Research Article

Interactions among Prescribed Fire, Soil Attributes, and Mycorrhizal Community Structure at Crater Lake National Park, Oregon, USA

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ABSTRACT

We identified relationships between prescribed burn treatments and selected soil and fuel attributes on mycorrhizal fungus fruiting patterns in an old-growth ponderosa pine (*Pinus ponderosa*) and white fir (*Abies concolor*) stand in Crater Lake National Park, Oregon, USA. Three prescribed burn treatments (early spring, late spring, and fall burns) plus non-burned controls were applied to 24 ~3 ha units in 2002. We sampled mycorrhizal fungus sporocarp production in the spring and fall in the ensuing three years, and collected data on surface fuels, soil C and N concentrations, $\delta^{13}C$ and $\delta^{15}N$ signatures, pH, and mineral soil bulk density. A gradient of C:N ratios and other soil attributes across the study area facilitated separation of the effect of fire from the effects of soil attributes on fungal fruiting patterns. Distinct guilds of fungal indicator species were identified, correlating more closely with soil C:N ratios than prescribed burn treatments. Although other habitat attributes (such as fuel levels) were correlated with C:N ratios, the C:N ratios were the most consistent predictor of fungal fruiting patterns. The fall burn treatment did reduce soil C:N ratios, and most of the fall burned units produced the fungal indicator species associated with lower C:N ratios, but the same fungal indicator species also fruited in the non-burned control units with lower C:N ratios. The spring burn treatments did not differ significantly from non-burned controls in fungal fruiting patterns or C:N ratios. Fall burn treatment units produced significantly fewer fungal species and collections than spring burn units, but did not differ significantly in fungal diversity and abundance from non-burned controls.

Keywords: C:N ratio, mycorrhizal fungi, ponderosa pine, prescribed fire

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INTRODUCTION

Prescribed fire is a valuable tool for returning forests of the western United States to their historic fire regimes and fuel levels after more than a century of fire exclusion (Agee 1993). Often the goal of prescribed fire is simply to reduce fuels and understory density, but prescribed fires affect other components of forest communities in many other, poorly understood, ways. Fire affects not only the habitat of aboveground biota but also the belowground environment (Neary *et al.* 1999).

Mycorrhizal fungi are critical to survival and growth of all forest tree species in the Pacific northwest by facilitating nutrient and water uptake through their symbiotic relationship with tree roots (Smith and Read 1997). These fungi exist as perennial networks of mycelia in the soil and on the tips of roots, where they interface with plant cortical cells and nutrient exchange occurs. It has been estimated that 1 g of healthy forest soil can contain more than 200 m of fungal mycelia (Leake *et al.* 2004), representing a nutrient foraging capacity far beyond that of fine roots alone. The sporocarps (mushrooms and truffles) are the ephemeral reproductive structures, or fruiting bodies, of these perennial organisms.

Most biomass of mycorrhizal fungi is in the top 10 cm of soil, a region likely to be affected by forest fire (Stendell *et al.* 1999). Even light intensity burns can alter the mycorrhizal fungal community (Smith *et al.* 2004); more intense fires may damage fungal individuals by burning fine roots where mycorrhizae reside (Jonsson *et al.* 1999, Dahlberg *et al.* 2001), impeding the plant community's survival, recovery, and growth. Therefore the implications of fire-induced changes in the mycorrhizal community can be significant to post-fire stand recovery and productivity. The response of mycorrhizal fungus fruiting patterns to fire is important because fungal sporocarps are a significant food source for wildlife (North *et al.* 1997, Cazares *et al.* 1999, Ashkannejhad and Horton 2006) and hence are an important response variable to evaluate effects of fire on food webs and wildlife carrying capacity.

Several researchers have attempted to link belowground mycorrhizal communities with aboveground sporocarps (Gardes and Bruns 1996, Dahlberg *et al.* 1997, Chen and Cairney 2002, Fujimura *et al.* 2004) with varying degrees of success, largely due to the fine spatial scale of mycorrhizal colonization on root tips and seasonal and annual variability in fruiting patterns. Because one of the main reasons for this study was to evaluate the impacts of prescribed burn treatments on sporocarps in the context of food webs, we decided to focus our sampling efforts on sporocarps rather than root tips. Sporocarp production responses to habitat conditions do not necessarily reflect belowground mycorrhizal community responses (Horton and Bruns 2001) and certainly a significant part of the mycorrhizal community in this ecosystem produced few or no sporocarps during our sampling, however an inventory based on sampling mycorrhizal root tips was beyond the scope of this project.

The timing of a prescribed burn affects fire severity, primarily as a function of fuel moisture, (e.g., in this climate, fuels are drier in the fall than in the spring, resulting in hotter burns) (Kauffman and Martin 1989, Monsanto and Agee 2008). Burn severity can affect soils by chemically transforming or volatilizing both C

and N (Knicker 2007), can damage fine roots near the soil surface (Smith *et al.* 2004), can reduce litter layer coverage and depth (Kauffman and Martin 1989), and increase or decrease levels of coarse woody debris (CWD) (Agee 1993, Cromack *et al.* 2000, Perrakis and Agee 2006). Soil moisture may conduct heat deeper into the ground while simultaneously regulating maximum soil temperatures (Hartford and Frandsen 1992, Campbell *et al.* 1995). Litter coverage and CWD enhance soil moisture retention that may be condusive to sporocarp production or fungal colonization and growth (Luoma *et al.* 1991), and CWD is important habitat for many small mammals that play a major role in fungal spore distribution (Maser and Trappe 1984). Fire has the potential to affect the mycorrhizal community by altering soil chemistry (C, N, pH, etc.), consuming fine roots where mycorrhizae reside, and impacting the availability of energy resources and suitability of the immediate environment (Smith and Read 1997).

Several studies have examined the effects of fire on soil attributes (Knicker 2007), mycorrhizae (Cairney and Bastias 2007), and fungal fruiting patterns (Visser 1995, Fujimura *et al.* 2004, Trappe *et al.* 2006), as well as the effects of soil attributes on fungal fruiting patterns (van der Heijden *et al.* 1999, Lilliskov *et al.* 2001, Högberg *et al.* 2007). Here we explore the relationships among seasonality of prescribed burning, an array of soil and fuel attributes, and mycorrhizal fungus fruiting patterns over three years in an effort to separate fire treatment effects from the effects of soil attributes on fungal fruiting patterns in a mixed ponderosa pine (*Pinus ponderosa* Doug.)-white fir (*Abies concolo*r [Gord. and Glend.] Lindl.) stand in Crater Lake National Park, Oregon, USA.

Our first hypothesis was that prescribed burning in the spring would have no significant effect on soil C, N, mineral soil bulk density, C:N ratios, pH, and $\delta^{13}C/^{15}N$ isotopic signatures of soil samples collected 3 yrs post-burn, as compared to unburned control units. We expected some reduction in surface fuels (litter and CWD) in the spring burn units. The fall burn units were expected to have lower levels of soil C and N, higher mineral soil bulk density, lower C:N ratios, higher pH, unchanged $\delta^{13}C/^{15}N$ isotopic signatures, and reduced levels of surface fuels.

Mineral soil C, N, and pH were chosen as measurement variables because they influence soil nutrient availability and can affect microbial communities over large-scale gradients (Lilliskov *et al.* 2001, Toljander *et al.* 2006, Högberg *et al.* 2007, Avis *et al.* 2008). Carbon transfer from photosynthesizing hosts to fine root biomass and mycorrhizal fungi also represent a major source of soil C (Högberg and Högberg 2002). Litter mass, fine woody debris (FWD), and CWD were selected because they affect mycorrhizal colonization and fruiting (Luoma *et al.* 1991), and their levels can be dramatically affected by fires (Monsanto and Agee 2008). Mineral soil bulk density provides an indication of soil compaction and organic content, and $\delta^{13}C/^{15}N$ isotopic signatures were selected because mycorrhizal fungi have been found to discriminate against heavier ^{15}N isotopes (Hobbie *et al.* 2005, Zeller *et al.* 2007). The relative abundance of lighter ^{12}C isotopes in the soil is an indicator of photosynthetic activity (Guy *et al.* 1993) and belowground C transport (Högberg and Högberg 2002, Leake *et al.* 2004).

