *P. contorta* sites to undisturbed 100-year-old *P. contorta* sites in and near Yellowstone National Park. As part of this study, the ratio of ascomycetes to basidiomycetes in the two stand types was also compared.

Methods

Site characteristics

The three clear-cut sites used for this study are in the Gallatin National Forest, Montana, on the Parched Gully clearcut. Parched Gully is 12 miles (1 mile = 1.609 km) south of West Yellowstone, Montana, and one-half mile from the western border of Yellowstone National Park, in the Hebggen Lake Ranger District. Each site was approximately 8 ha in size and ranged in elevation from 2300 to 2500 m. Forest vegetation was characterized by *P. contorta*, converting to *Abies lasiocarpa* (Hook.) Nutt., *Pinus albicaulis* Engelm., and *Vaccinium scoparium* Leiberg. in old growth.

Soil type was characterized by hard crystalline rocks, sandstone, or rhyolite flows. Soils had a moderately coarse to medium texture. Major soils were Dystric Cryochrepts and Typic Cryochrepts (Davis 1996). Regeneration of the forest after a disturbance has been ranked moderately limited, owing to the harsh subalpine climate and “droughty” soils.

The undisturbed sites were in Yellowstone National Park, near its western border. Clear-cut and undisturbed locations had the same vegetation type, a similar elevation (2300–2500 m), and similar soil types.

Site history

The clear-cut sites regenerated naturally. At the time of sampling, the clearcuts were 8 years old and were dominated almost exclusively by *P. contorta* and *Carex* spp. They were adjacent to an undisturbed forest dominated by *P. contorta*.

Sampling

Three clear-cut sites were chosen from the Parched Gully area. At each site, three sampling locations were chosen that were at least 20 m from the border of the clearcut and about 15 m from each other. Sampling was done in late August 1996. In each location, three soil cores were collected near *P. contorta* saplings, to maximize the quantity of roots in each sample. Each core was divided into three depths: (i) 0–5 cm, (ii) 5–10 cm, and (iii) 10–15 cm. Each core was 10 cm in diameter, making the volume of each core sample approximately 392.5 cm³.

Sorting and sampling of mycorrhizal root tips

Cores were kept on ice until returned to the laboratory and then stored at 4°C until ready for processing in early September. At that time, soil samples containing live root tips were sifted; washed; sorted by morphotype, according to color, hyphal type, and branching pattern; and placed in a 1.5-mL Eppendorf tube. A soil sample was defined as one layer (e.g., 0–5 cm) of a core. Root tips were freeze-dried and stored at –20°C pending analysis.

The internal transcribed spacer (ITS) region of the fungal nuclear ribosomal RNA gene repeat (nrRNA), consisting of approximately 600–800 bp, was amplified using primers ITS1 and ITS4B, to identify basidiomycetes, and ITS1F and ITS4, to identify ascomycetes, from individual mycorrhizae, using the method of Gardes and Bruns (1993). EM restriction fragment length polymorphism (RFLP) patterns were obtained by restriction digests (*AluI* and *HinfI*). Once RFLP patterns of root tips were produced, a letter code or species label was assigned to each unique pattern, and the abundance of each pattern was quantified. This procedure was done by differentiating RFLP patterns by measuring fragment lengths, and was repeated three times to ensure accuracy. Only unambiguous, clear patterns, indicating lack of dual infection or contamination, were scored as unique.

Fruit bodies were collected from the clear-cut and undisturbed locations during July and August of 1996. Additional fruit bodies had been collected from the undisturbed locations during the sum-

mer of 1995. Collections were made within 30 × 30 m plots that contained the coring locations. Fruit bodies were identified in the field while fresh, then oven-dried, and archived in the H. Thiers Herbarium at San Francisco State University.

EM RFLP patterns were identified to species by comparing them with those obtained from reference fruit bodies. As each species of fruit body produced a unique RFLP pattern, it was assumed that all EM patterns represented a unique species. In cases in which fruit bodies were not available for identification, fungi forming ectomycorrhizae were identified to class or order (by phylogenetic analysis of the 5.8S nrRNA sequence; Cullings and Vogler 1998) or to family (by phylogenetic analysis of the mitochondrial small subunit RNA sequence; Bruns et al. 1998).

