

Implications of Small Mammal Mycophagy to the Management of Western Coniferous Forests

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Management of our land and wildlife has been, and often still is, single-use oriented. However, we now have reached the stage in development of knowledge where the single-use concept is no longer valid or viable in land management. We can no longer afford a comfortably oversimplified economic view of our land and resources, "... therefore land management must evolve toward total ecosystem management, not only convenient fragments thereof." (Maser and Thomas 1978:1).

Fortunately, Leopold's (1966:251) statement—"The art of land doctoring is being practiced with vigor, but the science of land health is yet to be born."—is not so true today. Although our research and management often are problem-oriented, or crisis-oriented, or both, the finely tuned, delicately balanced inner workings of coniferous forest ecosystems are slowly becoming appreciated.

The purpose of this paper is to examine some interrelationships between small mammals, hypogeous ectomycorrhiza-forming fungi, and trees, and the implications of these relationships to management of western coniferous forests. It is not our intent to present data, because relevant data are available elsewhere (Maser, Trappe, and Nussbaum 1978, Rothwell and Coleman 1978, Trappe and Maser 1976, 1978).

Mycorrhizae

We begin with the premise that maximum wood-fiber production on a sustained basis is the primary goal of management in western coniferous forests. Many factors enter into achievement of this goal; among these are the mycorrhiza-forming fungi. Trees depend on these fungi for uptake of the non-mobile mineral nutrients required for survival and growth.

This paper is respectfully dedicated to the memory of Dick King, District Wildlife Biologist, USDI Bureau of Land Management, Coos Bay, Oregon, who strove for total ecosystem management throughout his professional career.

Mycorrhiza literally means "fungus-root" and denotes a symbiotic relationship between certain fungi and plant roots. The symbiotic association, termed "mycorrhizae," between mycelia (mold) of certain fungi and roots of vascular plants was discovered and described in the 1880s (Harley 1969). During the next 50 years, mycorrhizae were found on roots of most families of the world's vascular plants. Woody plants in the families Pinaceae, Fagaceae, Betulaceae, and several other tree and shrub families were found to be especially dependent on mycorrhiza-forming fungi for nutrient uptake (Harley 1969, Marks and Kozlowski 1973). Nonetheless, mycorrhizae were largely ignored by botanists and foresters alike until the last decade.

In recent years, the role of mycorrhizae in plant nutrition has been widely recognized. Their importance no longer can be overlooked. Forest managers must be aware of fungi and their diverse processes if they are to understand the ecosystems they manage.

The fungi grow into the tiny, nonwoody rootlets of host plants to form a balanced mycorrhizal symbiosis with no harm to the roots. The host provides photosynthetic products to the fungus, which in turn absorbs mineral nutrients from the soil and translocates them to the host. In effect, the mycorrhiza-forming fungi have evolved with the hosts as highly efficient extensions of the root system (Harley 1969).

Each host family characteristically forms a particular type of mycorrhizae with particular fungi. The most important family of trees in western coniferous forests is the Pinaceae, which includes pines (*Pinus* sp.), hemlocks (*Tsuga* sp.), spruces (*Picea* sp.), true firs (*Abies* sp.), Douglas-fir (*Pseudotsuga* sp.), and larches (*Larix* sp.). These hosts form ectomycorrhizae with thousands of fungal species that fruit in the form of mushrooms (epigeous or above-ground fruiting bodies) or truffles and false truffles (hypogeous or below-ground fruiting bodies) (Trappe 1962, 1969). In ectomycorrhizae, the fungal mycelia grow between outer rootlet cells, enclose the rootlets within a mantle of fungal tissue, and grow out from the rootlets into the soil. In addition to absorbing soil nutrients and translocating them to the host roots, ectomycorrhiza-forming fungi produce growth regulators that increase rootlet longevity and induce production of root tips. They also protect rootlets from pathogens by shielding root tips within a mycorrhizal mantle and by producing metabolites that often inhibit pathogenic growth (Harley 1969, Marks and Kozlowski 1973).

