

ENVIRONMENTAL CONSEQUENCES
OF TIMBER HARVESTING
in rocky mountain coniferous forests

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A REVIEW OF SOME INTERACTIONS BETWEEN HARVESTING,
RESIDUE MANAGEMENT, FIRE, AND FOREST INSECTS AND DISEASES

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ABSTRACT

Many species of insects and diseases create residues that predispose forests to fire. Conversely, natural factors such as fire, wind-throw, and other agents create forest residues that predispose forests to diseases and insects, including bark and cambium beetles, wood borers, and others. Man-made residues also predispose forests to insects and disease.

Harvesting practices, residue management, and fire management not only influence the behavior and impact of forest insects, but also can be used to suppress some insect and disease populations. These practices also have a profound influence--mostly negative--on forest floor and forest soil arthropods, many of which (in concert with wood-destroying fungi) are involved in both the micro- and macro-deterioration and dispersion of forest residues. Opinions vary concerning the value of removing residues through prescribed fire to manage forest insects and diseases. Harvesting, residue management, and fire management are inextricably tied to forest succession.

The interactions between harvesting, residues, fire, insects, and diseases have many implications for the resource manager. Future research should provide a better understanding of these interactions and will likely enhance our opportunity to reduce the negative impacts of many species of indigenous insects and diseases in managed forests.

KEYWORDS: arthropods, disease, fire, residue, harvesting, silviculture

INTRODUCTION

Harvesting, residue management, and prescribed fire can have both positive and negative effects in the removal of standing green or dead trees, the removal of forest residues, which through natural decomposition and decay form the humus and forest soil, or the consumption of residues and the resultant effect on forest floor and forest soil flora and fauna.

The interactions between harvesting activities, residue treatments, fire (both prescribed and wild), and forest insect and disease behavior and activity are extremely varied, usually complex, and most often mutually inclusive and reversible. This paper is a review of the literature and an interpretation of some of these interactions, with a discussion of the management implications. Because of the breadth of these interrelationships, the contents of the paper is presented below:

	<u>Page</u>
INSECT AND DISEASE INTERACTIONS.....	336
INSECTS CREATE RESIDUES AND PREDISPOSE FORESTS TO FIRE.....	339
RESIDUES PREDISPOSE FORESTS TO INSECTS AND DISEASES.....	344
Naturally Created Residues.....	344
Residues Created by Man.....	356
HARVESTING PRACTICES INFLUENCE BEHAVIOR AND IMPACT OF FOREST INSECTS...	359
RESIDUE AND FIRE MANAGEMENT TO "CONTROL" INSECTS AND DISEASE.....	362
Diseases.....	362
Insects.....	362
RESIDUE AND FIRE MANAGEMENT--SOME OPINIONS.....	366
IMPACT OF HARVESTING, RESIDUE MANAGEMENT AND FIRE ON FOREST FLOOR AND FOREST SOIL ARTHROPODS.....	367
Forest Floor Macrofauna.....	369
Forest Soil Mesofauna.....	380
RESIDUES, FIRES, INSECTS AND FOREST SUCCESSION.....	385
SOME MANAGEMENT IMPLICATIONS.....	388
Management of Forest Residues.....	388
Fire Management.....	391
Silvicultural Practices.....	392
RESEARCH NEEDS.....	393

INSECT AND DISEASE INTERACTIONS

Insects and diseases have many associations, often with the potential to stabilize populations or to alter the function of these organisms in the forest ecosystem. In addition to their often direct interdependence in dead plant materials, insects and diseases interact through their mutual or individual effects on live trees. In some cases, diseases predispose living host trees to insect attack (Miller

and Keen 1960; Felix and others 1971, 1974; Thomas and Wright 1961; Rudinsky 1962). In other cases, insect attack predisposes living trees to diseases (Wagner and Mielke 1961; Lorio 1966; Molnar 1965; Partridge and Miller 1972). In still other cases, insects and diseases may combine to kill or damage trees (Shea 1971).

Many insects utilize fungi, usually sporocarps, as their primary food base (Fogel 1975). In the process of eating fungal sporocarps, the insects ingest spores, which sometimes survive passage through the digestive tract (Nuorteva and Lain 1972). Thus, the fungus-eating insect has the ability not only to destroy but also to disperse and build fungal populations. The fungi affected in these ways are frequently tree pathogens (Powell and others 1972; Molnar 1965; Willhouse 1919), ectomycorrhizae (Zak 1965; Weiss and West 1920), or major decay fungi (Ackerman and Shenefelt 1973).

Insects and fungi can be mutualistic. The ability of many insects to exploit either live or dead wood as a food source may be entirely dependent upon a beneficial association with specific fungi (Graham 1967). Moreover, many species of insects, principally bark beetles and wood borers, contribute directly to the dispersal and effectiveness of many decay fungi. By ingesting and macerating woody tissue (Witkamp 1975; Graham 1925), and by their tunneling and boring activities, insects not only introduce fungi (fig. 1) but also create avenues of entry or "infection courts" for staining- or wood-destroying fungi (Thomas 1955; Orr 1959; Graham 1922). In fire-injured or fire-killed Douglas-fir, Pseudotsuga menziesii Britton, in Oregon, pin hole borers (ambrosia beetles), and sap-staining fungi, Ceratocystis minor (Hedge.) Hunt introduced by the Douglas-fir beetle Dendroctonus pseudotsugae Hopkins (Kimmy and Furniss 1943) seriously degraded sapwood causing it to turn dark a few weeks after attack (Furniss 1937).

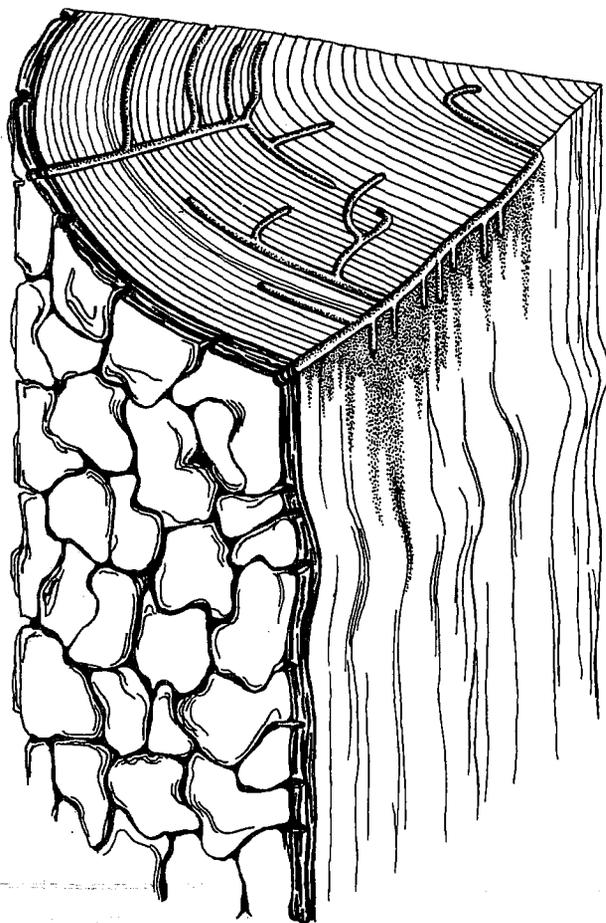


Figure 1.--Galleries of ambrosia beetles and associated stain. Beetle galleries and fungi cause degrade and hasten wood deterioration. Fungi also serve as source of food for these beetles.

Borden and McLaren (1970) reported that the year after Douglas-fir beetle attacks, hyphae of Polyporus volvatus Peck extrude through boring holes made by the beetles, suggesting the predator (Temnochila virescens var chlorodia (Mann.) (Ostomidae) as a likely vector. A few years later, Castello and others (1976) isolated P. volvatus from Douglas-fir beetles trapped in flight; their evidence suggested that the Douglas-fir beetle is the major vector of P. volvatus, a common cause of sapwood rot in beetle-killed trees. At other times, the brown rot fungus, Fomes pinicola (Schw. ex Fr.) Cke, is the most serious deteriorating agent in Douglas-fir killed by the Douglas-fir beetle (Wright and Harvey 1967). In some cases the blue fungus, Ceratocystis pilifera (Fr.) Moreau stains sapwood, and the red-rot fungus, Stereum sanguinolentum (Alb. and Schw. ex Fr.) Fr., causes decay in beetle-killed trees (Buttrick 1912).

In studying the rate of deterioration of Englemann spruce, Picea engelmanni Parry, killed by the Englemann spruce beetle, Dendroctonus rufipennis (Kirby) (= obesus Mann.), in Colorado, Mielke (1950) indicated that several root rot fungi may have weakened the trees before they were killed by beetles. An unidentified species of blue stain fungus that was probably carried into the trees by the beetles did not appear to be a serious defect. Although the rate of deterioration from decay in fallen trees was fairly rapid, Mielke anticipated that a high percentage of beetle-killed trees would remain standing and sound for at least 20 years.

On the Gaspè peninsula in eastern Canada, spruce killed by the eastern spruce beetle, Dendroctonus piceaperda, lost 8.7 percent of the merchantable volume to decay in 7 to 8 years (Riley 1940), while spruce killed by the European spruce sawfly, Diprion hercyniae (Htg.), lost 48.3 percent during the same period (Riley and Skolko 1942).

Insect-disease interactions also have been reported in wind-thrown white fir, Abies concolor (Gord. and Glend.), and California red fir, Abies magnifica A. Murr., in California. In one study (Gordon 1973), insects were attributed as killing many trees that were under physiological stress caused by root diseases or dwarf mistletoe, Arceuthobium americanum Nuttall ex Engelm.; mistletoe infections were judged to have severely reduced the vigor of 34 percent of the trees killed by bark beetles. Other trees physiologically stressed and mechanically weakened were wind-thrown; had they not been blown over, Gordon feels they would have been killed by beetles. In another study, Wickman (1965) reports that blue stain introduced by bark beetles and flatheaded borers was the most important single cause of degrade effecting an estimated 50 percent deterioration in the first and second years after the blowdown (Wickman 1965).

There are several reports of diseases associated with trees damaged by one or more species of spruce budworm, Choristoneura spp. Decay in grand fir, Abies grandis (Dougl.) Lindl., top-killed by the western spruce budworm, C. occidentalis Freeman, resulted in a serious loss in volume, with young saw timber-sized trees suffering a higher percentage of loss than older growth trees (Ferrell and Scharpf 1979). Stillwell (1956) found balsam-fir, Abies balsamea (L.) Mill., top-killed by the eastern spruce budworm, C. fumiferana Clem., to have a high incidence of decay. Butt rot has also been reported in balsam fir defoliated by the eastern spruce budworm; the rot is apparently related to high rootlet mortality (Sterner 1970).

Insects and fungi also can be antagonistic. At times trees do not appear to be predisposed to disease as a result of insect attack, nor predisposed to insect attack when diseased. In the west, Wickman and Scharpf (1972) found that white fir damaged by the Douglas-fir tussock moth, Orgyia pseudotsugata McDunnough, failed to show the presence of typical decay, although in 2 out of 21 top-damaged trees, the common brown rot fungus was present. In the east, Basham (1971) found no significant heart rot in eastern white pine, Pinus strobus L., damaged by the terminal weevil,

Pissodes strobi Peck. In a thinned red-pine, Pinus resinosa Ait., plantation in Ontario, stumps attacked by fungi appeared to be unsuitable or unattractive to insects, preventing the encroachment of bark- and wood-feeders (Martin 1965). Brown rots and carbonizing decays that attack cellulose seem to restrict insect activity, in contrast to white rots that do not seem to do so (Kimmev and Furniss 1943). Earlier in this Symposium, Dr. Mike Larsen discussed the relative significance of brown and white rots in the forest ecosystem. Some insect species parasitized by fungi reflect other cases of apparent antagonism (Roberts 1973).

Many insect and disease relationships in the forest ecosystem are very beneficial in that they contribute directly to the carbon and nutrient recycling process in dead plant residues and to the development of forest soil organic layers. Other insect-disease relationships are responsible for mortality and retarding growth in forest stands. An integrated insect-disease approach is often needed to fully understand the total forest pest impact (Wickman and Scharpf 1972). An excellent example of this concerns the need to very carefully consider the impact of dwarf mistletoe when contemplating partial cutting of lodgepole pine, Pinus contorta var latifolia Engelm., stands to manage the mountain pine beetle, Dendroctonus ponderosae Hopkins (D. Cole 1978).

INSECTS CREATE RESIDUES AND PREDISPOSE FORESTS TO FIRE

Insects and diseases kill forest trees and create dead plant bodies or residue. This material may decay, thus contributing to the recycling process by creating a reservoir both for nitrogen fixation as well as for pest inoculum. Or, these large accumulations of residues (fuels) may burn violently (fig. 2), consuming all or most of the residue as well as killing any living trees left in the insect or disease centers. Such wildfires affect the immediate recycling of nutrients as well as the removal of the pest inoculum; however, wildfires also increase genetic turnover because the survival potential of individuals with possible insect and/or disease resistant genotypes is negated by their increased probability of being burned. An ecosystem with these insect-disease-fire interactions may preserve endemic insect and disease activity, perhaps as a means of shortening the turnover time for available genes in long-lived trees.



Figure 2.--In August of 1961, a lightning ignited wildfire roared through 28,000 acres of jack-strawed lodgepole pine residue. The trees had been killed by the mountain pine beetle between 1926 and 1938 on the Bitterroot and adjacent National Forests in western Montana.

Bark Beetles

Of all forest insects that are reported to predispose forests to fire by creating residues, various species of bark beetles are perhaps the most significant. In the northern Rocky Mountains, as well as in the Pacific Northwest, the mountain pine beetle has been in the past and is currently responsible for killing millions of lodgepole pine. Dead trees, which as snags or windfalls, add to excessive residue (fuels) and increase the danger of devastating forest fires. Once ignited, the rate of consumption is magnified by these highly combustible fuels (Boag and Evans 1967).

Josef Brunner, an early day forest entomologist in the northern Rockies, recognized the predisposition of bark beetle-killed trees to fire. In 1917 he describes (Brunner 1917) the killing of millions of pine and Douglas-fir, by the mountain pine beetle and Douglas-fir beetle, respectively, and says, "These beetle-killed trees fall to the ground and form a veritable network of highly combustible material subject to ignition by lightning or other causes, which, other favorable conditions being present, result in conflagrations that kill all of the remaining living timber within its path." It was clear to Brunner that "there has been a most intimate interrelation of destructive bark beetles and forest fires in the denudation of the vast areas of once heavily forested lands in the Rocky Mountain region."

A classic example of this predisposition of bark beetle-killed forests to fire, and proof of Brunner's prediction, was the Sleeping Child burn (Mine Fire) on the Bitterroot National Forest in western Montana. Between 1926 and 1938, a mountain pine beetle epidemic killed lodgepole pine trees on 1.3 million acres on the Bitterroot and adjacent National Forests. In August of 1961, lightning ignited that residue, and the resultant fire consumed 28,000 acres of the beetle-killed, jack-strawed fuel (Lotan 1976). Earlier in the Symposium, Dr. Nellie Stark used this fire as a classic example of the impacts of wildfires on soil nutrient regimens.

The Sleeping Child wildfire and others like it also provide examples of the complex relationships between lodgepole pine and other conifers, the mountain pine beetle or other bark beetles, and wildfire. Many forests become predisposed to beetle infestations because of dense, overcrowded stands and competition between trees (Weaver 1961). At times, dense stands develop as a result of catastrophic fire, or because fire has not naturally thinned them; at other times overcrowding occurs in forests previously killed by insects (Weaver 1943). If bark beetle outbreaks occur during periods of drought, concurrent wildfires may check the excessive multiplication of beetles (Craighead 1925). Wildfires also provide a natural check on insects and disease; according to Lotan (1976), "the Sleeping Child burn will be relatively free of the mountain pine beetle and dwarf mistletoe for decades."

Fires, such as Sleeping Child, may serve to create lodgepole pine forests that may be predisposed to another mountain pine beetle outbreak in several decades, due to the ecological significance of the serotinous cone habit of lodgepole pine. Or, cone serotiny may lead to heavy overstocking and may actually delay beetle problems. Since the Sleeping Child fire, lodgepole pine has established itself over nearly all of the burned area, ". . . much of it with a density of tens of thousands of seedlings per acre" (Lotan 1976). In the first year of succession following the fire, lodgepole pine seedlings averaged over 8,500 per acre (Lyon and Stickney 1976).

