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Hypogeous Fungi Occurrence, Distribution and Mycorrhizal Hosts in Grand Teton National Park and John D. Rockefeller, Jr. Memorial Parkway

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Objectives

The persistence of mycorrhizal fungi in undisturbed coniferous forest ecosystems is assumed by the renewed appearance of their sporocarps each year. Sporocarps, however, are not produced in areas severely disturbed by fire or clearcutting; yet spores and other propagules of some species of hypogeous fungi are present in the soil in the absence of suitable mycorrhizal hosts, and are capable of forming mycorrhizae several years after clear-cutting or fire (Miller et al. 1989). In fact, hypogeous fungi such as Rhizopogon spp. are typically the first to recolonize root systems of new seedlings after large scale disturbance such as fire, insect attack, or clearcutting (Miller et al. 1989). Are these fungi residual in the soil from previously existing spore banks, or are they continuously being restocked into the area? Information on strategies for persistence, propagation and survival of ectomycorrhizal fungi is required before responses of forest ecosystems to fire and other disturbance can be understood.

The severe fire season of 1988 in the northwest corner of Wyoming left a large patchwork of burned and unburned areas that affected a variety of habitats. Although the native vegetation has already begun post-fire recovery, the effects of the fires will be evident for many years, and provides an outstanding opportunity to study closely the biotic and...
abiotic relationships comprising the recovery process. This study is a preliminary examination of the biology of hypogeous fungi in Grand Teton National Park and John D. Rockefeller, Jr. Memorial Parkway. Our objective is to examine the effect of hypogeous fungi on establishment of ectomycorrhiza-dependent tree species and the extent to which animal vectors facilitate tree survival and establishment by providing ectomycorrhizal spore inoculum.

Methods

Two permanent study areas were established in the Huck burn during July 1989, on opposite sides of the highway, in the John D. Rockefeller Memorial Parkway. Both sites have similar slopes, elevation and tree species composition. However, one site is east-facing and the other is west-facing. These specific sites were selected because each had (1) unburned mixed conifer forest composed of lodgepole pine (Pinus contorta) and subalpine fir (Abies lasiocarpa) (2) a severe burn in which both trees and ground litter were destroyed, and (3) a distinct "edge" where the ground cover was left intact but the trees were killed either by the intense heat or crown fires. These sites are considered replicated.

For small mammal trapping, four rectangular grids of 6 stations (10 m apart) were established in each treatment (forest, edge and burn) on the two study sites. On three collecting trips (one each in July, August, and September), small mammals were trapped with Sherman live traps baited with rolled oats and peanut butter on the trapping grid. Small mammals were identified to species, sexed and uniquely ear-tagged before release. The Lincoln-Petersen index was used to estimate total population size. Fecal pellets remaining in the trap were collected to sample for spores of fungal genera present. Randomly encountered scats of larger mammals were also collected for similar analysis.

In July and August, insects and soil arthropods were collected by using pitfall traps (partially filled with polyethylene glycol) installed near each trapping station. Insects have been sorted to families and those which are reported to be mycophagic will be sent to Oregon State Entomology Department for species identification. Smears of gut contents of specimens of confirmed mycophagic species will be made and examined for mycorrhizal spores.

In August soil was collected for analysis of mycorrhiza forming potential. Soil was collected from ash and subsoil
fractions in the burn and edge areas at both sites, and from whole soil in the unburned forest. The soil bioassay procedure of Miller et al. 1989 was used; each soil was composited, mixed in equal proportions with peat moss and vermiculite or perlite and placed into tubes or pots in the greenhouse. Lodgepole pine (*Pinus contorta*) or Yellow Blossom Sweet Clover (*Melilotus officinalis*) seeds were sown into respective tubes and the root systems will be examined this spring for the number and kinds of ecto- and endomycorrhizae formed. In addition, these soils are being directly subsampled for ectomycorrhizal fungal propagules present by using a sucrose gradient extraction process.

Nematodes were extracted from subsamples of this composited soil with Baermann funnels. Nematodes were counted by trophic category. Soil moisture was determined gravimetrically and nematode density is reported on a 100 g dry wt of soil basis.