Since this paper only considers coniferous trees, the discussion of mycorrhiza-forming fungi is limited to those fungi that form ectomycorrhizal relationships with conifers.

Dispersal of Mycorrhiza-forming Fungi and Coevolution with Trees and Mammals

The colonies of mycorrhiza-forming fungi in the soil and their association with roots are perennial. In contrast, fruiting bodies of mycorrhiza-forming fungi are ephemeral. Initiated from subterranean colonies, they enlarge, mature their spores, and decompose. Because the vast majority of mycorrhiza-forming fungi are obligate symbionts, requiring host roots for survival, spores must be deposited on or within soil where host roots will be available to establish new colonies.

Mycorrhiza-forming fungi that produce epigeous fruiting bodies discharge their spores into the air, and although spores may be moved long distances, a large proportion of them may be deposited where no host roots are available. Species that produce hypogeous fruiting bodies have evolved to a more specialized and habitat-specific means of spore dispersal: the fruiting bodies are eaten by animals. All tissues of a fruiting body are digested except the spores, which pass through an animal's digestive tract and are defecated, usually on or within soil. The spores are washed into soil by precipitation and are thus strategically placed for contact with host plant rootlets (Trappe and Maser 1978).

Animals that feed on hypogeous mycorrhiza-forming fungi apparently detect the fruiting bodies by odor. Each hypogeous fungal species produces a particular odor, which intensifies and becomes more penetrating as spores mature within a fruiting body. The digestible tissues of fruiting bodies have a high water content and also contain substantial protein, carbohydrates, vitamins, and minerals (Fogel and Trappe 1978). Stomach content analyses of many rodents indicate that, when hypogeous fungal fruiting bodies are maturing, these rodents appear to select them over other foods (Maser, Trappe and Nussbaum 1978, Trappe and Maser 1978).

The relationships between ectomycorrhiza-forming fungi, woody host plants, and rodents have probably resulted from a long evolution of the ecosystems involved. Because the interactions of these diverse organisms have been perceived only recently, it is important to realize that only our perception is new; the phenomena themselves are ancient. If we accept that ecosystems have evolved to a high degree of natural efficiency, then we must understand the processes involved before we can manage them effectively.

Mycorrhizae occur in the oldest known fossils of rooting structures: rhizomes of lycopods of some 400 million years ago (Harley 1969). This lends credence to the hypothesis that the origin of terrestrial plants required a symbiosis between fungi and photosynthesizing algae (Pirozynski and Malloch 1975). Evidence now points to simultaneous evolution of mycorrhizal tree hosts, hypogeous fungi, and the small mammals that eat them (Trappe 1977a).

Small Mammals and Mycorrhizal Fungi

The many reports of small mammal mycophagy in the literature, reviewed by Fogel and Trappe (1978), may leave an impression that epigeous fungi predominate over hypogeous fungi in mammalian diets. The great majority of these reports, however, were from observations of above-ground animal behavior and food caches. Stomach content analyses, in which the kinds of fungi actually eaten are identified, consistently confirm that rodents consume few epigeous fungi and that hypogeous species greatly predominate the fungal portion of their diets (Maser, Trappe, and Nussbaum 1978, Stienecker 1977, Stienecker and Browning 1970). Such data yield ecologically significant insights which have forest management implications.

We found over 1,000 fungal fruiting bodies in the stomach contents of approximately 500 small mammals, representing 3 orders, 8 families, 16 genera, and 29 species. All had consumed some fungi (Maser, Trappe, and Nussbaum 1978). Moreover, data suggest that spores are viable after passage through rodent digestive tracts. For example, the spores of one species of mycorrhiza-forming fungus

(*Glomus macrocarpus*) were germinated after passage through the digestive tract of an Oregon vole (*Microtus oregoni*) (Trappe and Maser 1976), and spores of *Glomus fasciculatus*, a related fungus, were capable of forming mycorrhizae after extraction from feces of mice in the family Cricetidae (Rothwell and Coleman 1978).

The following examples are given to illustrate some of our interpretations in terms of small mammal interactions with hypogeous mycorrhiza-forming fungi.