The mountain pine beetle is now killing millions of lodgepole pine trees in Montana, particularly on the Gallatin, Beaverhead, Kootenai, Lolo, and Flathead National Forests and in Glacier and Yellowstone National Parks; more than 1.4 million acres of forests are infested. There is, however, disagreement over whether these beetle-killed forests will be predisposed to huge forest fires (Kuglin 1980). Some

foresters feel as though "It's like a gasoline tank ready to explode out there" (Kuglin 1980). However, in 1979, concerns that the dead lodgepole could constitute an explosive fire hazard failed to materialize despite an unusually long and hazardous fire season (Schwennesen 1979). Cliff Martinka, research biologist in Glacier National Park, indicates that the relationship between fire and the mountain pine beetle is ". . . more complex than simply having an ignition source and a lot of dead trees" (Schwennesen 1979).

Early observations by Brunner (1917) might be an indication of what could happen on the Flathead and other National Forests where mountain pine beetle-killed trees are so numerous. In 1910 he observed the progress of two serious forest fires burning in beetle-killed timber. The first was in the Little St. Mary region, northeast of Belton, within Glacier National Park, where Douglas-fir had been killed by the Douglas-fir beetle between 1904 and 1910. In the second case, a fire burning in mountain pine beetle-killed (but still standing) western white pine, Pinus monticola Dougl., was so explosive that it jumped the north fork of the Flathead River and burned several sections of timber in Glacier National Park. Brunner's observations indicate that the length of time trees had been killed influence the potential fire danger. He says, "those which had been killed longest, previous to the fire, were burned to snags and those which had been dead but a season had the bark burned off to the very tops."

While National Park Service managers view the mountain pine beetle as just another protected species of wildlife (Kuglin 1980), Forest Service foresters are developing management plans to salvage beetle-killed trees as well as accelerate the harvest of green lodgepole pine. On the Flathead forest alone, 160 million board feet will be harvested between 1980 and 1982. According to Flathead Supervisor John Emerson, "It's time we start managing the beetle instead of letting it manage us" (Emerson 1979). The USDI Fish and Wildlife Service has recently been criticized by wildlife managers and conservationists for ruling that a proposed 22 million board foot salvage sale of beetle-killed lodgepole pine would not jeopardize endangered wildlife species such as grizzly bear and wolves (Schwennesen 1980).

In Oregon, the Forest Service is considering a 21-year, \$133 million project to remove mountain pine beetle-killed lodgepole pine to lessen the chance that a massive fire will cause further economic and aesthetic damage (Baum 1976). Over the 21-year period, potential resource damage and fire suppression costs have been estimated at \$260 million (Western Cons. Jour. 1976); the chance of a large fire is predicted to be multiplied 10 times if the dead tree residue is not removed (Baum 1976). Opponents argue that the expense of the salvage work is unjustified because the mountain pine beetle is nature's way of harvesting overmature trees (Western Cons. Jour. 1976; Baum 1976). It remains to be seen whether bark beetles have predisposed these forests to fire through the creation of some 1.4 million acres of lodgepole pine residue.

Defoliators

Some species of defoliating insects also produce forest residues that either decay and provide humus- and soil-building components, or--it is believed by some--fuel for wildfires. (Like bark beetles, outbreaks of defoliating insects also provide "fuel" for controversy.)

In the northern Rockies and the Pacific Northwest, the two insect species implicated in predisposing forests to wildfires are the western spruce budworm and the Douglas-fir tussock moth; transcontinentally, the entire spruce budworm complex is involved. In all cases, the insect-residue-fire interaction is inextricably related to the political, social, and emotional issues surrounding the use of insecticides.

In Canada Fettes and Buckner (1976) report that the eastern spruce budworm not only kills trees within 3 to 5 years of extreme defoliation--but also increases the threat of vast fires as an aftermath of epidemics. Others have also reported that many major forest fires have been associated with budworm outbreaks (USDA, FS 1975b). Notwithstanding these claims, I am not aware of any situations in the northern Rocky Mountains where either the forest residues created by defoliation or trees killed by the western spruce budworm have predisposed forests to major wildfires (fig. 3).

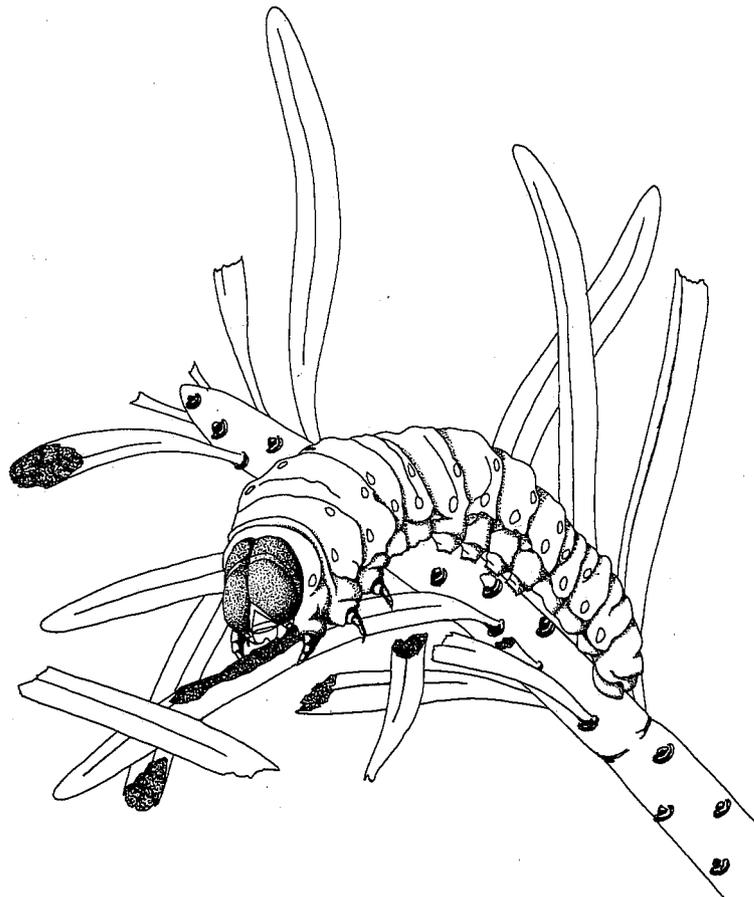


Figure 3.--A western spruce budworm larva feeding on Douglas-fir foliage. Though not substantiated in the northern Rockies, it is reported that many major forest fires have been associated with spruce budworm outbreaks (USDA, FS 1975b).

The large aerial spray programs against the eastern spruce budworm have been justified, in part, by the claim that not to take some kind of direct action would be to risk the development of thousands of acres of dead spruce-fir forests that when blown down could create a tangle, piled like criss-crossed matchsticks, that would not only create a tremendous fire hazard but also would make fire-fighting nearly impossible (Maine Forestry Dept. 1973). It has been said that "while such destruction has occurred historically and nature would in time heal the wounds, the risk in the present context of millions of Americans with all their needs and desires is quite unacceptable" (Maine Forestry Dept. 1973).

Most of us are aware of the controversy generated by using DDT against the Douglas-fir tussock moth in Oregon early in the 1970's. Not so well known are claims that the residues created by that insect predisposed defoliated stands to wildfire. Heavily-damaged stands were reported to be especially susceptible to wildfire (USDA, FS 1975a), and increased fire risk and fire protection costs were listed among the several disadvantages to not using direct control with DDT or other chemicals (Ellefson 1974). In addition to 852 million board feet of merchantable timber killed by the Douglas-fir tussock moth (with a loss value of \$28.1 million), an additional \$30.8 million in losses occurred in the form of damage to immature trees, reduced growth, increased reforestation expense, and increased fire protection costs (USDA, FS 1975a). (One might interpret these as economic losses only if they actually reduced the allowable cut.) Senator Robert Packwood (Oregon) was quoted as saying, "had we used DDT last year, we would not have seen the awesome increase in defoliation and environmental damage leading to increased fire damage in the affected areas that we did" (Crisp 1974). And Oregon's State Forester, Ed Schroeder, estimated that the "total economic impact on Oregon in terms of timber and growth lost, rehabilitation cost, increased fire protection cost, and diminished land value is \$9.5 million." He continued that "the esthetic and recreational appeal has been reduced, because of these forest residues and Oregonians will face increased fire danger for 20 years" (Crisp 1974). Again, as with the mountain pine beetle, it remains to be seen how serious the predisposition of Oregon forests to wildfires has been or will be, as a result of the Douglas-fir tussock moth.

Other Insects

In his unpublished manuscript, Brunner (1917) provides some interesting examples of insects contributing to the predisposition of trees to fire--less dramatic perhaps than the bark beetle and defoliator situations discussed above. He mentions several species of insects that feed in the cambium at the base of trees killing the bark in patches. In such cases, even light surface fires ignite and burn off the dead bark, especially of the resinous conifers, leaving basal wounds, which are often mistaken for fire wounds. He describes one situation where carpenter ants, Camponotus sp., often appropriate tunnels vacated by roundheaded wood borers, Pachyta sp., and ". . ." so honeycomb the bark with their mines as to provide a draft through it for a fire which, on this account, is able to scorch the cambium underneath, even on trees with very thick bark."

Naturally Created Residues

RESIDUES CREATED BY FIRE

As recently as 1970, some researchers long-involved with fire ecology felt there was little knowledge of insect-fire ecology (Komarek 1970). Of the studies in the field of fire ecology that had evolved by the mid 1970's, those dealing with plants and plant by-products predominated almost to the exclusion of any other type (Clayton 1974).

Brown and Davis (1973) remind us that there are so many variables operating on a forest fire that generalizations on specific fire effects can be misleading if taken by themselves. Lyon and Stickney (1976) indicate that most fires are characterized as variable both in pattern and intensity. Further, they say that "only in large, intense wildfires does variability approach a consistent and predictable level. Given such a fire, the crowns of both overstory and understory vegetation are destroyed and the organic mantle is reduced to mineral ash."

Some fire effects are immediately apparent, and others only years later, reflecting both direct, physiological injury to trees and long-term changes in the forest environment (Brown and Davis 1973). When a fire passes through an area, it can radically alter both plant and animal elements, not only by direct kill but also through sudden changes in food, shelter, competition, light, territoriality, reproduction, radiation input and other factors (Komarek 1967).

Fires also may destroy habitats for natural enemies of insects, at times allowing populations of some insect species to thrive after burns (Ahlgren and Ahlgren 1941) (fig. 4). In a study of woodpecker populations in a Douglas-fir/yellow pine forest near Libby, Montana, Blackford (1955) found three species of woodpeckers-hairy, Dendrocopos villosus, black-backed, Picoides articus, and three-toed-, P. tridactylus, and red shafted flickers, Colaptes cafer, had locally fluctuating populations that were greater on a burned area than on unburned areas. One year following the burn, however, he was not able to find even one woodpecker. In another study, wood borers persisted in burned areas because charcoal, ashes, and related fire debris deterred potential competitors and natural enemies (Linsley 1943).

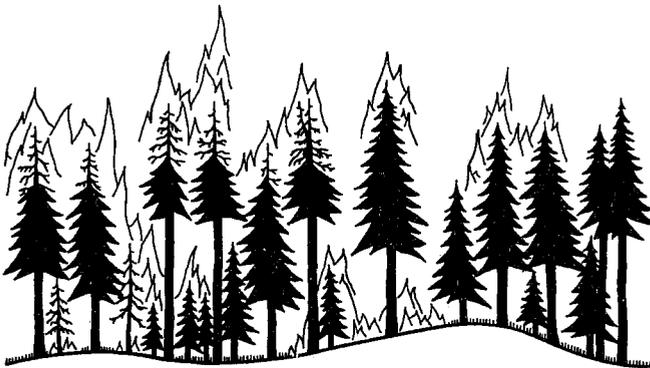


Figure 4.--Wildfires in undisturbed forests often create residues predisposing stands to a variety of insect species. Wildfire alters both plant and animal habitat as well as habitats for the natural enemies of insects, at times allowing some insect species to thrive following the fire.

Weakened living trees, or trees killed and reduced to residue by fire, provide a medium in which insects and disease can thrive (Ahlgren and Ahlgren 1941) and cause deterioration of the fire-created residues. The relationships between forest fires and disease or insect attack ". . . are exceedingly widespread, common and also complex" (Brown and Davis 1973), and are considered by some to be so intimately connected in causing deterioration of residues that they should be considered in combination rather than separately (Kimmey 1955; Kimmey and Furniss 1943).

Fire-Created Residues Predisposed to Diseases

The most comprehensive study of diseases in fire-created residues was conducted by Wallis and his colleagues (1971); they studied rate of decay in Douglas-fir, western hemlock, Tsuga heterophylla (Raf.) Sarge, and western redcedar, Thuja plicata Donn., after a wildfire, the Taylor River burn, in British Columbia. Three years after the burn, the upper bole of Douglas-fir, 8 inches and less in diameter, was of little economic value and 12 percent of the volume was decayed. Five years later, nearly all of the sapwood was decayed and significant deterioration of the heartwood had begun. By 7 years, salvageable material was usually limited to the lower bole and deterioration was complete after 11 years. They found no correlation between the extent of sap rot and insect attack in these three tree species 29 months after the fire.

The rate of deterioration in western hemlock and western redcedar differed from that in Douglas-fir. Deterioration of western hemlock progressed faster; nearly 3 months following the fire, 24 percent of the volume was decayed. In western redcedar, although some blue stain was found in most samples, no loss due to visible decay was present 3 years after the fire. Wallis and others (1971) concluded that fungal deterioration of mature, fire-killed western redcedar may not be significant for many years beyond that reported for Douglas-fir.

There were two reports in the 1930's of decay associated with fires. Three years after the Great Tillamook burn in Oregon in 1933, salvage of western hemlock was halted because of advanced decay and associated insect activities (Furniss 1937a). In an earlier study, investigators found that in the first year following a wildfire, the sapwood of Douglas-fir was stained by a fungus (Ascomycetes) that destroyed cell contents rather than wood fiber (Beal and others 1935).

Fire-Created Residues Predisposed to Insects

As a result of his research work with bark beetle problems in the northern Rockies in the early 1900's, Brunner (1917) wrote that "there is a current belief that outbreaks of serious insect devastations frequently follow in the wake of fires." He maintained that, in his opinion and that of his associates, this tenet cannot be maintained when subject to: 1) the "acid test" of careful observation, 2) a knowledge of the habits of the insects and 3) information concerning insect conditions prior to the occurrence of fires. He says that, "heavy killing near a burn after a fire . . .", usually taken as proof that the fire started the invasion, ". . . is but a centralization of an invasion which was already in existence before the fire occurred." Not only did he believe that serious invasions are not dependent on fires, but, in fact, that ". . . fire may be the means to end an impending infestation or at least to keep the killing of timber by the beetles at a nominal figure for many years."

In the more than 60 years since Brunner conducted his research, many investigators have reported on the interaction of fire and the predisposition of forests to a wide variety of insect species, principally bark and cambium beetles, wood borers, wood wasps, and other groups of lesser economic importance.

Bark and cambium beetles.--In the northern Rockies and other areas in the western United States, wildfires have predisposed forests to several species of bark and cambium beetles. In most cases, bark beetles, while present in large numbers, cause no direct damage (Gardiner 1957); they do, however, permit the entrance of wood-staining fungi that cause limited deterioration--changes affecting the original character of the wood but with the wood still being suitable for use as low-grade lumber--(Kimmey and Furniss 1943; Furniss 1937b).

The increased susceptibility of fire-injured Douglas-fir to the Douglas-fir beetle is probably the most notable example in the northern Rockies of fires predisposing forests to bark beetles. In a study in southern Idaho, Furniss (1965) found 70 percent of the trees on a burned area had been attacked within 1 year after the fire, but decreased abruptly with outright fire kill. The larger trees and those with most severe fire damage to the crown and cambium had the highest incidence of beetle attacks; however, trees killed by fire were less frequently attacked.

Elsewhere in the West, particularly in Oregon, the Douglas-fir beetle is the most important and abundant bark and phloem feeder in Douglas-fir predisposed by fire (Furniss 1937b; Kimmey and Furniss 1943). Beetles not only attack most of the fire-killed trees, but also scorched trees that survive the fire (Furniss 1937b), and at times healthy green trees surrounding the burn (Kimmey and Furniss 1943). Following the great Tillamook fire of 1933, many of the dead trees on the burn were attacked by that fall, more were attacked the following summer, and by the end of 1934 nearly all of the dead trees were infested by at least a few beetles (Furniss 1937a). Douglas-fir beetle populations developed in the scorched trees on that burn and killed some 200 million board feet of green timber in adjacent forests (Furniss 1941).