Some fungal taxa produce fruiting bodies in response to burning or disturbances (Pilz *et al.* 2004), while others respond to soil chemistry (Lilliskov *et al.* 2001, Carter and Tibbett 2003). Thus, our second hypothesis was that burning in the spring would not significantly change mycorrhizal fruiting patterns, as measured by sporocarp inventories conducted over multiple years. We did expect a shift in fruiting patterns in the fall burned units, with the extirpation of more sensitive taxa, the continu-

ation in fruiting of the more fire-adapted species, and the appearance of fire-associated taxa. We expected a decline overall in fungal diversity in the fall burned units compared to unburned control or spring burned units. We sought to identify guilds (assemblages of organisms that share a similar ecological niche [Landers 1983]) of mycorrhizal fungi that co-occurred under similar sets of soil attributes or fire histories.

We combined the fuels data of Perrakis and Agee (2006) with our soil attribute measurements to quantify many of the physical changes brought about by the different prescriptions and related these to mycorrhizal fungus fruiting patterns. In the course of soil analyses, we discovered a pre-existing gradient of soil attributes across the study area, which permitted us to separate burn treatment effects from the effects of soil attributes on mycorrhizal fungus fruiting patterns.

METHODS

Study Site

The study site at the south border of Crater Lake National Park in southern Oregon (42° 48'N, 122° 50'W) was characterized by McNeil and Zobel (1980). The topography is fairly flat with an elevation gradient from 1460 m to 1550 m. Average annual precipitation is about 65 cm to 85 cm, with most of this falling between October and May. The soils resemble Lapine and Stieger series and are highly porous with the base mineral soil dominated by volcanic pumice mixed with basaltic cobble from the eruption of Mt. Mazama about 7000 years ago. The litter (O horizon) is a fairly thick (to 20 cm) layer of ponderosa pine and white fir needles, ranging in dry mass from about 3 kg m^{-2} to 6 kg m^{-2}. The humus layer (A horizon) is quite variable in thickness and has diffuse interfaces with the litter above and mineral soil below.

The forest overstory is dominated by large ponderosa pine (60 cm to 200 cm dbh, to about 70 m tall) with some subdominant white fir (Perrakis and Agee 2006). The midstory primarily is composed of smaller white fir and lodgepole pine (*Pinus contorta* Doug.) (10 cm to 40 cm dbh, to about 30 m tall), and the minimal understory includes *Pyrola* spp., *Carex* spp., and a number of forbs. Canopy closure was highly variable with numerous gaps. *Ceanothus* spp. and *Arctostaphylos* spp. were also present but restricted to forest edges. Fire scar analysis by McNeil and Zobel (1980) indicated that fires affecting substantial portions of the study area occurred in 1782 to 1784, 1791, 1818, 1846, 1864, 1879, and 1902, with a mean fire return interval of 21.1 yr. There were no fires at the study site from 1902 until the 2002 prescribed burns.

Prescribed Burns

The site was divided into 24 treatment units averaging 2.8 ha in size, each of which was randomly assigned a burn prescription (Figure 1). Four prescriptions were applied: control (eight non-burned units: D, F, G, I, N, P, S, U), early spring burn (ignited 20-22 June 2002; 4 units: A, C, V, W), late spring burn (ignited 28 June 2002; 4 units: E, K, O, T), and fall burn (ignited 9-10 October 2002; 8 units: B, H, J, L, M, Q, R, X) (Perrakis and Agee 2006). The fall burn initially was planned to be applied in two treatments (early and late fall), but weather and fire crew logistical constraints permitted only one ignition weekend for all eight fall burn treatment units. Similarly, competing demands for the fire crew necessitated the close timing of the spring burn prescriptions. As a consequence of random treatment assignments, the early spring burn treatments were applied in the western half of the study area. Because our project began after prescribed burns were applied, we lack pre-treatment soil chemistry data.

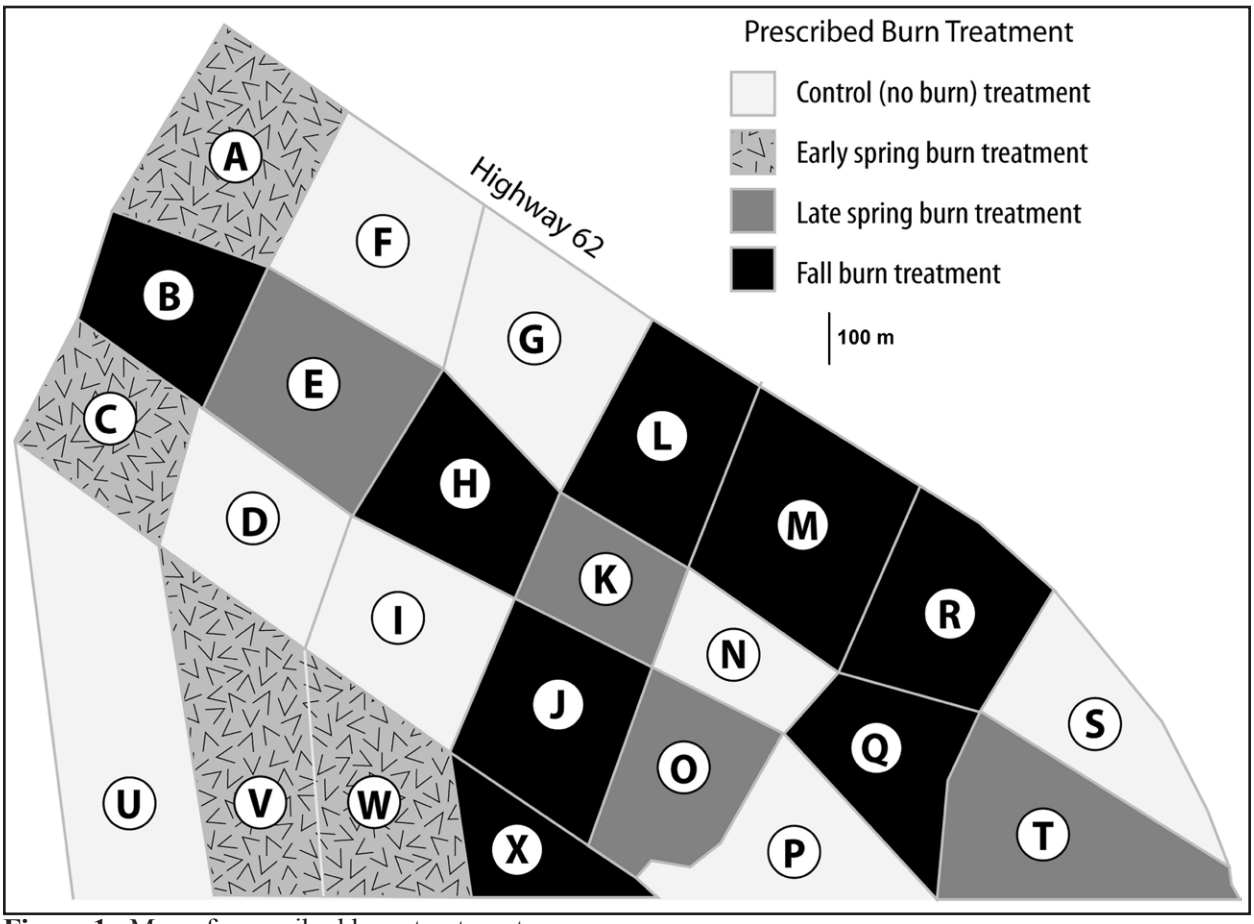

Figure 1. Map of prescribed burn treatments.

Both spring and fall burns reduced small tree abundance (>20 cm dbh) significantly compared to controls (ANOVA $P = 0.001$), but the spring and fall burns did not differ significantly from each other (Perrakis and Agee 2006). There were no significant differences between the density of large diameter trees (>20 cm dbh) between treatments (Perrakis and Agee 2006). The mean area of forest floor litter consumed was 30.5% (SD = 13.3) for the early spring burns, 45.0% (SD = 10.8) for the late spring burns, and 76.0% (SD = 8.0) for the fall burns (D. Perrakis, University of Washington, personal communication). Because the difference in levels of CWD between early and late spring burns was substantial (Table 1; $P = 0.06$) and the interval between the two spring burn ignitions was during a period of rapid drying, we decided to analyze the early and late spring burn treatments separately. Although the burn treatments reduced the midstory of white fir by varying degrees, it still was present on all sample plots.

