

INTENSIVE FIBER UTILIZATION AND PRESCRIBED FIRE:

EFFECTS ON THE MICROBIAL ECOLOGY OF FORESTS

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PREFACE

National projections show substantial increases in the demand for wood and wood fiber-based products, especially housing materials. Environmental considerations favor extending the use of wood, a renewable resource that can be processed with less energy and less pollution than alternative materials. Present utilization standards and logging practices leave large amounts of residue--small trees, cull and broken logs, tops, and dead timber--on the ground following harvesting. These residues can contribute to the forest's nutrient reservoir, reduce erosion, protect seedlings, improve soil quality (by either natural decay or as a fuel for natural wildfire) and provide wildlife cover. However, in the quantities that frequently occur, residues can also create an unnaturally high fire hazard, inhibit regeneration, detract from esthetic values, and waste scarce fiber resources.

Interactions between logging systems, silvicultural treatments (such as prescribed fire), and their respective residues will be manifested by changes in the soil microflora. These contributions are controlled by the basic physical and chemical aspects of the forest environment that are influenced by man's activities in the forests. Results of these activities will affect the nature and function of both individual and collective microbial populations. Microbial activities will be mediated primarily through changes in the soil which may have a subsequent effect on site quality.

Presently, little is known about the optimum amount and kinds of residue needed to maintain or improve soil quality after timber is harvested. This compendium was prepared as a basis for initiating research into the microbiological effects of alternative residues management procedures and to bring about an awareness of the potential problems and opportunities in this arena of environmental manipulation.

Past research reports many instances wherein management actions have had unforeseen effects on soil quality. This reflects a lack of knowledge of many forest environments and emphasizes the need to examine each forest condition individually. Only by better understanding the net effects wrought by management practices on each forest environment, can its soil be protected as a storehouse of essential microbial activity, mineral nutrients, and physical characteristics, which together comprise the substrate for growth of future forests.

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ABSTRACT

Reviews current knowledge of the effects of intensive wood utilization, prescribed burning, or a combination of both treatments, on the microbial ecology of forest soils. Identifies additional research that must be done to fill voids in knowledge.

THE EFFECTS OF INTENSIVE UTILIZATION AND FIRE ON SITE QUALITY

Intensive Utilization

Soils are developed by the integrated action of environmental forces upon parent materials. The soils produced have physical, chemical, and biological properties that derive from the relative influence of parent materials, climate, living organisms, topography, and time.

As forest soils mature, their properties become more distinct and more stable. The highly characteristic properties of forest soils are dependent on the presence of organic material on the soil surface, the continuous or periodic additions of fresh material as litterfall, and decaying woody materials. To the extent that it changes the rate of deposition and decay of organic material deposited on the forest floor, utilization may alter the rate or direction of soil formation processes.

When organic materials are removed from a site, such as by logging, the release of unavailable nutrients in soil is accelerated (Borman and others 1968). Likens and others (1969) demonstrated that severe treatments of watersheds result in the increase of nitrates and other mineral anions in streamflow. European experience has also shown that continuous litter and residue removal inhibits growth¹ (Krause and Hartel 1935; Weidemann 1934, 1935; Albert 1924). Close utilization of residues has not been widespread in North America. However, in certain loblolly pine stands in eastern Maryland where leaf litter had been regularly removed as a bedding material for animals, Cope (1925) reported a decrease of both height growth and volume. In Quebec, Weetman and Webbar (1972) indicated that on dry sites with low organic reserves, whole tree logging may deplete nutrients during the second rotation. Zinke and Colwell (1972) agree, and indicate that only stems and trunks should be removed during harvesting. Foliage, branches, and roots should be left as an organic resource.

Decaying woody materials contribute to the desirable properties of forest soils and persist for decades (McFee and Stone 1966). Further, decaying woody material constitutes the primary food base for a myriad of decay fungi that may serve as nutrient sinks that reduce losses from leaching of mineral nutrients (Stark 1972). Thus, removal of the organic material may reduce soil nutrients that require many decades to reconstitute, naturally or otherwise.

Even on favorable sites with stable soils, changes in organic resources could have short-term effects. For instance, any treatment that alters the relative ability of conifers and brush species to compete during recovery stages could affect early successional development. Whether or not such changes are desirable depends on management objectives.

Clearcutting has great impact on residue reduction and soil disturbance. Clearcutting temporarily interrupts the cycling of nutrients between the plants and the soil and it increases both soil temperatures (Day and Duffy 1963) and moisture (Bethlahmy 1962). Those changes favor decomposition of residues and other processes that increase nutrient release to the soil (Likens and others 1969). Removal of the plant cover also interrupts evapotranspiration and increases water movement through the soil system

¹Lesniká Práce. 1933. Damages caused by removal of forest litter. Vol. 12:137-146.

(Bethlahmy 1962; Coltharp 1960), increasing the probability of nutrient loss through leaching. However, most forest soils have a high capacity to retain nutrients against ground and surface runoff (Fredrickson 1972; Cole and Gessel 1965). If revegetation occurs rapidly, within a few years systems characteristic of the area are reestablished (Marks and Borman 1972).

The amount and distribution of slash and the extent of disturbance to the forest floor and soil systems are strongly influenced by the method of clearcutting (Bell and others 1974). Under some circumstances, even extensive thinning can cause site damage (Tamm 1969). Similarly, whole tree utilization may cause small losses of nutrients that could be significant after many harvest removals (Boyle and others 1973; White 1974). The needles and twigs contain a large proportion of the nutrients of the tree (Boyle and others 1973; Keays 1970, 1971). Thus, the combined effect of clearcutting, logging method, and intensive or whole tree utilization may have significant impacts on site quality. These impacts and the ability of specific sites to withstand them remain to be determined.

Literature Cited

Albert, A.

1924. Die ausschlaggebende bedeutung des wasserhaushaltes fur die ertragsleistungen unserer diluvialen samde, ermittelt durch bodenuntersuchungen in dem waldgebiet der standesherrschaft lieberose. N. - L. Zeitschr. Forest-u. Jagd. 56:193-202.

Bell, M. A. M., J. M. Beckett, and W. F. Hubbard.

1974. Impact of harvesting on forest environments and resources. Pac. For. Res. Cen., Can. For. Serv., Victoria, B. C.

Bethlahmy, N.

1962. First year effects of timber removal on soil moisture. Bull. Int. Assoc. Sci. Hydrol. 7:34-38.

Borman, F. H., G. E. Likens, D. W. Fisher, and R. S. Pierce.

1968. Nutrient loss accelerated by clearcutting of a forest system. Science 159: 882-884.

Boyle, J. R., J. J. Phillips, and A. R. Ek.

1973. "Whole tree" harvesting: nutrient budget evaluation. J. For. 71:760-762.

Cole, D. W., and S. P. Gessel.

1965. Movement of elements through a forest soil as influenced by tree removal and fertilizer additions. In: Forest soil relationships in North America, p. 95-104. C. T. Youngberg, ed., Oreg. State Univ. Press, Corvallis.

Coltharp, G. B.

1960. Some effects of a commercial-type clearcut on soil and water relations on a small wooded watershed. Diss. Abstr. 21:12.

Cope, J. A.

1925. Loblolly pine in Maryland. Univ. Maryland State Dep. For. 2nd ed., 96 p.

Day, R. J., and J. B. Duffy.

1963. Regeneration after logging in the Crowsnest Forest. Can. Dep. For. Publ. 1007, 31 p.

Fredrickson, R. L.

1972. Nutrient budget of a Douglas-fir on an experimental watershed in western Oregon. In: Proc., Research on coniferous forest ecosystems--a symposium, p. 115-131. J. F. Franklin, L. J. Demster, and R. H. Waring, eds. Pac. Northwest For. and Range Exp. Stn., Portland, Oreg.

Keays, J. L.

1970, 1971. Complete-tree utilization: an analysis of the literature in five parts. For. Prod. Lab., Can. For. Serv., Vancouver, B.C.

Krauss, G., and F. Hartel.

1935. Zur walsboden - untersuchngen. Soil Res. 4:207-216.

Likens, G. E., F. H. Borman, and N. M. Johnson.

1969. Nitrification importance to nutrient losses from a cutover forested ecosystem. Science 163:1205-1206.

- Marks, P. L., and F. H. Borman.
 1972. Revegetation following forest cutting: mechanisms for return to steady-state nutrient cycling. *Science* 176:914-915. McFee, W. W., and E. L. Stone.
 1966. The persistence of decaying wood in the humus layer of northern forests. *Proc. Soil Sci. Soc. Am.* 30:513-516.
- Stark, N.
 1972. Nutrient cycling pathways and litter fungi. *Bioscience* 22:355-360.
- Tamm, C. O.
 1969. Site damage by thinning due to removal of organic matter and plant nutrients. *Dep. Plant Ecol. For. Soils Publ.* 78. 6 p. Royal Coll. For., Stockholm.
- Weetman, G. F., and B. Webbar.
 1972. The influence of wood harvesting on the nutrient status of two spruce stands. *Can. J. Res.* 2:351.
- Weidmann, E.
 1934. Über die beziehungen des forstlichen sandortes zu dem wachstum und dem wirtschaftserfolg im walde. *Deut. Forsch.* 24:5-106.
- Weidmann, E.
 1935. Die ergebnisse 40-jähriger vorratspflege in den preussischen forstlichen versuchsflächen. *Forstarchive* 11:65-108.
- White, E. H.
 1974. Whole tree harvesting depletes soil nutrients. *Can. J. For. Res.* 4:530-535.
- Zinke, P. J., and W. L. Colwell, Jr.
 1972. Nutrient cycling in forests. *Proc. 1st Annu. Calif. Plant and Soil Conf.*, p. 51. (Sacramento, Calif., 1972).

Fire

The main ecological effect of fire is to compress the oxidative activities of decay into a very short time span. Most of the products of either biological or heat oxidation are similar in chemical composition and in quantity (Hall 1972; Komarek 1970). With the exception of charcoal, fire residues are eventually consumed by microbes as they would be in biological decomposition. Charcoal residues are not only highly resistant to decomposition, they also change the soil environment (Tyron 1948). Charcoal has been known to persist in soils for several hundred years (Soper 1919). Thus, fire or the lack of fire can have longstanding effects on forest soils.

Fires in heavy fuels can sterilize and change the biological, physical, and chemical characteristics of the upper soil horizons (Neal and others 1965). Changes include increasing soil pH from 0.3 to 1.2 units widening the C:N ratios of soil organic matter, and reducing soil pore size, aeration, water-holding capacity (Ralston and Hatchel 1971; Neal and others 1965), and water infiltration rates (DeBano and Rice 1973). These changes usually reduce microbial activities for varying periods after the burn (Ahlgren and Ahlgren 1965; Wright and Tarrant 1957). Reinoculation occurs from windblown spores or other debris, and through invasion from subsurface layers. Because burning changes the soil's physical and chemical properties and eliminates many potential competitors, microbes adapted to the changed soil environment have an advantage in the recolonization process.

When moisture is sufficient, the microbial population is quickly reconstituted, primarily from organisms adapted to the new soil environment. The reconstituted population may be greater and more active than the original one (Ahlgren and Ahlgren 1965), perhaps because of the large quantity of mineral nutrients released from the ash and because of other shifts in soil chemistry. For example, spores of the root pathogen *Rhizina undulata* Fr. germinate only after exposure to elevated temperatures (Gremmen 1971). It thereby gains access to soils that are rich in nutrients, that are likely to contain young and susceptible conifer roots, that harbor few competing organisms, and that have low concentrations of heat-labile growth inhibitors (Watson and Ford 1972). Increases in other potential conifer root pathogens have also been reported after burning (Wright and Bollen 1961; Tarrant 1956).

Temporary reductions in conifer-fungal mycorrhizal consociations have been found after burning (Wright 1971, 1958; Mikola and others 1964; Wright and Tarrant 1957; Tarrant 1956). Experimental heat sterilization of soils stimulates the production of biologically degradable phytotoxins (Rovira and Bowen 1966). Creation of such toxins by surface fires and their subsequent microbiological breakdown may represent important processes in forest soils. Mycorrhizal fungi have been reported to neutralize the effects of such toxins (Zak 1971). These changes will vary in degree and duration, depending on the intensity of the burn, soil type, climatic characteristics, and the type of vegetation that becomes established after the burn.

Most soil nitrogen (N) is present in the form of nitrogenous compounds contained in leaves, small twigs, and other materials of the decaying duff. Both laboratory (Knight 1966) and field studies (Metz and others 1961) have established that substantial net losses of N occur due to burning. However, N and other mineral nutrients in specific residue materials can increase. The apparent activity of micro-organisms active in the N cycle is increased in postburn soils (Jorgensen and Wells 1971; Neal and others 1965). Although net losses of N occur through volatilization and leaching, increases in N-fixing organisms of many soils may reconstitute a portion of this loss (Metz and others 1961; Wells 1971). Thus, the extent of N fixation and subsequent soil N transformations occurring after fire are critical factors in evaluating the long-term effects on site quality.

Although fire can have many detrimental effects on the soil environment, frequent burning on stable soils does not significantly damage site quality (Stone 1971; Wells 1971). Further, most forested ecosystems in North America have evolved under the direct influence of fire (Habeck and Mutch 1973; Komarek 1962; Ahlgren and Ahlgren 1960). In north temperate forests energy is stored at rates that exceed natural utilization (Olsen 1963). Therefore, fire or silvicultural alternatives may be required to maintain site quality by freeing energy and nutrients bound in forest residues. Not yet defined are the limits and conditions under which the rejuvenative (Lyons and Pengelly 1970; Komarek 1962) and protective silvicultural benefits (Davis 1959) provided by fire exceed its potential for damage.

Literature Cited

- Ahlgren, J. T., and C. E. Ahlgren.
1960. Ecological effects of forest fires. *Bot. Rev.* 26:483-533.
- Ahlgren, J. R., and C. E. Ahlgren.
1965. Effects of prescribed burning on soil microorganisms in a Minnesota jack pine forest. *Ecology* 46:304-310.
- Davis, K. P.
1959. *Forest fire: control and use.* 584 p. McGraw-Hill, New York.
- DeBano, L. T., and R. M. Rice.
1973. Water-repellent soils: their implications in forestry. *J. For.* 71:200-223.
- Gremmen, J.
1971. *Rhizina undulata*: a review of research in the Netherlands. *Eur. J. For. Path.* 1:1-6.
- Habeck, J. R., and R. W. Mutch.
1973. Fire dependent forests in the northern Rocky Mountains. *Quaternary Res.* 3:408-424.
- Hall, A. J.
1972. Forest fuels, prescribed fire, and air quality. USDA For. Serv., Pac. Northwest For. and Range Exp. Stn., 44 p.
- Jorgensen, R., Jr., and C. G. Wells.
1971. Apparent nitrogen fixation in soil influenced by prescribed burning. *Proc. Soil Sci. Soc. Am.* 35:806-810.
- Knight, H.
1966. Loss of nitrogen from the forest floor by burning. *For. Chron.* 42:149-152.

- Komarek, E. V.
1962. Fire ecology. Proc. Tall Timbers Fire Ecol. Conf. 1:95-107.
- Lyons, J. L., and W. L. Pengelly.
1970. Commentary on the natural role of fire in the Intermountain west. Intermt. Fire Res. Counc. Proc., Missoula, Mont. p. 81-84.
- Metz, L. J., F. Lotti, and R. A. Klawitter.
1961. Some effects of prescribed burning on coastal plain forest soil. U.S. Dep. Agric. For. Serv., Southeast. For. Exp. Stn. Pap. 133, 10 p.
- Mikola, P., O. Laiho, J. Erickainen, and K. Kuvaja.
1964. The effect of slash burning on the commencement of mycorrhizal association. Acta. For. Fenn. 77:1-11.
- Neal, J. L., E. Wright, and W. B. Bollen.
1965. Burning Douglas-fir slash. Physical, chemical, and microbial effects in soil. Oreg. State Univ. For. Res. Lab. Res. Pap. 1, 32 p.
- Olsen, J. S.
1963. Energy storage and the balance of producers and decomposers in ecological systems. Ecology 44:322-331.
- Ralston, G. W., and G. E. Hatchell.
1971. Effects of prescribed burning on physical properties of soil. Proc. Prescribed Burning Symp., p. 68-84. USDA For. Serv., Southeast. For. Exp. Stn.
- Rovira, A. D., and G. D. Bowen.
1966. The effects of microorganisms upon plant growth. II. Detoxication of heat-sterilized soils by fungi and bacteria. Plant and Soil 25:129-142.
- Soper, E. K.
1919. The peat deposits of Minnesota. Minn. Geol. Surv. Bull. 16.
- Stone, E. L.
1971. Effects of prescribed burning on long-term productivity of coastal plain soils. Proc. Prescribed Burning Symp., p. 115-127. U.S. Dep. Agric. For. Serv. Southeast. For. Exp. Stn.
- Tarrant, R. F.
1956. Effects of slash burning on some soils of the Douglas-fir region. Proc. Soil Sci. Soc. Am. 20:408-411.
- Tyron, E. J.
1948. Effects of charcoal on certain physical, chemical, and biological properties of forest soils. Ecol. Monogr. 18:82-115.
- Watson, A. G., and E. J. Ford.
1972. Soil fungistasis--a reappraisal. Annu. Rev. Phytopath. 9:327-348.
- Wells, C. G.
1971. Effects of prescribed burning on soil chemical properties and nutrient availability. Proc. Prescribed Burning Symp., p. 86-97. U.S. Dep. Agric., For. Serv., Southeast For. Exp. Stn.
- Wright, E.
1958. Occurrence of mycorrhizae after logging and slash burning in the Douglas-fir forest type. U.S. Dep. Agric., For. Serv., Pac. Northwest For. and Range Exp. Stn. Pap. 160, 7 p.
- Wright, E.
1971. Mycorrhizae on ponderosa pine seedlings. Oreg. State Univ. Bull. 13, 36 p.
- Wright, E., and W. B. Bollen.
1961. Microflora of Douglas-fir soil. Ecology 42:825-828.
- Wright, E., and R. F. Tarrant.
1957. Microbiological soil properties after logging and slash burning. U.S. Dep. Agric., For. Serv., Pac. Northwest For. and Range Exp. Stn. Pap. 157, 5 p.
- Zak, B.
1971. Detoxication of autoclaved soil by a mycorrhizal fungus. USDA For. Serv. Res. Note PNW-159, 4 p. Pac. Northwest For. and Range Exp. Stn., Portland, Oreg.

RELATIONSHIP OF UTILIZATION INTENSITY AND FIRE TO MICROBIAL ECOLOGY

The major microbial functions in a forest ecosystem are carried out in the soil environment. The surface layers of a forest soil may contain 10 to 100 million bacteria and 1 to 100 thousand fungi per gram (0.035 oz). The microbial mass in the top 6 inches (15.2 cm) of an acre of fertile agricultural soil has been estimated at 1,000 lb (450 kg) of bacterial and 2,000 lb (900 kg) of fungal biomass, on a dry weight basis (Bollen 1959). Soil, litter, and woody residue, largely in the form of cellulose and lignin, constitute the energy base for this intensely active component of a forest. The mineral nutrients required to maintain a forest ecosystem are largely derived from such residue and the microbial activity it supports.