Following wildfires, tree killing of ponderosa pine by the western pine beetle, Dendroctonus brevicomis Leconte, usually increases (Craighead 1925; Connaughton 1936; Stevens and Hall 1960) and is often catastrophic (Miller and Patterson 1927; Salman 1934; Miller and Keen 1960). Although mortality of fire-injured trees varies with the amount of damaged cambium and foliage (Salman 1934), trees most often attacked are usually those that have lost more than 50 percent of their foliage (Miller and Patterson 1927; Salman 1934). At other times, trees with light-to-medium fire injury attract more beetles than other trees in burned areas (Miller and Patterson 1927), and trees attacked are those that appear most likely to survive the fire. Fire-killed trees are not attractive to the western pine beetle (Furniss and Carolin 1977).

Most western pine beetle attacks in trees predisposed to fire occur during the first season after the fire (Miller and Patterson 1927), often accompanied by a decrease in the number of beetle attacks in the surrounding forest (Craighead 1925). Post-fire tree killing usually goes on at epidemic levels in the burned areas for 2 or 3 years (Miller and Keen 1960) and then wanes after 3 years (Connaughton 1936). The decline of attacks in burned areas has been attributed to high mortality of beetle broods (Craighead 1925). The cessation of beetle activity in the burned areas is often accompanied by an increase in beetle activity in the surrounding forest (Miller and Patterson 1927), often developing into outbreaks in the nearby green timber (Stevens and Hall 1960). With prescribed fire, the season when the burning is conducted is an important factor influencing the occurrence, the duration, and severity of beetle attack on fire-weakened ponderosa pine (Fischer In press).

The mountain pine beetle also is attracted to fire-killed or weakened western pines (Jaenicke 1921; Stevens and Hall 1960); in some cases beetle infestations are reported to have increased as much as 1,000 percent after "light burning" (Jaenicke 1921). More recently, Cronin and Gochnour (In Press) report two instances of increased activity of the mountain pine beetle following fire on the Kootenai National Forest in northern Idaho. They found: 1) a higher percentage of burned trees-- lodgepole, ponderosa, Pinus ponderosa Laws., and western white pine--successfully attacked than trees that were not burned, and 2) that the larger diameter trees were more often successfully attacked. Craighead (1925) reported that the mountain pine beetle was not attracted to fire-scorched trees.

A few other species of bark beetles are attracted to pines predisposed by fire. Sizeable populations of the red turpentine beetle, Dendroctonus valens LeConte, are often associated with fire-scorched trees (Eaton and Lara 1967) and can hasten the mortality of severely defoliated trees (Herman 1950).

Southern pines injured by fire are also very attractive to bark beetles, resulting in concentrations of beetles in scorched trees, as well as the killing of live green trees surrounding burns (Beal and Massey 1945).

In addition to the bark beetles discussed above, at least one species of engraver beetles (fig. 5) is associated with trees predisposed by fire to attack. In the northern Rockies, the pine engraver beetle, Ips pini (Say), at least during years of limited activity, not only confines its activities to slash but also to the ". . . tops of mature trees and smaller groups of standing saplings-and pole size trees that often have been damaged by the fire or broken off by wind or snow" (Schmitz and Taylor 1969). Ips beetles are also becoming an increasingly important problem in connection with prescribed fire. If flame length is not carefully managed, crown scorch predisposes small, pole-sized ponderosa pine to attacks by pine engravers (personal communication with William C. Fischer).

The discussion above describes the predisposition of burned forests to bark and cambium beetles through the weakening, scorching or killing of standing trees, usually in mature forests. Fires may also predispose forests to bark beetles in an indirect way when dense forests of a fire-associated species, such as lodgepole pine, regenerate on the burned areas and become "beetle-susceptible" several decades later (Lotan 1976).

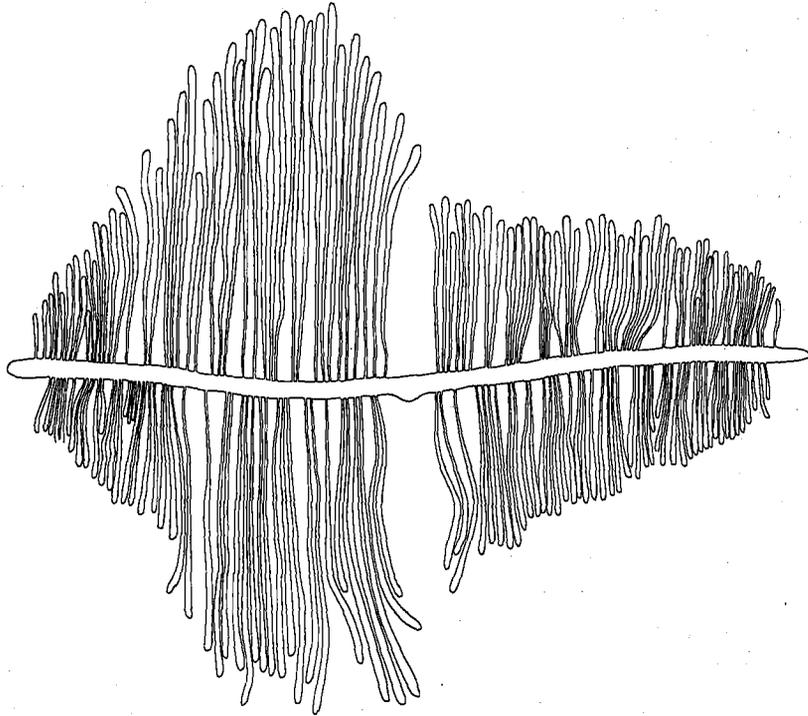


Figure 5.--Egg and larval galleries of the fir engraver *Scolytus ventralis* Leconte. Though not characteristically associated with trees and stands predisposed by fire, this engraver infests trees infected with root rot fungus and trees defoliated by the Douglas-fir tussock moth. The engraver also breeds in slash and windthrown trees (Furniss and Carolin 1977).

Wood borers.--In the Rocky Mountains and elsewhere in the West, wildfires create a residue of dead and dying trees that are often predisposed to a variety of wood-boring insects (Wallis and others 1974). Infestations of wood borers have been reported in, for example, (1) burned forests of Douglas-fir and ponderosa pine in California (Miller and Patterson 1927); (2) fire-killed pine in Ontario (Gardiner 1957); and (3) in fire-killed white spruce, *Picea glauca* (Moench) Voss, in Saskatchewan (Ahlgren and Ahlgren 1945). Most wood borers found in fire-killed conifers are "secondary" forms usually incapable of causing the death of the host; they usually infest only dead or dying trees (Gardiner 1957). The severity of attack by boring insects varies with the period of flight activity; due to the drying and subsequent detachment of bark, the further in time the fire is removed from the flight period the less severe the attacks (Buttrick 1912).

The galleries, or mines, of wood borers can seriously degrade some products, primarily peeler grade logs, but seldom become abundant enough to cause cull before fungi render the wood useless for lumber (Kimmey 1955). Wood borers related directly to the general deterioration of wood in fire-killed trees by providing entrance holes and galleries through which decay fungi can gain direct and early access to woody tissues (Basham 1956; Gardiner 1957; Stevens and Hall 1960; Wallis and others 1974).

"The most destructive wood borers belong to two families of beetles: the roundheaded borers and the flatheaded borers. Both groups contain a great many species, some of which are attracted to fire-killed timber even before the fire is out" (Stevens and Hall 1960).

Roundheaded wood borers (Cerambycidae).--Several species of beetles in this group attack sound heartwood, often of fire-killed or weakened trees. Roundheaded borers are usually the most important insects to consider in determining the salvability of fire-injured trees (Kimmey and Furniss 1943). Most heartwood damage to fire-predisposed trees is caused by a large roundheaded borer, Ergates spiculatus Leconte (Beal and others 1935). Beetles of this species usually do not become abundant in fire-killed trees until 5 or 6 years following the fire; beetle attacks continue as long as the wood remains sound (Kimmey and Furniss 1943).

The roundheaded borer, Criocephalus productus Leconte, causes considerable damage to the heartwood of Douglas-fir predisposed by fire (Kimmey and Furniss 1943). Adults of this group attack trees the first year after a fire (Kimmey and Furniss 1943), often while the trees are still smoldering (Furniss 1937b). By the third or fourth year after a fire, beetle larvae usually have not penetrated the heartwood of trees of average to large size, but in the smaller-to-medium-sized fire-killed trees, these borers will have done considerable damage (Furniss 1937b). Another borer, Leptura obliterated, along with several other wood-boring species and their associated fungi, destroy the sapwood and attack the heartwood of some conifers in the third year after fire has predisposed them to attack (Beal and Kimmey 1935).

Roundheaded wood-boring species of the genus Monochamus also damage fire-killed conifers by excavating tunnels into the heartwood usually after feeding for a time on the inner bark and outer layers of sapwood (Gardiner 1957). In a study of Monochamus damage to three species of fire-predisposed pine--eastern white pine, red pine, and jack pine, Pinus banksiana Lamb.,--Gardiner (1957) summarized: 1) the effect of the fire on wood borer damage varies with the tree species; 2) the severity of the burn governs the spread and nature of the attack; 3) the severity of the burn, which influences the attack pattern, indicates when trees should be harvested. In British Columbia, Monochamus oregonensis Leconte damage fire-killed white spruce (Ross 1960), and in New Hampshire M. scutellatus Say attacks spruce as severely as it does pine (Bess 1943).

Flatheaded wood borers (Buprestidae).--Probably the most notable flatheaded borers associated with fire-predisposed conifers are various species of the genus Melanophila, or metallic wood borers (fig. 6). Although living, uninjured green trees are either resistant to (Linsley 1943) or not killed (Furniss 1937b) by Melanophila, these beetles are definitely attracted to trees predisposed by wildfire (Evans 1966, 1971).

Perhaps the most interesting relationship between beetles in the genus Melanophila and fire-predisposed trees is how the insects are attracted to the fire. Some investigators feel that these beetles are attracted by volatile materials associated with smoke (Linsley 1943). Recent studies indicate that they are attracted to heat (Evans 1971), because heat is always a directional stimulus but smoke is affected by wind and is soon dissipated. Melanophila beetles apparently are able to detect

infra-red radiation for a distance of several miles through paired sense organs on the mesothorax (Evans 1964; Boag and Evans 1967); the organs are so sensitive that extraneous radiation from sources outside of the temperature range of wildfires is effectively filtered (Evans 1966). This feature allows Melanophila to be among the first insects to reach fire-killed trees--usually before competitors--and has resulted in the Holarctic distribution of at least one species, M. acuminata (Evans 1971). Buprestids of the genus Melanophila are known in some areas of North Carolina as "fire bugs," and have been observed landing on stumps that were still glowing (Linsley 1943). Another flatheaded borer, Asemum atrum Esch., infested the sapwood of the majority of fire-killed trees on the Great Tillamook burn in Oregon in 1933 (Furniss 1937b).

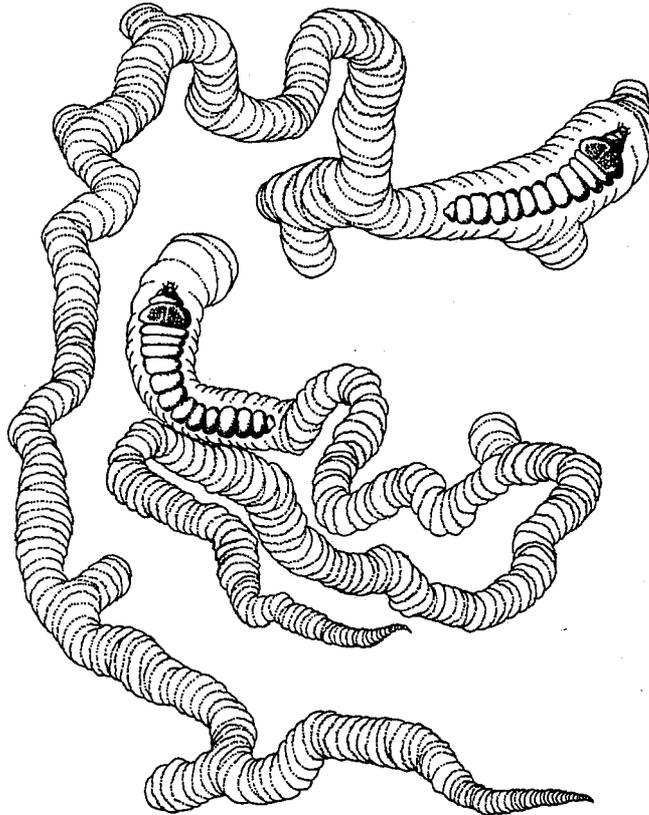


Figure 6.--Larvae and galleries of the flatheaded fir borer, Melanophila drummondi (Kirby). This species frequents fire-killed or otherwise injured trees. Larvae bore into the inner bark forming very characteristic frass-packed galleries.

Other wood borers.--Several species of ambrosia beetles, or pinhole borers, are associated with conifers predisposed by wildfire to beetle attack. Usually restricted to the sapwood, ambrosia beetles begin the process of wood deterioration (Beal and others 1935) through a combination of their galleries and an associated staining fungus (Kimmey and Furniss 1943); these beetles usually do not make wood completely useless (Furniss 1937b). In Colorado, some Engelmann spruce trees killed by the Engelmann spruce beetle showed evidence of ambrosia beetles, but most of the defect caused by these borers in the sapwood was removed with the slabs when the trees were cut into lumber (Mielke 1950).

Wood wasps (Siricidae) are also attracted to fire-killed trees, and may often severely damage the outer heartwood (Wallis and others 1971) (fig. 7). Siricids, along with roundheaded borers, produce larger holes than ambrosia beetles and are usually of more economic concern, even though their populations in the same tree may be lower. If lumber cut from fire-salvaged trees is not kiln-dried, siricids may emerge after the product is in use (Wallis and others 1971).

Other insect species.--Besides the more abundant and economically important bark beetles and wood borers, wildfires in coniferous forests attract a variety of other insects, some predatory, some scavengers (Boag and Evans 1967). Many species are attracted to fires by smoke and heat (Evans 1971); among those reported to be associated with fire are three species of Empidid or Platypezid smokeflies--Hermopezasp, and Microsania occidentalis (Komarek 1969) and M. imperfectus (Snoddy and Tippins 1968).

RESIDUES CREATED BY WINDTHROW

Windthrow represents a natural and often catastrophic event that, like wildfire, predisposes coniferous forests to insects and disease by creating tremendous amounts of residues. Throughout the West, as well as elsewhere on the Continent, several species of bark beetles and wood borers are known to degrade downed timber resulting from windthrow, and to threaten standing timber after breeding in the downed residues (Wickman 1965).

All known major outbreaks of the Douglas-fir beetle in western Oregon and Washington have been triggered by severe forest disturbances, particularly by residues created from extensive blowdown during storms (Wright and Harvey 1967). During the winters of 1949-1950 and 1950-1951, wind storms blew down some 10 million board feet of sawtimber and in the following 3 years another 3 billion board feet of standing timber were killed by beetles (Wright and Lauderbach 1958). A windstorm of hurricane force struck the Pacific Northwest on October 12, 1962, and in northern California alone blew down nearly a billion board feet of coniferous timber. Wickman (1965) caught, reared, or trapped at least 46 different species of insects degrading wood of those windblown trees. Species of Melanophila were the most numerous wood borers, and several species of Ips and Dendroctonus were the most common bark beetles. As a result of that storm, Douglas-fir beetles attacked injured trees (those felled, broken off or leaning), and then spilled over into live surrounding trees (Johnson and Belluschi 1969).

Windthrown ponderosa pine--as well as logging residue--is also predisposed to attacks by the western pine beetle (Mitchell and Sartwell 1974). Usually there is little population increase in such residues (Patterson 1927; Beal 1935), however, and over the course of many years residue-associated beetle damage has been rather minor.