Habitat Attribute Sampling

We collected data on ten habitat attributes for use as explanatory variables: mineral soil bulk density, total soil C, $\delta^{13}C$ depletion, total soil N, $\delta^{15}N$ enrichment, C:N ratio, CWD mass, FWD mass, litter mass, and mineral soil pH.

For mineral soil data, we took six soil cores with a 335 cm^3 sliding hammer corer (Blake and Hartge 1986) from random locations throughout each treatment unit. We labeled these samples before refrigerating them in sealed plastic bags. Due to the patchy nature

Table 1. Mean values of forest floor and soil habitat attributes by treatment. Superscripts indicate differences significant at $\alpha \leq 0.05$. Standard errors are in parentheses.

	Control	Early spring	Late spring	Fall	Overall
Total collections	144[a,b]	165[a]	154[a,b]	103[b]	566
Number of fungal species	69[a,b]	81[a]	81[a]	55[b]	133
Mineral soil bulk density (g cm^{-3})	0.779[a,b,c] (0.145)	0.665[b] (0.139)	0.856[c] (0.192)	0.866[a,c,d] (0.109)	0.802
Total C (%)	3.64[a] (0.99)	2.97[a] (0.97)	2.69[a] (0.79)	2.57[a] (0.72)	3.01
$\delta^{13}C$ (‰)	−25.72[a] (0.42)	−25.97[a] (0.45)	−25.27[a] (0.32)	−25.41[a] (0.34)	−25.58
Total N (%)	0.130[a] (0.049)	0.101[a] (0.031)	0.104[a] (0.028)	0.119[a] (0.036)	0.149
$\delta^{15}N$ (‰)	2.26[a] (0.62)	2.61[a] (0.64)	2.46[a] (0.66)	2.07[a] (0.61)	2.29
C:N ratio	26.35[a] (3.04)	29.18[a] (2.50)	26.29[a] (3.02)	22.39[b] (2.58)	25.5
Coarse woody debris (Mg ha^{-1})	122.38[a] (82.09)	105.43[a] (56.68)	71.25[a] (60.36)	36.06[b] (45.99)	82.13
Fine woody debris (Mg ha^{-1})	53.49[a] (22.91)	42.28[b] (19.06)	38.06[b] (11.37)	30.87[c] (13.08)	41.51
Litter mass (Mg ha^{-1})	103.11[a] (34.40)	73.72[a] (27.87)	60.23[a] (15.92)	31.98[b] (12.70)	67.36
Mineral soil pH	5.78[a] (0.28)	5.93[a,b] (0.46)	5.87[a,b] (0.32)	6.25[b] (0.26)	6.0

of fire in the burn treatments, some cores in the burned units were collected where the litter had not been consumed. Before coring, we removed the litter layer to expose the mineral soil surface. We oven dried the cores at 60 °C for 12 hours and screened them to remove >1 cm rocks and coarse organic debris. Bulk density was calculated after correcting for the volume and mass of rocks and debris removed. Subsamples were ground to flour consistency in an analytical mill and assayed for total C content, total N content, and $\delta^{13}C/^{15}N$ isotopic signatures by the University of California, Davis Stable Isotope Facility, using a Europa ANCA-GSL elemental analyzer interfaced to a PDZ 20-20 isotope ratio mass spectrometer (Sercon Ltd., Cheshire, United Kingdom). We measured the pH of mineral soil after mixing 1 g of finely ground soil sample in 5 cc of deionized water and allowing it to equilibrate for 1 hour.

Perrakis and Agee (2006) collected fuels data after application of the burn prescriptions. They established ten fuel inventory transects, each 20 m long, at predetermined, fixed locations in each unit for a total of 200 m of line transect (Perrakis and Agee 2006). Coarse woody debris (>7.6 cm diameter) was measured along these transects by Brown's (1974) planar intersect method, with the addition of litter depth measurements at three points along each transect. Coarse woody debris mass was calculated by use of the values for Pacific northwest mixed-conifer forests derived by van Wagtendonk *et al.* (1996), and litter mass was calculated by using regression equations from Agee (1973).

Fungal Sporocarp Sampling

In the three years following the burn applications, we collected fungal fruiting data in the spring and fall by time-constraint sampling (Claridge *et al.* 2000). Time-constraint sampling entails sampling of plots of a standard area for a standard number of person-minutes, allowing experienced surveyors to employ intuition to look in diverse microhabitats and maximize sporocarp detection. The method has been used successfully to quantify fungal diversity and habitat associations over broad ecotypes in southeastern Australia (Claridge *et al.* 2000).

We sampled all four units of both spring burn treatments in the spring and again in the fall. To balance samplings between treatments, four of the control units (G, P, S, U) and four of the fall burn units (M, Q, R, X) were sampled in the spring and the remaining four each (control units D, F, I, N; fall burn units B, H, J, L) were sampled in the fall. At each sampling iteration, we established one 1000 m^2 survey plot within each of the 16 treatment units. Plots were surveyed for 100 person-minutes for above- and belowground mycorrhizal fungal sporocarps.

Belowground fungi (truffles) were sought by gently raking away the surface litter and top layer of soil in both random locations and likely microhabitats, such as along downed logs. Samples of each putative species were collected for laboratory identification. A collection may be one sporocarp or many of a single species from a given plot. Survey plot placement was at least 50 m from the edge of the treatment unit, and the plots were moved within the treatment unit at each sampling to broaden the total area sampled and eliminate disturbance effects from previous sampling activities. Although the use of time-constraint sampling does not preclude comparisons of biomass and richness between species, this was not attempted because of great differences between fungal species in biomass and fecundity as well as the logistic problems of physically transporting all sporocarps from every plot for biomass analysis. Fungal species were identified by traditional taxonomic methods augmented by DNA sequencing when appropriate. All fungal collections were accessioned in the herbarium at Oregon State University.

Data Analysis

Two-way ANOVA tested for post-hoc differences between treatments for each habitat attribute, (i.e., are levels of mineral soil C significantly different between control units and fall burn units?) Bonferroni-adjusted Pearson's analysis identified post-hoc correlations among all habitat attributes (i.e., are levels of mineral soil C significantly correlated with levels of mineral soil N?). We chose this analysis because we expected correlations between some of the individual habitat attributes. By analyzing each pair of attributes independently, we avoided multicollinearity from these explanatory variables (Graham 2003).

We used non-metric multidimensional scaling (NMS) (Clark 1993), a form of ordination analysis (PC-ORD 4.33; McCune and Mefford 1999), to elucidate relationships among and between habitat attributes and the fruiting response of mycorrhizal fungi. Non-metric multidimensional scaling provides closeness-of-fit relationships between all explanatory and dependent variables for complex multivariate data sets and produces scattergrams that spatially orient experimental units based on minimized residuals between all variables. These scattergrams can identify patterns of association between habitat attributes and fungal species, probable indicator species for key habitat attributes, and guilds of species that occupy similar ecological niches. For readability, species with weaker ordination correlations (vector $r^2 < 0.500$) were not plotted.

For ordination analysis, we used three data sets. The first had habitat attribute data (mineral soil bulk density, total soil C, $\delta^{13}C$ depletion, total soil N, $\delta^{15}N$ enrichment, C:N ratio, CWD mass, FWD mass, litter mass, and mineral soil pH) for all 24 units; the second had fungal collection data for the 16 units sampled in the spring, with an overlay of habitat attribute data; and the third had fungal collection data for the 16 units sampled in the fall, with an overlay of habitat attribute data. Because robust patterns are not provided by sparsely dispersed collections, fungal species collected on fewer than four units in either spring or fall were not included in the ordination dataset; relationships between treatment and total species richness (including singletons) were tested with ANOVA. The ordination of habitat attributes shows similarities between units in physical properties (soil chemistry and fuels), and ordinations of species collections show similarities between units in fungal species assemblages.

