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FOREST SOILS OF THE DOUGLAS-FIR REGION

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Chapter VIII

FOREST SOIL BIOLOGY

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and
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The widely accepted assertion, "the soil is our basic resource," rarely evokes thought of the organisms that inhabit soil. Yet, without these myriad organisms no plant could survive. As often as not, forest practices indirectly affect tree growth by directly affecting the soil organisms. These organisms are vital in beneficial processes such as weathering of parent materials, soil aggregation, organic matter decomposition, nitrogen (N) transformation, gaseous nitrogen (N_2) fixation, phosphorus (P) and micronutrient solubilization and uptake, capture of nutrients that would otherwise be lost through leaching, and protection of tree roots from pathogens. Soil organisms can also harm forest productivity by aiding in formation of iron pans and highly acid raw humus, immobilizing N, or in the case of disease organisms, deteriorating roots of trees.

The kinds and activities of organisms in forest soils need to be recognized in predicting effects of forest practices on soil productivity. Unfortunately, the study of soil biology is extraordinarily difficult and time consuming, especially in forests with their diverse microsites. The many kinds of organisms require a multidisciplinary approach, and direct observations on soil in the forest itself are fraught with problems of technique. Perhaps for these reasons, forest soil biology has received relatively little study. The principles discussed below are well established by extensive research, but some are derived from agricultural work extrapolated to the forest system.

THE ORGANISMS IN FOREST SOIL

Virtually all life forms live in forest soil and interact with each other: viruses, bacteria, actinomycetes, fungi, algae, protozoa, nematodes, microarthropods (e.g., mites), macroarthropods (e.g., insects, millepedes), earthworms, slugs and snails, amphibians, reptiles, and mammals. Plant roots and rhizomes are also integral parts of the forest soil biota.

The specific identities, numbers, or biomass of the organisms are poorly known for any forest soil, again probably because of the difficulty of the undertaking. Recent research in the Douglas-fir Region (DFR) has concentrated on biological processes in soil rather than on relationships between organisms responsible for those processes. This approach is

practical in telling us what happens in soil. Unfortunately, it is of little help in learning how or why soil biotic processes are changed by forest practices, because these changes largely result from shifts in species populations. The forester needs to know the identity and ecological requirements of the vegetation to predict the outcome of a management practice; for the same reasons, the soil biologist must also strive to know the major organisms involved in soil processes. Examples of the importance of such understanding for predicting effects of management practices are detailed in compendia such as those of Dickinson and Pugh (1974) and Dindal (1973).

The numbers and biomass of organisms in soil are as difficult to comprehend as the national debt. A single gram of soil may contain between 10 million and 100 million bacteria and actinomycetes, 1,000 to 100,000 fungal propagules, and several km of fungal hyphae. The top 15 cm (6 in) of 1 ha of fertile soil may include as much as 1,100 kg of bacteria (1,000 lb/acre), 1,100 kg of actinomycetes, and 2,200 kg of fungi (2,000 lb/acre) (Bollen 1974). The soil of an old-growth Douglas-fir stand in Oregon has been estimated to contain about 4,200 kg/ha (3,700 lb/acre) dry weight of fungal mycelium, 5,400 kg/ha (4,800 lb/acre) of mycorrhizal root tips, and 41,000 kg/ha (36,500 lb/acre) of woody roots (Fogel et al 1973). These figures should be compared with a total dry weight of about 55,000 kg/ha (49,000 lb/acre) of a forest floor 7 cm thick and 200,000 to 700,000 kg/ha (180,000 to 625,000 lb/acre) weight of organic matter incorporated in mineral soils as representative of the DFR. Mites and nematodes may number from thousands to hundreds of thousands per m^2 of soil; insects, earthworms, and animals of similar size, from dozens to hundreds (Dindal 1973). The list of estimated numbers could go on, but the point is that these myriad organisms interact both with each other and with the physical and chemical environment of the soil to profoundly affect soil productivity.