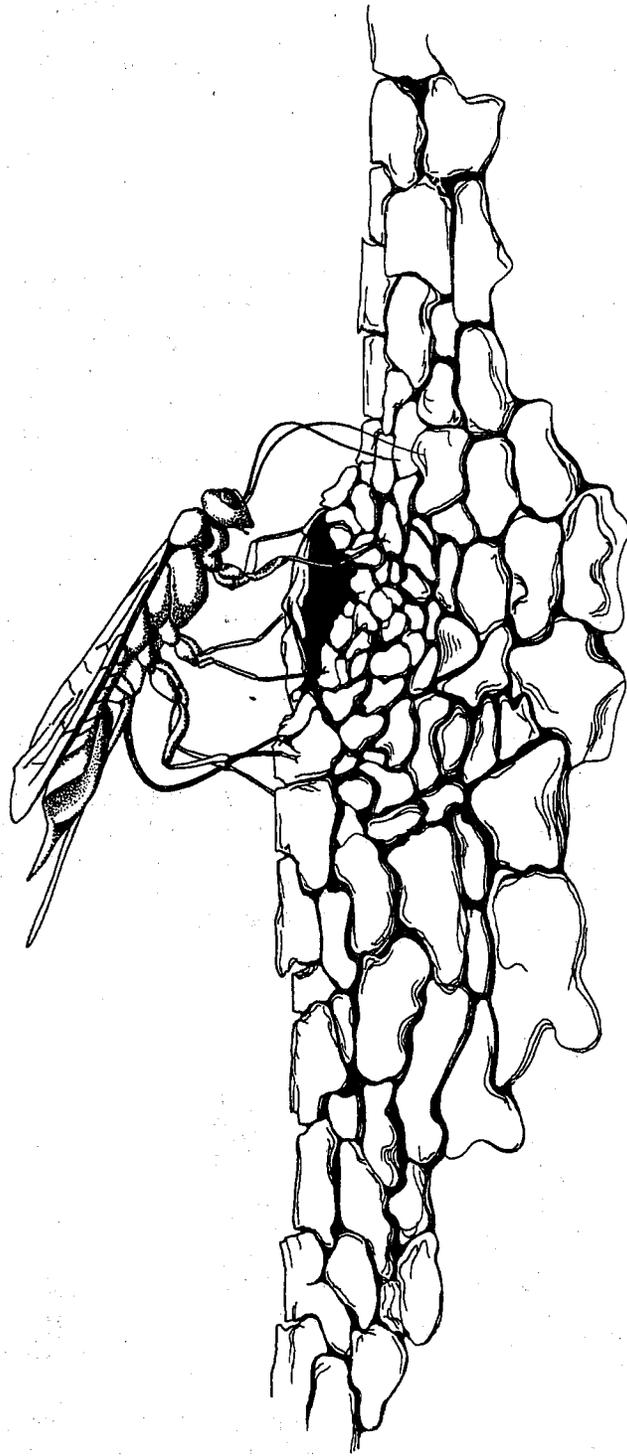


Figure 7.--An adult horntail (Siricidae) laying eggs in fire-killed tree. Eggs are layed deeply into the wood through the long, flexible ovipositor of the female. At times they are unable to extract their ovipositor from the wood and die in this position. Adult horntails are known to emerge from dimension lumber cut from fire-killed trees, at times creating emergence holes in walls, floor, and ceilings (Furniss and Carolin 1977).

Deterioration of spruce (*Picea* spp.) and jack pine blowdown in northern Ontario between 1969 and 1972 was caused by several species of wood borers, especially *Tetropium* spp. and sawyer beetles, *Monochamus* spp. (Gardiner 1975). Milling studies showed a 10 to 20 percent loss in all material combined, 1 and 2 years after the storm. In this case, trees left standing after the storm were not attacked due in part to rapid salvage of the windthrown material as well as the attraction of emerging beetle populations to fresh breeding material provided by further blowdown (Gardiner 1975).

In the central Rocky Mountains, major outbreaks of the Engelmann spruce beetle have generally been associated with residues created by windthrow, as well as residues created by logging (Massey and Wygant 1954; Schmid and Beckwith 1972). A severe wind storm in Colorado in mid-June of 1939 blew down groups of Engelmann spruce in which comparatively large populations of the Engelmann spruce beetle subsequently developed. Beetles spread from the windthrow residue to the surrounding forests, and by 1948, 4 billion board feet of spruce timber had been killed (Mielke 1950).

Perhaps the most notable occurrence of windthrown forests creating residues predisposed to insects in the northern Rocky Mountains involved the Engelmann spruce beetle. During the fall of 1949, hurricane-force winds whipped through northern Idaho and northwestern Montana, transforming countless stands of Engelmann spruce into large volumes of spruce residue. Severe epidemics of the spruce beetle developed in much of this downed timber during 1950 and 1951, spreading in 1952 to standing spruce throughout most of the Engelmann spruce timber type in the northern Rockies (fig. 8). As a result, approximately 2.5 billion board feet of spruce timber was attacked by this beetle between 1952 and 1956 (Tunnock 1959). During this same period, the forest management plan was modified on several national forests as thousands of acres of spruce forests were clearcut in northern Idaho and western Montana to salvage damaged and/or beetle-killed trees, both standing and windthrown. The outbreak steadily declined following its peak in 1953; by the late 1950's no infestations were reported in many forest compartments.



Figure 8.--Besides fire, windthrow is another natural and catastrophic agent that creates residues and predisposes forests to insects. In western Montana, between 1952 and 1956, 2.5 billion board feet of green spruce timber was killed by beetles developing in residues created by hurricane-force winds in 1949.

There are at least three interesting and significant residue management implications related to this Engelmann spruce beetle outbreak; the first involved the utilization of these wind- and beetle-created residues. While foresters were struggling to remove the standing and downed residual trees before they deteriorated too badly, several species of woodpeckers--known to increase their numbers in such outbreaks (Yeager 1955)--were feeding on the beetles in the infested standing trees. However, to reach the beetles in the cambium, the woodpeckers removed large quantities of the scaly bark. This accelerated checking and substantially reduced the period of time that residue trees could be salvaged for sawtimber (Fellin 1955). A similar instance was reported from the Gaspè Peninsula in eastern Canada, where beetle-killed spruce dried more rapidly when woodpeckers removed the bark in search of beetle larvae (Riley 1940).

The second residue management implication was both biological and socio-political; at issue was whether the removal of beetle-infested trees from the forest would effect some control--assuming that the beetles were still present in the trees--or would the removal be strictly a residue-salvage situation. This was an exceedingly volatile issue because forest pest "control" funds were available for access and removal of trees that were still beetle-infested, but not to remove the residue or salvage the trees.

One of the most controversial Engelmann spruce stands was in Bunker Creek, a roadless area about 15-20 miles from the Spotted Bear Ranger Station and contiguous to the western edge of the Bob Marshall Wilderness. Proponents argued that a road must be built to remove the beetle-infested trees; opponents argued that whether the trees were infested or not, a road in that area would jeopardize the wilderness. I personally spent 15 days in that forest in 1956 with a bark beetle survey crew. We determined that, in fact, the standing trees, though they had been infested, were now residue; and the beetles were gone. As a result of our survey findings, pest "control" funds, though requested, were not authorized to access those beetle-killed spruce. In 1971, 15 years later, a road was built and Bunker Creek was made accessible. The Engelmann spruce beetle residues were salvaged and ended up at the Hoerner-Waldorf pulp mill in Missoula, Montana. Payne (1969), in discussing the role of politics in the coniferous forests, cited the Bunker Creek controversy as a classic example of how pressure and political groups are involved in the management decisions in northern Rocky Mountain forests.

The Engelmann spruce windthrow illustrates a third implication of residue management: how our forest insect and disease problems change as old-growth forests are converted to stands of young trees. As the Engelmann spruce beetle problem diminished with the logging of progressively more mature and over-mature spruce during the past two decades, an increasing number of clearcuts have been planted to, or have naturally regenerated with, young Engelmann spruce. Damage to these young trees by the Engelmann spruce weevil, *Pissodes strobi* (Peck) (= *engelmanni* Hopkins) has steadily increased. These small weevils attack and kill or seriously injure terminal shoots of young trees, causing crooks in the trunk or a stunted, forked, and worthless tree (Keen 1952). By 1966, terminals destroyed by weevils were noticeable in most stands of spruce reproduction in the Northern Rockies; some were recurrently damaged (Tunnock 1966). By 1971, the weevil was distributed throughout young spruce stands in this region (McGregor and Quarles 1971) and terminal killing was prevalent in many areas. In some young trees, repeated attacks to live portions of the main bole killed the trees outright, or predisposed them to death by secondary insects. "In some areas," according to McGregor and Quarles (1971), "large blocks of young even-aged spruce offer ideal conditions for buildup and maintenance of weevil populations." No doubt this weevil will continue to be a serious problem in the management of young Engelmann spruce in the Northern Rockies.

The eruption of Mount Saint Helens has raised fears of windthrown residues predisposing forests to insects. High winds accompanying the 18 May 1980 eruption blew down millions of board feet of Douglas-fir timber growing on the mountain. Foresters are now worried that the downed residues may become infested with the Douglas-fir beetle, which may then spread to standing healthy trees farther from the mountain. Frank Kopecky, deputy regional forester in Portland, Oregon, says that the beetles could become "a major problem" in two or three years (Missoulia 1980).

RESIDUES CREATED BY OTHER AGENTS

Lightning may predispose trees and forest stands to insect attack when the struck trees do not ignite and burn. In the northern Rockies, Schmitz and Taylor (1969) document an instance where a 79-foot-tall, 24-inch-diameter (24 m, 0.6m) tree struck by lightning was infested along its entire length by bark beetles--the upper two-thirds by the pine engraver beetle, the mountain pine beetle at near mid-bole, and the western pine beetle and a pine engraver in the lower bole. Moreover, 76 percent of the immature trees within 80 feet (24.3 m) of the struck tree were attacked and became infested with pine engraver beetles (fig. 9). Schmitz and Taylor (1969) speculated that the infested trees surrounding the lightning-struck tree suffered lightning damage to their roots, predisposing them to pine engraver beetle attack. Schmitz (personal communication) believes that a lightning-struck tree is probably the most attractive of what we call "weakened" trees.

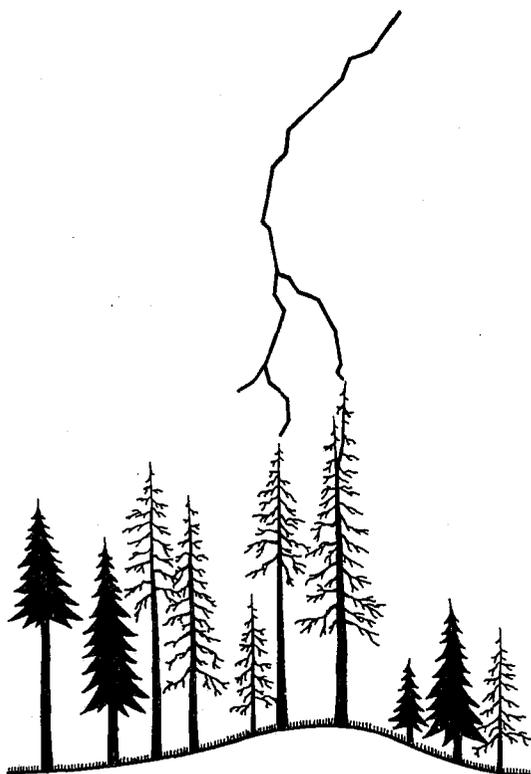


Figure 9.--Lightning, in addition to igniting fires predisposing forests to insects, often predisposes struck trees (when not ignited) and those surrounding them to various species of bark and engraver beetles. In the opinion of Dr. R. F. Schmitz (personal communication), lightning-struck trees are probably the most attractive to some insect species of those trees we call "weakened", by one cause or another.

In the South, the southern pine beetle, Dendroctonus frontalis (Zimm.), and Ips spp. are attracted to lightning-struck trees. Hodges and Pickard (1971) believe that lightning strikes are important in sustaining populations of the southern pine beetle. Hetrick (1949) has presented evidence that only when there is electrical injury to the roots of pines are the trees attacked by the southern pine beetle; electrical injuries confined only to the tops and trunks of trees are not followed by beetle attacks. In the West, Hopping (1925) found fire-scarred or lightning-struck pines to be more susceptible to insect attack than trees weakened by fungi or mistletoe.

Residues Created by Man

In the northern Rocky Mountains, the most significant forest insect problems associated with forest residues created by man's activities have developed as a result of precommercial thinning, particularly in species of pine. Probably the most widespread problem involves pine engraver beetles in ponderosa pine thinning slash.

In many cases, populations of engraver beetles, Ips spp., develop in thinning residue, often depending on the time at which residue is created. In the Northern Region (Tunnock, personal communication) as well as in the Pacific Northwest (Sartwell 1970; Mitchell and Sartwell 1974), thinning slash-residue deposited in the spring and summer is particularly attractive to engraver beetles. But if the material is thinned earlier, in March for example, the residue is unattractive by the time Ips begin flying.

Whether or not Ips broods that develop in the thinning residue "spill over" and infest crop trees or green trees in adjacent unthinned forests usually depends on the weather. If there has been a so-called "wet spring", residual crop trees are usually not infested. However, if the spring has been "dry", particularly during April-June, there will usually be significant mortality to residual trees. This latter situation has occurred in the northern Rockies, most recently in 1977. Also in the Pacific Northwest, residual trees are killed when drought accompanies thinning slash that is heavily infested with Ips engraver beetles (Dolph 1971).

In nearby Alberta, "flash insect outbreaks in lodgepole pine stands frequently result from the breeding of certain bark beetles..." (primarily several species of Ips) in slash remaining after logging operations (Reid 1955).

Graham (1922), in discussing insects that breed in residues and consequently are potentially injurious to standing green timber, cites Ips pini Say as a species that occasionally kills a few trees. Says Graham (1922): "...this species only kills living trees when it occurs in such large numbers that the attacked tree is quickly girdled, thus stopping the flow of resin."

Besides engraver beetles, some bark beetle populations develop as a result of residues created by man. In 1970 and 1971, populations of the Douglas-fir beetle built up in residues resulting from clearing operations associated with the construction of Dworshak Dam near Orofino, Idaho. Between 1972 and 1975, 111 million board feet of standing Douglas-fir were killed in forests adjacent to the reservoir (McGregor and others 1974).

In the interior of British Columbia, infestations of the Douglas-fir beetle are usually found where excess residue had been produced by logging operations, as well as in overmature stands (Walters and Graham 1952).

Bark and engraver beetles infesting thinning and logging residue are only a few of a series of insect species that successively inhabit and feed on slash and other forest residue until the wood has disintegrated completely (Adams 1915; Savely 1939). Thomas (1955) lists a series of four groups of arthropods that successively infest red and white pine logging slash: 1) bark beetles, 2) borers and weevils of the families Cerambycidae, Buprestidae, Pythidae, and Curculionidae, 3) parasites, 4) predators entirely dependent for food on the presence of insects in the first two groups.

In addition to bark and engraver beetles, thinning and logging slash predisposes forests to other types of forest insects (fig. 10). In Montana, Fellin and Schmidt (1966) observed a very close relationship between residues created by thinning young lodgepole pine stands and infestations of a needle-eating weevil, Magdalis gentilis Leconte. Although they were apparently neither feeding on or breeding in the residue, weevils were attracted to the thinned stands and fed on current year needles of crop trees, often resulting in a loss of 75 to 100 percent of the foliage. Fellin (1973) found that time of thinning was significant in determining whether these crop trees would be infested; when residues were not created before late July to mid-August, Magdalis infestations did not develop. In 1974, Magdalis populations were attracted to lodgepole pine thinning slash throughout 700 acres in the Moose Creek drainage of the Lewis and Clark National Forest in west-central Montana. There was heavy defoliation of the 1974 growth in most areas; in some stands 100 percent of the new growth was destroyed (Hamel and McGregor 1974).



Figure 10.--Although fire, windthrow, and other natural factors create substantial amounts of residue, predisposing forests to insects, man--through his own management actions--also creates vast amounts of forest residue through logging slash, precommercial thinnings, etc., predisposing forests to a wide variety of insect species.

In red pine stands in Ontario, Magdalis perforatus causes damage to young trees as a result of adult feeding, but population increases are usually related to pruning operations or mortality in young stands and not to thinning in older stands (Martin 1965).

In the Southeast, other species of weevils are influenced by forest residues, including stumps, also depending on when timber is harvested. In east Texas, Thatcher (1960) determined a relationship between the season in which pines were cut and emergence of the pitch-eating weevil, Pachylobius picivorus (Germar). Later, Speers

(1974) determined that the time of year in which timber is harvested affects the severity of killing of pine seedlings by both the pitch-eating weevil and the pales weevil, Hylobius pales (Herbst). In pine cuttings made after June and through the summer and fall, older weevils were attracted to the fresh stumps, from which they emerged to attack newly winter-planted seedlings.

Residues created by pruning in red pine forests also have been associated with populations of the pine root collar weevil, Hylobius radialis Buchanan, but were related to a decrease, rather than an increase, in populations and damage (Wilson 1967). Based on his previous research (Wilson 1966), and behavioral studies with the weevil, Wilson pruned the lower 3-5 whorls of branches from young red pines. This pruning, along with duff removal and soil scraping, allowed heat and light to penetrate the normally cool, dark daytime habitat of the weevil, reducing larval populations below an economic level for at least 1 year (Wilson 1967). Branch pruning to snow depth also has been reported (Miller 1967) to adequately and permanently control populations of the European pine shoot moth, Rhyacionia buoliana (Schiff).