Squirrels

Townsend chipmunks (*Eutamias townsendi*) inhabit all forest successional stages of Oregon forests from the Cascade Mountains westward to the coast (Gashwiler 1959, 1970). Their stomach contents proved them to be avid mycophagists (Maser, Trappe, and Nussbaum 1978, Tevis 1952) and potentially important vectors of mycorrhiza-forming fungal spores. These chipmunks travel relatively long distances in a short time, visiting clearcuts from old-growth timber (Gashwiler 1959). They are normally more numerous in old-growth timber than in adjacent clearcuts in the first few years following logging and burning, but become more numerous in clearcuts as succession advances (Gashwiler 1959, 1970, Tevis 1956). During these early years, chipmunks transfer mycorrhiza-forming fungal spores from standing timber into clearcuts. As succession progresses, cover increases as do associated fruits, seeds, and other foods. The chipmunks' ingestion of appropriate fungi in standing timber, and their subsequent defecating of the spores in clearcuts make them the most important diurnal vector of hypogeous fungal spores in western Oregon.

Red squirrels (*Tamiasciurus hudsonicus*) occupy the forests of northeastern Oregon, whereas chickarees (*T. douglasi*) inhabit coniferous forest throughout the rest of the state. The specimens examined had been feeding primarily on hypogeous fungi (Maser, Trappe, and Nussbaum 1978). Much of the time spent on the ground by red squirrels and chickarees is probably employed in gathering hypogeous fungi.

Northern flying squirrels (*Glaucomys sabrinus*) are associated generally with coniferous forests in Oregon. Stomachs of these nocturnal squirrels contained mostly hypogeous fungi (Maser, Trappe, and Nussbaum 1978). McKeever (1960) found scant mention of fungi in the literature on food habits of northern flying squirrels. However, his own data on stomach-content analysis of 24 flying squirrels trapped throughout a 12-month period indicated dependence on both fungi and lichens. Despite the availability of various seed crops in the three forest communities of McKeever's study (ponderosa pine (*Pinus ponderosa*), lodgepole pine (*P. contorta*), and mixed true firs (*Abies* spp.)) no seeds were found in the stomachs. Our data on northern flying squirrels (unpublished) from Oregon concur with McKeever's observations, but with differences in fungal fruiting season.

Chickarees, red squirrels, and northern flying squirrels all reproduce in arboreal nests and descend to the ground to gather fruiting bodies of hypogeous fungi. However, both chickarees and red squirrels (allopatric—do not coexist with one another) are diurnal while northern flying squirrels (sympatric—coexist with both chickarees and red squirrels) are nocturnal. This difference in times of activity allows use of the same hypogeous fungal food supply without interspecific contact during foraging. The available fungal flora is thus partitioned as a source of food

and fungal spores are dispersed through defecation both day and night by two genera of squirrels occupying the same habitat.

Pocket Gophers

Mazama pocket gophers (*Thomomys mazama*) occur in Oregon from the Cascade Mountains westward to the coast. Individuals of this species taken from grassy areas within ponderosa pine forests in central Oregon had eaten small amounts of both hypogeous and epigeous fungi (Maser, Trappe, and Nussbaum 1978).

In the Oregon Cascade Range, the Mazama pocket gopher is primarily associated with grassy areas and mountain meadows, often within the forest. During snow-free months they stay underground except for foraging, but during winter they are active above ground under snow cover. Similarly, their fecal chambers are subterranean part of the year and often above ground part of the year. Since these gophers eat hypogeous mycorrhiza-forming fungi, the spores would accumulate within the fecal chambers. Even if an individual gopher ate few mature hypogeous fungal fruiting bodies at any one time, the location-specific defecation of the individual would concentrate spores in a given area, increasing the probability of mycorrhiza-forming fungi colonizing the rootlets of conifer seedlings that germinate on the site.

The following is a speculative example: Lost Prairie, in the Cascade Range in Linn County, Oregon, is a small, natural prairie, which conifers did not invade until recently, even though it is largely surrounded by forest. They have done so only at a narrowed end of the meadow where gopher activity had become concentrated throughout the year. The gophers had foraged both within the forest and the prairie. It is possible that gophers, eating hypogeous mycorrhiza-forming fungi in the forest and then defecating in their fecal chambers located near their nesting chambers in the prairie, could build up a localized spore concentration for mycorrhizal inoculation of conifer seedlings.

