Results From Green-Tree Retention Experiments: Ectomycorrhizal Fungi

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ABSTRACT

The ecosystem effects of natural disturbances differ dramatically from those engendered by even-aged management practices that emphasize commodity production. Because forest management activities can reduce ectomycorrhizal (EM) fungus diversity and forest regeneration success, management approaches are needed to sustain these essential forests organisms. We present selected results from experiments that test biodiversity assumptions behind current guidelines for ecosystem management. We examine contrasts in structural retention as they affect biodiversity and sporocarp production of EM fungi—a functional guild of organisms well suited as indicators of disturbance effects on below-ground ecosystems.

Overstory removal significantly reduced EMF sporocarp production but, in contrast to the initial hypothesis, the effects were not always proportional to basal area retained. The effect of spatial pattern of retention varied between retention levels and mushroom and truffle sporocarp groups. Management implications include the need to address the conservation of rare truffle and mushroom species in a manner that recognizes their different responses to forest disturbance. We also raise the hypothesis that fire suppression may favor mushroom production over truffle production. Because fire seems to be important in the reproductive evolution of EMF, our results also add further impetus to the development of management plans that seek to restore forest health from the effects of decades of fire suppression.

Experimental results suggest using dispersed green-tree retention in combination with aggregated retention to maintain sporocarp production. Such a mix ameliorates disturbance effects and may maintain higher levels of sporocarp production in the aggregates by reducing edge effects. It remains unclear how short-term reductions in sporocarp abundance will affect EM fungus populations for future forests. After disturbance, spores are a form of legacy and key to enabling adaptations by other species in the face of environmental change. Long-term silvicultural experiments are essential for monitoring trends in the EM fungus community.

KEYWORDS: Fungi, hypogeous, epigeous, mycorrhizae, biomass, diversity, disturbance.

INTRODUCTION

Fungi profoundly affect nearly all terrestrial ecological processes and events; accurate information on the fungal component is required to adequately understand how ecosystems function (Trappe and Luoma 1992). When fungal mycelia form particular associations with a host plant's fine roots, a symbiotic organ forms, called a mycorrhiza. Through this structure the plant provides carbohydrates to the fungus, which in turn facilitates uptake of nitrogen, phosphorus, other minerals and water to the plant (Allen 1991, Marks and Kozlowski 1973, Smith and Read 1997). The fungus also protects plant roots from attack by pathogens and the effects of heavy metal toxins, promotes fine root development, and may produce antibiotics, hormones and vitamins useful to the plant (Smith and Read 1997). Mycorrhizal associations are vital to the existence of most vascular plants (Smith and Read 1997, Trappe 1987).

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Availability of mycorrhizal fungi determines patterns of primary plant succession on new soils such as moraines, fresh volcanic deposits, and mine spoils (Allen 1991, Cázares 1992, Helm et al. 1999, Trappe and Luoma 1992). Mycorrhizal fungi are associated not only with increased plant productivity but also with developing community diversity following disturbance (Allen et al. 1995, Cázares 1992). Mycorrhizal fungal species differ in their ability to provide particular benefits to their hosts, and their presence and diversity change during plant succession (Cázares 1992, Helm et al. 1996, Mason et al. 1983, Trappe 1977). A diversity of mycorrhizal fungi is likely essential for successful shifts of geographic range by plants due to climate change (Perry et al. 1990).

The ectomycorrhiza type is characterized by a mantle of fungal hyphae encasing the root tips of the associated plant. Ectomycorrhizae are characteristic of the Pinaceae and Fagaceae which dominate most forests in the Pacific Northwestern United States, and are required for survival of these hosts in field soil (Trappe and Luoma 1992). We are able to reasonably infer the mycorrhizal status of diverse forest fungi by their placement in certain fungal genera (Molina et al. 1992, Trappe 1962) despite the reservations expressed by Arnolds (1991). Ectomycorrhizal fungi (EMF) form a functional guild linking primary producers to soil systems, are important in ecosystem response to disturbance (Janos 1980, Perry et al. 1989), and may be sensitive indicators of environmental changes (Arnebrant and Söderström 1992, Arnolds 1991, Termorshuizen and Schaffers 1987, Termorshuizen et al. 1990). Ectomycorrhizal fungi mostly produce macroscopic sporocarps in the form of mushrooms and truffles (epigeous or above-ground fruiting bodies and hypogeous or below-ground fruiting bodies, respectively). Sporocarps produce the spores that disseminate the species and provide for genetic recombination within and among populations.