INTERACTIONS BETWEEN SOIL ORGANISMS AND ENVIRONMENT

Soil organisms are strongly interdependent. Any two may interact in one or more of a variety of ways: *competition* for the same sources of life-sustaining elements; *saprophytism* of one on the dead remains of another; *predation* or *necrotrophic*

symbiosis, one killing and consuming the other; *biotrophic symbiosis*, one obtaining physiological benefits from the other or both from each other without causing death; *antibiosis* between microorganisms or *allelopathy* between roots, one producing metabolites that inhibit or overcome the other; *synergism*, the activities of two organisms producing a greater effect than the sum of the effects of the two acting individually. An association of two organisms without any detectable effect on either is termed *commensalism*, regarded as rare in soil (Griffin 1972).

All these forms of interaction continually occur in soil. In an undisturbed forest, the balance of the various soil organisms and their activities may shift in one direction or another with the change of seasons. After the initial period of stand establishment, however, overall populations are relatively stable and change almost imperceptibly as the stand ages. A strong disturbance of the stand—e.g., by fire, insect attack, disease, timber harvest, or heavy fertilization—will upset the equilibrium. A struggle to occupy the changed soil environment ensues. Some of the former resident organisms may not be well adapted to the new environment and may disappear altogether. Others may increase in population. New organisms may invade. These changes may help or hinder the forest manager in achieving his goals.

To exemplify these phenomena, let us consider a few of the biological relationships in the soil of a typical mature Douglas-fir forest and the changes that follow clearcutting, burning, and invasion by red alder (*Alnus rubra* Bong.). Our hypothetical example draws on research reported or reviewed in publications listed in the bibliography at the end of this chapter. In reading the example, one may get an impression of an even, tidelike flow of events. In reality, many of the events occur as dramatic upswings or declines in populations and activities and can vary markedly from one pocket of soil to the next at any time.

In a well-stocked Douglas-fir stand, relatively little sunlight reaches the forest floor. Understory vegetation is often scattered, consisting mostly of ferns and occasional vine maple (*Acer circinatum* Pursh). Several cm of humus are present, and often about a fourth of the ground surface is occupied by rotten wood, some of it so decomposed and covered by litter that it is not evident to the casual observer. Fine roots of trees and understory vegetation profusely permeate the humus, rotten wood, and upper mineral soil. Larger, woody roots penetrate more deeply, often growing down channels formed by long-dead roots.

The population of soil organisms is in dynamic equilibrium; activity of some surges in one season, that of others in other seasons. Population changes occur most rapidly on or near root tip surfaces in the zone known as the *rhizosphere*. As

tips grow through the soil, they exude carbohydrates, amino acids, and other organic compounds that stimulate growth of various bacteria, actinomycetes, and fungi. These, in turn, produce metabolites that antagonize some other microorganisms and stimulate still others. Protozoa that feed on the bacteria also begin to increase with the increased food supply. Most fine root tips are occupied by mycorrhizal fungi, *Ascomycetes* and *Basidiomycetes* on the Douglas-fir and *Endogonaceae* (*Phycomycetes*) on the ferns and maple. The mycorrhizal fungi grow through the humus and mineral soil, absorbing water and nutrients that they translocate to their host plants; in turn, they receive carbohydrates and other photosynthates from the hosts. In spring and fall, the Douglas-fir mycorrhizal fungi produce mushrooms and truffles that are eaten by slugs, squirrels, chipmunks, and red-backed voles or are inhabited by insects and other invertebrates. Mycorrhizal *Endogonaceae* of the ferns and maples, in contrast, form single spores or spore clusters that are eaten more by deer mice, jumping mice, earthworms, and millepedes. Of the many fungal species that form mycorrhizae with Douglas-fir, some may attract aphids or nematodes to the roots, others may repel them (Zak 1965, 1967). As rootlets age, their succulent tissues collapse, fewer exudates are leaked out, and the biotic activity around them wanes. Occasional rootlets are colonized by pathogens which kill the succulent tissues and sometimes work into the woody root system.

The soil away from root surfaces also witnesses much biological activity, albeit with lower populations and at a slower pace than near roots. Wood and litter are decomposed by a succession of fungi with associated bacteria, mites, insects, centipedes, millepedes, earthworms, etc. Low nitrogen supplies limit the rate of decomposition, especially of lignins in rotten wood. The decomposer organisms are, in turn, parasitized or preyed upon by still other organisms; ultimately, the nutrients from their digested or decomposed remains are released to absorption by the mycorrhizal fungi, which recycle them into the host tree, fern, or maple. Meanwhile, mobile organisms—such as burrowing mammals, salamanders, earthworms, and ants—are transporting and excreting nutrients from one microsite to another, mixing and cultivating the soil in the process.