Patterns from the clear-cut sites were compared with patterns from undisturbed sites, to determine if species overlap existed. Matching patterns were given the same species label. To obtain further evidence that they were the same species, those patterns thought to be identical were run side-by-side on the same gel to make a more accurate comparison.

Analysis

The most abundant species were identified by comparing root tip RFLP patterns to patterns generated from identified mushrooms. Contingency tables and a χ^2 test were used to determine differences in species composition between the clear-cut and undisturbed locations. In addition, a multivariate analysis of variance of a mixed two-factor design was used to analyze variation in species richness, root-tip abundance, and ascomycete–basidiomycete ratio between clear-cut and undisturbed sites and between layers within sites. Sites were compared using evenness and diversity indices, to determine differences in community structure, and the Sorenson index (a distance measure) (Krebs 1989), to determine differences in community composition.

Results

Fifty unique RFLP patterns were identified in the three clear-cut sites (an average of 16.7 species and 135 root tips per site), with an average of 4.05 species being found per core. Seven species contributed to 50% of the EM fungi root tips (Fig. 1). One of these was an ascomycete (*Cenococcum geophilum* Fr.; 52 root tips) and 6 were basidiomycetes (150 root tips).

Undisturbed sites yielded 66 species (an average of 33 species and 174 root tips per site), with an average of 8.25 species being found per core. Seven species contributed to 50% of the root tips in these sites (Fig. 2). One species was an ascomycete (23 root tips) and 6 were basidiomycetes (155 root tips).

Among both clear-cut and undisturbed locations, a total of 106 species were identified. Ten species were found in both clear-cut and undisturbed sites. Forty species were unique to the clear-cut sites and 56 species were unique to the undisturbed sites. Restriction fragment sizes for the unique patterns found in both clear-cut and undisturbed sites are listed in Table 1. The sum of fragment sizes equaled approximately 600–800 bp, the length of the ITS region amplified. This indicated a lack of dual infection or contamination for each pattern; a greater sum of base pairs would indicate more than one DNA fragment in the sample.

Although undisturbed forest locations had more species, the relative abundance of species in the two treatments was similar, as illustrated by the species-distribution curves,

Fig. 1. The most common species found in clear-cut sites. Seven species comprised 50% of the root tips from the clear-cut sites analyzed. The most dominant was an ascomycete and the other six were basidiomycetes. The footnotes in the figure indicate: ¹, the code assigned to each RFLP pattern; ², the species was identified by the fruit body; ³, the species was identified by methods in Bruns et al. (1998); ⁴, the species was identified by methods in Cullings and Vogler (1998).

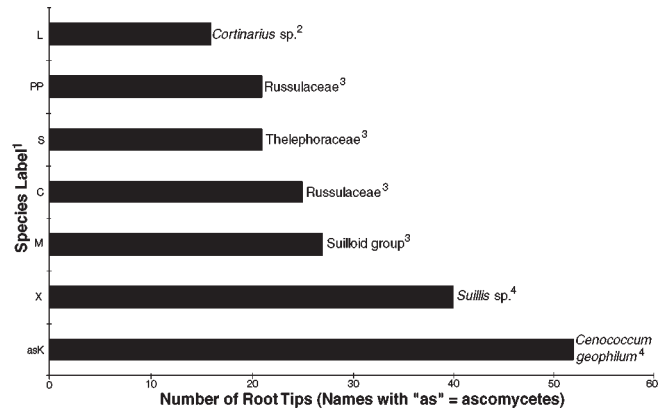
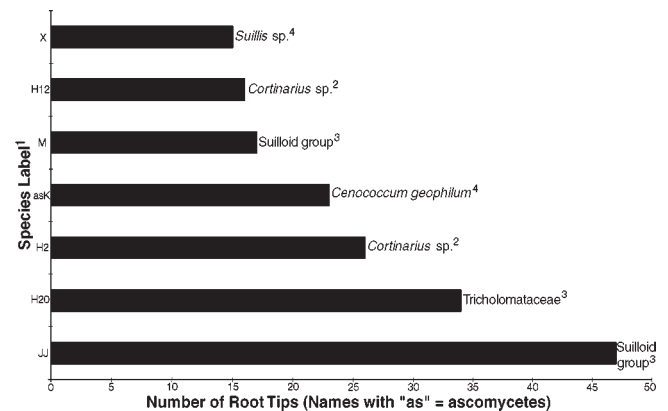