Plant nutrients are derived directly from the atmosphere or soil parent materials, mainly through microbial metabolism. The accumulation of organic materials in or on forest soils provides not only the energy source for microbial growth, but also a reservoir for available nutrients. Thus, a forested ecosystem is characterized by a large, highly efficient, internal circulation system that transfers mineral nutrients between the plant cover and the soil. Production of large quantities of biomass from forest soils is the result of this system (Ovington 1962).

How forest residues contribute to the soil resource, through natural decay or prescribed fire, must be understood and managed if extreme changes in soil properties are to be avoided. The soil is a dynamic system that is maintained by an unstable equilibrium of physical, chemical, and biological processes. Residue effects are mediated primarily through changes in soil parameters, e.g., temperature, moisture, aeration, acidity, nutrient and energy supply, and available biota (Bollen 1974). It is appropriate to examine in detail how close utilization or burning of residues affects the six factors directly involved in this delicate equilibrium.

Temperature

Each micro-organism has an optimum temperature both for growth and for each of many metabolic processes that contribute to its ecological functions. Outside these temperature optima, growth or function ceases or changes (Raney 1965). Within any given forest, micro-organism populations are comprised primarily of those well adapted to the prevailing temperature regime. Radical changes in soil temperatures, such as those resulting from clearcutting, particularly when associated with residue removal or burning, can engender radical changes in microbial populations (Parr 1968). These fluctuations are most pronounced in the uppermost soil layers where temperatures are strongly influenced by radiation exchange or short-term effects of burning. The success of the subsequent forest depends upon this layer.

Moisture

The optimum moisture content of forest soils for microbial activity is near 50 percent of its water-holding capacity (Bollen 1974). As moisture decreases below that level, growth and metabolism of the soil microflora are reduced. When soil becomes air-dry, both processes essentially cease. On the other hand, as moisture increases, the air supply is reduced (displaced). As air displacement increases beyond 50 percent, microbial growth and metabolism are again reduced, until all aerobic processes come to a near standstill (Stolzy and Van Gundy 1968). Treatment of forest residues profoundly

affects buffering of soil moisture extremes, particularly the rapidity of drying of upper soil layers during the summer (Day 1963; Day and Duffy 1963). Drying rate is also strongly affected by climate and site. For example, residues in wet spots remain saturated for most of the year and decompose very slowly; and soil moisture loss in the summer will be more critical to the microbial activity of a southwest-facing slope than of a north-facing slope.

Aeration

Gaseous oxygen (O_2), carbon dioxide (CO_2), and nitrogen (N_2) are components of the atmosphere vital to microbial metabolism. Oxygen is required for most processes that decompose carbon compounds, to produce energy for growth. Most micro-organisms require at least a trace of CO_2 to initiate growth. This compound is also an end product of energy-related metabolism. Excessive amounts of CO_2 can retard microbial activity (Wimpenny 1969). Certain N-fixing organisms incorporate gaseous nitrogen directly into cellular constituents. Thus, movement of atmospheric gases into the soil must be adequate for satisfactory exchange. Any residue treatments that impede ventilation will predictably reduce microbial activity by restricting O_2 supplies or by permitting gases to reach toxic concentrations (Clark and Kemper 1967). Treatments that encourage compaction or the formation of impermeable soil layers can be exceedingly detrimental. Accumulation of organic soil residue does not adversely affect the gas exchange process.

Hydrogen Ion Concentration (pH)

Concentration of hydrogen ions in the soil strongly affects microbial activity. The observed effects of soil acidity on micro-organisms may be attributed to (1) changes in organic matter availability; (2) pH-caused nutrient deficiencies; (3) toxic effects of hydrogen or aluminum ions; or (4) a combination of the above factors (Jurgensen 1973). Micro-organisms differ in their degree of tolerance to pH change. Some thrive only in a very narrow range and others tolerate wide extremes (Davey and Danielson 1968).

Radical changes in soil pH result from the effects of residue management, especially fire (Wells 1971). The presence of ash or charcoal increases basicity. When such a change occurs, organisms with either a wide pH range or a narrow pH range suitable to the new regime replace the previously existing biota. This effect is particularly pronounced as soil pH nears neutrality and the acid-base activities approach balanced levels. Thus, the microbiological activities of weakly acid forest soils are highly susceptible to drastic change.

Forest soils are typically acid. Leaching increases acidity through loss of mineral elements. The extent and rate of nutrient loss is a function of cation exchange capacity in areas of sufficient rainfall. Partially decomposed residues provide an important source of exchange sites, particularly in coarse-textured soils.

Nutrient and Energy Supply

Because most soil organisms are heterotrophic, they require a source of energy in the form of carbon compounds. The effect of forest litter and woody residues on soil microbial activity depends on the type of material, its nutrient content, and on the initial fertility of the soil (Davey and Danielson 1968; Waksman and Tenney 1928). A lack of suitable organic substrates normally limits the growth of heterotrophic micro-organisms in soil (Gray and Williams 1971).

Although an abundance of carbon (C) compounds is desirable, excessive amounts can produce marked expansion of microbial populations and excessive competition for mineral nutrients. Soil micro-organisms require many of the same nutrient elements as do

higher plants and can, at times, provide intense competition to plants for these nutrients. Because of the low N supply in most woody residues and other similar materials, competition generally results in severe N deficiencies termed "immobilization" (Zoettl 1965). The immobilized N is used in the production of microbial cells and, although it is not lost to the site, it is unavailable to higher plants until death and decomposition of the microbes exceed their population growth (Mulder and others 1969). For an optimum rate of decomposition, the C to N ratio should approximate 25:1. In decay-resistant woody residues, the ratio is much wider (approximately 400:1), but much of this C is in the form of lignins, which break down slowly (Allison and others 1963). Thus, lignicolous materials exert low but long-term N demands. Humus, and therefore most soils, should have a narrow C-to-N ratio (approximately 20:1).

Humus is mostly made up of highly decomposed material. The material that is not decomposed is highly resistant to further breakdown. Humus also contains a large quantity of the available cation exchange capacity for nutrient storage. Mineralized soil N is easily released from these cation exchange sites and is readily available for plant or microbial growth. N deficiencies in humus normally occur only when high C-to-N ratio, readily decomposable residues become incorporated. This begins a rapid decay process that quickly immobilizes much of the soil N supplies (Bartholomew 1965). On the other hand, residues that remain on but not in the soil may, through slow decay, actually increase N supplies to the soil under the right conditions.

Available Biota

Soil organisms compete for mineral nutrients, food supplies, and possibly oxygen (Clark 1969), which leads to highly refined competitive mechanisms adapted for specialized niches. Production of antibiotics, and parasitism, predation, and symbiosis serve as examples. Competition sometimes limits the development of certain species and leads to successions of organisms as decomposition proceeds (Alexander 1964).

Frequently, the nature of the microbial successions is dictated by the pioneer organisms present when a food source becomes available. Pioneer organisms are largely controlled by the previously described physical and chemical parameters that govern macrohabitat. Pioneer species may impose permanent changes on the subsequent successions of micro-organisms until a specific food source is exhausted (Shigo and Ellis 1973). Residues and residue treatments directly influence the successional patterns. Thus, the pioneer organisms prevalent during the season in which the residues are generated may control subsequent microbial populations.

As indicated previously, available moisture, temperature, and amount and kind of organic substrate dictate the type of organisms active in the soil at any given time. Biotic history can also influence soil microflora. For example, previous activity of soil pathogens or stem decays may affect reforestation. Residues indirectly affect soil activity just as they affect the establishment of higher plants on the site, e.g., the establishment of *Alnus* or *Ceanothus* species following burning provides host roots for certain symbiotic organisms (Youngberg and Wollum 1970). Similarly, specific conifers are hosts for certain ectomycorrhizal fungi.

The roots of pioneering plants directly influence the soil. The soil area surrounding the roots of higher plants, termed the rhizosphere, is characterized by very intense microbial activity. This activity is based on leakage or sloughing of food materials, such as certain sugars and amino acids, from the roots (Rovira 1969; Slankis and others 1964). The extent and influence of such root systems in soils are little appreciated. A single rye plant grown in 2 ft³ (0.06 m³) of soil had 13,800,000 roots with a total length of 387 mi (619.2 km), and 14 by 10⁹ root hairs with a total length of 6,600 mi (10,619 km), and provided a total surface area of 6,874 ft² (638.6 m²). The total external surface of the shoots and leaves of this plant provided only 51.38 ft² (4.72 m²) of surface area (Ditmer 1937). A 55-year-old Douglas-fir is reported

to have 464 ft (141.4 m²) of roots greater than 1 cm in diameter (McMinn 1963), but the greatest length and surface area would be contributed by smaller roots. Dead roots are also important as food supplies for decay organisms in deep soil strata.

Literature Cited

- Alexander, M.
1964. Biochemical ecology of soil microorganisms. *Annu. Rev. Microbiol.* 18:217-252.
- Allison, F. E., R. M. Murphy, and C. J. Klein.
1963. Nitrogen requirements for the decomposition of various kinds of finely ground woods in soil. *Soil Sci.* 96:187-190.
- Bartholomew, W. V.
1965. Mineralization and immobilization of nitrogen in the decomposition of plant and animal residues. *In: Soil Nitrogen, Agron. Monogr.* 10, p. 295-306. W. V. Bartholomew and F. E. Clark, eds. Am. Soc. Agron., Madison, Wisc.
- Bollen, W. B.
1959. Microorganisms and soil fertility. *Oregon State Monographs, Studies in Bacteriology*, No. 1, Oreg. State Coll., Corvallis.
- Bollen, W. B.
1974. Interaction between soil microbes, forest residues, and residue treatments. *In: Environmental effects of forest residues management in the Pacific Northwest.* O. P. Cramer (ed.) USDA For. Serv. Gen. Tech. Rep. PNW-24. Pac. Northwest For. and Range Exp. Stn., Portland, Oreg.
- Clark, F. E.
1969. Ecological associations among soil microorganisms. *In: Soil biology, reviews of research.* *Natl. Resour. Res. UNESCO* 9:125-161.
- Clark, F. E., and W. D. Kemper.
1967. Microbial activity in relating to soil water and soil aeration. *In: Irrigation of agricultural lands*, p. 472-480. H. R. Haise and T. W. Edminster, eds. Am. Soc. Agron.
- Davey, C. B., and R. M. Danielson.
1968. Soil chemical factors and biological activity. *Phytopathology* 59:900-908.
- Day, R. J.
1963. Spruce seedling mortality caused by microclimate in the Rocky Mountains. *Can. Dep. For., Publ.* 1003, 35 p.
- Day, R. J., and P. J. B. Duffy.
1963. Regeneration after logging in the Crowsnest Forest. *Can. Dep. For. Publ.* 1007 31 p.
- Ditmer, H. J.
1937. A comparative study of the subterranean members of three field grasses. *Science* 88:2290.
- Gray, T. R. G., and S. T. Williams.
1971. Microbial activity in soil. *In: Microbes and biological productivity*, p. 255-286. D. E. Hughes and A. H. Rose, eds., 21st Symp. Soc. Gen. Microbiol. Cambridge Univ. Press.
- Jurgensen, M. F.
1973. Relationship between nonsymbiotic nitrogen fixation and soil nutrient status. *J. Soil Sci.* 24:512-522.
- McMinn, R. G.
1963. Characteristics of Douglas-fir root systems. *Can. J. Bot.* 41:105-122.
- Mulder, E. G., T. A. Lie, and J. W. Woldendorp.
1969. Biology and soil fertility. *In: Soil biology, reviews of research.* *Nat. Resour. Res. UNESCO* 9:163-208.
- Ovington, J. D.
1962. Qualitative ecology and the woodland ecosystem concept. *Adv. Ecol. Res.* 1:103-192.

- Parr, J. F.
 1968. The soil microbiological equilibrium: nature and duration of changes induced by cultural practices. *In: Forest fertilization--theory and practice*, p. 28-37. Tenn. Valley Auth., Muscle Shoals.
- Raney, W. A.
 1965. Physical factors of the soil as they affect soil microorganisms. *In Ecology of soil-born plant pathogens*, p. 115-119. R. F. Baker and W. C. Snyder, eds. Univ. Calif. Press, Berkeley.
- Rovira, A. D.
 1969. Plant root exudates. *Bot. Rev.* 35:35-57.
- Shigo, A. L., and W. E. Ellis.
 1973. Heartwood, discolored wood, and microorganisms in living trees. *Annu. Rev. Phytopath.* 11:197-221.
- Slankis, V., V. C. Runeckles, and G. Krotov.
 1964. Metabolites liberated by roots of white pine (*Pinus strobus* L.) seedlings. *Physiol. Plant.* 17:310-313.
- Stolzy, L. H., and S. D. Van Gundy.
 1968. The soil as an environment for microflora and microfauna. *Phytopathology* 58:889-899.
- Waksman, S. A., and F. E. Tenney.
 1928. Composition of natural organic materials and their decomposition in the soil: II. The influence and nature of plant upon the rapidity of its decomposition. *Soil Sci.* 25:155-171.
- Wells, C. G.
 1971. Effects of prescribed burning on soil chemical properties and nutrient availability. *Proc. Prescribed Burning Symp.*, p. 86-97. U.S. Dep. Agric. For. Serv., Southeast. For. Exp. Stn.
- Wimpenny, J. W. T.
 1969. Oxygen and carbon dioxide as regulators of microbial growth and metabolism. *In: Microbial growth*, p. 161-197. P. M. Meadow and S. J. Pirt, eds. 19th Symp. Soc. Gen. Microbiol.
- Youngberg, C. T., and A. G. Wollum II.
 1970. Nonleguminous symbiotic nitrogen fixation. *In: Tree growth and forest soils*, p. 385-395. C. T. Youngberg and C. B. Davey, eds. Oreg. State Univ. Press, Corvallis.
- Zoetl, H.
 1965. Accumulation and transformation of nitrogen in forest soils. *Berich. Deutsch. Bot. Gesell.* 78:167-180.

IMPACT OF RESIDUE MANAGEMENT PRACTICES ON CRITICAL MICROBIAL ACTIVITIES

Of the many important activities of soil micro-organisms likely to be influenced by residue management practices, the following are critical and are considered priority items for research: (1) Recycling of materials bound in woody residues through decomposition and decay; (2) establishment and function of mycorrhizal activities; (3) accumulation and retention of soil N in the forest ecosystem; and (4) activities of indigenous plant pathogens.

Decay

For purposes here, decomposition or decay is defined as the enzymatic oxidation of chemically complex woody plant materials by micro-organisms, predominantly fungi (Satchell 1971), to more simple compounds and nutrients that become part of the soil. These materials make up the nutritional organic base of the forest. Woody materials in the various stages of decay may be at the soil surface or be totally or partially imbedded in it. Tree residues, depending on size, persist up to 150 years or more (McFee and Stone 1966; Dimbelby 1953). In the surface foot of soil, woody residue comprises a significant volume, up to 30 percent (McFee and Stone 1966). Hence decomposing woody tissues are an important component of the organic-containing soil layers in temperate forests. As integral parts of the soil system and function, their impact is yet to be fully elucidated.

The Role of Residue Decay in the Forest Ecosystem

The decay and decomposition of plant materials have long been the subject of papers and discussions in both forestry and agriculture. The Carbon Cycle is particularly important to both disciplines. This is the process by which C is photochemically fixed, assimilated by the plant and, after its death, reduced to a variety of simple organic compounds and CO₂ by the soil microflora (fig. 1). The left side of figure 1 encompasses the processes involved in CO₂ fixation by tree growth, the right side depicts CO₂ release through decomposition associated with fungi and other micro-organisms. The decomposition of plant materials in a forest is one of the more complex phenomena associated with this cycle.

In any ecosystem, there is a balance between fixed and decomposed carbon. The principal controlling factors in this cycle are:

1. Light
2. Temperature
3. Moisture and Moisture Regimes
4. Latitude, Slope, and Aspect (insolation)

Restrictive limitations imposed by any one of these factors normally result in responses from the plant community that are reflected in the rate of biomass production and its decomposition (Loman 1965, 1962; Olson 1963; Spaulding 1929a, 1929b).

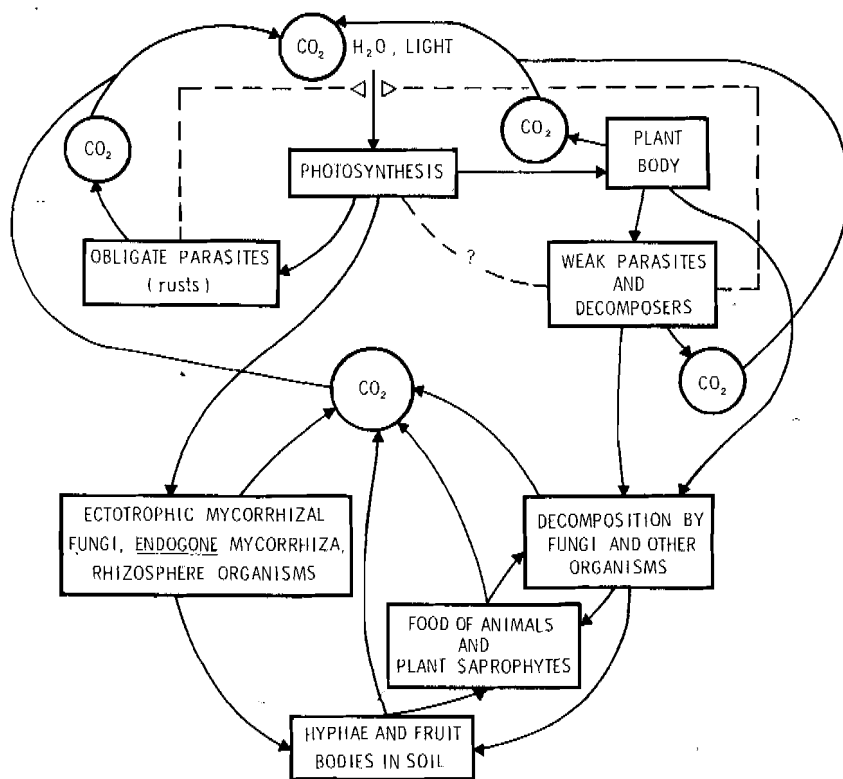


Figure 1.--The role of fungi in cycling carbon within an ecosystem. On the left is the symbiotic cycle directly using photosynthetic products. The decomposition cycle is shown on the right (after Harley 1971).

When examining the C cycles of forest trees and agricultural crops, the major differences between the two are readily apparent. Agricultural practice usually involves annual harvest and site management (with appropriate mineral and organic fertilizer amendments). In forest practice, harvest occurs between 80 to 150 years (sawtimber) or 15 to 25 years (pulpwood) and site management related to fertility and production of the new crop is left primarily to natural processes. Man's interference with these processes has been restricted to (1) limited forest fertilization, (2) nursery-grown outplants, (3) broadcast seeding (often with rodent control), and (4) silvicultural practice that may change forest type.