New organisms continually attempt to invade the soil. However, nearly all microsites are fully occupied by resident organisms which attack, antagonize, or strongly compete with invaders. Invasion success rate is therefore extremely low.

After the mature Douglas-fir stand is clearcut, its soil biology changes considerably. The upper soil is moved about and mixed during log removal. Quantities of fresh limbs and Douglas-fir needles are deposited. Some of the soil surface is newly exposed to solar radiation. Many soil organisms adapted to the environment of the mature forest cannot survive in this

suddenly new situation. Mycorrhizal fungi of the Douglas-fir, being dependent on living trees as an energy source, begin to die as carbohydrates stored in rootlets of the stumps are depleted. As surviving ferns and maples recover from the shock of sudden release, their root systems begin to grow vigorously and their mycorrhizal fungi occupy some of the soil vacated by dying Douglas-fir mycorrhizae. Other organisms also find microsites vacated, and populations begin to change markedly. Warming of the upper soil layers by the sun increases activity of decomposers and speeds decomposition of organic matter. The small mammals that depended on the mature forest habitat and the food produced by mycorrhizal fungi of Douglas-fir disappear. Populations deeper in the soil also change but more slowly.

Slash burning after logging additionally changes succession of populations initiated by clearcutting. With a severe burn, much of the carbon (C) and N in the forest floor are lost in combustion. Many mineral elements previously bound in surface organic matter are left as soluble fractions of ash and begin leaching into the soil with winter rain. The pH of the upper soil rises slightly. Many of the organisms at or near the surface are killed outright, and the survivors' food supply is reduced. Windborne bacteria and spores of many fungi alight and are washed into the soil by rain. Spores of others, present before the burn or even before the cutting, require a heat treatment to break dormancy. The burn accomplishes this, and they germinate. Wind-disseminated seeds of trees and annual and perennial weeds are scattered over the burned clearcut. Some of the ferns and vine maples survive at the root crown, and some are untouched.

A new succession has begun. Nitrifying bacteria and N_2 -fixing bacteria and algae colonize the burned areas, and in spring, available N content of the upper soil rises. Seeds germinate, and the seedlings rapidly extend roots into the soil. Grass and weed roots encounter spores of the mycorrhizal Endogonaceae of the ferns and maples. All can share the same mycorrhizal fungi, so the grass and weeds soon form mycorrhizae. Their ability to take up nutrients is thereby enhanced, and they flourish. At the same time, the mycorrhizal Endogonaceae acquire the host-produced energy they need to multiply in the soil.

The Douglas-fir and red alder seedlings are slower to get started. Many mycorrhizal Ascomycetes and Basidiomycetes of the previous forest have died. Growth of seedlings whose roots fail to contact newly deposited spores of appropriate mycorrhizal fungi is slowed. Many alders, however, quickly become infected by the actinomycetes that form N_2 -fixing nodules with their roots. The alders respond with increasingly vigorous growth. As they expand their root systems, mycorrhizal fungi compatible with alder are contacted. More mycorrhizal fungi grow out from the roots into the soil, and

the alders thrive. Unfortunately, the alder mycorrhizal fungi are host-specific and do not form mycorrhizae with the Douglas-fir. Rapid early growth rate of the alder compared with Douglas-fir, together with the antagonism and competition of alder mycorrhizal fungi against those of Douglas-fir, soon results in dominance by alder. In a few years, many of the Douglas-fir die.

The alders dominate the site over several decades. Vine maple is soon overtopped but survives at reduced vigor. Sword fern, in contrast, is well adapted to shade and provides plenty of photosynthate to its mycorrhizal fungi. It flourishes, also, with the increased availability of soil N, thanks to the N_2 -fixing actinomycetes that nodulate the alder. The grass and weeds of the clearcut are replaced by shade-tolerant vegetation that forms mycorrhizae with the same Endogonaceae.

