Proceedings of the California Forest Soils Council Conference on Forest Soils Biology and Forest Management

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Contents

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Preface[1]

Soil biology should be a conscious consideration in forest management. Yet, it is not. Historically, managers of western forests have focused on harvesting methods, regeneration practices, vegetation control, and means of protecting their stands from fire and pests. Management has centered on the stand, with emphasis on efficient wood production and extraction. More recently, attention has turned to broader issues and the management and sustenance of whole ecosystems (Sierra Nevada Ecosystem Project 1996). On both public and private lands, scientists, planners, managers, and the general public are weighing other values along with the sustained production of wood. Increasingly, attention is turning to streamside protection, wildlife habitat, and the development of plant communities and forest structures mimicking late seral stages of forest succession. "Restoration ecology" has come into vogue, and a cottage industry has emerged to certify what is, and is not, "sustainable forestry."

Despite this broadening view of forest ecosystem management, the soil often is overlooked or remains an afterthought for many "ecosystemologists." Even within the field of forest soils research, certain aspects of soil science have drawn more attention than others of similar significance (Powers 1987, Stone 1987). True strides have been made in our understanding of how nutritional and physical properties of forest soils are affected by forest management. But our appreciation of the diversity, function, and importance of forest soil biology seems rooted in generalities, overlooked and misunderstood by well-meaning people who treat the soil ecosystem as a "black box" (Tate 1995).

Plant production is the source of organic carbon that drives ecosystem processes including soil genesis. But the transport and transformation of organic carbon in plant detritus is entirely due to the work of soil organisms—a silent community, which, because it literally is underfoot and out of sight, seems equally out of mind. In fact, plant detritus is the immediate currency for litter and topsoil fauna, which, through chewing and mixing, alter the surface area of fresh materials and to some degree, their chemistry. In turn, faunal feces become substrate for smaller soil invertebrates as well as fungi and bacteria that reduce them further, releasing plant nutrients, creating soil humus, continuing soil development. *Figure 1* illustrates the general pathway of forest detritus in the food web of soil organisms.

The significance of soil fauna to soil properties important to management has been previously described (Hole 1981). Ecological functions of soil fauna and other biota include mounding, mixing, void creation and filling, formation and destruction of natural soil aggregates, and the production of special products that range from soil-binding polysaccharides to edible mushrooms. Such activities affect water and air movement, nutrient cycling and availability, and soil aggregation and stability. Eight biologically mediated processes by which this occurs (Tate 1987) are:

- Catabolism of colloidal soil organic matter
- Modification of soil pH

[1] An abbreviated version of this paper was presented at the California Forest Soils Council Conference on Forest Soils Biology and Forest Management, February 23-24, 1996, Sacramento, California.

- Synthesis of chelators
- Alteration of soil redox potential
- Oxidation or reduction of soil cations and anions
- Synthesis of polysaccharides
- Physical shredding of organic debris
- Production of cell or mycelial biomass.

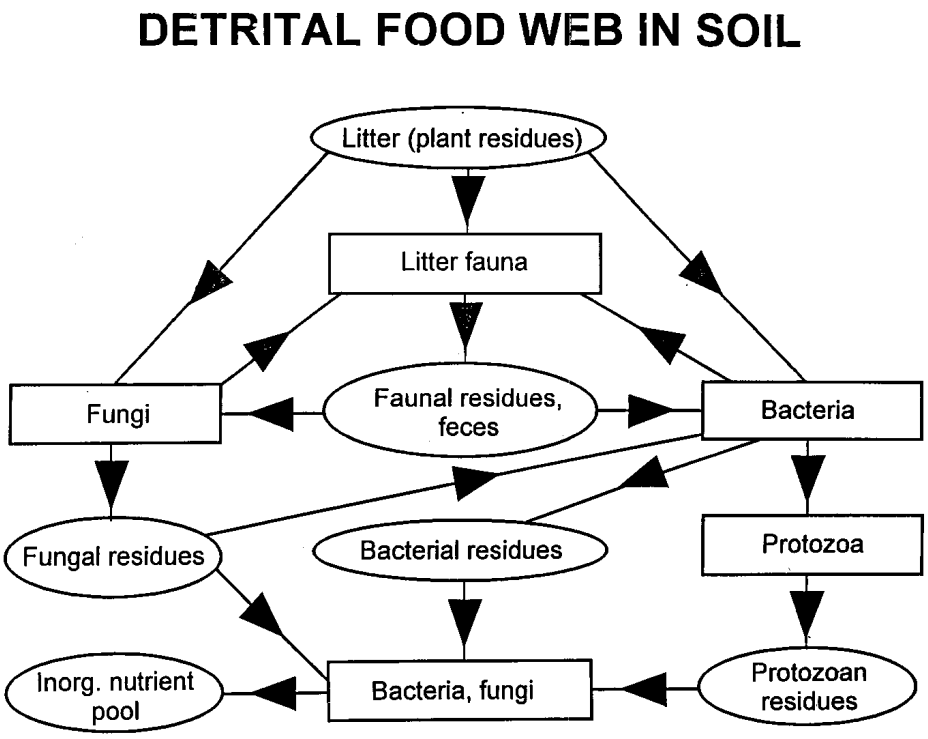

Figure 1—Simplified flow of organic matter in the detrital food web of forests (Richards 1974).

Decomposition of plant residues illustrates the relevance of soil biota in an important process. Sterilization/inoculation techniques and mesh-size screening treatments have demonstrated clearly the effectiveness of organisms of differing size on litter breakdown. For example, Vossbrinck and others (1979) have shown that excluding soil mesofauna (organisms between 0.2 mm and 1 cm in size)--thereby creating a purely fungal and bacterial system—reduces the decomposition of grassland litter by 50 percent (*fig. 2*). Such work also shows that decomposition still proceeds in the absence of meso- and macrofauna, but it proceeds much more slowly. The consequence is residue buildup, surface thermal insulation, and lessened nutrient availability.

One test of true understanding by a scientific discipline is the ability to answer the question "What does it mean?" True understanding extends beyond such questions as "What exists?" (simple taxonomic survey), and "How does it function?"

(observations of behavior under controlled conditions). Important as these questions are, we must also address the question "What is its significance to human endeavor?" If human endeavor—forest management, in this case—is associated with a lessened abundance of a soil organism, *what is the significance of lower abundance*?

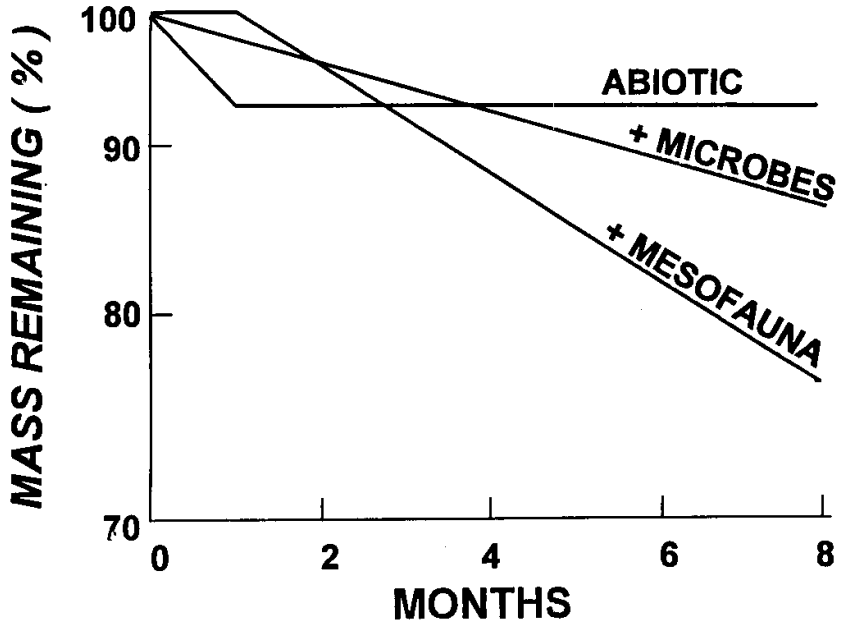

Figure 2—Eight-month trend in decomposition (mass loss) of grass residues by abiotic and biotic agents of decomposition (Vossbrinck and others 1979). Initial mass loss due to abiotic factors is the physical leaching of water soluble compounds.

Often we assume that if an organism behaves in a way that seems beneficial to things that humans value, then reduced abundance of that organism means a loss of that which is valued. Pankhurst (1997) cites evidence that beyond a certain minimum diversity of soil organisms, most species probably have redundant ecosystem functions. But Pankhurst also adds that redundancy may impart greater resistance to a loss of function caused by disturbance. Therefore, a profound question is "What is the minimum diversity needed to assure that important processes will continue to function in the face of forest management disturbances?" Does a measurable decline in the number of soil organisms mean a significant loss of function? What is the difference between statistical significance, biological significance, and practical significance? If changes triggered by forest management do occur, how long do they last? Do we underestimate (or overestimate) the resiliency of soil ecosystems?

These are the sorts of questions addressed in the pages that follow. Sometimes, data are available to support a conclusion. Other times, deductive reasoning can provide valuable insight. For other questions, only relevant factors can be discussed in the absence of quantitative data. As you read these proceedings, we ask that you raise these questions, as well:

- What are the roles of soil organisms in the function of managed forest ecosystems?
- Is there a perfect soil organism or suite of organisms?
- How stable are biotic soil populations or communities over time and how resilient are they to management disturbances?
- What is myth, what is fact, and what is speculation?

We organized this symposium not simply to summarize what already is known in the broad field of soil biology. Other symposia and volumes (Hatfield and Stewart 1994, Pankhurst and others 1997, Ritz and others 1994) have done this. Rather, we invited key research specialists to address questions of soil biology that may have great consequences for forest management.

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The Functional Roles of Forest Soil Arthropods: The Soil Is a Lively Place[1]

Andrew Moldenke,[2] Maret Pajutee,[3] and Elaine Ingham[4]

Abstract

Plant growth depends upon the activity of numerous types of organisms within the environment. The recycling of nutrients in the forest floor involves the interaction of a vast diversity of bacteria, fungi, protozoa, and invertebrates. Arthropods are integral to the initial shredding of the litter, which exposes nutrients to microbial digestion. Hundreds of California species either feed directly upon decomposer microorganisms or prey upon microbivorous taxa. Microbivory enhances the succession of microbial taxa with different enzymatic capabilities for processing soil resources. The final step of recycling, the entry of soil nutrients back into a root, is largely the result of invertebrates feeding upon microbes which have immobilized nutrients within the rhizosphere. Forest management practices can significantly alter soil foodwebs, which may in turn have significant effects on long-term soil productivity. Because arthropods facilitate a number of different soil processes, assays of soil arthropod abundance and community composition may prove to be useful in developing an understanding of the effects of forest management on nutrient cycles in forest soils.

Introduction

No one would deny that there is a formidable biological component to soils (Dindal 1990, Edwards and others 1988, Eisenbeis and Wichard 1987, Petersen and Luxton 1982). It is also undeniable that the fauna, microbes, and roots in healthy soils play a number of interactive functional roles (Benckiser 1997, Coleman and Crossley 1996, Fitter and others 1985). It is unfortunate, therefore, that as scientists and managers we are still rather naive in our understanding of soil ecology.

Can we delineate some of the most important functional roles played by the fauna in the soil? Can we associate these roles with individual species or groups of species? Can we devise simple cost-effective methodologies to evaluate both the effectiveness and the unintended nontarget effects of silvicultural practices (cool-burning, fertilization, herbicide application, compaction) on the integrity of soil ecosystems? We certainly can, but it will require the impetus of research managers and new collaborations between resource managers and university and government scientists.

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[1] An abbreviated version of this paper was presented at the California Forest Soils Council Conference on Forest Soils Biology and Forest Management, February 23-24, 1996, Sacramento California.

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The Plant-Soil Interface: The Microbial Sheath

In natural ecosystems, plant roots do not function all by themselves. A growing body of research has demonstrated that nearly all plant species form symbiotic associations with fungi known as mycorrhizae. The majority of the absorptive surfaces of the roots of each mycorrhizal species are likely to be intimately involved in these symbioses. Less easy to quantify are the ensheathing populations of bacteria. The extent to which these neighboring microbes dominate the flow of nutrients into and out of plant roots is not generally appreciated.

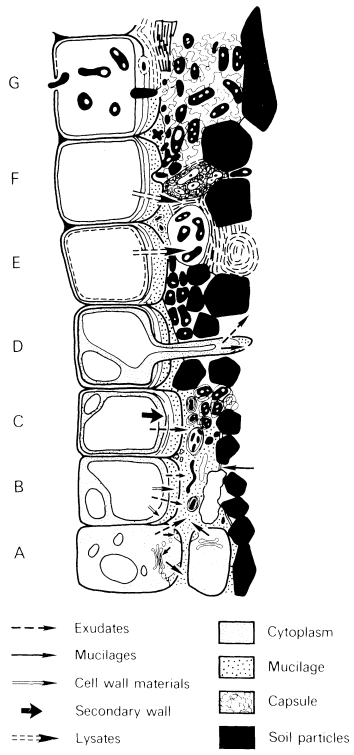

Figure 1—Stages in the life of a root surface cell and nearby rhizosphere. At A, the root cap zone, there is massive excretion of gel by the dictyosome vesicles into the rhizosphere. At B, the epidermal cells are emerging from beneath the root cap and beginning to extend; at this stage the cell is enclosed only by a primary wall. With cessation of longitudinal extension, the cell secretes a secondary wall (stage C) that the developing root hair must penetrate (stage D). With mechanical and microbial lysis of the cuticle, further mucilages are released into the soil. These organic materials together with the products of cell autolysis provide substrates for microorganisms, which proliferate in the rhizosphere (stage E). These microorganisms break down the primary wall (stage F) and invade the epidermis and cortex (stage G). At this stage the outer cortex ceases to function physiologically (Foster and others 1983).

Roots larger than several millimeters in diameter serve to anchor the plant and transport water and water-soluble nutrients. Active physiological metabolism and uptake of nutrients are confined largely to the tips of fine roots. The growing tip of the rootlet secretes a wide variety of chemicals that are easily metabolizable carbohydrates (*fig. 1*; Foster and others 1983). These carbohydrates fuel rapid

bacterial growth and reproduction throughout the immediate vicinity of the rootlet (the rhizosphere). Fungal growth in the rhizosphere may be saprophytic, parasitic, or symbiotic. Symbiotic growth may form diverse compound structures, but two common forms predominate (Allen and others 1994). Fungal hyphae may completely envelop the rootlet with a thick covering (interwoven with the underlying root epidermal cells), thence radiating out for as much as several meters, often as individual fungal strands (ectomycorrhizae; *fig. 2*). Other fungi grow inward to penetrate through the cell wall of root cells, expanding into numerous pouches in direct contact with the plant cell membrane, simultaneously growing outward into the soil for several centimeters (endomycorrhizae; *fig. 3*).

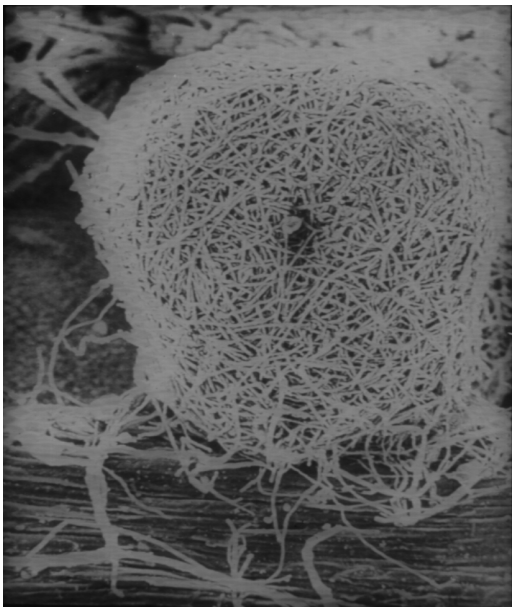

Figure 2—*Pinus strobus* root tip with ectomycorrhizal sheathing of *Pisolithus tinctorius* (Slide by James Trappe).

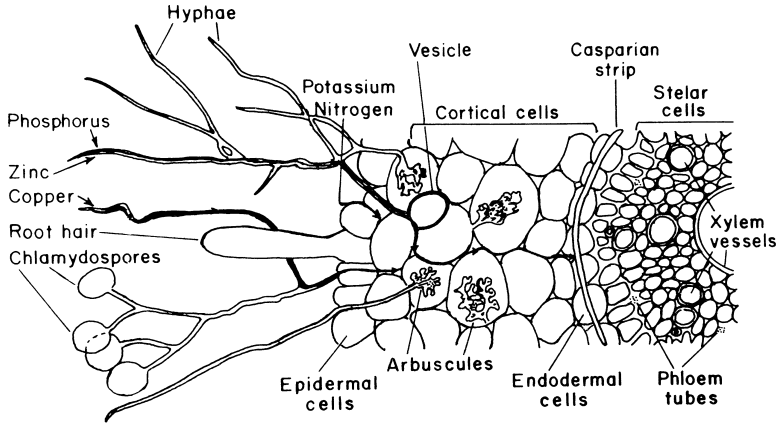

Figure 3—A typical endomycorrhiza showing hyphae extending beyond the root epidermis into the rhizosphere (Curl and Truelove 1986).

As a plant root matures, it is encased by a gelatinous sheath populated with bacteria and mycorrhizae (Curl and Truelove 1986, Foster and others 1983). As the outer epidermis ruptures, fine roots leak significant quantities of nitrogenous amines and micronutrients into the rhizosphere *(fig. 1)*. In this manner the root provides large amounts of carbohydrates and smaller amounts of various other substances that facilitate microbial growth in the rhizosphere. Subsequently, bacterial and fungal metabolism produces catalytic exoenzymes, proteins secreted into the soil, which enzymatically degrade organic chemicals and alter inorganic chemicals. The majority of these soluble nutrients, which may be useful for plant growth, are probably captured by the bacteria or fungi within the rhizosphere. The root becomes encircled by microbes, and microbial metabolic levels far exceed that of the root itself.

Without fauna in the soil to graze upon bacteria and fungi, most of the nutrients would eventually accumulate in microbial tissue (Moore and others 1988).

The Nature of Recycling

The Faunal Factor

From the plant's point of view, nutrient recycling must make available the limiting chemicals incorporated within the forest floor litter and provide a supply of required chemicals from the inorganic geologic substrate. Because plant roots are incapable of secreting enzymes to carry out these chemical transformations (Curl and Truelove 1986), plants are ultimately and completely dependent upon exoenzyme production by bacteria and fungi in the soil, and to a lesser degree upon the enzymes secreted within the digestive systems of soil-inhabiting fauna (from protozoa to vertebrates). Some abiotic chemical degradation occurs in the most extreme environments (deserts, bare rock surfaces), but these are exceptions to the general case of dependence upon microbial enzymatic degradation. Microbial degradation of resources within the soil matrix leads primarily to growth of microbes themselves because the potential absorptive surface area of microbes greatly exceeds that of roots. Thus, microbes can generally compete more efficiently for soluble nutrients. Microbial exoenzymes benefit plants only if some of the enzyme catalysis occurs directly next to a root tip or if mycorrhizal fungi directly share resources with the plant. Bacteria and fungi serve as a biological sponge in the soil, "immobilizing" or "pooling" nutrients from dead organic residues and the inorganic substrate by incorporating them into their own living biomass.

Soil fauna facilitate microbial growth and chemical degradation by:

- Shredding the dead plant parts in forest litter and burrowing into coarse woody debris.
- Moving either the resources or the microbial inocula in a continual homogenization of the soil.
- Improving the water-holding and oxygen-penetrating capabilities of the soil through the *geometry* and chemistry of their fecal pellets, which is soil itself.
- Enhancing the expression of the full range of chemical potentials of soil microbes by facilitating the succession of taxa with different exoenzymic capabilities.

- Liberating into the soil solution (also known as "mobilizing" or "mineralizing") the nutrients pooled within the microbial biomass of the rhizosphere by grazing upon the bacteria and fungi currently active around or within the microbial sheathing of physiologically active roots (Moldenke and others 1994, Seastedt 1984, Setala and Huhta 1991, Visser 1985, Webb 1977).

Shredding and Burrowing

The half-life of different species of coarse woody debris on the forest floor is largely a function of the abundance and diversity of wood-boring insects (largely ambrosia, long-horned or metallic woodboring beetles) (Schowalter and others 1988). Boring insects carry microbial inocula and provide increased access for fungal attack (Ingham and Moldenke 1995). Often these beetles require the presence of actively growing fungi to concentrate limiting nutrients within the wood (Crowson 1981, Martin 1987).

Nutrients in dead leaves or needles are largely unavailable to most microbes. A bacterium in the leaf litter is analogous to a person in a pantry without a can opener. Eventually a person can beat a can open, but it is much more effective to have a can opener. The arthropod shredder is the bacterium's can opener. Bacteria and fungi will eventually use all of a dead leaf, but they are far more efficient if the leaf is shredded first. Shredders (i.e., millipedes, earthworms, sowbugs) crush vast quantities of plant cells from which they extract only the most readily available nutrients--the rest enter the normal soil recycling chain as the shredders defecate the crushed fragments (Hopkin and Read 1992). Passage through numerous shredding devices (the mouthparts of even much smaller organisms, i.e., penknife mites) is required before all the resources are finally available for complete enzymatic digestion (Dawod and FitzPatrick 1993). This process of continually refined shredding takes time, which accounts for the persistence of humus layers in the soil.

Transportation and Homogenization

People take mobility for granted until they become physically disabled. There may be 500 million bacteria in a teaspoon of forest soil, but each one is largely incapable of movement even though some bacteria have flagella that permit limited movement. Each bacterium needs diverse nutrients for growth and reproduction. From a bacterium's point of view, a resource that is several microns away is infinitely far away, because some other competitor is likely to be closer to the resource. There are several solutions: find a method of travel to cross the distance (hitchhike); have someone bring the resource to you; or hope that all your competitors between you and the resource already have enough of the resource and will not steal it before it diffuses back to you. Soil fauna fill the first two roles and provide a better chance of success for the bacterium.

Bacterial and fungal inocula can be carried either on the outer body surfaces of invertebrates or in their intestinal tracts (Anderson 1988, Visser 1985). In general, the number of spores carried phoretically is directly proportional to the surface area of an organism. The viability of ingested inocula is generally proportional to the time it requires to pass through the length of the gut (Anderson 1975). Well-fed individual invertebrates have high percentages of viable inocula in their feces, whereas poorly

fed individuals produce feces with minimal viable inocula. The best-known transporters of both organic substrates and microbial inocula are anecic earthworms (species that feed largely on the soil surface, defecate deep in the soil, and construct extensive tunnels in the rooting zone) (Lavelle 1988).

Building the Fabric of the Soil

Kubiena (1938) at the University of Iowa was the first American to carefully document the contribution of different invertebrates to the microstructure of the soil. Pawluk (1985) at the University of Alberta has recently documented the invertebrate biogenic characteristics of all natural Canadian soils. Thin-section photography has revealed that the humus, A-layer, and much of the litter and B-layers are mostly invertebrate feces *(fig. 4)*. Living between (and sometimes within) these feces are the occasional roots, microbes, protists, and invertebrates, together with scattered undigested dead plant and animal material (Bal 1982, Rusek 1985). The content of the feces can be largely organic (litter consumers), inorganic (deep soil endogeic earthworms), or heterogeneous mixes (mobile millipede coprovores). Only in soils with very low organic content (deserts) or frequent disturbance (annual row crop agriculture) do invertebrate feces fail to be the predominant structural elements (Pawluk 1985).

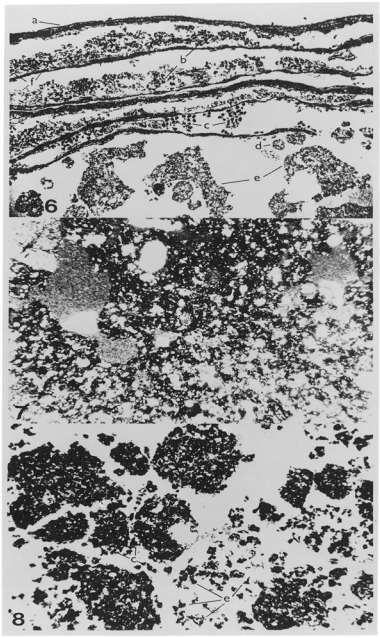

Figure 4—Thin sections of Bohemian oak soils. Top: oak leaves partially metamorphosed into feces by Collembola (f), Enchytraeidae (b), oribatid mites (c). Below the leaves are droppings of fungus-gnat larvae (d) and the epigeic earthworm *Dendrobaena rubida*. Middle: soil fabric of mineral soil composed entirely of feces of endogeic earthworms. Bottom: Droppings of epigeic earthworms near surface of a mull soil subsequently partially disintegrated by enchytraeids (e) and Collembola (c) (Rusek 1985).

The size, shape, and percentage of organic content in the feces control many physical and chemical properties of different soil types (Martin and Marinssen 1993). A matrix of large fecal pellets promotes macropore formation, facilitating aeration and infiltration. Dense mixes of small feces promote wettability and refugia from predators. The majority of soil-dwelling arthropod species probably feeds principally upon the fungi growing on the surface of fecal pellets (Anderson 1975). As they graze on the hyphae they often physically abrade the pellets themselves, exposing additional nutrients to microbial attack.

Each time an annellid worm or arthropod ingests solid food it secretes copious carbohydrate lubricants (mucus). These carbohydrates do act as energy sources for intestinal microbes, but in most instances the mucus ultimately surrounds and embeds the fecal material as well (Edwards and Lofty 1972, Lee 1985). When the content of the fecal material is largely inorganic, as it is for most deep-dwelling earthworms, this input creates a branching "drilosphere" throughout the soil of additional resources and subsequent microbial growth (Barois and others 1993, Bouche 1975).

The feces of earthworms are continually reingested to exploit the nutrients filtered from the soil solution by microbial populations. Thin-section soil micrographs document that soil structure is dominated by invertebrate feces, but it is the largely unstudied rate of re-consumption that drives the turnover of the embedded nutrients.

Microbial Succession

There may be as many as 40,000 kinds of microbes in a single teaspoon of soil (Tiedje 1994). These different microbes exhibit a wide variety of chemical capabilities (Fox 1994, Hawksworth 1991, Palleroni 1994). This level of specialization for resources is mediated by the fauna. The vast majority of microbes is inactive at any given time; only the subset of species capable of using the actual specific chemical composition of resources currently available is metabolically active (Lavelle 1994). As such species grow, and consequently change the chemistry of the remaining resources, the fauna consume them (presumably after most of them have reproduced), which permits other species to succeed them.

Although the rate of microbial grazing by soil fauna in different soil types remains largely unquantified, such grazing rates may be very high (Coleman and Crossley 1996, Visser 1985). More than 200,000 individual fungivorous arthropods can inhabit every square meter of conifer forest soil on average (Moldenke 1990, Petersen and Luxton 1982). The most frequently occurring fungivorous arthropods are oribatid mites, endeostigmatid mites, and springtails. The fungivorous springtail, *Onychiurus*, is the prime determinant of the fungal community composition of a conifer soil in Scotland (Newell 1984). By preferentially consuming a fast-growing species, it keeps fungal diversity high; when *Onychiurus* is removed, a single fungal species predominates, representing 90 percent of the fungal biomass.

Microbial Grazing and Consumption of Microbes

Plant growth depends upon nutrient uptake by the roots. When nitrogen, either as NO_3 or NH_4 ions, is released as an enzymatic byproduct into the soil solution, how does it enter a root? Since the carbon:nitrogen ratio of bacteria and fungi is very low compared to that of the plant material and organic matter they "eat," these organisms

act as accumulators ("sinks") of nitrogen. Bacteria growing within the rhizosphere mucigel have ample supplies of labile carbon. They require nitrogen and other soluble nutrients that are being drawn toward the root as water enters the root's vascular system.

A large fraction, perhaps most, of the nitrogen in growing plants enters a root as the result of fauna grazing the microbes in the rhizosphere (de Ruiter and others 1993, Moore and others 1988). As rhizosphere-grazers (the protozoa, rhabditid nematodes, bacteria- and fungus-feeding mites, and springtails) scrape bacteria and fungi off the root surface and consume them, they defecate (Kuikman and others 1990). Some of the nitrogenous byproducts in these feces can penetrate the disturbed microbial sheaths of the roots. As long as the populations of microbial grazers do not get too dense, they stimulate mycorrhizal growth and exoenzymic activity (Finlay 1985).

Two studies substantiate this interpretation. First, a culture of fungi, bacteria, protozoa, and nematodes from native grassland soil was incubated in a microcosm, and the rate of nitrogen mineralization was estimated by intermittent drainage of soil water (Hunt and others 1987). When biocides were added to kill the protozoa and nematodes grazing on microbes, mineralization rate decreased by more than 82 percent.

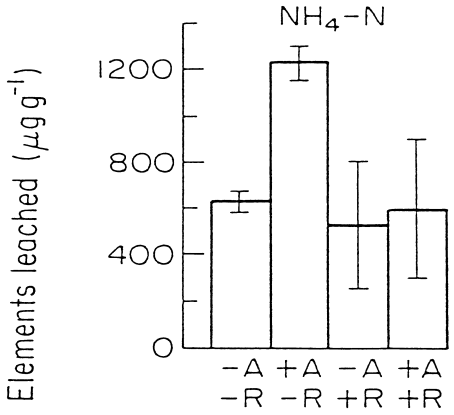

Figure 5—Total ammonium released as leachate from microcosms with 6-week incubation under four experimental treatments. A = arthropods; R = roots of oak seedlings; + = presence; - = absence. Incubation with arthropods alone mineralized significantly more nitrogen (Anderson and others 1985).

Second, normal soil profiles of English oak forests containing natural populations of soil microbes and protozoa were reconstituted in the laboratory (Anderson and Ineson 1982, Anderson and others 1985). Nitrogen mineralization was monitored in the leachate, and a base rate for microbes in the absence of any plant roots or arthropods was established *(fig. 5)*. Addition of a growing oak seedling did not affect the rate. The oak root cannot directly cause mineralization, and it can act only as a passive sponge. Addition of an arthropod shredder greatly enhanced nitrogen mineralization. The increased rate of nutrient mineralization was directly

correlated with the biomass of shredders added (relatively independent of specific taxon). Surprisingly, synchronous addition of both oak seedling and arthropod shredders resulted in no detectable difference from the basal rate of nitrogen leaching with only microbes present. The "missing" nitrogen that should have leached in their combined presence manifested itself in an increased rate of seedling growth (more than fourfold higher than in the absence of arthropods).

Biodiversity Is "Politically Correct," But Are So Many Kinds Really Needed?

We estimate that there are probably 200-250 species of soil arthropods per square meter and 2,500 per square kilometer of western coniferous forest soil[5] (Parsons and others 1991). There are dramatic changes in the soil fauna as one compares north-facing versus south-facing slopes, young stands and mature forest, and pine forest and oak forest.[6] Among all of this diversity, are there certain species that may perform special roles?

The Unique Role of the Macroshredder

Different ecosystems throughout the world are characterized by fundamentally different soil chemical and physical properties. The fundamental chemical differences result largely from the geologic substrate, but the physical attributes (the development of horizons, the microporosity, structure, and wettability) are largely a result of the biota.