Man's most recent intercession in the natural events of forest regeneration and stand development (in addition to previous and existing timber harvesting and management practices) has been the removal of both natural and manmade forest residues--a practice stimulated by increased needs for wood fiber (Foulger and Harris 1972; Gardner and Hann 1972). These practices have generated questions regarding the effects of residue removal on fungal populations as they relate to mycorrhizal and disease activity, and nutrient release through decomposition. Survival of conifer seedlings during the initial period of establishment is intimately related to these populations and processes. Survival becomes especially critical on the drier sites (Day 1963; Day and Duffy 1963).

The Nature of Residue Decay

The form and age of residues influence the rapidity of decay. Residues formed from young materials have a fast turnover rate, under optimum decay conditions, due to their high carbohydrate content (or lower lignin contents). Residues formed from old-growth timber are more resistant to decay (Waksman and Tonney 1928). Polyphenolic material (tannin) derived from lignin or lignin like compounds are a component of forest

soils in the form of residues at various stages of decay. They ultimately control the nature of the organic resource and the nutritional, physical, and biological quality of the soil (Davies 1971). For example, Bollen and Lu (1969) reported that tannins (polyphenols) in bark of Douglas-fir stimulate certain molds in the soil.

Studies on the decomposition of forest litter have been conducted by Adam and Cornforth (1973), Kowal (1969), Daubenmire and Prusso (1963), Witkamp (1966), and Hayes (1965a, b). These workers have dealt primarily with leaves, small twigs, and bark. Allison and Murphy (1963) and Allison (1961) studied the decomposition of wood and bark particles in soil but did not examine whole wood or bark. In most of the above work, the specific fungi associated with the decomposition processes were not indicated. Agrawal (1971), in contrast, did utilize specific litter fungi to assay for cellulytic capacity. His experiments, however, were confined to prepared cellulose which does not lend itself to accurate ecological interpretation.

Wagener and Offord (1972) have presented data on the relationship of time to slash decay in northern California. After 34 years, 43 and 85 percent volume reductions of piled slash were observed in two different experimental areas. Estimates of slash volume decayed over periods of time have also been provided by Toole (1965), Roff and Eades (1959), Gil and Andrews (1956), Kimmey (1955), Spaulding and Hansbrough (1944a, b), Kimmey and Furniss (1943), Childs (1939), Spaulding (1929a, b), Hubert (1920), and Long (1917).

The Function of Residue Decay

In addition to the function of decay as a mineral recycling agent, Seidler and others (1972) have recently suggested that the decomposition of woody tissues in conifer stems of the Pacific Northwest may provide a significant ecological niche for N-fixing bacteria of the genus *Clostridium*. Cornaby and Waide (1973) reported the microbial fixation of atmospheric nitrogen in decaying and decayed logs of *Castanea dentata* in the southeastern United States and presented convincing evidence to support the hypothesis as stated by Cowling and Merrill (1966): the possible dependence on external sources of N to support decay fungi in woody materials. The association of N-fixing organisms with the decay process may be extremely important in two ways: (1) by affecting the rates of decay in forest residues, and (2) by site N-replenishment as affected by kinds and amounts of woody residues.

Another important effect of residues, buried or otherwise, is their moisture-holding capacity (Barr, 1930). Large (log-sized) residues act as perched water tables that may eventually dry out, but at much slower rates than the associated soil or small (litter and branch) residues. Such residues provide, in many cases, well-defined ecological niches in or on which fungi survive and function in an environment otherwise unfavorable to them (Zak 1969).

Decaying residues strongly influence nutrient accumulation through fungal activity and nutrient release (Stark 1973). Stark (1972) has presented data suggesting that fungal hyphae act as "nutrient sinks" by incorporating and binding (concentrating?) essential nutrients into their structures. The fungal soma is eventually decomposed, resulting in slow nutrient release. That fungi are accumulators of substrate nutrients has also been pointed out by Harley (1971).

The Fungi Associated With Residue Decay

Many species of decay fungi have been collected and studied by mycologists and pathologists. These fungi have been detailed as parts of checklists in monographs, or noted as occurring in restrictive ecological niches (Richards 1970). For the most part they have not been related as particular species, or even as broad taxonomic groups, to ecological functions (Hering 1972). The fungi responsible for decomposition are in

themselves complex in genetical, physiological, and ecological makeup. They constitute a group of organisms that are both adaptable and unstable. Their survival, growth, and reproduction may frequently be limited by their ecological requirements. Only recently have investigators attempted to establish more precisely the roles of decay fungi in the forest environment (Aho 1974; Shea 1960). It is not enough to know the fungi present; knowing why they are or are not present under particular forest environments, manmade or otherwise, is equally important.

Conclusions

Processes involved in decomposition are essential aspects of carbon, nitrogen, and mineral cycling, all of which are intimately related. However, present knowledge is fragmentary, particularly when ecologically interrelated processes concerned with residue decay are examined. Tentative conclusions are that continuous cropping and intensive utilization decrease site productivity (Pierovich and Smith 1973; White 1974). In ecologically sensitive areas, residues, as substrates for specific fungi, may have to be managed as intensively as the trees themselves if productivity is to be maintained.

Research Needs

The following questions remain to be answered. How much hetero- and autotrophic plant biomass is a particular site producing? How much does the N economy of a forested site depend on residue decay and associated micro-organisms? In terms of site maintenance, do more desirable or less desirable populations and species of fungi occur? How does one manage or select for fungal populations and species most beneficial for site maintenance? These complex, interrelated questions reflect the kinds of research that must be done.

Literature Cited

- Adams, S. N., and I. S. Cornforth.
1973. Some short-term effects of lime and fertilizers on a Sitka spruce plantation. II. Laboratory studies on litter decomposition and nitrogen mineralization. *Forestry* 46:39-47.
- Agrawal, S. S.
1971. The cellulolytic capacity of some forest litter fungi. *Phyton* 28:169-175.
- Aho, P. E.
1974. Decay of forest residues. *In: Environmental effects of forest residues management in the Pacific Northwest--a state-of-knowledge compendium*, p. 91-913. USDA For. Serv. Gen. Tech. Rep. PNW-24, Pac. Northwest For. and Range Exp. Stn. Portland, Oreg.
- Allison, F. E.
1961. Comparative rates of decomposition in soil of wood and bark particles of several softwood species. *Proc. Soil Sci. Soc. Am.* 25:193-196.
- Allison, F. E., and R. M. Murphy.
1963. Comparative rates of decomposition of wood and bark particles of several species of pines. *Proc. Soil Sci. Soc. Am.* 27:309-312.
- Barr, P. M.
1930. The effect of soil moisture on the establishment of spruce regeneration in British Columbia. *Yale Univ. Sch. For. Bull.* 26, 45 p.
- Bollen, W. B., and K. C. Lu.
1969. Douglas-fir bark tannin decomposition in two forest soils. USDA For. Serv. Res. Pap. PNW-85, 12 p. Pac. Northwest For. and Range Exp. Stn., Portland, Oreg.
- Childs, T. W.
1939. Decay of slash on clear-cut areas in the Douglas-fir region. *J. For.* 37:955-959.
- Cornaby, B. W., and J. B. Waide.
1973. Nitrogen fixation in decaying chestnut logs. *Plant and Soil* 39:445-448.

- Cowling, E. B., and W. Merrill.
1966. Nitrogen in wood and its role in wood deterioration. *Can. J. Bot.* 44:1539-1544.
- Daubenmire, R., and D. C. Prusso.
1963. Studies of the decomposition rates of tree litter. *Proc. Soil Sci. Soc. Am.* 27:589-592.
- Davis, R. I.
1971. Relation of polyphenols to decomposition of organic matter and to pedogenetic processes. *Soil Sci.* III:80-85.
- Day, R. J.
1963. Spruce seedling mortality caused by microclimate in the Rocky Mountains. *Can. Dep. For. Publ.* 1003, 35 p.
- Day, R. J., and P. J. B. Duffy.
1963. Regeneration after logging in the Crowsnest Forest. *Can. Dep. For. Publ.* 1007, 31 p.
- Dimbleby, G. W.
1953. Natural regeneration of pine and birch on the heather moors of northeast Yorkshire. *Forestry* 26:41-52.
- Foulger, A. N., and J. Harris.
1972. Wood, bark, and needle residue volumes in a west Wyoming lodgepole pine stand. U.S. Dep. Agric. For. Prod. Lab., Madison, Wisc.
- Gardner, R. B., and D. W. Hann.
1972. Utilization of lodgepole pine logging residues in Wyoming increases fiber yield. USDA For. Serv. Res. Note INT-160, 6 p. Intermt. For. and Range Exp. Stn., Ogden, Utah.
- Gill, L. S., and S. R. Andrews.
1956. Decay of ponderosa pine slash in the southwest. USDA For. Serv., Intermt. For. and Range Exp. Stn. Note 19, 2 p. Ogden, Utah.
- Harley, J. L.
1971. Fungi in ecosystems. *J. Ecol.* 59:653-668.
- Hayes, A. J.
1965a. Studies on the decomposition of coniferous leaf litter. I. Physical and chemical changes. *J. Soil Sci.* 16:121-140.
- Hayes, A. J.
1965b. Studies on the decomposition of coniferous leaf litter. II. Changes in external features and succession of microfungi. *J. Soil Sci.* 16:242-257.
- Hering, T. F.
1972. Fungal associations in broad-leaved woodlands in northwest England. *Mycopath. Mycol. Appl.* 48:15-21.
- Hubert, E. E.
1920. The disposal of infected slash on timber-sale areas in the northwest. *J. For.* 18:34-56.
- Kimney, J. W.
1955. Rate of deterioration of fire-killed timber. U.S. Dep. Agric. Circ. 962:1-22.
- Kimney, J. W., and R. L. Furniss.
1943. Deterioration of fire-killed Douglas-fir. U.S. Dep. Agric. Tech. Bull. 851, 61 p. Washington, D. C.
- Kowal, N. E.
1969. Effects of leaching on pine litter decomposition rate. *Ecology* 50:739-740.
- Loman, A. A.
1962. The influence of temperature on the location and development of decay fungi in lodgepole pine logging slash. *Can. J. Bot.* 40:1545-1559.
- Loman, A. A.
1965. The lethal effects of periodic high temperatures on certain lodgepole pine slash decaying basidiomycetes. *Can. J. Bot.* 43:334-338.
- Long, W. H.
1917. Investigations of the rotting slash in Arkansas. U.S. Dep. Agric. Tech. Bull. 496, 15 p. Washington, D.C.
- McFee, W. W., and E. L. Stone.
1966. The persistence of decaying wood in humus layers of northern forests. *Proc. Soil Sci. Soc. Am.* 30:513-516.

- Olson, J. S.
1963. Energy storage and the balance of producers and decomposers in ecological systems. *Ecology* 44:321-322.
- Pierovich, J. M., and R. C. Smith.
1973. Choosing forest residues management alternatives. USDA For. Serv. Gen. Tech. Rep. PNW-7, 11 p. Pac. Northwest For. and Range Exp. Stn., Portland, Oreg.
- Richards, M. J.
1970. Studies on *Russula emetica* and other agarics in a Scots pine plantation. *Trans. Brit. Mycol. Soc.* 55:217-229.
- Roff, J. W., and H. W. Eades.
1959. Deterioration of logging residue on the British Columbia coast (western hemlock, amabilis fir, and Sitka spruce). Can. Dep. North. Affairs Nat. Resour., For. Br., Forest Prod. Lab., FPL Note 11, 38 p.
- Satchell, J. E.
1971. Feasibility study of an energy budget for Methop Wood. In: Productivity of forest ecosystems. P. Duvigneaud, ed. UNESCO.
- Seidler, R. J., P. E. Aho, P. N. Rahu, and H. J. Evans.
1972. Nitrogen fixation by bacterial isolates from decay in living white fir trees (*Abies concolor* (Gord. & Glend.) Lindl.). *J. Gen. Microbiol.* 73:413-416.
- Shea, K. R.
1960. Fungus succession and significance of environment in the deterioration of logs. Weyerhaeuser Co. For. Res. Note 30, 7 p.
- Spaulding, R.
1929a. The decay of hardwood slash in northern New England. *J. For.* 27:241-245.
- Spaulding, R.
1929b. Decay of slash of northern white pine in southern New England. U.S. Dep. Agric. Tech. Bull. 132, 20 p. Washington, D.C.
- Spaulding, R., and J. R. Hansbrough.
1944a. Decay of logging slash in the northeast. U.S. Dep. Agric. Tech. Bull. 876, 22 p. Washington, D.C.
- Spaulding, R., and J. R. Hansbrough.
1944b. Decay in balsam fir in New England and New York. U.S. Dep. Agric. Tech. Bull. 872, 30 p. Washington, D.C.
- Stark, N.
1972. Nutrient cycling pathways and litter fungi. *Bioscience* 22:355-360.
- Stark, N.
1973. Nutrient cycling in a Jeffrey pine ecosystem. *Mont. For. Conserv. Exp. Stn.*, 389 p.
- Toole, E. R.
1965. Deterioration of hardwood logging slash in the south. U.S. Dep. Agric. Tech. Bull. 1328, 27 p. Washington, D.C.
- Wagener, W. W., and H. R. Offord.
1972. Logging slash: its breakdown and decay at two forests in northern California. USDA For. Serv. Res. Pap. PSW-83, 11 p. Pac. Southwest For. and Range Exp. Stn., Berkeley, Calif.
- Waksman, S. A., and F. E. Tenney.
1928. Composition of natural organic materials and their decomposition in the soil: III. The influence of nature of plant upon the rapidity of its decomposition. *Soil Sci.* 25:155-171.
- White, E. H.
1974. Whole tree harvesting depletes soil nutrients. *Can. J. For. Res.* 4:530-535.
- Witkamp, M.
1966. Decomposition of leaf litter in relation to environment, microflora, and microbial respiration. *Ecology* 47:194-201.
- Zak, B.
1969. Characterization and classification of mycorrhizae of Douglas-fir.
I. *Pseudotsuga menziesii* + *Poria terrestris* (Blue- and orange-staining strains). *Can. J. Bot.* 47:1833-1840.

Mycorrhiza Formation

Within the zone influenced by plant roots exists a wide variety of functional associations between roots and certain micro-organisms (Lewis 1973). Perhaps the most specialized of these are the mutualistic (symbiotic) associations, termed mycorrhizae, that occur between the roots of most higher plants and certain fungi. Most participating fungi and their hosts have evolved a strong interdependence for survival in natural ecosystems (Harley 1971, 1969). In mycorrhizal associations, each partner benefits from the other (Trappe and Fogel 1974). This is illustrated by the complete failure of afforestation from seed or seedling in areas where soils lack the appropriate mycorrhizal-forming fungi (Mikola 1973; Vozzo and Hacskaylo 1971; Trappe and Strand 1969) and by the difficulty in culturing the fungi in the absence of the host root (Palmer 1971; Gerdemann 1968). Many fungi form mycorrhizae on one, or only a few species or types, of host plant (Gerdemann and Trappe 1974; Chilvers 1973), so changes in vegetation can result in direct alterations in populations of mycorrhizal fungi. Thus, site treatments that affect populations of mycorrhizal fungi, either directly or through competition, or the ability of these fungi to form the mutualistic association, could create highly significant impacts on growth or regeneration of the succeeding stand.

Mycorrhizal Anatomy and Development

Four major types of mycorrhizae are recognized on the basis of internal and external anatomy. The orchidaceous and ericaceous mycorrhizae are a diverse group of fungi with septate hyphae, normally found on members of the Ericaceae and Orchidaceae. These are characterized by intracellular penetration that ultimately digests the host cells. The vesicular-arbuscular mycorrhizal fungi have nonseptate hyphae and usually occur on members of the Cupressaceae, Taxodiaceae, Accraceae, some species of the Ericaceae, most herbaceous species, and all woody plants not ectomycorrhizal. These fungi occur on more plant species than any other type. They penetrate the root but form spores external to the root and cause little, if any, change in morphology. The ectomycorrhizal fungi are found on members of the Pinaceae, Fagaceae, Betulaceae, Tiliaceae, and several other minor plant families. The ectomycorrhizae are characterized by a highly specialized morphology and are required for the survival of the Pinaceae and several other woody plant families in temperate ecosystems (Trappe and Fogel, in press; Meyer 1973). The fungi involved are generally higher basidiomycetes or ascomycetes that form a characteristic mantle of fungal tissue completely enclosing the host rootlet. Penetration by the fungus is largely limited to the intercellular regions and only rarely occurs within the cell. Intercellular ramification by the fungi, with the absence of cellular digestion, results in the formation of a netlike structure, termed the "Hartig net," wherein fungal tissues completely surround the cortical cells. Invasion does not proceed beyond the endodermis (Harley 1969). In some instances, intermediary types (ectendomycorrhizae) are formed and are characteristic of certain species (Zak 1971). The following discussion will emphasize the ecologically obligatory associations between members of the Pinaceae and the ectomycorrhizal fungi because of the direct relationship with regeneration of the important western timber-producing species.

Normally, a young conifer seedling is infected during the first growing season (Robinson 1967). The fungus spreads as a web of mycelium (fungal strands) over the young roots until the entire surface of the root, including the apex, is covered. Ultimately, a typical thick mantle of fungal tissue is formed. Penetration into the root generally coincides with but can precede the maturation of the mantle. As root systems enlarge, each new crop of roots becomes infected. Infected young rootlets, devoid of root hairs, emerge from the lateral root completely ensheathed by the fungus and are gradually transformed into a characteristic mycorrhizal structure. Young lateral roots become transformed into an easily recognizable series of short, often much branched series of clublike root tips. Branching patterns, colors, and other characteristics are often associated with particular host-fungus combinations (Zak 1971; Wilcox 1968).

Mycorrhizal Physiology

Mycorrhizae are substantially longer lived than nonmycorrhizal roots (Harley 1969; Orlov 1968). In addition, the fungal hyphae function as extensions of the root system, absorbing and translocating soil nutrients and water to the host (Bowen 1973; Harley 1969). They may also act, in concert with other fungi, as nutrient sinks for conservation of nutrients on the site (Stark 1972; Harley 1971).

The fungal symbiont is not generally capable of utilizing complex carbohydrates as an energy source and is, therefore, largely dependent on the host for a supply of simple sugars (Hacskaylo 1973; Harley 1969). During times of extreme drought, the surface soil layers which normally contain the mycorrhizal fungi are most affected and the host may supply both water and nutrients from deep soil horizons (in addition to the energy source) and enable a mycorrhizal partner to survive.

Mycorrhizal Function

Ultimately, mycorrhizal hyphae and structures derived from them can fuse, forming large networks of interconnected fungal bodies, permitting increased absorption and translocation of nutrients between hosts sharing a common fungal network (Furman and Trappe 1971; Reid and Woods 1969). Among trees direct grafting of roots also occurs (Borman 1966; McMinn 1963). Thus the forest soil consists of an interconnected series of pipelines that acquire and share required materials through a highly sophisticated and delicate balance of structures derived from both higher plants and their fungal symbionts. Photosynthate (sugars) and mineral nutrients can be transferred between plants through the various components of this system (Reid and Woods 1969; Borman 1966; Woods and Brock 1964). Of particular significance are the possible increases in uptake and transport of ammonium nitrogen (Melvin and Nilsson 1952), synthesis of amino acids in the mycorrhizal structures (Krupa and others 1973), and increased absorption of phosphate (Bielecki 1973; Bowen 1973).