Alder leaf litter is unusually rich in N, so it supports a rich flora and fauna of decomposing organisms. The annual accretion of soil N under the alder ranges from 100 to 300 kg/ha (90 to 270 lb/acre). This may double the N content over that originally present in a low-N-status Douglas-fir soil. Earthworms and other invertebrates find conditions amenable under alder, and their populations increase markedly. In a few years, rapid incorporation of litter into the soil by many kinds of decomposer organisms and burrowing or tunneling creatures produces a mull soil with a light litter layer, high porosity, and good vertical distribution of organic matter.

Surviving Douglas-fir which are overtopped by alder grow slowly. As their crowns overtop the alders, their increased photosynthesis now boosts root growth and mycorrhizal development. These phenomena, coupled with the high soil nitrogen content, lead to a rapidly accelerating growth which surpasses that of similar size Douglas-fir growing in pure stands. As the Douglas-fir crowns increasingly occupy the canopy, understory alders decline and die. However, much of the N added by alder nodules is captured by the soil organisms and is recycled into trees and other forest organisms. Site productivity is thereby increased indefinitely.

BIOLOGICAL PROCESSES IN SOIL

Numerous processes in the preceding sketch are vital to site productivity and can be particularly affected by forest management practices. The following discussion deals with some of these individual processes, but remember that in soil they proceed simultaneously and in complex interrelationship.

Nitrogen Fixation and Transformation

N is the element that most commonly limits growth of forest vegetation in the Douglas-fir Region. N added to an

ecosystem by biological N_2 fixation is converted to ammonium (NH_4^+), amino acids, and cell protein. N_2 can be fixed by certain free-living bacteria and blue-green algae or lichenized algae, as well as by symbiotic bacteria that nodulate legumes or actinomycetes that nodulate species of alder, *Ceanothus*, and several other nonleguminous woody genera.

The amount of N contributed to forest ecosystems by free-living N_2 fixers has not been evaluated but may be significant. N_2 -fixing bacteria have been discovered in association with decay fungi in heartrot of standing trees (Seidler et al 1972). Possibly they are active also in the trees fallen on the forest floor.

Symbiotic N_2 fixation is better understood. The *Rhizobium*-legume association in agriculture has been extensively studied; similar N_2 -fixing activities can be assumed for wild legumes such as lupines in the DFR. In general, however, legumes are rather shade intolerant and not abundant in well-stocked stands after initial establishment. Nodulated woody plants such as alder and *Ceanothus* spp., in contrast, commonly occur in DFR forests and can potentially contribute substantial N to the ecosystem on a continuing basis (Tarrant and Trappe 1971, Trappe et al 1968, Wollum and Youngberg 1964).

Some of the N_2 fixed by free-living bacteria and blue-green algae is liberated in soluble form from living cells. Much is incorporated into cell protein, however, and becomes available to other organisms only after the bacteria or algae die. The nodule organisms similarly dispose of their fixed N_2 but differ in that most of the N is liberated directly to host roots. Living parts of the host, especially leaves, are consequently high in N content. The N is then added to soil by litter fall and rain washing (Tarrant and Trappe 1971).

Regardless of the form in which N reaches the soil, once there it is beset by a series of transformations in which all soil organisms, large and small, are involved. Proteins are decomposed by animal digestion or microbial or fungal action to yield ammonia (NH_3). NH_3 rapidly combines with water to form NH_4OH , which in turn yields NH_4^+ . Some NH_4^+ is oxidized by nitrifying bacteria to nitrite (NO_2^-) and nitrate (NO_3^-). Under waterlogging, compaction, or other situations that produce anaerobic conditions, NO_3^- is utilized by certain bacteria as an oxidant in lieu of O_2 . The NO_3^- is reduced to gaseous N oxides and free N_2 which are lost to the air. This process is known as denitrification.

Nutrient Capture and Cycling

The soluble forms of N, particularly NO_3^- , might be lost from an ecosystem through leaching. Thanks to the soil organisms, however, much of this N is captured and recycled,

except when disturbance leaves the soil underpopulated. In the transforming process, N is successively assimilated and released through the web of diverse soil organisms. Bacteria incorporate it into protein and release it in death to predators or decomposers. Saprophytic fungi similarly use N for growth and production of enzymes that are essential for decomposing organic matter. Mycorrhizal fungi assimilate it for their own needs and, in addition, translocate it in various forms to host roots for use by the host plant. Fungal fruiting bodies provide a protein source to the animals that feed on them, and the animals, in turn, release N to the soil by excretion or death.