Forest Management

Studies from the Pacific Northwest indicate that forest management activities can reduce ectomycorrhizal fungi, forest regeneration success, and influence patterns of plant succession (Amaranthus et al. 1994; Harvey et al. 1980a, 1980b; Waters et al. 1994; Wright and Tarrant 1958). Development of management approaches to sustain these essential organisms in forests has been hampered by a lack of knowledge of EMF community structure, diversity, and spatial and temporal variability across stands and landscapes.

Many EMF species, especially those that produce truffles, are also important dietary items for vertebrates and invertebrates: some small mammal species rely on them for over 90 percent of their diet (Carey et al. 1999, Claridge et al. 1996, Hayes et al. 1986, Jacobs 2002, Maser et al. 1978, Maser et al. 1985). Truffle species diversity provides necessary nutritional diversity to the diet of mammal mycophagists (see review by Luoma et al. 2003). Small mammals, in turn, form important links in the trophic structure of forest ecosystems as prey for raptors (e.g., owls and goshawks) and mammalian carnivores (e.g., martens and fishers) (Carey 1991, Fogel and Trappe 1978, Hayes et al. 1986, McIntire 1984).

Few studies have examined silvicultural effects on EMF sporocarp production (Colgan et al. 1999, Waters et al. 1994). Although EMF sporocarps do not reveal as complete a picture of the below-ground EMF community as root tip studies (Dahlberg et al. 1997, Gardes and Bruns 1996, Horton and Bruns 2001, Yamada and Katsuya 2001), silvicultural effects on sporocarp production mirror the effects found in root-tip studies: species diversity and community composition can change dramatically. Thinning affects the composition and diversity of EMF in the stand as well as the frequency of sporocarps (Carey et al. 2002, Colgan et al. 1999, Waters et al. 1994). For example, stands that were heavily thinned showed increased dominance by one fungal species. Thinning also reduced truffle biomass, frequency of truffles, and shifted overall species composition (Carey et al. 2002, Colgan et al. 1999). However, total truffle biomass and frequency of sporocarps may recover 10 to 17 years after thinning, whereas shifts in species dominance persist longer (Waters et al. 1994).

Green-tree retention, the practice of leaving live, structurally-sound, large trees in a stand after extracting timber, is an alternative forest management method designed to accelerate the development of late-successional forest characteristics in young, managed stands (Aubry et al. 1999). The Demonstration of Ecosystem Management Options (DEMO) experiment is a long-term study designed to examine the effects of different levels and patterns of green-tree retention on multiple forest attributes (see Aubry et al. 1999). Studies of disturbance effects on the below-ground ecosystem are relatively rare. These studies are critical to forest managers seeking to incorporate basic ecological knowledge into forest management policies and practices. Here we focus on initial results from an experiment that tested some of the assumptions behind the current guidelines for ecosystem management as they affect a functional guild of organisms (EMF) that are well suited as indicators of disturbance effects on the below-ground ecosystem. Detailed reporting of the DEMO fungi study can be found in Luoma et al. (2004).

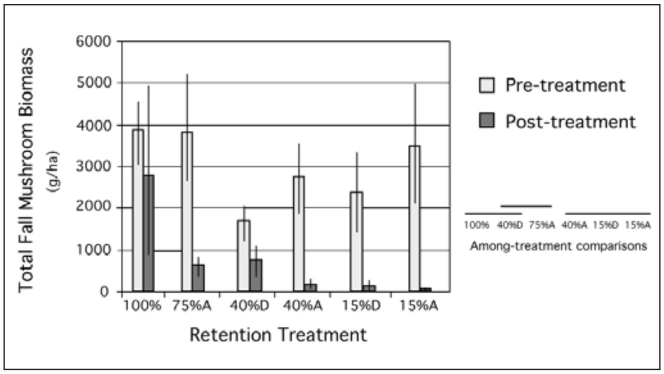

Figure 1—Mean total ectomycorrhizal mushroom standing crop biomass for the fall samples from three DEMO blocks. Standard errors are indicated by vertical bars. Among-treatment comparisons were derived from multiple analysis of variance, repeated measures contrasts of the time * treatment interaction using transformed data. Treatments (see methods) without a shared horizontal bar above them are significantly different at $p \leq 0.1$ (adapted from Luoma et al. 2004, used with permission). D = dispersed retention; A = aggregated retention.