Voies

California red-backed voles (*Clethrionomys californicus*) are the most specialized mycophagists that we have thus far studied (Maser, Trappe, and Nussbaum 1978). Hypogeous fungi constituted 74 percent of the volume of 123 vole stomachs. However, differences in subspecies dependence upon fungi were apparent: *C. californicus californicus* had 90 percent hypogeous fungi by volume in 51 stomachs and *C. californicus mazama* had 70 percent hypogeous fungi by volume in 72 stomachs (Maser, Trappe, and Nussbaum 1978). The California red-backed vole depends on fungi for sustenance and probably also for a source of water (Getz 1968, Maser, Trappe, and Nussbaum 1978).

Oregon voles (*Microtus oregoni*) trapped in the coniferous forest of western Oregon also proved to be mycophagists, but the degree to which they consumed fungi was habitat dependent (Maser, Trappe, and Nussbaum 1978). The Oregon vole feeds either primarily on hypogeous fungi or primarily on vascular plants, depending on the habitat, but its main orientation is toward vascular plants.

An understanding of relative dependence on hypogeous fungi by these two species of voles permits interpretation of their population changes in relation to

plant succession. Western Oregon coniferous forests may be divided into six generalized successional stages: (1) grass-forb, (2) brush-seedling, (3) pole-sapling, (4) young forest, (5) mature forest, and (6) old-growth forest. The dietary specialization of the California red-backed vole and dietary flexibility of the Oregon vole allow both to co-exist in stages 3 through 6. Their food source is partitioned in all but one successional stage (pole-sapling), which represents the primary change in dominance between Oregon voles (declining in numbers) and California red-backed voles (increasing in numbers). The abundance of hypogeous fungi begins to increase in this stage while ground vegetation declines (Maser, Trappe, and Nussbaum 1978).

Population shifts due to silvicultural treatment, such as clearcutting, can be understood only when differences in dependency on hypogeous fungi as food by these two species is recognized. In Oregon, the California red-backed vole occurs only in coniferous forests and depends strongly on hypogeous, ectomycorrhiza-forming fungi for food. The Oregon vole, sympatric with the California red-backed vole in these forests, also feeds on hypogeous fungi, but its usual diet is forbs and grasses. Changes in small mammal populations that accompany the clearcutting of old-growth coniferous timber have been extensively studied (Gashwiler 1959, 1970, 1972; Goertz 1964; Hooven 1973; and others). All studies reached the same conclusions about habitat "preferences" of the California red-backed vole and the Oregon vole: the California red-backed vole is most abundant in old-growth timber; the Oregon vole is most abundant in clearcuts. The food habits of the voles had not been studied, however, and we think the explanations, based largely on visible habitat alteration, were unsatisfactory.

California red-backed voles normally disappear from clearcuts within a year after logging and burning (Gashwiler 1959, 1970). We hypothesize that they disappear because they are left without their specialized food supply—hypogeous ectomycorrhiza-forming fungi, which do not fruit without their coniferous hosts (Maser, Trappe, and Nussbaum 1978). Oregon voles, on the other hand, increase in numbers following logging and burning as their primarily herbaceous diet becomes available (Gashwiler 1959, 1970, Hooven 1973, Maser, Trappe, and Nussbaum 1978).

Small Mammals, Mycorrhizal Fungi, and Forest Management

System management presupposes that every component of a naturally functioning system serves a purpose and that each component benefits the entire system in some way. The approach to understanding how a particular system functions, therefore, is objective and positive. Conversely, product management often presupposes that any noncommercial component of a system that visibly "damages" a commercial component is necessarily detrimental. In the latter case, the approach is largely subjective and negative.

The following few examples serve to illustrate the positive system approach to forest management while at the same time emphasizing certain products.