Other soil nutrients, such as potassium, are similarly captured and recycled by the soil biota. Moreover, less soluble elements, such as P and micronutrients, are extracted from soil minerals by organisms and thereby enter the nutrient cycle for use by forest vegetation (Trappe and Fogel 1977). Indeed, a lack of mycorrhizae on Douglas-fir typically manifests itself as P deficiency (Trappe and Strand 1969).

Carbon Cycling

Compounds of C provide the energy for growth of all organisms and are the "building blocks" of their structure. C enters an ecosystem primarily through photosynthesis. Much of it leaves the ecosystem through respiration by green plants and by organisms that derive their energy directly from the green plant, including mycorrhizal fungi, nodule-forming bacteria and actinomycetes, pathogens, and feeding animals. Much C remains, however, as a component of the cellulose, lignin, protein, and other compounds that comprise the biomass of the ecosystem. When part or all of an organism dies, it is sooner or later added to the soil organic matter.

The C cycle differs from that of soil nutrients in that much of the C is released as CO_2 respired by the soil organisms. Some C is incorporated into the structure of soil organisms, and some serves as their source of energy. The CO_2 respired by soil organisms is important in soil chemical processes (see chapter XI). That which escapes the soil may be recycled into the ecosystem in photosynthesis by algae and higher plants.

C is more tightly captured and recycled in some successional stages of an ecosystem than in others. If we recall the sequence of events in our earlier hypothetical example of a Douglas-fir stand replaced by alder, we can exemplify these stages. In the mature forest at the start, the C entering the ecosystem equals losses. The stand is at equilibrium, with organisms and their parts dying and decomposing at the same overall rate as new ones grow. Clearcutting and log removal abruptly remove a large proportion of C incorporated in the biomass. Further losses ensue in burning of slash and the forest

floor and because the CO_2 respired by decomposers is not fully replaced by photosynthesis of the remaining vegetation. As green plants subsequently occupy the site, however, photosynthetic assimilation of C begins to increase. Once the site is well populated with green plants, photosynthetic incorporation of C catches up with and then exceeds respiration losses.

Water and Oxygen Exchange

In common with all other life forms, soil organisms need water to grow. During drought, many can extract water bound in organic matter. Many, especially microorganisms and fungi, form drought-resisting spores to survive times of extreme drying. Inadequate moisture probably slows biotic activities in the soil during most summers in the DFR. However, rotten logs hold large quantities of water and can maintain soil processes such as decomposition even during dry spells (Fogel et al 1973).

Oxygen (O_2) is as vital to the soil biota as other elements already mentioned, although many soil organisms are adapted to lower O_2 pressures than those required by life forms above ground (Griffin 1972). Of the soil organisms, only algae produce O_2 by photosynthesis. The rest must obtain O_2 from the soil solution or soil atmosphere for their life processes (Griffin 1972). O_2 may become available in the soil through chemical reactions or diffusion from the air above. In the DFR, however, precipitation is probably an important factor. O_2 enters the soil dissolved in rainwater. Moreover, periodic heavy wetting of the soil displaces and flushes out much of the CO_2 -charged soil atmosphere, which is replaced by O_2 -bearing air as the soil dries. A soil structure that permits ready entry of precipitation and drainage of excess water is important, then, to provide both moisture and O_2 to the soil organisms.

SILVICULTURAL IMPROVEMENT OF SOIL BIOTIC ACTIVITY

Fortunately, good soil management practices generally favor desirable biological activity. For example, minimizing soil compaction during timber harvest is useful to maintain not only good soil physical properties but also optimum populations of soil organisms. Fertilizing an N-deficient stand will benefit soil organisms, through which most of the added N will pass before reaching the trees.

Less obvious, perhaps, are opportunities for using soil organisms to achieve specific silvicultural goals. A few examples are noted below.