The sequoia pitch moth, Vespamima sequoiae Hy. Edw., which infests pruned conifers, provides an interesting example of forest residues predisposing trees to insects through intense cultural practices. Fresh pruning scars, often associated with fuel-break pruning (Powers and Sundahl 1973), and associated resin flow where the living limbs are attached, attract the pitch moth (Weidman and Robbins 1947). Pitch moth attacks cause an additional accumulation of pitch, but larvae and pupae both tolerate it and are not drowned in the excessive amount of pitch exuded by attacked trees (Weidman and Robbins 1947). Although pitch moths usually do not kill trees, their attacks may weaken trees and render them more susceptible to bark beetles, Dendroctonus and Ips (Weidman and Robbins 1947). Aesthetic changes in trees, resin masses, and flowing pitch, may be the most important consequences of pitch moth attacks (Powers and Sundahl 1973). Pitch moths are also attracted to the large flow of resin at sapsucker drillings (Weidman and Robbins 1947) and to the wounds in the tree boles resulting from increment borings made by the investigators (Powers and Sundahl 1973).

In the stumps and slash of thinned red pine in Ontario, Martin (1965) found three groups of insects of potential economic importance--wood borers, bark beetles, and weevils. Although the wood borers are usually economically important because they downgrade sawn products, the red pine thinnings in this case were used for pulp, and wood borers were not of particular importance. One species of weevil, Pissodes approximatus, breeds in stumps, slash, logs, and dead standing trees; in Martin's study, this species killed many trees that may otherwise have survived drought, disease, planting shock, or other factors. Martin (1965) found that insects avoided or were not successful in establishing themselves in living stumps that were root-grafted to living trees.

In eastern Canada, many balsam fir trees damaged by the eastern spruce budworm are reportedly killed by the secondary attacks of the balsam bark beetle, Pityokteines sparsus Leconte. More trees are killed by the beetle in logging areas, indicating that logging residues are associated with an increase in beetle activity, since fewer trees were killed by beetles in areas where both logging and slash were absent (Graham 1922). In many areas of Montana and Utah, populations of Pityokteines and Pityogenes build up in logging and thinning slash, then move to the tops and branches of large residual ponderosa pine. In some areas, nearly every branch is attacked during the year when residues are created, with some branch killing the following year. Populations appear to wane after the second year.

In the northern Rockies, one conifer with minimal residue-insect problems, is western larch, Larix occidentalis Nutt. Though standing, live western larch has essentially no bark beetle (Dendroctonus) problems, long-butt residues are attractive to and suitable as a breeding substrate for the Douglas-fir beetle (R. F. Schmitz, personal communication).

HARVESTING PRACTICES INFLUENCE BEHAVIOR AND IMPACT OF FOREST INSECTS

Many species of forest insects are known to be influenced by the environmental changes brought about by silvicultural and stand management practices such as thinning, overstory removal, clearcutting, and prescribed burning. The ecological consequences of all types of cuttings--but especially clearcutting, which has been most intensively and most widely employed in coniferous forests of the northern Rocky Mountains--are incompletely or only partially understood and are the subject of increasing attention and debate. Changes in the forest alter micro (and macro) meteorological conditions such as light, wind, temperature (air and soil), evapotranspiration rates, and in turn affect nearly all flora and fauna either by outright killing of some plants or animals or by altering the environment, resulting in a modification of the behavior of the organism. The combined influence of all or some forest manipulations usually increases or decreases most species of forest insects by influencing the food supply, shelter, competition, vulnerability to predation, reproduction, and other behavioral habits, such as oviposition, dispersal, and feeding (fig. 11).

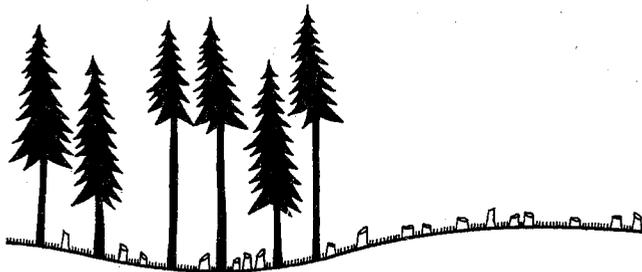


Figure 11.--A shelterwood and a clearcut with intensive residue utilization (mechanically removed). These harvesting practices, coupled with intensive fiber utilization, have varying effects on the behavior and impact of a variety of flying, surface, and soil insects.

In the northern Rockies, two widespread and destructive forest insects have plagued resource managers for decades--the western spruce budworm, principally in Douglas-fir and several other economically valuable species, and the mountain pine beetle, principally in lodgepole pine. Managers are interested in stand management practices that will reduce or ameliorate the impacts of either of these two, or any other insect species.

Western Spruce Budworm

In their most recent western spruce budworm management plan, resource managers in the Northern Region have chosen "silvicultural practices" over other alternatives, including the use of chemicals (USDA, FS 1977). This decision was largely intuitive because few studies have been made and little information exists relative to the relationships of stand manipulation and the behavior and impact of the western spruce budworm. Pursuant to the needs of resource managers, the entire western spruce budworm research effort in the northern Rockies is designed around silvicultural-entomological objectives. We are in our second year of three closely related and coordinated studies involving 1) the reciprocal relationships among the western spruce budworm and cone and seed production, 2) the influence of stand manipulations on behavior of the budworm, particularly dispersal patterns of both larvae and adults, and 3) the impact of the budworm on regeneration and residual stands within a matrix of variables involving cutting systems, forest series, size of cuttings, etc. (USDA, FS 1978a).

Mountain Pine Beetle

Based on empirical models that identify stand characteristics conducive to mountain pine beetle epidemics, W. Cole (1978) feels that harvesting or management strategies can be applied to prevent mountain pine beetle epidemics in lodgepole pine stands. Managers are faced with the challenge of lowering the probability that epidemics will occur within any given stand. W. Cole (1978) feels that managers can predict these probabilities from stand structure--i.e. principally diameter distribution and phloem distribution within diameters. In considering the alternatives presented, the manager must "...decide how much risk he is willing to accept if he desires large diameters, or be willing to accept and manage for smaller diameter stands" (W. Cole 1978). Amman (unpublished data) lists four main conditions that must be met for epidemics of mountain pine beetle to occur in lodgepole pine stands. These conditions are: 1) sufficient numbers of large diameter trees, 2) thick phloem in many of the large trees, 3) optimal temperature for beetle development, and 4) optimal tree age.

Other researchers agree that losses are related to tree diameter and phloem thickness, but feel that the most important factors in susceptibility are reduction of tree vigor and associated resistance; this, they feel, is why larger trees are successfully attacked. D. Cole (1978) recognizes the circumstantial evidence presented by both groups, but says "...neither has proved its case, especially as to whether managed stands will be more or less susceptible to attack than unmanaged stands and whether they will be susceptible sooner or later than unmanaged stands." Not unexpectedly, this research controversy presents the practicing silviculturist with a serious dilemma in determining the actual consequences of specific practices intended to minimize losses.

D. Cole (1978) discusses several silvicultural practices for reducing losses from the mountain pine beetle in lodgepole pine. He indicates that practices are available in each regeneration system for reducing losses either by lowering risk or recovering losses; however, the practices must be carefully selected and applied. He issues some reminders: 1) managers must be extremely cautious when using partial cutting, for any purpose, in lodgepole pine stands where sustained timber productivity is important; 2) practices implemented for reducing mountain pine beetle losses must be compatible with the major requirements of lodgepole pine silvicultural management systems; 3) "It is the forest that must be the primary focus of lodgepole pine

management, and not the beetle." If we fail to recognize this, "...silvicultural recommendations may evolve that are too narrow in scope--perhaps solving some immediate problem, but creating greater long-term forest management problems" (D. Cole 1978).

At the present time, management of lodgepole pine stands in the northern Rockies is directed toward prevention, with emphasis on green stands and concurrently salvaging infested stands (McGregor 1979). In addition, research continues to develop methods 1) to prevent outbreaks from developing, 2) to obtain maximum wood and fiber production, 3) to develop knowledge of beetle-host tree interactions, and 4) to determine desirable stocking levels of insect and disease-free growing stock of desired species (McGregor 1979).

Researchers and managers in the northern Rocky Mountains and elsewhere in the West are also concerned with the mountain pine beetle in ponderosa pine forests. In Montana, McGregor (1973) indicates that thinning of second-growth ponderosa pine stands prior to beetle infestation will reduce susceptibility of individual trees to attack and decrease the number of attacked trees. As an example, on the Ninemile Ranger District in western Montana, second-growth ponderosa pine stands that were thinned to a basal area of 120 or less were not infested with the mountain pine beetle. At the same time beetles continued to infest stands with a basal area of more than 120, even more severely where the basal area exceeded 150.

In Oregon, Sartwell (1970, 1971) established that the severity of tree killing by the mountain pine beetle in second-growth ponderosa pine stands was related to stand density, and that thinning dense stands could be used to prevent outbreaks. He believes that beetles kill a larger proportion of trees in dense, overcrowded, and less vigorous stands, than in sparsely stocked stands. Sartwell (1971) and Sartwell and Stevens (1975) established that stands with well-spaced, thrifty trees can resist even the infestation pressures of an outbreak population.

Western Pine Beetle

Fifty-five years ago, Craighead (1925) recognized that each species of Dendroctonus presented a different problem in different regions as well as in different forest types, so that "control" methods could not be generalized to envelop the entire genus. Because the western pine beetle prefers overmature, slow-growing, decadent trees on poorer sites, Craighead suggested short rotations and cutting practices to encourage more rapid growth; light cutting in narrow strips, he said, "would largely prevent losses from the the beetle."

The Pine Engrayer

In Alberta, Reid (1957) studied the bark beetle complex, especially Ips pini Say associated with slash created by five different cutting practices. He concluded that: 1) cutting to a diameter limit of 6.5 inches (16.5 cm) does not produce enough residue to constitute a beetle hazard; 2) clearcutting, or similar treatments, result in large volumes of slash and create the greatest beetle hazard; and 3) selection cutting, though creating large volumes of residue, provides environmental factors that favor predators and parasites of Ips, thereby reducing the beetle hazard to residual stands.

A multitude of interactions with several different diseases and a variety of insect species and groups (with different habits and economic impact) exist with both residue and fire management. In discussion some of these interactions, I use the word "control" with caution and interpret the word "residue" very broadly.

Diseases

The most noteworthy examples of fire and residue management involve three forest diseases: brownspot needle blight, Scirrhia acicola (Dearn.) Siggers, dwarf mistletoe, and root pathogens, principally Fomes annosus (Fr.) Cke.

As noted by Martin and others (1977) and Miller (1978), prescribed burning to control brownspot needle blight on long leaf pine, Pinus palustris L., seedlings provides a classic and outstanding example of the use of fire to control disease. Fire has been implicated in many aspects of the spread and intensification of dwarf mistletoes (Alexander and Hawksworth 1975), and fire is often used to burn the slash of infected trees in order to reduce the infection of new seedlings (Martin and others 1977). In discussing fire and dwarf mistletoe relationships in the northern Rocky Mountains, Wicker and Leaphart (1976) plead for planning management activities on the basis of habitat types. The authors are convinced that although fire, pests, and plants should be managed, "Man should strive to manage the total forest ecosystem and not to control or eradicate certain segments of it" (Wicker and Leaphart 1976). Repeated burning is known to have a suppressive effect on certain root pathogens (Froelich and others 1978). Prescribed fire reduces the incidence of Fomes annosus root rot (Martin and others 1977) and controls many other plant diseases (Hardisan 1976; Harvey and others 1976).

There are some other fire-disease interactions. Fire can act as a sterilizing agent in controlling some plant diseases by destroying insects acting as plant disease vectors (Ahlgren and Ahlgren 1960). Fire scars can serve as avenues of entry for many forest pathogens (Harvey and others 1976), and infested residues act as reservoirs that tend to propagate and increase pathological activity (Nelson and Harvey 1974; Mitchell and Sartwell 1974; Parmeter 1977). In some cases fire may favor the increase of disease by producing thick stands of the host plant, thereby inducing multiplication and spread (Ahlgren and Ahlgren 1960).

Insects

In the late 1800's and early 1900's, entomologists used prescribed fire to suppress insect populations (Komarek 1970), but fire prevention campaigns and insecticidal developments influenced later generations of entomologists to use methods other than fire. "Today, modern fire-use technology and renewed interest in alternative methods make fire attractive again as an insect management tool" (Miller 1978). Komarek (1970) summarizes the actions of fire on regulating insect populations and lists several variables that must be considered when studying or evaluating the effect of fire. Yet, he concludes that "...to what extent and how these changes occur has not been investigated," and "There appears to have been very little

investigation regarding controlled burning and its effect on regulating forest insects" (Komarek 1970). Moreover, if an insect pest is to be controlled with fire, its life history must be known in detail in order for fire to be used at the most appropriate time (Lyon and others 1978). I will summarize a few fire-residue-forest insect relationships--bark and engraver beetles, wood borers, weevils and others.

BARK BEETLES

Of all the forest fire-forest - residue-forest insect interactions in the northern Rocky Mountains, probably the most interesting, controversial and socio-political event involves the tremendous amounts of lodgepole pine residues created by the mountain pine beetle and fire management related to those residue.

D. Cole (1978) recommends consideration of prescribed fire as an important long-range management alternative in integrated programs for controlling losses to the mountain pine beetle in commercial lodgepole pine forests in the northern Rocky Mountains. Stagnated stands, past the point of responding to cultural treatments, eventually will be susceptible to the beetle. In these kinds of stands, D. Cole (1978) indicates that "...prescribed fire can be a valuable silvicultural practice for bringing the stands under management by 'starting over'"--a different aspect of insect control through prescribed fire. Martin and others (1977) report that fire may be used to control spacing and thus reduce the severity of attacks by the mountain pine beetle.

Management of lodgepole pine residues--created by the mountain pine beetle--in Glacier National Park and the adjacent Flathead National Forest is at this time embroiled in controversy. One element of the controversy involves restraining the "spread" of the infestation. At this time there are some 30-40 million dead lodgepole pine trees--standing residue--killed by the mountain pine beetle on the east side of the Flathead River in Glacier National Park (Scott Tunnock, personal communication). Mark McGregor, a Forest Service entomologist, "is irritated because the National Park Service did nothing to stop the beetles from spreading..." from inside the Park to infest thousands of acres on the adjacent Flathead National Forest (Kuglin 1980). McGregor feels that "the infested stands could have been logged in an attempt to stem the infestation." National Park Service biologist Robert Hall responds that the national park manages its forests, not to produce timber but for people to enjoy. Hall said, "Tourists are curious when they see thousands of red-brown trees. We try to explain to people that this is a natural thing and that we don't log in National Parks" (Kuglin 1980).

Another element of the controversy involves the use of prescribed fire in managing the lodgepole pine residues. During the summer of 1979, park personnel planned to prescribe-burn patches of the residues to break up and diversify the stands. [One of the alternatives of the park's fire management plan is to introduce fire where a specific major need is demonstrated (Glacier Nat. Park 1978)]. The plan was not effected because of an extreme fire season. While some parks allow certain wildfires to burn under a pre-determined prescription--a "let burn policy"--some critics considered the Glacier Park burning plan tantamount to forest management, thus contrary to national park management philosophy.

In other fire-residue-insect relationships, Mitchell and Sartwell (1974) cite several authors who generally have supported the recommendation that tree killing can be prevented by burning or otherwise removing bark beetle-infested residues from

which beetle progeny presumably emerge and attack live standing trees (fig. 12). Contemporary investigators, as well as some who worked in the 1920's, feel that this "build up" philosophy is too simplistic, that residues attract beetles and concentrates them in smaller areas where they can do more damage to standing trees than if widely dispersed. They support their contention by citing the behavioral patterns of the Douglas-fir beetle, when outbreaks of this beetle develop, "...many standing trees are killed during the time nearby residues are under attack" (Mitchell and Sartwell 1974).



Figure 12.--A shelterwood cut with intensive residue utilization (mechanically removed) and residues being burned. Removal and utilization of residues obviously eliminates the problems of insects developing in the residue. Prescribed burning of the residues usually prepares the site for regeneration, and kills most "destructive" as well as "beneficial" species inhabiting the residues.