Most of the California and Oregon conifer forest soil is what Europeans call a "mor" soil, with rather distinct strata separating litter, humus and mineral soil (Klinka and others 1981). In perennial Valley Grassland soil (called "mull"), on the other hand, there is rapid incorporation of organic materials into the subsoil and consequently an indistinct separation of organic and inorganic layers within the rooting zone. Mull soils are created largely by the activity of earthworms, a critical subset of which are called anecic worms *(fig. 6)*. Anecic worms have vertical burrows and take living or dead leaves from the surface to feed upon and excrete deep in the soil (Lavelle 1988). In the conifer forest, characterized by few earthworms, earthworms have horizontal burrows. Consequently, there is little mixing between the upper soil layers, resulting in a mor structure. A majority of the species of invertebrates living in our forest soils are either fungivorous or predaceous. Very few species fill the functional role of large-bodied (> 5 mm) detritus consumer or macroshredder.

In Oregon forests the millipede Harpaphe is the principal macroshredder (Moldenke 1990). In northern California ponderosa pine forests it is the spirobolid millipede (Moldenke 1992). These two keystone species regulate the rate of initial shredding of fallen leaf resources. The more common the millipede, the thinner the litter layer becomes and the faster it is metamorphosed into humus. Our own investigations throughout the Northwest have shown that macroshredder populations decrease along a latitudinal gradient along the West Coast conifer belt of North America: California has significant populations of both earthworms and millipedes;

[5] Unpublished data on file at Department of Entomology, Oregon State University, Corvallis, OR 97331.
[6] Unpublished data on file at Department of Entomology, Oregon State University, Corvallis, OR 97331.

Oregon has dense populations of millipedes but scant earthworms; mainland British Columbia possesses few millipedes and no earthworms; Alaska has no macroshredders at all. The litter layer builds up more rapidly as you go north, because of the absence of macroshredders. In Alaska, for example, litter decomposition is so slow under conifer forests that as the forests age, the insulating litter layer passes a critical point and permafrost results. Shredding of forest floor litter in Alaska is left only to the microshredder mites and springtails, and, as a consequence of slower activity, much of the ecosystem nutrient supply becomes immobilized in the permafrost and forest growth becomes extremely slow (Flanagan and van Cleve 1977).

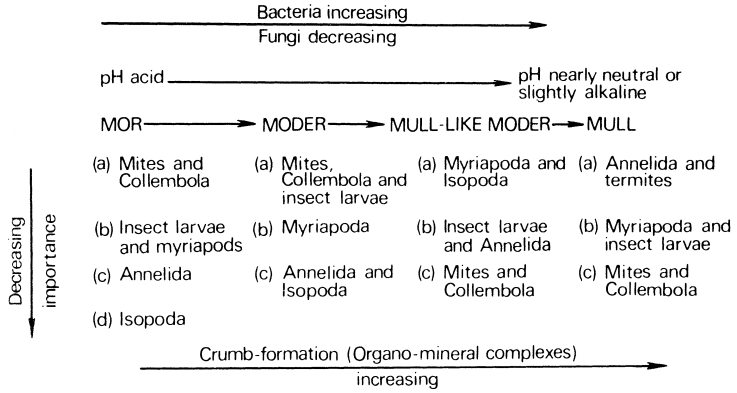

Figure 6—Soil categories, pH, and biota responsible for soil structure (Wallwork 1970).

The Big Tree and the Tiny Springtail: Physical Size Is Not Necessarily an Adequate Measure of Importance

In the French Alps, oak forests growing on clay soils are tall, provide good timber, grow vigorously throughout the year, produce large annual crops of leaves that are shed in the fall, and are associated with soils characterized by a thin litter and a thick humus layer (Kilbertius and Vannier 1981). Oaks on sandy soils, however, are stunted, grow few leaves during an annual season, and are associated with soils with deep litter and very thin humus layers.

Decomposition of oak leaves is largely limited by the presence of high concentrations of phenols. These phenols can polymerize into a macromolecule that fills the entire digestive system, as either a caterpillar ingests a green oak leaf or a millipede ingests a dead leaf. This polymerization impedes digestive enzymes from supplying nutrients and reduces consumption of additional resources (Schultz 1989).

Springtails of the genus *Tomocerus* are abundant on clay soils but are scarce on sandy soils. *Tomocerus* is uniquely able to feed on the fungi growing on the decaying oak leaves because it can prevent the phenol chain reaction from occurring. *Tomocerus* fills its midgut with inorganic clay particles from the mineral soil in which it resides during the hot dry daytime. When it surfaces in the evening to feed, the phenols are bound to the charged clay particles. This adaptation allows *Tomocerus* to thrive and indirectly benefits the entire community by detoxifying the phenols within its feces. Litter resources on clay soils are rapidly incorporated into

microbial biomass, but the insufficiency of clay particles on the sandy soils retards decomposition. Consequently a large percentage of the nutrients are locked up in the dead litter layer and are not available to the ecosystem on sandy soil (Kilbertius and Vannier 1981).

Management Applications

Can Invertebrates Be Useful?

Soil arthropod biodiversity can be useful as indirect assays of ecosystem function or productivity, or as direct estimators of ecosystem responses to differing management protocols.

Soil Compaction: A Foodweb Research Example

A number of techniques have been developed to ameliorate compacted soils. "Subsoiling" (subsurface fracture of compacted soil with restricted surface disruption) is currently being used throughout the Pacific Northwest. Studies of the impacts of subsoiling on biotic processes are generally lacking. We took soil samples from a ponderosa pine *(Pinus ponderosa)* forest in the Deschutes National Forest, Oregon, in an area that had been harvested several times over a 20-year period with partial cuts and machine piling.[7]

Table 1—*Characteristics of soil foodweb composition under ponderosa pine forests in Deschutes National Forest, Oregon. Fungal and bacterial biomass expressed as µg/g dry weight soil; density of nematodes per gram dry weight soil; density of arthropods per 25 x 25 cm^2. Arthropod density pooled from both horizons.*

Condition	Soil depth	Total fungal biomass	Active fungal biomass	Active bacterial biomass	Total nematode density	Total arthropod density
	cm	µg/g	µg/g	µg/g	number	number
Control forest	0-5	718.5	12.5	6.0	20.4	
	15-20	548.5	1.3	3.4	5.7	581
Compacted skid trail	0-5	540.7	9.2	9.4	175.6	
	15-20	349.7	1.9	6.2	45.5	556
Subsoiled skid trail	0-5	495.1	11.5	7.4	20.4	
	15-20	295.4	4.5	4.7	19.0	534

Results indicated the following scenario of events. Initial compaction caused by the use of skid roads removed approximately one-third of the soil fungal biomass *(table 1)*. Fungi inhabiting the deeper layer of soil remained largely metabolically active. This fungal demise led to the stimulation of soil bacteria by 1.5- to 2.0-fold, and an 8- to 9-fold increase in predominantly bacteria-feeding nematodes. Total

[7] Unpublished data on file at Sisters Ranger District, Deschutes National Forest, USDA Forest Service, Sisters, OR 97759.

arthropod densities remained constant *(table 1)*, but the species composition shifted from a community overwhelmingly dominated (78 percent) by fungivorous mites to one with a large component of bacterivores (11 percent) and predators (9 percent) of bacteria-feeding nematodes (*fig. 7).*

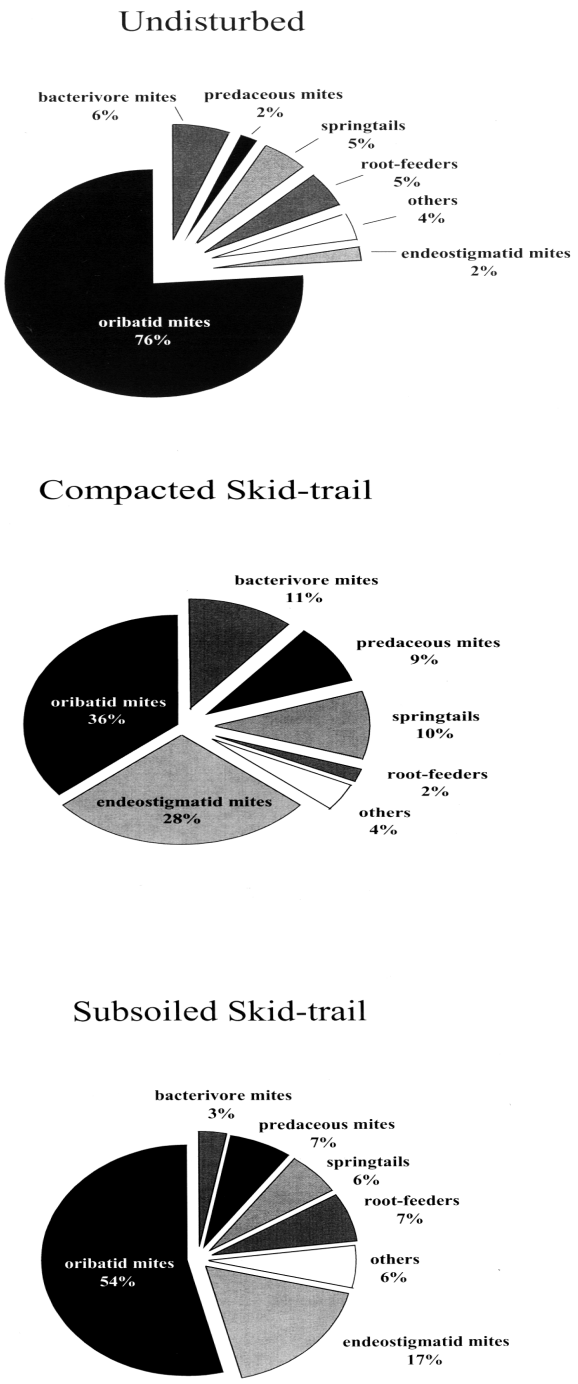

Figure 7—Arthropod community composition in undisturbed and skid-trail soils of ponderosa pine forests in Deschutes National Forest.

Subsoiling continued to reduce total fungal biomass but did enhance the active component within both soil layers *(table 1)*. This shift of increased fungal activity accompanies a decrease in active bacterial biomass and an enormous decrease in bacteria-feeding nematodes. It is likely, though we did not examine for it directly, that the active fungi in both the compacted and subsoiled cores was largely saprophytic, whereas that in the adjacent noncompacted forest floor was predominantly ectomycorrhizal. Total arthropod density did not change, but subsoiling resulted in a species composition far more similar to the fungivore-dominated noncompacted forest floor *(fig. 7)*.

We conclude from these data on skid trails and a parallel study on compacted landings that compaction: shifts the entire foodweb to one that utilizes primarily bacteria (rhabditid nematodes, gamasid mites); reduces the general size categories of soil inhabitants (rhabditids in place of tylenchids; oppioids and endeostigmatids in place of ceratozetoids; and shifts their life history towards short-lived species (oribatids shift to endeostigmatids and springtails).

In this example, arthropods provided a useful indicator for determining the effects of subsoiling as a management option, but the ability to understand the results was greatly enhanced by expanding the breadth of the analysis to include soil microbes and nematodes.

Conclusion

Arthropods open up spatial and temporal scales of examination that reveal something about how an ecosystem works--scope and knowledge that are unavailable with the usual analyses. Soil chemical and physical properties are usually examined with soil cores. But soil cores inherently contain information limited to one random point and only one instant of time. Tree-ring analysis, on the other hand, reveals different information about soils. Think of the level of understanding we need between these contrasting, conventionally explored scales.

Arthropods that live in the soil perform a number of critical soil functions. Soil is made mostly of the feces of arthropods. Microbe-grazing by arthropods mineralizes nutrients to complete the nutrient recycling process. We need to study arthropods for their own sakes, as well as for their indicator roles of additional soil processes being carried out at ever finer scales of resolution.

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Ecological Significance of Nitrogen Fixation by Actinorhizal Shrubs in Interior Forests of California and Oregon[1]

Matt D. Busse[2]

Abstract

Biological nitrogen fixation (BNF) is vital to the terrestrial nitrogen (N) budget, balancing N losses from denitrification and providing N for organism growth and maintenance. Limited information exists, however, to verify the importance of BNF by actinorhizal shrubs in moisture- and nutrient-limited forests of the interior west. A series of studies are presented that evaluate BNF by actinorhizal shrubs in central Oregon and northeastern California ponderosa pine forests and examine the effects of several forest management practices on shrub growth and potential N fixation. Nitrogen fixation rates were determined for *Ceanothus velutinus* (snowbrush) and *Purshia tridentata* (bitterbrush) in central Oregon by ^{15}N isotope dilution methods and for *Purshia* and *C. prostratus* (mahala mat) in northeast California by ^{15}N natural abundance. Both *C. velutinus* and *Purshia* were efficient N fixers in the ponderosa pine understory of central Oregon; about 85 percent of their total plant N was derived from fixation. *Ceanothus velutinus* fixed an average of 10 kg N ha^{-1} annually at sites with low to moderate shrub cover. Although this rate is substantially lower than that reported for *C. velutinus* shrub fields on the western slopes of the Cascades, it would provide enough N to offset losses from periodic prescribed fire or harvesting. *Purshia* fixed about 1 kg N $ha^{-1}yr^{-1}$ or less as an understory species at sites in Oregon and California and showed little or no stimulation from several management treatments, including overstory removal, organic residue removal, prescribed fire, and fertilization. *Ceanothus prostratus* also fixed less than 1 kg N ha^{-1} yr^{-1} at the California site. Of the three species, only *C. velutinus* produces biomass and, consequently, fixes sufficient N to replace N lost during perturbation.

Introduction

Terrestrial ecosystems gain an estimated 130-170 million metric tons of nitrogen (N) annually from biological nitrogen fixation (BNF) (Galloway and others 1995), with about 40 million metric tons, or 23-31 percent of the total, attributed to forested ecosystems (Burns and Hardy 1975). Although these estimates are admittedly crude, they underscore both the magnitude and the significance of BNF to the global N budget. At the forest stand level, high rates of BNF are most often reported for actinorhizal and leguminous plants which fix N in symbiosis with soil prokaryotes. Examples include *Alnus rubra* (red alder), 130 kg N ha^{-1} yr^{-1} (Binkley 1981); *Casuarina equisetifolia,* 12-85 kg N ha^{-1} yr^{-1} (Diem and Dommergues 1990); and *Ceanothus velutinus* (snowbrush), 20-100 kg N ha^{-1} yr^{-1} (McNabb and Cromack 1983, Youngberg and Wollum 1976, Zavitkovski and Newton 1968). By comparison, asymbiotic N fixation by free-living soil prokaryotes typically contributes 1 kg N ha^{-1} yr^{-1} or less in forest ecosystems (Jurgensen and others 1992), whereas associative N

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fixation, although controversial, has been suggested to fix up to 50 kg N ha^{-1} yr^{-1} in the rhizosphere of conifer roots (Bormann and others 1993).

Not satisfied with the intrinsic rates of N fixation, soil and plant biologists have long had the goal to enhance BNF through better understanding of its biochemistry, physiology, and ecology. Unfortunately, what can be described by a simple chemical equation, the conversion of atmospheric N to ammonium by the enzyme complex *nitrogenase*, belies a complexity and elegance that is often frustrating to the scientific community. Although a wealth of knowledge has been gained in the study of BNF, translation of this knowledge to on-the-ground improvements has been slow, particularly in temperate agricultural ecosystems. It is important to ask, therefore, whether similar obstacles should be expected in forested ecosystems. Have we as a scientific community set our expectations of BNF too high?

If BNF is indeed besieged by predictions or unrealistic expectations, they are a likely indication that the long-standing goal of providing sizable improvements in N yield has been overemphasized. Instead of asking how much additional N can be fixed by advances in breeding programs, inoculum technology, or other scientific improvements, a more apropos question is to first ask how much added N is required by forested ecosystems. For example, if providing sufficient N for tree growth is required, then, as suggested by Turvey and Smethurst (1983), "initial fixation rates should be between 50 and 100 kg ha^{-1} yr^{-1}." An alternative approach is to provide sufficient N input from BNF to meet the needs of long-term ecosystem sustainability. The value of such an approach is subtle, yet would be of considerable importance if BNF could replace N losses from prescribed fire, wildfire, denitrification, or harvesting. For example, use of prescribed fire to reduce fuel buildup can result in N losses of between 50 and 150 kg ha^{-1} in central Oregon pine forests (Landsberg 1993, Monleon and Cromack 1996, Simon 1990). Assuming a prescribed-fire program with a mean return interval of 15 years, complete replacement of N losses would be met by N fixation rates between 3 and 10 kg ha^{-1} yr^{-1}. This example accentuates a proclivity to become entranced by high rates of N fixation without first taking into consideration the basic needs of an ecosystem.

Nitrogen fixation by actinorhizal shrubs is a viable means to replace N lost by perturbation in pine forests. Actinorhizal plants fix N in symbiosis with members of the genus *Frankia*, a soil actinomycete, and are common in the understory of pine and mixed conifer forests of central Oregon and northeastern California (Benson and Silvester 1993, Schwintzer and Tjepkema 1990). These N-fixing plants are early seral, establishing after natural or anthropogenic disturbances, and often persist until shaded by overstory trees. In addition to providing fixed N, actinorhizal shrubs are acknowledged for their importance as wildlife browse species (Conard and others 1985, Guenther and others 1993), erosion control (Conard and others 1985), and improvement of soil quality (Busse and others 1996, Dyrness and Youngberg 1966, Johnson 1995). Johnson (1995) found that stands of *C. velutinus* in the eastern Sierra Nevada had higher levels of soil carbon (C) and N compared to adjacent Jeffrey pine stands. Higher levels of C and N have also been reported in central Oregon soils when actinorhizal shrubs are present in the understory of ponderosa pine stands (Busse and others 1996).

Although actinorhizal shrubs are common to the dry, pine forests of central Oregon and northeastern California, little is known of their contribution to the N budget. The objectives of my research were to compare rates of N fixation by *Purshia, C. velutinus*, and *C. prostratus* in these forests and to evaluate their response

to a variety of forest management practices. The ecological importance of BNF by these species is discussed in the context of managing understory vegetation for a variety of uses, including wildlife habitat, timber production, and soil productivity.

Materials and Methods

Actinorhizal Species

More than 200 actinorhizal species representing 8 plant families are known (Berry 1994). The following species were selected for study on the basis of their relative abundance in pine forests of central Oregon and northeastern California:

- *Purshia*, or bitterbrush, a member of the *Rosaceae* family, is found throughout pine forests and rangelands of the interior west of North America. Its geographical distribution, estimated at 138 million hectares (Hormay 1943), extends from southern British Columbia to New Mexico, and includes all 11 western states. Noted characteristics include its high value as a wildlife browse (Guenther and others 1993), intolerance to fire (Driscoll 1963, Hormay 1943), and extensive phenotypic variation (Klemmedson 1979). Nodulation was first identified by Wagle and Vlamis (1961), and ability to fix N was confirmed several years later (Webster and others 1967). Current knowledge of the N-fixing capacity of *Purshia* under natural conditions is limited. Dalton and Zobel (1977) estimated annual rates well under 1 kg N ha^{-1} in central Oregon pine forests and attributed this, in part, to low nodulation rates resulting from restrictive soil temperature and moisture.

- *C. velutinus*, or snowbrush, a member of the *Rhamnaceae* family, is also widespread in the western states and can flourish in a variety of forested habitats (see Conard and others 1985 for a review of the genus *Ceanothus*). It is a fast-growing, seral species capable of seed germination, even after several hundred years of dormancy (Conard and others 1985), and is fire tolerant with rapid resprouting typical after fire. The N-fixing ability is well characterized for pure stands of *C. velutinus*. Studies from shrub fields on the western slopes of the Cascade Range in Oregon estimate annual rates of fixation as high as 100 kg N ha^{-1} yr^{-1} (Binkley and others 1982, McNabb and Cromack 1983, Youngberg and Wollum 1976). On a drier site in central Oregon, fully stocked *C. velutinus* contributed an estimated 71 kg N ha^{-1} yr^{-1} (Youngberg and Wollum 1976).

- *C. prostratus* is a mat-forming species found on dry sites in pine forests in the Sierra Nevada and southern Cascade Range and is credited as a valuable species for erosion control (Conard and others 1985). Nitrogen fixation by *C. prostratus* was first identified by Delwiche and others (1965), yet no additional information exists with regard to its N-fixing ability in field conditions.

Measurement of BNF

Measurement of N fixation is problematic; the lack of a simple and accurate method to determine annual rates continues to be a limitation. Several methods have been used, including ^{15}N isotope dilution, ^{15}N natural abundance, acetylene reduction, N accretion, and N difference, each with their own assumptions and inaccuracies. Of

these, the ^{15}N stable-isotope methods are currently considered to have the least drawbacks for the quantitative measurement of BNF (Warembourg 1993). Their advantages rest in the ability to measure BNF cumulatively over one or more growing seasons, the high degree of precision of stable isotopes, and the capability of assessing the relative efficiency of N fixation, or the proportion of plant N derived from fixation (Ndff). Stable-isotope methods are not without their limitations, however. Several assumptions, which primarily involve the selection of the reference plant, must be satisfied to ensure an accurate measurement of BNF. Reference plants are required in order to estimate the relative proportion of plant N derived from fixation versus soil N uptake. They must have a similar rooting profile, timing of N uptake, and internal isotopic discrimination as N-fixing plants. Finding an appropriate reference plant, unless non-nodulating isolines are available, is a difficult task at best.

I used ^{15}N isotope dilution to measure BNF in central Oregon and ^{15}N natural abundance to measure BNF in northeastern California as summarized below.

Quantification of BNF by C. velutinus *and* Purshia *in Central Oregon Ponderosa Pine Stands*

Rates of N fixation by *C. velutinus* and *Purshia* were quantified at three sites on the eastern slope of the central Oregon Cascades, along a north-south transect of the Deschutes National Forest. Site characteristics are listed in *table 1*. Criteria for site selection were to provide: (i) 20 to 60 percent ground cover of *C. velutinus* in the understory of ponderosa pine and (ii) a range of ponderosa pine stand ages. Although occupancy by *Purshia* was not one of the original criteria, the species was included in this experiment given its presence at two of the sites.

Table 1—*Site characteristics for the ^{15}N-isotope-dilution study in central Oregon.*

	Swede Ridge	Walker	Mt. Jeff
Elevation (m)	1520	1470	1950
Annual precipitation (cm)	53	38	89
Site index (m)	33	23	29
Stand age in 1991 (yr)	48	125	26
C. velutinus cover (pct)	23	31	59
Purshia cover (pct)	15	9	0

The Mt. Jeff site is about 60 km north of Bend, Oregon, on the eastern flank of the Mt. Jefferson Wilderness. *Ceanothus velutinus* established after a wildfire in 1954. The site was planted to ponderosa pine in 1963 and sprayed with 2,4-D ([2,4-dichlorophenoxy] acetic acid) to delay growth of competing vegetation. The understory is dominated by *C. velutinus* and *Arctostaphylos patula* (greenleaf manzanita). The Swede Ridge site is a ponderosa pine/ *Purshia-C.velutinus*/*Stipa occidentalis* (needlegrass) plant community (Volland 1985) about 18 km southwest of Bend, Oregon. The area was logged between 1920 and 1940, and an even-aged pine stand has regenerated in the exclusion of fire. The Walker site is a mixed-

conifer/*C. velutinus*-*Castanopsis chrysophylla* (golden chinkapin) plant community about 77 km south of Bend, at the base of Walker Mountain. Understory shrubs at Walker resprouted or germinated from seed following a moderate-intensity prescribed fire in 1976. Soils at the three sites are Cryandepts, with pumice and ash parent material derived primarily from the eruption of Mt. Mazama (Crater Lake) about 7,000 years ago.

Four 25-m^2 replicate plots were installed at each site. Aqueous ^{15}N-ammonium sulfate (10 percent atom excess) was applied to the surface of the mineral soil at a rate of 5 kg ha^{-1} in late summer 1989 and again in April 1990 immediately after snow melt. Forest floor material was carefully removed from each plot immediately before application of ^{15}N and replaced after 48 h. Actively growing foliage and stems were sampled monthly from actinorhizal and reference plants beginning in May 1990, and $^{15}N/^{14}N$ and total N concentration was determined by the Stable Isotope Research Unit, Oregon State University. Thirty-one *C. velutinus* and 53 *Purshia* plants were compared. Species tested for applicability as reference plants included *Arctostaphylos*, *Ribes cereum*, and *Carex rossii*. *Arctostaphylos* was eventually chosen as the reference plant on the basis of similarity in rooting profile and synchronicity of N uptake with respect to the actinorhizal shrubs.

The relative contribution of atmospheric N to the actinorhizal plants was calculated by the equation:

$$Ndff = ([\delta^{15}N_r - \delta^{15}N_a]/ \delta^{15}N_r) \times 100 \quad (1)$$

where Ndff is the percentage of plant N derived from atmospheric N; $\delta^{15}N_r$ is the per mil ^{15}N excess of the reference plant; and $\delta^{15}N_a$ is the per mil ^{15}N excess of the actinorhizal plant. Equation (2) was used to determine total N fixed:

$$\text{Total N fixed (kg ha}^{-1}) = (\text{Ndff}) \times (\text{plant biomass}) \times (\text{plant N concentration}) \quad (2)$$

Plant biomass was determined by destructively sampling each plant within the study plots after the last sampling date in 1991. Plants were excavated for both above- and below-ground biomass. Because of the extensive rooting system of *C. velutinus* and the amount of labor required to exhume all of its fine roots, only roots >1 cm in diameter were sampled. Although omitting fine roots of *C. velutinus* led to an underestimation of plant biomass, it was considered well under a detectable range of error for total biomass. Age of each shrub was also determined by counting annual rings in order to convert total N fixed to an average annual rate.

Quantification of BNF by Purshia *and* C. prostratus *in Northeastern California Pine Stands*

Nitrogen fixation by *Purshia* and *C. prostratus* was measured by the ^{15}N-natural abundance method (Shearer and Kohl 1993) at Blacks Mountain Experimental Forest on the Lassen National Forest in northeastern California. The study area was part of a larger experiment, installed in the late 1930's through the early 1940's, designed to test the effect of harvest intensity on stand growth (Dolph and others 1995). Five levels of harvesting (100, 85, 50, 20, and 0 percent overstory removal) were compared in the original study. Two of these treatments were selected in the present study: 85 and 0 percent removal. Three replicate plots (8.2 ha) of each treatment were arranged in a randomized complete block design.

Blacks Mountain is located in the eastside pine type (Society of American Foresters forest cover type 237; Barrett and others 1980) and has an overstory dominated by mixed-age ponderosa pine and Jeffrey pine. Dominant understory plants include *C. prostratus*, *Purshia*, *Arctostaphylos*, *Artemesia tridentata*, and *Festuca idahoensis*. The climate is characterized by warm, dry summers and cold, wet winters, and the mean annual precipitation is about 50 cm. The soil is a loamy-skeletal, mixed, mesic Typic Argixeroll, about 1 m deep above basalt bedrock.

Foliage from five plants per species (*Purshia, C. prostratus, Arctostaphylos*) was collected at nine randomly selected subplots (0.05 ha) per treatment, for a total of 90 samples of each species. *Arctostapholus patula* was chosen as the reference plant based on the results from the ^{15}N isotope dilution study. Plants were sampled in early November, and every attempt was made to sample species in proximity to each other in order to reduce potential variation in natural ^{15}N abundance. Nitrogen fixation was calculated by equations (1) and (2).

Predictive equations of plant biomass, based on canopy size, were developed in order to avoid destructive sampling. Fifty-four *C. prostratus* plants were measured for crown length and width (cm) and excavated for above- and below-ground dry weight determination. *Ceanothus prostratus* biomass (g plant^{-1}) was predicted by the equation ($r^2 = 0.89$):

$$\ln(\text{biomass}) = -5.3 + 2.54\,(\ln[\text{mean crown length}]) \quad (3)$$

Purshia biomass was estimated by the ratio of mean crown length to biomass for 72 plants. Mean crown length (cm) of each shrub within the 0.05-ha subplots was measured, and total plant biomass per area was calculated using the predictive equations. The ages of 10 randomly selected shrubs per species were also determined to convert total N fixed to average annual N fixation.

Response of Purshia *to Forest Management Practices*

A logical progression after the measurement of BNF is to ascertain the effect of forest management practices on actinorhizal plant growth. To address this effect, results are presented from the "Black Bark" study in central Oregon. The study was designed to test the effect of several types of organic-residue treatments on ponderosa pine ecosystem processes. Sixteen treatments, arranged in 4 x 4 factorial treatment design, were replicated at three sites on the Deschutes National Forest, including the Swede Ridge site from the ^{15}N isotope dilution study (see Monleon and Cromack 1996 for location and stand characteristics of the other two sites). The treatments included four levels of organic matter removal after thinning: (1) whole tree removal; (2) bole removal only; (3) no removal; and (4) no thinning, in combination with four silvicultural treatments: prescribed fire; fertilization; prescribed fire + fertilization; and no treatment (control). Plots receiving prescribed fire were burned in spring 1991, and fertilizer (200 kg N ha^{-1}, 100 kg phosphorus [P] ha^{-1}, 33 kg sulfur [S] ha^{-1}) was applied in fall 1991.

A nondestructive sampling protocol was used to predict *Purshia* biomass. Fifty plants per site, encompassing a range of shrub sizes, were collected adjacent to the experimental plots and measured for mean crown length (cm) and biomass (g plant^{-1}). The resulting regression equation was:

$$\ln(\text{biomass}) = -161 + 0.115\,(\ln[\text{mean crown length}]) \quad (4)$$

with $r^2 = 0.93$. Canopy size of each shrub within three 0.01-ha subplots was measured in every plot at the end of the third growing season after treatment, and biomass was estimated using the regression equation. Total N fixed was then calculated using values for Ndff and N concentration from the Swede Ridge site as determined in the ^{15}N isotope dilution study.

Results and Discussion

BNF by C. velutinus *and* Purshia *in Central Oregon*

Plant N derived from fixation averaged 87 percent for *C. velutinus* and 83 percent for *Purshia* at the combined sites in 1990. Differences in Ndff between sites were not significant for either species ($\alpha = 0.05$), indicating a high N-fixing efficiency regardless of the level of shrub coverage or stand age. The Ndff of the young pine stand at Mt. Jeff, with 59 percent *C. velutinus* coverage, was only nominally lower than the Ndff of Swede Ridge (80 vs. 91 percent, respectively), which is a dense pine stand with only 23 percent *C. velutinus* coverage. Results for *C. velutinus* and *Purshia* compare favorably with those for other actinorhizal species. Previous studies, although limited to actinorhizal trees, have reported Ndff values of 68 to 100 percent for *Alnus glutinosa* (Beaupied and others 1990, Cote and Camire 1984, Domenach and others 1989) and 48 to 67 percent for *Casuarina equisetifolia* (Gauthier and others 1985, Parrotta and others 1994). From a practical standpoint, the Ndff values indicate that N fixation is not a limiting process in the growth of these shrubs in central Oregon pine ecosystems and that little opportunity (or need) exists to improve their N-fixing efficiency. Development of selected *Frankia* inoculum for outplanting of nursery-grown stock, therefore, would likely have minimal or no impact on BNF and plant growth rates.