Reducing Post-Harvest Stream and Air Pollution

As stated earlier, few nutrients escape an ecosystem if its soil is fully populated with soil organisms. Clearcutting depopulates the soil more abruptly than partial cutting, especially of organisms depending on living roots for survival. Burning additionally depletes substrates for decomposing organisms and converts much of the mineral nutrient bound in organic matter into soluble ash. The radical decrease in green plants minimizes the living biomass reservoir into which nutrients can be cycled.

Nitrification speeds up in some soils after timber harvest, so they experience a buildup of NO_3^- . The combination of these events can and probably usually does lead to temporary but substantial increases of ions leaching into stream water (Borman et al 1968). NO_3^- is of particular concern because of its toxicity at higher concentrations to many organisms, including fish and man.

These leaching losses can be minimized by maintaining soil organic matter and restocking the site as quickly as possible with trees and other desirable vegetation. As a result, the populations below ground will be higher. Also, tannins from bark have been shown to slow nitrification in soil (Bollen and Lu 1969), suggesting that timber harvest residues should be left on the site rather than burned. Bollen (1974) has detailed the factors involved and has recommended specific ways of dealing with residues in lieu of burning. Properly timed fertilization of unburned sites with N can improve the C:N ratio to increase reproduction and activity of soil microbes and fungi without contributing to water pollution. It may offer the bonus of increasing populations of microorganisms antagonistic to root pathogens (Nelson 1972, 1975).

Adding Nitrogen by Biological Fixation

Biological N_2 fixation ranks high among the world's sources of available soil N. Production of synthetic N fertilizers, especially urea, requires large amounts of energy. Additional energy is used to transport and apply these fertilizers. Man's fascination with technology has led to devoting immense resources to research on fertilizer production and application. Meanwhile, study of how to manage the highly effective biological system for N_2 fixation in forests has received relatively little attention.

The N_2 -fixing organisms that nodulate alders and *Ceanothus* spp. are known to add substantial N to an ecosystem. Over a 5-year period, a red alder forest contributes a conservatively estimated 780 kg of N/ha (690 lb/acre), which

represents about \$600/ha (\$240/acre) worth of forest fertilization as practiced in the DFR on the basis of 1975 costs, a sixfold increase from 1970 costs (Tarrant and Trappe 1971). The dollar values of N_2 fixation will further rise with increases in the price of natural gas used in the manufacture of urea.

However, the rosy benefits afforded by management of biological N_2 -fixing host plants are clouded by the fact that the nodulated host plants other than red alder are small trees, shrubs, or herbs. All of these plants, especially red alder, will compete with conifers in mixed stands. Only red alder offers an economically usable wood product, but it is not yet as valuable as most conifers.

Alternating rotations of alder and conifers may well be a useful management practice on some sites, especially where *Phellinus (Poria) weirii* root rot is a problem on the conifers (Tarrant and Trappe 1971). Otherwise, the silviculture of growing nodulated host plants together with conifers remains to be developed.

Managing Mycorrhizae

Nearly all forest plants have evolved with a strong dependence on mycorrhizal fungi for extracting nutrients from soil. The ectomycorrhizae of Pinaceae (including Douglas-fir, hemlocks, spruces, true firs, and pines) and certain other woody plant families serve additional functions as well, such as protecting root tips from attack by pathogens (Trappe and Fogel 1977).

Each species of Pinaceae in the DFR can form mycorrhizae with hundreds of fungal species. A single tree typically has mycorrhizae formed respectively with several different fungi. The wide array of fungi suitable for a tree species encompasses broad physiological diversity. Some may be especially tolerant of temperature extremes or drought, some may be particularly effective in absorbing nutrients such as P, some may protect root tips from pathogenic invasion more than others, etc. (Trappe and Fogel 1977).

Nursery stock bears mycorrhizal fungi from the nursery. These have been fungi adapted to the fertilizer and irrigation regimes of the nursery soils but not necessarily suited to help the seedlings become established at the planting site. Fumigation of nursery soils can effectively eliminate mycorrhizal fungi (Trappe and Strand 1969). The void thus created can be filled by inoculation with fungi selected for specific qualities, such as adaptability to the planting site for which a given lot of seedlings is destined. The technology for such practices is currently being developed in several DFR nurseries. In addition, containerized production of seedlings opens opportunities for inoculation.