Fig. 2. The most common species found in undisturbed sites. Seven species comprised 50% of the root tips from the undisturbed sites analyzed. One species was an ascomycete and the other six were basidiomycetes. The footnotes in the figure indicate: ¹, the code assigned to each RFLP pattern; ², the species was identified by the fruit body; ³, the species was identified by methods in Bruns et al. (1998); ⁴, the species was identified by methods in Cullings and Vogler (1998).



which closely mirror each other (Fig. 3). The diversity indices and evenness measures of the clear-cut and undisturbed sites support this finding, as they were also very similar (Tables 2 and 3). However, those species most abundant in the clear-cut sites were not the same as those most abundant in the undisturbed sites.

Chi-square tests indicated a significant difference in species composition between the clear-cut and undisturbed sites ($P = 0.0001$). The multivariate analysis of variance disclosed no significant differences between the clear-cut and undisturbed sites in any of the three tests: species richness, root-tip abundance, and percentage of ascomycetes. In addition,

Table 1. Restriction fragment sizes (in bp) for the restriction patterns identified.

(A) Basidiomycetes.																
Undisturbed sites							Clear-cut sites									
Species label	<i>Hinf</i> I			<i>Alu</i> I			Species label	<i>Hinf</i> I			<i>Alu</i> I					
BB	320	280	124		280	240	124	AA	400	190	124		400	240		
CC	320	250	110		600			B	520	340			500	300		
F	380	320			520	300		BB	320	280	124		280	240	124	
FS	320	242	147		500	300		C	480	320			500	300		
H10	400	320	67		400	250		CC	320	250	110	67	600			
H11	300	300			260	220	100	D	260	190			700			
H12	450	320			500			DD	380	300	147		300	250	190	
H13	500	100			500	200		E	380	320			420	242		
H14	300	280	124		400	242		F	380	320			520	300		
H15	360	320	110		360	242		FF	400	320			500	400	280	
H16	340	340	100		700	80		G	380	260			320	242	180	
H17	320	180	150	100	600	150		GG	340	300			700			
H18	340	200	130	50	400	280	80	H	500	400	320		450	300		
H2	380	340	124		500	100		HH	340	320			700			
H20	404	90			400	90		I	340	360			380	260		
H21	380	64			480	300		J	340	200			480	260		
H51	400	400			400	300		JJ	380	160			400	220		
H23	360	242			320	220		L	340	124			520	147	80	
H25	400	300	124		400	240		M	250	200	124	110	70	450	360	
H27	380	320			700			N	320	200	147	124		500	160	
H52	400	400			500	110		O	340	300	124		300	140		
H28	330	350			500	300		PP	300	220			404	200		
H53	300	124			450	280		Q	320	280	200		500			
H31	300	180	140		400	330		R	350	124			380	220		
H33	360	340	100		300	260	190	S	320	190	170	124	500	124	70	
H34	380	300			500	400		X	220	190	120	67	400	300		
H35	400	242	30		750			Z	320	300	110		500	400	260	220
H36	400	280			700											
H38	500	400	147		400	147										
H39	500	250			550	147										
H40	450	400			400	250										
H41	400	300			500	300	190									
H42	320	250	64		500	250	147									
H44	300	300			500	250	147									
H45	500	400			380	200										
H46	500	300			500	190										
H47	350	67			500	300	250									
H49	400	300			480	300										
H5	380	300	100		400	140	60	50								
H50	350	124			500	300	250									
H6	440	260	140		480	340										

H8	320	180	140			400	300	
JJ	380	160				400	220	
L	340	124				520	147	80
M	250	200	124	110	70	450	360	
S	320	190	170	124		500	124	70
X	220	190	120	67		400	300	

(B) Ascomycetes.