Small Mammal Control

Many western forest ecosystems are characterized by summer drought and early fall frost. Even maritime zones occasionally experience this pattern during

exceptional years. Such climatic regimes operate against spore dispersal by epigeous mycorrhiza-forming fungi; epigeous fungi typically abort when dried or frozen. Hypogeous fungi, in contrast, are protected from the vagaries of weather by the overlying humus and soil and can fruit in all but the most severe weather conditions. Small mycophagous mammals, therefore, may be critical to the dispersal of mature spores throughout such forest ecosystems, to maintain maximum diversity of the fungal flora. In addition, the mammals may be the primary mechanism through which genetic diversity is maintained within a given subterranean species of fungus by transporting spores from one colony to another.

Available data indicate that in many cases the newly perceived beneficial aspects of small forest mammals may outweigh the visibly detrimental aspects. Although some small mammal control may be warranted, we suggest that each species' role in a forest be objectively evaluated—not unilaterally determined. It is conceivable, as data accumulate, that the roles played by small mammals will prove to be compatible with timber production, and those of some species, such as the California red-backed vole, to be decidedly beneficial.

Management of Dead Woody Material

Management of standing, dead trees (snags) and down, dead woody materials (especially logs) as wildlife habitats has been discussed by Thomas et al. (1978) and Maser et al. (1978). Neither of these discussions were oriented toward the dispersal of mycorrhizal inoculum by small mammals, but techniques of managing snags and logs as habitats for wildlife were outlined.

Snags have a two-fold importance to mycophagous mammals. While standing, their natural and excavated cavities serve as homes for northern flying squirrels, chickarees, red squirrels, and bushy-tailed woodrats (*Neotoma cinerea*), all of which feed on hypogeous mycorrhiza-forming fungi (Maser, Trappe, and Nussbaum 1978). As snags fall, they enter one of five log classes and serve as homes for a different clientele of small forest mammals (Maser et al. 1978). Snags, therefore, are logs for the future.

Logs have many attributes that are critical to the well-being of forest ecosystems (Maser et al. 1978), but we are only beginning to understand and appreciate them. Protective cover for small animals is perhaps the most obvious use of logs. Most small forest mammals, such as California red-backed voles, concentrate their activities in and around decaying logs. Well-rotted logs contain concentrations of mycorrhiza-forming root tips (Harvey et al. 1976, Trappe unpublished data) and act as seed beds for coniferous tree seedlings, such as western hemlock (*Tsuga heterophylla*), in western Oregon and Washington (Franklin and Dyrness 1973). Such concentrations of roots and seedlings may be due in part to deposition of spore-rich mammalian fecal pellets in and around these logs.

Available data show logs to be something more than simply "debris," "residue," or "fuel" (Maser et al. 1978). When considered in a forest sense, logs can be managed in ways to aid the dispersal of mycophagous mammals into clearcuts, harsh sites, or other areas that would benefit from increased inoculum of mycorrhiza-forming fungi to insure optimum tree growth.

Clearcuts

Clearcuts can be designed to facilitate both the dispersal of small mycophagous mammals and natural regeneration of trees. For example, it may be desirable to modify the size and shape of clearcuts, create maximum edge effect (Thomas, Maser, and Rodiek 1978), and manage for snags and logs.

Shelterwood Cuts

Shelterwood cuts may have a decided advantage over clearcuts in some circumstances, especially on harsh sites. The living trees that form a shelterwood will insure the survival of part of the existing mycorrhiza-forming fungal flora necessary for regeneration of conifer seedlings. Further, root grafting may occur which will keep both stumps and their attendant mycorrhiza-forming fungi alive (Lanner 1961, McMinn 1963, McQuilkin 1935). In turn, the live trees and stumps act as reservoirs for mycorrhiza-forming fungi and thereby for mammalian dispersal of mycorrhizal inoculum.

Outplanting Nursery Seedlings

Mycorrhizal inoculation of soils is important for the establishment of conifer seeds and seedlings as well as for outplanted nursery stock, but the fungi that form mycorrhizae on seedlings in nurseries may not be adaptable to the soils or climate of the planting site (Trappe 1977b). We hypothesize that fungi endemic to nurseries will not function effectively at all planting sites and must be replaced by fungi native to a site if a plantation is to thrive. Dispersal of mycorrhizal fungi by small mammals, therefore, may be a critical factor in plantation establishment and survival.