Percentage Ndff was plotted as a function of shrub age in order to determine the optimum plant age for *nitrogenase* activity (*fig. 1*). If a peak age (followed by a decline in activity) could be identified, it would provide forest managers with a target period in which to regenerate shrubs by low-intensity underburning or other silvicultural methods. *Ceanothus velutinus* had consistently high values of Ndff for plants between 8 to 22 years old. *Purshia* also failed to show a clear change in Ndff with increasing plant age from 8 to 45 years, yet had considerably more variation in Ndff compared to *C. velutinus*. This variation was possibly due to inconsistent nodulation attributed to *Purshia* (Dalton and Zobell 1977, Righetti and Munns 1982, Righetti and others 1986). Evidently, ability to fix N does not decline for either species with increasing age.

Total N fixed by *C. velutinus* was significantly different between sites ($\alpha = 0.05$), ranging from 83 to 246 kg ha^{-1} (*table 2*). The highest level was found at Mt. Jeff, which has shrub coverage between 2- and 2.5-fold greater than the other sites. Annual N fixation followed the same trend: the rate increased as a function of *C. velutinus* coverage, from a low at Swede Ridge to its highest rate at Mt. Jeff. It is important to note, however, that the annual rate of 10 kg ha^{-1} yr^{-1} is a linear average for the life of the stand. The extent to which this overestimates the annual rate of a young *C. velutinus* stand and underestimates the annual rate of a stand at its peak age of growth is unclear and requires further attention. Youngberg and Wollum (1976) found *C. velutinus* plants well nodulated in the first growing season after wildfire and salvage logging in central Oregon. The maximum level of N accretion did not occur, however, until the seventh growing season after disturbance. Failure to account for

the loss of plant biomass from root mortality and leaf fall in the present study also resulted in an underestimation of annual N fixation. Production and turnover of fine root biomass can account for a large percentage of net primary productivity of conifer forests (Fogel 1990, Grier and others 1981, Ruess and others 1996), although limited information suggests that annual root production and turnover are less prolific for shrubs than for other vegetation lifeforms (Aerts and others 1992, Persson 1979). Leaf fall would not be expected to have a major impact on the estimation of N fixation because *C. velutinus* is an evergreen shrub that typically does not lose a large percentage of its foliage in central Oregon except during winters with low snowfall.

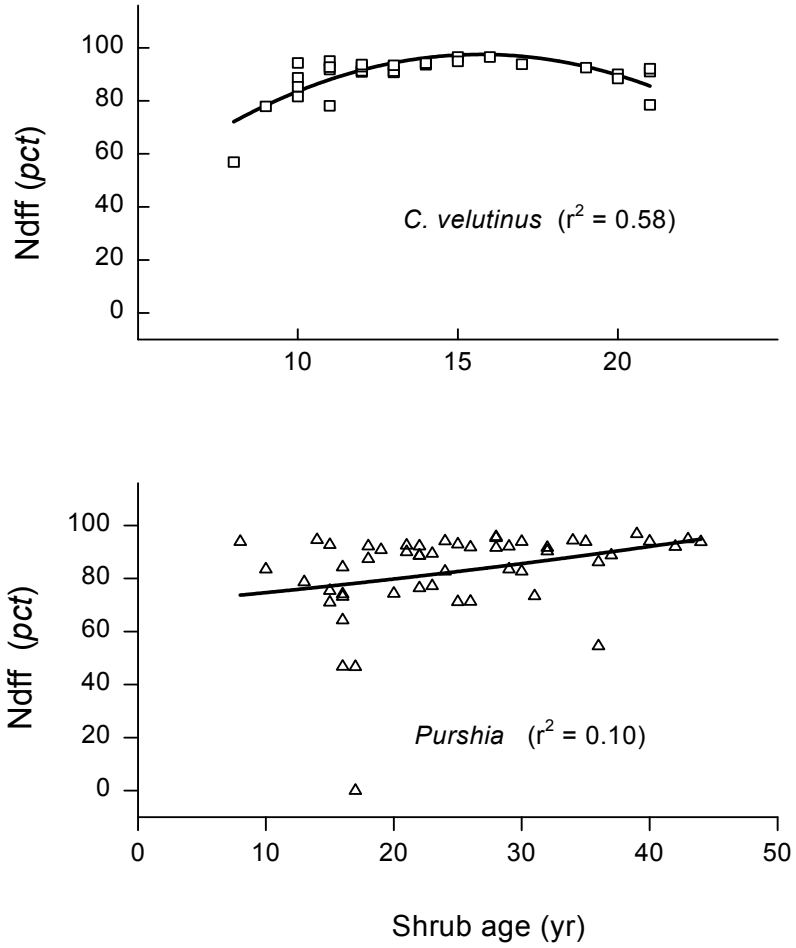

Figure 1—Percentage of plant N derived from N_2 fixation (Ndff) for shrubs of different ages.

Table 2—*Nitrogen fixing characteristics of* C. velutinus *and* Purshia *at three ponderosa pine sites in central Oregon.*

Site	Biomass[1]	Ndff[2]	*C. velutinus* Total N_2 fixed[3]	Annual N_2 fixed[4]
	Mg ha^{-1}	pct	kg ha^{-1}	kg ha^{-1} yr^{-1}
Swede Ridge	7.8 (1.4)[5]	91 (5)	83 (3)	4.0 (0.7)
Walker	11.8 (2.1)	90 (3)	165 (20)	11.1 (3.1)
Mt. Jeff	24.5 (2.8)	80 (7)	246 (26)	15.1 (1.8)
Average	14.7 (8.7)	87 (6)	165 (82)	10.1 (5.6)
Site	**Biomass**	**Ndff**	***Purshia* Total N_2 fixed**	**Annual N_2 fixed**
	Mg ha^{-1}	pct	kg ha^{-1}	kg ha^{-1} yr^{-1}
Swede Ridge	2.4 (0.6)	85 (12)	30 (4)	1.5 (0.4)
Walker	0.4 (0.4)	82 (10)	11 (5)	0.4 (0.3)
Mt. Jeff	---	---	---	---
Average	1.4 (1.4)	83 (2)	21 (14)	0.9 (0.8)

[1] Aboveground + belowground.
[2] Nitrogen derived from fixation.
[3] Total N_2 fixed = (Biomass) x (Plant N concentration) x (Ndff).
[4] Annual N_2 fixed = $\sum$ total N fixed for each shrub within a plot, divided by its measured shrub age.
[5] Values in parentheses are one standard deviation (n = 4).

The annual rate of N fixation was considerably lower for *Purshia* than for *C. velutinus* at Swede Ridge and Walker (*table 2*). The average rate of 1.1 kg ha^{-1} yr^{-1} is in general agreement with the conclusion of Dalton and Zobel (1977) that *Purshia* is a minor contributor to the total N economy in central Oregon pine stands. They estimated an annual rate of 0.057 kg ha^{-1} yr^{-1} at a ponderosa pine site in central Oregon, using the acetylene reduction method. The difference in annual rate between the two studies is not surprising given the differences in methods used and the inconsistent nodulation found in the earlier study. It should be emphasized that these findings are only relevant for *Purshia* in the understory of ponderosa pine, where low N fixation rates are most likely dictated by the slow growth rate of the shrub. This conclusion may not apply, however, throughout its entire range, particularly in nonforested lands where the faster growing, erect form of *Purshia* can be found.

Although the annual rates of N fixation for *C. velutinus* were as much as 18 times greater than those for *Purshia*, they were still substantially below the levels measured in the western Oregon Cascade Range (*table 3*). With one exception (Zavitkovski and Newton 1968), the previous studies have found up to 10-fold higher annual rates of N accretion in comparison with those in the present study. Several factors, including climatic differences, stand conditions, and methodology, can help

explain this discrepancy. For example, rainfall is considerably higher and temperature fluctuations less extreme west of the Cascade crest. The study site used by McNabb and Cromack (1983) received 250 cm of annual rainfall in comparison to an average of 60 cm for the three sites used in the present study. Growth rates and, consequently, BNF rates are higher in the wetter and milder climate west of the Cascade crest. Differences in stand conditions also contributed to the lower rate of BNF in central Oregon and are a reflection of the contrasting objectives of these studies. The earlier studies were conducted in *C. velutinus* shrub fields with the objective of predicting the maximum amount of N accretion on a disturbed site. By comparison, my objective was to measure the amount of N input by *C. velutinus* as a component of a ponderosa pine understory. Not only is plant coverage reduced from shading in the understory, but competition from overstory trees for limited site resources further reduces the potential for growth (Riegel and others 1992). Finally, caution must be used in comparing these studies because of the inconsistency of methods used to quantify N fixation. Correlation between acetylene reduction, N difference, and ^{15}N isotope dilution as measures of N fixation has never been made in forested ecosystems, and, therefore, their relative accuracy is unclear.

Table 3—*Summary of N_2 fixation by* C. velutinus.

Location	Stand condition	Cover	N_2 fixation		Source
			Annual rate	Method	
		pct	kg ha^{-1} yr^{-1}		
Western Oregon	Shrub field	19-86	0-20	N accretion	Zavitkovski and Newton 1968
Cascade Range	Shrub field	58	108	N accretion	Youngberg and Wollum 1976
	Shrub field	Not available	94-100	N accretion	Binkley and others 1982
	Shrub field	≈ 100	101	Acetylene reduction	McNabb and Cromack 1983
Central Oregon	Shrub field	70	72	N accretion	Youngberg and Wollum 1976
	Pine understory	23-59	10	^{15}N isotope dilution	This study

The N-fixing potential of *C. velutinus* and *Purshia* in central Oregon was estimated for a range of shrub coverages (*fig. 2*.). Total N fixed was calculated by multiplying aboveground biomass values measured at known coverages (Martin 1981) by the N concentration and Ndff values from the present study. All biomass

values were corrected to include an estimate of belowground biomass as determined at the Swede Ridge site (belowground biomass = 45 percent of total biomass for *C. velutinus* and 19 percent of total biomass for *Purshia*). Based on these estimates, *C. velutinus* fixes about three times more N than *Purshia* at given canopy coverage. For example, BNF at 60 percent shrub coverage is 20 kg ha^{-1} yr^{-1} for *C. velutinus* and 7 kg ha^{-1} yr^{-1} for *Purshia* for a stand age of 15 years. It should be noted, however, that it is uncommon to find *Purshia* coverage as high as 60 percent in pine understories. Seldom will it exceed 40 percent, which is equivalent to approximately 4.5 kg N fixed ha^{-1} yr^{-1}.

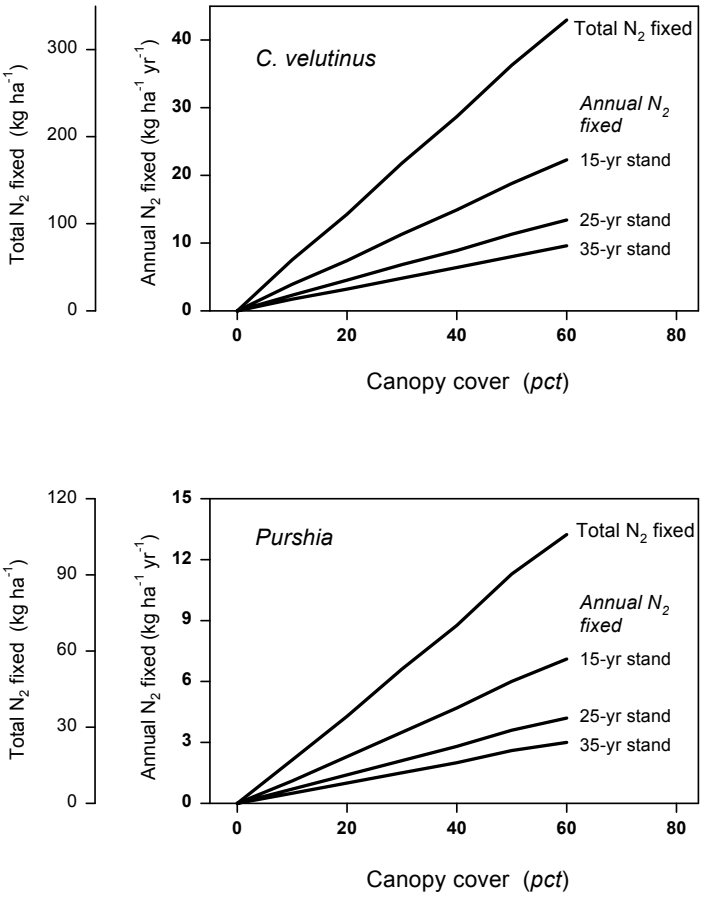

Figure 2—Nitrogen-fixing potential of *C. velutinus* and *Pushia* in the understory of central Oregon ponderosa pine stands.

BNF by Purshia *and* C. prostratus *in Northeastern California*

Preliminary results from the study at Blacks Mountain are presented in *table 4*. Shrub growth and N-fixing characteristics were compared after more than 50 years after harvesting (85 percent overstory removal) with an unharvested control. Neither species was capable of a long-term response to the more open conditions created by

harvesting. There were no significant effects of harvesting on shrub coverage, biomass, or N-fixing characteristics of either species ($\alpha = 0.05$). Average annual N fixation was well under 1 kg ha^{-1} yr^{-1} for *Purshia* and *C. prostratus* in both harvested and control treatments.

Nitrogen fixation efficiency (Ndff) for *Purshia* was lower and more variable at Blacks Mountain than at central Oregon. Whether this is a reflection of site differences in infectivity and/or effectivity of indigenous *Frankia*, or, more simply, is due to differences in ^{15}N methodologies between the two studies is unknown. It is unlikely, however, that improving Ndff at Blacks Mountain by inoculating with selected *Frankia* strains would result in measurable increases in plant biomass due to the inherent slow growth of *Purshia* in pine understory.

Table 4—*Nitrogen-fixing characteristics of* Purshia *and* C. prostratus *at Blacks Mountain Experimental Forest.*[1]

			Above + belowground				
Species	**Overstory treatment**	**Cover**	**Biomass**	**Biomass N**	**Ndff[2]**	**Total N_2 fixed[3]**	**Annual N_2 fixed[4]**
		pct	kg ha^{-1}	kg ha^{-1}	pct	kg ha^{-1}	kg $ha^{-1}yr^{-1}$
Purshia	0 pct removal	8.4 (4.1)[5]	856 (665)	6.2 (4.9)	63 (42)	5.3 (5.0)	0.3 (0.3)
	85 pct removal	6.8 (4.3)	724 (697)	5.3 (4.5)	36 (22)	2.1 (1.7)	0.1 (0.1)
	Average	7.6 (1.1)	790 (93)	5.8 (0.6)	50 (19)	3.7 (2.3)	0.2 (0.1)
C. prostratus	0 pct removal	13.3 (9.2)	1588 (1162)	11.9 (8.7)	83	9.9 (7.3)	0.6 (0.4)
	85 pct removal	14.4 (6.6)	1968 (953)	14.7 (7.1)	83	12.2 (5.9)	0.7 (0.3)
	Average	13.8 (0.8)	1778 (269)	13.3 (2.0)	83	11.1 (1.6)	0.7 (0.1)

[1] Results are preliminary.
[2] Nitrogen derived from fixation.
[3] Total N_2 fixed = (Biomass N) x (Ndff).
[4] Annual N_2 fixed = (Total N_2 fixed)/(mean shrub age).
[5] Values in parentheses are one standard deviation ($n = 3$).

The natural abundance method appears ineffective at estimating Ndff for *C. prostratus* even though all plants sampled for biomass determination were well nodulated. This species had a much higher percentage of fine roots in the upper 20 cm of mineral soil than *Arctostaphylos* had, which conflicted with the assumption that both the N-fixing plant and reference plant have the same rooting profile and access to the same pool of available N in the soil profile. As a result, total and annual

N fixation were calculated with the Ndff value determined for *C. velutinus* in central Oregon (83 percent). Using this value, in effect a "best case scenario" of N fixation, still resulted in a rate of less than 1 kg ha^{-1} yr^{-1}. Low biomass production, even at a relatively high coverage, appears to be the controlling factor limiting N input from *C. prostratus*.

Effects of Forest Management Practices

The response of *Purshia* to organic residue removal, prescribed fire, and fertilization was measured after three growing seasons on the "Black Bark" Study in central Oregon. Results are presented in *table 5* for the main factors (organic residue and silvicultural treatment) only, as there were no significant interactions ($\alpha = 0.05$) between factors. *Purshia* biomass and cover were unresponsive to the combination of treatments. The only exception was a significant decline in both biomass and cover ($\alpha = 0.05$) after prescribed fire. Of the four organic-residue treatments, thinning with minimal soil disturbance (thin, no removal) had the greatest biomass and cover. Fertilization with N, P, and S resulted in a slight, nonsignificant ($\alpha = 0.05$) decline in biomass and cover. The inability of *Purshia* to respond to fertilization is in direct contrast to the response of the herbaceous layer. Total herbaceous biomass increased an average of 500 percent during the first three growing seasons (data not shown).

Table 5—*Effect of organic residue removal, fertilization, and prescribed fire after overstory thinning on* Purshia *growth characteristics and estimated N_2 fixation.*

Treatment [1]	Above-ground biomass	Cover	Estimated N_2 fixation	New seedlings
	Mg ha^{-1}	pct	kg ha^{-1} yr^{-1}	no. ha^{-1}
Organic residue				
Whole-tree removal	0.78a[1]	7.5a	0.7a	741a
Bole-only removal	0.60a	6.6a	0.7a	924a
Thinning, no removal	1.00a	10.2a	1.1a	745a
No thinning	0.60a	5.5a	0.6a	488a
Silvicultural practice				
Control (no treatment)	1.60a	16.1a	1.6a	341b
Fertilize	1.21a	12.3a	1.2a	225b
Burn	0.10b	1.1b	0.1b	1328a
Burn + fertilize	0.05b	0.4b	0.2b	1004a

[1] For organic residue or silvicultural practice, means within a column followed by the same letter are not significantly different at the 0.05 level.

Annual N fixation was estimated using N concentrations and Ndff values determined previously at the Swede Ridge site. Prescribed fire was the only treatment that had a significant effect ($\alpha = 0.05$) on N fixation. The decline after burning was

nominal, however, considering the low average annual N fixation rate of 0.8 kg ha^{-1} yr^{-1} for all treatments. No effects due to organic residue removal or fertilization were found. The inability of *Purshia* to respond to any of the treatments, in conjunction with its overall low N fixation rate, raises doubt as to the potential for using management options to improve the biomass production or N fixation rate of *Purshia*.

Purshia is generally known for its intolerance to fire (Driscoll 1963, Horsay 1943). Simon (1990) found greater resprouting after spring burning when the fire intensity was limited by high moisture content in the O horizon and recommended using a mosaic pattern of burning to maintain a viable population of *Purshia*. In the present study, only 11 percent (274 out of 2,496 plants) of the shrubs resprouted. Seed germination, by comparison, responded more favorably to prescribed fire; seedling number was significantly greater ($\alpha = 0.05$) on burned plots than on unburned plots (*table 5*). Continued monitoring of seedling survival is required to determine whether *Purshia* biomass and N fixation will eventually benefit from a single-entry prescribed burn.

Ecological Significance of N Fixation by Actinorhizal Shrubs

The rates of N fixation by *Ceanothus* and *Purshia* in central Oregon and northeastern California are low, especially when compared with other ecosystems or other actinorhizal species. The amount of N input, which reached a maximum of 15 kg ha^{-1} yr^{-1} for *C. velutinus*, should not come as a surprise, however, considering the adverse climate and fierce competition for moisture, nutrients, and light in ponderosa pine stands (Riegel and others 1992). Whether this observation diminishes the importance of these species as N fixers depends on the criteria used to assess ecosystem needs. Replenishing N lost during low-intensity prescribed fires, for example, can easily be met by the N fixation rate of *C. velutinus* (*table 6*). Coverage between 5 and 23 percent is sufficient to replace volatilized N for a fire-return interval of 15 years.

A similar approach can be used to estimate the level of N input required to balance expected N losses from overstory harvesting. An estimated 189 kg N ha^{-1} are sequestered in 45-year-old stands of ponderosa pine in central Oregon (Little and Shainski 1995). Assuming that stands are harvested at 90 years and average N uptake between years 45 and 90 is double the rate of that during the first 45 years, then only 6 kg N ha^{-1} yr^{-1} are needed to replace the harvested N. This rate can be supplied by a low to moderate coverage of *C. velutinus*. It is unlikely that N fixation by *Purshia* would be sufficient to replace N losses from either harvesting or prescribed fire; the canopy coverage requirements would be uncharacteristically high for *Purshia* in pine understories and would present an unwanted risk of potential wildfire damage.

Shrubs are often viewed as unwelcome competitors for site resources, and their role as a fuel ladder, increasing the potential damage from wildfire, is an added concern. Should *Purshia*, *C. velutinus*, and *C. prostratus* then be managed for their role as N fixers? Or, are the costs too high? The relatively low rate of N fixation by *Purshia* and *C. prostratus* would indicate, at first glance, little benefit to pine forests of central Oregon and northeastern California. These ecosystems acquire limited exogenous inputs of N, however. Estimates of N input from dry deposition are about 1 kg ha^{-1} yr^{-1} (Dalton and Zobel 1977). Consequently, about 50 percent of the annual N addition in these ecosytems is derived from N fixation by *Purshia* and *C.*

prostratus. Potential benefits to ecosystem N levels from managing *C. velutinus* are even more tangible. Nitrogen-fixation rates for *C. velutinus* found in this study are sufficient to replace ecosystem N losses due to periodic disturbance. Developing a balance, therefore, between the concerns of wildlife habitat, overstory competition, potential fire danger, and N fixation should be considered in the management of these species.

Table 6—*Nitrogen fixation and canopy coverage requirements by actinorhizal shrubs to replace N lost from periodic disturbances.*[1]

Disturbance	Estimated N removed[2]	N_2 fixation required for N replacement[3]	Shrub coverage required to replace N	
			C. velutinus	*Purshia*
	kg ha^{-1}	kg ha^{-1} yr^{-1}	——— pct———	
Low-intensity prescribed fire	50-150	2-9	5-23	20-80
Overstory harvest	570	5	16	42

[1]Coverage requirements were determined from *figure 2* for a 15-yr-old shrub stand.
[2]Values for low-intensity prescribed fire from Simon (1990), Landsberg (1993), Monleon and Cromack (1996). Value for overstory harvest from Little and Shainski (1995).
[3]Assumes a 15-yr fire-return interval, a 90-yr rotation age for harvesting, and 1 kg ha^{-1} yr^{-1} supplied by atmospheric deposition.

It is well established that competition by shrubs for water, nutrients, and light can limit conifer growth in plantations (Conard and Radosevich 1982, Conard and Sparks 1993, Lanini and Radosevich 1986, McDonald and Fiddler 1993). Conventional wisdom suggests that control of understory shrubs is required to meet the objective of optimizing tree growth. The effects of shrub competition, however, can vary with site quality. Powers and Ferrell (1996) found that dry, nutrient-poor sites had the greatest reduction in ponderosa pine seedling growth due to competing shrubs, whereas sites with adequate rainfall and nutrient resources showed little inhibition in seedling growth. Furthermore, whether the competitive advantage provided by eliminating shrubs in young plantations lasts throughout an entire rotation is not clear. Oliver (1990) found that ponderosa pine growth was reduced by shrub competition for the initial 20 years after planting. Barrett (1982) found similar results at 20 years for naturally regenerated pine stands in central Oregon dominated by *C. velutinus*, *Purshia*, *and Arctostaphylos.* After 35 years, however, trees free of shrub competition were larger but had similar growth rates as trees grown with shrub competition (Busse and others 1996). In addition, indices of soil quality (total C, N, and microbial biomass) had increased after 35 years in the presence of shrubs. Long-term improvement of soil quality by actinorhizal shrubs (Binkley and others 1982, Busse and others 1996, Johnson 1995) could counterbalance the reductions in initial tree growth resulting from competition for site resources.

Conclusions

A series of studies were presented which evaluated BNF by actinorhizal shrubs in the understory of ponderosa pine forests. Results showed that *Purshia* and *C.*

velutinus are efficient N fixers, providing the majority of N required for their biomass production. Nevertheless, their annual N fixation rates are comparatively low, apparently controlled by the slow growth of shrubs in these moisture-limited forests. Only in the case of *C. velutinus*, which fixed an average of 10 kg ha^{-1} yr^{-1}, was N fixation considered sufficient to offset N losses from perturbation. Maintaining low to moderate coverage of *C. velutinus* (between 5 and 23 percent) is adequate to replace N lost during prescribed fire or harvesting. These results contrast with previous studies from *C. velutinus* shrub fields in the western Oregon Cascades which showed N accretion rates of about 100 kg ha^{-1} yr^{-1}. This discrepancy can be attributed to differences in climatic regime, stand conditions, and methods. The rate of N fixation in both *Purshia* and *C. prostratus* averaged 1 kg ha^{-1} yr^{-1} or less.

Actinorhizal plants serve numerous functions in forest ecosystems. They are valued for wildlife browse and habitat, erosion control, improvement of soil quality, and N fixation. They also compete for site resources and contribute to fuel loading and potential wildfire danger. Future work is needed to identify an appropriate balance between these factors in the management of understory shrubs.

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Fungal Succession and Diversity in Ectomycorrhizal Associations: A Case Study Approach[1]

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Abstract

This paper examines fungal succession among ectomycorrhiza-forming fungi by reviewing several studies. The first group of studies confirmed that common nursery fungi were replaced by other species over time. The second series of experiments showed that the root system underwent a succession of fungi as the stand aged. Fungi were apparently associated with certain parts of the root system: the youngest roots with early-succession species and the older part of the root system with later-stage species. The next series of studies showed that disturbing tree roots of existing plants changed the fungal species that formed mycorrhizas on roots of newly planted seedlings adjacent to the existing plants. Other studies showed that the removal of the surface layers of the forest floor increased both fungal species richness and abundance of fruiting bodies. However, the increase in fruiting body production was observed to occur primarily in early succession fungal species. Finally, it was shown that the youngest stands had few very abundant fungal species, with other species present in low to very low quantities. Over time, the fungal population changed with more species present, but the roots were still dominated by relatively few species.

Introduction

This review paper focuses on fungal succession among ectomycorrhiza-forming fungi. Most of the work presented will center on the fruiting bodies of the fungi that form mycorrhizas and not on the actual infected root. Deacon and Fleming (1992) and Sagara (1992) have written more detailed review papers. I have purposefully chosen these articles to represent fungal succession as seen in: newly or recently planted forests; managed forests, or what could be called plantation forests; and a forest naturally regenerating after disturbance.

Some characteristics about the ectomycorrhizal condition are well understood and taken as fact. A review of any of the major books written about ectomycorrhizal associations (Harley and Smith 1983, Marks and Kozlowski 1973) confirms that the association changes the shape of the short root and extends the effective root area of the host plant by several mechanisms. These include increased physical size of the root due to the fungus, extension of fungal hyphae into the soil, and increased number of small roots. This increase in size along with changes in anatomy may in turn lead to improved uptake of mineral nutrients and water, increased availability of

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some mineral nutrients, greater resistance to some root diseases, and more tolerance to environmental factors like high temperature and drought. However, further evaluation shows that most studies have been done with seedlings and with relatively few fungal species. Indeed, relatively few fungi have been proven to form associations in pure culture experiments. However, it is commonly assumed from location and frequency of fruiting bodies that many other fungal species do in fact form associations.

It is important to recognize that these advantages are collective and no single fungus gives all of these advantages. Instead, one particular fungus may do little more than improve the availability of phosphorus, while another may be better at protecting against temperature extremes. An interesting argument to advance is one that says that even though a single fungus may do only one thing well, the many different fungal species present on the root system of a single tree collectively confer all these benefits. This is an idea that is apparently difficult to demonstrate scientifically. At the beginning of this paper it seems appropriate to add a bit of skepticism to the topic. This is best summarized by Tacitus (54-119 A.D.): "*Omne ignotum pro magnifico*," i.e., "Anything unknown is assumed wonderful."

Succession on Planted Pine Seedlings

A good starting point for discussion is to show that succession does in fact take place among the mycorrhiza-forming fungi. Chu-Chow (1979, 1980) conducted one of the simpler studies on fungal succession in New Zealand. She went to many nurseries and to many stands in an area growing *Pinus radiata* and collected fruiting bodies and mycorrhizal roots. She plated out over 7,000 mycorrhizal root pieces and keyed out the results after using sterile inoculation techniques to synthesize known mycorrhizal pairs. Chu-Chow (1980) found that *Rhizopogon* sp. was very common nursery fungi and that "after outplanting" they were replaced by other species over time. She also found that *Amanita muscaria* was present only in the middle age to older stands and that unidentified basidiomycetes became more prominent as the forest stands became older.

Some points should be made about this study. First, this was a very exhaustive study with many roots and fruiting bodies observed in different age classes and locales. Second, it was shown that there were some species common to young plants, while different species occurred only on more mature plants. Third, with different sites, growing conditions, and probably different fungal species present, different fungi would be early-stage associates, and so on, to climax. In other words, even with the same tree species, there can be a different fungal succession on different sites with different conditions.

When discussing fungal succession, it is worthwhile to examine the idea of fungus-host specificity. The question really is just how exacting are trees and their fungal partners in the range of associations. Harley and Smith (1983) stated rather unequivocally that there are no cases in which a particular fungus is found only on one particular species of higher plant. Some species seem to be narrower in host range and others seem to be very broad. Most of early-stage fungi are not at all particular about the host species with which they associate, and to some extent this is true of the climax species. In fact, it is not unusual for the same fungus to form mycorrhizas with conifers and with associated hardwoods or woody shrubs. This is important in the concept of a refuge for the fungi when trees that are normally

dominant in an ecosystem are temporarily not available as a host. In other words, a fungus that is normally associated with a dominant conifer species may be able to form an association with a shrub, brush, or hardwood species and survive without the more usual host.

In studies of naturally regenerating slash *(Pinus elliottii)* and Monterey pines *(P. radiata)* in Australia, Lamb (1979) showed that mycorrhiza-forming fungi were neither exclusive nor specific and that they can travel considerable distances from the source of inoculum. There are at least three noteworthy findings from this study. First, the Monterey pine had fewer fungal species associated with it than did the slash pine. Second, the study used, not nursery seedlings, but natural regeneration that was as much as 5 years old. Lamb (1979) collected hundreds of specimens and noted that by the time the seedlings were 5 years old he was able to isolate as many as 42 species. Third, the distances are extreme—Lamb (1979) noted that at the Cloud's Creek site he was unable to find any mycorrhizas once he was 2 kilometers from the forest edge, but he did find them at 1 kilometer. At distances of 200 to 400 meters, there was relatively little falloff in the number of species compared to what was in the plantation.