An interesting twist to bark beetle control through fire has been reported with the western pine beetle in ponderosa pine. Miller and Patterson (1927) reported that although fire-injured trees attracted beetles to concentrate within trees in the burned area, the trees afforded a very unfavorable breeding ground for the insects and in the end contributed toward an actual reduction of their numbers. Nevertheless, Miller and Patterson (1927) concluded that fires do not markedly assist in eliminating populations of the western pine beetle unless the fires are severe enough to kill the trees.

ENGRAVER BEETLES

The philosophy that fire may be used to destroy infested residue or logs, aiding in the control of insects (Martin and others 1977), often applies to engraver beetles, especially *Ips* spp., in some pine species. If crop trees are only scorched, however, prescribed burning may merely predispose them to *Ips* attack. Some species of engraver beetles spend part of their life cycle in the forest floor (duff); the deeper the litter, the better the protection for the beetles. Eliminating prescribed fire in pine stands where slash has been created not only benefits beetles in the residue but also those aestivating in the forest floor (R. F. Schmitz, personal communication).

WOOD BORERS

Mitchell and Martin (In Press) suggest that prescribed burning to reduce fuel loads of residues serves two functions: 1) it not only consumes the residues, but also 2) attracts wood borers to the larger partially burned or unburned logs. Borers will initiate decomposition by loosening the bark, creating holes in the wood and introducing wood-destroying fungi. Evans (1971) suggests that the role of Melanophila wood borers should be considered in any prescribed burn program, not only because of their usefulness in residue deterioration but also because of their contribution to fire-induced increases in species diversity. Dahl (1971) found no relation between the mortality of Monochamus wood borers and the height of lodgepole pine slash above the ground in prescribed fires of low and moderate intensity, although at the ground level Monochamus mortality was increased.

OTHER INSECT SPECIES

Several species of weevils, some cone and seed insects and some other insect species that spend a portion of their life cycle in the forest floor, are also involved in the interactions of residue and fire management.

Earlier I mentioned that the killing of pine seedlings by two weevils, the pales weevil and pitcheating weevil, is influenced by the time of year during which timber is harvested. Fox and Hill (1975) studied the effects of prescribed burning in standing and cutover areas on the behavior of these two weevil species and found that: 1) the pales weevil showed a positive preference for cutover areas, but residues and debris burned after logging were a deterrent for this species; and 2) both burned and cutover areas were attractive to the pitcheating weevil. These differences in the relative attractiveness of burned and unburned areas can influence the management of pine forest land, especially when prescribed fire is used in preparing the site (Fox and Hill 1973).

Prescribed fire can aggravate damage to conifer seedlings by another species of weevil. In British Columbia, the weevil, Steremnius carinatus Boh. recently began causing significant damage to seedlings. Prescribed burning of surface residue, "...often necessary to reduce brush competition for seedlings, destroys the natural vegetation and materials the weevils normally eat, and focuses the attention of the weevils on newly planted seedlings" (Condrashoff 1969). "In some plantations, weevils have killed or damaged over 40 percent of Douglas-fir seedlings planted on recently logged and burned sites along the west coast of Vancouver Island (LeJeune 1962).

Logging and residue removal has been shown to kill sugar pine cone beetles, Conophthorus lambertianae Hopkins. In the laboratory, Bedard (1966), found high mortality rates in these beetles exposed to temperatures greater than 47° C, indicating that high temperatures from direct sunlight could have the same effect. Bedard (1966) noted that when logging operations open up the tree canopy, and when the residues have been removed, ideal conditions of radiation are established for high temperature mortality of this beetle. In seed production areas in the Lake States, burning is reported to be effective in controlling the red pine cone beetle (Miller 1978).

In the Lake States Simmons and others (1977) determined that prescribed burning to control the maple leaf cutter (Paraclemensia acerifoliella (Fitch)), which pupates in the forest floor, was more effective than insecticide treatments.

RESIDUE AND FIRE MANAGEMENT--SOME OPINIONS

Since the early 1900's, there has been an evolution in philosophy and strategy concerning the management of forest residues. Two issues are involved: 1) residue management and utilization as it involves protection from wildfire, and 2) residues triggering forest insect and disease outbreaks.

In the early 1900's, Mitchell (1913) indicated that in California the piling and burning of residue was the accepted method because of 1) a desire to render the cutover area as fireproof as possible, 2) the belief that protection of litter was not necessary to insure reproduction, and 3) a desire to make the area as sightly as possible. There was considerable controversy as to whether the increased protection from wildfire by prescribed burning offset the danger involved, the expense, and the damage to reproduction and standing timber.

The issue of the expense of burning forest residue was echoed the following year by Koch (1914) in the northern Rocky Mountains. Citing examples on the Lolo National Forest in western Montana, Koch 1) questioned the risk (to wildfire) of unburned residue, and 2) chided the Forest Service for "...piling brush just because we have always piled brush...", adding, "it is time for us to quit blindly following precedent and at least make a serious investigation of the possibility of less expensive methods of protection."

Shortly thereafter, Hopping (1915) acknowledged Mitchell's and Koch's concerns about protection and cost-benefits, but mentioned another protection aspect--the dangers of insect infestations that can result from destructive insects breeding in unburned forest residues. Citing several examples to support his point, Hopping concluded by saying that "...the consideration of the burning or non-burning of brush must be taken up from a broad protection standpoint and not from the standpoint of fire risk or cost alone."

Later, in studying residue management in the Lake States, Mitchell (1921) advocated intensive protection rather than prescribed burning. He felt that destroying the residue by burning did not materially reduce the fire hazard because 1) of the litter accumulation normally present and 2) the close utilization of cedar and spruce for pulp and posts resulted in little residue created. Moreover, Mitchell believed that prescribed burning actually increased the fire hazard by killing, but not consuming, reproduction, as well as damaging or destroying the soil organic layer.

The following year, Graham (1922) discussed the entomological aspect of the residue management problem, and pointed out that 1) "...we are burning up valuable humus in our slash piles," 2) smaller pieces of residues are unfavorable to insect development, while larger branches, tops and broken logs are the most suitable breeding places, and 3) larger pieces of residue are more difficult to burn, do not materially increase the danger of wildfire, and after burning usually remain on the ground uncharred. Graham (1922) concluded that in the Northeast prescribed burning is not the best way to manage residue, nor can it be recommended or is "...as effective a factor in forest insect control as has been generally believed."

Still, by 1938, there was a feeling that fire was commonly used for forest insect "control" (Haig 1938), and as recently as 1973 the disposal of forest residues by fire was often being prescribed to prevent insect populations from developing in forest residue, or to prevent insect populations from moving from the residue to green standing timber (Brown and Davis 1973).

Prior to concluding this discussion of fire and residue management opinions, I must mention that Mitchell (1913) not only had strong feelings of how residues should be managed in California, but also of the kind of labor that should be used. His words are rather strong and may be as controversial now as they probably were then. Sixty-six years ago, Mitchell (1913) wrote:

"In California foreign labor, preferably Italian, for this class of work is, if properly supervised, probably the cheapest. There are two fundamental reasons for this aside from wages. In the first place, the foreigner is usually not afraid of work, and in the second does not consider his work beneath him. In addition, he is usually as quick to grasp the idea of how the work is to be done as the average "white man" and can generally be trusted not to soldier on the job. On the other hand, the average woods worker who has not raised himself out of the "swampers" class is too often either lazy, incompetent, or both. As a rule, too, he is too good for his job, takes little or no interest in his work, and if left alone is pretty apt to spend his time in seeing how little he can accomplish."

In concluding these thoughts, observations, and opinions concerning residue and fire management in relation to insects and diseases, we are reminded that there are some who feel that fires have historically kept pest populations at low levels before the Forest Service existed (USDA, FS 1975c).

IMPACT OF HARVESTING RESIDUE MANAGEMENT AND FIRE ON FOREST FLOOR AND FOREST SOIL ARTHROPODS

Of all the interactions among forest residues, fires, and insects, probably none has received less attention and is as casually dismissed as the interaction among residues, fire, forest floor, and forest soil arthropods. Research scientists and land managers in the western States recently considered this as one of a dozen areas of fire ecology research needs (Kickert and others 1976).

It is a common practice in the northern Rocky Mountains and elsewhere to burn forest residues and unmerchantable trees after logging. Such fires consume varying levels of duff, exposing proportionate amounts of mineral soil. Partially or completely exposing mineral soil is desirable as a seedbed for germinating many species of trees and as a planting site for coniferous seedlings. Burning also removes vegetation that competes with developing young trees, and logging followed by prescribed burning usually provides desirable habitat for wildlife, particularly ungulates--a habitat that often is more favorable than that provided by dense forest cover.

While providing a desirable environment both for forest regeneration, and for many forest animals, fires also influence other forest flora and fauna, and fire variability makes generalizations concerning fire effects difficult (Lyon and others 1978). However, fires not only affect the flora and fauna within deteriorating residues, but also the habitat of the fauna that utilize the forest floor and the upper layers of mineral soil by altering the environment and food supply on and in the ground. Generally, invertebrates, often "undesirables," decrease in number following a burn (Reichert and Reeder 1972), usually because the animals or their eggs are killed by flame or heat, and their food supply and shelter are diminished. The effects of fire on invertebrate populations may be transitory or long lasting, as well as selective and varying among species; in some cases burning also destroys natural predators of pest species. Analyzing the effect of residue management and prescribed fire on forest floor and soil invertebrates is complicated by the fact that we still do not always know which are our friends and which are our enemies.

Most of the organisms that live in forest residues, the forest floor, and forest soil, are decidedly beneficial. The species and groups involved include not only natural enemies of pests, but also organisms that decompose residues. The series of events in the decomposition and fragmentation of residues is initiated by several species of beetles that loosen the bark on the residues as well as introduce wood-decaying fungi. As described by Mitchell and Sartwell (1974):

"This is followed by a progression of other arthropods, each contributing to the fragmentation of the material (Wickman 1965; Elton 1966). Following bark beetles are wood borers such as ambrosia beetles (Scolytidae), flat-and round-headed borers (Buprestidae and Cerambycidae), termites (Isoptera), horntails (Siricidae), carpenter bees (Apidae), and carpenter ants (Formicidae). These insects bore holes deep into the wood and also introduce wood-destroying fungi (Boyce 1923, Shea and Johnson 1962, Wright and others 1956, Wright and Harvey 1967, Kimmey and Furniss 1943)."

Although decomposition itself is largely a microbial process, fragmentation of the material is largely an arthropod process. This fragmentation may increase the area of residues exposed to microbial activity by up to 15 times compared to unfragmented residues (Witkamp 1971). Moreover, the fecal material produced by these species of arthropod "fragmenters" encourages the growth of decomposing microbes, particularly bacteria (Crossley 1970).

Following the arthropod "fragmenters", forest floor and forest soil mesofauna (intermediate-sized organisms) are the next arthropod group in the decomposition process; most are various species of mites and Collembola with a wide variety of feeding habits. Many are saprophytes that feed on bacteria, fungal hyphae, or other living plants or animals. Although they do not directly contribute to chemical decomposition of litter nor to the turnover of plant nutrients, they play a major role in the process by breaking organic tissue into smaller pieces. The smaller these particles become, the more susceptible they are to action by other organisms, such as bacteria and fungi, involved directly in the decomposition process (Metz and Farrier 1971).

"Harmful" forest floor or forest soil fauna can only be categorized as such insofar as they act or feed in a way that is in competition with, or counter to, what man wants out of the resource. For the most part, harmful insects include those that feed on seeds, seedlings, or sprouts of desirable coniferous and broad leaf species.

Different investigators have used several systems to categorize the arthropods in the forest floor and forest soil. In the following discussion, I will refer to those invertebrates that inhabit and move about in the forest litter as forest floor macrofauna, (surface arthropods) and to those that are generally smaller, less mobile, and occupy the humus and forest soil, as forest soil mesofauna.

Forest Floor Macrofauna

Many studies have been made throughout the United States concerning the impact of harvesting, residue management, and fire on forest floor macrofauna. Some of these studies were concerned with the effects of macrofauna on direct seeding. Though not designed to determine effects of residue and fire management, results of these studies could have implications in the management of residues and prescribed fire; the studies will be reviewed here.

RESEARCH IN THE NORTHERN ROCKY MOUNTAINS

In the northern Rocky Mountains three studies in the past 10 years have focused on the effects of forest residue and prescribed fire management or wildfire on forest floor macrofauna (Fellin and Kennedy 1972; Clayton 1975; and Fellin 1980b). These three studies were preceded by, and related to, several studies involving forest floor macrofauna and direct seeding and planting.

In the northern Rockies, most evidence that insects are involved in direct or indirect seeding efforts has been circumstantial (Kennedy and Fellin 1969). Wahlenberg (1925) summarized the results of past direct-seeding projects in the northern Rocky Mountain region and attributed the death of an undetermined number of western white pine seedlings to cutworm larvae. Haig (1936), and Haig and others (1941) noted that soil insects, chiefly cutworm (*Noctuidae=Phalaenidae*) larvae, were one of the most important direct agents of conifer seedling mortality in the western white pine type in northern Idaho. Schopmeyer (1939), and Schopmeyer and Helmers (1947), determined that either cutting or clipping were the major kinds of injury to direct-seeded western white pine during the first growing season. They observed several forms of cutting in both screened spots and unscreened spots; they speculated that "cutworms, grasshoppers, and other insects may have had a part" in causing the damage.

Fellin and Kennedy (1972) studied the abundance of some arthropods inhabiting the forest floor in three clearcut areas that were prescribed burned in 1960, 1961, and 1962, in north-central Idaho. Generally, they found more arthropods present and more taxa represented on the older burns, and attributed this greater relative abundance of individuals to movement from adjacent unburned forests, and repopulation from survivors within the burned areas. The most abundant arthropod in soil samples on the oldest burn was the carabid, *Amara erratica* (Sturm). A projection based on sample data from the 1960 burn indicated there could have been up to 100 carabids per square yard (0.836m^2) of soil surface. Because of the abundance of this carabid --and its seed-eating behavior--and because of one or more species of grasshoppers and cutworms, Kennedy and Fellin (1969) recommended that direct seeding of western white pine and perhaps other conifers be done the first or second season after prescribed burning.

The second research program on forest floor macrofauna in the northern Rockies was conducted by Clayton (1975). He studied forest floor insects where a wildfire had been allowed to burn as a "prescribed fire" in a wilderness fire management area. The fire was ignited by lightning on August 10, 1973, burned for 43 days and eventually covered 1,200 acres (486 ha). Although the fire did burn intensely in some stands of trees, most of the area was only lightly burned by surface fire. By summer of 1974 one had to look closely in places to see exactly where the fire had burned and where it had not.

Regardless of the light burn, Clayton (1975) found that 7 out of the 13 groups of arthropods studied showed a significantly greater number of individuals in the burned areas of hillsides and streamside than in unburned areas. On the other hand, four groups were more numerous in the control areas than in the burns. Clayton concluded that the effects of even a relatively light fire on the arthropod community can be easily seen a year later.

The third study of forest residues, prescribed fire and forest floor macrofauna was done between 1975 and 1977; results of that study are reported elsewhere in this proceedings (Fellin 1980b).

RESEARCH ELSEWHERE IN THE UNITED STATES

Probably the first research done in this country concerning prescribed burning and forest floor fauna was done by Pearse (1943) on the Duke University forest. He found that earthworms, centipedes, millipedes, ants, and nesting pollinators were "significantly--often seriously--reduced" in numbers after a prescribed fire. Moreover, mechanical removal of litter was even more detrimental to these organisms than was prescribed burning. One deficiency in Pearse's study was that samples were hand-sorted without magnification, so many small arthropods were no doubt overlooked in his sampling.

Several researchers have reported the effects of macrofauna on seeds and seedlings. The importance of soil-inhabiting invertebrates in the destruction of sown Douglas-fir seed in Washington was clearly demonstrated in a detailed study of the fate of 440 radio-tagged seeds by Lawrence and Rediske (1962). Soil-surface invertebrates were found to have destroyed 11 percent of the seeds observed over a period of 22 weeks. In a northern California study of 3,200 tagged seeds, 29 percent were destroyed by soil-surface-inhabiting invertebrates (Johnson and others 1966). Also in California, cutworms damaged pine seedlings (Fowells 1940), usually by clipping seedlings in groups. In Florida, tiger moth larvae *Apantesis radians* Wlk. (Arctiidae) damaged pine seedlings (Ebel 1967). In a study of seedspotting in Oregon (Franklin and Hoffman 1968), insects and other animals (rodents, birds, slugs, and shrews) were believed responsible for one-third of the mortality of western white pine germinants.