The environmental indicator value of each fungal species for each habitat attribute was quantified using Indicator Species Analysis (PC-ORD 4.33). This method combines information on the concentration of species occurrence in a particular group and the faithfulness of occurrence in that group (Dufrêne and Legendre 1997, McCune and Mefford 1999) to assign indicator values for each species in each group. These indicator values are then tested for significance using Monte Carlo randomization. To cross-check these results, we then employed logistic regression to analyze correlations between individual habitat attributes and the likelihood of occurrence of individual fungal species. The logistic regression, ANOVA, and correlation analyses were performed with SAS 9.1 statistical analysis software (SAS Institute, Cary, North Carolina, USA).

RESULTS

Habitat Attributes

The mean values of each habitat attribute by treatment are displayed in Table 1, and the ordination of units by habitat attributes is presented in Figure 2. In this ordination, the treatments are separated along the dominant horizontal axis, with the fall burn units to the left with higher mineral soil pH and lower fuel levels, and the control units to the right with lower mineral soil pH and higher fuel levels. There was a secondary stratification along the vertical axis, further separating units most notably by total N above and C:N ratio below.

The patterns seen in this ordination are supported by correlation analysis (Table 2). Above mean levels of $\delta^{13}C$ depletion, $\delta^{15}N$ enrichment, C:N ratios, and fuels were correlated and tended to occur together as a suite of characteristics, mostly on control and early spring burn treatments (Table 1). In contrast, higher soil bulk density, total N, and pH levels occurred on a separate suite of units, including most of the fall burn units but also three control units. Most of the late spring burn units had habitat attributes intermediate between these groups, except unit T (at the east end of the study area), which was more similar to the fall burn treatments. Control units S, G, and N differed from other controls by their high levels of total N and correspondingly lower C:N ratios. All spring burn units had above mean C:N ratios except unit T (late spring burn). Fall burn units B, H, and J had below mean C:N ratios, but had lower axis 1 values due to reduced total N.

Species Assemblage Ordinations

We made a total of 566 collections representing 133 species of mycorrhizal fungi over three years. Of these 133 species, 77 were found in only one or two units during a col-

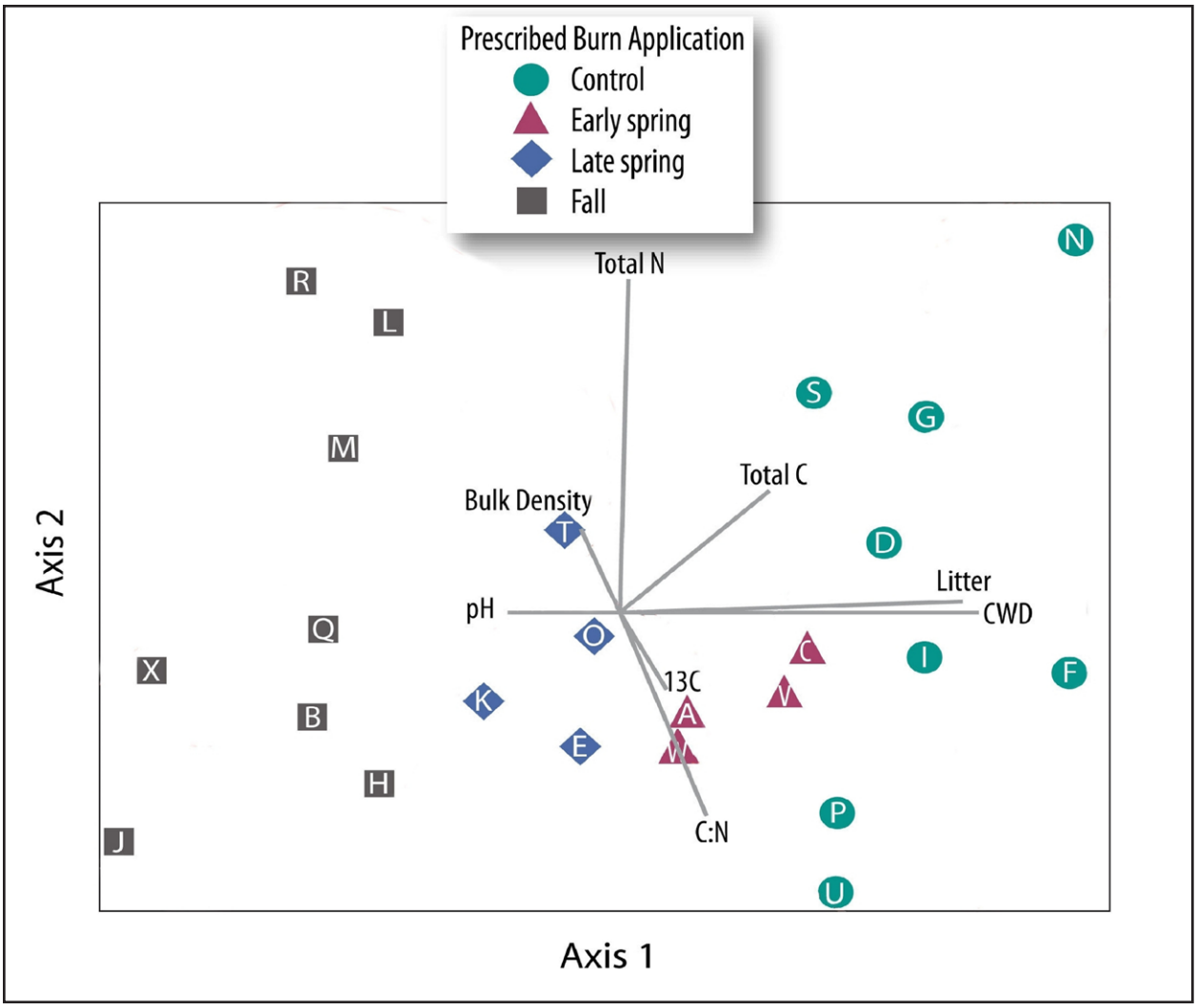

Figure 2. Ordination of habitat attributes for all units.

lecting season (spring or fall) and were not used in ordination analysis. Of the remaining 56 species, 14 were collected in the spring and 44 in the fall (four species were collected in both seasons).

The ordination by species collected on the units surveyed in the spring is presented in Figure 3, and by species collected on the units surveyed in the fall in Figure 4. Soil attribute data are displayed in the vector overlays but do not affect the position of the scattergram points. In the ordination of fungi collected in the spring (Figure 3), the vectors of *Amanita pantherina*, *Morchella angusticeps,* and *Sarcosphaera coronaria* were associated with units typified by lower C:N ratios, fuel levels, and higher pH, which were primarily, but not exclusively, late spring and fall burn treatments. The opposing vector of *Gautieria monticola, Hysterangium separabile, Hydnotrya variiformis, Ramaria rasilispora,* and *Rhizopogon salebrosus* associated with units of higher C:N ratios, higher fuel levels, and lower pH; but not consistently with the control treatments.

In the ordination of fungi collected in the fall (Figure 4), *Boletus chrysenteron, B. zelleri, Rhizopogon vulgaris*, *Russula densifolia*, and *R. tyrrhenica* were associated with units having lower C:N ratios, lower fuel levels, and higher bulk density; *Cortinarius caperatus, C. rigidus, Gautieria monticola, Gomphus floccosus, Ramaria flavobrunnescens, Russula integ-*

Table 2. Bonferroni-adjusted Pearson's correlations between habitat attributes. Estimates are above *P* value. A negative sign preceding the estimate indicates an inverse correlation; *P* values significant at $\alpha \leq 0.05$ are bolded.