The advantages of an underground pipeline, particularly to plants growing in a harsh and infertile forest soil environment, are readily apparent. Mineral nutrients, water, and even photosynthate may be supplied to new seedlings or to individual trees occupying extremely harsh microsites. An early acquisition of the benefits provided by this soil pipeline is particularly critical to seedling survival. In the absence of mycorrhizae, seedling root penetration below the summer drought zone and root surface area are not adequate to provide sufficient mineral nutrients during the first several seasons in even the most moderate forest soil conditions. Thus, some of the most successful plants that occupy rigorous nondesert sites, such as timberline or coal spoil banks, are ectomycorrhizal (Schramm 1966). Fungi adapted to particular environments appear to have evolved concomitantly with the ability of certain plants to survive in extreme environments (Marx and Bryan 1971; Moser 1958). Many species of mycorrhizal fungi associate with only a single genus or even subgenus of host, others are apparently nonspecific (Chilvers 1973; Smith 1971; Trappe 1962, 1971).

The large assemblage of mycorrhizal fungi encompasses a wide spectrum of physiological and ecological capabilities. Potential functional differences between species are expressed in habitat preferences and successional changes in fungi with the age of host and season (Anderson 1966; Mikola 1965; Dominik 1961, 1958). Fungal species have demonstrated differences in resistance to temperature or moisture stress (Mexal and Reid 1973; Hacskaylo and others 1965; Moser 1958), and nitrogen utilization (Bowen 1973; Lundeberg 1970). Differential growth responses of vascular plants to different mycorrhizal fungi have frequently been observed (Bowen 1973; Mikola 1973; Laiho 1970). Mycorrhizae can in some instances be pivotal factors controlling plant succession (Robinson 1972; Handley 1963). Nitrogen-fixing organisms may be stimulated by mycorrhizae (Rambelli 1973; Silvester and Bennett 1973).

Mycorrhizal seedlings resist drought better than nonmycorrhizal seedlings (Bowen 1973; Shemakhanova 1962). In one case a severed spruce shoot survived for 8 months as a result of an intact connection between a mycorrhizal root and the rhizomorph of a mycorrhizal fungus emanating from the soil on which it lay (Simonsberger and Koberg 1967). Seedling losses related to desiccation are particularly severe in clearcuts where soil and plant surface temperatures can kill tissues (Day 1963). Limited water supplies make seedlings even more susceptible to heat injury, and resultant losses impose long delays in restocking cut units (Day 1963; Day and Duffy 1963). Early formation of mycorrhizal structures may be particularly significant in reducing heat mortality by increasing the seedlings' access to soil moistures.

In summary, contact with specific mycorrhizal networks and soil conditions appropriate for mycorrhizal establishment are essential to the survival and growth of conifer regeneration (Zerling 1960).

Distribution of Mycorrhizal Fungi

Little is known about the distribution and persistence of ectomycorrhizal fungi apart from their hosts. As a rule, mycorrhizal fungi do not produce fruiting bodies or sporulate in the absence of live host roots (Romell 1938). Survival in the form of saprophytic hyphae in the soil is probably limited (Harley 1969; Gerdemann 1968). Hyphal aggregations termed rhizomorphs may persist for some time due to their tough outer layers and ability to transport nutrients, but they are probably limited to within a few feet of active host roots. Mycorrhizal short roots may survive a short while after tree harvest due to the tough outer mantle and possible storage of food materials. However, evidence to support any of the latter contentions is not as yet available.

At present, it is generally thought that mycorrhizal fungi do not survive for extended periods in the absence of host roots (Hacsckaylo 1973), and that they reinvade through airborne spores (Lamb and Richards 1974) only after the appearance of suitable hosts on the site. Thus, clearcutting may drastically reduce the populations of mycorrhizal fungi in direct proportion to the removal of the hosts, particularly conifers. Little or nothing definitive is known concerning spore dispersal patterns and their germination requirements, or their effectiveness in reestablishing mycorrhizal fungi other than they have been observed to act in some instances as effective inoculum (Theodorou and Bowen 1973).

Potential Impacts of Residues Management on the Mycorrhizal Association

In addition to the requirement for a suitable host and fungus, the environment in which the two meet imposes a strong influence on their ability to form a successful mycorrhizal association (Björkman 1970). Thus, the soil factors affected by clearcutting and burning cause site changes that could alter mycorrhizal symbiosis.

Temperature directly affects root colonization by mycorrhizal fungi (Bowen and Theodorou 1973; Theodorou and Bowen 1971) and their growth in vitro (Harley 1969; Hacsckaylo and others 1965). The related factor of soil moisture can also limit growth of mycorrhizal fungi (Bowen and Theodorou 1973), and in some instances low soil moisture may be responsible for the replacement of some mycorrhizal fungi by others (Worley and Hacsckaylo 1959). Similarly, soil aeration as related to soil water content has been reported to affect mycorrhiza formation (Mikola 1973; Mikola and Laiho 1962; Heikurainen 1955). Soil acidity appears particularly critical in successfully controlling species of mycorrhizal fungi on the site and in the ability of the fungi to form the mycorrhizae (Bowen and Theodorou 1973; Theodorou and Bowen 1969; Richards 1961). The complex series of physical, chemical, and biotic changes wrought by forest burning result in temporary reductions in mycorrhizal roots on conifer regeneration (Wright 1971; Mikola and others 1964; Wright and Tarrant 1958; Tarrant 1956).

Other more subtle effects of management on the quality of forest soils may control the ability of mycorrhizal fungi and their hosts to form the mycorrhizal association. Availability of nutrients, organic matter, and an energy supply in the form of simple sugars are critical to mycorrhizal fungi. In general, mycorrhiza formation is enhanced when there is a mild deficiency of mineral nutrients (Hesterberg and Jurgensen 1972). Hatch (1937) reported a deficiency of nitrogen, phosphorus, potassium, or calcium stimulated mycorrhizal development. Björkman (1942) found the amount of soil nitrogen and phosphorus to be decisive factors in the formation of the association. He also found that the addition of ash to certain soils increases the numbers of mycorrhizae (Björkman 1941).

Though plants with mycorrhizae can be cultivated in soils with a low organic content (Björkman 1956, 1954), high levels of organic matter are reported to have favorable effects on mycorrhizal development (Rubtov 1964; Rayner 1936, 1938). As a single amendment, organic matter can promote formation of mycorrhizae in deficient soils (Mikola 1973). Forest residue levels would greatly affect the subsequent organic matter content of the soil. Similarly, the presence of decaying roots appears to promote mycorrhiza formation (McMinn 1963).

One of the most notable physiologic characteristics of most mycorrhizal fungi is their requirement for simple sugars as energy sources. Such substances are generally thought to be supplied through plant root exudation (Hacskeylo 1973). Thus, factors that influence sugar levels in the host plant and its transport to and liberation from roots, such as sunlight and mineral nutrition, may affect mycorrhizal development (Björkman 1970).

Stand composition, at the time of harvesting, may condition the soil either favorably or unfavorably for the succeeding crop through the influence of roots and their exudates. Rhizosphere microflora that compete for simple sugars exuded from roots may directly affect mycorrhizal fungi (Harley 1969); antagonistic rhizosphere fungi may have suppressive effects (Levisohn 1957); root pathogens may influence development of mycorrhizae or vice versa (Marx 1973); and certain micro-organisms common in the vicinity of roots may be synergistic to the formation of mycorrhizal structures (Voznyakovskaya and Ryzhkova 1955). Higher plants or lichens may release soil chemicals that trigger allelopathic responses among mycorrhizal fungi (Handley 1963; Wilde 1954; Brown and Mikola 1974). Early succession of shrub species, which are typically vesicular-arbuscular mycorrhizal, may affect the establishment of ectomycorrhizal fungi and therefore their hosts, such as pines (Trappe, personal communication).

Conclusions

Management of temperate forests for optimal tree growth and to favor selected species will also require the management of the fungal symbionts on which these trees depend. Present and contemplated forest residue practices will directly influence the symbiotic mycoflora. Examination of the net effects of these influences will provide valuable information regarding biological impacts of management and may provide direct inputs into management tactics designed to achieve optimal growth of predetermined species.

Research Needs

Before it is possible to assess the environmental impacts of treatments on various sites in forested ecosystems, the following questions that relate mycorrhizal development to intensive utilization and prescribed burning, or to both, must be answered. Does extensive removal or burning of host trees or organic material reduce or change populations of mycorrhizal fungi at specific sites? If so, how quickly and by what means do these populations reconstitute themselves? If effects are significant, do they constitute a hazard to, or delay, the establishment and growth of the succeeding stand?

Literature Cited

- Anderson, J.
1966. Indagini sulla micorrizia in alcune specie di eucalitto nell'Italia centrale. Publ. Cent. Agric. For. (Roma) 8:259-274.
- Bielecki, R. L.
1973. Phosphate pools, phosphate transport, and phosphate availability. Annu. Rev. Plant Physiol. 24:225-252.
- Björkman, E.
1941. The development and incidence of mycorrhiza among forest trees on ash-fertilized and unfertilized sectors of drained marshes. Medd. Stat. Skogsforsanst. 32:255-296.
- Björkman, E.
1942. Über die Bedingungen der Mykorrhizabildung bei Kiefer und Fichte. Symb. Bot. Upsal. VI(2):1-196.
- Björkman, E.
1954. Betzdelsen av godsling i skogstradsplantaskolar för plantornas första utveckling i skogsmarken. Norrlands Skogsvårdsf. Tidskr. 543.
- Björkman, E.
1956. Über die Natur der Mykorrhizabildung unter besonderer Berücksichtigung der Waldbäume und die Anwendung in der forstlichen Praxis. Forstwiss. Zentralbl. 75:265-286.
- Björkman, E.
1970. Forest tree mycorrhiza--the conditions for its formation and the significance for tree growth and afforestation. Plant and Soil 32:589-610.
- Bormann, F. H.
1966. The structure, function, and ecological significance of root grafts in *Pinus strobus* L. Ecol. Monogr. 36:1-26.
- Bowen, G. D.
1973. Mineral nutrition of ectomycorrhizae. In: Ectomycorrhizae--their ecology and physiology, p. 151-206. G. C. Marks and T. T. Kozlowski, eds. Academic Press, New York.
- Bowen, G. D., and C. Theodorou.
1973. Growth of ectomycorrhizal fungi around seeds and roots. In: Ectomycorrhizae--their ecology and physiology, p. 107-150. G. C. Marks and T. T. Kozlowski, eds. Academic Press, New York.
- Brown, R. T., and P. Mikola.
1974. The influence of fruticose soil lichens upon the mycorrhizae and seedling growth of forest trees. Acta For. Fenn. 141:1-22.
- Chilvers, G. A.
1973. Host range of some eucalypt mycorrhizal fungi. Aust. J. Bot. 21:103-111.
- Day, R. J.
1963. Spruce seedling mortality caused by microclimate in the Rocky Mountains. Can. Dep. For. Publ. 1003, 35 p.
- Day, R. J., and P. J. B. Duffy.
1963. Regeneration after logging in the Crowsnest Forest. Can. Dep. For. Publ. 1007, 31 p.
- Dominik, T.
1958. Studium nad mikotrofizmem rodzaju *Populus*. Inst. Badaw. Lesn. Pr. 181:117-172.
- Dominik, T.
1961. Studies on mycorrhizae. U.S. Dep. Comm. Transl. TT 65-50333 (1966), from Folia For. Polon. A 5:3-160.
- Furman, T. E., and J. M. Trappe.
1971. Phylogeny and ecology of mycotrophic achlorophyllous angiosperms. Quart. Rev. Biol. 46:219-225.
- Gerdemann, J. W.
1968. Vesicular-arbuscular mycorrhiza and plant growth. Annu. Rev. Phytopath. 6: 397-418.

- Gerdemann, J. W., and J. M. Trappe.
1974. The endogonaceae in the Pacific Northwest. Mycol. Mem. 5:1-75.
- Hacsckaylo, E.
1973. Dependence of mycorrhizal fungi on hosts. Bull. Torrey Bot. Club 100:217-223.
- Hacsckaylo, E., J. G. Palmer, and J. A. Vozzo.
1965. Effect of temperature on growth and respiration of ectotrophic mycorrhizal fungi. Mycologia 57:748.
- Handley, W. R. C.
1963. Mycorrhizal association and *Calluna* heathland afforestation. For. Comm. Bull. 36:1-70.
- Harley, J. L.
1969. The biology of mycorrhiza. Leonard Hill, London. 334 p.
- Harley, J. L.
1971. Fungi in ecosystems. J. Appl. Ecol. 8:627-642.
- Hatch, A. B.
1937. The physical basis of mycotrophy in *Pinus*. Black Rock For. Bull. 6, 168 p.
- Heikurainen, I.
1955. Der wurzelaufbau der kiefernbestände auf reisermoorboden und seine beeinflussung durch die entwässerung. Acta For. Fenn. 65. No. 3.
- Hesterberg, G. A., and M. F. Jurgensen.
1972. The relation of forest fertilization to disease incidence. For. Chron. 48:92-96.
- Krupa, S., A. Fontana, and M. Palenzona.
1973. Studies on nitrogen metabolism in ectomycorrhizae. I. Status of free and bound amino acids in mycorrhizal and nonmycorrhizal root systems of *Pinus nigra* and *Corylus avellera*. Physiol. Plant. 28:1-6.
- Laiho, O.
1970. *Paxillus involutus* as a mycorrhizal symbiont of forest trees. Acta For. Fenn. 106:1-72.
- Lamb, R. J., and B. N. Richards.
1974. Survival potential of sexual and asexual spores of ectomycorrhizal fungi. Trans. Brit. Mycol. Soc. 63:181-191.
- Levisohn, I.
1957. Antagonistic effects of *Alternaria tenuis* on certain root-fungi of forest trees. Nature 179:1143-1144.
- Lewis, D. H.
1973. Concepts in fungi nutrition and the origin of biotrophy. Biol. Rev. 48:261-278.
- Lundeberg, G.
1970. Utilization of various nitrogen sources, in particular bound soil nitrogen, by mycorrhizal fungi. Stud. For. Suec. Skogshögsk. 79:1-95.
- Marx, D. H.
1973. Mycorrhizae and feeder root diseases. In: Ectomycorrhizae--their ecology and physiology, p. 351-382. G. C. Marks and T. T. Kozlowski, eds. Academic Press, New York.
- Marx, D. H., and W. C. Bryan.
1971. Influence of ectomycorrhizae on survival and growth of aseptic seedlings of loblolly pine at high temperatures. For. Sci. 17:37-41.
- McMinn, R. G.
1963. Characteristics of Douglas-fir root systems. Can. J. Bot. 41:105-122.
- Melvin, E., and H. Nilsson.
1952. Transfer of labelled nitrogen from an ammonium source to pine seedlings through the mycelium of *Voletus variegatus* Fr. Svensk Bot. Tidskr. 46:281-285.
- Meyer, F. H.
1973. Mycorrhizae in native and man-made forests. In: Ectomycorrhizae--their ecology and physiology, p. 79-106. G. C. Marks, and T. T. Kozlowski (eds.) Academic Press, New York.

- Mexal, J., and C. P. P. Reid.
1973. The growth of selected mycorrhizal fungi in response to induced water stress. *Can. J. Bot.* 51:1579-1588.
- Mikola, P.
1965. Studies on the ectendotrophic mycorrhizal of pine. *Acta For. Fenn.* 79:1-56.
- Mikola, P.
1973. Mycorrhizal symbiosis in forestry practice. *In: Ectomycorrhizae--their ecology and physiology*, p. 388-412. G. C. Marks, and T. T. Kozlowski (eds.) Academic Press, New York.
- Mikola, P., J. Erickainen, and K. Kuvaja.
1964. The effect of slash burning on the commencement of mycorrhizal association. *Acta For. Fenn.* 77:1-11.
- Mikola, P., and O. Laiho.
1962. Mycorrhizal relations in the raw humus layer of northern spruce forests. *Commun. Inst. For. Fenn.* 55:1-13.
- Moser, M.
1958. Der einfluss tiefer temperturen auf das washstum und die lebenstatigheit hoherer pilze mit spezieller berucksichtigung von mykorrhizapilzen. *Sydowia* 12:386-399.
- Orlov, A. J.
1968. Development and live duration of the pine feeding roots. *In: Methods of productivity studies in root systems and rhizophere organisms*, M. S. Ghilarov and others, eds. Publ. House Nauka, Leningrad.
- Palmer, J. G.
1971. Techniques and procedures for culturing ectomycorrhizal fungi. *In: Mycorrhizae*, p. 145-150. E. Hacskaylo, ed. U.S. Dep. Agric. For. Serv. Misc. Publ. 1189, Washington, D.C.
- Rambelli, A.
1973. The rhizosphere of mycorrhizae. *In: Ectomycorrhizae--their ecology and physiology*, p. 299-350. G. C. Marks and T. T. Kozlowski, eds. Academic Press, New York.
- Rayner, M. C.
1936. The mycorrhizal habit in relation to forestry. II. Organic composts and growth of young trees. *Forestry* 10:1-22.
- Rayner, M. C.
1938. The use of soil or humus inocula in nurseries and plantations. *Emp. For. J.* 17:236-243.
- Reid, C. P. P., and F. W. Woods.
1969. Translocation of C¹⁴ labeled compounds in mycorrhizae and its implications in interplant nutrient cycling. *Ecology* 50:179-187.
- Richards, B. N.
1961. Soil pH and mycorrhiza development in *Pinus*. *Nature* 190:105-106.
- Robinson, R. K.
1967. *Ecology of fungi*. English Univ. Press Ltd., London. 116 p.
- Robinson, R. K.
1972. The production by roots of *Calluna vulgaris* of a factor inhibitory to growth of some mycorrhizal fungi. *J. Ecol.* 60:219-224.
- Romell, L. G.
1938. A trenching experiment in spruce forest and its bearing on problems of mycotrophy. *Svensk Bot. Tidskr.* 32:89-99.
- Rubtov, S.
1964. Humusul di larice-stimulator puternik al cresterii puielor de larice in pepiniere. *Rev. Padurilor* 69:279.
- Schramm, J. R.
1966. *Mycotrophy of Woody Plants*. Akad. Naul. S.S.S.R., Moscow. U.S. Dep. Comm. Transl. TT 66-51073, Washington, D.C.
- Shemakhanova, N. M.
1962. Mycotrophy of woody plants. (Rus.) Iz dated. Akad. Nauk SSSR. Moscow. 375 p.