Several studies have shown that populations of surface arthropods (macrofauna) in the forest floor decreased after fire. Buffington (1967) compared populations of invertebrates in the forest floor and surface soil of burned and non-burned areas about a year after a wildfire in the pine barrens of New Jersey. His samples from unburned areas were usually richer than those from burns, in numbers of both taxa and individuals. In an area of shrub steppe vegetation in southeastern Washington, two species of beetles were significantly reduced by a wildfire (Rickard 1970). In Australia, both wild and prescribed fires reduce populations of phasmatids

if the forest floor is completely consumed (Campbell 1961), and "fuel reduction fires" of low intensity substantially reduce populations of forest floor fauna (Leonard 1977). In African soils, burning destroys populations of termites and results in impoverishment of these tropical soils (Reichert and Reeder 1972).

Although most groups of macrofauna are reduced by fire, in some instances, prescribed burning, often in prairies and grassland, increases arthropod density and biomass. Following a prescribed burn in a grassland area (formerly a pine-hardwood forest), populations of herbivores (phytophagous) increased, presumably as a result of an increase in the food supply; at the same time, other groups such as predaceous spiders, flies, and scavengers showed less response to burning (Hurst 1970).

There are at least three reports of grasshoppers being more numerous in burned than unburned areas. In the northern Rockies, Clayton (1975) found the orthopteran family Acrididae to be more numerous in burned than in unburned coniferous forests, and Hurst (1970) reports grasshoppers to have increased in numbers after prairie and grassland fires. In a northern Minnesota jack pine burn, grasshoppers increased after a fire, possibly due to recolonization from adjacent unburned forests or from survival in patches of unburned ground (Ahlgren 1974). This recolonization from without or repopulation from within burned areas could be a very significant behavioral mechanism regarding the long-term effects of fire on forest floor macrofauna.

There are some interesting evolutionary adaptations and implications among some groups of insects surviving fires or inhabiting or recolonizing burned areas. In Montana, Clayton (1975) collected grasshoppers from burned and unburned areas, ranked them from dark to light and determined that out of 60 specimens, the 20 most darkest were from the burned area. Several investigators have reported melanistic forms of grasshoppers and other orthopterans, pentatomid bugs and noctuid larvae to inhabit burned areas in African savannas (Reichert and Reeder 1972). Many species of rodents and birds in grassland fire environments have color patterns that harmonize with burned or partially burned vegetation. Such camouflage is useful to these species, since some predators seem also to be adapted to fires, and will congregate at fires to feed on prey animals previously out of sight in the grass (Stoddard 1963; Komarek 1969).

RESEARCH ON IMPORTANT ARTHROPOD GROUPS

Of the forest floor macrofauna influenced by harvesting residue and fire management practices, at least three orders of arthropods deserve special attention because of their feeding behavior or their response to silvicultural or residue treatment. They are: Coleoptera (beetles), Hymenoptera (mainly ants), and Araneida (spiders).

Coleoptera

Of all the forest floor macrofauna, the beetles are probably the most abundant. Two to four families usually predominate. In a study of soil invertebrates in two aspen forests in northern Minnesota, Wagner and others (1977) collected 22 families of beetles in the soil litter environment. The numerically dominant taxa were rove beetles (Staphylinidae), ground beetles (Carabidae), click beetles (Elateridae), and soldier beetles (Cantharidae). In a recent study in Montana (Fellin 1980b), carabids and staphylinids were the predominant families.

Some investigators have found that burning reduces beetle populations. Ahlgren (1974) reports that in forested areas fire reduced most beetle genera at least temporarily; she found fewer beetles on burned than on unburned land the first three months after prescribed burning in Minnesota jack pine stands. In southern pine stands, a 60 percent decrease in beetle populations was noticed in burned areas (Pearse 1943; Heyward and Tissot 1936). In the New Jersey pine barrens, four times more beetles were found on unburned than on burned land (Buffington 1967).

In other studies, researchers report that beetle populations increased following burning: 1) Tester and Marshall (1961) found beetle numbers to increase following burning in a Minnesota prairie, 2) beetles increased in number on burned transmission lines in Mississippi, and 3) in an Illinois prairie, after an initial reduction, beetles recolonized rapidly following burning (Rice 1932). Ahlgren (1974) reports that beetle populations in grasslands and prairies are not as affected by fire as they are in the forest, partly because of lower soil temperatures during fires and partially because of the safety in partially burned grass tussocks. It would appear that in prescribed burning in coniferous forests, particularly in partial cuttings where residue is not as abundant, that beetles, as well as other arthropods, could seek refuge from which burned areas could be quickly repopulated following burning.

In Finland, Huhta and others (1962) found the density of adult Coleoptera to be very high the first year after clearcutting and to remain high also during the second year, but to begin to decrease in the third year after clearcutting. Subsequent burning apparently had no serious effect on the beetles. These investigators felt that adult beetles are so swift that they can presumably escape danger by running into cracks and holes, which if deep enough, will allow the animals to survive until the fire passes by. Later, in comparing types of clearcutting, Huhta (1976) found beetles (other than Staphylinidae) to be most abundant in a young clearcut area stocked with pine seedlings and without a shrub layer. All clearcut areas harbored significantly lower numbers of beetle larvae than the untreated control site. Huhta (1976) cites other investigators who report a decrease in total density of Coleoptera after cutting.

Coleoptera (Carabidae).--Probably one of the most important groups of forest floor arthropods are the ground beetles, or carabids. Though a few species climb, fly, or both, most are restricted to the ground level (Kulman 1974) and are vulnerable to harvesting, residue, and fire management practices. Among the numerous species are those that are both "beneficial" and "harmful". I would like to review four aspects of carabid ecology: 1) as affected by fire, 2) as biological control agents, 3) as seed eaters, and 4) as influenced by the forest environment.

Carabids and fire.--As with some other groups of Coleoptera, some species of carabids are influenced by prescribed burning and wildfire. In an area where wildfire had been allowed to burn in western Montana, Clayton (1975) found carabids to be more numerous on unburned control areas than on burned sites. Within the burned area, he found more carabids in a riparian woodland along a creek bank than on a south slope ponderosa pine savanna. In a study of carabids in Florida pine forests which had either been burned annually or unburned for 10 years or longer, Harris and Whitcomb (1974) collected 85 percent of the beetles (representing 7 species in 4 genera) in plots that had not been burned for 10 years, and where leaf litter was present following fire, compared to annually burned forests. In Australian Pinus radiata plantations, French and Keirle (1969) found that carabids were reduced immediately after fire, but they were the first group of insects to recolonize burned areas.

Carabids as biological control agents.--Many species of carabids feed on other insects near, on, or in the ground, as well as larvae that drop to the forest floor from trees above (Kulman 1974). As such, they effect a certain amount of biological control against several species of forest insects, including the gypsy moth, Porthe-
tria dispar (L.), the eastern spruce budworm, and a species of sawfly.

Kulman (1974) cites earlier investigators who report that in some areas the ground beetle, Calosoma sycophanta was the most important single control factor of the gypsy moth. More recently, however, Campbell (1967) considers that C. sycophanta probably can be an effective population influencing factor only in areas where dense host populations have persisted for several years.

Calosoma frigidum (Kearby), is reported as a predator of the eastern spruce budworm. In two white spruce plantations near Sault Ste. Marie, Ontario, these large black carabids were observed crawling over the foliage and eating budworm larvae; they also seized and ate larvae placed in front of them (fig. 13). Although no quantitative data is available on the impact of these carabids on budworm populations, investigators (Sanders and Van Frankenhuyzen 1979) feel that the size, numbers, and manner of searching the current foliage suggests that the beetles may have played an important role in reducing spruce budworm populations in these two white spruce plantations.

As a portion of a larger study of natural enemies of the eastern spruce budworm (Jennings and others 1979) Reeves and Jennings (1977) are studying carabid beetles associated with the spruce budworm. One of their objectives is to determine if stand composition and spruce budworm infestation can be correlated with carabid beetle populations. Other studies show that some species of ground beetles are efficient predators of spruce budworm larvae that reach the forest floor (Krahl and Simmons 1977, 1979). This happens most commonly when all the new foliage has been consumed and budworm larvae spin down to the ground or low vegetation.

In a study of two jack pine stands lightly infested with Neodiprion swainei Midd., Tostowaryk (1973) found three species of Pterostichus preyed to a limited amount on sawfly cocoons, but the ground beetles preferred fly puparia. Tostowaryk (1973) concludes that these carabids are probably only of minor importance in the control of N. swainei.

Carabids as seed eaters.--Many species of carabids are phytophagous (plant feeders), often feeding on conifer seeds or seedlings. Johnson and Cameron (1969) list 159 species of Carabidae belonging to 33 genera that are known to use vegetable matter as food in varying degrees, with some species using it almost exclusively. Certain genera feed on berries, seeds, tender shoots, and pollen and foliage of plants (Essig 1942). Species in the genera Harpalus, Zabrus, Omophran, and Amara eat cereal and seeds of plants (Imms 1948). Of those species that use vegetable matter as food, species in nine genera are known to feed on coniferous seeds and seedlings.

In the northern Rockies, Kennedy and Fellin (1969) found the carabid, Amara erratica to be the principal insect destroying western white pine seeds after direct seeding in clearcut areas that had been prescribed burned in northern Idaho. They indicated that spring sowing of seeds treated with Endrin, Arasan, and aluminum powder prevented carabid damage to seeds. However, Johnson and others (1966) indicate that "apparently the protective coatings currently in use for reducing seed losses to birds and rodents have little adverse effect on the ground beetles."

In Washington, Johnson and others (1966) found the carabid, Amara sp. to be of minor importance as a seed-eater, but at least six other species of carabids were found to feed on conifer seed. One species was most abundant in open areas and recently logged habitats; another species ate seeds over which bark or wood chips had

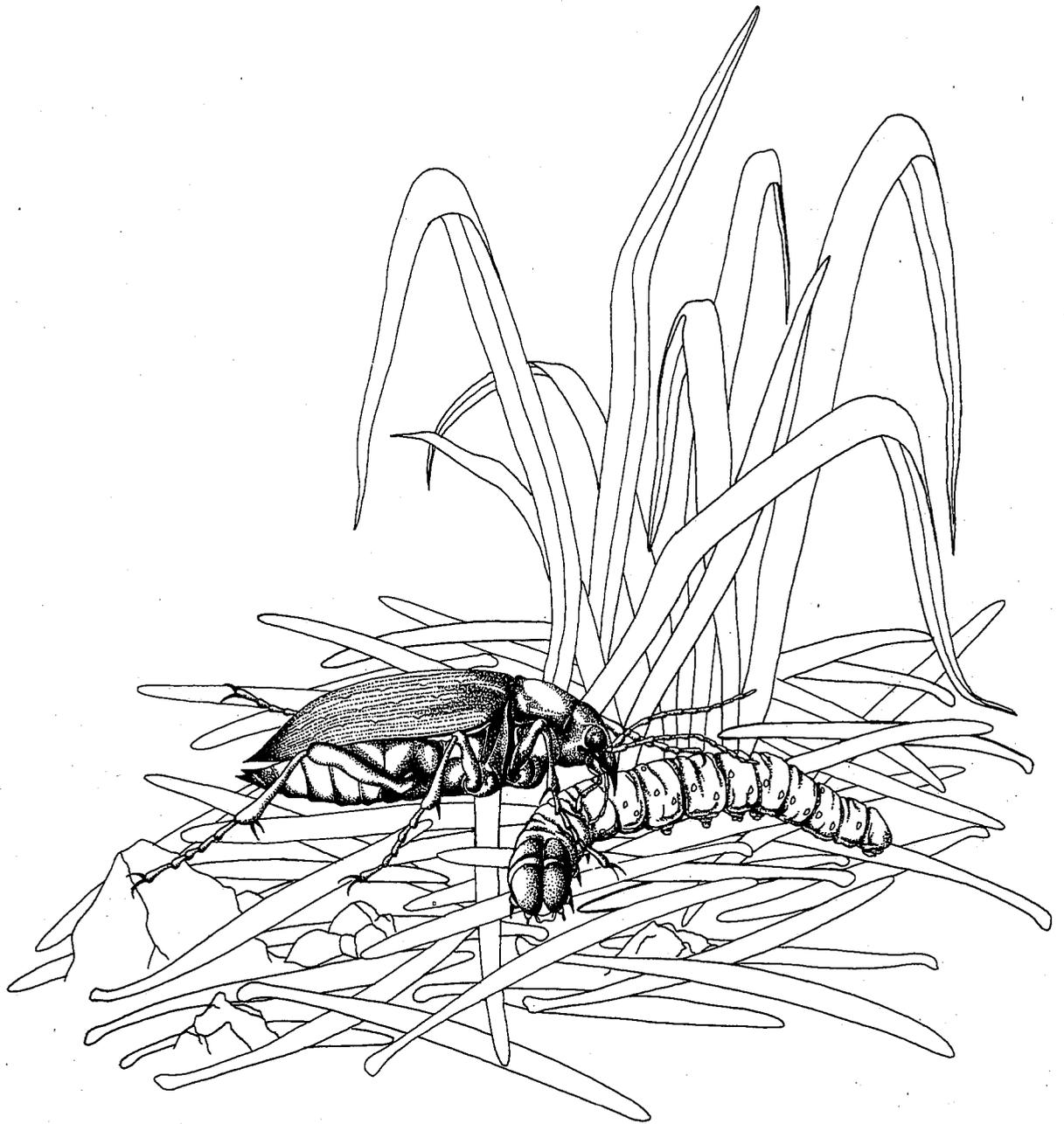


Figure 13.--Ground beetles (*Carabidae*) are one of the more important groups of forest floor arthropods. Some species feed on plant materials, including conifer seeds. Most species are predators, feeding on insects and other arthropods on the soil surface, as well as larvae, such as spruce budworm, that drop to the forest floor from trees above (Kulman 1974).

been placed for protection from rodents (Dick and Johnson 1958). One species, Harpalus cautus (DeJean) was often found under pieces of bark or wood lying on the ground, but quickly moved to a new place of shelter if the wood chip was removed. This behavioral trait, probably common to many carabid species, has implications in residue management practices and forest regeneration programs.

Seed caching has been reported for at least 3 species of carabids--Harpalus pennsylvanicus (DeGeer), H. erraticus Say (Kirk 1972), and Synuchus sp. (Manley 1971). Some species, even though they cache seeds, apparently do not eat them.

Carabid beetle damage to conifer seed is common in Europe (Nüsslin and Rhumbler 1922; Gäbler 1954). Harpalus pubescens (Müll) feeds on seed and seedlings of conifers (usually chewing seedlings off just above the ground surface). Species of Pterostichus, Calathus, Poecilus, Bembidion, and Harpalus feed on seed in nurseries (Nüsslin and Rhumbler 1922; Gäbler 1964.) Beetles in the genus Harpalus have destroyed up to 80 percent of the seeds and seedlings in nursery beds.

Carabids and the forest environment.--Several investigations have shown some important relationships between the forest environment and carabid behavior. Johnson and his colleagues (1966) studied the relative abundance and seasonal occurrence of six species of Pterostichus--all seed eaters--in three vegetation cover types near Chehalis, Wash. Of the six species, P. algidus (LeConte) was the most abundant, especially during October in an open grown and recently logged habitat. Another species, P. vulgaris was the most abundant from July to September and also more abundant in open stands and on recently logged land than in dense forest cover. Peak numbers occurred during the period of natural seed fall and prior to the time that direct seeding would take place.

From the results of a study of carabids in trembling aspen, Populus tremuloides Mich., stands defoliated by the forest tent caterpillar, Malacosoma disstria Hübner, Kulman, Grim, and Witter (In Press) speculated that several species of ground beetles preferred stands with less ground cover and greater humidity--both factors being related to less exposure of the forest floor in non-defoliated stands. Stands exposed and grassy from 4 years of defoliation were apparently unattractive to at least three species studied.

Studies in Minnesota show the relationships of tree species cover on carabid fauna. In northern Minnesota, Kulman and Cushwa (In Press) found Synuchus impunctatus Say to be most abundant in aspen stands and Calathus ingratus (DeJean) most abundant in jack pine stands. Pterostichus adstrictus was the most abundant beetle in all stands. In southern Minnesota, the abundance of several carabid species varied between stands of red oak, Quercus borealis Mich., trembling aspen, and sugar maple, Acer saccharum Marsh (Kulman, Witter, and Skalbeck, In Press).

Martin (1965) studied the abundance of carabids in red pine plantations of varying ages in four stages of development: 1) establishment, 2) transitional, 3) monoculture, and 4) young forest stages. He found four species to appear only in the open or semi-open conditions prior to crown closure (stages 1 and 2). Several species of Harpalus were abundant only prior to crown closure. Several species were found in all four developmental stages, though most common or extremely abundant in the latter stages of stand development.