	Mineral soil bulk density	**Total C %**	**δ^{13}C depletion**	**Total N %**	**δ^{15}N enrichment**	**C:N ratio**	**Coarse woody debris mass**	**Fine woody debris mass**	**Litter mass**	**Mineral soil pH**	**Collections**
Total C %	−0.5926										
	0.7833										
δ^{13}C depletion	0.6000	−0.1487									
	0.0019	0.4881									
Total N %	0.3552	0.5702	-0.4222								
	0.0892	**0.0030**	**0.0378**								
δ^{15}N enrichment	−0.1918	0.0469	-0.0495	−0.1794							
	0.3693	0.8277	0.8183	0.3970							
C:N ratio	−0.5008	-0.0756	−0.6379	−0.6954	0.1736						
	0.0065	0.8699	**0.0004**	**0.0001**	0.2016						
CWD mass	−0.2772	0.5580	−0.3842	0.1304	0.1491	0.4811					
	0.2134	**0.0059**	0.0702	0.6629	0.4949	**0.0154**					
FWD mass	−0.1979	0.3883	−0.0890	0.2560	0.1117	0.2022	0.7458				
	0.3539	0.0608	0.6789	0.3529	0.6033	0.1324	**0.0001**				
Litter mass	−0.2813	0.5716	−0.2798	0.2947	0.0604	0.2771	0.8911	0.8928			
	0.1830	**0.0035**	0.1855	0.2345	0.7792	0.1024	**0.0001**	**0.0001**			
Mineral soil pH	0.1772	−0.2076	−0.0673	0.0745	−0.2037	−0.3766	−0.4623	−0.5109	−0.4762		
	0.4874	0.3025	0.7784	0.8700	0.3191	0.1105	**0.0147**	**0.0115**	**0.0154**		
Collections	−0.5979	0.1333	−0.4795	−0.3219	0.1366	0.5962	0.2336	0.1167	0.1943	−0.2776	
	0.0070	0.5558	−0.0618	−0.1117	0.3573	**0.0047**	0.2412	0.6428	0.4014	−0.2401	
Number of fungal species	−0.5861	0.0950	−0.4737	−0.3222	0.1009	0.5818	0.2293	0.1223	0.1989	−0.2535	0.9963
	0.0098	0.7940	0.0744	0.1126	0.4571	**0.0072**	0.2677	0.6577	0.4174	0.2975	**0.0098**

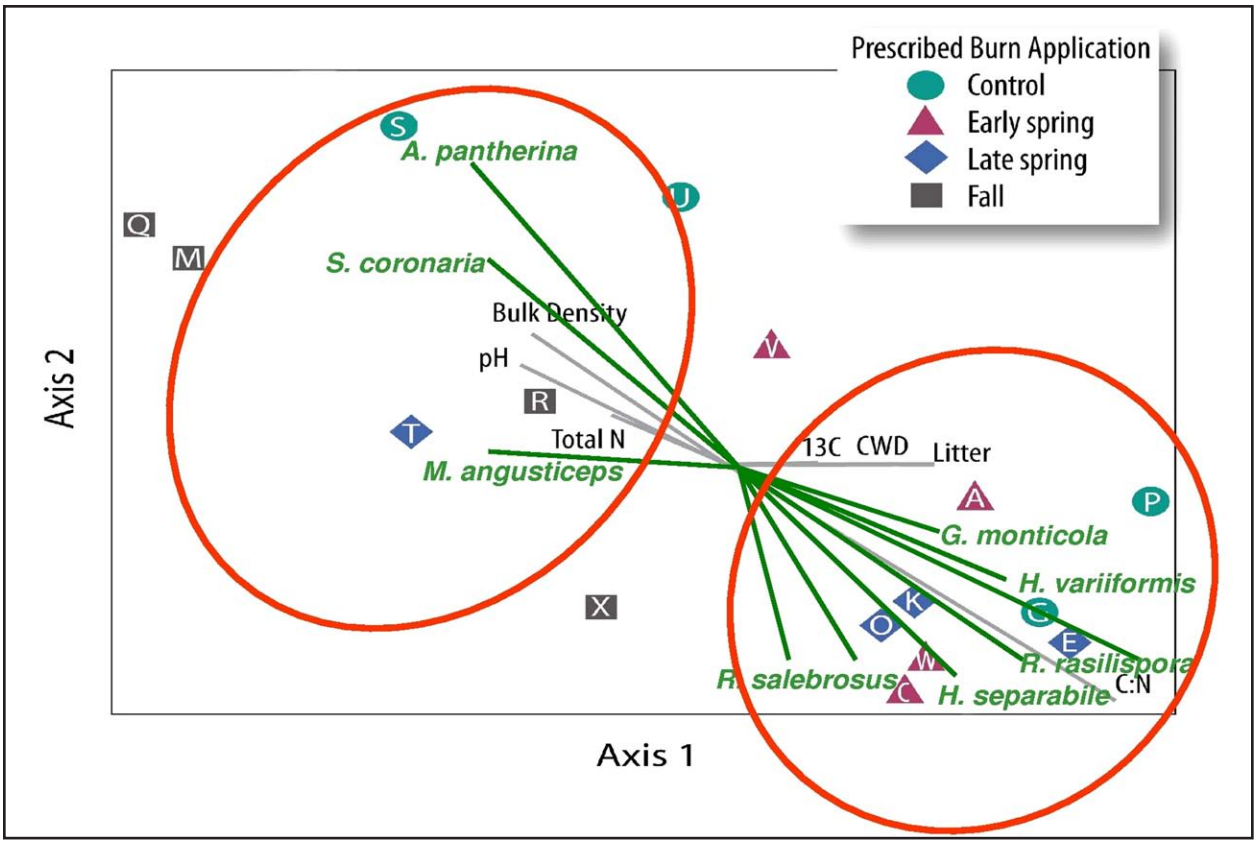

Figure 3. Ordination of spring collection units by fungal species assemblage.

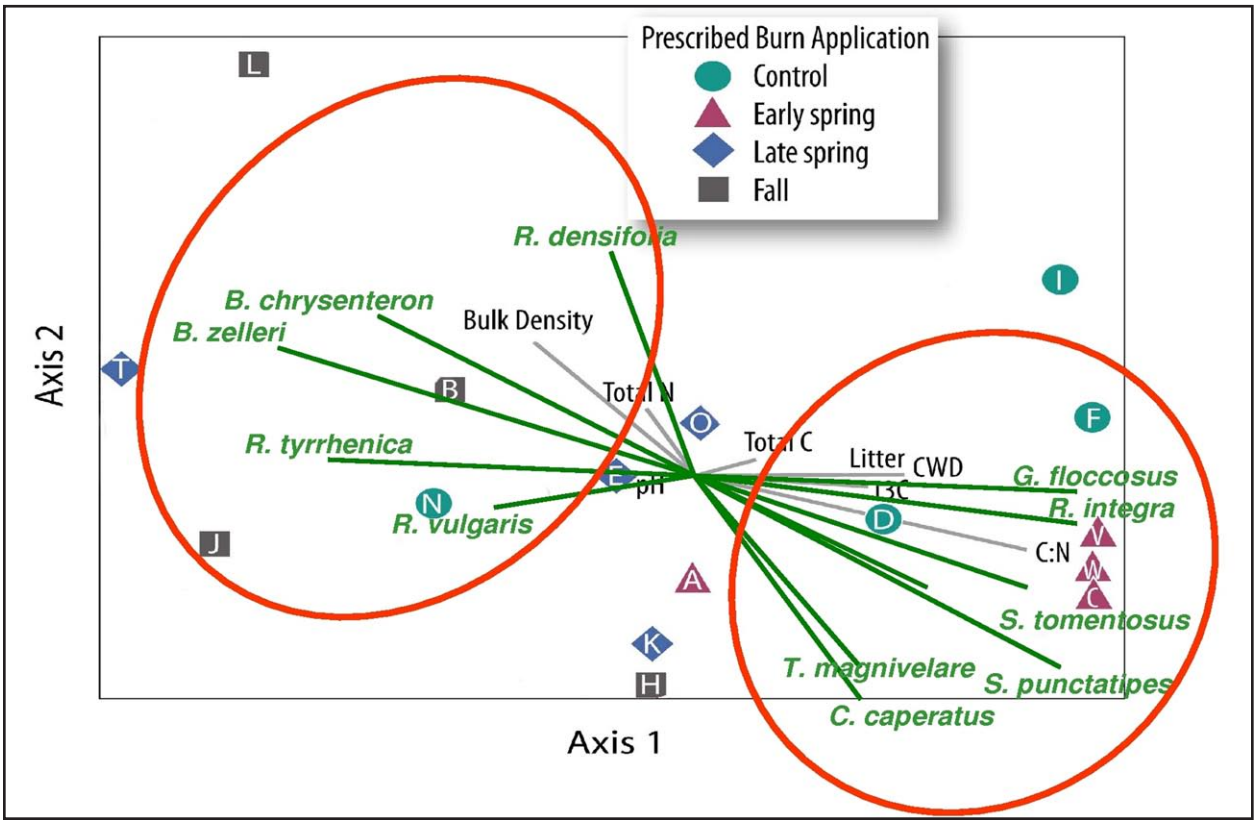

Figure 4. Ordination of fall collection units by fungal species assemblage.

ra, Suillus punctatipes, S. tomentosus, and *Tricholoma magnivelare* were associated with units having higher C:N ratios, higher fuel levels, and lower mineral soil bulk density.