- Silvester, W. B., and K. J. Bennett.
1973. Acetylene reduction by roots and associated soil of New Zealand conifers. *Soil Biol. Biochem.* 5:171-179.
- Simonsberger, P., and H. Koberg.
1967. Der pilz als lebensrette--mykorrhizapilz *Thelephora terrestris* bewahrt abgeschnittenen fichtensampling vor dem vertrocknen. *Mikrokosmos* 5:147-149.
- Smith, A. H.
1971. Taxonomy of ectomycorrhizal-forming fungi. *In: Mycorrhizae*, p. 1-8. E. Hacsckaylo, ed. U.S. Dep. Agric. For. Serv. Misc. Publ. 1189. Washington, D.C.
- Stark, N.
1972. Nutrient cycling pathways and litter fungi. *Bioscience* 22:355-360.
- Tarrant, R. F.
1956. Effects of slash burning on some soils of the Douglas-fir region. *Proc. Soil Sci. Soc. Am.* 20:408-411.
- Theodorou, C., and G. Bowen.
1969. The influences of pH and nitrate on mycorrhizal associations of *Pinus radiata* D. Don. *Aust. J. Bot.* 17:59-67.
- Theodorou, C., and G. Bowen.
1971. Influence of temperature on the mycorrhizal associations of *Pinus radiata* D. Don. *Aust. J. Bot.* 19:13-20.
- Theodorou, C., and G. D. Bowen.
1973. Inoculation of seeds and soil with basidiospores of mycorrhizal fungi. *Soil Biol. Biochem.* 5:765-771.
- Trappe, J. M.
1962. Fungus associates of ectotrophic mycorrhizae. *Bot. Rev.* 28:538-606.
- Trappe, J. M.
1971. Mycorrhiza-forming ascomycetes. *In: Mycorrhizae*, p. 19-37. E. Hacsckaylo, ed. U.S. Dep. Agric. For. Serv. Misc. Publ. 1189. Washington, D.C.
- Trappe, J. M., and R. D. Fogel.
Ecosystematic functions of mycorrhizae. *In: Belowground ecosystems*. Academic Press, New York. (In press).
- Trappe, J. M., and R. F. Strand.
1969. Mycorrhizal deficiency in a Douglas-fir region nursery. *For. Sci.* 15:381-389.
- Voznyakovskaya, M., and A. S. Ryzhkova.
1955. Microflora accompanying mycorrhizas. *In: Mycotrophy in plants*. A. A. Imshenetskii, ed. Program for Scientific Translations, 1967.
- Vozzo, J. A., and E. Hacsckaylo.
1971. Inoculation of *Pinus caribaea* with ectomycorrhizal fungi in Puerto Rico. *For. Sci.* 17:239-245.
- Wilcox, H. E.
1968. Morphological studies of the roots of red pine, *Pinus resinosa*. II. Fungal colonization of roots and the development of mycorrhizae. *Am. J. Bot.* 55:686-700.
- Wilde, S. A.
1954. Mycorrhizal fungi: their distribution and effect on tree growth. *Soil Sci.* 78:29-31.
- Woods, F. W., and K. Brock.
1964. Interspecific transfer of Ca⁴⁵ and P³² by root systems. *Ecology* 45:886-889.
- Worley, J. F., and E. Hacsckaylo.
1959. The effect of available soil moisture on the mycorrhizal association of Virginia pine. *For. Sci.* 5:267-268.
- Wright, E.
1971. Mycorrhizae on ponderosa pine seedlings. *Oreg. State Univ. Res. Bull.* 13, 36 p.
- Wright, E., and R. F. Tarrant.
1958. Occurrence of mycorrhizae after logging and slash burning in the Douglas-fir type. U.S. Dep. Agric. For. Serv., Pac. Northwest For. and Range Exp. Stn. Pap. 160, 7 p. Portland, Oreg.

Zak, B.

1971. Characterization and identification of Douglas-fir mycorrhizae. *In*: Mycorrhizae, p. 38-53. E. Hacskaylo, ed. U.S. Dep. Agric. For. Serv. Misc. Publ. 1189. Washington, D.C.

Zerling, G. I.

1960. Die mykorrhizabildung bei larche unter der bedingungen des transwolga-tschernosems und ihre stimulierung. *Mikrobiologiya* 29:401.

Soil Nitrogen Fixation and Transformations

Of the many elements essential for plant growth, nitrogen (N) is required in greater amounts than any other mineral nutrient and has been found to be a limiting factor for tree growth in both eastern and western forest soils (Stone 1973; Heilman 1961). The amounts of N present and its subsequent availability in forest soils depend on a variety of chemical, physical, and biological processes.

Nitrogen values vary from less than 0.02 percent in subsoils to greater than 2.5 percent in organic soils. The average N content in the surface layer of most soils ranges from 0.03 to 0.4 percent; the amount decreases with soil depth (Bremner 1967). Spatial variations in N distribution are especially evident in forest soils where considerably greater amounts of N are found in the litter layer than in the mineral soil (Gessel and others 1973). Estimates of N levels present in the litter beneath western stands have ranged from 80 kg/ha for pinon pine-juniper to over 1,300 kg/ha in second-growth Douglas-fir (Zavitkovski and Newton 1967; Youngberg 1966).

Man, by his intervention in the forest ecosystem, can have a significant impact on the N cycle and consequently on site productivity (Wollum and Davey 1975). Nitrogen is unique among the soil nutrients because it is present in the soil almost entirely as organic forms. No inorganic reserve is normally present to alleviate soil N lost to tree removal, to volatilization, or to leaching (Zoetl 1965). In natural ecosystems the atmosphere supplies N to the soil through the fixation of inert N₂ into forms useful to plants. However, these gains in total N can be balanced by losses through biological conversion of nitrate to the gases N₂ or N₂O (denitrification), removal by timber harvesting or burning, and by leaching into the subsoil (Knight 1966; Norris 1962). Each process in the N cycle is related to site productivity and would be strongly subject to change by forest management practices.

Nitrogen Fixation

Considerable work has been done in attempting to evaluate the relationship of N-fixation (dinitrogen fixation) to the overall soil N balance and to increase the extent of fixation in the soil. However, the significance and contribution of N-fixation in many ecosystems have still not been resolved. Generally, small amounts of N are added to the soil by precipitation (Allison 1965) and absorption of NH₃ from the air by soil and plants (Malo and Purvis 1964). It has been advocated that the slow oxidation of soil organic matter coupled with sunlight fixes sizable portions of N (Dhar 1960). However, few if any other investigators support the latter view. Therefore, most of the N added to the soil is considered to have come from biological fixation.

Symbiotic

Probably the best known symbiotic relationship associated with N fixation is the bacterial genus *Rhizobium* and the root nodule it forms on members of the legume family *Leguminosae*. Leguminous plants, such as soybean, pea, and alfalfa, are part of food and forage production and have been found to add up to 200 kg N/ha/yr to the soil

under proper management (Stewart 1966). However, most work has centered on agricultural systems and, with the exception of black locust (Ike and Stone 1958), very little is known regarding the extent and significance of the *Rhizobium*-like legume association in forest ecosystems (Wollum and Davey 1975). Information is needed on the distribution of legumes in forest stands, and should include the widely distributed herbaceous and shrubby species.

Possibly of greater importance than legumes to the forest ecosystem is the occurrence of nonleguminous but nodulated plants. More than 113 species have been reported to form nodules. Included are the common western plants red alder *Alnus rubra* and snowbush *Ceanothus velutinus* (Youngberg and Wollum 1970). The exact nature of the nodule-forming endophyte has not been determined. Various investigators have isolated *Streptomyces* from surface sterilized roots of several nodule-forming genera (e.g., Wollum and others 1966). However, these actinomycetes did not cause nodulation when grown under sterile culture conditions.

Nonleguminous plants have been found to fix appreciable amounts of N. Laboratory studies have reported fixation rates equivalent to 56 kg/N/ha/yr for *Alnus rugosa*, 15 kg/N/ha/yr for *Hippophae rhamnoides*, and 4 kg/N/ha/yr for *Myrica cerifera* (Akkermans 1971; Silver and Mague 1970). Considerably higher values have been reported from field studies on snowbush and red alder (VanCleve and others 1971; Youngberg and Wollum 1970; Newton and others 1968).

Certain lichens are another example of a symbiotic N-fixing relationship; in this case, between blue-green algae and fungi. A number of species have been found to fix N both in the laboratory and in the field (Henriksson and Simu 1971; Fogg and Stewart 1968). The actual contributions of lichens to the soil N supply would depend on weather, soil properties, and extent of lichen cover. A study on various volcanic and arid soils found 2 to 4 times greater amounts of N associated with lichen crusts than with the bare soil surface (Shields 1957). Fixation rates from 10 to 100 kg/N/ha/yr have been attributed to lichens in desert soils of Utah (Rhychert and Skujins 1974). The occurrence and development of lichens on certain forest sites have been investigated (Pike and others 1972), but the significance of these organisms to the forest N balance is unknown.

Nonsymbiotic

In contrast to symbiotic N-fixation, the importance of free-living N-fixing micro-organisms in soil is still uncertain. It is generally conceded that the nonsymbiotic N-fixing microflora contribute only small amounts of N to arable soils (Jensen 1965; Menzell and Norris 1962). However, in noncultivated soils such as grasslands and forests where organic matter is not removed from the site, N gains may be significant (Moore 1966). Studies on soil N accumulation and cycling on forested sites have indicated substantial gains of N. In temperate zones, annual N additions have been reported to range from 4 kg/ha/yr in young stands to between 10 and 25 kg/ha/yr in mature stands (Richards and Voigt 1965), although considerably higher values may be obtained on certain sites (Richards 1964). Tropical rain forests appear to have a much higher fixation rate, likely averaging over 50 kg/ha/yr (Greenland and Kowal 1960). Recent soil studies using direct measurement techniques in the field have indicated far lower fixation rates, averaging in the order of 1 to 10 kg/ha/yr (Hardy and others 1973).

This anomaly between the extent of N gains on forest sites and the measurement of nonsymbiotic N fixation in soil may be in part explained by the enhanced microbial activity in the rhizosphere. N-fixing micro-organisms would be stimulated by the generally low N content of organic materials secreted and sloughed off by plant roots (Starkey 1958). Nitrogen gains occurring in this narrow zone around the root would not normally be measured in studies on soil N-fixation. Recent investigations have shown considerably higher N fixation rates associated with the rhizosphere of conifer roots

than with root-free soil (Richards 1973; Silvester and Bennett 1973). Similar stimulation of N-fixation has been reported in the rhizosphere of various grasses, corn, and rice (Dommergues and others 1973; Yoshida and Ancajas 1973). Some investigators have indicated that N-fixing micro-organisms are favored in the rhizosphere of mycorrhizae, as compared to nonmycorrhizal roots (Rambelli 1973; Silvester and Bennett 1973). However, the reduced rhizosphere fixation rates associated with slash pine mycorrhizae (Richards 1973) show that this aspect of nonsymbiotic N-fixation must be studied further.

Another source of N in forest systems may be the leaf surface of plants or "phyllosphere." Ruinen (1956, 1965) isolated N-fixing organisms from the leaves of numerous plant species and showed that leaf exudates were suitable substrates for their development. Various species of *Azotobacter* have been found in the phyllosphere of over 50 species of trees, crops, ornamentals, and aquatic plants (Iswaran and others 1973). Vlassak and others (1973) have isolated blue-green algae from phyllosphere samples of *Ceratodon purpureus*. The algae showed appreciable N-fixing capabilities. In studies on the tropical grass *Tripsacum laxum*, less than 1 kg/N/ha to 3.5 kg/N/ha have been attributed to phyllosphere fixation (Bessems 1973; Ruinen 1970). In a similar laboratory study, Jones (1970) attempted to determine the extent of N-fixation occurring on the leaves of Douglas-fir where he isolated nitrogen-fixing bacteria. Jones concluded that as much as 65 g/ha/day of N could be fixed in some Douglas-fir stands. Although such N gains under natural conditions would appear unlikely, this source of added N to forest sites could be of importance.

In the past, the ability of micro-organisms to grow on so-called "N-free" media was considered proof of N-fixing capacity. However, growth on these media is not positive proof because small amounts of fixed N are always present, and ammonia can be absorbed from the air. Although the incorporation of ^{15}N is the most definitive method by which N-fixation is established, the acetylene reduction technique is now normally used for field investigations. Many studies have shown that micro-organisms able to fix N also have the ability to reduce acetylene to ethylene (e.g., Hardy and others 1973). Production of ethylene from acetylene is almost completely restricted to N-fixing organisms, and is considered presumptive evidence for the occurrence of N-fixation. Because of its sensitivity, ease in measurement, and economy (Hardy and others 1968), the acetylene reduction technique is preferred over the ^{15}N analysis.

Numerous genera of bacteria and blue-green algae have been found to contain species or strains having an N-fixing ability. Various fungi and yeasts have also been reported to fix N, although more recent evidence indicates that N fixation does not occur in these groups (Postgate 1971). Several of the nonsymbiotic N-fixing micro-organisms, such as *Azotobacter* and the blue-green algae, are normally restricted to nearly neutral or alkaline soils. However, many others, particularly the spore-forming anaerobes, are so widely distributed that a lack of N-fixing microflora would not likely be a factor limiting N-fixation in forest soils (Jurgensen and Davey 1970).

Mineralization

Nearly all of the N in soil is tied up as organic complexes which, with the possible exception of a few amino acids, are not available for plant uptake. The N must first undergo biological transformation by various components of the soil microflora to be eventually released as ammonium, an N form readily used by plants. This release, or "mineralization" of organic N, together with N present in precipitation, fulfill the N requirements of the plant community (Wollum and Davey 1975).

Nitrogen mineralization is generally determined by the factors that influence decomposition of organic matter, such as kind of organic material, soil moisture, nutrient levels, and the soil macro- and microflora (Bartholomew 1965; Witkamp and van der Drift 1961). Species variation has been linked to changes in decomposition rates of forest tree litter (Witkamp 1966). Mineralization rates generally are the

highest at soil moisture levels near field capacity (Stanford and Epstein 1974). Ammonium production decreases at higher moisture tensions but still occurs even when the soils are below the permanent wilting point (Miller and Johnson 1964). A similar reduction in N release is observed in wet and poorly drained soils (Tusneem and Patrick 1971). Soil chemical properties are significant because the application of fertilizer and lime can cause large increases in mineralization rates (Williams 1972; Broadbent 1965).

Nitrification

Nitrification, the conversion of ammonium to nitrate by soil micro-organisms, has recently been receiving considerable attention because of increased awareness of the role of nitrates in stream, lake, and ground water pollution. In contrast to the positively charged ammonium ion, the nitrate anion is not tightly held on soil exchange sites and is readily leached through the soil profile. Differences in the uptake or "preference" of trees for ammonium vs. nitrate have also been found (Krajina and others 1973; van den Driessche 1971), thus making soil nitrification a factor in developing and evaluating forest fertilization programs.

The bulk of nitrate produced in soils is generally assumed to come from the activity of a select group of autotrophic bacteria, particularly *Nitrosomonas* and *Nitrobacter*. These organisms obtain their energy solely from the oxidation of N compounds. The levels of soil organic matter have little or no direct effect on nitrifying bacteria because they use carbon dioxide as a carbon source (Wallace and Nicholas 1969). However, organic matter indirectly affects nitrification by influencing soil moisture levels, soil temperature, and cation exchange capacity. Nitrifying organisms are much more sensitive to variations in the soil environment than micro-organisms active in mineralization. Nitrification is drastically reduced at low soil moisture levels and under acid soil conditions (Siefert 1970; Merrill and Dawson 1967; Reichman and others 1966).

The Relationship of Residues Management to Nitrogen Transformations

The type and levels of wood residue affected by various management practices greatly influence the development of the soil microflora, especially those active in the N-cycle. Increased residue utilization and prescribed burning would reduce the amount of organic material incorporated into the soil. Because many diverse micro-organisms function in the cycling of soil N, such reductions in residue could have many ramifications. In order to fully evaluate the possible significance of residue practices on soil N transformation, all aspects of the N-cycle must be considered.

Nitrogen Fixation

The impact of forest management practices on the incidence and activity of symbiotic N-fixing associations deserves study, particularly the less conspicuous symbiotic plants. Opening of the forest canopy, either through harvesting or fire, and the resultant change in soil chemical and physical properties could favor or restrict the development and efficiency of an N-fixing flora (Loneragan 1972; Nutman 1972). In either case, the potential of such changes should be considered.

Most of the N-fixing micro-organisms, other than the blue-green algae and the anaerobic phototrophic bacteria, require a supply of organic carbon as an energy source. Adequate energy sources would seem particularly important for these organisms because they are inefficient users of carbohydrates (Stewart 1969). The relationship of soil organic matter to N fixation depends on the type of material, its nutrient content, and on the initial fertility of the soil (Rice and others 1967). Thus, the removal of organic matter from the site by logging or residue utilization could affect the

activity of nonsymbiotic N-fixers in soil or in woody residue. This may be accomplished by reducing the organic sources available to these organisms or by changing the physical and chemical environment of the soil (Jurgensen 1973).

The breakdown and decay of woody tissue could also influence the forest ecosystem by directly affecting N-fixation. The N content of wood/unit carbon is lower than most other types of plant tissue. However, in spite of these low levels of N, wood-destroying fungi are able to metabolize the carbon-rich substrate and produce sporocarps and large numbers of spores comparatively rich in N (Merrill and Cowling 1966). One possible explanation for this phenomenon is fungal use of N produced by N-fixing organisms present in the wood. The N-fixing population could use simple sugars produced by the fungal breakdown of wood and in return, supply N to the primary decomposers. The possibility of such a synergistic relationship was strengthened by the recent study of Cornaby and Waide (1973) who showed low but significant amounts of N were being fixed in decaying chestnut logs. Seidler and others (1972) and Aho and others (1974) have found that a sizable fraction of bacteria isolated from decay zones in white fir had an N-fixing capability. Knutson (1973) has observed that bacteria isolated from healthy and water-soaked aspen were able to grow on N-free media.

Reductions in residue levels by fire would have far different consequences on N-transformations than wood removal through logging. As noted earlier, studies conducted in the Southeast over a 20-year period have shown no significant loss of N from the soil due to prescribed burning; in fact, soil N increases of 23 kg/N/ha/yr associated with annual burning on some sites have been reported (Jorgensen and Wells 1971). Other investigations have also reported increases in the soil N content upon burning (e.g., Klemmedson and others 1962). These N gains have been attributed to an increased legume component in the ground vegetation after fire (Stone 1971). Another possibility is the greater activity of nonsymbiotic N-fixers, particularly the autotrophic blue-green algae. The increased light and nutrient levels of the soil surface as a result of burning would favor the development of such organisms (Jurgensen and Davey 1968).

Mineralization

The mineralization of N from soil organic matter can be altered by forest management practices. Harvesting, fire, and site preparation techniques have all been shown to accelerate the release of organic N (DeBell and Ralston 1970; Likens and others 1970; Neal and others 1965). This is due, at least in part, to the resultant changes of microclimate on the soil microflora (Borman and others 1968). The release of nutrients and pH increase after burning or logging may also favor the organisms responsible for N mineralization. Much of the ammonium released may be immobilized in the breakdown of woody materials. Additional N will enter the soil and become available for uptake by trees. However, some may be leached below the root zone or lost through overland flow if the topography is steep (DeByle and Packer 1972).

Nitrification

Effects of forestry practices on soil nitrification rates and the nitrate content of water supplies are now being questioned. Likens and others (1970) showed that clearcutting and herbiciding of northern hardwoods in New Hampshire greatly increased the soil populations of nitrifying bacteria and, consequently, the levels of nitrate in neighboring watersheds. However, the loss of nitrate after clearcutting has been found to be much lower in other parts of the country (Reinhart 1973). These differences seem to be related to soil type, with podzols being especially susceptible to nitrate losses.