Chu-Chow (1979) offered an opinion as to why Lamb (1979) had found relatively fewer species than she had in her work. Specifically, she criticized the strong sterilant Lamb (1979) used in his isolation work. She said that he "… used 1 percent calcium hypochlorite as a surface sterilant, but I used 0.7 percent. The recovery rate in my study dropped from 67 to 38 percent when calcium hypochlorite was increased from 0.7 to 1.0 percent. Moreover, I found that certain cultural types of *Rhizopogon* did not grow well on Hagem medium containing yeast…" (Chu-Chow 1979).

Three summary points can be made from these early articles. First, the fungi that form mycorrhizas are not exclusive or specific. Second, they may travel considerable distances. Third, laboratory technique may have considerable effect on results of the experiment.

Succession on Birch Trees

The succession of mycorrhizal fungi on tree roots has been the subject of several studies done at Bush Estate near Edinburgh, Scotland. The site had been used agriculturally for many years, when it was decided to use it for a provenance test for *Betula pendula*, and *Betula pubescens* (Mason and others 1982). The original objective of the study was to determine how well birches of different latitudes grew in the selected area. In a serendipitous fashion, Mason and others (1982) found the patterns of fungal succession on the planted birch trees to be equally interesting. Birch is ectomycorrhizal and has some of the same mycorrhizal fungi as does Scots pine (*Pinus sylvestris*). They kept track of the number of each mushroom that appeared around certain trees. The locations of fruiting bodies surrounding a *B. pedula* after 5 years are shown in Ford and others (1980). Their figures can be generalized as a bulls-eye target with the stem of the birch tree located at the bulls-eye. Furthermore, Ford and others (1980) showed that *Laccaria laccata* was located in the outermost ring of the target or at the ends of the roots, which are the youngest portion of the root system. The next inner ring showed *Hebeloma* spp.; and finally, nearest the trunk, was *Lactarius pubescens*. By the 10th year, *Cortnarius* spp. had been added to the innermost ring of the bulls-eye. Finally, in the 12th year, *Russula*

species began to appear (Last and others 1984, Mason and others 1983). Furthermore, the numbers of fruiting bodies had increased considerably over time (Mason and others 1982). There were no fruiting bodies in the first year, but in the second, fourth and sixth years, the numbers increased from 0.4 to 28 to 170 (per tree).

In summary, the root system underwent a succession of fungi as the tree aged. Fungi were apparently associated with certain parts of the root system—the youngest roots with early-successional species, while the older part of the root system had later-stage species. That is to say, the succession was based not only on the age of the whole plant, but also on the age of the individual root. These studies showed that *Lactarius* was occupying some root sites that had been previously occupied by the *Hebeloma*.

Bruns (1995) suggested a leaky garden hose as a conceptual model of infection along a root extending from the stem into the soil. At the end closest to the stem of the tree, or supply end, there is more material in the hose and more material is used as it travels along the main root. This means that the older, more proximal parts of the root system can support later-successional species and the young, mostly distal ends support only early succession species.

Ford and others (1980) concluded that the distribution of fruiting bodies could be the result of a mycorrhizal infection with the following four characteristics:

- "A tree root system that is branched, and provides a limited and non-spatially uniform medium for infection."
- "A low density *initial* infection possibly conditional upon a developing state of the host root system which results in the outward spread of the infection."
- "Spread by hyphal growth."
- "Infections by different species of mycorrhizal fungi, each of which can be viewed as non-interacting low density epidemics spreading across the root system by hyphal growth at different rates…" (Ford and others 1980).

The distribution of fruiting bodies depends on structure of the root system, and the infection being at a relatively low density and dependent on the development of the host root system. Ford and others (1980) point out that the mycorrhizas are acting like a group of spatially separated communities, not as one large interacting community. Two points are worth repeating. First, the study was done on an area that had no ectomycorrhiza-forming trees for several years before the study started, and the seed source for the trees studied was from a different geographic area. These factors should eliminate much of the natural inoculum normally found in soil. Second, the fungal species appeared over time as the plants became receptive. This implies that the inoculum was continuously available and had only to wait for the roots to be sufficiently developed for infection to take place. Because the area is relatively close to a mature forest, this seems to indicate that spores were the primary means of infection.

Fleming (1984, 1985) used the same birch plantation at Bush Estate to show how disturbing existing tree roots changed the fungal species that formed mycorrhizas on roots of newly planted seedlings. Three treatments were used in these experiments. First, six trapezoid-shaped areas were placed around two 11-year-old

Betula pendula trees (*fig. 1*). The inner and outer edges of the trapezoid were 30 and 80 cm from the tree, respectively. Around three of these areas, a trench was dug deep enough to sever all roots (35 cm deep by 10 cm wide). These trenches were then lined with plastic and refilled with soil. These trenched areas and the undisturbed areas constituted two of the treatments. In the final treatment, cores of soil, 10 cm in diameter by 8 cm in depth, were lifted and replaced with minimum disturbance. These cores were taken inside and outside the trenched areas and were repeatedly lifted and replaced throughout the study. By lifting and replacing the same core, it was possible to prevent re-invasion of the cored area by roots or by mycelium from the birch sapling. The core removal experiment was done to remove concerns about changes at the micro-site, such as nutrient or water availability, due to the plastic barrier in the trenched areas. Finally, nonmycorrhizal seedlings grown in sterile vermiculite-peat in 1-cm diameter tubes were planted in all areas. Seedlings were placed both inside and outside the trenches and in the middle of all cores.

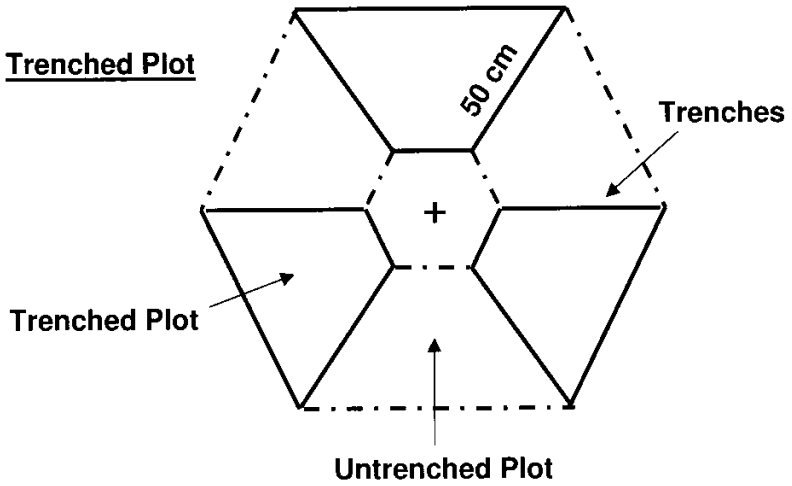

Figure 1—Arrangement of trenched (solid lines) and untrenched plots (dashed lines) surrounding a birch tree (+). Seedlings were planted in both cored areas and noncored areas within the trenched and untrenched areas (Fleming 1984).

The mycorrhizal types found on the seedlings showed that in the trenched and cored areas the bulk of the mycorrhizas was formed by early-stage fungi, whereas in the non-isolated areas, more mycorrhizas were formed by late-stage fungi. This is what would be expected if the late-stage fungi depended more on infection caused by mycelial contact and not by spores. In general, late-stage fungi have been shown to need a larger supply of carbohydrates, particularly glucose (Hacskaylo 1973). In practical terms, this means that they need to be attached to a mature host. Additionally, seedlings in the trenched study had the largest percentage of uninfected tips.

Dry weights of seedlings in the non-isolated treatment that contained the most late-stage fungi were significantly smaller than the weights of seedlings in the trenched treatment, which in turn were smaller than seedlings in the core treatment. It is tempting to make some hypothetical statements about what is causing the

differences. First, the late-stage fungi may have been using carbohydrate at the expense of seedling growth. Second, lighter infection in the trenched study probably meant less mineral nutrients and less water being supplied to the seedlings than to the core treatment. In this context, it seems likely that infecting a seedling with late-stage fungi may not lead to a more vigorous plant if the fungal partner was using carbohydrate at the expense of seedling growth.

The studies of Fleming (1984, 1985) and Mason and others (1982, 1983) help clarify two points. First, there is a distinct succession of mycorrhizal types with the younger roots or younger trees having one group of fungi present and older trees or older parts of a root system having a different group present. Second, it is possible to cause an infection by later-stage fungal species onto small plants but probably at the expense of seedling vigor.

These studies, along with those presented earlier in the paper, seem to indicate that spore infection is common among early-stage fungi. With this in mind, it seems that an absence of mycorrhizal infection would be unlikely. I can attest that Douglas-fir and ponderosa pine seedlings, grown in a clean, stainless steel growth chamber with peat and perlite growing media, routinely become infected with ectomycorrhizas. In fact, producing uninfected control plants is difficult in production nursery conditions when the nursery is in a forested area.

These studies also seem to indicate that the specific mycorrhizal fungi that inhabit the roots of trees are a function of several factors, which in turn affect the aboveground community: soil, climate, topography, age of the stand, and past history. I believe that the belowground community probably mirrors the aboveground community. In general, as a forest stand ages from seedlings to saplings to mature trees, it becomes more diverse. This diversity is not only in the vegetation present but also in the ages of the individuals within the stand. All of these factors should influence the mycorrhizal fungi that are present. Older, more complex forests should have greater diversity above- and belowground.

Succession in Mature Forests

The examples given so far have concentrated on plantations or seedlings. The remaining studies deal with older stands. DeVries and others (1995) studied five Scots pine stands in Holland. These Dutch forests have changed in recent years in that the diversity of mycorrhiza-forming fungi has declined. DeVries and others (1995) investigated whether "the cessation of former management practices like litter raking have further contributed to an accelerated build-up of a humus profile. Ectomycorrhizal fungi are sensitive to thick, nitrogen-rich organic layers." In effect, this study intended to approximate earlier practices to see if this would restore species diversity within the fungi. In each stand, litter and humus layers, including vegetation, were removed from around the Scots pines.

The removal of the surface layers increased both species richness and abundance of fruiting bodies. However, the effects on richness did not last past the first 4 years after removal. Furthermore, the increase in fruiting body production was seen to be primarily in early-succession species. De Vries and others (1995) also noted that the numbers of species were still not close to what was seen in the forest in the past and that the fungi present were not those that would have been expected in a true

succession. Finally, it was noted that many fungi, which had become rare, did not reappear in these stands.

There are two ideas to be highlighted here. The first concerns past practices being used as comparisons. Although DeVries and others (1995) do not discuss this, it seems reasonable to assume that past practices were such that they caused fungal associations different from what would have been present in an unmanaged, untouched forest. In other words, defining "normal conditions" for an area that has seen forestry/agriculture/management practiced for many years must be difficult, if not impossible. The second point concerns reasons why the treatments did not return the stand to the previously observed conditions. The authors note three reasons: absence of the appropriate inoculum, high amounts of nitrogen in the upper mineral soil, and additional nitrogen from air pollution. All three seem to be aspects of the changes seen when comparing more highly industrialized areas to earlier, less developed areas.

The final study to be discussed concerns stands naturally regenerated after fires. These stands are located in or near Wood Buffalo National Park in Alberta, Canada. Visser (1995) found stands that were 6, 41, 65, and 122 years old. She notes that the pH, soil texture, and bulk densities were all similar and that the soils on this site were degraded eutric brunisols developed on calcareous, lacustrine, and very fine sands to silts. Although all the stands were jack pine (*Pinus banksiana*), they differed by density of stems, basal area, and biomass. This was especially true for the youngest stand. Visser collected fruiting bodies and took soil cores to examine the roots, evaluating up to 900 root tips in each sample.

Visser found some definite trends in what species were present and when they first appeared. For example, *Coltricia perennis* was not found in the older stands, whereas species from *Russula* were not seen in the youngest stand. This is the same trend seen in earlier studies done on planted forests.

A second aspect of the study needs some preliminary information. Three distributions have been used for species abundance curves (Ludwig and Reynolds 1988). Two of these can be seen in the species-relative abundance curves for ectomycorrhizal root tips in these jack pine stands. The first is the geometric distribution, and it is characteristic of a species-poor community. This distribution represents a situation in which there are a few but very abundant species present. Visser's results show the ectomycorrhizal root tips on the 6-year-old stand had a geometric distribution. The 6-year-old stand had a few very abundant species (*Suillus brevipes*, 77.4 percent) with other species present in low to very low quantities. Furthermore, this young stand had 12 mycorrhizal types present. The geometric distribution is considered to be characteristic of a community that has a critical and very limiting resource. This limiting resource is used in a hierarchical fashion with a single dominant species using the largest amount of the resource. A lengthy dialog could ensue as to what exactly is the limiting resource and what causes it to be changed over time. Two interesting candidates for the limiting resource seem likely: having an adequate amount of spores or inoculum of the mycorrhiza-forming fungus, and having enough trees or, more specifically, tree roots.

Visser identifies the second distribution as the lognormal. A lognormal distribution of species takes place when there is interaction between several approximately independent factors (May 1981). In contrast to the 6-year-old stand, the 122-year-old stand had four species represented on between 10 and 20 percent of

the tips, and a further six species on between 3 and 10 percent of the root tips (*Suillus brevipes*, 5.3 percent). This stand had 27 mycorrhizal types present. Visser lists canopy closure, alterations in host physiology, and changes in the soil environment as the interacting, more or less independent, factors. On a conceptual basis this closely parallels what was seen in the birch succession study discussed earlier. The resource of most concern is the root system of the tree. It seems clear that the physiology of the trees would change over time. For example, more and perhaps different carbohydrates would be available, while hormones, vitamins, and other growth factors would change in abundance and availability. Furthermore, as Visser points out, the soil would be altered by the addition of leaf and root litter. All of these factors would lead to many different physical and physiological environments. This means that different environments could be used by different fungi, leading to a richer, more diverse fungal community.

There are a few points worth emphasizing. First, this study was done in a virgin forest and with natural regeneration. The forest was disturbed, but it was disturbed by a natural agent: fire. Second, the trees seem able to reestablish the mycorrhizas after disturbance. This may be because there are refuges for the fungi, characteristic of later stages available on brush species that regenerate by sprouting. Finally, it should be noted that part of this study was done by counting the actual infected tips, not by counting fruiting bodies.

A good discussion might entertain the hypothesis that fungi associated with fire-adapted species like jack pine would have a fundamentally different reproduction strategy than species found in later stages of forest succession. I want to make this point because one purpose of this paper is to point out some concepts that seem to contradict logical explanation. Part of the problem is that there can be many different environments present in soil within a very short distance. This means that there are many different possibilities for succession. Succession in ectomycorrhizal associations is not a subject that can be easily summarized. Indeed the same can be said for much of the mycorrhizal association. As was pointed out earlier, different fungi confer different advantages and many different fungi can form associations with many different woody plants. As a consequence, overly simplistic answers may be wrong, or may not take into account the complexity of different ecosystems or the vast array of associations that can plausibly form. However, it does seem probable that any disturbance will cause only a temporary disruption of the mycorrhizal community.

Several problems are fairly unique to the study of mycorrhizas and their hosts. The most important is that the fungal half of the relationship does not necessarily fruit in any regular or predictable fashion. Identification of most fungi that form mycorrhizas is based on the fruiting body; an enduring difficulty is the ability to identify the fungal agent involved. The logical answer is to evaluate the mycorrhiza, not the fruiting body. The problem with this idea is the very nature of root systems, where an infected short root, usually a few millimeters long, is hidden in the soil. Additionally, it is very difficult in a forest to tell which root belongs to which plant. Finally, even the gentlest excavation of a root system can destroy many, if not all, of the mycorrhizal roots. However, new methods using DNA are making this type of study more feasible, yet still not simple.

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Influence of Forest Harvesting on Soil Organisms and Decomposition in Western Washington[1]

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Abstract

Clearcutting has created a fragmented landscape with many forest edges in the Pacific Northwest—a condition different from that created by natural disturbances. Recently ecosystem management has been proposed as an alternative method to clearcutting whereby coarse woody debris (CWD) (snags and logs) and green trees are retained to provide important structures. Knowledge of how harvesting practices affect soil microbiology is far from complete. The objectives of this paper are to discuss (1) the influence of clearcutting on respiration of forest floor/soil and coarse woody debris and invertebrate density; (2) the influence of forest edges on litter decomposition and nitrogen release, soil moisture, and fruiting of epigeous mycorrhizal fungi; and (3) the influence of ecosystem management practices on soil moisture and temperature, microbial biomass, and Douglas-fir seedling growth and survival in western Washington. Sites on the Olympic Peninsula and in the Puget Sound region were studied. Clearcutting influenced microclimate, soil respiration, decomposition, nitrogen release, and invertebrates to varying degrees, but the mild environment of this area tended to dampen the effect. Decomposition and nitrogen release, soil moisture, temperature, and the patterns of fruiting of mycorrhizal fungi are strongly influenced by forest edges. Ecosystem management, specifically green-tree retention treatments, generally created an intermediate microclimate between forests and clearcuts, but did not strongly influence soil microbial biomass. Douglas-fir seedlings were successfully grown under tree canopies for 1 year, but survival and growth need to be evaluated over time.

Introduction

Forest harvesting has dramatically changed the forest landscape in the Pacific Northwest region of the United States. Recent clearcutting has created a fragmented landscape consisting mostly of relatively young forests and clearcuts with kilometers of edges between cutover and forested lands *(fig. 1)*. Portions of the Pacific Northwest landscape have always supported younger forests because of natural disturbances such as fire, wind, flooding, volcanic eruptions, and insects and diseases. However, natural disturbances create patterns different from clearcutting. For example, fire causes mosaic patterns on the landscape, and even if trees are killed, they are not removed from the site.

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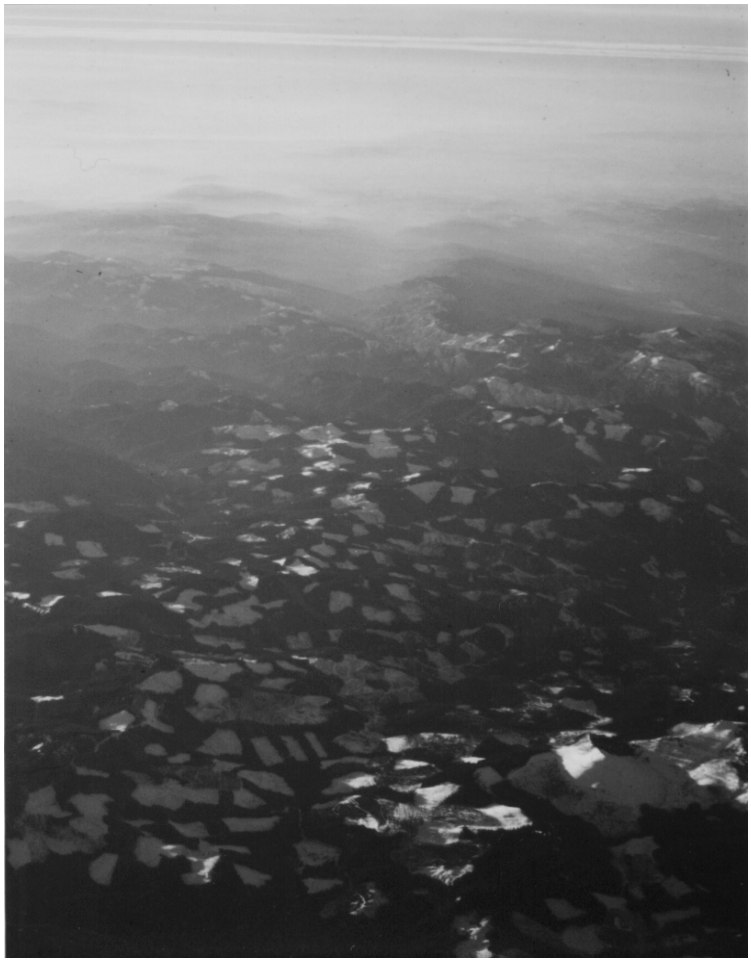

Figure 1—Aerial view of clearcuts in the central Oregon Cascades. Note the varieties of shapes and sizes and the many forest edges.

Studies of forest fragmentation and edge effects have been conducted, investigating wildlife (Walters 1991), microclimate and vegetation (Chen and others 1992), ectomycorrhizal roots (Harvey and others 1980), and mushroom diversity and abundance (Saari 1993). In addition to being influenced directly by the changed physical environment at forest edges, mycorrhizal fungal populations may also be influenced indirectly by changes in the foraging behaviors of small mammals that feed on fungi, such as the red-backed vole (Walters 1991). Belowground properties such as soil temperature and moisture, pH, decomposition rates, tree root abundance and fungal species and populations are also likely to be strongly influenced by edges.

Extensive clearcutting has been challenged as an ecologically sound silvicultural technique in the Pacific Northwest because it changes forest composition and structure, thereby altering wildlife habitats. It also increases the potential for soil erosion and siltation of salmon streams. Invertebrate and soil microbial populations (including mycorrhizal fungi), and decomposition and nutrient cycling processes in the forest floor and mineral soil are also changed by clearcutting (Abbott and Crossley 1982, Abbott and others 1980, Amaranthus and others 1989, Barber and Van Lear 1984, Borchers and Perry 1992).

Ecosystem management has recently been proposed as an alternative to clearcutting (FEMAT 1993, Franklin 1992, Swanson and Franklin 1992). Thinning and retention of green trees as well as retention and recruitment of standing dead and downed coarse woody debris (CWD) are important components of ecosystem management. CWD is a dominant feature of old-growth forests in the Pacific Northwest (Agee and Huff 1987, Harmon and Chen 1991, Harmon and others 1986) and is purported to promote ecosystem stability, habitat diversity, and long-term productivity in the Pacific Northwest (Franklin 1992, Swanson and Franklin 1992). Forest managers are urged increasingly to leave CWD at the time of harvest to provide critical habitat components for a variety of vertebrate and invertebrate organisms. In addition, CWD may help maintain the productive capacity of the soil by increasing soil moisture levels, moderating soil surface temperatures, inhibiting surface erosion, and providing a source of inputs for nutrients and soil organic matter (Edmonds 1991, Franklin and Maser 1988, Harmon and others 1986).

Thus, harvesting practices are at the center of a great deal of debate. Retention of live trees and CWD may have substantial effects on soil processes, but we need experiments to find out what these effects are before we can conclude whether they have implications for long-term productivity. This paper compiles data from a number of western Washington studies investigating the influence of harvesting on the soil ecosystem. Some studies are experimental, whereas others are more anecdotal with little or no replication. Taken collectively, however, they may provide inferences. The objectives of this paper are to discuss (1) the influence of clearcutting on respiration of forest floor/soil and coarse woody debris and invertebrate density; (2) the influence of forest edges on litter decomposition and nitrogen release, soil moisture, and fruiting of epigeous mycorrhizal fungi; and (3) the influence of ecosystem management practices on soil moisture and temperature, microbial biomass, and Douglas-fir *(Pseudotsuga menziesii)* seedling growth and survival.

Materials and Methods

Clearcut Studies

Study Sites

Two clearcuts and two forested sites were studied on the western and eastern sides of the Olympic Peninsula *(fig. 2)*. The forested site on the western side was pristine old growth and was located in the Twin Creeks Research Natural Area, Olympic National Park, at a distance of 32 km from the Pacific Ocean just inside the park boundary. Climate is generally moderate, and the average annual temperature is 9.3 °C at the Hoh Ranger Station. Annual rainfall averages approximately 3,500 mm.

The overstory vegetation is an uneven-aged forest dominated by western hemlock *(Tsuga heterophylla)*, Douglas-fir, and western redcedar *(Thuja plicata)*. The overstory on the older terraces adjacent to the Hoh River are dominated by Sitka spruce *(Picea sitchensis)*, western hemlock, and western redcedar. However, on the slope between two terraces, the location of this study, Douglas-fir dominates. Douglas-fir trees in the West Twin Creek watershed ranged in age from 237 to 635 yr, western redcedar from 123 to 600 yr, and western hemlock up to 262 yr (Edmonds and others 1993). Understory vegetation is dominated by sword fern *(Polystichum munitum)* and Oregon oxalis *(Oxalis oregana)*. Forest floor depth was typically 5 cm, and soils were Inceptisols.

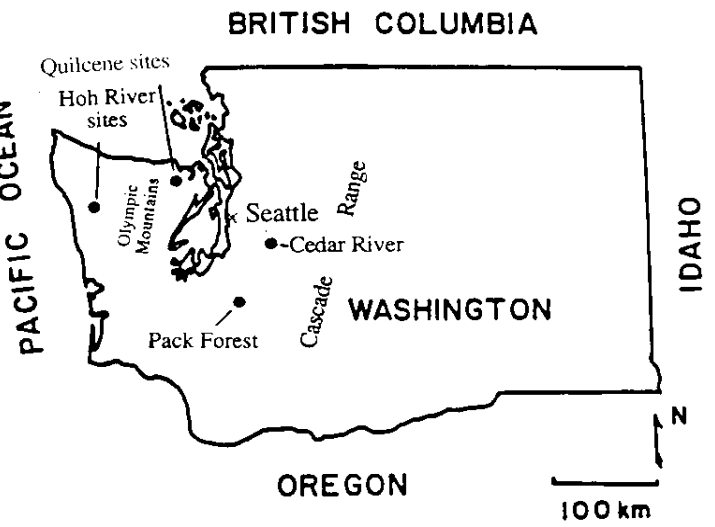

Figure 2—Study sites in Washington.

The adjacent clearcut site was located 2 km from the old-growth site on Washington State Department of Natural Resources land, just outside the boundary of Olympic National Park. Elevation in the clearcut ranged from 300 to 340 m; slope was 38 percent and aspect was 225°. Overstory vegetation before harvest was similar to the forested site, and the understory was dominated by sword fern and Oregon oxalis. The stand was harvested in 1988 and 1989 and replanted to Douglas-fir in 1992. Post-harvest vegetation was dominated by thistle (*Carduus* spp.), trailing blackberry *(Rubus ursinus)*, sword fern, and several unidentified composites.

Clearcut and forested sites on the eastern side of the Olympic Mountains were located approximately 5 km south of Sequim Bay in the USDA Forest Service Quilcene Ranger District of Olympic National Forest. Mean annual temperature for Quilcene is 10.1 °C (Henderson and others 1989). Annual precipitation is 762 mm. Elevation at the forested site ranged from 290 to 320 m, and slope was 25 percent. The clearcut site ranged in elevation from 305 to 320 m, and slope was 5 percent. These sites had an overstory dominated by Douglas-fir, western hemlock, and western redcedar, with an understory of sword fern and salal *(Gaultheria shallon)*. The forested site had been selectively cut at an unknown time, and trees were in the 80- to 90-year-old age class. The clearcut site was harvested in 1989 and 1990 and replanted with Douglas-fir seedlings. Regeneration on the clearcut site included salal and a number of composite species.

Procedure for Measuring Respiration

Carbon dioxide evolution from the forest floor in the forest, mixed forest floor/soil in the clearcut, and CWD in both the forest and clearcut were determined only on the sites in the Hoh River Valley. Respiration rates were determined using the soda lime trap method (Marra and Edmonds 1994, 1996). CWD decay classes were assessed using the system of five decay classes based on structural characteristics outlined in Maser and Trappe (1984). Nurse logs (logs with tree seedlings) were avoided to minimize the influence of root respiration. Decay classes 1 and 2 (least decomposed) were classified as a single decay class (1-2) for the

purposes of this study. Respirometers, constructed of white plastic buckets (20.3 cm in diameter) with the bottoms removed *(fig. 3)*, were installed on three decay classes of logs (1-2, 3 and 5) of two species (Douglas-fir and western hemlock) as well as on the forest floor or soil in the clearcut. No species identification of logs in decay class 5 was possible. Log diameters ranged from 28 to 163 cm.

Figure 3—Static carbon dioxide trap on a log in the clearcut in the Hoh River Valley, Washington.

Respirometers were installed in July and August of 1991, and measurements began in October 1991. Three replicates were used for each category. Respiration from a total of 30 logs and the forest floor in the old-growth forest and 30 logs and the soil in the clearcut was measured every 4 weeks from October 22, 1991 to November 19, 1992. Respiration was expressed as g CO_2 m^{-2} day^{-1}.

Procedure for Sampling Invertebrates

Three replicate western hemlock logs in decay class 3 and forest floor and mineral soil samples were taken from the forested and clearcut sites at both the Hoh and Quilcene sites (Marra 1995). Samples were taken in May, June, and August 1992. Log disks approximately 20 cm wide were removed with a chainsaw, placed in plastic bags, and transported to the laboratory, where they were cut into smaller pieces with a bandsaw (approximately 10 cm^3). Forest floor and soil samples were approximately 20 cm x 10 cm x 5 cm deep. After initial hand sorting for macroinvertebrates, Berlese high-gradient extraction was used for the smaller invertebrates. Samples were gradually extracted over a 2-week period. Methods were adapted from Moldenke (1994). Densities of mites, springtails, and beetles were expressed as number of individuals per cubic meter for logs and per square meter for forest floor in the old-growth forest and the forest floor/soil in the clearcut.

Statistical Analysis

Student t tests were used to determine whether significant differences ($p < 0.05$) occurred in respiration rates and invertebrate densities in the various substrates between clearcut and forested sites (Wilkinson 1989).

Forest Edge Studies

The influence of forest edges on needle litter decomposition and nitrogen release was studied at Pack Forest, while the influence on microclimate and fungal fruiting patterns was studied in the Cedar River Watershed *(fig. 2)*.

Study Sites

The site at the Charles Lathrop Pack Forest of the College of Forest Resources, University of Washington, was located approximately 100 km south of Seattle at an elevation of approximately 400 m (Edmonds and Bigger 1984). Average annual temperature and rainfall at Pack Forest are 9.2 °C and 1040 mm, respectively. A small clearcut (1.3 ha) was located on a low-productivity site (Class IV; King 1966) with a 30 percent southwest slope. The soil is a rocky, thin Inceptisol derived from residual andesite. The forest before cutting consisted of 53-year-old Douglas-fir with a salal understory. A second small clearcut (3.4 ha) was located on a slightly higher-productivity site (Class II; King 1966). Soil is a silty Inceptisol on relatively level terrain. The Douglas-fir forest also was 53 years old at the time of cutting with an understory dominated by sword fern. Stands were cut in February and March 1980 and the litter decomposition study was established shortly thereafter. The clearcuts were adjacent to each other.

The Cedar River sites were located approximately 70 km southeast of Seattle at an elevation of approximately 450 m. Annual rainfall averages about 1,900 mm, with precipitation occurring predominantly from October through May, and average air temperature is 8.5 °C. Soils are mostly Inceptisols and are derived from glacial outwash, glacial till, and volcanic ash. Naturally regenerated second-growth forests in the area are dominated by Douglas-fir and western hemlock and are 60-70 years old. Western redcedar, Pacific silver fir *(Abies amabilis)*, and red alder *(Alnus rubra)* are also present. Common understory species are sword fern, Oregon grape *(Berberis nervosa)*, salal, and huckleberry (*Vaccinium* spp). The 2-to-5 year-old clearcuts selected for study were replanted with Douglas-fir and western redcedar. Natural regeneration of red alder and western hemlock also occurred. Other common species in clearcuts were salal, huckleberry, Oregon grape, salmonberry, sword fern, fireweed *(Epilobium angustifolium)*, foxglove *(Digitalis purpurea)*, and two species of blackberry (*Rubus* spp.).