Indicator Species Analysis and Logistic Regression Correlations

Indicator species analysis and logistic regression analysis generally agreed with each other and with the ordination results (Table 3). This table presents data for the 27 fungal species that had significant correlations with one or more habitat attribute in either analysis.

DISCUSSION

Our first hypothesis was that prescribed burning in the spring would have no significant effect on soil C, N, mineral soil bulk density, C:N ratios, pH, and $\delta^{13}C/^{15}N$ isotopic signatures of soil samples collected 3 yr post-burn, as compared to unburned control units. We expected some reduction in surface fuels (litter and CWD) in the spring burn units. The fall burn units were expected to have lower levels of soil C and N, higher mineral soil bulk density, lower C:N ratios, higher pH, unchanged $\delta^{13}C/^{15}N$ isotopic signatures, and reduced levels of surface fuels. The treatment effects on soil properties and fuel levels were as expected with the exception of mineral soil bulk density (Table 1). Bulk density might be anticipated to increase with fire severity as a function of increased consumption of organic soil components; however, here the bulk density was lowest in the spring burn units and was not correlated with total C (Tables 1 and 2). This pattern is difficult to explain until analyzed spatially: the units with the highest soil bulk densities were at the lower (eastern) end of the project area and concentrated adjacent to Highway 62. An artifact of random treatment assignment was that all of the early spring burn treatment units were placed in the western (least dense) end of the project area (Figure 1), and half of the fall burn treatments (as well as several control units) were located in the densest end of the geographic gradient. We observed a similar spatial pattern with soil N and $\delta^{13}C$ depletion. This gradient helped us to distinguish the effects of the burn treatments from the effects of the soil chemistry.

Our second hypothesis was that burning in the spring would not significantly change mycorrhizal fruiting patterns, but we expected a shift in fruiting patterns in the fall burned units as compared to controls. We expected a decline overall in fungal diversity in the fall burned units compared to unburned control or spring burned units. The fall burned units did not differ significantly from controls in either numbers of collections or numbers of species, but did differ from spring burn units (Table 1).

We identified guilds of indicator mycorrhizal fungal species that co-occurred under similar sets of soil attributes. This pattern was more closely correlated with soil C:N ratios than burn treatment (Figures 3 and 4). While all of the units with above-mean C:N ratios were either control or early spring burn treatments, three of the units with below-mean C:N ratios were unburned controls that produced fungal fruiting patterns similar to the fall burned units (units N, S, and U).

The fall ordination also suggested a transitional group of treatment units: A (early spring burn), E (late spring burn), H (fall burn), K (late spring burn), and O (late spring burn). These units tended to group with the fall burn units in habitat attribute space due to their moderate to low fuel levels, but none of them produced the low C:N indicators *Boletus chrysenteron* or *B. zelleri*, and all three produced the high C:N indicators, *Suillus punctatipes* and *S. tomentosus*.

Although mineral soil bulk density was negatively correlated with the C:N ratio (Table 2), several units that had above-mean bulk densities also had above-mean C:N ratios and

Table 3. Logistic regression and Indicator Species Analysis of habitat attributes on fungal taxa. Collection season S = spring, F = fall; positive correlations ++ = $P < 0.05$, + = $P = 0.05$ - 0.10; negative correlations -- = $P < 0.05$, - = $P = 0.05$ - 0.10; n = $P > 0.10$.

Species	Collection season	Mineral soil bulk density	Total C %	‰ $\delta^{13}C$ depletion	Total N %	‰ $\delta^{15}N$ enrichment	C:N ratio	Coarse woody debris	Fine woody debris	Litter mass	Mineral soil pH
Alpova trappei	S	n / n	n / n	n / n	n / n	n / n	n /++	n / n	n / n	n / n	- / -
Amanita muscaria	S	n / -	n / n	+ / n	n / n	n / +	n / n	n / n	n / +	+ / +	n / n
Amanita pantherina	S	n / +	n / n	n / n	n / n	n / n	-- / --	n / n	n / n	n / n	n / +
Boletus chrysenteron	F	n / +	n / n	n / n	n / n	n / --	- / -	n / n	n / +	n / n	+ / ++
Boletus zelleri	F	+ / ++	n / n	- / -	n / -	n / +	- / --	-- / --	- / --	- / --	n / n
Cortinarius caperatus	F	- / --	n / n	n / n	n / n	+ / ++	n / ++	n / n	n / n	n / n	n / n
Cortinarius claricolor	F	n / n	n / n	n / n	n / n	n / n	n /++	n / n	n / n	n / n	n / n
Cortinarius rigidus	F	n / n	+ / ++	n / n	n / --	n / ++	n / ++	+ / +	n / ++	+ / ++	- / n
Gastroboletus subalpinus	F	n / n	n / n	n / n	n / n	n / n	n / n	n / n	n / n	n / ++	- / n
Gautieria monticola	S	n / n	- / n	n / n	n / n	n / n	+ / ++	n / ++	n / n	+ / ++	n / --
Gautieria monticola	F	n / -	n / n	n / n	n / n	n / n	n / +	+ / +	n / ++	n / +	n / n
Gomphus floccosus	F	- / -	n / ++	n / n	n / ++	n / ++	+ / +	+ / ++	+ / ++	n / ++	n / n
Hysterangium separabile	S	n / -	n / n	n / n	n / n	n / n	+ / +	n / n	n / n	n / n	n / --
Hydnotrya variiformis	S	n / n	n / n	n / n	n / n	n / n	n / +	n / n	+ / +	n / ++	- / --
Melanogaster tuberiformis	S	n / n	n / n	n / n	n / n	n / n	n / ++	n / n	n / n	n / n	n / n
Morchella angusticeps	S	n / n	n / n	n / n	n / n	n / n	n / n	-- / --	n / -	- / --	n / n
Ramaria cartilaginea	F	-- / --	n / n	n / n	n / n	n / n	n / n	n / -	- / n	-- / --	-- / --
Ramaria flavobrunnescens	F	n / --	n / n	n / n	n / n	n / n	+ / +	n / ++	+ / ++	n / ++	n / --
Ramaria rasilispora	S	n / -	n / n	n / n	n / n	n / n	++ / ++	n / n	n / n	n / n	n / --
Rhizopogon evadens	F	n / n	n / n	n / n	n / -	n / n	n / n	n / -	n / -	n / n	n / n
Rhizopogon salebrosus	S	n / n	n / --	n / -	n / --	n / n	n / n	n / n	n / +	n / n	n / n
Rhizopogon vulgaris	S	n / n	n / --	n / n	n / n	+ / n	n / -	n / n	n / +	n / n	n / n
Rhizopogon vulgaris	F	n / n	- / --	n / n	n / -	n / n	n / n	- / --	n / +	n / ++	n / n
Russula cascadensis	F	n / -	n / n	n / n	n / n	n / n	n / ++	n / n	n / n	n / n	n / n
Russula claroflava	F	n / ++	n / n	n / n	n / +	n / +	n / --	n / n	n / n	n / n	n / n
Russula densifolia	F	n / n	n / n	n / n	n / n	n / n	n / --	n / n	n / n	n / n	n / n
Russula integra	F	- / n	+ / ++	n / n	n / -	n / ++	n / ++	+ / ++	n / ++	n / ++	n / n
Russula tyrrhenica	F	n / n	n / -	n / n	n / n	n / -	- / --	n / --	n / --	n / -	n / n
Sarcosphaera coronaria	S	n / n	n / n	n / n	n / n	++ / n	- / --	n / n	n / n	n / n	n / +
Sarcodon imbricatus	F	n / n	n / n	n / n	n / n	n / n	n / --	n / --	- / n	n / n	n / n
Suillus punctatipes	F	-- / --	- / n	n / n	n / n	+ / ++	++ / ++	n / n	n / n	n / n	n / n
Suillus tomentosus	F	- / --	n / n	n / n	n / n	+ / +	++ / ++	+ / ++	++ / ++	+ / +	n / n
Tricholoma focale	F	n / n	n / n	n / n	n / n	n / n	+ / ++	n / n	n / n	n / n	n / n
Tricholoma magnivelare	F	n / --	n / n	n / n	n / n	n / n	n / ++	n / n	n / n	n / n	n / n

produced high C:N (control units F and P) or intermediate fungal guilds (unit O). Conversely, units B, N, U, and X had below-mean bulk densities and C:N ratios, and produced the low C:N fungal guilds, indicating that C:N ratios were more consistently correlated with fruiting patterns than bulk density.