THE FORESTERS' ALLIES IN THE SOIL

Research has a vital responsibility to continually expand our understanding of soil organisms and their activities and to develop ways of using this understanding to achieve management goals. The forester who is truly attuned to the ecosystem will assimilate the concepts and knowledge and put them to intelligent use.

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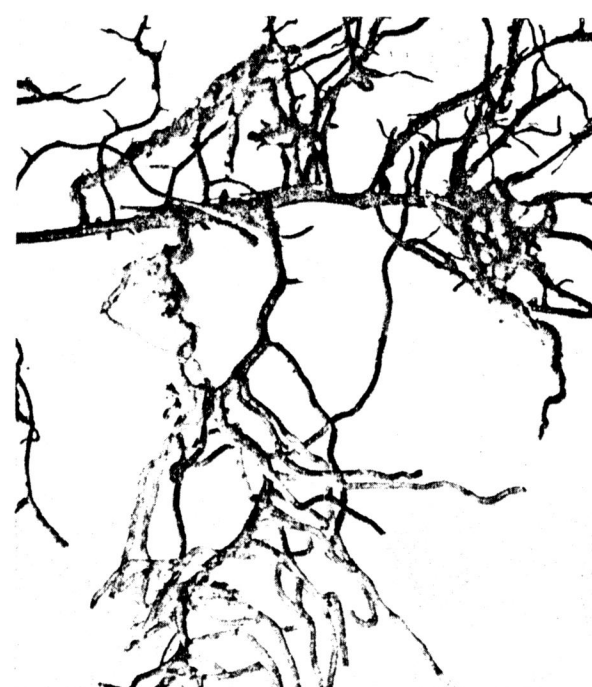
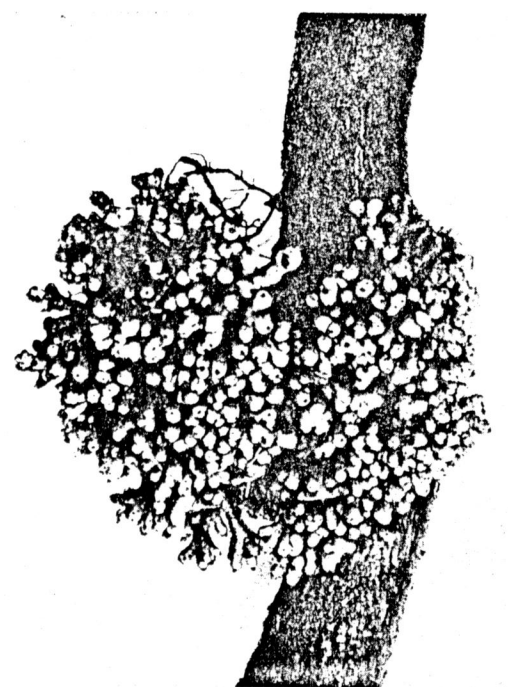
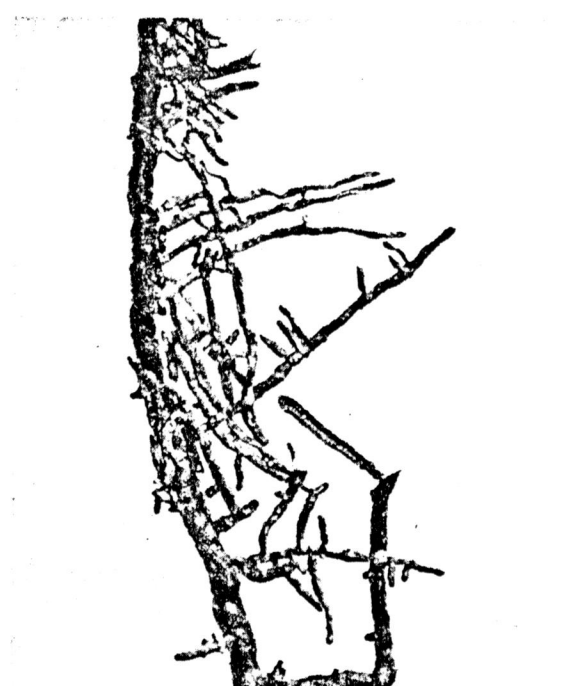
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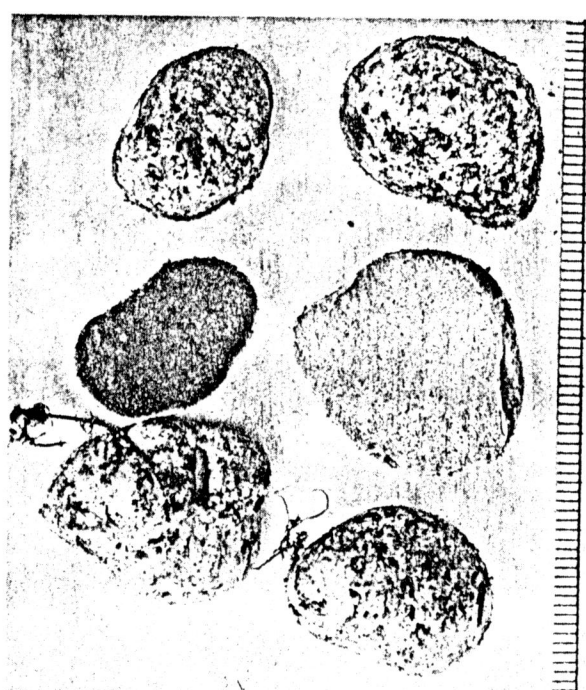
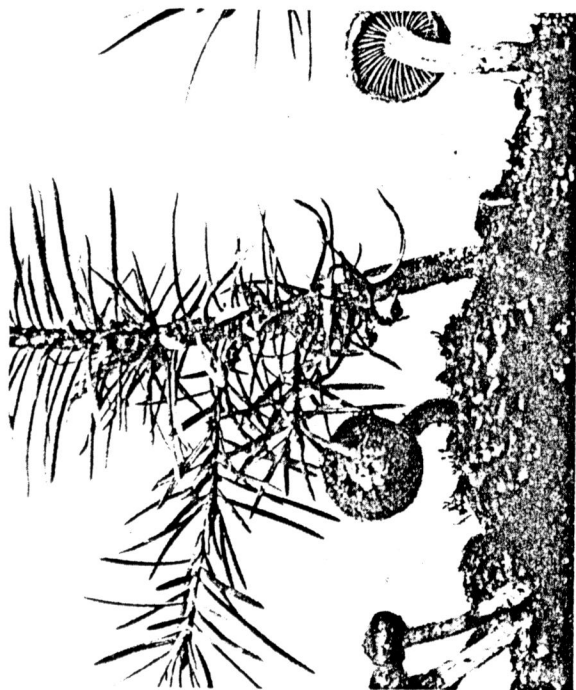
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(Trappe) Plate 1. Alder Nodules and Alder and Maple Mycorrhizae