Litter Decomposition and Nitrogen Release

Litter decomposition was determined at Pack Forest by collecting green needle litter from freshly downed trees after clearcutting. Air-dried needles (equivalent to 13.08 g oven-dry mass) were placed in 25 cm x 18 cm nylon litterbags (1 mm mesh) in the clearcut and at forest edges. Litterbags were placed inside the forest 5 m from the southwest-facing edge of the low-productivity clearcut and 20 m inside the east-facing edge of the high-productivity clearcut. Five litterbags were collected after 1

and 2 years from duplicate plots. The dry mass (75 °C) remaining was determined. Total nitrogen in the initial needles and after 2 years of decomposition was determined using the wet oxidation method (Parkinson and Allen 1975) and a Technicon Autoanalyzer 11.[4]

Influence of Forest Edges on Soil Moisture and Mycorrhizal Fungi

Three replicate sites involving clearcut/forest edges were selected in the Cedar River Watershed. Transects were established at each site that extended from the edges into both the forest and the clearcut on the north, east, and west sides. Clearcut sizes were 8, 73, and 82 ha, and the topography was relatively level. Rectangular plots (1 m x 4 m) for soil moisture and fungal sporocarp sampling were established at 16 locations along each transect, ranging from 240 m deep into the forest to 90 m into the clearcut. Moisture contents of the forest floor (3-4 cm deep) and upper mineral soil (to a depth of 6-7 cm) were determined gravimetrically. Epigeous fungal sporocarps and moisture in the forest floor and soil were sampled twice during autumn 1995. Autumn is the optimal time for fruiting for most species in this area. Specimens were identified to genus and dry biomass determined by drying to a constant weight at 45 °C.

Statistical Analysis

Student *t*-tests were used to determine if significant differences ($p < 0.05$) occurred in decomposition rates and nitrogen release between clearcuts and forest edges (Wilkinson 1989). No statistical tests were conducted for soil moisture and fruiting body biomass but standard deviations are presented.

Ecosystem Management Studies

Study Site and Treatments

Studies involving green-tree retention were also established in the Cedar River Watershed *(fig. 2)* (Barg 1996). Treatments consisted of uncut 60- to 70-year-old second growth forest, partially cut sites, and clearcut sites with three replicates of each treatment. A 200-square meter plot was established at each site, with all sites within 8 km of each other. The harvested sites were cut 2 to 5 years before research began. The clearcut and forested sites are described in the forest edge section above. The three green-tree retention areas were 19, 20, and 24 ha and had 30, 20, and 30 trees/ha, respectively. Tree density in the forested sites ranged from 204 to 408 trees/ha. Understory vegetation in the green-tree retention areas had species that also occurred in the clearcut, but western hemlock was a more important component than in the clearcut sites.

Microclimate

Current, maximum, and minimum air temperatures were recorded in each plot every 2 to 4 weeks between July 1994 and June 1995 using a Taylor max-min

[4] Mention of trade names or products is for information only and does not imply endorsement by the U.S. Department of Agriculture.

thermometer that was mounted 1 m above the ground in a white shelter box facing north. Soil temperature was measured at 48-min intervals at 10-cm depth using Hobo-Temp dataloggers. Soil moisture was determined gravimetrically (oven dried at 104 °C for 24-48 hours) at 1- to 2-month intervals from July 1994 to August 1995.

Soil Microbial Biomass

Mineral soil samples to a depth of 10 cm were taken from each plot using a 6-cm diameter soil corer at each sampling time in July, September, and October 1994 and March, May, and June 1995. Soil microbial biomass, expressed as mg C per gram dry soil, was determined using the fumigation-incubation method (Jenkinson and Powlson 1976) with modifications (Barg 1996).

Seedling Survival and Growth

Douglas-fir seedlings were planted in three circular plots throughout one green-tree retention site and an adjacent clearcut. Within each plot, the seedlings were planted in four transects radiating at distances of 0.5, 2.0, 3.5, 5.0, 6.5, and 8.0 m from the plot center. Seedling diameters and heights were measured after planting in April 1994 and again in October 1995. Seedling survival was recorded.

Statistical Analysis

ANOVA for repeated measures was used to determine if significant differences ($p < 0.05$) occurred in microclimate variables and microbial biomass among treatments and in seedling growth in green-tree retention and clearcut treatments (SAS 1989).

Results and Discussion

Influence of Clearcutting on CO_2 Evolution

Studies comparing soil or forest-floor respiration in forested and clearcut environments have reported increases, decreases, or no significant differences due to clearcutting in respiration rates (Ceulemans and others 1987, Ewel and others 1987, Fernandez and others 1993, Hendrickson and others 1989, Luizao and others 1992, Mattson and Swank 1989, Nakane and others 1986, O'Connell 1986, Vermes and Myrold 1992). We found no significant differences in respiration rates between the clearcut and the nearby old-growth forest for the forest floor/soil *(table 1)*. Forest floor and soil were mixed in the clearcut. The average daily respiration rate for the forest floor in the old-growth site was 5.50 g CO_2 m^{-2}, which was similar to the soil respiration rate in the clearcut (5.22 g CO_2 m^{-2} day^{-1}). Vermes and Myrold (1992), on the other hand, found that forest floor respiration rates in a mature coastal western hemlock forest in Oregon were double those in a clearcut site. However, they found no differences between clearcuts and forests at Douglas-fir sites in Oregon. In contrast, Maybury (1993) found soil respiration rates to increase after clearcutting of Douglas-fir at Pack Forest, Washington.

Carbon dioxide evolution from the forest floor is the sum of microbial and root respiration, and clearcutting affects both. Reduction in root biomass after harvesting causes root respiration to decline. The effect of harvesting on microbial respiration is

more variable and difficult to predict, which probably explains the often-conflicting influence of clearcutting on forest floor respiration, as reported in the literature. For example, on hot dry sites, post-harvest conditions may inhibit microbial decomposition as well as decreasing root respiration. On the other hand, increases, due to harvesting in cooler climates, in forest floor temperature and moisture may increase microbial respiration and more than compensate for the loss of root respiration. The moderate temperature and moisture regimes in the western Olympic Mountains probably explain why we found no significant differences in respiration between the forest and clearcut sites.

Table 1–*Average forest floor, soil, and coarse woody debris respiration (g CO_2 $m^{-2}day^{-1}$) in an old-growth forest and nearby clearcut in the Hoh River Valley, Washington. Respiration was determined every 4 weeks from October 1991 to November 1992.*

Category	Old-growth forest	Clearcut
Western hemlock logs	4.37 (1.95)[1]	4.05 (1.66)
Douglas-fir logs	3.23 (0.86)	2.94 (1.05)
Decay class 1-2 logs	4.46 (2.05)	3.71 (1.87)
Decay class 3 logs	3.23 (0.69)	3.37 (1.06)
Decay class 5 logs	4.07 (0.66)	4.28 (0.74)
Forest floor/soil	5.50 (0.39)	5.22 (1.26)

[1]Standard deviations in parentheses.

There were no significant differences between the forest and the clearcut for CWD, much as there were no significant differences between the forest floor and the soil *(table 1)*. Respiration rates of Douglas-fir logs averaged 3.23 g CO_2 m^{-2} day^{-1} in the forest and 2.94 g CO_2 m^{-2} day^{-1} in the clearcut, whereas western hemlock logs averaged 4.37 g CO_2 m^{-2} day^{-1} in the forest and 4.05 g CO_2 m^{-2} day^{-1} in the clearcut *(table 1)*. There were also no significant differences in respiration rates for the different decay classes of CWD between the clearcut and the forest *(table 1)*. Other researchers have noted that decomposition of small diameter wood in clearcuts may be inhibited in hot, dry environments (Barber and Van Lear 1984, Erickson and others 1985). Moisture does not appear to be an important factor limiting CWD decomposition in the Olympic Peninsula, and logs in the clearcut remained moist even during the summer (Marra and Edmonds 1996). However, there were some seasonal differences in patterns of CO_2 evolution in the clearcut and old growth (Marra and Edmonds 1996).

Influence of Clearcutting on the Density of Invertebrates in Soil and CWD

The most abundant invertebrates observed in the forest floor or soil in the clearcuts and forested sites on the Olympic Peninsula were mites and collembola. Clearcutting influenced mite populations. Mite density was significantly lower in clearcuts (4,472 m^{-2}) than in the forests (6,694 m^{-2}), but there was no significant difference for collembola (1,234 m^{-2} in the forest and 2,185 m^{-2} in the clearcut soils) *(table 2)*. Beetles were the most abundant insect order with significantly lower populations in the clearcuts than in the forests (78 and 120 m^{-2}, respectively). There were no significant differences in mites, collembola, and beetles in the CWD

between clearcuts and forests. Densities were 52,272 and 50,358 m^{-3} for mites, 24,053 and 47,394 m^{-3} for springtails, and 2,375 and 3,179 m^{-3} for beetles in the forests and clearcuts, respectively.

Table 2—*Average density of mites (Acari), springtails (Collembola), and beetles (Coleoptera) in forest floor/soil and decay class 3 western hemlock logs in clearcut and forested sites on the Olympic Peninsula, Washington.*

Treatment	Acari	Collembola	Coleoptera
		Forest floor/soil (No. m^{-2})	
Clearcut	4,472 (2,681)[1,2]	2,185 (6,472)	78 (83)[2]
Forest	6,694 (3255)	1,234 (1,083)	120 (72)
		Decay class 3 western hemlock logs (No. m^{-3})	
Clearcut	50,358 (35,497)	47,394 (31,449)	3,179 (2,590)
Forest	52,272 (26,966)	24,053 (11,470)	2,375 (1,316)

[1]Standard deviations in parentheses.
[2]Means are significantly different between clearcut and forest ($p<0.05$).

Others have found that the density of microarthropods in litter, soil, and small diameter woody debris decreased after clearcutting (Abbott and Crossley 1982, Abbott and others 1980, Blair and Crossley 1988, Maybury 1993, Seastedt and Crossley 1981,). Maybury (1993), working at Pack Forest, found that both mites and springtails in soil tended to be reduced by clearcutting of Douglas-fir forests.

Influence of Forest Edges on Decomposition and Nitrogen Release

Decomposition rates of Douglas-fir needles in forest edges at Pack Forest varied considerably, depending on the edge direction and how far from the edge needles were placed. Needles placed 5 m from the southwest-facing edge of the low-productivity site clearcut decomposed at a higher rate than needles in the adjacent clearcut *(table 3)*. Only 35.8 percent of the mass remained after 1 year at the edge compared to 42.9 percent in the clearcut. The decomposition rate of needles placed 20 m from the east-facing edge of the high-productivity site was slow, and 63.0 percent of the mass remained after 1 year. Here, decomposition was not significantly different from that in the clearcut (56.9 percent remaining after 1 year). The decomposition rate of Douglas-fir needles in a closed canopy forest in the Cedar River Watershed was similar to that in the high-productivity sites with 53.5 percent mass remaining after 1 year (Edmonds 1980) *(table 3)*. After 2 years of decomposition, there were no significant differences between clearcut and forest edge treatments *(table 3)*.

The microclimate at forest edges is usually different from that of interior forests. For example, Chen and others (1992) found that soil temperature and moisture were higher closer to a forest edge than in deep forest interiors. Differences in slope, aspect, and distance from the edge probably influenced decomposition rates in the high- and low-productivity sites. This could possibly explain the very rapid decomposition near the southwest-facing edge of the forest. The east-facing edge of the forest received less radiation and would have lower temperatures than a southwest-facing edge. However, because the litterbags were placed at different distances from the edge, it is difficult to separate the influence of aspect and distance. This preliminary study points out that more research needs to be done on the influence of edges.

Table 3—*Percent mass remaining after 1 and 2 years decomposition and mass of N remaining after 2 years decomposition of Douglas-fir needles in forest edges and clearcuts in low and high productivity sites at Pack Forest and under a closed canopy at Cedar River, Washington.*

	Low productivity site		High productivity site		
Years of decomposition	**5 m from SW facing edge**	**Clearcut**	**20 m from E facing edge**	**Clearcut**	**Cedar River forest[1]**
			Percent mass remaining		
0	100.0	100.0	100.0	100.0	100.0
1	35.6 (1.4)[2]	42.9 (5.8)[3]	63.0 (8.2)	56.9 (15.1)	53.5 (4.4)
2	35.8 (11.3)	34.9 (6.8)	55.9 (7.9)	46.1 (13.2)	43.7 (9.5)
			Percent N mass remaining		
0	100.0	100.0	100.0	100.0	100.0
2	44.2 (13.9)	56.7 (11.1)[3]	77.0 (10.9)	79.9 (23.0)	87.9

[1]Edmonds (1980)
[2]Numbers in parentheses are standard deviations
[3]Significant difference between clearcut and forest edge

As well as influencing decomposition rates, forest edges also appeared to influence the rate of nitrogen release from the decomposing needles. In the closed canopy forest at Cedar River, 87.9 percent of the original nitrogen mass in the decomposing needles still remained after 2 years *(table 3)*. In the needles near the southwest-facing edge of the clearcut at Pack Forest, only 44.2 percent of the initial nitrogen remained after 2 years, whereas 56.7 percent remained in needles in the adjacent clearcut. In contrast, 77 and 79.9 percent of initial nitrogen remained in needles near the east-facing edge and adjacent clearcut, respectively, in the high-productivity site *(table 3)*.

The most rapid nitrogen release was observed on the low-productivity site. Some of this nitrogen release may have been dissolved organic nitrogen (DON) rather than mineral nitrogen. Northup and others (1995) found considerable release of

DON from decomposing *Pinus muricata* litter in a low-productivity site in coastal northern California. They suggested that the polyphenol concentration of decomposing litter controls the proportion of nitrogen released in DON relative to mineral forms, and litter polyphenol concentrations increased as productivity decreased; DON is available to mycorrhizal fungi and is less subject to leaching losses from ecosystems.

Influence of Forest Edges on Soil Moisture and Mycorrhizal Fruiting

Forest edges are likely to influence fungal fruiting, as well as influencing decomposition rates. Saari (1993) found that mushroom diversity and abundance of certain species was greater along the edges of power line corridors than in forest interiors or corridor centers in Finland. Moisture in the forest floor and mineral soil was extremely variable near forest edges at Cedar River *(fig. 4)*. In September 1995, moisture appeared to be lowest for the first 15 m inside the forest, and highest for the first 15 m into the clearcuts, probably because of higher evapotranspiration by trees near the edge. Soil temperatures in autumn 1994 were also higher between the very edge of the forests and 30 m into the clearcuts than deep within forests or clearcut centers (Grace Sparks, personal communication).

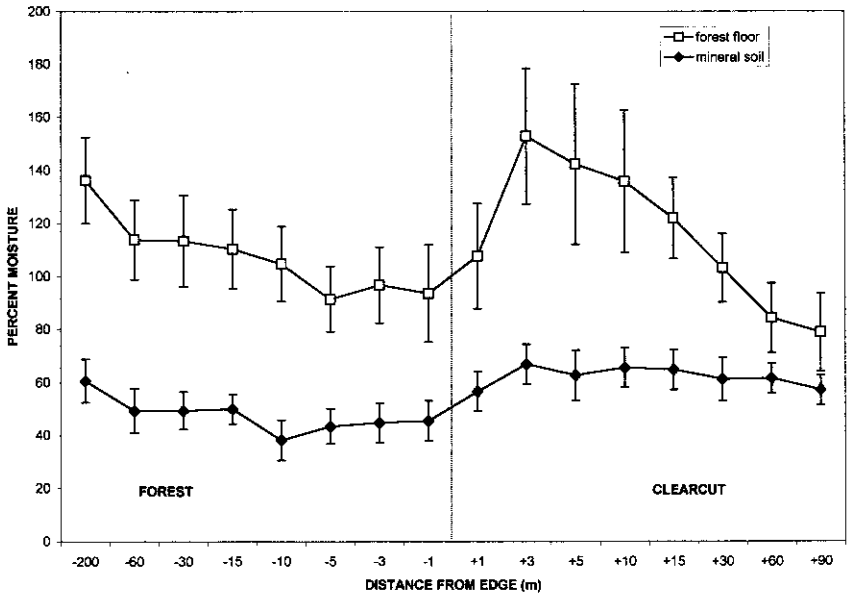

Figure 4—Average percent moisture in forest floor and mineral soil in September 1995 along transects from 200 m into 60- to 70-year Douglas-fir forests across forest edges 90 m into clearcuts in the Cedar River Watershed, Washington. Data represent the average of nine transects in three replicate clearcuts; the vertical bars represent standard errors. (Unpublished data on file at College of Forest Resources, University of Washington, Seattle, WA 98195.)

Changing conditions of temperature and moisture near forest edges would be expected to influence decomposition rates and would also be expected to influence

the fruiting of mycorrhizal fungi. *Figure 5* shows the production, in autumn 1995, of epigeous sporocarps for three common ectomycorrhizal genera (*Cantharellus*, *Russula* and *Lycoperdon* spp.). Each showed a distinct pattern of biomass production. *Cantharellus* spp. fruited in the forest away from the edge, with maximum biomass produced 60 m from the edge. *Russula* spp. produced sporocarps from the interior forest to the edge, with some production 5 m into the clearcut. *Lycoperdon* spp. produced sporocarps from 15 m into the forest to 90 m out into the clearcut. These patterns suggest that these species are responding to different microenvironments and that they may possess varying dependencies on their hosts. Ectomycorrhizal fungal species may have narrow or wide host ranges, and *Lycoperdon* spp. are reported to have a broad host range (Molina and others 1992). Biomass production, however, was not well related to moisture and temperature at the time of sampling. This research is ongoing and the results are likely to be extremely important with respect to mycorrhizal establishment on seedlings as well as commercial mushroom harvesting.

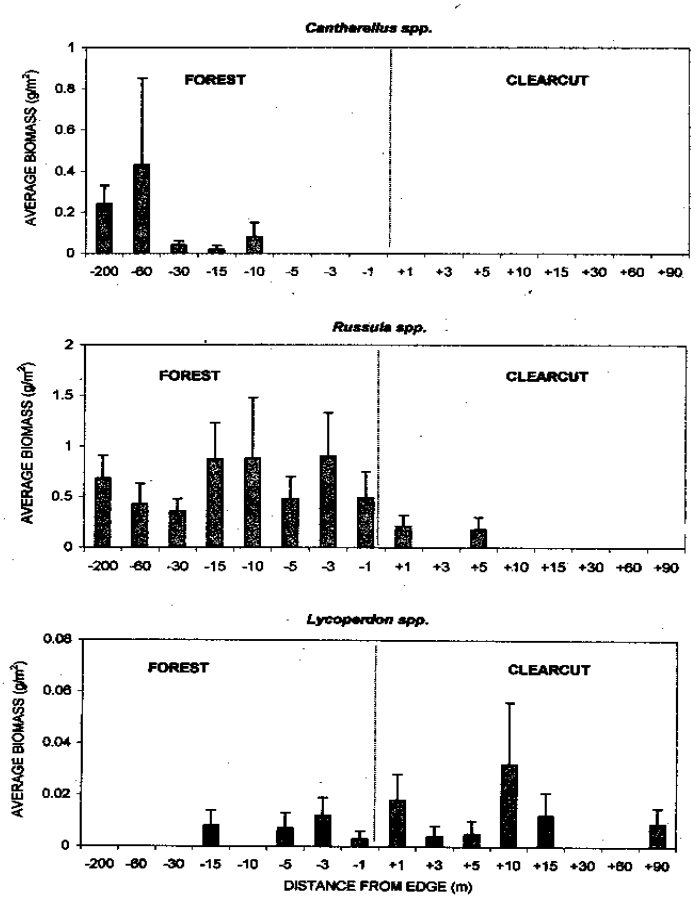

Figure 5—Average biomass in autumn 1995 of three common mycorrhizal fungal genera (*Cantharellus* spp., *Russula* spp. and *Lycoperdon* spp.) along transects from 200 m into 60- to 70-year Douglas-fir forests across forest edges 90 m into clearcuts in the Cedar River Watershed, Washington. Standard errors are shown. (Unpublished data on file at College of Forest Resources, University of Washington, Seattle, WA 98195.)

Influence of Ecosystem Management (Green-Tree Retention) on Temperature, Moisture, Microbial Biomass, and Douglas-fir Seedling Survival and Growth

Retention of both CWD and green trees is an important aspect of the ecosystem management strategy currently applied in Douglas-fir stands in western Washington. In this section, we will focus on how retention of green trees influences soil properties and seedling growth. Two main approaches have been used for retention of green trees: (a) leaving dispersed trees with densities of 20-30 trees/ha, and (b) leaving clumps of trees in areas that are mostly clearcut. The research reported here investigates dispersed retention of green trees and its influence on air and soil temperatures, soil moisture, microbial biomass, and seedling survival and growth.

Table 4—*Average and absolute maximum and minimum air and soil temperatures (°C) in forest, clearcut, and green tree retention plots in the Cedar River Watershed from July 1994 to June 1995.*

Treatment	Average maximum	Average minimum	Average	Absolute maximum	Absolute minimum
Air temperature					
Forest	18.6 (8.0)[1]	4.0 (5.3)	11.1 (5.3)	28.6	-7.3
Green tree retention	22.1 (10.2)	3.4 (4.8)	12.7 (7.3)	34.2	-9.3
Clearcut	24.9 (9.8)	1.4 (4.8)	13.2 (7.3)	36.6	-12.0
Soil temperature at 10 cm					
Forest	10.9 (4.2)	10.1 (4.1)	10.5 (1.3)	19.5	2.6
Green tree retention	11.0 (5.3)	9.6 (4.7)	10.3 (0.5)	20.5	2.3
Clearcut	12.1 (5.5)	10.8 (5.0)	11.3 (1.3)	21.9	2.9

[1]Standard deviations in parentheses.

In general, the most extreme microclimatic conditions were observed in the clearcut sites; the forested sites were the most buffered and the retention sites were intermediate. Average air temperatures were warmest in the clearcut (13.2 °C), lowest in the forest (11.1 °C), and intermediate in the green tree retention sites (12.7°C) *(table 4)*. The absolute maximum and minimum air temperatures (36.6 °C and -12.0 °C, respectively) occurred in the clearcut with temperatures in the green-tree retention areas being intermediate. Average maximum and minimum temperatures were also intermediate in the green-tree retention sites. Maximum air temperatures were significantly higher ($p > 0.05$) in clearcut and retention sites than in forest sites in the warmer months. Soil temperatures at a depth of 10 cm were

lower than air temperatures, but there were no significant differences among treatments *(fig. 6)*. In most cases, however, soil temperatures in green-tree retention sites were intermediate relative to those in the forest and clearcut treatments. There were also no significant differences in soil moisture among treatments throughout the year ($p < 0.05$), but there were some interesting trends. Soils in the upper 10 cm in the forest and retention treatments lost moisture in spring (May) earlier than soils in the clearcut treatment, probably because of increased evapotranspiration. By June, however, the clearcuts had the lowest soil moisture. In the fall (late September and October), soils in the clearcut treatment had the highest soil moisture because of direct input of precipitation and lower evapo-transpiration.

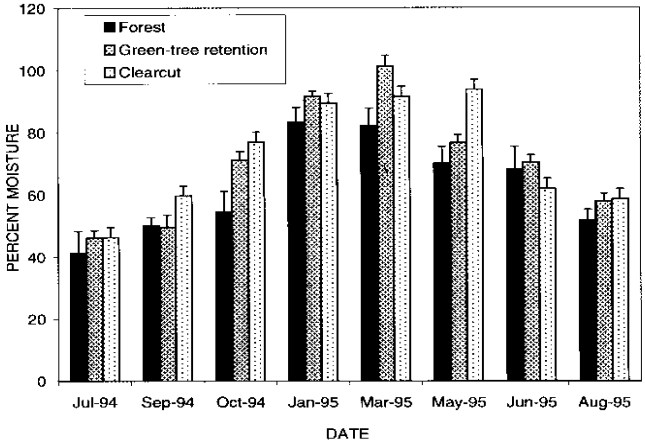

Figure 6—Average percent moisture of mineral soil (top 10 cm wet mass basis) from July 1994 to August 1995 in 60- to 70-year-old forest, green-tree retention areas, and clearcuts in the Cedar River, Watershed (Barg 1996). Standard errors are shown.

Many studies have demonstrated that partial canopy retention moderates microclimatic variables more than clearcut sites (Holbo and Childs 1987, Maybury 1993,Valigura and Messina 1994). Working with clearcut, seed tree, and shelterwood treatments at Pack Forest, Maybury (1993) found that increased canopy retention moderated temperatures, but there was little difference in soil moisture among treatments.

Soil microbial biomass was not significantly different among treatments *(fig. 7)*, averaging 1.5, 1.6, and 1.7 mg C per gram soil in the forest, green-tree retention, and clearcut treatments, respectively, during the study period. A clear seasonal trend was not apparent. Increases in microbial biomass in harvested treatments, due to increases in harvesting residues and changes in soil moisture and temperature, have been noted in studies in the Rocky Mountains (Entry and others 1986) and in western Washington (Maybury 1993). In contrast, reduced microbial biomass was found in clearcut sites in Finland (Pietikainen and Fritze 1995) and in forest gaps in Germany (Bauhus and Barthel 1995). These studies attributed these declines to reduced mycorrhizae, litterfall, root exudates, and changes in microclimate.

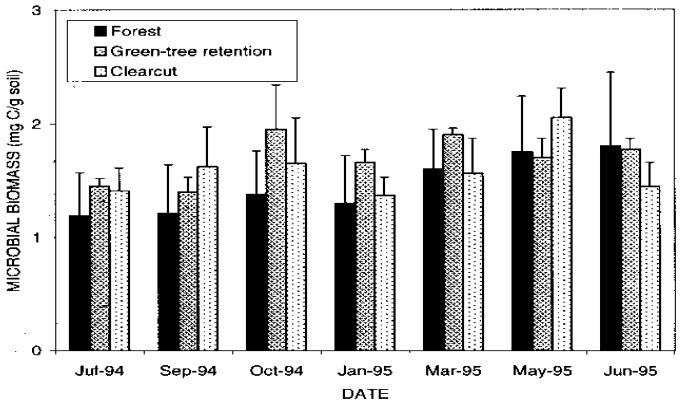

Figure 7—Microbial biomass in the top 10 cm of mineral soil in 60- to 70-year-old forest, green-tree retention areas, and clearcuts in the Cedar River from July 1994 to June 1995 (Barg 1996). Standard errors are shown.

It has been argued that Douglas-fir seedlings cannot be grown successfully under a canopy because Douglas-fir is a shade-intolerant species. This did not appear to be the case in our study. First-year seedling survival was greater than 90 percent in both the retention and clearcut sites. Increases in stem diameter and height were not significantly different between treatments *(table 5)*. However, there was a trend showing that diameter growth was greater in clearcuts, whereas height growth was greater in the partial-retention sites. Stronger trends in seedling growth could emerge with more time in the field (Dunlap and Helms 1983).

Table 5—*Douglas-fir seedling diameter and height growth in a clearcut and green tree retention site in the Cedar River Watershed from April 1994 to October 1995.*

Treatment	Diameter growth	Height growth
	(mm)	(cm)
Clearcut	9.5 (4.5)[1]	35.7 (18.9)
Green tree retention	8.5 (3.6)	39.1 (18.5)

[1]Standard deviations in parentheses.

Conclusions

Forest harvesting in the Pacific Northwest has created a fragmented landscape that is now comprised of clearcuts, young forests, and many forest edges. To varying degrees, this practice has influenced microclimate, soil respiration, decomposition, soil nitrogen dynamics, microbial biomass, fungal fruiting, and invertebrates. Soil organisms respond very differently depending on the specific site conditions and harvesting practices. For example, forest edges appear to be extremely dynamic. In contrast, ecosystem management, specifically green-tree retention treatments, seem

to moderate microclimate conditions between forests and clearcuts. Contrary to popular opinion, Douglas-fir seedlings were successfully grown under tree canopies for 1 year, but survival and growth need to be followed for more years. More research is needed to examine the influence of forest harvesting practices on soil microbial and invertebrate populations and processes. We have examined only a few pieces of the puzzle.

Acknowledgments

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Northern Flying Squirrel Mycophagy and Truffle Production in Fir Forests in Northeastern California[1]

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Abstract

In this paper we summarize the results of four studies in which we either examined the feeding habits of the northern flying squirrel (*Glaucomys sabrinus*), a mycophagous (consuming fungi) small mammal, or compared the abundance of truffles (sporocarps of hypogeous mycorrhizal fungi) among different types of fir (*Abies*) forest. The studies were conducted within the Lassen National Forest in northeastern California between 1990 and 1994. In the first study, we found that abundance of northern flying squirrels was significantly less in old-growth fir stands that had been shelterwood-logged 6 to 7 years previously than in nearby, unlogged old-growth and mature fir stands. Truffles were common in the diet of flying squirrels, truffle frequency was low in the shelterwood-logged stands compared to the unlogged old-growth and mature stands, and abundance of flying squirrels was correlated with truffle frequency across the 12 stands in which we estimated both. In the second study, we found no significant effects on total truffle frequency and biomass of truffles from commercial thinning or broadcast burning that had occurred about 10 years previously, but there were significant effects of thinning on frequencies of individual truffle genera. In the third study, we compared food preferences of captive northern flying squirrels among sporocarps of five species of fungi, two species of lichens, and fir seeds. Foods most preferred were two species of truffles, and consumption rate differed significantly among the five species of fungi. In the fourth study, we found that total truffle frequency and biomass and species richness did not differ significantly between old-growth and nearby, mature fir stands. We also observed that abundance of truffles (pooled across species) was not significantly associated with decayed wood, depth of the organic soil, or other habitat features. We collected 46 species of truffles in these floristically simple forests, however, and there was significant association between age class and frequencies of individual truffle species. Our data suggest that the effects of disturbance on truffle assemblages are species specific, and that predicting the effects of forest management on mycophagous small mammals may be difficult until more is known about the effects of disturbance on truffle production and the nutritional values of different truffle species.

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Introduction

Most species of fungi that produce hypogeous sporocarps (truffles) are ectomycorrhizal (Miller 1983; Trappe 1962, 1971), though a few species of vesicular-arbuscular mycorrhizal fungi also form macroscopic sporocarps (Janos and Sahley 1995, Maser and others 1978). Spores of hypogeous fungi are believed to be primarily dispersed by animals that eat truffles (Fogel and Trappe 1978, Maser and others 1978). Spores are viable after passage through the digestive tracts of small mammals (Cork and Kenagy 1989, Trappe and Maser 1976), and truffles are common in the diets of small mammals in temperate forests dominated by ectomycorrhizal fungi (Fogel and Trappe 1978, Hall 1991, Johnson 1994, Maser and others 1978, Taylor 1992, Tevis 1953, Ure and Maser 1982), as well as in New World tropical forests dominated by vesicular-arbuscular mycorrhizal fungi (Janos and Sahley 1995).