Likewise, coarse woody debris levels were positively correlated with C:N ratios, and all of the high C:N fungal guild-producing units had above-mean CWD levels. However, four of the units producing the low C:N fungal guild (units N, S, T, and U) had above-mean CWD levels, and three of them (N, S, and U) were unburned control units and also had above-mean FWD and litter levels. Again, fungal fruiting patterns correlate more closely with C:N ratios than fuel levels or prescribed burn timing.

The suites of attributes indicated by these groupings are consistent with what we might expect would separate burned from non-burned sites, however these fungi were collected over a continuum of burn severities from non-burned controls to fall burns, suggesting that the relationships are not as simple as burned versus not burned. For example, *Gautieria monticola,* associated with higher C:N ratios, was collected on four control units but also on five spring burn units. Conversely, *Sarcosphaera coronaria,* associated with lower C:N ratios, was collected on two control units as well as on nine burned units. Only *Morchella angusticeps* consistently fruited on burned units to the exclusion of control units.

These patterns are further supported by logistic and indicator species analysis of each species against each habitat attribute (Table 3). Indicator species analysis tended to identify more variables as significant than did logistic regression. All of the species identified in the ordination had significant correlations with habitat attributes, most frequently the C:N ratio.

Categorizing Units by Fungal Guilds

The units can be grouped into three categories based on the fungal guild indicator species they supported (Figures 5, 6): the low C:N guild in units B, J, L, M, N, Q, R, S, T, U, and X; intermediate or transitional units A, E, H, K, and O (inconsistent or without either high or low C:N indicator species); and the high C:N guild in units C, D, F, G, I, P, V, and W. Four of the intermediate units (A, E, K, and O) produced the high C:N guild in the spring (Figure 3) and the low C:N guild in the fall (Figure 4). Unit H was only sampled in the fall and did not produce any C:N ratio indicator species.

Of the late spring burn units, only unit T produced a clearly low C:N guild both spring and fall, while the other late spring burn units (E, K, and O) were intermediate. Three of the four early spring burn treatment units (units C, V, and W) produced high C:N-associated guilds, and the fourth (unit A) was intermediate. In total, more spring burn units produced the high C:N guild than did control units.

No fall burn units produced high C:N fungal guilds. However, three of the control units produced the low C:N fungal guild. All but one of the units (unit G; control) having above-mean C:N ratios produced the high C:N guild. Unit G is spatially transitional between high and low C:N units, and the apparent inconsistency between its C:N ratio and the fungal guild produced may be an artifact of the random locations from which soil cores were taken within the unit. All of the intermediate units also had above-mean C:N ratios. Only one of the low C:N guild producing units had an above-mean C:N ratio (unit J, a fall burn). The three control units (units S, N, and U) that produced the low C:N guild all had below-mean C:N ratios. The correlation between the C:N ratio (Figure 5) and fungal guilds (Figure 6) is much closer than that of burn treatment (Figure 1) and fungal guild (Figure 6), and explains

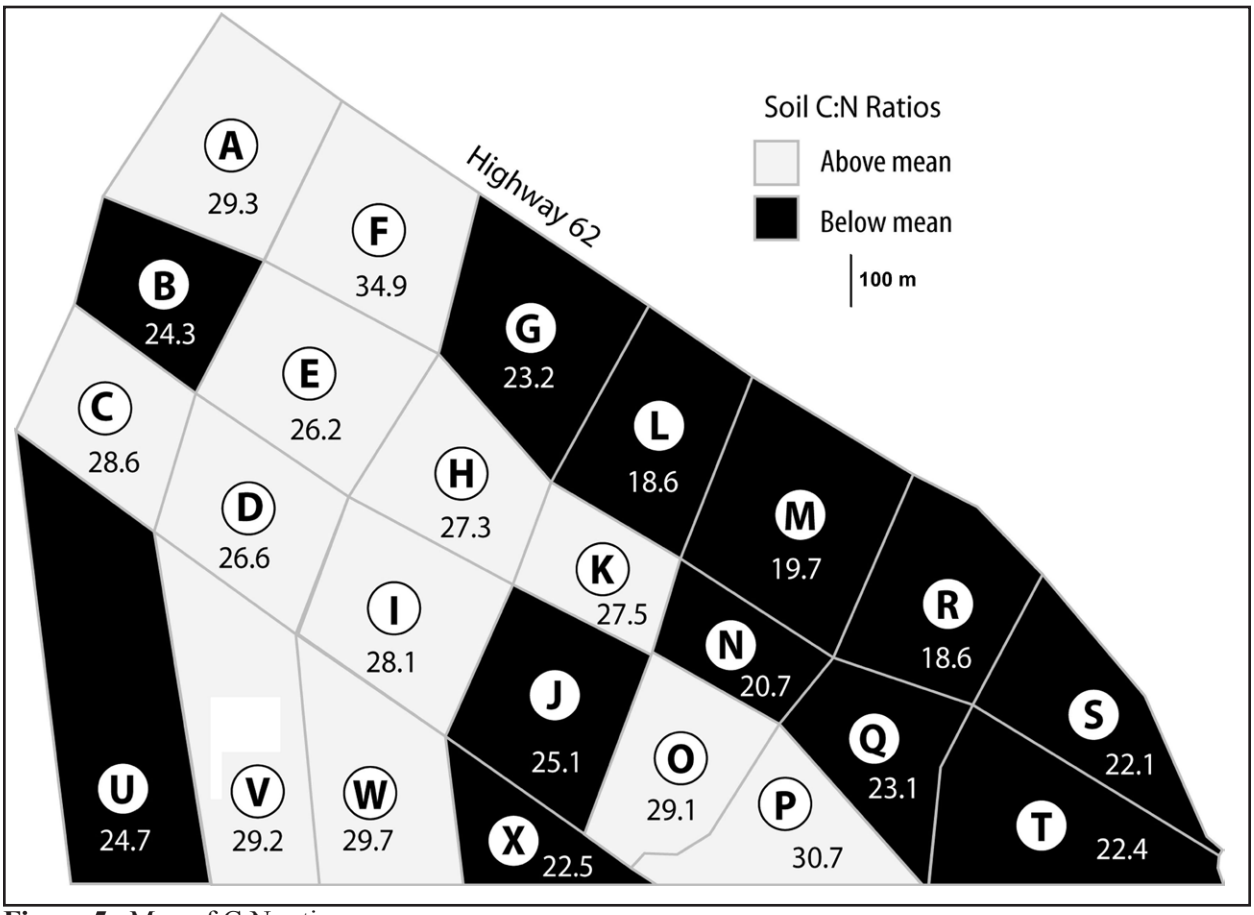

Figure 5. Map of C:N ratios.

the occurrence of low C:N fungal guilds in control units N, S, and U.

The seven units at the east end of the study area all had low C:N ratios and produced low C:N guilds, irrespective of burn treatment. One clue to the effect of the fall burn treatment on the units is to compare the C:N ratios from control units G and S to those of proximate fall burn units L, M, and R. The C:N ratios of control units G and S were 22.1 and 23.2, respectively, and fall burn units L, M, and R ranged from 18.6 to 19.7. If we assume that the C:N ratio of control units G and S did not change appreciably from before the burn treatments, then we can infer that the fall burn treatment itself reduced the C:N ratio by 2.4 to 4.6 in units L, M, and R. By this estimate, it is quite possible that these units were producing the low C:N fungal guild even before the burn prescriptions were applied. The contrast in C:N ratio between fall burn units B, J, and X, and their neighboring control and spring burn units is also striking (Figure 5), suggesting direct influence by the fall burn treatment.