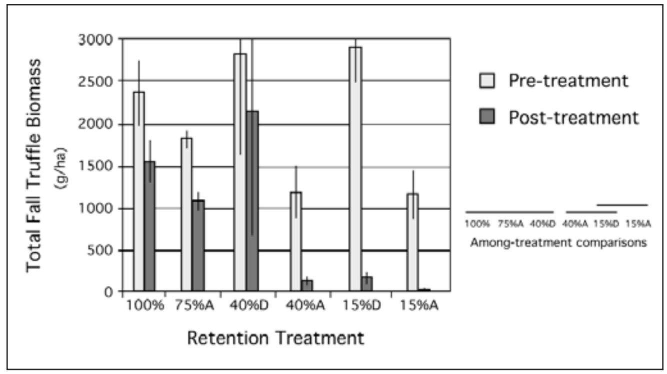

Figure 2—Mean total truffle standing crop biomass for the fall samples from three DEMO blocks. Standard errors are indicated by vertical bars. Among-treatment comparisons were derived from multiple analysis of variance, repeated measures contrasts of the time * treatment interaction using transformed data. Treatments (see methods) without a shared horizontal bar above them are significantly different at $p \leq 0.1$ (adapted from Luoma et al. 2004, used with permission). D = dispersed retention; A = aggregated retention.

The DEMO Experiment

The objective of the DEMO fungi study was to compare pre- and post-treatment standing crop biomass of EMF sporocarps within no harvest, 75-percent, 40-percent (dispersed and aggregated), and 15-percent (dispersed and aggregated) retention treatments. The DEMO experiment replicated six green-tree retention treatments in six geographic locations (Aubry et al. 1999). The treatments consisted of four levels of live tree retention (15, 40, 75, and 100 percent of existing live-tree basal area), with two patterns of retention, aggregated (A) and dispersed (D), applied to the 15- and 40-percent retention treatments. The aggregated pattern consisted of residual trees retained in clumps of about 1 ha and the dispersed pattern has residual trees homogeneously dispersed throughout the unit. For the 75-percent retention treatment, all of the harvest occurred in approximately 1-ha patches dispersed throughout the unit. Fungal sporocarp sampling was limited to 3 blocks.

Study Area

General environmental characteristics of the sites are described by Halpren et al. (1999). The Butte block is located on the Gifford Pinchot National Forest in southwestern Washington. The Dog Prairie and Watson Falls blocks are located on the Umpqua National Forest in southwestern Oregon. Prior to harvest, all blocks were dominated by *Pseudotsuga menziesii* (Mirb.) Franco. The importance of other tree species varied by block (Halpren et al. 1999).

RESULTS

Luoma et al. (2004) found that total fall biomass exceeded total spring biomass for both epigeous and hypogeous sporocarps except in the Watson Falls block where spring biomass of *Gautieria* was a major contribution to greater spring hypogeous sporocarp biomass. In particular, total fall mushroom biomass decreased significantly in the 40-percent aggregated, 15-percent dispersed, and 15-percent aggregated treatments as compared to the other treatments (fig. 1). No treatment effect was detected on the fall mushroom standing crop in the 40-percent dispersed treatment (fig. 1). Total fall truffle biomass was significantly reduced in the 40-percent aggregated, 15-percent dispersed, and 15-percent aggregated treatments as compared to the control, 75-percent aggregated, and 40-percent dispersed treatments (fig. 2). No treatment effect was detected on the fall truffle standing crop in the 40-percent dispersed treatment (fig. 2).

DISCUSSION

Relevance to Ecosystem Management

Standing crop data are useful to interpret the role of fungal species as a food source for animals or the energy expanded in an ecosystem for species reproduction. Standing crop of hypogeous sporocarps may underestimate actual sporocarp biomass productivity because animals utilize a proportion of the fruiting bodies (Luoma et al. 2003). The degree of underestimation is most pronounced at periods of low productivity, when consumptive pressure on the available food resource is proportionally high (North et al. 1997).

When both epigeous and hypogeous species are simultaneously assessed, new understanding of overall diversity phenomena emerges. For example, the more equable biomass distribution of hypogeous sporocarps compared to epigeous between spring and fall (Luoma et al. 2004, Smith et al.