Forest management may affect truffle production because ectomycorrhizal fungi are dependent on their host plants for carbon (Hacskaylo 1973, Harley 1971, Last and others 1979), and both ectomycorrhizae (Harvey and others 1978, 1979) and truffles (personal observation) develop primarily in organic soil layers and the upper mineral soil where they are vulnerable to disturbance of the forest floor. Several studies have examined seasonal and annual variation in truffle production (Fogel 1976, Fogel and Hunt 1979, Hunt and Trappe 1987, Luoma 1991, States 1985) or compared truffle production among different age classes of forest (Amaranthus and others 1994, Clarkson and Mills 1994, Luoma and others 1991, North and others 1997, O'Dell and others 1992, Vogt and others 1981). The effects of forest management, especially partial-harvesting practices, on truffle production is still poorly understood.

In this paper we summarize results of four studies conducted in the Lassen National Forest in northeastern California between 1990 and 1994. In each study, we either examined the feeding habits of the northern flying squirrel (*Glaucomys sabrinus*), a mycophagous (consuming fungi) small mammal, or compared fruiting patterns of truffles among different types of fir (*Abies*) forest. In the first study, we compared abundance of flying squirrels among three types of forest that varied in age and stand structure and evaluated the correlation between the abundance of flying squirrels and truffle frequency. In the second, we evaluated the effects of commercial thinning and broadcast burning on truffle frequency and biomass 10 years after treatment. In the third, we determined whether captive flying squirrels preferred sporocarps of certain species over others, and whether flying squirrels preferred truffles over other types of food available to them. And in the fourth, we compared truffle frequency, biomass, number of truffle species, and relative frequencies of individual species between old-growth and mature fir forests to determine whether old-growth fir forests had unique truffle communities.

Study I: Patterns of Flying Squirrel Abundance

A study of home range size and habitat use patterns of California spotted owls (*Strix occidentalis occidentalis*) in the Lassen National Forest indicated that owls selected stands with relatively dense canopy cover (Zabel and others 1992b). One of the most striking patterns of habitat use by spotted owls was a clear avoidance of old-growth forests within Swain Mountain Experimental Forest that had been shelterwood-logged in 1984-1985 (Zabel and others 1992a). Radiotelemetry positions of owls were rarely located in shelterwood-logged areas but frequently were located

in unlogged stands of old-growth and mature forest adjacent to shelterwood-logged areas. Analysis of pellets egested from spotted owls indicated that the northern flying squirrel was the owl's primary prey within the Lassen National Forest, occurring in about 80 percent of the pellets analyzed.

We hypothesized that the lack of use of the shelterwood-logged forests within Swain Mountain Experimental Forest by spotted owls could be related to prey abundance. To test this hypothesis, we compared abundance of flying squirrels in the shelterwood-logged old-growth forests and in nearby, unlogged old-growth and mature forests (Waters and Zabel 1995). We also sampled truffles within each forest type to determine whether truffle frequency was correlated with abundance of flying squirrels.

Study Area and Methods

Stands of unlogged old-growth, unlogged mature, and shelterwood-logged old-growth fir forest were located within or near Swain Mountain Experimental Forest, which is located at the southern end of the Cascade Range within the Lassen National Forest in northeastern California. Soils were well drained and derived from mafic andesite. Forests were high elevation (1,800-2,000 m) and dominated by white fir (*A. concolor*) or a mixture of white and red fir (*A. magnifica*). Scattered sugar pine (*Pinus lambertiana*), Jeffrey pine (*P. jeffreyi*), ponderosa pine (*P. ponderosa*), and lodgepole pine (*P. contorta*) occurred within some of the grids.

Unlogged old-growth forests (hereafter, old-growth forests) were characterized by multilayered canopies and large logs, stumps, and snags. Dense patches of small firs occurred in the understory, but herbaceous plants (e.g., *Pyrola picta*, *Viola purpurea*, and *Corallorhiza maculata*) and shrubs (primarily *Chrysolepis sempervirens*) were uncommon. The organic soil included layers of litter and humus and large pieces of buried, decayed wood. From counts of growth rings on cut stumps in adjacent shelterwood-logged areas, we estimated that the majority of codominant and dominant trees in the old-growth and shelterwood-logged forest types were 200 to 400 years old.

Unlogged mature forests (hereafter, mature forests) were characterized by even-aged stands that grew back after stand-replacement wildfires (this forest type was referred to as "young" by Waters and Zabel [1995]). These forests were in the stem-exclusion phase (Oliver and Larson 1996) of forest development. They were dense and had closed canopies, and virtually no herbaceous plants or shrubs were present in the understory. Old, dead stems on the forest floor indicated that shrubs were abundant for some period after wildfires occurred. The organic soil included well-developed layers of litter and humus. From counts of growth rings of cored trees within each stand, we estimated that most codominant and dominant trees in this forest type were 80 to 100 years old.

Shelterwood-logged old-growth forests (hereafter, shelterwood-logged forests) were located in Swain Mountain Experimental Forest. The experimental forest was dominated by old-growth fir forests until 1984-1985 when large areas were logged to study natural regeneration rates using the shelterwood silvicultural system. These timber harvests left an open stand structure of widely spaced, large-diameter trees. The ground was intentionally disturbed to expose mineral soil for natural regeneration. Tractors with brush blades were used to remove logs and disturb soils,

and slash was piled and burned or broadcast burned. At the time of our study, grasses, forbs, and low shrubs (primarily *Ceanothus cordulatus* and *Ribes roezlii*) had become established, and the little organic soil present on the forest floor was primarily characterized by undecomposed litter.

We selected four areas within each of the three forest types that were similar in elevation and tree species composition, at least 150 m apart, relatively homogeneous, and sufficiently large. Within each of the 12 areas we established a 12- to 13-ha rectangular or square grid. During August or September of 1991 and 1992, we livetrapped flying squirrels during a single trapping session that was 15 to 16 nights long. Flying squirrels were captured in Tomahawk livetraps (41 x 13 x 13 cm) and individually eartagged. Fecal pellets were also collected from captured flying squirrels and analyzed to describe diet. We used the first-order jackknife estimator (Burnham and Overton 1979, Rosenberg and others 1995) to estimate population size within each grid. Abundance of flying squirrels was estimated by dividing the jackknife population estimate by the effective area trapped. The effective area trapped was estimated by adding to the area of each grid a strip equal in width to one-half the mean maximum distance moved by flying squirrels captured at least twice (Wilson and Anderson 1985).

During summer 1991, we sampled truffles and vegetation within each of the 12 grids. We used a rake to search for truffles within a 4-m^2 circular plot (1.13-m radius) located at each grid point (91-104 truffle plots/grid). We raked through the litter, humus, and upper 5 to 10 cm of mineral soil. As a measure of truffle abundance we used truffle frequency, which was the percentage of 4-m^2 plots in which we found $\geq$1 truffle. We sampled vegetation within circular plots at every third grid point within each grid. We measured the diameter at breast height (dbh) of trees and the length and midpoint diameter of logs within each circular plot. Size of vegetation plot differed among the three forest types because of large differences in the densities of trees. In old-growth forests, small trees (< 18 cm in dbh) were measured within a 6-m radius and larger trees and logs within a 16-m radius. In mature forests, all trees and logs were measured within a 6-m radius. In shelterwood-logged forests, all trees and logs were measured within an 18-m radius. We used a spherical densiometer to obtain a relative measure of canopy cover at each vegetation plot (we used the average of three densiometer readings taken 8 m from the plot center). Ground cover was estimated using a point-intercept method; type of ground cover was recorded at 52 points per vegetation plot (13 points per transect along four transects following cardinal directions). We also dug a small soil pit at each point in the grid and measured the depth of organic soil (combined depth of litter, humus, and buried, decayed wood).

We used repeated-measures analysis of variance (ANOVA) to compare estimates of flying squirrel abundance in 1991 and 1992 among the three forest types. If variances differed significantly among forest types, we used Welch's variance-weighted ANOVA (SAS Institute 1997) and a variance-weighted multiple comparison test (SAS Institute 1997). If variances did not differ significantly among forest types, we used traditional ANOVA tests and the Ryan-Einot-Gabriel-Welsch multiple-range test (SAS Institute Inc. 1989) to compare means following ANOVA. We considered tests significant if $\alpha < 0.05$. Spearman ranked correlation analysis was used to evaluate the correlation between abundance of flying squirrels (averaged between 1991 and 1992) and truffle frequency across the 12 grids.

Results and Discussion

Measures of vegetation structure differed greatly among the three forest types. Compared to old-growth forests, shelterwood-logged forests had significantly less basal area and canopy cover, fewer large-diameter snags, greater ground cover of forbs, less ground cover of small-diameter and large-diameter logs, and a thinner layer of organic soil *(table 1)*. Also, compared to old-growth forests, mature forests had significantly greater basal area and canopy cover, more small-diameter snags and fewer large-diameter snags, and less ground cover of large-diameter logs *(table 1)*. Each of the three forest types had its own characteristic distribution of diameter size classes of trees *(fig. 1)*.

Table 1—*Means (x) and standard errors (SE) of variables measured in three forest types (n = 4 grids in each forest type) in northeastern California in 1991. The alpha (α) value is from an ANOVA test, and means with the same letter did not differ at an experimentwise α of 0.05.*

Variable	Old-growth		Mature		Shelterwood		
	x	*SE*	*x*	*SE*	*x*	*SE*	α
Basal area ≥5 cm dbh (m^2 ha^{-1})	72.6A	1.7	92.1B	1.5	22.6C	1.6	<0.01
Canopy cover (pct)	66.0A	0.4	78.3B	1.8	24.3C	1.7	<0.01
Snags ha^{-1} 13-52 cm in dbh	69.3A	22.5	176.1B	42.6	5.0A	1.9	0.01
Snags ha^{-1} > 52 cm in dbh	9.7A	1.4	0.7B	0.7	5.8C	1.0	<0.01
Shrub cover (pct)	0.9A	0.4	0.5A	0.3	6.3A	3.6	0.15
Grass cover (pct)	1.4A	0.8	0.0A	0.0	3.6A	1.6	0.10
Forb cover (pct)	0.4A	0.3	0.0A	0.0	2.2B	0.6	0.01
Ground cover (pct) of logs ≤52 cm in diameter	2.1A	0.4	1.3A,B	0.1	0.6B	0.1	0.01
Ground cover (pct) of logs > 52 cm in diameter	3.3A	0.3	0.0B	0.0	0.5B	0.1	<0.01
Organic soil depth (cm)	6.8A	0.3	7.9A	0.4	1.7B	0.4	<0.01

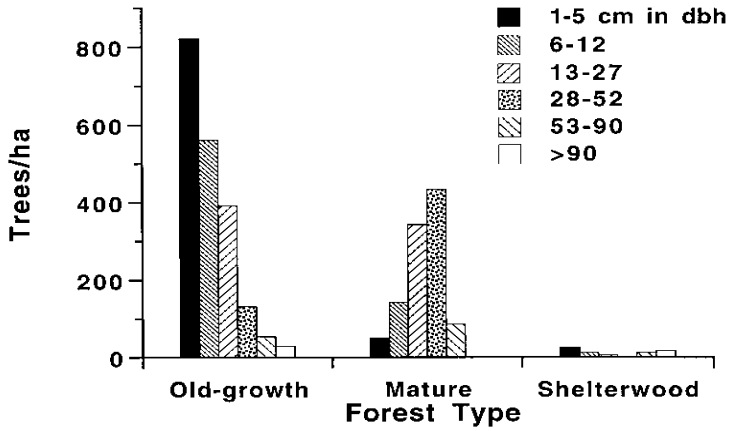

Figure 1—Mean densities of trees sampled in 1991 in old-growth (n = 4 grids), mature (n = 4), and shelterwood-logged (n = 4) fir forests in northeastern California.

Flying squirrel abundance was significantly less in shelterwood-logged forests than in old-growth and mature forests *(fig. 2)*. Mean abundance was greater in old-growth forests than in mature forests in both 1991 and 1992, but in neither year was that difference significant. These results suggest that within our study area, flying squirrels were not old-growth specialists, but that their populations were negatively affected by the logging that occurred within Swain Mountain Experimental Forest.

Few studies have compared flying squirrel abundance among different forest types, and none have compared abundance among forests that were similar in composition and age to those in our study. Carey and others (1992) found that the mean density of flying squirrels in old-growth stands in Oregon and Washington was approximately twice that in managed conifer stands that were 40 to 70 years old. Rosenberg and Anthony (1992) found that densities of flying squirrels were similar in old-growth and 30- to 60-year-old stands of Douglas-fir (*Pseudotsuga menziesii*) in Oregon.

We found that truffles were common in the diet of northern flying squirrels. Truffle spores were found in each of the 165 fecal samples analyzed. Lichen, unknown vegetative matter, spores of epigeous fungi, pollen from staminate cones of conifers, and insect and seed parts were also observed. Truffles have been shown to be a primary food of flying squirrels in the northern Sierra Nevada (Hall 1991) and Oregon (Maser and others 1985, Maser and others 1986). McKeever (1960) found that the most common foods found in the stomachs of flying squirrels trapped in Swain Mountain Experimental Forest were fungi and lichens, but he did not distinguish between hypogeous and epigeous fungi.

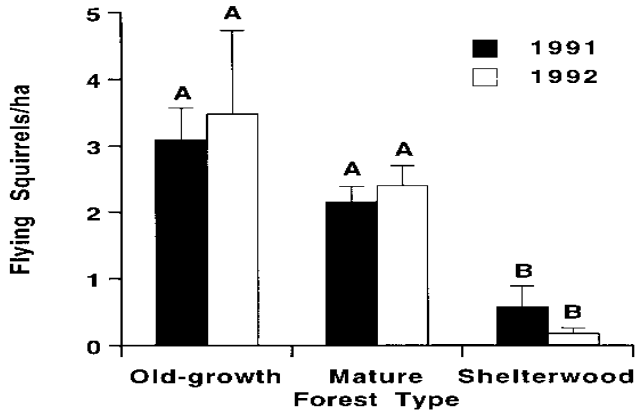

Figure 2—Mean estimates of abundance of northern flying squirrels in old-growth (n = 4 grids), mature (n = 4), and shelterwood-logged (n = 4) fir forests in northeastern California. Repeated-measures ANOVA indicated that abundance differed significantly among the three forest types (F = 20.2; d.f. = 2, 9; $\alpha < 0.01$), but not between 1991 and 1992 (F = 0.2; d.f. = 1, 9; $\alpha = 0.66$). Multiple comparisons were performed separately for each year; within each year, columns with the same letter did not differ at an experiment α of 0.05.

Abundance of flying squirrels was positively correlated with truffle frequency across the 12 grids ($r_S = 0.86$, $\alpha < 0.01$). Because truffles were so common in the diet of flying squirrels in our study area, the correlation between abundance of flying

squirrels and truffle frequency suggests that truffle abundance may have influenced habitat selection by flying squirrels. Other factors that we did not measure, however, undoubtedly affect the quality of habitat for flying squirrels. For example, lichens are especially common in the diets of flying squirrels during winter when conditions are harsh (Hall 1991, Maser and others 1986, Maser and others 1985, McKeever 1960), and their availability may be an important determinant of the quality of flying squirrel habitat.

Truffle frequency during summer 1991 differed significantly among the three forest types (F = 9.71; d.f. = 2, 9; $\alpha < 0.01$). Multiple comparisons indicated that truffle frequency did not differ significantly between old-growth forests (x = 27.8 percent, SE = 6.0) and mature forests (x = 17.5 percent, SE = 1.6), but was significantly less in shelterwood-logged forests (x = 4.2 percent, SE = 2.2). Because we sampled truffles only once, interpretations from these data are limited. The much lower frequency of truffles in shelterwood-logged forests compared to that in nearby, unlogged old-growth forests, however, suggests that the logging and/or site preparation that occurred within Swain Mountain Experimental Forest resulted in reduced truffle production.

Other species of forest rodents were abundant in shelterwood-logged forests. Mean abundance was greatest in shelterwood-logged forests for golden-mantled ground squirrels (*Spermophilus lateralis*), yellow pine chipmunks (*Tamias amoenus*), lodgepole chipmunks (*Tamias speciosus*), and deer mice (*Peromyscus maniculatus*) (Waters and Zabel [In press]). These species are known to eat truffles, but they have varied diets that also include seeds, leaves, fruit, flowers, and insects (Fogel and Trappe 1978; McKeever 1964; Nowak 1991; Sutton 1992; Tevis 1952, 1953), and are not considered to be as mycophagous as northern flying squirrels. The only other species whose abundance we compared among forest types and that is considered to be highly mycophagous is the California red-backed vole (*Clethrionomys californicus*; Maser and others 1978, Ure and Maser 1982). We captured 22 California red-backed voles in old-growth forests, four in mature forests, and none in shelterwood-logged forests (Waters and Zabel [In press]).

Study II: Effects of Thinning and Broadcast Burning on Truffle Abundance

We considered the silvicultural treatments within Swain Mountain Experimental Forest to be relatively severe, especially the site preparation techniques, which left highly disturbed soils with large areas of exposed mineral soil. To evaluate the effects of less severe silvicultural treatments on the abundance of truffles, we sampled truffles at a site (Jennie Springs) near Swain Mountain Experimental Forest that had been used by other researchers to study the effects of commercial thinning and broadcast burning on various stand conditions (Oliver and others 1981).

Study Area and Methods

The Jennie Springs site was located at an elevation of 1,860 m about 1 km south of Swain Mountain Experimental Forest. The site is characterized by an even-aged, mature (stem-exclusion phase) stand of white fir that originated after a stand-replacement wildfire.

We sampled truffles in 21 units, a subset of the units originally treated (Waters and others 1994). The 0.4-ha units were square. Seven were heavily thinned (about 70 percent of basal area removed), seven moderately thinned (about 35 percent of basal area removed), and seven not thinned. Thinning occurred in 1982. Logs were removed by horse or cable to minimize ground disturbance. Within each thin level, four of the seven units were burned, and three were not. Two of the four units were burned in the spring and two in the fall, but we pooled spring and fall burned units for these analyses. Burn intensities were light to moderate with flame lengths averaging about 0.5-1.0 m (Weatherspoon 1994).

Within each unit we established a 5 x 6 grid with 8-m spacing between grid points. In June 1992 we searched for truffles in a 4-m^2 circular plot located at each grid point (30 truffle plots/unit). In September 1992 we searched for truffles in a 4-m^2 circular plot located midway between adjacent grid points (15 truffle plots/unit). Truffles were placed in paper bags and stored in a cooler or refrigerator until they could be identified to genus, dried, and weighed. Vegetation was sampled in four systematically located 0.02-ha circular plots (8-m radius) within each unit. Within each vegetation plot we measured the dbh of all trees and snags $\geq$8 cm and the length and midpoint diameter for all logs $\geq$12 cm wide at the midpoint. We also estimated canopy cover using a spherical densiometer at three systematically located points within each vegetation plot. At 12 systematically located points within each unit, we dug a small soil pit and measured the depths of the litter and humus layers. We collected a sample from the litter, humus, and mineral soil (5 cm below the top of the mineral soil) at each of the 12 points and combined these subsamples into one composite sample for each unit. These composite samples were oven-dried, and soil moisture was determined gravimetrically for each layer. A separate composite sample (six systematically located subsamples) of mineral soil was collected from each unit. These samples were used to determine percent total nitrogen, percent total carbon, and pH by a soils laboratory at Oregon State University in Corvallis.

We tested for effects due to thinning and burning on truffle frequency (proportion of truffle plots in which we found $\geq$1 truffle) and biomass using two-factor ANOVA. Truffle biomass in this and following studies was the dry weight of all truffle collections found during a particular sampling interval (standing crop); we made no attempt to estimate annual production. Variables whose distribution was not normal were transformed using a log or arcsine transformation.

Results and Discussion

During the June sample period, we found truffles in 206 of the 630 plots sampled; the biomass of all truffles collected was the equivalent of 1.56 kg ha^{-1}. During the September sample period, soils were dry, and we found truffles in only 13 of the 315 plots sampled (most of those truffles appeared old); results reported here are thus only from the June sample period.

Compared to unthinned units, heavily thinned units had significantly fewer trees, less canopy cover, more undecayed logs, a thinner organic layer, and less moisture in the litter and humus layers *(table 2)*. Truffle frequency and biomass did not differ significantly among the three thin levels *(fig. 3)*. Truffle biomass was more variable than frequency, with mean biomass of truffles greatest in the heavily thinned units. Truffle frequency was similar among thin levels because some genera such as *Gymnomyces* (includes genus *Martellia* because we could not reliably separate these

two similar genera at the time) had significantly greater frequencies in thinned units, and others (*Hysterangium* and *Gautieria*) had significantly greater frequencies in unthinned units *(table 2)*.

Table 2—*Means (x) and standard errors (SE) of variables measured at the Jennie Springs site in June 1992. For each thin level (n = 7), values were averaged across four broadcast burned units and three unburned units. The alpha (α) value is from effect due to thinning in two-factor ANOVA.*

Item	Thinning level						
	Heavy		Moderate		Unthinned		
	x	*SE*	*x*	*SE*	*x*	*SE*	α
Tree density (stems ha^{-1})	101.2	6.3	248.7	24.1	749.6	74.0	<0.01
Canopy cover (pct)	41.7	2.7	66.5	3.1	85.2	1.0	<0.01
Undecayed logs (m^2 ha^{-1})	417.5	57.4	435.0	61.2	160.0	36.7	<0.01
Decayed logs (m^2 ha^{-1})	59.9	13.0	91.4	23.9	79.0	17.3	0.42
Depth of organic soil (cm)	3.1	0.6	3.7	0.5	4.9	0.5	<0.01
Litter moisture (pct)[1]	4.9	0.7	8.5	1.1	15.2	1.7	<0.01
Humus moisture (pct)[1]	14.3	2.3	17.6	2.8	26.2	3.0	0.01
Mineral soil moisture (pct)[1]	22.7	1.7	25.0	1.2	24.4	0.6	0.77
Alpova frequency (pct)	1.9	1.4	3.3	1.8	4.8	2.2	0.42
Gautieria frequency (pct)	0.0	0.0	1.4	1.0	5.2	1.9	0.02
Hysterangium frequency (pct)	1.4	1.0	2.4	1.2	12.4	4.6	0.01
Gymnomyces frequency (pct)[2]	25.7	5.5	18.1	5.7	6.2	1.1	0.02
Balsamia frequency (pct)	2.4	0.6	1.9	1.0	2.4	1.2	0.61

[1] $n = 6$ units for each thin level.
[2] Includes genus *Martellia*.

Table 3—*Means (x) and standard errors (SE) of variables measured at the Jennie Springs site in 1992. For broadcast burned units (n = 12), values were averaged across four heavily thinned units, four moderately thinned units, and four unthinned units. For unburned units (n = 9), values were averaged across three heavily thinned units, three moderately thinned units, and three unthinned units. The alpha (α) value is from effect due to burning in two-factor ANOVA.*

Item	Burn level				
	Broadcast burned		Unburned		
	x	*SE*	*x*	*SE*	α
Tree density (stems ha^{-1})	350.2	71.2	388.2	128.9	0.48
Canopy cover (pct)	61.8	5.9	68.0	6.1	0.02
Undecayed logs (m^2 ha^{-1})	295.9	57.7	393.0	52.1	0.14
Decayed logs (m^2 ha^{-1})	64.1	13.6	93.6	16.0	0.19
Depth of organic soil (cm)	2.9	0.3	5.2	0.3	<0.01
Litter moisture (pct)[1]	8.5	1.4	11.5	2.5	0.06
Humus moisture (pct)[1]	16.2	1.7	25.6	3.5	<0.01
Mineral soil moisture(pct)[1]	23.5	1.0	25.1	0.8	0.30
Soil pH	5.87	0.03	5.72	0.05	0.03
Alpova frequency (pct)	5.0	1.6	1.1	0.6	0.10
Gautieria frequency (pct)	1.7	0.9	3.0	1.6	0.60
Hysterangium frequency (pct)	4.7	2.4	6.3	3.1	0.46
Gymnomyces frequency (pct)[2]	15.3	3.9	18.5	5.2	0.49
Balsamia frequency (pct)	2.5	0.7	1.9	0.8	0.52

[1] $n = 12$ for broadcast burned units and $n = 6$ for unburned units.
[2] Includes genus *Martellia*.

Compared to unburned units, burned units had significantly less canopy cover, a thinner organic soil layer, less moisture in the humus layer, and higher soil pH *(table 3).* Truffle frequency and biomass did not differ significantly between burned and unburned units *(fig. 3).* Unlike differences among thin levels, however, frequencies of the five most common genera did not differ significantly between burn levels *(table 3),* suggesting that thinning affected truffle frequencies more than broadcast burning.

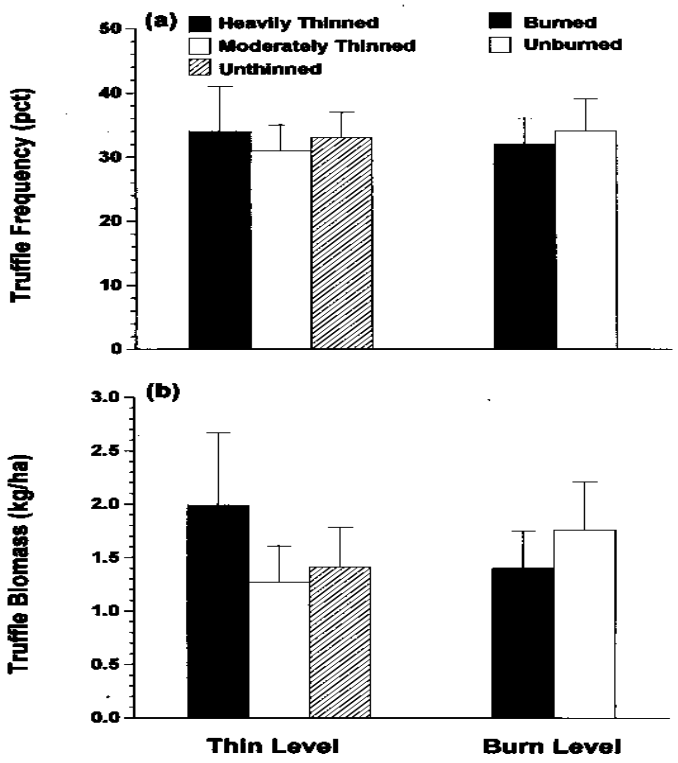

Figure 3—Means and standard errors of (a) truffle frequency and (b) truffle biomass by thin level and burn level in northeastern California in 1992. For each thin level (n = 7), values were averaged across four broadcast burned units and three unburned units. For broadcast burned units (n = 12), values were averaged across four heavily thinned units, four moderately thinned units, and four unthinned units. For unburned units (n = 9), values were averaged across three heavily thinned units, three moderately thinned units, and three unthinned units. Two-factor ANOVA indicated that for truffle frequency, neither the effect due to thinning (F = 0.04; d.f. = 2, 15; α = 0.96) nor the effect due to burning (F = 0.06; d.f. = 1, 15; α = 0.80) was significant. Similarly, for truffle biomass, neither the effect due to thinning (F = 0.11; d.f. = 2, 15; α = 0.90) nor the effect due to burning (F = 0.29; d.f. = 1, 15; α = 0.60) was significant.

Unfortunately, we were unable to continue this study, so caution must be taken in interpreting the results because of its short duration. The similarity in mean truffle frequency among thin levels and between burned and unburned units, however,

contrasts greatly with the significant difference in mean truffle frequency between shelterwood-logged old-growth forests and unlogged old-growth forests found in the previous study.

Study III: Food Preferences of Northern Flying Squirrels

Because results of the previous study suggested that thinning could lead to changes in relative frequencies of truffle species, we wanted to know whether northern flying squirrels preferred sporocarps of certain fungal species over others. We also wanted to know whether flying squirrels preferred sporocarps over other naturally occurring food types. In this study, we compared preferences of captive flying squirrels among sporocarps of five species of fungi, two species of lichens, and fir seeds (Zabel and Waters 1997). Although many studies have shown that truffles are common in the diets of small mammals, we know of no published studies comparing preferences of mycophagous small mammals among different kinds of truffles.

Methods

We captured flying squirrels in two stands of old-growth fir in Swain Mountain Experimental Forest in August 1994. Fungal sporocarps and lichens were collected in old-growth and mature fir stands, also within Swain Mountain Experimental Forest. Fir seeds (*A. concolor* and *A. magnifica*) were obtained from the USDA Forest Service Nursery in Placerville, California. Choice of fungal species was determined by availability; we used sporocarps of the five most commonly found species at the time of sampling (August 1994): *Gautieria monticola*, *Alpova trappei*, *Gymnomyces abietis*, *Endoptychum depressum*, and *Arcangeliella lactarioides*. All are ectomycorrhizal basidiomycetes, except *Endoptychum depressum*, which is a saprobic basidiomycete. *Endoptychum depressum* and *Arcangeliella lactarioides* are secotioid fungal species, which exhibit morphological and fruiting characteristics intermediate between those of epigeous and hypogeous fungi. The two lichen species were *Bryoria fremontii* and *Letharia vulpina*, which were common epiphytic species in fir stands within Swain Mountain Experimental Forest.

After capture, flying squirrels were transported to and housed in outdoor pens at Humboldt State University in Arcata, California. Feeding trials were conducted in two 1.2 x 1.2 x 1.0-m cages built with wood and hardware cloth. Size of food samples was standardized across foods and tests; samples were 2-3 cm in diameter. Food samples were weighed before and after each feeding trial to determine the proportion eaten. Each food sample was placed in a randomly assigned grid cell across the bottom tray of the feeding cage. The tray was filled with peat moss to a depth of about 8 cm. Truffle food samples were buried 2-3 cm, and all other food samples were placed on top of the peat moss. Peat moss was thoroughly mixed after each experiment and changed nightly. Experiments began shortly after sunset when squirrels were moved from their outdoor cages into the test rooms, which were illuminated with a red light. Flying squirrels entered the center of the feeding cage through a plastic tube (8 cm in diameter). An observer used a tape recorder and described behavior of the flying squirrels from behind a blind 1 m from the cage. Feeding trials were performed on seven male squirrels for 45 minutes each night for four consecutive nights.

We used the proportion of food samples eaten (averaged across the four nights) as a measure of food preference. We tested whether this measure varied among the eight food types using ANOVA with a randomized complete-blocks design (each squirrel was a block). Mean proportion of food eaten was compared among the eight foods following ANOVA using the Ryan-Einot-Gabriel-Welsch multiple-range test.

Results and Discussion

Mean proportion of food samples eaten varied significantly among the eight foods *(fig. 4)*. Among the five species of fungi, mean proportion of food eaten ranged from 0.90 (SE = 0.05) for *Gautieria monticola* sporocarps to 0.11 (SE = 0.04) for *Arcangeliella lactarioides* sporocarps. Multiple comparisons indicated that samples of the hypogeous species *Gautieria monticola* were eaten significantly more than samples of the hypogeous species *Gymnomyces abietis*, and samples of the secotioid species *Endoptychum depressum* were eaten significantly more than samples of the secotioid species *Arcangeliella lactarioides (fig. 4)*. North and others (1997) concluded that palatability varied greatly among truffle species in their study area because consumption rates, determined by comparing truffle biomass between open plots and exclosures, varied greatly among truffle species. The three hypogeous species used in our study were consumed more than the two secotioid species, which is consistent with results of other studies that showed truffles were more common than mushrooms in the diets of mycophagous small mammals (Maser and others 1978, 1985, 1986; North and others 1997; Taylor 1992; Ure and Maser 1982).