Burning of logging residues has resulted in large increases in soil ammonium levels (Christensen 1973; Neal and others 1965), which may increase soil nitrification rates. The rise in soil pH after a fire would also favor the nitrifying bacteria.

Vegetational changes following harvesting or fire may affect the levels of soil nitrate. The nitrate content of soils supporting red alder is considerably greater than soil under western conifers (Trappe 1972). This species difference may be related to the tannin contents of tree bark and its effect on nitrification (Bollen and Lu 1969). Plant species invading a forest site after disturbance have been associated with nitrification rates higher than rates in climax ecosystems (Rice and Pancholy 1972).

Nitrification is an inevitable process occurring in mildly acid to alkaline soils. Although there has been considerable interest in suppressing the nitrifying bacteria by applying chemicals (Parr 1973), these treatments, even if successful, would likely be limited to relatively small areas of particular environmental concern. Increases in nitrification will generally occur after harvesting or site treatment operations, and due to the nature of the nitrate ion, will result in increased N loss from the soil. The effect of N loss on site productivity depends on the amount of N lost, initial soil fertility, and the extent of N gains coming from N-fixation.

Conclusions

Nitrogen is subject to various biological transformations, many of which occur simultaneously in the soil. Any natural or man-induced changes in the physical and chemical properties of a forest site will greatly affect the activity of the responsible soil micro-organisms. It is important to understand the impact forest management techniques and objectives have on these processes. By investigating the N cycle and the organisms active in its functioning, problem areas can be identified and resolved by appropriate management and silvicultural action.

Research Needs

Of particular interest are the sources of N-fixation in forest soils and their contribution to the soil N status. The importance of this information for evaluating the nutrient changes in soil and water systems has been stressed (Reinhart 1973). The effects of harvesting, fire, and residue removal on rates of N-fixation, N-release from soil organic matter, and nitrification need to be known. Also required is the effect of the vegetational changes occurring after site disturbance on N transformations and if increased residue removal will significantly alter the N balance in forest soils, especially on steep terrain. Such information will be required to evaluate the potential long-term impact of intensive forestry operations on site productivity.

Literature Cited

- Aho, P. E., R. J. Seidler, H. J. Evans, and P. N. Raju.
1974. Distribution, enumeration, and identification of nitrogen-fixing bacteria associated with decay in living white fir trees. *Phytopathology* 64:1413-1420.
- Akkermans, A. D. L.
1971. Nitrogen fixation and nodulation of *Alnus* and *Hippophae* under natural conditions. Ph.D. Thesis. University of Leiden, Holland
- Allison, F. E.
1965. Evaluation of incoming and outgoing processes that affect soil nitrogen. *In: Soil nitrogen*, Agron. Monogr. 10, p. 578-606. W. V. Bartholomew and F. E. Clark, eds. Am. Soc. Agron., Madison, Wisc.
- Bartholomew, W. V.
1965. Mineralization and immobilization of nitrogen in the decomposition of plant and animal residues. *In: Soil nitrogen*, Agron. Monogr. 10, p. 285-306. W. V. Bartholomew and P. E. Clark, eds. Am. Soc. Agron., Madison, Wisc.
- Bessems, E. P. M.
1973. Nitrogen fixation in the phyllosphere of Gramineae. *Wageningen Agric. Res. Rep.* 786, 68 p.

- Bollen, W. B., and K. C. Lu.
1969. Douglas-fir bark tannin decomposition in two forest soils. U.S. Dep. Agric. For. Serv., Pac. Northwest For. and Range Exp. Stn. Res. Pap. PNW-85, 12 p.
- Bormann, F. H., G. E. Likens, D. W. Fisher, and R. S. Pierce.
1968. Nutrient loss accelerated by clearcutting of a forest system. *Science* 159:882-884.
- Bremner, J. M.
1967. Nitrogenous compounds. *In: Soil biochemistry*, p. 19-66. A. D. McLaren and G. H. Peterson, eds. Marcel Dekker, New York.
- Broadbent, F. E.
1965. Effect of fertilizer nitrogen on release of soil nitrogen. *Proc. Soil Sci. Soc. Am.* 29:692-696.
- Christensen, N. L.
1973. Fire and the nitrogen cycle in California chaparral. *Science* 181:66-68.
- Cornaby, B. W., and J. B. Waide.
1973. Nitrogen fixation in decaying chestnut logs. *Plant and Soil* 39:445-448.
- DeBell, D. S., and C. W. Ralston.
1970. Release of nitrogen by burning light forest fuels. *Proc. Soil Sci. Soc. Am.* 34:936-938.
- DeByle, N. V., and P. E. Packer.
1972. Plant nutrient and soil losses in overland flow from burned forest clearcuts. *In: Watersheds in transition*, p. 296-307. Sandor C. Csallany, Thad G. McLaughlin, and William D. Striffler, eds. Am. Water Resour. Assoc., Urbana, Ill.
- Dhar, N. R.
1960. Role of organic matter in soil fertility. *Trans. 7th Int. Congr. Soil Sci.* 7(4):314-320.
- Dommergues, Y., J. Balandreau, G. Rinaudo, and P. Weinhard.
1973. Nonsymbiotic nitrogen fixation in the rhizospheres of rice, maize and different tropical grasses. *Soil Biol. Biochem.* 5:83-89.
- Driessche, R. van den.
1971. Response of conifer seedlings to nitrate and ammonium sources of nitrogen. *Plant and Soil* 34:421-439.
- Fogg, G. E., and W. D. P. Stewart.
1968. *In situ* determinations of biological nitrogen fixation in Antarctica. *Bull. Brit. Antarct. Surv.* 15:39-46.
- Gessell, S. P., D. W. Cole, and E. C. Steinbrenner.
1973. Nitrogen balance in forest ecosystems of the Pacific Northwest. *Soil Biol. Biochem.* 5:19-34.
- Greenland, D. J., and J. M. L. Kowal.
1960. Nutrient content of the moist tropical forests of Ghana. *Plant and Soil* 12:154-174.
- Hardy, R. W. F., R. D. Burns, and R. D. Holsten.
1973. Application of the acetylene-ethylene assay for measurement of nitrogen fixation. *Soil Biol. and Biochem.* 5:47-81.
- Hardy, R. W. F., R. D. Holsten, E. K. Jackson, and R. C. Burns.
1968. The acetylene-ethylene assay for N₂ fixation: laboratory and field evaluation. *Plant. Physiol.* 43:1185-1207.
- Heilman, P. S.
1961. Effects of nitrogen fertilization on the growth and nitrogen nutrition of low site Douglas-fir stands. Ph.D. Thesis. Univ. of Washington, Seattle.
- Henriksson, E., and B. Simu.
1971. Nitrogen fixation by lichens. *Oikos* 22:119-121.
- Henzell, E. F., and D. O. Norris.
1962. Processes by which nitrogen is added to the soil/plant system. *In: Bull. Commonw. Bur. Past. Field Crops* 46:1-18.
- Ike, A. F., and E. L. Stone.
1958. Soil nitrogen accumulation under black locust. *Proc. Soil Sci. Soc. Am.* 22:346-349.

- Iswaran, V., A. Scri, and R. Apte.
1973. *Azotobacter chroococcum* in the phyllosphere of water hyacinth (*Eichhornia crossipes* (Mort.) Iolma). *Plant and Soil* 39:461-463.
- Jensen, H. L.
1965. Nonsymbiotic nitrogen fixation. *In: Soil nitrogen*, Agron. Monogr. 10, p. 436-480. W. V. Bartholomew and F. E. Clark, eds. Am. Soc. Agron., Madison, Wisc.
- Jones, K.
1970. Nitrogen fixation in the phyllosphere of the Douglas-fir, *Pseudotsuga douglasii*. *Ann. Bot.* 34:239-244.
- Jorgensen, J. R., and C. G. Wells.
1971. Apparent nitrogen fixation in soil influenced by prescribed burning. *Proc. Soil Sci. Soc. Am.* 35:806-810.
- Jurgensen, M. F.
1973. Relationship between nonsymbiotic nitrogen fixation and soil nutrient status-- a review. *J. Soil Sci.* 24:512-522.
- Jurgensen, M. F., and C. B. Davey.
1968. Nitrogen-fixing blue-green algae in acid forest and nursery soils. *Can. J. Microbiol.* 14:1179-1183.
- Jurgensen, M. F., and C. B. Davey.
1970. Nonsymbiotic nitrogen-fixing micro-organisms in acid soils and the rhizosphere. *Soils Fert.* 33:435-446.
- Karjina, V. J., S. Madoc-Jones, and G. Mellor.
1973. Ammonium and nitrate in the nitrogen economy of some conifers growing in Douglas-fir communities of the Pacific Northwest of America. *Soil Biol. Biochem.* 5:143-147.
- Klemmedson, J. O., A. M. Schultz, H. Jenny, and H. H. Biswell.
1962. Effect of prescribed burning on forest litter and total soil nitrogen. *Proc. Soil Sci. Soc. Am.* 26:200-202.
- Knight, H.
1966. Loss of nitrogen from the forest floor by burning. *For. Chron.* 42:149-152.
- Knutson, D. M.
1973. The bacteria of sapwood, wetwood, and heartwood of trembling aspen. *Can. J. Bot.* 51:498-500.
- Likens, G. E., F. H. Bormann, N. M. Johnson, D. W. Fischer, and R. S. Pierce.
1970. Effects of forest cutting and herbicide treatment on nutrient budgets in the Hubbard Brook watershed ecosystem. *Ecol. Monogr.* 40:23-47.
- Loneragan, J. F.
1972. The soil chemical environment in relation to symbiotic nitrogen fixation. *In: Use of isotopes for study of fertilizer utilization by legume crops.* Int. Atomic Energy Agency Tech. Rep. 149:17-54.
- Malo, B. A., and E. R. Purvis.
1964. Soil absorption of atmospheric ammonia. *Soil Sci.* 97:242-247.
- Merrill, L. G., and J. E. Dawson.
1967. Patterns observed for the oxidation of ammonium to nitrate by soil organisms. *Proc. Soil Sci. Soc. Am.* 31:757-760.
- Merrill, W., and E. B. Cowling.
1966. Role of nitrogen in wood deterioration: amount and distribution of nitrogen in fungi. *Phytopathology* 56:1083-1090.
- Miller, R. D., and D. D. Johnson.
1964. The effect of soil moisture tension on carbon dioxide evolution, nitrification, and nitrogen mineralization. *Proc. Soil Sci. Soc. Am.* 28:644-647.
- Moore, A. W.
1966. Nonsymbiotic nitrogen fixation in soil and soil-plant systems. *Soils Fert.* 29:113-129.
- Neal, J. L., Jr., E. Wright, and W. B. Bollen.
1965. Burning Douglas-fir slash. Physical, chemical, and microbial effects in soil. *Oreg. State Univ. For. Res. Pap.* 1, 32 p.

- Newton, M., B. A. El Hassan, and J. Zavitkovski.
1968. Role of red alder in western Oregon forest succession. *In: Biology of alder*, p. 73-84. J. W. Trappe, J. F. Franklin, R. F. Tarrant, and G. M. Hanson, eds. U.S. Dep. Agric. For. Serv., Pac. Northwest For. and Range Exp. Stn.
- Norris, D. O.
1962. The biology of nitrogen fixation. *Bull. Commonw. Bur. Past. Field Crops* 46:1113-127.
- Nutman, P. S.
1972. The influence of physical environmental factors on the activity of *Rhizobium* in soil and in symbiosis. *In: Use of isotopes for study of fertilizer utilization by legume crops*. Int. Atomic Energy Agency Tech. Rep. 149:55-84.
- Parr, J. F.
1973. Chemical and biochemical considerations for maximizing the efficiency of fertilizer nitrogen. *J. Environ. Qual.* 2:75-84.
- Pike, L. H., D. M. Tracy, M. A. Sherwood, and D. Nielsen.
1972. Estimates of biomass and fixed nitrogen of epiphytes from old-growth Douglas-fir. *In: Proc. Research on coniferous forest ecosystems--a symposium*, p. 177-187. U.S. Dep. Agric. For. Serv., Pac. Northwest For. and Range Exp. Stn., Portland, Oreg.
- Postgate, J. R.
1971. Relevant aspects of the physiological chemistry of nitrogen fixation. *Symp. Soc. Gen. Microbiol.* 21:287-307.
- Rambelli, A.
1973. The rhizosphere of mycorrhizae. *In: Ectomycorrhizae: their ecology and physiology*, p. 299-349. T. T. Kozlowski, ed. Academic Press, N. Y.
- Reichman, G. A., D. L. Grunes, and F. G. Vietx, Jr.
1966. Effect of soil moisture on ammonification and nitrification in two northern plains soils. *Proc. Soil Sci. Soc. Am.* 30:363-366.
- Reinhart, K. G.
1973. Timber-harvest clearcutting and nutrients in the northeastern United States. USDA For. Serv. NE-170, 5 p. Northeast For. Exp. Stn. Upper Darby, Pa.
- Rhychert, R. C., and J. Skujins.
1974. Nitrogen fixation by blue-green algae-lichen crusts in the Great Basin desert. *Proc. Soil Sci. Soc. Am.* 38:768-771.
- Rice, E. L., and S. K. Pancholy.
1972. Inhibition of nitrification by climax ecosystems. *Am. J. Bot.* 59:1033-1040.
- Rice, W. A., E. A. Paul, and L. R. Wetter.
1967. The role of anaerobiosis in asymbiotic nitrogen fixation. *Can. J. Microbiol.* 13:829-836.
- Richards, B. N.
1964. Fixation of atmospheric nitrogen in coniferous forests. *Aust. For.* 28:68-74.
- Richards, B. N.
1973. Nitrogen fixation in the rhizosphere of conifers. *Soil Biol. Biochem.* 5:149-152.
- Richards, B. N., and G. K. Voigt.
1965. Nitrogen accretion in coniferous forest ecosystems. *In: Forest soil relationships in North America*, p. 105-116. C. T. Youngberg, ed. Oreg. State Univ. Press, Corvallis.
- Ruinen, J.
1956. Occurrence of *Beijerinckia* species in the phyllosphere. *Nature* 177:220-221.
- Ruinen, J.
1965. The phyllosphere. III. Nitrogen fixation in the phyllosphere. *Plant and Soil* 22:375-394.
- Ruinen, J.
1970. The phyllosphere. V. The grass sheath, a habitat for nitrogen-fixing microorganisms. *Plant and Soil* 33:661-671.

- Seidler, R. J., P. E. Aho, R. N. Raju, and H. J. Evans.
1972. Nitrogen fixation by bacterial isolates from decay in living white fire trees (*Abies concolor* (Gord. and Glend.) Lindl.). *J. Gen. Microbiol.* 73:413-416.
- Seifert, J.
1970. The influence of moisture on the degree of nitrification in soil. *Acta Univ. Carol.-Biol.* 1969:353-360.
- Shields, L. M.
1957. Algal and lichen floras in relation to nitrogen content of certain volcanic and arid range soils. *Ecology* 38:661-663.
- Silver, W. S., and T. Mague.
1970. Assessment of nitrogen fixation in terrestrial environments in field conditions. *Nature* 227:378-379.
- Silvester, W. B., and K. J. Bennett.
1973. Acetylene reduction by roots and associated soil of New Zealand conifers. *Soil Biol. Biochem.* 5:171-179.
- Stanford, G., and E. Epstein.
1974. Nitrogen mineralization-water relations in soils. *Proc. Soil Sci. Soc. Am.* 38:103-107.
- Starkey, R. L.
1958. Interrelationship between microorganisms and plant roots in the rhizosphere. *Bacteriol. Rev.* 22:152-172.
- Stewart, W. D. P.
1966. Nitrogen fixation in plants. Athlone Press, London, 168 p.
- Stewart, W. D. P.
1969. Biological and ecological aspects of nitrogen fixation by free-living organisms. *Proc. Roy. Soc.* 172B:367-388.
- Stone, E. L.
1971. Effects of prescribed burning on long-term productivity of coastal plain soils. *In: Proc. Prescribed Burning Symp.*, p. 115-127. U.S. Dep. Agric. For. Serv., Southeast For. Exp. Stn.
- Stone, E. L.
1973. Regional objectives in forest fertilization, current and potential. *In: Forest fertilization*, p. 10-18. U.S. Dep. Agric. For. Serv., Northeast. For. Exp. Stn.
- Trappe, J. M.
1972. Regulation of soil organisms by red alder: a potential biological system for control of *Poria weirii*. *In: Managing young forests in the Douglas-fir region*, vol. 3, p. 35-51. A. B. Berg (ed.). *Oreg. State Univ. Press, Corvallis.*
- Tusneem, M. E., and W. H. Patrick, Jr.
1971. Nitrogen transformations in waterlogged soil. *La. State Univ. Agric. Exp. Stn. Bull.* 657, 75 p.
- VanCleve, K., L. A. Viereck, and R. L. Schlentner.
1971. Accumulation of nitrogen in alder (*Alnus*) ecosystems near Fairbanks, Alaska. *Arct. and Alp. Res.* 3:101-114.
- Vlassak, K., E. A. Paul, and R. E. Harris.
1973. Assessment of biological nitrogen fixation in grassland and associated sites. *Plant and Soil* 38:637-649.
- Wallace, W., and D. J. D. Nicholas.
1969. The biochemistry of nitrifying microorganisms. *Biol. Rev.* 44:359-391.
- Williams, B. L.
1972. Nitrogen mineralization and organic matter decomposition in Scots pine humus. *Forestry* 45:177-188.
- Witkamp, M.
1966. Decomposition of leaf litter in relation to environment, microflora, and microbial respiration. *Ecology* 47:194-201.
- Witkamp, M., and J. van der Drift.
1961. Breakdown of forest litter in relation to environmental factors. *Plant and Soil* 15:295-311.

- Wollum, A. G. II, C. T. Youngberg, and C. M. Gilmour.
 1966. Characterization of a *Streptomyces* sp. isolated from root nodules of *Ceanothus velutinus* Dougl. Proc. Soil Sci. Soc. Am. 30:463-467.
- Wollum, A. G. II, and C. B. Davey.
 1975. Nitrogen accumulation, transformation, and transport in forest soils. In: Proc. 4th N. Am. For. Soils Conf., Quebec, 1973.
- Yoshida, T., and R. R. Ancajas.
 1973. The fixation of atmospheric nitrogen in the rice rhizosphere. Soil Biol. Biochem. 5:153-155.
- Youngberg, C. T.
 1966. Forest floors in Douglas-fir forests: 1. Dry weight and chemical properties. Proc. Soil Sci. Soc. Am. 30:406-409.
- Youngberg, C. T., and A. G. Wollum II.
 1970. Non-leguminous symbiotic nitrogen fixation. In: Tree growth and forest soils, p. 383-395. C. T. Youngberg and C. B. Davey, eds. Oreg. State Univ. Press, Corvallis.
- Zavitkovski, J., and M. Newton.
 1967. The role of snowbrush (*Ceanothus velutinus* Dougl.) and red alder (*Alnus rubra* Bong.) in forest regeneration in the Pacific Northwest. Proc. IUFRO Congr., Sec. 21, p. 429-440.
- Zoettl, H.
 1965. Accumulation and transformation of nitrogen in forest soils. Ber. Deutsche Bot. Gesell. 78:167-180.