- a. L Large mature alder nodule (X 1).
- b. Immature and mature alder nodules (X 1.2).
- c. Red alder root with 2 types of ectomycorrhizae—2 different fungi (X 2):
 - 1. Pale and smooth-fungus unknown.
 - 2. Pink and tomentose from outgrowing hyphae—fungus unknown.
- d. False truffle fruiting body of *Alpova diplophloeus*, (Scale in mm).
- e. Bigleaf maple root with endomycorrhizae (X 4).
- f. Vine maple root with endomycorrhizae (X 4).



(Trappe) Plate 2. Douglas-fir Mycorrhizae

- a. Douglas-fir seedling with mushrooms of a mycorrhizal fungus, *Inocybe lacera*, fruiting from the mycorrhizae (X1).
- b. Mushroom of *Russula cascadenis*, a mycorrhizal fungus of Douglas-fir (X 1).
- c. False-truffle fruiting body of *Rhizopogon vinicolor*, a mycorrhizal fungus of Douglas-fir (Scale in mm).
- d. Douglas-fir root with two types of ectomycorrhizae—2 different fungi (X 4):
 - 1. Black and tomentose—formed with *Cenococcum geophyllum*.
 - 2. Light pinkish tan and smooth—fungus unknown.
- e. Bronze-green mycorrhizae of Douglas-fir formed with the fungus *Lactarius sanguifluus* (4 X).
- f. White mycorrhizae of Douglas-fir with abundant hyphae and rhizomorphs (X 4).