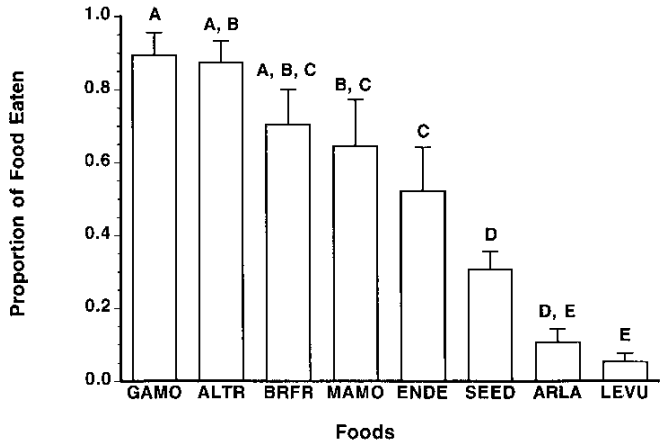

Figure 4—Means and standard errors of proportion of food sample eaten (averaged across a four-night period) by seven captive northern flying squirrels (all male) in 1994. The eight food types were *Gautieria monticola* sporocarps (GAMO), *Alpova trappei* sporocarps (ALTR), the lichen *Bryoria fremontii* (BRFR), *Gymnomyces abietis* sporocarps (GYAB), *Endoptychum depressum* sporocarps (ENDE), fir seeds (SEED), *Arcangeliella lactarioides* sporocarps (ARLA), and the lichen *Letharia vulpina* (LEVU). Mean proportion of food eaten varied significantly among the eight foods (F = 31.75; d.f. = 7, 42; $\alpha < 0.01$). Foods with the same letter did not differ at an experiment α of 0.05.

The relatively high preference for the lichen *Bryoria fremontii* is consistent with dietary studies, which have shown that lichens were a common food of northern flying squirrels (Hall 1991, Maser and others 1985, 1986; McKeever 1960). These studies, however, showed that lichens were less common in the summer diets of flying squirrels than in the winter diets, suggesting that lichens were eaten more when other foods like truffles were unavailable. The low preference for fir seeds is also consistent with dietary studies, which have not found conifer seeds to be common in the diets of northern flying squirrels.

We showed that preference varied significantly among the eight foods tested, but we do not know how the nutritional values of these foods varied. Cork and Kenagy (1989) found that the nutritional value of one truffle, *Elaphomyces granulatus*, was low for the ground squirrel *Spermophilus saturatus* because digestibility of the sporocarps was low. They hypothesized that truffles generally have relatively low nutritional value for small mammals but are commonly consumed because they are seasonally abundant and highly detectable because of the strong odors they develop when mature. Claridge and Cork (1994), however, found that the nutritional values of two truffle species were high for a forest-dwelling marsupial (*Potorous tridactylus*) in Australia. Because of their high water content, fungal sporocarps may be important during certain periods or in certain areas as a source of water (Fogel and Trappe 1978).

Study IV: Truffle Production in Old-Growth and Mature Forests

Great concern has been expressed over the potential loss of biodiversity due to logging of remaining old-growth forests in the western United States. The Forest Ecosystem Management Team (FEMAT) identified more species of fungi (527 species, 80 of which were truffles) as being closely associated with late-successional and old-growth forests in the Pacific Northwest than any other group of organisms evaluated (arthropod associations were not evaluated; FEMAT 1993). Large decayed logs are considered to be important habitat features of late-successional forests (Harmon and others 1986, Perry and Amaranthus 1997), and at least two published studies have shown that truffle production was positively associated with decayed wood (Amaranthus and others 1994, Clarkson and Mills 1994). We wanted to know whether truffle production and number of truffle species were greater in old-growth fir forests than in younger forests. We also wanted to know whether truffle presence was associated with habitat features such as decayed logs and organic soil depth. In this study, we compared truffle fruiting patterns between old-growth and nearby, mature fir forests, and evaluated associations between truffle abundance and measures of habitat structure and composition within those forests (Waters and others 1997).

Study Area and Methods

We located four areas in which a stand of old-growth fir forest was located near a stand of mature (stem-exclusion phase) fir forest. The old-growth and mature stand within each of these four areas were similar in elevation, slope, aspect, and tree species composition *(table 4)*. Within each of the eight stands we established a 6 x 6 grid with 10-m spacing between grid points (0.25 ha). In three of the pairs, the two

grids were less than 0.4 km apart and in the fourth, the two grids were 0.7 km apart. The eight grids were located in Swain Mountain Experimental Forest and were within stands of similar age, structure, and composition to old-growth and mature stands used in Study I.

In 1993, we measured vegetation characteristics within 50.3-m^2 circular plots (4-m radius) centered at each grid point. Within each of these vegetation plots, we measured the dbh of all trees ≥12 cm in dbh and tallied trees 1-5 cm and 6-11 cm in dbh. We also determined decay class (Maser and others 1979) and measured the length and mid-point diameter of portions of all logs within the vegetation plot with a mid-point diameter ≥10 cm.

Table 4—*Stand information for old-growth and paired, mature stands. Percent red fir was the percentage of total basal area.*

Pair	Stand type	Elevation	Aspect	Slope	Red fir
		m		pct	pct
1	Old-growth	1988	NW	9	90
	Mature	2003	NW	11	99
2	Old-growth	1796	SE	16	41
	Mature	1811	NE	18	10
3	Old-growth	1799	SE	19	60
	Mature	1823	SE	19	19
4	Old-growth	1945	NE	16	87
	Mature	1954	NE	14	100

Truffles were collected within a 4-m^2 circular plot positioned systematically near each of the 36 grid points. In 1993, truffles were collected during four sample periods; the four truffle plots were clustered around each grid point (total of 144 truffle plots per grid). In 1994, truffles were collected during three sample periods, and the three truffle plots were clustered around each of 36 points offset from the 1993 points (total of 108 plots per grid). Plots were never located on previously sampled areas. The fourth sample period in 1994 was canceled because soils were dry and we found few truffles. We also measured the length and diameter of portions of decayed logs (classes 4-5; Maser and others 1979) within the 4-m^2 truffle plot (decayed logs were soft and elliptical to flat in cross-sectional shape) and the depth of the organic soil layer at three systematically positioned points within each truffle plot. Decayed logs and organic soil depth were measured within truffle plots in all sample periods except the first sample period of 1993.

We used repeated-measures ANOVA (sample period was the repeated factor) with a randomized-blocks design (each pair of grids was a block) to test whether truffle frequency and biomass and number of truffle species differed significantly between the two age classes in 1993 and 1994. We also compared frequencies of truffle species between old-growth and mature forests using a contingency table to test the null hypothesis of no association between age class and frequencies of the 10 most common truffle species; numbers of truffle collections were pooled across sample periods and years for this test.

We used two methods to evaluate potential associations between truffle abundance and measures of habitat structure and composition. First, we evaluated

Spearman ranked correlations across the eight grids between truffle abundance (truffle frequency and biomass pooled across sample periods and years for each grid) and eight habitat measures (we used the mean value from the 36 vegetation plots sampled in each grid). The eight habitat measures were basal area of white fir, basal area of red fir, basal area of snags, number of fir stems 1-5 cm in dbh, number of fir stems 6-11 cm in dbh, surface area of undecayed logs, surface area of decayed logs, and average organic soil depth. We performed multiple regressions to evaluate the association between truffle abundance in 1993 within the area of the 50-m^2 vegetation plots and the same eight habitat variables used above. We were able to perform this analysis for the 1993 data only because the four truffle plots sampled in 1993 were located within the 4-m-radius vegetation plots, but the truffle plots sampled in 1994 were not. We performed two multiple regressions. In one, the dependent variable was the number of truffle plots at each grid point in which $\geq$1 truffle collection was found (values ranged from 0 to 4) and in the other, the dependent variable was the sum of the dry weights of truffle collections found in the four truffle plots at each grid point. We pooled across forest type (n = 288 vegetation plots) for each multiple regression.

We also evaluated associations between truffle presence and (1) presence of decayed wood and (2) organic soil depth within the 4-m^2 truffle plots. We used a 2 x 2 contingency table to test for association between truffle presence (plots with $\geq$1 truffle and plots with no truffles) and presence of decayed wood (plots with at least some decayed wood and plots with no decayed wood). We used the Wilcoxon rank-sum test (SAS Institute 1989) to compare organic soil depth values between plots with truffles and plots without truffles. Tests were performed separately for three sample periods in 1993 and three sample periods in 1994.

Results and Discussion

We sampled 8,064 m^2 over 2 years and found truffles in 30.4 percent of the 2,016 plots; truffle biomass was equivalent to 2.43 kg/ha. A total of 46 species were found. Truffle frequency *(fig. 5)* and biomass *(fig. 6)* did not differ significantly between the two age classes in 1993 or 1994. Number of truffle species also did not differ significantly between age classes in 1993 (F = 0.74, d.f. = 1, 3, α = 0.45) or 1994 (F = 0.16, d.f. = 1, 3, α = 0.72). A total of 38 species were found in old-growth forests and 38 in mature forests. There was significant association between age class and frequencies of the 10 most common species *(fig. 7)*. Frequencies of *Gautieria monticola*, *Gymnomyces abietis*, *Thaxterogaster pingue,* and *Leucophelps spinispora* were similar between old-growth and mature forests, but frequencies of *Hysterangium crassirhachis* and *Hysterangium coriaceum* were greater in mature forests, and frequencies of *Alpova trappei*, *Rhizopogon evadens*, *Melanogaster varigatus*, and *Hymenogaster sublilacinus* were greater in old-growth forests.

None of the correlations between the eight habitat measures and truffle frequency were significant ($\alpha > 0.31$), nor were any of the correlations with truffle biomass ($\alpha > 0.13$). Also, little of the variation in either measure of truffle abundance within the 288 50-m^2 circular areas was explained by the eight habitat measures. R^2 was only 0.06 for the multiple regression using number of truffle plots with $\geq$1 truffle collection as the dependent variable, and 0.02 using the total dry weight of truffles as the dependent variable.

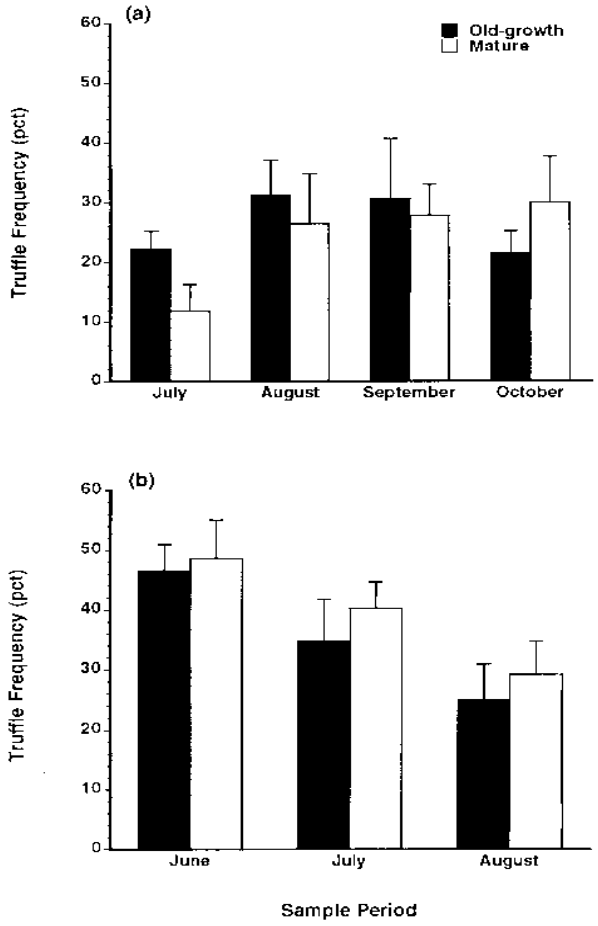

Figure 5—Means and standard errors of truffle frequency in four old-growth and four mature fir stands in northeastern California during (a) four sample periods in 1993 and (b) three sample periods in 1994. Repeated-measures ANOVA (sample period was repeated measure) indicated effect of age class was not significant in 1993 (F = 0.10; d.f. = 1, 3; α = 0.78) or 1994 (F = 0.62; d.f. = 1, 3; α = 0.49). Sample period effect was nearly significant in 1993 (F = 3.32; d.f. = 3, 9; α = 0.07) and significant in 1994 (F = 13.39; d.f. = 2, 6; α = 0.01).

Not only were decayed wood and organic soil depth not good predictors of truffle abundance among grids or among vegetation plots, they were not good predictors of truffle presence among 4-m^2 truffle plots. We found a significant association between presence of decayed wood and presence of truffles in only one of six tests *(fig. 8)*. Association was greatest in both years during the last sample period, however, when soils were dry. Decayed logs retain large amounts of water and may influence truffle production most when soils are driest (Amaranthus and others 1994). Mean values of organic soil depth were greater in plots with truffles than in plots without truffles in each sample period, but ranked values were only marginally significant in one of six tests *(fig. 9)*.

Truffle production has been shown to be low in young (< 30 years) conifer stands after stand-replacement events like clearcutting (Amaranthus and others 1994,

Clarkson and Mills 1994, Vogt and others 1981). North and others (1997) found that 60-year-old stands that had originated after clearcutting in Washington had significantly lower truffle biomass than old-growth (≥300-year-old) stands, but that truffle biomass did not differ significantly between old-growth and natural, mature stands (stands that developed after windstorms in the early part of the century and that were dominated by trees about 70 years old). Luoma and others (1991) did not statistically compare truffle biomass among stand age classes, but found that standing crop biomass of truffles was greater in mesic, mature stands (80 to 199 years old) of Douglas-fir in Oregon than in mesic, old-growth stands (≥200 years old).

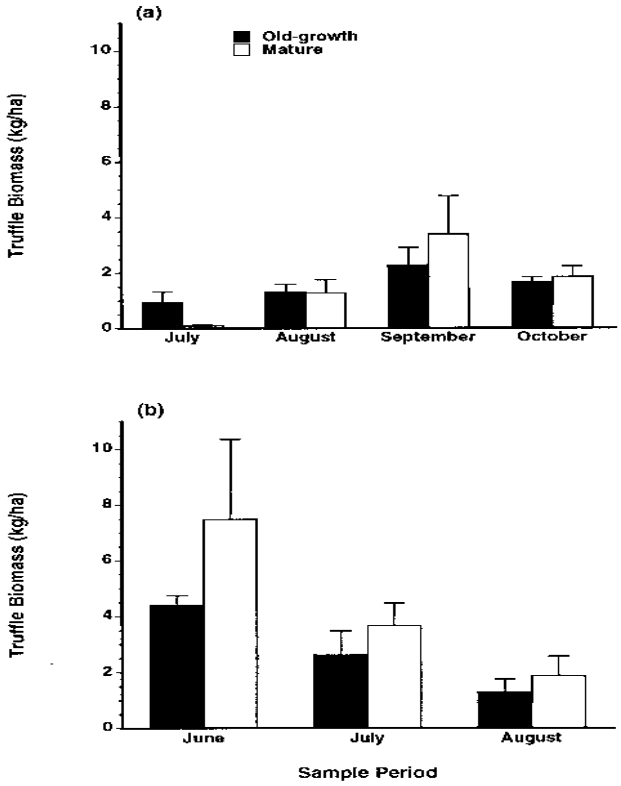

Figure 6—Means and standard errors of truffle biomass in four old-growth and four mature fir stands in northeastern California during (a) four sample periods in 1993 and (b) three sample periods in 1994. Repeated-measures ANOVA indicated effect of age class was not significant in 1993 (F = 3.38; d.f. = 1, 3; α = 0.16) or 1994 (F = 0.68; d.f. = 1, 3; α = 0.47). Sample period effect was significant in 1993 (F = 23.17; d.f. = 3, 9; α < 0.01) and 1994 (F = 8.14; d.f. = 2, 6; α = 0.02).

The lack of significant associations between truffle abundance and habitat measures suggests that truffle collections (pooled across species) were more or less randomly distributed within the stands in which we sampled. Each of these stands, however, was densely stocked, unmanaged, and relatively homogeneous. Associations may be greater in more disturbed or heterogeneous stands.

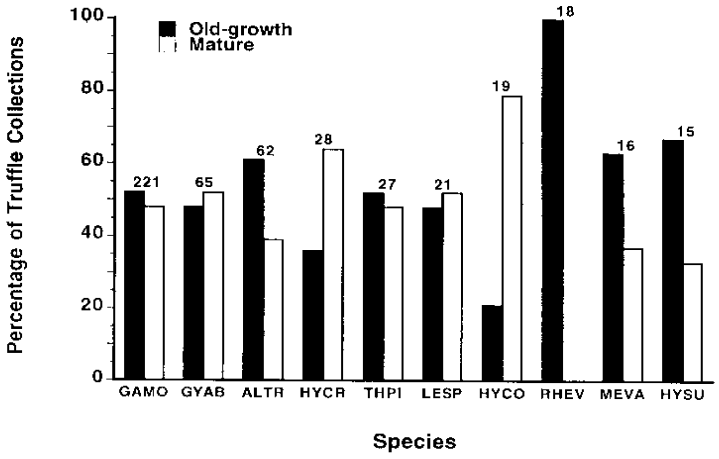

Figure 7—Percentages of truffle collections found in four old-growth and four mature fir stands in northeastern California. Total number of collections found in 1993 and 1994 for each species is listed above bars. Contingency table analysis indicated significant association between age class and numbers of collections of 10 most common truffle species (χ^2= 31.58, d.f. = 9, $\alpha < 0.01$). Ten species were *Gautieria monticola* (GAMO), *Gymnomyces abietis* (GYAB), *Alpova trappei* (ALTR), *Hysterangium crassirhachis* (HYCR), *Thaxterogaster pingue* (THPI), *Leucophelps spinispora* (LESP), *Hysterangium coriaceum* (HYCO), *Rhizopogon evadens* (RHEV), *Melanogaster varigatus* (MEVA), and *Hymenogaster sublilacinus* (HYSU).

Conclusions

We began our research with the goal of trying to understand patterns of spotted owl habitat use observed in and around Swain Mountain Experimental Forest in the Lassen National Forest. We tested the hypothesis that abundance of the owl's primary prey was lower in old-growth forests that had been shelterwood-logged 6 to 7 years previously (where owls were rarely detected) than in nearby, unlogged old-growth forests (where owls were frequently detected). Abundance of flying squirrels was significantly less in shelterwood-logged old-growth forests than in unlogged old-growth and mature forests. Spotted owls may have avoided the open, shelterwood-logged forests for additional reasons, but low abundance of flying squirrels made these forests poor foraging habitat for the owl.

Consistent with other studies, dietary analysis showed that truffles were a common food of flying squirrels in our study area. The food preference study showed that the foods most preferred by captive squirrels were two species of truffles, although the lichen *Bryoria fremontii* was also readily eaten. Truffle frequency was correlated with abundance of flying squirrels across the 12 grids in which we sampled, suggesting that truffle availability may have influenced habitat selection by flying squirrels.

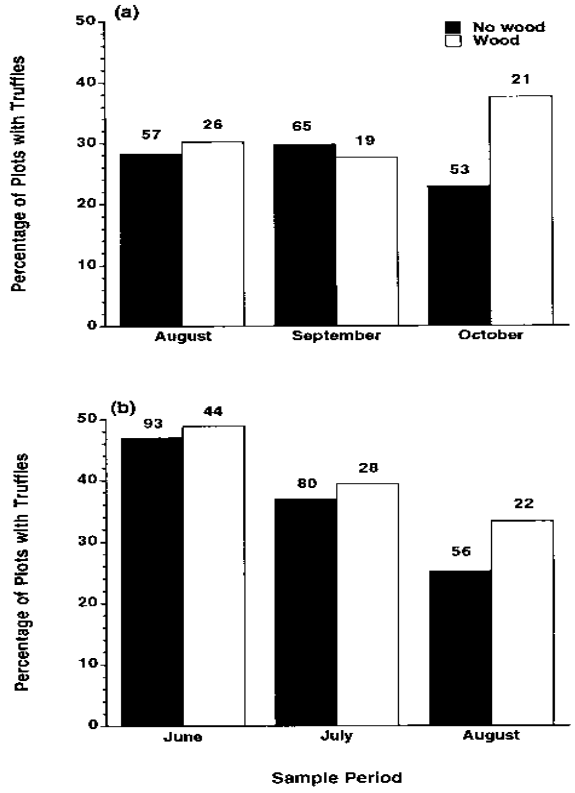

Figure 8—Percentages of 4-m^2 truffle plots (pooled across four grids in old-growth stands and four grids in mature stands) in (a) 1993 and (b) 1994 without decayed wood and with at least some decayed wood that had $\geq$ 1 truffle collection (n = 288 truffle plots for each sample period). Number of plots with truffles is listed above each bar. The α values from 2 x 2 contingency tables (d.f. = 1) testing for association between truffle presence and presence of decayed wood were 0.73 in August 1993, 0.73 in September 1993, 0.02 in October 1993, 0.76 in June 1994, 0.70 in July 1994, and 0.19 in August 1994.

Low truffle frequency in shelterwood-logged forests suggests that silvicultural treatments within Swain Mountain Experimental Forest negatively affected truffle production. Our study was not designed to determine the relative impacts of harvest level and ground disturbance. We note, however, that harvest level in the shelterwood-logged forests (where mean basal area in the four grids was about 30 percent of that in the four grids in old-growth forests) was roughly similar to harvest level in the heavily thinned units at the Jennie Springs site, but in that study, truffle frequency and biomass were not significantly less in heavily thinned units than in unthinned units. Unlike disturbance to the forest floor in the shelterwood-logged forests, disturbance to the forest floor was minimized at the Jennie Springs site, suggesting that the ground disturbance associated with site preparation in Swain Mountain Experimental Forest may have had a greater effect on truffle production than harvest level. Longer-term studies specifically designed to determine the relative impacts of tree harvest and ground disturbance on sporocarp production would provide useful information for forest managers.

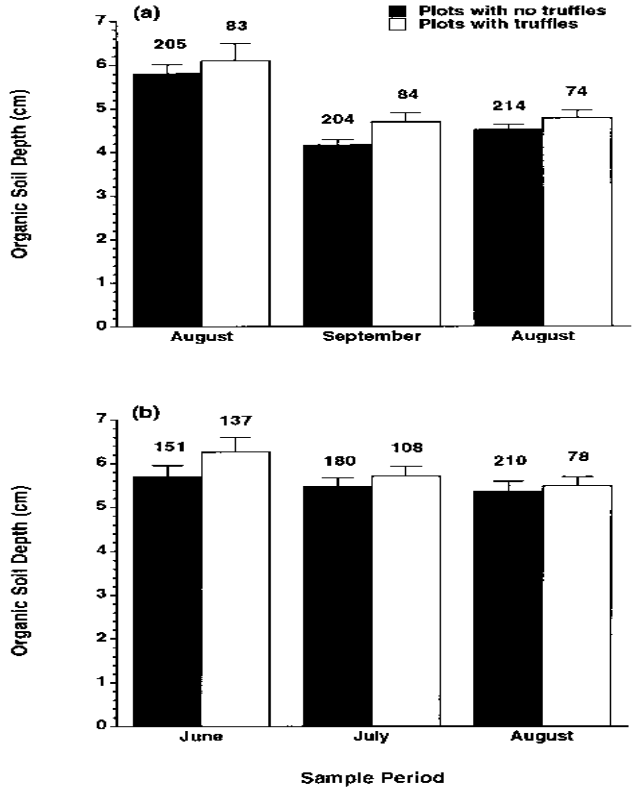

Figure 9—Means and standard errors for organic soil depth in (a) 1993 and (b) 1994 within 4-m^2 truffle plots with no truffles and plots with $\geq$ 1 truffle collection (pooled across four grids in old-growth stands and four grids in mature stands). Number of truffle plots is listed above each bar. The α values from Wilcoxon rank-sum tests comparing ranked values between plots without truffles and plots with truffles were 0.45 in August 1993, 0.06 in September 1993, 0.33 in October 1993, 0.35 in June 1994, 0.49 in July 1994, and 0.10 in August 1994.

We found that by the stem-exclusion phase of forest development, truffle production and species richness were similar to that found in old-growth forests. Thus, we found no evidence indicating that old-growth fir forests in the Lassen National Forest were unique in truffle production or diversity of truffle species. Even though the old-growth and mature forests we sampled were floristically simple, 46 species of hypogeous ectomycorrhizal fungi were found in 2 years, and we do not know how many epigeous ectomycorrhizal species were present. The functional significance of this high diversity of mycorrhizal fungi is poorly understood. Even though truffle frequency (pooled across truffle species) did not differ significantly among thinning levels or between old-growth and mature forests, frequencies of individual taxa did. This suggests that the effects of forest management on truffle production and assemblages of mycorrhizal fungi are species specific and complex. Different species may perform different functions and be adapted to different environmental, substrate, and host conditions (Perry and Amaranthus 1997, Trappe 1977). It may be difficult to make predictions or generalizations until we have more information on species-specific effects of disturbance. Similar disturbances may have

different overall effects in areas with different assemblages of truffle species, and the same species may react differently under different environmental conditions. This implies that the effects of forest management on mycophagous mammals are also complex, especially because our food preference study and other studies suggest that different truffle species have different palatabilities, and so little is known about the nutritional values of different truffle species. Acknowledgment of the complexities of forest ecosystems and the limitations of current knowledge argues for an adaptive approach to forest management (Kohm and Franklin 1997).

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American Matsutake *(Tricholoma magnivelare*) across Spatial and Temporal Scales[1]

Michael P. Amaranthus,[2] David Pilz,[3] Andrew Moore,[4] Rick Abbott,[5] Daniel Luoma[6]

Abstract

Thousands of people annually harvest American matsutake *(Tricholoma magnivelare* [Peck] Redhead) from private, State, and Federal lands. Yet, spatial and temporal uncertainties about matsutake ecology and production hinder efforts to manage this valuable resource on a sustained basis. Our studies indicate that production and value of American matsutake vary strongly over time, are spatially related to individual host plants, and can be enhanced by certain practices at various spatial scales. Managers wishing to predict matsutake production at individual shiro, stand, landscape, and regional scales need information for a wide variety of habitat types over the long term. Understanding local, regional, national, and international production and market factors will aid decision-making and policy-making. Biological, social, and economic influences function across many scales and are key to sustainable management of American matsutake.

Introduction

Current forest management decisions integrate increasingly complex and changing social, economic, and ecological values. The decision-making process requires in-depth knowledge of the function and abundance of organisms in forest ecosystems across various spatial and temporal scales. Usually, ectomycorrhizal fungi (EMF) have been overlooked when forest ecosystems are considered. However, foresters, ecologists, managers, and policymakers are beginning to recognize that EMF influence forest productivity, recovery, and wildlife food webs (Amaranthus and Perry 1987, 1989; Harley and Smith 1983; Waters and others 1995). This paper explores another EMF product of forest ecosystems: the expanding industry that harvests wild edible fungi.

Harvesting wild edible fungi in the Northern Hemisphere is a major industry, with sales estimated to exceed $1 billion (Hall and others [In press]). Interest in wild edible fungi stimulated early research on EMF (Frank 1885). Over the past century, we have developed a general understanding of the geographic range, host

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associations, and mycorrhizal characteristics of important edibles, such as *Boletus, Cantharellus, Tricholoma,* and *Tuber* species. However, we have poor understanding of their ecology and productivity (factors greatly influencing spatial and temporal variability) and their interaction with other forest vegetation and wildlife species. The decline of wild edible mushrooms in Europe and Japan (Arnolds 1991, Kawai and Ogawa 1981) has created the need to understand these EMF species over expanding temporal and spatial scales (*table 1).* This is particularly true of the American matsutake because the dramatic decline in Japanese matstuake production has created enormous market demand for related species.

Table 1—*Factors that influence matsutake production and harvest levels at various spatial scales.*

Spatial scale	Factor
Individual shiros 1-50 m^2	Mushroom harvest method Host presence Soil compaction/ripping Watering Host productivity
Stand and landscapes 1-100 km^2	Silvicultural method Temperature/rainfall Stand density/composition/age Plant community/seral stage Wildlife interactions
Regional and global >1,000 km^2	Market demand International production Socioeconomic forces Disturbance agents Policy and regulations Access to roads/airports

Individual Shiro Scale

The American matsutake and related species form a distinctive fungal colony in the soil called a "shiro," the Japanese term for "white," "castle," or "place." The shiro is a dense mass of mycelia that form a white to pale gray mat beginning just below the litter layer *(fig. 1)*. Across its range, American matsutake is an EMF symbiont with true firs, pines, hemlocks, Douglas-fir, and some hardwood species. Within a particular habitat type and when conditions are right, the matsutake mushroom will fruit in association with the mycorrhizae and hyphae of specific host plants in the shiro colony.

The American matsutake industry employs thousands of commercial harvesters from British Columbia to Mexico. Accelerated harvest of the mushroom has heightened concern that matsutake production may not be sustainable and that harvesting adversely impacts productivity of both plant host and matsutake. Government agencies operating in the Pacific Northwest, such as the USDI National Park Service, USDA Forest Service, and the State of Washington Department of Natural Resources, have recently restricted matsutake harvest in some areas because of uncertainties over production and environmental impacts. Many questions arise concerning the scale of the individual shiro. What are the spatial relationships to

hosts or indicator plants? What are the impacts of litter removal, raking, and other mushroom harvest practices? What are the effects of harvesting mushrooms before spore maturation? Can shiro production of matsutake mushrooms be enhanced? Answers to these questions are needed by resource specialists, managers, and policymakers to make informed decisions about the sustainability of the resource and how it should be managed.

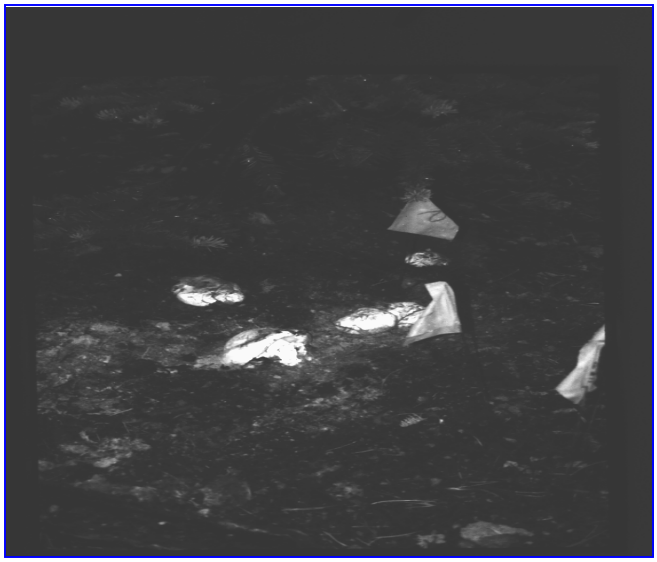

Figure 1—Raking exposes matsutake mushrooms and shiro-white mass of mycelia beneath the litter layer. Yellow flags indicate location of harvested matsutake mushrooms.