Soils collected from the study site were also analyzed for organic matter, pH, electrical conductivity, phosphorus, magnesium, calcium, potassium, sodium, and texture according to techniques outlined in the University of Wyoming soil testing laboratory manual of standard fertility tests and laboratory procedures (Shreve 1989). Soil pits were excavated and generally described in the field. Two soil surveys from adjacent areas of Teton County, Wyoming, (Young 1982, Nordin and Blackwell 1989) were used to establish a probable series name and taxonomic name for the soil on the study site.

At each sampling time conifer seedlings were excavated and examined for ecto- and endomycorrhizal infection and hypocotyl and epicotyl production. In addition, within each of the rodent trapping grids, at least 20 seedlings (when present) were permanently marked by small stakes in July. Survival of these seedlings was followed through August and September.

Results

Many portions of the study are still ongoing and only preliminary results can be presented at this time.

Five species of small mammals were trapped from the study sites, *Clethrionomys gapperi* (red-backed vole), *Peromyscus maniculatus* (deer mouse), *Eutamias minimus* (least chipmunk), *Neotoma cinerea* (woodrat), and *Sorex cinereus* (masked shrew) from pitfall traps.
Capture success increased from July through September (Fig. 1). Population size (Lincoln-Petersen index) was slightly higher in September (27/600m², SD = 5.45) than in August (30/600m², SD = 3.63) on the west-facing slope. On the east-facing slope, the density in September (30, SD = 3.63) was significantly higher than the density in August (14, SD = 2.07) (t-test, P < 0.5). In August and September more animals were trapped in the edge and burn than in the forest. Overall trap success was higher in the burn (but not significantly so) than in the forest and edge (Fig. 1).

On both sites, C. gapperi was captured only in the forest and edge (Fig. 2). Trapping success for P. maniculatus was highest in the burns, intermediate in the edge and lowest in the forest. Eutamias minimus was more abundant on the west-facing slope and trapping success was approximately equal in all treatments. On the east-facing slope Eutamias minimus was rare and was captured only in the burn. Only one individual of N. cinerea was captured on a single trapping night in the east-facing forest in September. One S. cinereus was caught in the forests on each site in July.

Fecal pellets from C. gapperi contained the greatest number and diversity of fungal spores (Table 1) with spores from ectomycorrhizal, saprophytic and facultative genera; however, most spores were from ectomycorrhizal taxa. Eutamias minimus pellets contained Hysterangium and Thaxterogaster spores (both ectomycorrhizal genera), but remnants from a variety of vascular plants were also found.

Peromyscus maniculatus fecal pellets contained few spores of ectomycorrhizal or saprophytic fungi, but occasionally contained Morchella spores, a facultative mycorrhizal fungus common to recently burned areas.

Few spores of mycorrhizal fungi have been found thus far from soil extractions. However, sclerotia of Cenococcum geophilum, a common ectomycorrhizal colonizer of early successional conifer species, were found in soils from all treatments. Cenococcum sclerotia appeared to be most abundant in soil from the burn treatments, averaging 3,900/l of soil, while only 1,240 and 1,400 sclerotia/l of soil were found in the forest and edge soils respectively.

Two species of newly germinated conifer seedlings were encountered in the Huck fire research sites, Pinus contorta (lodgepole pine) and Abies lasiocarpa (subalpine fir). Lodgepole pine (Pinus contorta) seedlings germinated throughout the growing season on both east-facing and west-facing slopes.
Figure 1. Number of small mammals trapped each month in forest, edge and burn treatments along the John D. Rockefeller Memorial Parkway. Histograms reflect captures by species for both east- and west-facing sites.
Figure 2. Total number of small mammal captures in forest, edge and burn treatments along the John D. Rockefeller Memorial Parkway. Histograms reflect captures by species for both east- and west-facing sites.
Table 1. Fungal genera present in fecal pellets from small mammals trapped at field sites in the Huck fire, Grand Teton National Park and John D. Rockefeller Memorial Parkway.