Pathogen Activity

Forest diseases have been referred to as negative influences in the forest environment (Boyce 1961; Hubert 1931). However, in terms of productivity and stabilization over many generations, many diseases may prove useful to natural forest ecosystems, particularly in north temperate forests where organic matter is generally produced at a higher rate than it can be recycled through the process of decay (Olsen 1963).

Possible Ecological Functions of Pathogens

It is generally thought that overmature forests are more prone to fiber-destroying disease, particularly stem decays, than young vigorous forests (Boyce 1961). As more and more of a site's raw materials become tied up in plant bodies, the plants occupying that site become less thrifty and more prone to insect and disease attack. This condition will eventually lead to an ecosystem whose productivity, in terms of usable fiber production and game habitat, may be extremely low. Other aspects of productivity, for example, watershed protection, may not be greatly impaired. As dead plant bodies (fuel) accumulate, they become subject to fires during dry seasons. Eventually, insect and disease attacks, in coordination with dry seasons and lightning storms, provide conditions in which wildfires are the primary means of rejuvenating the system (Lyons and Pengelly 1970; Komarek 1963). Under natural conditions this process (cycle) is repeated frequently.

Disease "losses," as traditionally viewed by foresters and pathologists, may be natural site characteristics similar to sunlight, moisture, and other factors. In at least one case, a stem decay has been cited as an agent that may help to preserve a forest climax timber type, the California redwood (Stone and others 1972). In this case, stem decay contributes to stem breakage during high winds which in turn prevents uprooting, thus stimulating root sprout regeneration. Excess losses, however, can be interpreted as a biotic indicator that site rejuvenation is required or an inappropriate stand composition must be changed in order to maintain stability.

Introduced pathogens, such as white pine blister rust, are notable exceptions to a system within which endemic diseases may serve a natural function. Imported diseases interrupt natural flow of energy by creating fire-conducive conditions in unnatural circumstances. Harvesting activities, when not conducted within the framework of the natural ecosystem, may also serve to interfere with natural site development to create biotic problems. Management should complement the flow of the ecosystem and could improve the efficiency of natural processes.

Fire as an Evolutionary Factor

By removing resistant hosts from the proximity of heavily infected stands, fire may have changed the genetic evolution of hosts and parasites in fire-dominated forests. The accumulation of resistance, normally associated with delicately balanced host-parasite coevolution, may have been prevented through elimination of the best source of genes to provide resistance. Thus, resistant individuals, due to their close proximity to heavy fuels (dead or dying neighbors), have a high likelihood of destruction by wildfire. Such an explanation has been suggested for the lack of resistance to certain dwarf mistletoes (Roth 1966). Certainly, the relative efficiency of wildfire sanitation has been a major factor in limiting dwarf mistletoes in some situations and dispersing them in others (Alexander and Hawksworth 1975). Other diseases, particularly of the aerial parts of forest trees, have probably been constrained to varying degrees (Chapman 1927), depending on their dispersal capability. As a recycling agent in the forest ecosystem, disease may be so important that internal mechanisms have developed to discourage the incorporation of resistance genes in host populations. This would assure a continuing role for pathogens. The apparent lack of effective resistance to many forest diseases may, therefore, be a direct result of natural wildfire.

As management becomes more intensive and utilization replaces or moderates some of the effects of fire in many aspects of the energy cycling of forests, perhaps the eradicated effect of wildfire on resistant genotypes can be reversed. Considerable benefit may be available through permitting resistance to diseases to be incorporated into the gene pools of forest plants. This could be done through management of fuels by prescribed fire and increased utilization in concert with selection of leave trees, planting stock, or both.

Fire as a Dispersing Agent

Although wildfire is mainly an agent of sanitation, its varying intensities sometimes creates discontinuous effects. Several generations (cycles) of fire may be required to fully cover a forest ecosystem. On a more localized and time-limited basis, particularly in areas with relatively low fire frequency and discontinuous spread, increases in the intensity and losses from diseases can result.

Fire frequency varies with specific conditions and is characteristic of the site (Habeck and Mutch 1973). Presumably, site, species, and fire frequencies have evolved so as to balance the ecosystem at the maximum production level consistent with stability. Although a specific stand may not be optimally productive or stable, the ecosystem is. When fire occurs, it acts as a natural sanitizing and rejuvenating agent (Muller 1929; Weir 1923), which serves to balance energy flow. In the natural state, this system provides a heterogeneous forest of highly mixed ages and species (Habeck and Mutch 1973), a situation that can be considered ideal with respect to minimizing most disease losses. Conversely, fire exclusion over a long period, or devastating fires over large areas, produce a situation analogous to agricultural monoculture: large expanses of frequently overstocked single-age forests with limited numbers of species. This situation is ideal for maximizing spread and intensity of most diseases (Day 1955).

Fire scars represent a major natural infection court for many root and butt rot fungi (Hepting and Shigo 1972; Toole 1959; Nordin 1958; Basham 1957; Toole and Furnival 1957; Burns 1955; Gustafson 1946; Garren 1941; Hepting 1941; Hart 1938; Stickel and Marco 1936; Hepting and Hedgecock 1935; Kaufert 1933; Nelson and others 1933; McCarthy 1928; Schmitz and Jackson 1927; Lachmund 1923, 1921; Boyce 1921), and at least a significant one for several stem canker fungi (Haig 1938; Dearness and Hansbrough 1934). Incomplete postfire removal of dwarf mistletoe-infected overstory creates a situation ideal for the spread and intensification of damage from the mistletoe parasites (Alexander and Hawksworth 1975). Wildfire also contributes to increased disease problems by creating thick stands in which intense competition for space, moisture, and nutrients weakens trees. Such a stand is an ideal substrate for root and stem decay fungi (Baxter 1967; Boyce 1961).

Diseases, like dwarf mistletoe, whose distribution and intensity are directly dependent on fire history (Alexander and Hawksworth 1975), should gradually be eliminated through improved harvesting practices. The effects of most other endemic pathogens can be minimized by controlling stand age, vigor, composition, and inoculum. They probably have been reduced through the sanitizing effect of natural wildfire (Heinselman 1971; Chapman 1927).

Past Efforts of Disease Control Through Use of Fire

The effectiveness of prescribed fire and removal of residues as a sanitizing treatment for disease is widely recognized and has provided the impetus for a number of both successful and unsuccessful attempts to control forest pathogens. In Michigan, attempts to eradicate the sweetfern blister rust (*Cronartium comptoniae*) by burning the infected pines and the alternate host were unsuccessful (Baxter 1967). In the late 1940's, prescribed burning to control the fusiform rust (*Cronartium fusiforme*) in the southern United States failed (Siggers 1949). In the latter case, inoculum was reduced, but counterbalancing epidemiological factors were sufficient to offset the gain. Inoculum reduction and lowered disease incidence were achieved by fire in the southeast, and in India with the brown-spot needle disease (*Seirrhia acicola*) and *Septoria pini* of longleaf pine (Siggers 1944, 1932; Gibson 1938; Chapman 1927).

In many sections of the country, fire is associated with an increase in *Ribes* populations (Davis and Klehm 1939) that support white pine blister rust, and an increase in oaks that serve as alternate hosts for the fusiform rust in the southeast. The spread and intensification of *Nectria* and *Cytospora* canker (Haig 1938; Dearness and Hansbrough 1934) and modification of several other fungal diseases have been associated with burning (Muller 1929). The use of prescribed fire appears well suited as an agent useful for the control of dwarf mistletoe under certain site conditions (Alexander and Hawksworth 1975). Weir (1923) observed that broadcast burning reduced growth and fruiting of the most important cull-producing fungi in Idaho and Montana. He noted that charred stumps and logs are rarely reinfected by the cull fungi of the living tree. Boyce (1961) observed that charring of stumps in the Southwest controlled fruiting of cull-producing fungi, and Roth (1956, 1943) reported reductions in defect of fire-thinned oak when compared to normally harvested or thinned stands. Many of the above cited effects of fire could be duplicated by clearcutting and intensive utilization.

Residue as a Dispersing Agent

Whether related to biotic forces, physical forces such as high winds and wildfires, or to man's activities, plant residues left in place can pose disease problems. Cull-causing decay fungi produce spores from fruiting structures that develop on stumps of fallen trees and other woody residue (Gill and Andrews 1956; Spaulding 1934; Wright 1934; Hubert 1920). Many root diseases are dependent on stumps and roots in the soil or decaying tree butts in contact with the forest floor (Boyce 1961; Kaarik and Rennerfelt 1957). These residues act as a substrate for growth and sporulation and provide the inoculum for new infections.

No other class of forest diseases causes more timber damage than root decays (Nelson and Harvey 1974). The saprophytic stages of these fungi are completely dependent on woody residue to survive from one generation of host plants to the next. Thus, residues may enable the intensification of root disease in proportion to their volume and suitability for colonization by increasing the probability of survival of the causal fungi (Hudson 1968). *Armillaria mellea*, *Poria weirii*, and *Fomes annosus* are important examples of this type of pathogen. Heart-rotting fungi can also be propagated in this manner (Hudson 1968; Meredith 1960). However, standing dead or live defective trees are probably more important as a source of inoculum for heart-rot fungi. Diseases that attack foliage, and then produce spores on dead and fallen needles, may also represent residue hazards. *Lophodermium*, *Herpotrichium*, and *Neopeakia* are representative genera (Hepting 1971; Hudson 1968; Boyce 1961).

Survival of pathogens on residue depends on many factors: (1) size and species of residue; (2) charring; (3) soil physical and chemical characteristics; (4) site; (5) host trees available; (6) relative location of residues to the soil and host plants; (7) species of pathogenic fungi present; (8) relative vigor of the hosts; and (9) the adaptive capacities of the pathogens and their potential hosts. Through adequate reduction of forest residues, intensive utilization and fire can suppress many types of diseases. Conversely, allowing residues to accumulate can encourage these same diseases.

Residual Effects of Fire and Harvesting on Site Factors That Influence Disease Problems

In addition to the sanitation influence provided by physical removal of wood or burning, the six macroenvironmental parameters that change as a result of these treatments (temperature, moisture, aeration, acidity, nutrient and energy supply, and available biota) also provide direct influences on disease organisms on, in, or associated with soil components. For example, survival and distribution of cull-producing fungi in slash can be directly influenced by temperatures brought about by exposure to insolation (Loman 1965, 1962).

Soil temperatures of 60° to 70° C for 10 minutes are normally sufficient to kill most root pathogens (Johnson 1946). Surface fires may cause temperatures in this range within the upper 4 inches of forest soils (Van Wagner 1970; Beadle 1940; Raymond Shearer, personal communication). Therefore, substantial reductions in the numbers of certain feeder root pathogens in these shallow soil layers (2 to 4 inches) may occur. However, the reported reduction in fungal and bacterial populations induced by surface fire (Neal and others 1965) and possible concomitant heat or nutrient-induced elimination of soil fungistasis² (Watson and Ford 1972, Dobbs and others 1960) could lead to increases in any pathogenic organisms surviving in these soil layers. Pathogens could be introduced on or in the seed (Bloomberg 1966). Increased nutrient availability and reduced competition can contribute to soil colonization advantages by surviving feeder root pathogens and may lead to the fire related buildup of these pathogens (Hartley and Pierce 1917). In addition, the suppressive effects of heat and fire generated soil extracts on soil fungi have been reported to be greater on fungi normally antagonistic to feeder root pathogens than on the pathogens (Widden and Parkinson 1975; Bollen 1969).

The potential for fire-induced feeder root disease damage by *R. undulata* to conifer regeneration in the Northern Rocky Mountains is poorly defined. It is known, however, to be present in western Montana and northern Idaho (Weir 1915). The lack of recent reports on the fungus in this area may be due, at least in part, to effective fire exclusion and limitation. This parasite has demonstrated its potential to cause extensive damage to conifer seedlings and even mature trees in Great Britain and Europe (Gremmen 1971; Jalaluddin 1967; Murray and Young 1961). It has also been reported to be destructive to conifer seedlings in western Washington (Morgan and

²An inhibitory factor that limits germination of fungal spores in soils. Such a factor has been reported present in forest soils (Dobbs and Bywater 1959).

Driver 1973, 1972). One report associated this organism with a diseased condition in an 80-year-old spruce in Vermont (Thompson and Tattar 1973). Thus, although its potential in the Intermountain region is unknown, its presence here and its capability to infect conifer regeneration in recently burned areas are recognized.

After the initial soil microflora reductions following fire, microbial populations greater than the original can occur (Renbuss and others 1973; Ahlgren 1965). The presence of potentially damaging feeder root diseases, including *Phytophthora*, *Pythium*, *Fusarium*, and *Rhizoctonia* in natural forest soils, and their survival after burns of various intensities has been documented (Wright and Bollen 1961). Increases in damaging feeder root pathogens have been reported in postfire soils (Hartley and Pierce 1917; Wright and Bollen 1961; Tarrant 1956). Conversely, charcoal has been reported to reduce damping-off of conifer seedlings (Beltram 1963; Radovanovic 1962; Commonwealth of Pennsylvania 1930; Boyce 1925). Very short exposures to increased soil temperatures resulting from prescribed fires or wildfires may cause shifts in species composition and numbers of soil fungi (Peterson 1970; Seaver and Clark 1910). Increases in the activity of ascomycetes such as the root pathogen *Rhizina undulata* (Morgan and Driver 1972; Ginns 1968; Jalaluddin 1968) after burning provide a specific example.

Alkaline shifts in soil pH have been well documented subsequent to site burning (Neal and others 1965) and weakly acid, neutral, or alkaline soils are generally favorable to soil feeder-root pathogens. Seedling damping-off has been correlated directly to raising forest soil pH levels (Tarrant 1956). In addition, high moisture and lack of aeration may be caused by fire or harvesting practices (Ralston and Hatchell 1971; Bethlahmy 1962) and are generally conducive to soil-inhabiting plant diseases (Raney 1970). The effects of fire and nitrogen fertilization are similar (Sagara 1973) and high nitrogen levels contribute to an increased susceptibility to feeder root diseases (Rowan 1971; Foster 1968). This indicates a real possibility of feeder-root pathogen problems, particularly on regeneration established during the early postburn period. The potential effects of these factors on the establishment of mycorrhizal associations (Björkman 1970) and the apparent resistance to feeder-root pathogens provided by mycorrhizae (Marx 1973) provide an additional and potentially significant factor.

Clearcutting or burning may threaten the subsequent timber crop through excessive release of nutrients. Changes in soil nutrients, particularly nitrogen, can influence disease (Hesterberg and Jurgensen 1972; Foster 1968; Sadasivan 1965). For instance, because the addition of nitrogen to forest nurseries increases incidence of damping-off diseases, applications are delayed until seedlings have grown beyond the susceptible stage (Rowan 1971; Foster 1968). Additions of nitrogen, phosphorus, and potassium to young slash pine increased incidence of fusiform rust (Blair and Cowling 1974; Hollis and others 1972; Gilmore and Livingston 1958; Bogess and Stahelin 1948). Conversely, regulation of soil nutrient balance can reduce incidence of this destructive pathogen (Hollis, personal communication).

Root disease caused by *Fomes annosus* decreased when potassium and magnesium were added to the soil, but increased with additions of manganese and increasing soil pH (Yde-Anderson 1970). Froelich and Nicholson (1973) reported a reduction of *F. annosus* root rot as large quantities of sulfur were added. This may have been more the result of a lowering in soil pH than the increased levels of available sulfur in the soil. Additions of nitrogen alleviate little leaf disease (Roth and Copeland 1957; Roth and others 1948), *Verticillium* wilt of maple (Caroselli 1956), and maple decline (Mader and Thompson 1969).

Addition of soil nutrients probably influences disease through control of plant health and vigor. However, nutrients may also directly affect the survival and growth of the saprophytic stage of many root pathogens. Again, nitrogen or the form of nitrogen can be significant (Huber and Watson 1974). Nitrogen level appears to regulate the formation and germination of *Fusarium* chlamydospores (Garrett 1970).

Nitrate favors *Curvularia* disease as compared to ammonium (Sadasivan 1965), and nitrate is a poor nitrogen source for *Fomes annosus* (Johanson 1970), *Poria weirii*, and *Armillaria mellea* (Cowling 1970).

Any sudden increase in available nutrients will alter the quantity and quality of root exudation and therefore the rhizosphere. Both fertilization and liming have greater influences on the rhizosphere microflora than on organisms in the surrounding soil (Voznyakovskaya and Avrova 1968; Welte and Trollendenier 1961). Thus, rhizosphere-dependent micro-organisms, such as feeder root pathogens and mycorrhizae, should be the first affected.

Conclusions

Although the effects of intensive utilization and prescribed burning on disease organisms are likely to be complex, treatments which direct the change in disease status are possible in managed forests. Potential for damage and opportunities for control can be anticipated.

Forest managers must become acquainted with the natural roles of diseases in fire-dependent forests. Harvesting, utilization intensity, and prescribed fires could be used in concert to discourage, emulate, or supplement these functions. Comparisons of the effects of intensive utilization and prescribed fire on forest pathogen activities should provide considerable insight into their functions and means to control them.

Research Needs

In the Intermountain West, forest operations using both prescribed burning and clearcutting in conjunction with intensive fiber utilization are likely to depend on natural regeneration. Therefore, assessment and diagnosis of seedling mortality after such treatments are imperative. If seedling loss is significant, the contributing factors should be investigated. If disease is evident, its significance to the regeneration and growth of the subsequent crop should also be assessed. Disease, active or potential, will likely limit the management options for many sites.

Literature Cited

- Ahlgren, I. F.
1965. Effects of prescribed burning on soil microorganisms in a Minnesota jack pine forest. *Ecology* 46:304-310.
- Ahlgren, I. F., and C. E. Ahlgren.
1960. Ecological effects of forest fires. *Bot. Rev.* 26:483-533.
- Alexander, M. E., and F. G. Hawksworth.
1975. Wildland fires and dwarf mistletoes: a literature review of ecology and prescribed burning. USDA For. Serv. Gen. Tech. Rep. RM-14. Rocky Mt. For. and Range Exp. Stn., Ft. Collins, Colo.
- Basham, J. T.
1957. The deterioration by fungi of jack, red, and white pine killed by fire in Ontario. *Can. J. Bot.* 35:155-172.
- Baxter, D. V.
1967. Disease in forest plantations: thief of time. 250 p. Cranbrook Inst. Sci., Bloomfield Hills, Mich.
- Beadle, N. C. W.
1940. Soil temperatures during forest fires and their effect on the survival of vegetation. *J. Ecol.* 28:180-192.
- Beltram, V.
1963. Drveni vglasi-selektivni sterilizator-trajno posredno dubrivo. *Sumarski list.* 87:175-185.