To study the spatial relationship between the American matsutake and individual plants, we established two study blocks within 5 km of each other in an area of known production. The study area occurs on the Diamond Lake Ranger District of the Umpqua National Forest in the southern Oregon Cascade Mountains. Soils are deep and derived from volcanic ash parent material. Block 1 is a north-facing slope and Block 2 is a west-facing slope. Slope steepness ranges from 0 to 5 percent on block 1 and from 10 to 45 percent on block 2. Block 1 occurs at a mean elevation of 1,450 m and block 2 at 1,370 m. In each block, a first point was randomly established. From this starting point, a 6 x 6 array of grid points (30-m spacing) was established.

In September and October 1995, each matsutake mushroom that fruited within the grid was located and marked by a wire engineering flag. In blocks 1 and 2, respectively, 86 and 82 matsutake mushrooms were located and flagged. For each matsutake, the distance to the base of the nearest Shasta red fir (*Abies magnifica* var. *shastensis*), mountain hemlock (*Tsuga mertensiana*), western white pine (*Pinus monticola*), candystick plant (*Allotropa virgata*; an achlorophyllous plant whose roots have been observed to be colonized by matsutake mycelium), and neighboring matsutake was measured to the nearest 0.1 m. Only trees that were of intermediate, codominant, or dominant crown class were used for measurements. The distance from each of the 36 grid points to the base of the nearest Shasta red fir, mountain hemlock, western white pine, candystick, and neighboring matsutake sporocarp was also measured to the nearest 0.1 m. Again, only trees that were of intermediate, codominant, or dominant crown class were measured. A Wilcoxon signed rank test

was used in a nonparametric paired comparison of matsutake distances to random points, as represented by the grid points or other plants. A significant difference between the distance of the matsutake to a random point or to one of the trees—the candystick or another mushroom—indicated an association.

Results from this study indicate that at the Diamond Lake study site, American matsutake production is spatially related to the occurrence of individual Shasta red fir *(fig. 2),* candystick plants, and other matsutake mushrooms *(fig. 3)*. Matsutake were distributed spatially in proximity to Shasta red fir *(fig. 4)*. Matsutake are symbiotic and form mycorrhizae on the site with Shasta red fir—the Shasta red fir translocates tree carbohydrates to the matsutake fungus, and in return, the matsutake provides the Shasta red fir with the moisture and mineral nutrition absorbed from its filaments in the soil.

Figure 2—Open understory and Shasta red fir (*Abies magnifica* var. *shastensis*) from the Diamond Lake study area are indicators of productive matsutake habitat.

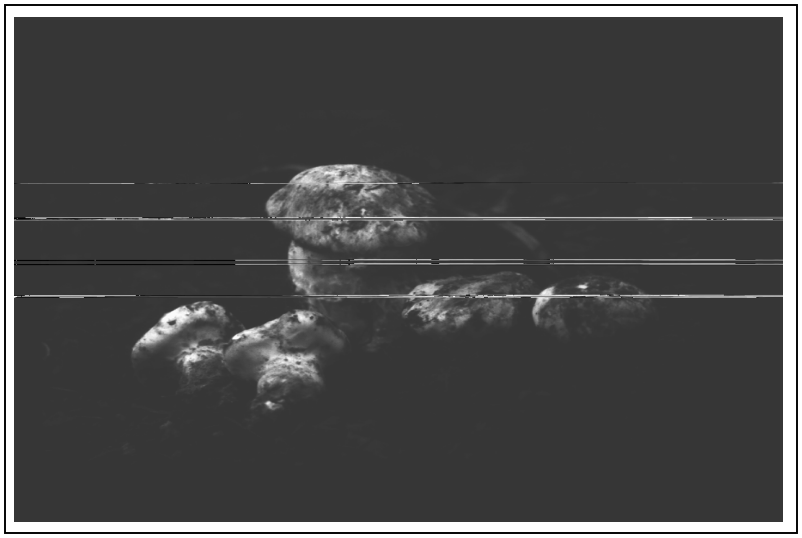

Figure 3—American matsutake (*Tricholoma magnivelare*) harvested from the Diamond Lake study area.

Matsutake were also distributed spatially in proximity to candystick (*Allotropa virgata*) *(fig. 4)*. Although this species is often referred to as a saprophyte, candystick is a mycotroph that obtains nutrients and carbon compounds via a mycorrhizal fungus associated with its roots (Castellano and Trappe 1985). American matsutake has been observed to occupy the roots of candystick in Idaho (Lichthardt 1995), and it is likely that the Shasta red fir, matsutake, and candystick have a complex functional relationship in which compounds are transferred between all three partners.

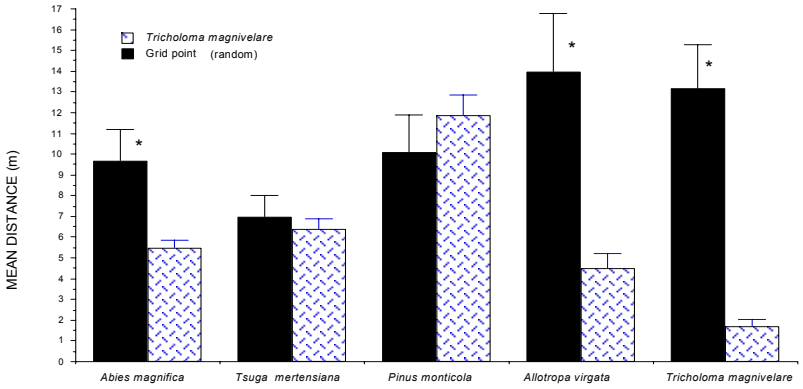

Figure 4—Comparison of distance from random points and individual *Tricholoma magnivelare* to nearest *Abies magnifica* var. *shastensis*, *Tsuga mertensiana*, *Pinus monticola, Allotropa virgata,* and neighboring *Tricholoma magnivelare.* Asterisk (*) indicates significantly closer to *Tricholoma magnivelare* than random point. Wilcoxon signed rank test $P \leq 0.05$.

The presence of Shasta red fir and candystick is an "indicator" of matsutake production that can be used by managers, researchers, and commercial and recreational harvesters for locating and managing matsutake in the southern Oregon Cascades. It is likely that other associations exist with specific trees and substrates in other areas of commercial production. For example, harvester activity is concentrated in tanoak (*Lithocarpus densiflorus*) areas in the Klamath Mountains of southwest Oregon and northwest California and in lodgepole pine (*Pinus contorta*) areas in the coastal dunes of the Oregon Coast. The significant spatial relation between American matsutake and other matsutake mushrooms reflects the clustering of fruiting-body production into the distinctive fungal colony or shiro. This clustered nature of production has implications for developing inventory and monitoring sampling designs for estimating matsutake production.

Research and monitoring of the effects of mushroom harvesting practices on sustainablilty of production is needed at this smaller scale. Activities such as litter removal, raking, compaction, timber harvest, and harvesting immature mushrooms before spore maturation may all influence matsutake production at the scale of the individual tree or cluster. A study is underway in four habitat types in Oregon to evaluate effects of various matsutake harvesting techniques on production (Pilz and others 1996). Research is also needed on the physiology, life cycle, and reproduction of shiros. Only by determining how matsutake typically grows, reproduces, and

disperses into new habitat can we begin to understand the impacts of our land management practices on long-term viability of the fungus and its sporocarps.

There is also opportunity to enhance production at the scale of individual shiros. Near block 2 of the Diamond Lake study, we chose three pairs of matsutake clusters to determine whether watering would increase production. In September 1994, each matsutake mushroom was carefully located, flagged, harvested, and weighed. In summer 1995, pairs of matsutake mushroom clusters that had similar mushroom numbers and biomass production during the fall 1994 season were selected for treatment. One cluster in each pair was selected for treatment and 2.5 cm of water was sprinkled on each cluster once a week for 4 weeks, beginning August 3, 1995. Although the watered areas did not have an increase in the number of matsutake harvested, the average weight of individual mushrooms was greatly increased *(fig. 5)*. Although these results cannot be applied to all matsutake areas throughout its range, watering, where feasible, is a potential enhancement tool for increasing the biomass and value of individual clusters.

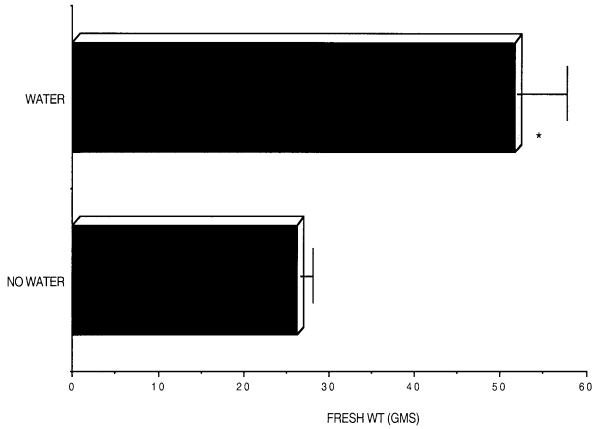

Figure 5—Average fresh weights of grade 1 *Tricholoma magnivelare* in watered and non-watered paired plots. Asterisk (*) indicates significantly greater fresh weight. Wilcoxon signed rank test $P \leq 0.05$

Stand and Landscape Scale

The potential interactions between matsutake, stand, landscape conditions, and management practices are numerous, complex, and site-specific. For example, clear-cutting is an efficient means of timber harvest, but it removes the photosynthetic host and energy source upon which the matsutake depends. Spores or mycelium of the matsutake may persist in the soil and colonize young trees, but fruiting typically ceases for at least two or three decades (Ogawa 1982). On the other hand, matsutake may fruit more abundantly in the middle-age stands that eventually develop with even-aged management than in late successional forests.

Japanese foresters utilize management techniques to increase or enhance the natural production of Japanese matsutake (*Tricholoma matsutake*) (Ogawa 1982). Pines 40 to 50 years old are most productive, whereas those more than 50 years in age decrease in productivity. Forests with a high density of pines and low density of other trees and shrub species are favored for matsutake stand-level treatments (Kawai

and Ogawa 1981, Ogawa 1982). Foresters promote a pine canopy that allows light to penetrate to a sparsely vegetated or open forest floor. Forest practices in Japan include thinning of pines and other competing tree species and removal of shrubs, herbs, dead branches, and damaged and diseased trees. This allows the forest floor to dry and to receive more light with better air circulation. Soils that are relatively warm, well drained, and with thin litter and organic layers are favorable to the development of the Japanese matsutake mycelium. Pine forests positioned on southwestern slopes and ridgetops tend to be most suitable. Most sites lack optimal conditions for matsutake mushroom production.

Unfortunately, in North America, there is little analogous information on which to base forest management practices to enhance production of matsutake or any other EMF mushroom or truffle species. We are currently designing and implementing studies in Oregon to evaluate the influence of overstory and understory density and litter thickness on matsutake production. Manipulating overstory and understory vegetation and removing surface soil organic layers to improve matsutake production will result in a variety of other ecosystem effects related to changing forest structure and composition.

Our research indicates that tremendous variability in matsutake production can occur across stand and landscapes from year to year. Production records from 1992 to 1996 on our 160-hectare study site in tanoak/mixed conifer habitat in the Klamath Mountains of southwest Oregon exemplify this variation *(fig. 6)*. Commercial harvesters located and harvested matsutake daily during the fruiting season, and all sporocarps were tallied and weighed fresh. In 1992, the study area produced four times more matsutake by weight than in 1993 and 1995 and 620 times more than in 1994.

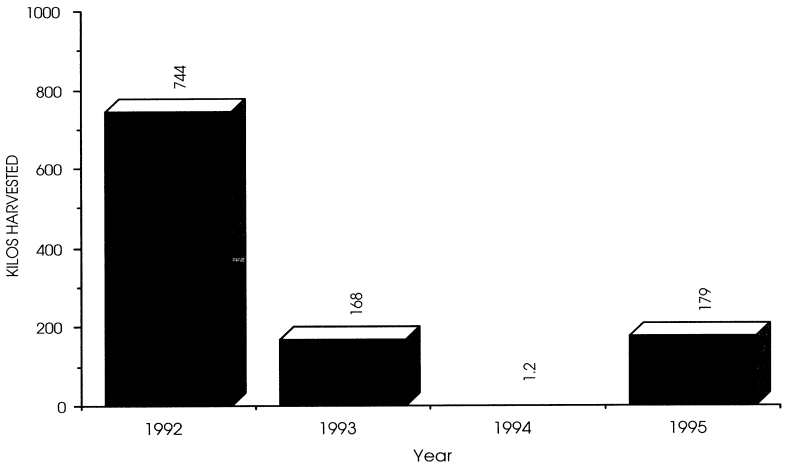

Figure 6—Total kilograms (fresh wt.) of *Tricholoma magnivelare* harvested from 160-hectare study area in the Klamath Mountains from 1992 to 1995.

Such dramatic swings in production from year to year have important implications for management and administration of the commercial harvest. Migrant harvesters account for a majority of the commercial work force and are important for providing a reliable supply of matsutakes to mushroom buyers and brokers. Large and sudden pulses of matsutake production lead to large and sudden influxes of migrant pickers that can catch public land agencies and local communities

unprepared to provide adequate lodging, camping, sanitation, and garbage facilities. Influx of harvesters can stimulate rural economies but large numbers of people in the woods also can create problems: increased litter, noise, fire danger, traffic hazards, disturbance of wildlife, and conflicts with big-game hunters and recreational mushroom harvesters. Ongoing studies are improving our ability to predict the level of matsutake production in various habitats. The ability to predict the magnitude of matsutake production in advance would aid management and administration of the mushroom harvest.

Temporal variation in fruiting necessitates long-term monitoring to characterize abundance, distribution, and trends that are essential to the management of commercial harvest. Currently, poorly documented historical levels of production, ephemeral fruiting patterns, and natural variation in habitat are complicating efforts to provide reliable estimates of production at the stand and landscape scale.

Regional and Global Scale

The American matsutake is commercially harvested from the northern interior of British Columbia to Mexico. In British Columbia, the harvest begins in August and September, moving generally from north to south and from high to low elevations. In the Pacific Northwest, the harvest generally ends in January in the coastal areas of northern California. In 1992, nearly 1 million pounds of American matsutake were harvested. The mean price in 1992 was more than $8 per pound when averaged for all stages of development or "grades" (Schlosser and Blatner 1995). Grade 1 matsutake brings the highest price and is characterized by unopened caps in which the mushroom veil is still completely intact with the mushroom stem. Once the matsutake begins to open, it is downgraded to 2, 3, 4, 5, or 6, with the lowest grade reflecting a fully open matsutake that is often affected by insects or other damage agents. The average prices paid in 1992 for matsutake from the 160-hectare study site of tanoak/mixed conifer habitat in southwest Oregon was $20 for grade 1, compared to $1.50 for grade 5. For the period from 1992 to 1995, the price to harvesters ranged widely, from $0.25 to $100 per pound depending upon the grade and demand for the mushroom.

Unlike other harvested wild mushrooms, the market for the American matsutake is largely international, with most exported to Japan. The American matsutake closely resembles the Japanese matsutake (Redhead 1984) in shape, odor, and flavor. Demand for Japanese matsutake has increasingly exceeded supplies during the past 30 years because of the decline of Japan's matsutake habitat and growing demand from a larger and wealthier consumer population (Kawai and Ogawa 1981). Hence, Japanese entrepreneurs began importing similar mushrooms to supplement supply, especially during the past decade (Hosford and others [In press]). Japanese matsutake and related species are also harvested from China, North and South Korea, and Russia, but most studies of the Japanese matsutake have been conducted in a limited geographical area (Japan) and a narrow range of ideal habitats (red pine forest). By contrast, the American matsutake is widely distributed throughout North America and is harvested from diverse forest habitats where it develops mycorrhizal associations with numerous tree species.

Regional biological disturbance agents and climatic and socioeconomic forces can greatly influence production. Since 1905, the matsutake forests of Japan have

been plagued by the pine short nematode (Hosford and others 1997). A combination of climatic, socioeconomic, and biological factors in Japan has increased the magnitude of the plague. Pine mortality from nematode disease often increases after a prolonged period of scarce rainfall and high temperatures. This apparently weakens the pines' resistance to the parasite. In addition, a change in the use of the forest has also had an adverse effect. Traditional harvesting of wood for charcoal from understory shrubs and trees, such as oaks, has historically favored the growth of shade intolerant pines. The conversion from wood burning stoves to natural gas burners has promoted conditions leading to pine mortality and the growth of the dense, brushy understory unfavorable to Japanese matsutake production. In contrast, matsutake production has increased dramatically in Korea where pine plantations of 40 to 50 years of age are widespread and prime for matsutake production. These pine plantations are a result of reforestation after the Korean war.

At the largest scale, a variety of global factors influence the demand for and value of matsutakes. Global weather patterns and fluctuating international trade creates large variations in local prices paid to pickers. Consequently, landowners or land managers in America have difficulty calculating fair market value and reasonable compensation for the harvest of matsutakes from their forests. Managers also have difficulty calculating the quantities of matsutakes collected from their lands. Harvesters often cross property boundaries in their search for mushrooms to sell to buyers of their choosing. Federal mushroom permits in the Pacific Northwest are not currently based on a percentage of the market value of the crop, as they are with many other products. Higher permit fees are problematic because harvesters may not be able to predict harvesting expense. Many factors determine harvester success, including fruiting abundance and density, competition from other harvesters, timing, price, and hunting and harvesting methods and conditions.

The monetary value of this relatively new, special forest crop and the conflict over its proper use have brought attention to and underscore the need to understand the American matsutake at both regional and global scales. Regional, social, and economic studies of matsutake harvesting and commerce would help managers develop fair harvest regulations and supply agency personnel and lawmakers in local, county, State, Provincial, and Federal governments with necessary information.

Conclusions

Today, tens of thousands of harvesters pick matsutake from private, State, and Federal lands in many countries across the world. Yet, uncertainty regarding managing matsutake hinders efforts to manage this valuable resource on a sustained basis. At the center of the management issue is a lack of information regarding productivity and management across a variety of spatial and temporal scales. In spite of the notable effort applied to matsutake research in recent years, several important topics remain to be addressed. Managers wishing to predict matsutake production and management effects at the individual shiro, stand, landscape, and regional scales will need reliable and long-term information for a wide variety of habitat types. Understanding local, regional, national, and international production and market factors will aid decision-making and policy-making. Ectomycorrhizal fungi, such as the matsutake, have co-evolved over millennia as a component of diverse and complex natural forest ecosystems operating across a variety of spatial and temporal scales.

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Managing Our Grandchildren's Forests: The Role of Soil Biology and Soil Ecology[1]

James R. Boyle[2]

The papers of this volume provide some "nuggets" of insight into the complexity of soil biology and its potential relevance for considering options for forest management. The authors have presented a special perspective from which to view the rich diversity of soil biota and their roles in forest ecosystems.

Soil arthropods make the soil a lively place and can give us insights into soil processes. Matsutake mushrooms, fruiting bodies of mycorrhizal symbionts, are important as specialty human foods and indicators of intimate and crucial associations with tree roots. Truffle fungi provide significant connections between soil conditions and biota with flying squirrels and predators. Actinorhizal shrubs have important roles in a variety of forest ecosystems. In some cases their accretion of nitrogen appears to have a major significance for forests. Various forest cutting practices in the Pacific Northwest have different effects on soil organisms and organic matter decomposition processes. Effects are site- and cutting system-specific. Generalizations are risky and more research is needed to completely define important interactions and processes. Ectomycorrhizal associations undergo successional processes and are influenced by forest conditions and disturbance. Spatial variability in soils and variations of fungus-root associations over time mean that simple evaluations of possible mycorrhizal conditions are not likely to provide useful information. New techniques may help overcome some of this limitation.

The papers in these Proceedings suggest that we are challenged to take a truly holistic view of forest-soil systems and forest management. Thus, the sometimes-controversial concept of "ecosystem management" can have relevance for our consideration of soil biology and forest management. The term "ecosystem management" means managing forests with ecosystem principles in mind. This is an appropriate mental framework for putting forest soils in appropriate context within forest management. Because soils are essential, interactive components of forest ecosystems (*fig.* 1), let us consider some ecosystem principles and how soils relate to them.

A forest ecosystem can be viewed as a defined unit of forest landscape that lets us think usefully about inputs and outputs of matter and energy, essential structures and components of human value, and critical processes and dynamics (e.g., nitrogen compound transformations). An ecosystem is a "holistic system for accounting." For

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convenience, we establish artificial boundaries to help define interactions with adjacent air, land, and water systems. Boundaries let us set the ecosystem of interest in an appropriate landscape setting. They give us points to measure incoming precipitation and outgoing water and sediments. An ecosystem has physical and biotic components: rocks, soils, microorganisms, and fauna above- and below-ground. It has structure: physical arrangement of slopes, herbs, shrubs, trees and water. And it is continuously being modified by myriad physical, chemical, and biological processes that move and transform matter and energy, water and nutrients, organic matter, and gases.

Soils within forest ecosystems support roots, water, and nutrients; store and transmit organic matter; and are habitats for a fantastic array of organisms. These organisms carry on numerous vital ecosystem processes. These include "chopping and shredding" organic matter as it passes through their guts, "tilling" the forest floor and mineral soil, burrowing and creating pores, "recycling" through decomposition processes, controlling each other by grazing and predation, and joining in symbioses of mycorrhizae and root nodules.

In relation to managed forests, it is appropriate to ask which critical forest ecosystem properties and processes influenced by soil biota are (1) *essential* to system maintenance, (2) *desirable* for system characteristics, and, (3) *likely to be influenced* by forest management. If we accept the "view from the bottom" (*fig. 1)*, we believe that any organisms involved in the following processes will be critical for forest productivity: effective plant rooting, water supply, plant nutrition, symbioses and rhizosphere processes. Plus, if we expand our view of critical processes to include those related to hydrology, we would consider habitats and other values of forests. By taking a "systems view" of potential forest management impacts on soil biology, we can evaluate changes to inputs of matter and energy to soils; transformation processes and related properties within soils (e.g., soil structure); and outputs from soils.

Forest management activities most often have two major effects on forest ecosystems: (1) simplification of the composition and diversity of plants at a site due to favoring desired crop trees and reducing or eliminating competing vegetation; and (2) altering, controlling, and reducing amounts and composition of organic residues by removing logs and "slash disposal." (Consider the implications of the latter: "slash" is bad; get rid of it; burn it; pile and burn it; windrow and burn it.) Of course, there are other management impacts on soils, including compaction and exposure to erosion, but these are likely to be under control via enlightened practices based on numerous workshops and current literature and knowledge. Thus, this discussion is limited to soil biota.

For context, consider the status of the "original" forests and soils that confronted our predecessor foresters. These were sites of some inherent natural productivity that had developed over hundreds or thousands of years of vegetation growing, shedding, dying and decaying—being "processed" by soil organisms—and interacting with other soil formation processes. Natural disturbances—such as periodic fires, windstorms, insect and disease epidemics and erosion, and slides and slumps—affected ecosystem conditions. Many of today's forest sites have had some harvesting and perhaps some management. (In the past, harvesting and "forestry," or forest management, were not necessarily synonymous!) Thus, soils of today's forests may or may not be the same as the first forests that were cut. It is relevant that today we

do have some reserved uncut lands in parks, wilderness, and other areas that can serve as baselines for comparisons of soils and other forest properties.

The ideal baseline conditions of soil properties (*fig. 1*) have been created and maintained by soil biological processes (i.e., soil organisms) interacting with parent materials and topography, vegetation, and dynamic climactic conditions over time (time is significant only in its substitution for some measures of numbers of chemical reactions, volumes of percolating water, heating and chilling cycles, etc.) For example, when a good forester decides that there will be no more tanoak, ceanothus, bearclover, alder or vine maple, or tops and branches left throughout the site, he or she has decided to change the physical and biochemical composition of organic matter potentially recycled through the soil ecosystems. This means that the diverse populations of millipedes, mites, springtails, bacteria, actinomycetes, fungi, protozooans, worms and gophers that have evolved in the forest soils and have developed the productive capacity of the site are now confronted with new "diets," differing in composition and timing from those of a previous time. The good forester expects that the soils will continue to be as productive as they previously were (or based on the findings of the Fast Fix Fertilizer Co-Op, the forester may need to apply a little N).

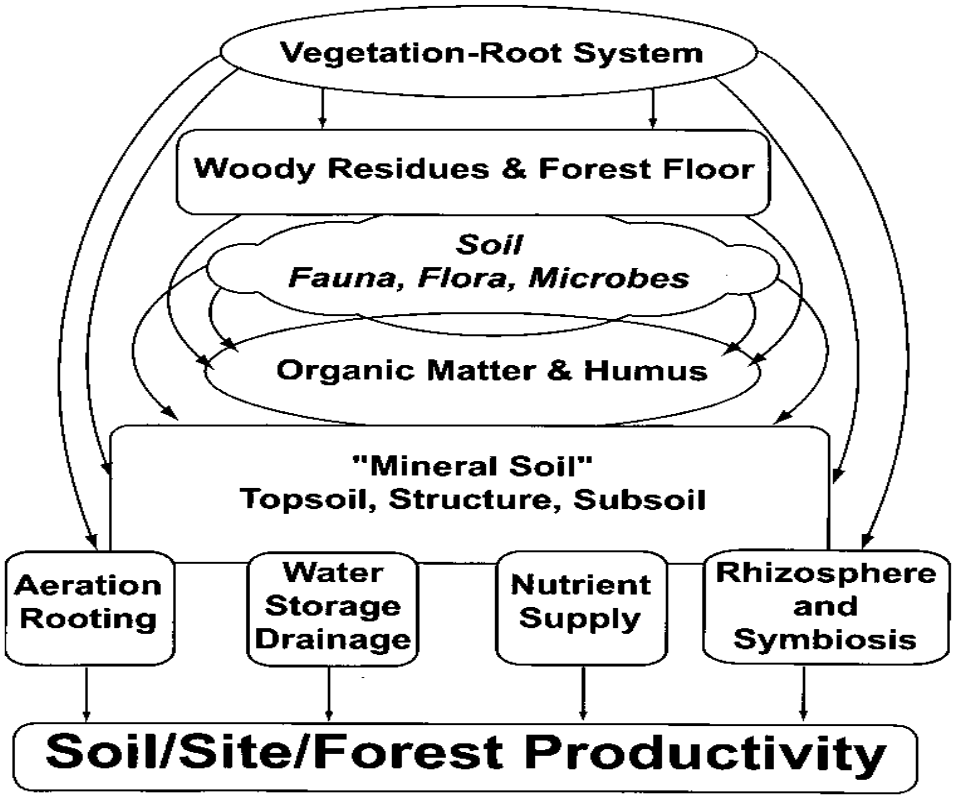

Figure 1—Forest productivity: a view from the bottom.

However, are we sure that soils will continue to be equally productive, harvest after harvest? If not, what indication will the forester have if there is a change? What will be the properties of the forest soils of our grandchildren's forest? How can we know the answers? What are the risks? What are the management options? In our

quest for ecosystem management, should we view all sites the same? How can we evaluate forest management interactions with soil biology and related forest ecosystem properties and processes?

Here are some suggestions. All sites and soils are not the same. We can learn about soil management from our colleagues in agriculture. Soil zoologists, biologists, and ecologists provide clues, but they do not always have definitive answers. It is wise to recognize resilient and sensitive soils and to maintain options. Consideration of a "land ethic" seems useful in thinking about forest management and long-term productivity.

Obviously, all forest sites are different. It follows that management impacts on soil biology will differ as well. Steep, rocky, shallow soils developed from granites on south-facing slopes are likely to need more care in ensuring maximum organic matter retention than deep, nutrient-rich, gently-sloping soils developed from marine sediments. These contrasting site-types are surely different in soil biology and in the historic processes that have contributed to their present-day productive capacity. The more resilient sites have greater reserves of nutrients and rooting capacities and likely have more diverse biota and more efficient processes for recycling organic matter and nutrients than do the sensitive sites. It is logical to think of contrasting forest ecosystems in terms of differentially managing forestry impacts on soil biology and other critical ecosystem properties.

Experience in agriculture long ago led to crop rotations for managing soil properties related to organic matter and nutrients. Even today, in the most intensive Iowa corn and soybean cropping, farmers rotate corn and beans and use "no-till" practices to retain organic matter. This, of course, influences soil biology, soil structure, rooting, and nutrient- and water-retention capacity. Certainly, fertilizers and other chemicals are used extensively, but now they are applied with much more efficiency than they were previously. Extrapolating from agriculture, forestry can take advantage of longer crop rotations, potentially more diverse vegetation, and less frequent machine entries to effectively minimize impacts on soils. In the process, we can potentially manage forests—our renewable resources—with fewer inputs of non-renewable energy- and petroleum-based resources.

The information on soil biology from these Proceedings provides some interesting and important understandings of relationships between soil organisms and forests. However, except for extreme situations, many of the relationships involved in long-term productivity are not definitive. Foresters are challenged to intimately know their individual forest ecosystems, including soils and soil ecology, and to have the wisdom to know and apply relevant information about management-soil biology interactions. The links between amounts and types of organic residues are becoming clearer with research, but holistic interpretations are needed to apply reasonable constraints on forestry and to avoid needless panic reactions. I recommend the book *Soil Ecology* (Killham 1994), as a thorough, concise reference for understanding this important and complex subject.

It seems wise, in most cases, to maintain a number of options for long-term productivity by keeping maximum amounts and diversity of organic residues available for biological recycling. (Yes, there are cold, wet sites where maximum organic matter could be too much of a good thing. Such sites are common in British Columbia but are rarely found in most parts of California, Oregon, and Washington.) However, if a management practice drastically alters a soil's capacity to supply

water, nutrients, structure, and biological function, how long will the condition persist? How extensively should the practice be applied? What amendments or alternative practices might be used to prevent adverse impacts? There is no substitute for local, site-specific knowledge and understanding. For instance, where are the "soil monitoring plots" analogous to the forest inventory plots? How often does a field forester examine a forest floor, dig a spadeful of soil, or even think about the basic soil resource in relation to his or her grandchildren's forest? Is this the place to start?

In considering this matter of forest management and soil biology, I return to Aldo Leopold's concepts in his essay, "The Land Ethic." In his view, land is an "energy circuit" (a holistic ecosystem). Land is not merely soil: native plants and animals keep the energy circuit open. Human changes are of a different order than evolutionary ones and often have effects more comprehensive than is intended or foreseen. For forest management and soil biology, the processes of this energy circuit mean that:

- Forest land is not merely soil, but a forest-soil system where the soil ecosystem and soil biology are connected to the forest.
- Soil biology and soil organisms have kept the forest-soil system going, while modified soil ecosystems may or may not do so.
- Changes made by forest management may be more drastic than evolutionary changes, causing effects to our grandchildren's forests that may or may not be foreseen.

Thus, foresters and soil scientists can use the best aspects of the "ecosystem management" concept to help us view forest-soil systems as holistic systems connected to atmospheric and aquatic systems. In this way, we might begin to perceive "soil ecosystems" and soil biology as important factors in the process of forest management. We can thus help manage our grandchildren's forests with a "view from the bottom" as well as with a view from the forest. We can see the trees *and* the soil. The papers of this volume direct us toward this holistic vision.

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