<table>
<thead>
<tr>
<th>SMALL MAMMALS</th>
<th>FUNGI</th>
<th>Epigeous</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Hypogeous</td>
<td></td>
</tr>
<tr>
<td>Clethrionomys gapperi</td>
<td>Rhizopogon--e</td>
<td>Morchella--f</td>
</tr>
<tr>
<td></td>
<td>Hysterangium--e</td>
<td>Peziza--u</td>
</tr>
<tr>
<td></td>
<td>Gautieria--e</td>
<td>Russula--e</td>
</tr>
<tr>
<td></td>
<td>Thaxterogaster--e</td>
<td>Pholiota--s</td>
</tr>
<tr>
<td></td>
<td>Geopora--e</td>
<td>Hypholoma--s</td>
</tr>
<tr>
<td>Eutamias minimus</td>
<td>Hysterangium--e</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Thaxterogaster--e</td>
<td></td>
</tr>
<tr>
<td>Peromyscus maniculatus</td>
<td></td>
<td>Morchella--f</td>
</tr>
</tbody>
</table>

1 ectomycorrhizal habitat; 2 facultative habit; 3 habit unknown; 4 saprophytic habit
facing sites and continued to be abundant even during the September collecting visit. Subalpine fir (Abies lasiocarpa) on the other hand, only germinated on both sites during May and June, and was rarely encountered during September.

From July through September, survival of lodgepole pine seedlings was about 50% for the east-facing burn and edge and the west-facing burn treatments. Mortality was highest in the west-facing edge at about 80% where most seedlings were fir.

Lodgepole pine seedlings collected in July and August from both sites had allocated more biomass to epicotyl production than to hypocotyl production, whereas seedlings collected during September had allocated more biomass to hypocotyls than epicotyls, regardless of site or treatment. Few or no ectomycorrhizae were formed until September, although abundant short roots were present. By September, however, 100% of surviving seedlings were ectomycorrhizal. In addition, the number of ectomycorrhizae root tips was positively correlated with the number of primary needles.

Analysis of the mycorrhization potential of soils from the study sites is still underway. Preliminary data from the endomycorrhizal bioassay, however, shows that vesicular-arbuscular mycorrhizal fungi are most prominent in soil from the west-facing control and edge ash fractions.

Soil from the burn treatment had the lowest average density of nematodes at 42/100 g of soil, while the forest soil was intermediate with 83 and the edge supported the highest populations at 621/100 g of soil. In the edge and the burn, bacterial feeders constituted the largest trophic group. Omnivores and fungal feeders were also present but at low densities. Five trophic groups were collected from the forest soil. Dorylamidae (omnivores) were most abundant followed by bacterial feeders. Also present in lower densities were plant parasites, fungal feeders and predators. The trophic diversity ($H'$, Shannon-Wiener diversity index) was 0.50 in the forest soil, 0.18 in the burn soil and 0.10 in the edge soil reflecting these differences. Soil moisture (from the bulked soil) averaged 10.25% in the burn, 17% in the edge and 11.5% in the forest.

Both east-facing and west-facing slope soils are in the Hechtman-Rock outcrop association and are members of the loamy-skeletal, mixed lithic Cryochrepts. The major factors resulting in this classification are the relatively steep slopes, rhyolitic parent material and largely coniferous macrovegetation. Soil chemistry data are provided in Table 2.
Table 2. Soil Characteristics of various soil fractions from east facing and west facing sites in the Huck fire, Grand Teton National Park and John D. Rockefeller Memorial Parkway.