- Bethlahmy, N.
1962. First year effects of timber removal on soil moisture. Bull. Inst. Assoc. Sci. Hydrol. 7:34-38.
- Björkman, E.
1970. Forest tree mycorrhiza--the conditions for its formation and the significance for tree growth and afforestation. Plant and Soil 32:589-610.
- Blair, R. L., and E. B. Cowling.
1974. Effects of fertilization, site, and vertical position on the susceptibility of loblolly pine seedlings to fusiform rust. Phytopathology 64:761-762.
- Bloomberg, W. J.
1966. The occurrence of endophytic fungi in Douglas-fir seedlings and seeds. Can. J. Bot. 44:413-420.
- Bogess, W. R., and R. Stahelin.
1948. The incidence of fusiform rust in slash pine plantations receiving cultural treatments. J. For. 46:683-685.
- Bollen, G. J.
1969. The selective effect of heat treatment on the microflora of a greenhouse soil. Neth. J. Plant Path. 75:157-163.
- Boyce, J. S.
1921. Fire scars and decay. The Timberman 22:7.
- Boyce, J. S.
1925. Report on forest tree diseases observed in Great Britain and Denmark. A report of the Office of Investigations in Plant Pathology. Bur. Plant Ind., Washington, D.C. 87 p.
- Boyce, J. S.
1961. Forest pathology. Third ed. 572 p. McGraw-Hill, New York.
- Burns, P. Y.
1955. Fire scars and decay in Missouri oaks. Univ. Mo. Coll. Agric. Bull. 642.
- Caroselli, N. E.
1956. The effect of various soil amendments on maple wilt incited by *Verticillium* sp. (abstr.). Phytopathology 46:240.
- Chapman, H. H.
1927. Use of fire in regeneration of certain types of forests in India. J. For. 25:92-94.
- Commonwealth of Pennsylvania.
1930. Mont Alto State Forest Nursery. Dep. For. and Water Bull. 49, 57 p.
- Cowling, E. B.
1970. Physiology of *Fomes annosus*. In: Proc. Third Int. Conf. *Fomes annosus*, P.192-201. U.S. Dep. Agric. For. Serv., Southeast For. Exp. Stn., Asheville, N.C.
- Davis, K. P., and K. A. Klehm.
1939. Controlled burning in the western white pine type. J. For. 37:399-407.
- Day, W. R.
1955. Forest hygiene in Great Britain. Univ. Toronto For. Bull. 4, 26 p.
- Dearness, J., and J. R. Hansbrough.
1934. *Cytospora* infections following fire injury in western British Columbia. Can. J. Res. 10:125-128.
- Dobbs, C. G., and J. Bywater.
1959. Studies in soil mycology. II. G.B. For. Comm. Rep. For. Res. 1958, p. 98-104.
- Dobbs, C. G., W. H. Hinson, and J. Bywater.
1960. Inhibition of fungal growth in soils. In: The ecology of soil fungi, p. 130-147. D. Parkinson and J. S. Waide, eds. Liverpool Univ. Press, Liverpool.
- Foster, A. A.
1968. Damage to forests by fungi and insects as affected by fertilizers. In: Forest fertilization--theory and practice, p. 42-46. Tenn. Valley Auth., Muscle Shoals, Ala.
- Froelich, R. C., and J. D. Nicholson.
1973. Spread of *Fomes annosus* reduced by heavy application of sulfur. For. Sci. 19:75-76.

- Garren, K. H.
1941. Fire wounds by loblolly pine and their relation to decay and other cull. J. For. 39:16-22.
- Garrett, S. D.
1970. Pathogenic root-infecting fungi, p. 284. Cambridge Univ. Press, Cambridge.
- Gibson, J. M.
1938. Comments. J. For. 36:1049-1051.
- Gill, L. S., and S. R. Andrews.
1956. Decay of ponderosa pine slash in the Southwest. USDA For. Serv., Rocky Mt. For. and Range Exp. Stn. Res. Note 19, 2 p.
- Gilmore, A. R., and K. W. Livingston.
1958. Cultivating and fertilizing a slash pine plantation: effects on volume and fusiform rust. J. For. 56:481-483.
- Ginns, J. H.
1968. *Rhizina undulata* pathogenic on Douglas-fir seedlings in western North America. Plant Dis. Rep. 52:579-580.
- Gremmen, J.
1971. *Rhizina undulata*: a review of research in the Netherlands. Eur. J. For. Path. 1:1-6.
- Gustafson, R. O.
1946. Forest fires, basal wounds, and resulting damage to timber in an eastern Kentucky area. Ky. Agric. Exp. Stn. Bull. 493, 15 p.
- Habeck, J. R., and R. W. Mutch.
1973. Fire-dependent forests in the northern Rocky Mountains. Quaternary Res. 3:408-424.
- Haig, J. R.
1938. Fire in modern forest management. J. For. 1045-1051.
- Hart, A. C.
1938. The relation of fire scars to decay in living trees. M.S. thesis, Yale Univ.
- Hartley, C., and R. G. Pierce.
1917. The control of damping-off of coniferous seedlings. p. 1-32. U.S. Dep. Agric. Bull. 453, Washington, D.C.
- Heinselmann, M. L.
1971. The natural role of fire in northern conifer forests. In: Proc. Fire in the Northern Environment: a summary. 275 p. C. W. Slaughter, R. J. Barney, and G. M. Hansen, eds. U.S. Dep. Agric. For. Serv. Pac. Northwest For. and Range Exp. Stn. Portland, Oreg.
- Hepting, G. H.
1941. Prediction of decay following fire in Appalachian oaks. J. Agric. Res. 62: 109-120.
- Hepting, G. H.
1971. Diseases of forest and shade trees of the United States. U.S. Dep. Agric. Handb. 386, 658 p. Washington, D.C.
- Hepting, G. H., and G. C. Hedgcock.
1935. Relation between butt rot and fire in some eastern hardwoods. U.S. Dep. Agric. For. Serv. Tech. Note 14, 2 p. Washington, D.C.
- Hepting, G. H., and A. I. Shigo.
1972. Difference in decay rate following fire between oaks in North Carolina and Maine. Plant Dis. Rep. 56:406-407.
- Hesterberg, G. A., and M. F. Jurgensen.
1972. The relation of forest fertilization to disease incidence. For. Chron. 48:92-96.
- Hollis, C. A., W. H. Smith, R. A. Schmidt, and W. L. Pritchett.
1972. Relation between nutritional status of slash pine and fusiform rust. Proc. 2nd North Am. For. Biol. Workshop, Oreg. State Univ. 51 p.
- Huber, D. M., and R. D. Watson.
1974. Nitrogen form and plant disease. Annu. Rev. Phytopath., p. 139-166.

- Hubert, E. E.
1920. The disposal of infected slash on timber sale areas in the Northwest. *J. For.* 18:34-36.
- Hubert, E. E.
1931. An outline of forest pathology. John Wiley & Sons, N.Y. 543 p.
- Hudson, H. J.
1968. The ecology of fungi on plant remains above the soil. *New Phytol.* 67:838-874.
- Jalaluddin, M.
1967. Studies on *Rhizina undulata*. II. Observations and experiments in East Anglian plantations. *Trans. Brit. Mycol. Soc.* 50:461-472.
- Jalaluddin, M.
1968. Fire as an agent in the establishment of a plant disease. *Pak. J. Sci.* 21:42-44.
- Johanson, M.
1970. Discussions on *Fomes annosus*. In: Proc. 3d Int. Conf. *Fomes annosus*, p. 62-65. U.S. Dep. Agric. For. Serv., Southeast. For. Exp. Stn., Asheville, N.C.
- Johnson, J.
1946. Soil-steaming for disease control. *Soil Sci.* 61:83-91.
- Kaarik, A., and E. Rennerfelt.
1957. Investigations on the fungal flora of spruce and pine stumps. *Statens Skogsforskningsinst. (Sweden), Medd.* 47:1-88.
- Kaufert, F. H.
1933. Fire and decay in the southern bottomland hardwoods. *J. For.* 31:64-67.
- Komarek, E. V.
1963. Fire research and education. *Proc. Tall Timbers Fire Ecol. Conf.* 2:181-187.
- Lachmund, H. G.
1921. Some phases in the formation of fire scars. *J. For.* 19:638-640.
- Lachmund, H. G.
1923. Bole injury in forest fires. *J. For.* 21:723-731.
- Loman, A. A.
1962. The influence of temperature on the location and development of decay fungi in lodgepole pine logging slash. *Can. J. Bot.* 40:1545-1559.
- Loman, A. A.
1965. The lethal effect of periodic high temperatures on certain lodgepole pine slash decaying basidiomycetes. *Can. J. Bot.* 43:334-338.
- Lyons, J. L., and W. L. Pengelly.
1970. Commentary on the natural role of fire. In: Symposium on the role of fire in the Intermountain West, p. 81-84. Intermt. Fire Res. Council., Missoula, Mont.
- Mader, D. L., and B. W. Thompson.
1969. Foliar and soil nutrients in relation to sugar maple decline. *Proc. Soil Soc. Am.* 33:794-800.
- Marx, D. H.
1973. Mycorrhizae and feeder root diseases. In: *Ectomycorrhizae--their ecology and physiology.* 444 p. G. C. Marks and T. T. Kozlowski, eds. Academic Press, N.Y.
- McCarthy, E. F.
1928. Analysis of fire damage in southern Appalachian forests. *J. For.* 26:57-68.
- Meredith, D. S.
1960. Further observations on fungi inhabiting pine stumps. *Ann. Bot.* 24:63-78.
- Morgan, P., and C. H. Driver.
1972. *Rhizina* root rot of Douglas-fir seedlings planted on burned sites in Washington. *Plant Dis. Rep.* 56:402-409.
- Morgan, P., and C. H. Driver.
1973. *Rhizina* root rot in conifer plantations in western Washington. *Plant Dis. Rep.* 57:167-169.
- Muller, K. M.
1929. Aufbau, wuchs, und verjungung der sudosteuropaischen urwalder. Reviewed by M. Hanover and H. Schaper. *J. For.* 28:744.
- Murray, J. S., and C. W. T. Young.
1961. Group dying in conifers. *For. Comm. For. Rec.* 46, 19 p.

- Neal, J. L., E. Wright, and W. B. Bollen.
1965. Burning Douglas-fir slash: physical, chemical, and microbial effects in the soil. Oreg. State Univ. For. Res. Lab. Res. Pap. 132 p.
- Nelson, E. E., and G. M. Harvey.
1974. Residues and forest disease. *In: Environmental effects of forest residues management in the Pacific Northwest--a state-of-knowledge compendium*, p. 51-511. USDA For. Serv., Gen. Tech. Rep. PNW-24. Pac. Northwest For. and Range Exp. Stn. Portland, Oreg.
- Nelson, R. M., I. H. Sims, and M. S. Abell.
1933. Basal fire wounds on some southern Appalachian hardwoods. *J. For.* 31:829-837.
- Nordin, V. J.
1958. Basal fire scars and the occurrence of decay in lodgepole pine. *For. Chron.* 34:257-265.
- Olsen, J. S.
1963. Energy storage and the balance of producers and decomposers in ecological systems. *Ecology* 44:322-331.
- Peterson, P. M.
1970. Danish fireplace fungi--an ecological investigation of fungi on burns. *Dansk Bot. Ark.* 27:1-97.
- Radovanovic, Z.
1962. Uticaj drvenog uglja na razvitak bora smrce ijele. *Sumarstvo* 15:113-129.
- Ralston, C. W., and G. E. Hatchell.
1971. Effects of prescribed burning on physical properties of soil. *Proc. Prescribed Burning Symp. USDA For. Serv., Southeast. For. Exp. Stn.*, p. 68-84.
- Raney, W. A.
1970. Physical factors of the soil as they affect soil microorganisms. *In: Ecology of soil borne plant pathogens*, p. 115-119. K. F. Baker, W. C. Snyder, eds. Univ. Calif. Press, Berkeley.
- Renbuss, M., G. A. Chilvers, and L. D. Pryer.
1973. Microbiology of an ashbed. *Proc. Linn. Soc. N.S.W.* 97:302-310.
- Roth, E. R.
1956. Decay following thinning of sprout oak clumps. *J. For.* 54:26-30.
- Roth, E. R., and O. L. Copeland.
1957. Uptake of nitrogen and calcium by fertilized shortleaf pine. *J. For.* 55:281-284.
- Roth, E. R., and G. H. Hepting.
1943. Origin and development of oak stump sprouts as affecting their likelihood to decay. *J. For.* 41:27-36.
- Roth, E. R., E. R. Toole, and G. H. Hepting.
1948. Nutritional aspects of the little leaf disease of pine. *J. For.* 46:578-587.
- Roth, L. F.
1966. Foliar habit of ponderosa pine as a heritable basis for resistance to dwarf mistletoe. *In: Breeding pest resistant trees*, H. D. Gerhold and others, eds., p. 221-227. Pergamon Press, London.
- Rowan, S. J.
1971. Soil fertilization, fumigation, and temperature affect severity of black root rot of slash pine. *Phytopathology* 61:184-187.
- Sadasivan, T. S.
1965. Effect of mineral nutrients of soil microorganisms and plant disease. *In: Ecology of soil borne plant pathogens*, p. 460-468. K. F. Baker and W. C. Snyder, eds. Univ. Calif. Press, Berkeley.
- Sagara, N.
1973. Proteophilous fungi and fireplace fungi. *Trans. Mycol. Soc. Japan* 14:41-46.
- Schmitz, H., and L. W. R. Jackson.
1927. Heart rot of aspen with special reference to forest management in Minnesota. *Minn. Agric. Exp. Stn. Tech. Bull.* 50, 43 p.
- Seaver, F. J., and E. D. Clark.
1910. Studies in pyrophilous fungi. II. Changes brought about by heating of soils and their relation to the growth of *Pyronema* and other fungi. *Mycologia* 2:109-124.

- Siggers, P. V.
1932. The brown spot needle blight of longleaf pine seedlings. *J. For.* 30:579-593.
- Siggers, P. V.
1944. The brown spot needle blight of pine seedlings. U.S. Dep. Agric. Tech. Bull. 870, 36 p. Washington, D.C.
- Siggers, P. V.
1949. Fire and the southern fusiform rust. U.S. Dep. Agric., For. Pathol. Spec. Release 33, 4 p. Washington, D.C.
- Spaulding, P.
1934. Persistence of heart-rotting fungi in girdled trees. *Phytopathology* 24:17-18 (Abstr.)
- Stickel, P. W., and H. F. Marco.
1936. Forest fire damage studies in the Northeast. III. Relation between fire injury and fungal infection. *J. For.* 34:420-423.
- Stone, E. C., R. F. Grah, and P. J. Zinke.
1972. Preservation of the primeval redwoods in the Redwood National Park. *Am. For.* 78:48-59.
- Tarrant, R. F.
1956. Effects of slash burning on some soils of the Douglas-fir region. *Proc. Soil Sci. Soc. Am.* 20:408-411.
- Thompson, J. E., and T. A. Tattar.
1973. *Rhizina undulata* associated with disease of 80-year-old red spruce in Vermont. *Plant Dis. Rep.* 57:394-396.
- Toole, E. R.
1959. Decay after fire injury to southern bottomland hardwoods. U.S. Dep. Agric. Tech. Bull. 1189. Washington, D.C.
- Toole, E. R., and G. M. Furnival.
1957. Progress of heart rot following fire in bottomland red oaks. *J. For.* 55:20-24.
- Van Wagner, C. E.
1970. Temperature gradients in duff and soil during prescribed fires. *Can. Bimon. Res. Notes* 26:42.
- Voznyakovskaya, Yu M., and N. P. Avrova.
1968. Effect of fertilizers on microorganisms producing vitamins in the rhizosphere of wheat. *Mikrobiologiya* 37:110-114.
- Watson, A. G., and E. J. Ford.
1972. Soil fungistasis--a reappraisal. *Annu. Rev. Phytopath.* 9:327-348.
- Weir, J. R.
1915. Observations on *Rhizina inflata*. *J. Agric. Res.* 4:93-97.
- Weir, J. R.
1923. The effect of broadcast burning on sale areas on the growth of cull-producing fungi. *J. For.* 21:183-184.
- Welte, E., and G. Trollendenier.
1961. The influences of the hydrogen ion concentration of the soil on the rhizosphere effect. *Naturwissenschaften* 48:509.
- Widden, P., and D. Parkinson.
1975. The effects of a forest fire on soil microfungi. *Soil Biol. Biochem.* 7:125-138.
- Wright, E.
1934. Survival of heart rots in down timber in California. *J. For.* 32:752-753.
- Wright, E., and W. B. Bollen.
1961. Microflora of Douglas-fir forest soil. *Ecology* 42:825-828.
- Yde-Anderson, A.
1970. Discussions on *Fomes annosus*. In: *Proc. 3d Int. Conf. Fomes annosus*, p. 137-148. U.S. Dep. Agric. For. Serv., Southeast. For. Exp. Stn., Asheville, N.C.

SUMMARY

From the many potential effects on microbial ecology that could result from the practices of intensive fiber utilization or prescribed burning in forested ecosystems, four major functional areas directly influence subsequent site quality. These include: (1) decay with its effects on carbon transformations, carbon, and mineral cycling, and the associated soil development; (2) the formation and function of mycorrhizal roots; (3) fixation of N and its transformations; and (4) the development and damage caused by plant disease fungi. The existing literature on each of these subjects was intensively reviewed to provide the basis for the following tentative conclusions.

The processes and organisms involved in residues decomposition are essential to soil development through carbon and mineral cycling and conservation, and may contribute indirectly to nitrogen acquisition. Therefore, the rate of timber harvesting in conjunction with prescribed burning or intensive fiber utilization should be adjusted to provide an adequate organic matter base for these processes. Failure to do so in the past has resulted in decreased site productivity.

The obligate association between most conifers and their mycorrhizal partners emphasizes that management of forest ecosystems for optimal growth of selected species will require management of the fungal symbionts on which the trees depend. In several instances postharvest site treatments directly affected the ability of conifer seedlings to establish mycorrhizal associations.

Nitrogen is subject to various transformations by soil micro-organisms. Any changes in the physical and chemical properties of a forest soil will affect the activity of these organisms. The most important nitrogen-related microbial activities are the fixation of atmospheric N into a form usable by plants and the conversion of other forms of N into nitrate that is subject to leaching losses. These are directly responsible for the input and outflow of nitrogen in forest soils. Because of its importance to forest ecosystems, management activities should be directed toward providing maximum input and minimum outflow of nitrogen. Both burning and extensive fiber removal are known to influence nitrogen transformation.

Disease problems are not currently known to be greatly affected by residues management. Prescribed burning may increase the activities of the potentially damaging *Rhizina* root rot or other feeder root diseases on young conifer seedlings. Large buried residues, stumps, and roots infected by or subject to infection by several root pathogens are known to perpetuate such pathogens. In some circumstances proper management of such materials, or a lack thereof, could create significant impacts in post-treatment forests.

Harvey, A. E., M. F. Jurgensen, and M. J. Larsen
1976. Intensive fiber utilization and prescribed fire: effects on the microbial ecology of forests. USDA For. Serv. Gen. Tech. Rep. INT-28, 46 p. Intermountain Forest & Range Experiment Station, Ogden, Utah 84401.

Reviews current knowledge of the effects of intensive wood utilization, prescribed burning, or a combination of both treatments, on the microbial ecology of forest soils. Identifies additional research that must be done to fill voids in knowledge.

OXFORD: 83/86; 436; 44.

KEYWORDS: utilization, residue management, prescribed fire, microbial ecology, decay, mineral cycling, mycorrhizae, nitrogen fixation, nitrification, mineralization, pathogen, disease, regeneration, forest ecology, site quality.

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