Conclusions

Hypogeous fungi depend upon their ectomycorrhizal host trees for photosynthates. The host trees, in turn, depend upon the mycorrhizal fungi for nutrient absorption. The most obvious spore-dispersal mechanism of hypogeous mycorrhiza-forming fungi is mycophagy by small mammals.

Tevis (1952:200) thought about fungal spore viability in the feces of mycophagous mammals 20 years ago and pointed to the need for study of "... reinoculation of devastated ground ... [with the aid of] rodents." To understand the significance of small mammal mycophagy within a forest ecosystem and to forest management will require imaginative research. Although it is immediately apparent that mycophagy results in partitioning the available food resource among mammalian species, the implications to establishment, survival, and growth of plant communities and terrestrial ecosystems are just being perceived.

Much emphasis, time, and money have been expended on control of small mammal species, such as Townsend chipmunks and deer mice (*Peromyscus maniculatus*), that visibly damage economically valuable trees in commercial forests (Abbott 1961, Crouch 1976, Hoooven 1953, 1975, Kverno et al. 1965, Moore 1940, Pank 1974). For the most part, subjective and quantitative questions have been asked, and standardized methods have been employed in attempts to find an-

swers: (1) What species occur in the area? (2) How many individuals occur in the area? (3) Does a potential problem exist, in the control sense, with respect to reforestation? (4) How successful has the control program been?

If we are to understand the positive aspects of plant-animal interrelationships, however, then we need to be objective and ask qualitative as well as quantitative questions: (1) Why are the species there? (2) Why do they do what they do? (3) How do they interrelate with the existing plants and with each other? (4) How do they use the available habitat? Only when we objectively seek to understand a system can we improve timber production by working knowingly with the system rather than inadvertently against it (Buckner 1964, Hamilton and Cook 1940).

We stress that both qualitative and quantitative research are needed, and that such research will be most beneficial if it is system-oriented. Moreover, a different perspective of existing data, such as that collected during rodent control programs, may lend new insights to forest management and timber production.

We hypothesize an interwoven relationship of organisms: host trees, hypogeous mycorrhiza-forming fungi, and small mycophagous mammals. The obligatory symbiotic relationship between hypogeous mycorrhiza-forming fungi and most higher plants—notably the commercially valuable Pinaceae—forms part of the fabric. Small mycophagous mammals—those that feed on fungal fruiting bodies and thereby disperse viable spores—complete the fabric.

If our hypothesis is correct, then a critical thread of importance to the optimum functioning of coniferous forest ecosystems has been identified. We are, then, dealing with an open system that cannot be unilaterally compartmentalized by management into discrete, disjunct components.

... man has defined species as economically desirable, undesirable, or neutral—good, bad, or indifferent. This may be good, short-term economics, but it is very poor ecology. We must consider both direct and indirect cost/benefits of our management decisions. No longer can we afford wildlife sacrifices on the altar of cost-effectiveness or allow wildlife scapegoats to take the blame for interrelationships that we do not fully understand. (Maser and Thomas 1978:2)

We cannot validly oversimplify that species, such as deer mice and chipmunks, impede reforestation. Although they eat some tree seeds, they also disperse inoculum of mycorrhiza-forming fungi. Thorough study of these relationships can lead to an improved understanding of the role that some small mammals play in the functioning of forest ecosystems. It can also lead to new and better approaches to managing those ecosystems.

The outstanding scientific discovery of the twentieth century is not television, or radio, but rather the complexity of the land organism. ... The last word in ignorance is the man who says of an animal or plant: 'What good is it?' If the land mechanism as a whole is good, then every part is good, whether we understand it or not. If the biota, in the course of aeons, has built something we like but do not understand, then who but a fool would discard seemingly useless parts? To keep every cog and wheel is the first precaution of intelligent tinkering. (Leopold 1966:176-177)

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