<table>
<thead>
<tr>
<th>Subsoil</th>
<th>Control</th>
<th>Edge Ash</th>
<th>Edge Subsoil</th>
<th>Burn Ash</th>
<th>Burn</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>WF</td>
<td>EF</td>
<td>WF</td>
<td>EF</td>
<td>WF</td>
</tr>
<tr>
<td>OM</td>
<td>5.2</td>
<td>14.4</td>
<td>16.7</td>
<td>5.9</td>
<td>4.5</td>
</tr>
<tr>
<td>pH</td>
<td>5.0</td>
<td>7.1</td>
<td>6.7</td>
<td>5.8</td>
<td>5.3</td>
</tr>
<tr>
<td>Elect. con.</td>
<td>0.2</td>
<td>0.6</td>
<td>0.7</td>
<td>0.5</td>
<td>0.5</td>
</tr>
<tr>
<td>Phosphorus</td>
<td>20</td>
<td>216</td>
<td>110</td>
<td>48</td>
<td>66</td>
</tr>
<tr>
<td>Magnesium</td>
<td>1.5</td>
<td>3.6</td>
<td>2.2</td>
<td>2.4</td>
<td>1.2</td>
</tr>
<tr>
<td>Calcium</td>
<td>5.6</td>
<td>42.1</td>
<td>19.3</td>
<td>11.8</td>
<td>5.5</td>
</tr>
<tr>
<td>Potassium</td>
<td>1.4</td>
<td>6.1</td>
<td>4.7</td>
<td>1.5</td>
<td>1.8</td>
</tr>
<tr>
<td>Sodium</td>
<td>0.5</td>
<td>0.6</td>
<td>0.4</td>
<td>0.4</td>
<td>0.4</td>
</tr>
</tbody>
</table>
Additional chemical analyses such as total N, nitrate and ammonium are still in progress.

Conclusions

In this study, *C. gapperi* was trapped only in the edge and forest treatments, which is consistent with its preferred habitat in mesic areas under log cover (Maser et al. 1979). Fungal fruiting body production is also increased under these conditions and fungi are a major food resource for red-backed voles (Maser et al. 1978). Therefore, *C. gapperi* did not appear to be a major vector of ectomycorrhizal fungal spores into burned areas at our study sites. *Peromyscus maniculatus*, a trophic generalist and the most widely distributed rodent in North America, is frequently the only species found in severely disturbed habitats. The lush regrowth after burns may be providing an easily accessible seed source for *P. maniculatus*, and even fungi such as *Morchella*, which was abundant in the burn treatment throughout the summer, are only rarely eaten. Furthermore, our pitfall traps yielded large numbers of insects in the burn and the lack of ground cover may also make foraging for insects relatively easy for *P. maniculatus*.

*Eutamias minimus*, the most omnivorous of the species trapped, does not have highly specific habitat requirements. However, even though fewer fungi were eaten by *E. minimus* than *C. gapperi*, spores of the ectomycorrhizal fungi that were eaten appear to be dispersed through the burn treatment. *Eutamias minimus* showed the greatest potential for ectomycorrhizal spore dispersal at our sites.

Although both lodgepole pine and subalpine fir had germinated abundantly by July, only lodgepole pine seedlings survived throughout the summer. This appeared to be due to differences in strategies for growth and water use efficiency by both species and by early and late season lodgepole seedlings. Subalpine fir produced a large tap root early in the season, but few short roots and needles. Early season lodgepole pine produced many more needles and allocated less energy to the roots. Many individuals of both species had desiccated by mid-summer. However, lodgepole seedlings that germinated in response to August rain allocated much less energy to the stem and needles and more to roots. By September, over half of all short roots on all surviving seedlings were ectomycorrhizal. This suggests that colonization by ectomycorrhizal fungi influences allocation of energy to the roots, increases the root-to-shoot ratio and prevents excessive transpirational
loss and desiccation.

The nematode community in soil from the forest was typical for undisturbed coniferous forests: trophic diversity was high and all major feeding groups were present. In the burn and edge, food web complexity was reduced and bacterial feeders assumed dominance. The dead roots may have provided an abundant substrate for bacteria that were fed upon by microbivores. Low densities in the burn probably resulted from lack of litter due to intense ground fire and high soil temperatures. Soil moisture content may also have been a factor and, in fact, highest densities were found in the edge which had a significantly higher soil moisture. Furthermore the trees on the edge were killed but the litter did not burn. Thus the litter layer provided insulation while the dead roots provided a major resource input to the decomposer community and the bacterial populations responded accordingly. Thus the litter layer provided insulation while the dead roots provided a major resource input to the decomposer community and the bacterial populations responded accordingly.

Literature Cited