2002) has important implications to mycophagous mammals. Fungal diversity in the diet of such animals appears to be nutritionally important (Claridge et al. 1999, Johnson 1994, Maser et al. 1978). Clearly, animals that depend on fungi as major food items (Fogel and Trappe 1978, Luoma et al. 2003) could not rely on epigeous fungi for diet diversity over the spring. Quite possibly, the decline in populations of some mycophagous animals could relate to decline in diversity of the fungal populations due to habitat disturbance (Claridge et al. 1996, Pyare 2001). Results from the DEMO study show that truffle genera important in the diets of small mammals were significantly affected by the treatments (Jacobs 2002).

Maintenance of EM fungal diversity is important for ecosystem health and resilience (Amaranthus 1997; Amaranthus and Perry 1987, 1989; Perry et al. 1990). Disturbance, whether natural or human caused, can drastically alter populations of EM fungi (Amaranthus et al. 1990, 1994, 1996; Colgan 1997; Pilz and Perry 1984; Schoenberger and Perry 1982).

The Secotioid Syndrome

Some sporocarps have morphology that is intermediate between truffles and mushrooms. Such sporocarps have been referred to as "secotioid" (Singer 1958). In addition to epigeous secotioid taxa, Thiers (1984) included all truffle-like taxa in his analysis of the "secoitioid syndrome." He proposed that in the Mediterranean and semi-arid climates of the western United States, high summer temperatures combined with extended drought stress were primary drivers in the evolution of hypogeous sporocarp formation (i.e., the truffle form). Bruns et al. (1989) documented that such morphological divergence (from mushroom to truffle) can proceed relatively rapidly, possibly as a result of selective pressures on a small number of developmental genes. Hibbett et al. (1994) present a case in which a simple secotioid phenotype, arising from a mutation at one locus, has persisted over a wide geographic range in wet environments that presumably do not exert the selective pressures that drive the secotioid syndrome toward evolution of more strongly sequestrate (Trappe et al. 1992) sporocarps. Baura et al. (1992) speculate that such mutations will not persist long in a population. Kretzer and Bruns (1997) found that secotioid forms of the important EM mushroom genus *Suillus* evolved at least twice and have persisted for evolutionarily significant periods of time over a wide range of summer-dry habitats in the western United States. They noted that the selective forces that favor a secotioid lineage were unclear.

We propose that results from Luoma et al. (2004) represent the first experimental evidence to support Thiers' hypothesis (1984). Even the relative small (1 ha) gaps created in the 75-percent aggregated retention treatment significantly reduced fall production of EM mushrooms in the surrounding uncut forest. Those same gaps, however, did not significantly reduce truffle production. The formation of gaps likely influenced the thermal properties, humidity, and evapotranspiration of the remaining intact forest (e.g., Zheng and Chen 2000). Based on these results, we extend Thiers' hypothesis to encompass the influence of fire in the broader context of forest disturbance in the summer-dry climates of the western United States. Fire is an important agent for producing the patterns of forest fragmentation (e.g., Heyerdahl et al. 2001) that would select for hypogeous sporocarp production via the "secotioid syndrome."

CONCLUSIONS

Even though green-tree retention can preserve ectomycorrhiza diversity (Stockdale 2000), sporocarp production and EM species richness was significantly reduced at all levels of retention except the control. These effects, however, differed by season and treatment (Luoma et al. 2004).

The DEMO study demonstrated the importance of pretreatment sampling. Experimental units within blocks were intended to be as similar as possible in overstory vegetation and site characteristics (Aubry et al. 1999), yet pretreatment results showed that uniformity of fungal populations in forests based on stand structure alone can not be assumed (see also Cázares et al. 1999).

Management implications include the need to address the conservation of rare truffle and mushroom species in a manner that recognizes their different responses to forest disturbance. We also raise the hypothesis that fire suppression may have favored mushroom production over truffle production. Because fire seems to be important in the reproductive evolution of EMF, our results also add further impetus to the development of management plans that seek to restore forest health from the effects of decades of fire suppression (Agee 1997).

Luoma et al. (2004) also found that overstory removal significantly reduced EMF sporocarp production but, in contrast to their initial hypothesis, the effects were not always proportional to basal area retained. The effect of spatial pattern of retention varied between retention levels and mushroom and truffle sporocarp groups. Though not directly studied in the DEMO experiment, Luoma et al. (2004) concluded their results supported the use of dispersed green-tree retention in combination with aggregated retention when maintenance of sporocarp production is a goal. Continuing study of retention level and spatial pattern relationships is important for development of scientifically sound silvicultural techniques for use in the pursuit of science-based forest management.

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