Undisturbed sites								Clear-cut sites									
Species label	<i>HinfI</i>				<i>AluI</i>				Species label	<i>HinfI</i>				<i>AluI</i>			
asK	340	300	160	124	110	400	190	asA	404	260	160	110	450				
asT	300	190	170			600		asB	340	300			500	400			
FasI	320	250	147			500	400	242	asC	380	240	190	500	147			
FasL	380	300				680			asD	320	240	147	450	190			
Has1	380	170				600			asE	280	242	147	500	300			
Has10	360	340				650			asF	380	340		500	240			
Has11	380	242	190			750			asG	380	340		500	330	124		
Has12	240	200				500			asH	360	200		450	180			
Has13	360	190	60						asK	340	300	160	124	110	400	190	
Has16	340	190	147			600			asQ	380	190	147	600	80			
Has18	260	220	147			600			asR	320	242		320	242			
Has2	360	300				360	200	60	asT	300	190	170	600				
Has20	380	170				500	200		asX	260	200	130	124	404	320		
Has21	404	260				600			asM	340	300		600	500			
Has3	400	320				320	200	190	asN	340	300		300	190	170		
Has4	300	200	124			600			asO	190	160	147	500				
Has6	350	340	70			650	150		asS	380	160		380	200			
Has8	404	320				600			asU	242	180	67	450	160			
Has9	400	360				520	200		asL	340	300		400	190			
									asW	380	360		600				
									asY	340	320		400	190			
									asZ	340	320		480	190			
									asI	500	320	160	400	190			

Note: In species labels as, ascomycete; H, found in mature sites only.

Fig. 3. Logarithmic distribution of species, ranked according to the number of individuals of each species, for clear-cut and undisturbed sites. The rank of each species from 1 (the most abundant species) to n (the rarest species) is plotted on the x -axis (Krebs 1989). The y -axis represents the logarithm of the relative abundance of each species. The most dominant species in clearcuts was represented by 12.84% of the individuals and seven species made up 50% of all individuals. The most dominant species from the undisturbed sites represented 13.51% of all individuals and seven species made up 50% of all individuals.

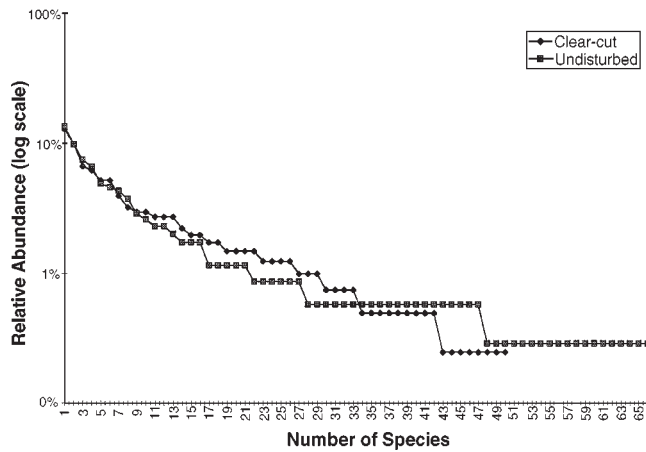


Table 2. Diversity indices for undisturbed and clear-cut sites.

Index	Undisturbed sites	Clear-cut sites
Simpson's (1-D)	0.946	0.952
Shannon-Wiener	4.987	4.86

Note: (1-D), 1 - Simpson's index or 1 - (probability of picking two organisms that are the same species) (Krebs 1989).

Table 3. Evenness measures of undisturbed and clear-cut sites.