Possible explanations for the spatial pattern of bulk density, total N, $\delta^{13}C$ depletion, and C:N ratios include the adjacent Highway 62, historic human use, or natural causes. Isotopic patterns do not support the effect of motor vehicle traffic as a source of C or N deposition. Both petrocarbon deposition (Wilkes *et al.* 2000) and N fertilization (Temple *et al.* 2005) would tend to increase $\delta^{13}C$ depletion, and at our site the low C:N units are less $\delta^{13}C$ depleted.

From about 1925 to 1932, there was a park entry station and maintenance camp in the vicinity of units Q, R, S, and T (S. Mark, Na-

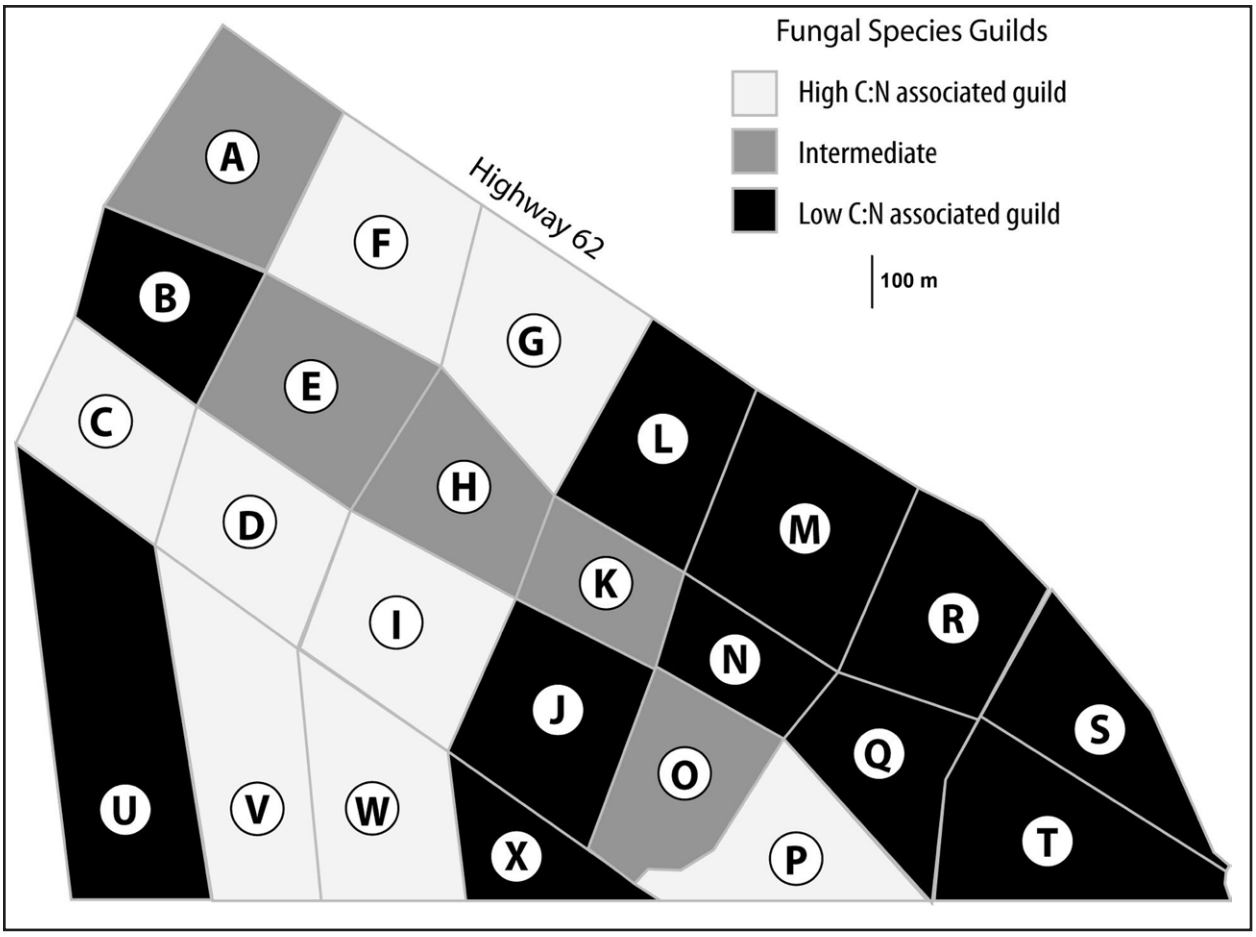

Figure 6. Map of mycorrhizal fungi guild fruiting patterns.

tional Park Service, personal communication). All of these units had above-mean bulk density, and unit S (a control) had the highest bulk density of the entire project area. It is possible that this area is still responding to an intense and prolonged disturbance from 75 years ago, either from the camp itself or from related highway construction activities.

All five of the units intermediate between the high and low C:N fungal guilds were in a line between unit O and unit A (Figure 6). This line marked the transition from high C:N (to the west) to low C:N soils (to the east). Four of these five units were spring burn treatments; one (unit H) was a fall burn treatment. Unit H was the only fall burn unit that did not clearly produce a low C:N fungal guild; it had the highest C:N ratio and CWD levels of the fall burn treatment units.

Fall burn treatment units B, J, and X all had below-mean C:N ratios and produced the low C:N fungal guild, but in their cases the lower C:N ratios were due to lower levels of total C, rather than to higher levels of total N. The fall burns may have reduced total C but the difference is non-significant (P = 0.123). These units were surrounded by control and spring burn treatment units (Figure 1) that maintained higher C:N ratios (Figure 5), suggesting that the fall burn treatment changed the soil C:N ratio enough to shift mycorrhizal fungus fruiting patterns.

All fall-burned units produced low C:N guilds except unit H. The burn treatment may have reduced the C:N ratio enough to suppress fruiting of high C:N guild species, but not enough to produce the low C:N guild. Of all the spring burn units, only unit T produced the

low C:N fungal guild. It was among the band of low C:N ratio units along the highway, and based on the spatial pattern of soil properties, also may have produced the low C:N fungal guild before the burn treatment was applied.

While the development of sporocarps in saprobic (wood-decaying) fungi can be very sensitive to substrate chemistry (Moore 1998), we know very little about sporocarp initiation factors in mycorrhizal fungi. Primary elements in mycorrhizal morphogenesis are thought to be available energy, temperature patterns, and moisture availability (Smith and Read 1997). Mycorrhizal fungi presumably have steady access to photosynthetically fixed C, but relative levels of organic and inorganic forms of N may be differentially influential to sporocarp morphogenesis between species.

The meaning of the C:N ratio threshold of 26 as a divide for the fruiting of some fungi and not others at this site is unknown, but may be a consequence of the varying abilities of different species to access the energy required to produce fruiting bodies under differing soil chemistry or water potential conditions. Although it is unknown whether the fruiting patterns we observed are a consequence of spatial patterns of mycorrhizal fungi across the landscape or fruiting responses to environmental conditions, it seems unlikely that mycorrhizal fungi could colonize an area where they were previously absent and initiate fruiting in the three years since the burn treatments were applied. It seems more likely that those fungi we detected were there before the treatments and what we observed is a fruiting response, rather than newly arrived fungal individuals. Conversely, however, it is easy to imagine sensitive species being extirpated by the effects of more severe fires.

With the exception of *Morchella angusticeps,* which responded more to the treatment itself than to the effects on soil properties, the timing and consequent severity of prescribed burn treatments influenced fungal communities only indirectly as a function of their effects on soil attributes. Burn treatments may adjust pre-existing soil chemistry that in turn influences fungal community composition. Although the differences in the number of fungal collections and species between control and fall burn treatments were not significant, it is likely that some mortality of fungal individuals occurred in the fall burn units. In no unit or treatment was mycorrhizal fungal fruiting suppressed entirely. The observed indicator species tended to be mutually exclusive, and given the short duration of time since treatments, it is more likely that the patterns observed represent sporocarp morphogenesis rather than mycorrhizal colonization. This site offers and excellent opportunity for studying the long-term effects of the prescribed burn treatments on the stand structure, species composition, and soil chemistry on mycorrhizal fruiting patterns.

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