Index	Undisturbed sites	Clear-cut sites
Simpson's	0.957	0.969
Shannon-Wiener	0.808	0.863

the soil-core layers within each treatment did not differ significantly in any of the tests.

Although there was no significant difference in species richness between clear-cut and undisturbed sites, in the undisturbed locations, there was a trend indicating increasing species richness with soil depth (Fig. 4). Unlike species richness, root-tip abundance decreased with soil depth in the undisturbed sites (Fig. 5). A few common species dominated the upper core layers, while the lower layers consisted of many rare species. In contrast, there was little difference among the soil cores in the clearcuts with respect to depth.

Ascomycetes comprised 38.8% of the root tips in the clearcuts (23 of 50 species) and 28.7% of the root tips in the undisturbed locations (19 of 66 species). No significant difference in ascomycete proportions was found between the clear-cut and undisturbed sites. However, in both clear-cut and undisturbed site, the ascomycete proportion decreased with soil depth (Fig. 6).

Ten species were present in both the clear-cut and undisturbed sites: two ascomycetes and 8 basidiomycetes (Fig. 7).

Fig. 4. Species richness for each depth for clear-cut and undisturbed sites. Species richness in each core layer was determined using a multivariate ANOVA of the percentage of species in each core layer. Species richness was greater in the undisturbed sites than in the clear-cut sites in core layers from depths of 5–10 and 10–15 cm.

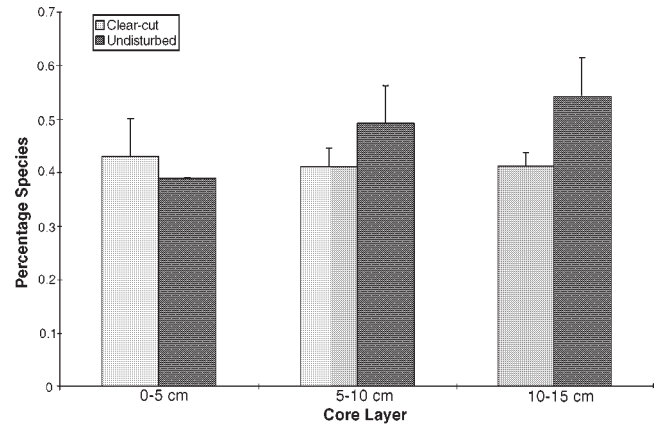
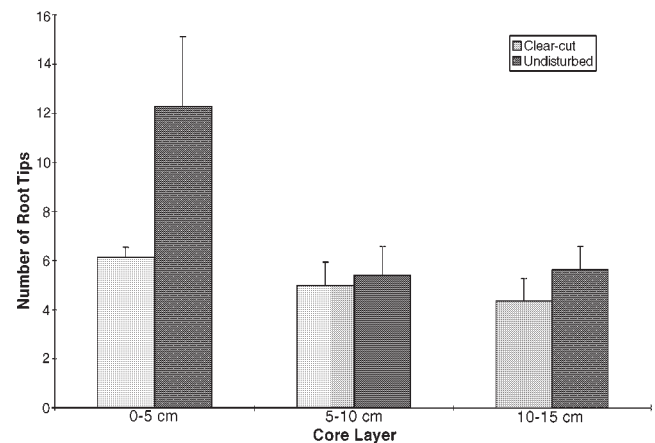


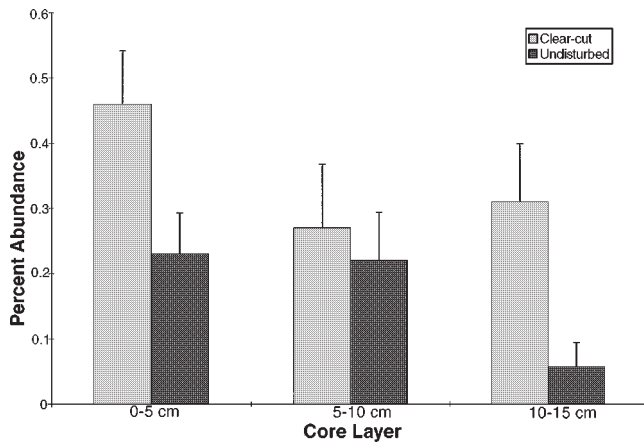
Fig. 5. Root-tip abundance for each depth for clear-cut and undisturbed sites. The root-tip abundance in each core layer was determined using a multivariate ANOVA. There were more root tips in the undisturbed sites than in the clear-cut sites in core layers from each depth, with the greatest difference being found in core layers from a depth of 0–5 cm.



All species except one were abundant in the clear-cut sites but rare in undisturbed sites. While there was a significant distinction ($P = 0.0001$) between the clear-cut and undisturbed sites, there was also overlap in species composition. Nine of the 14 most common species in the clear-cut sites were also found in the undisturbed sites. This comprised 202 root tips—one-half of the clear-cut root tips. In contrast, only 34% of the undisturbed stand root tips (119 root tips) were of a species found in both the clear-cut and undisturbed sites.

To determine whether any of the difference in species composition between the clear-cut and undisturbed sites was due to site effects or treatment effects (i.e., clear-cutting), the average distance between sites of the same treatment was compared with the average distance between sites of different treatments. This analysis was conducted with presence-absence data (Sorenson index) and relative-abundance data

Fig. 6. The percentage of ascomycetes for each depth in clear-cut and undisturbed sites. The percent abundance of ascomycete root tips in each core layer was determined using a multivariate ANOVA. The ascomycete abundance was greater in the clear-cut sites than in the undisturbed sites in core layers from each depth.



(Euclidean distance). In both cases, the average distance between sites of different treatments was greater than the average distance between sites of the same treatment. These results support the finding that the treatment effect was greater than the site effect (Table 4).

Discussion

The fungal community structure was similar in clear-cut and undisturbed locations, as indicated by the relative-abundance curves. Generally, steep curves indicate an early successional community, while a relatively flat curve indicates a more undisturbed community (Krebs 1989). However, in this study, as indicated in Fig. 3, clear-cut and undisturbed stands had similar community structures despite differences in age. This suggests that mycorrhizal dominance patterns did not change after the clear-cut disturbance but, instead, were maintained.

While clear-cut and undisturbed sites were similar in terms of relative EM species abundance (Fig. 3), species composition between the clear-cut and undisturbed sites was significantly different. Also, trends suggest differences in species richness between the clear-cut and undisturbed sites, although these trends were not significant. Species richness decreased after disturbance and ascomycete proportions increased. Reduction in species richness parallels previous studies that showed a decrease in mycorrhizal abundance after clear-cutting (Perry et al. 1987, 1990; Pietikäinen and Fritze 1995). The response of ascomycetes to clear-cutting is similar to their response to fire disturbance (Wicklow and Hirschfield 1979; Wicklow 1988). After both disturbances, ascomycetes became more dominant in relation to basidiomycetes. Post fire in a lodgepole pine forest, ascomycetes became dominant through the colonization of fine-root biomass, woody roots of dying or dead trees, and the breakdown of litter or humus (Wicklow 1988). These conditions may be present in a clear-cut stand as well, leading to the same increase in the proportion of ascomycetes.

Although not quantified, *P. contorta* appeared to have regenerated relatively poorly in the clear-cut sites, based on

Fig. 7. Relative abundance of species found in both clear-cut and undisturbed sites. Ten species were present in both clear-cut and undisturbed sites, eight of which were basidiomycetes. In general, these 10 species were more dominant in the clear-cut sites than in the undisturbed sites. The footnotes in the figure indicate: ¹, the code assigned to each RFLP pattern; ², the species was identified by the fruit body; ³, the species was identified by methods in Bruns et al. (1998); ⁴, the species was identified by methods in Cullings and Vogler (1998).

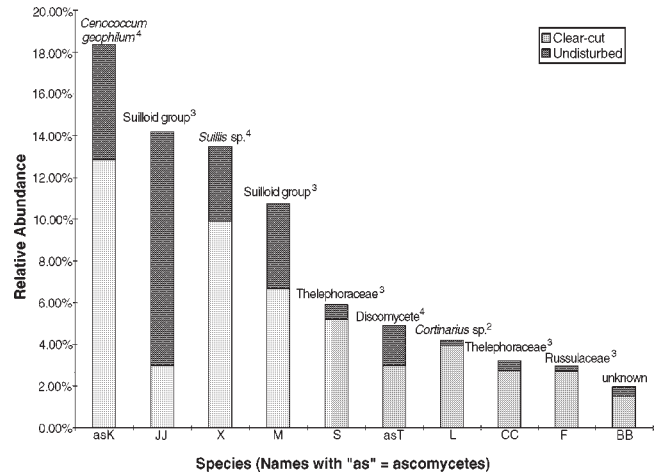


Table 4. Distance measures (a greater value indicates more distance and, therefore, less similarity).

	Undisturbed sites	Clear-cut sites	Undisturbed sites/clear-cut sites
Presence-absence data (Sorenson)	0.417	0.404	0.655
Relative-abundance data (Euclidean)	346	208	413

observations of the number of saplings in each type of stand. Loss of EM species richness could be associated with poor regeneration of *P. contorta*. Poor regeneration could also be due to environmental stress resulting from relatively steeper slopes (e.g., less soil moisture, nutrient loss in runoff) and competition from *Carex* spp., which were abundant in clear-cut sites. Competition from *Carex* spp. in disturbed forests has been documented by Abrams and Dickmann (1982), who found that these became the dominant species and caused a reduction in diversity in *Pinus banksiana* Lamb. sites that had been clear-cut and (or) burned.

As mentioned earlier, 9 of the 14 species most commonly found in clear-cut sites were also found in the undisturbed sites, but in much lower abundance. One hypothesis that could explain this observation is that these 9 species in the clear-cut sites may have been less abundant prior to disturbance and became more abundant after clear-cutting, perhaps as a result of a functional shift or by chance. Over successional time their relative abundance may decrease as new species become established, and may continue to decrease until their numbers are more characteristic of an undisturbed stand.

The large number of basidiomycete species found in common in the two forest types suggests that there is a shift

from ascomycetes to basidiomycetes over successional time. Eight of the 10 species shared between clear-cut and undisturbed sites are basidiomycetes. However, ascomycetes were present in the clear-cut sites as well as in the undisturbed sites. This pattern can be explained by one of two hypotheses. (i) Mainly basidiomycetes remained in the soil after clear-cutting. The clear-cut site, while at first containing only basidiomycetes that remained after the disturbance, may then have been invaded by ascomycete species or by germinating pre-existing ascospores. (ii) All species may have been present in the clearcuts after disturbance, but in different proportions. Ascomycetes may have become more dominant, as indicated by their relatively high abundance in the clear-cut sites, as a result of changes in soil conditions following clear-cutting.

Our results indicate that clear-cutting can have significant effects on EM fungal species richness and composition. Some fungal species responded positively to clear-cutting, and it is possible that they remained in the soil after treatment. However, an overall loss of species richness after clear-cutting and significant changes in species composition indicate that clear-cutting can negatively alter the EM fungal community, and this may have profound effects on ecosystem function.

For example, a loss of EM species richness can have negative impacts on forest ecosystems. Greater fungal diversity may provide resilience, buffering changes in forest ecosystems caused by natural disturbances. Thus, loss of EM diversity could reduce forest resilience, which could, in turn, have detrimental effects, such as a loss in the plant–soil link, which would then lead to a reduction in forest regeneration (Perry et al. 1989).

Continued research in mycorrhizal fungus community ecology will greatly improve our understanding of ecosystem processes by enhancing the perception that microorganisms as well as macroorganisms greatly influence ecosystem processes and change. This more inclusive view will strengthen decisions in ecosystem management, as managers will be obliged to incorporate the influence of biotic interactions on an ecosystem's response to human manipulation.

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