In his treatise of carabids and their environments, Thiele (1977) notes that "characteristic societies of carabids can be assigned to some forest plant community", but that "it is not to be expected that a particular species be found exclusively in any one plant community." In Europe, carabid fauna in forests has little in common with that of adjoining fields (Thiele 1977).

Coleoptera-Staphlinidae.--Although probably not as important as carabids, some species of staphylinids (rove beetles) are influenced by forest management practices. In Finland, Huhta (1976) found the density of staphylinids to be very high in some clearcut areas where stocked pine saplings had failed to grow, but where spruce, birch, and mountain ash formed a sparse shrub layer. Ten years earlier, Huhta and others (1967) reported a strong but transitory increase in Staphylinidae soon after clearcutting. Huhta (1976) cites other authors who report a decline in staphylinid populations, accompanied by alterations in species composition, in clearcut areas in Poland.

Hymenoptera (Formicidae)

The formicids, or ants, are also an important component of the forest floor macrofauna. Like the carabids, ant populations are known to be influenced by fire, and many species of ants are effective predators.

Ants and fire.--Although most groups of forest floor arthropods are either decimated or reduced by burning, several investigators have reported ants to be more numerous in burned areas. According to Ahlgren (1974), ants are less affected by fire than many other groups because of their adaptations to hot xeric conditions of early postfire topsoil. Moreover, their cryptic habits enable them to survive fire below the levels of intense heat and their colonization habits and social organization adapt them to rapid re-establishment on burned land. Even though ant populations are destroyed by fire or are less numerous in burned areas, they are often the first to recolonize burned areas (French and Keirle 1969), at times within 1 hour after a fire (Komarek 1970).

Two studies in the northern Rockies report that ants were generally more abundant on burned than unburned areas. In his study in western Montana where a wilderness wild-fire was allowed to burn, Clayton (1975) found that by both numbers of individuals and species ants were more numerous on the burned than on the unburned areas. Of five genera studied, he found: 1) three genera to be more numerous on burned sites, 2) one genus more abundant in an unburned area, and 3) one genus with no difference in populations between burned and unburned areas. More recently Fellin (1980b) reported Formicidae were more numerous in burned areas after prescribed fire than in unburned areas.

Studies elsewhere also report ants to be abundant in burned areas. Although both Pearse (1943) in the long leaf pine region, and Buffington (1967) in New Jersey reported a reduction in ant populations following burning, Pearse reported an increase in the species proportion on the burned area and Buffington found two ant species strikingly more numerous on burned land. In the pine regions of the South, Heyward and Tissot (1936) found more ants in burned 0 to 2 inch mineral soil layers than in unburned soil. In grass and prairie habitats, both Rice (1932) and Hurst (1970) found ants to be more numerous following fire or on burned areas.

Ants as predators.--Several species of ants are reported to be associated as predators of both the eastern and western spruce budworm and the jack pine budworm. Ants also interact with both carabids and spiders in a predaceous or competitive-type relationship.

In his studies with the jack pine budworm, Allen (1968) found Camponotus noveboracensis (Fitch) to be a common inhabitant in all jack pine stands studied, and two species of Formica were also associated with jack pine budworm populations. At some sites, Allen found from 100 to 400 nests of F. exsectoides (Forel) per acre

with every tree in the stand continually covered with ants. Budworm larvae falling to the ground were immediately attacked by a worker ant and dragged to a nest, and ants would commonly scurry down silk threads after budworm larvae spinning down from a feeding site. Allen and his colleagues (1970) report that both C. noveboracensis and F. exsectoides had little success preying on budworm larvae in the foliage because of the larval feeding tunnels and the silk surrounding them. This is probably why neither ant species was able to influence jack pine budworm populations. Jennings (1971) reports that 6 species of Formica actively preyed on late instar jack pine budworm when the larvae were dislodged from their feeding sites with long poles.

In a study of the introduced wood ant, Formica lugubris, McNeil and his associates (1978) found that large numbers of the eastern spruce budworm were removed from the population by the ants. They believe that this introduced wood ant could play a role in an integrated control program against the spruce budworm.

In Montana, Bain (1974) studied the relationship of two wood ant species, Formica obscuripes (Forel) and F. criniventris (Wheeler) with the western spruce budworm. He found that ants foraging in the foliage of budworm-infested trees was an important factor in causing larvae to fall to the ground where they were further preyed upon by ants. Bain estimated that during the period of larval development, as many as 12,000 budworm larvae could be gathered by the ants from a single nest. He acknowledges that while this pressure may not be sufficient to completely suppress the budworm population, predation by ants represents a formidable factor in slowing the rate of increase in budworm populations and reducing the overall economic damage caused by the budworm.

Populations of predaceous ants are also reported to influence carabid numbers in some habitats, but apparently to have little influence on spiders. Thiele (1977) reports that ants can exert a considerable influence on carabid populations and the habitats they occupy. Carabids are attacked and severely injured by ants; in the vicinity of Formica nests, there was a sharp decrease in numbers of both species and individuals of carabids. Although some investigators have reported a competitive-type relationship between ants and spiders, Van der Art and DeWit (1971) found no significant difference in the composition of the fauna of wandering spiders, or in the total number of spiders caught between a habitat in which ants were numerous and a comparable habitat without ants.

Ants and the forest environment.--In his studies discussed earlier, Martin (1965) lists five species of ants in four genera that generally occur prior to crown closure, while two other species only appeared in the last two stages of stand development, macroculture and young forest stages. Wagner and others (1977) observed 12 species of ants, mostly woodland species, in two aspen forests in northern Minnesota.

Araneida (Spiders)

A third group of important forest floor macrofauna are the spiders. As with the beetles and ants, many species of spiders are known to be predaceous. Some species are associated with forest development and populations of many species are affected by fire.

Spiders and fire.--Several studies of the effects of fire on spiders have been made in this country; however, the most exhaustive research on spider-fire interactions has been done in Finland.

In the northern Rockies where a wildfire had been allowed to burn, Clayton (1975) found spiders to be more numerous in areas that had been burned than in control areas. Within the burned areas, spiders were definitely more numerous and more species were represented in a riparian woodland than on a south slope ponderosa pine savanna. Elsewhere in these proceedings, Fellin (1980b) reports the results of a recent study of the effect of prescribed burning and harvesting practices on spiders and other forest floor macrofauna in western Montana.

Reichert and Reeder (1972) studied the immediate and long-term effect of burning on spiders in Wisconsin prairies. They found that species active on the surface at the time of burning were eliminated, while those occupying subsurface burrows, or sacs under rocks or clumps of dense vegetation escaped thermal damage. The greatest decrease in numbers was noticed two weeks after the burn, followed by a slow increase. Even after 45 days, however, the numbers in the burn were not equal to those in the controls.

Reichert and Reeder (1972) recognize that some spider species may be indirectly affected by a burn through changes in the plant cover and that "seasonal activity patterns largely determine the different response of spider populations to the immediate effects of burning." They concluded that the abundance and species composition of spiders are both relatively stable, and that species inhabiting the prairie have adapted to the effects of periodic burning.

In other studies, Pearse (1943) considered spiders, along with roaches and ants, to be well adapted for existence in a burned area; but Rice (1932), Buffington (1967), and Heyward and Tissot (1936) thought spiders to be one of the groups least well adapted to burning. Algren (1974) cites several authors in reporting that spiders, primarily surface dwellers, are drastically reduced by fire in most areas, with population decreases of from 9 to 31 percent. In one study, Hurst (1970) reported an increase, primarily ground and wolf spiders, following fire.

Huhta (1965, 1971) has intensively studied ecology of spiders in the litter and soil of Finnish forests, mostly in relation to silvicultural practices and prescribed burning. He found that after clearcutting, the abundance of typical species decreased, and species foreign to the original fauna spread into the cutover areas; though the species were varied, the total numbers of individuals were about 60 percent less than in the uncut area (Huhta and others 1967). Following burning, which almost totally destroyed most of the original populations (Huhta and others 1967), the number of individuals remained continuously low and the composition of the fauna was unstable; most species were markedly less frequent after burning and occurred only sporadically in the burned soil (Huhta 1965). Between years 7 and 13, following cutting and burning, the composition of the spider community reverted towards the original forest situation. In a more recent study, Huhta (1976) confirmed his earlier observations that the density of spiders decreased considerably after clearcutting, but in two of his clearcut areas, he was not able to show signs of spider recovery.

Elsewhere in Europe, Brabetz (1978) studied the effects of controlled burning in some uncultivated grasslands. In March and April of 1975 and 1976, two parcels of land (20 x 56 meters) were burned, and two parcels set aside as a control. In the spring and summer after the first burning, significantly more spiders were trapped in the burned area; however, after the second burning, spiders were more numerous in unburned areas.

Spiders as predators.--Studies have shown that several species and groups of spiders are associated as predators of the spruce and jack pine budworms. Though all of these studies have involved spiders in the arboreal, rather than the forest floor environment, many species do move from the duff and litter onto the boles and into the crowns.

Some studies began when it was discovered that spiders constituted about 90 percent of the total invertebrate predator fauna and that in New Brunswick spider populations may have been as high as 250,000 per acre. These early studies indicated: 1) a functional response of spider predation to budworm populations, 2) a seasonal pattern of predation, 3) the relative importance of various spider families, and 4) an explanation for previously unknown mortality. Investigators established that spiders may significantly influence budworm populations (Loughton and West 1962; Loughton, Derry and West 1963).

In a study of invertebrate predators of the jack pine budworm, Allen (1968) collected 51 species of spiders representing 15 families from the foliage and bark of jack pine; of those collected, nearly 75 percent were 5 families of hunting spiders with some potential as predators (Allen and others 1970). Several species of the important groups collected on the tree boles were actually ground dwellers that foraged on the boles and exerted some predatory influence. The spiders were commonly observed below tanglefoot barriers or scurrying around the bases of trees in the duff.

Although it has been reported that the selection of moving prey by spiders precludes their having any effect on the egg stage of the budworm (Loughton, Derry and West 1963), it has been recently determined that spiders do prey on spruce budworm egg masses (Jennings and Houseweart 1972).

The impact of spiders as predators of other soil-dwelling invertebrates is poorly known (Wagner and others 1977), but there are some data that spider predation is an important subtractive process acting on populations of some fauna. After removing spiders from enclosed experimental areas, Clarke and Grant (1968) found centipedes and Collembola, known spider prey, at higher densities than in the controls. Millipedes, not taken by spiders, were not consistently higher on areas where spiders had been removed. Although one spider species is reported to prey on certain species of carabids, ground beetles do not account for a large part of the prey (Thiele 1977).

Spiders and the forest environment.-Tolbert (1975) studied the preference of insects and spiders inhabiting the forest floor on one or more slopes and aspects on a small mountain in the Southeast. He found 20 of 34 species demonstrated shifts to slopes offering different exposures with time. Southfacing slopes were preferred by 50 percent of the species collected, while southeast and northwest exposures were least preferred. Tolbert (1975) recognized that since plants have distributional preference, the herbivorous arthropods may have been responding to specific food plants rather than slope conditions. Likewise, predaceous species may have been responding to the distribution and abundance of prey.

Physical aspects of deciduous forest litter habitat, either as structural micro-habitats or refuges from predation, are suggested as being important in regulating within-habitat species diversity with some species of wandering spiders (Uetz 1975). A distinct litter layer is important in the seasonal and daily activity of forest floor fauna in different habitats; the layer, in wooded areas, provided extra food and retreats during periods of inactivity (Williams 1959b).

During four stages in the development of red pine plantations, spider and harvestmen (Phalangida) made up about one third of the arthropod fauna during the first two stages--establishment and transitional. However, in the latter two stages--macroculture and young forest--of community development, spiders made up 50 percent of the total arthropod fauna (Martin 1965).

Forest Soil Mesofauna

Many studies, principally in North America and Europe, have dealt with the effect of harvesting, and residue management, and fire management on forest soil biota. Most of the research has involved the effect of fire, both prescribed and wildfire, on soil mesofauna, but some investigators have studied the response of mesofauna to silvicultural practices. There is a general feeling that harvesting stimulates the development of soil organisms, while prescribed fire substantially reduces populations, at least temporarily. Recovery is usually fairly rapid, especially in the upper layers of soil (Bell and others 1974). I will review the studies of harvesting, residue management and fire as related to soil mesofauna by geographic regions, and conclude the section by discussing soil and surface temperature during fires and its effect on mesofauna.

RESEARCH IN WESTERN UNITED STATES

In the northern Rockies, Fellin and Kennedy (1972) studied the relative abundance of forest soil fauna 1, 2, and 3 years after western white pine forests were clearcut and prescribed burned. Considering all taxa, the total number of individuals collected in samples from the 1962 burn was nearly half again as great as samples from either the 1961 or 1960 burn. Excluding the mites (Acarina), arthropods in samples from the 1960 burn outnumbered those from the 1961 burn by more than five times and were nearly four times more abundant than those from the 1962 burn. The Acarina--which comprised 77 percent of the total fauna--were most abundant on the 1962 burn, more than twice as numerous as on the 1960 burn, and 25 percent more abundant than on the 1961 burn.

A recent study investigated the effects of harvesting and residue management practices, including prescribed fire, on forest soil mesofauna in northwestern Montana. Partial results of that study are presented elsewhere in this proceedings (Fellin 1980c).

Vlug and Borden (1973) studied soil Acari and Collembola populations for 1 year in clearcut areas that were burned and not burned, and in adjacent unlogged areas, in a coastal British Columbia western hemlock and western redcedar forest. They found the density of mites, Collembola, and other arthropods was reduced by logging, and was even further reduced by slash burning. Population levels and diversity in the logged and burned areas was relatively high, however, indicating that neither treatment induced total mortality. Moreover, there was a rapid reinvasion of treated areas. The density of some mites and of one family of Collembola in the litter and upper two layers of soil was progressively reduced by logging and slash burning, but population densities increased in the third and fourth soil levels. This indicated that either migration to deeper levels or adaptation to conditions further below the surface had occurred.

At least two studies have been made of mesofaunal populations in California forest soils. Price (1973), in a study of the fauna in the organic and upper soil layers under a ponderosa pine stand near Grass Valley, Calif. showed a population density of about 200,000 arthropods per square meter of forest floor. About 150 species were encountered, mostly mites (primarily oribatids), followed by springtails (Collembola). Wenz (1976) investigated the effects of wildfire on forest soil microarthropod populations in California. He found that of two wildfires studied both reduced virtually all arthropod groups, and the effects were still evident 2 and 3 years after the fires.

RESEARCH IN EASTERN UNITED STATES

Some of the most comprehensive research in this country on the effect of silvicultural practices and prescribed fire on soil mesofauna has been conducted by Metz and his co-researchers (fig. 14). Metz and Farrier (1971, 1973) presented the first information concerning the effects prescribed burning of forest residues has on forest soil mesofauna under defined conditions and frequency. Metz and Farrier define the forest floor as all organic debris overlying the mineral soil, and divide it into three layers: the L, or litter layer, made up of freshly fallen undecomposed material; the F, or fermentation layer, consisting of partially decomposed L still recognizable as to origin; and the H, or humus layer, consisting of well-decomposed organic matter unrecognizable as to origin.

In their first study (1971), they found that mite populations were reduced more in the surface 3 inches (75 mm) of mineral soil than in the forest floor, while numbers of collembolans decreased in the forest floor with little change in the mineral soil. In 1973, Metz and Farrier studied mesofaunal populations in unburned areas and in periodically and annually burned areas. They found annual burns had the most serious impacts on animals, while the number of animals on the periodically burned plots was significantly greater. The number of animals in the controls was not significantly different from those in the periodically burned areas. They conclude that there are more mesofauna 1) in a coniferous forest floor than in the soil beneath it, 2) in the surface of the mineral soil than in the underlying layers, 3) in the lower layers of the forest floor than in the surface, and 4) when sampled immediately before and after burning on annually burned plots, the number of animals was reduced drastically. Metz and Farrier (1973) point out that there are no data in the literature to indicate that their results are applicable to other forest types or burning regimes.

Hill, Metz, and Farrier (1975) reviewed the effects of four silvicultural practices--fertilizers, insecticides, fire, and cutting--on forest floor mesofauna. With respect to fire, they note that when fire destroys much of the forest floor, the mesofauna are considerably reduced, either as a result of death from heat and suffocation or by the removal of much of their food supply and living space. They indicate that light prescribed burns where only the L and part of the F layers are consumed, and where there is no erosion problem, have no lasting effects on mesofauna, but that the effects of wildfire are more drastic and longer lasting. Metz and Dindahl (1975) report that species diversity of collembolans was increased by both annual and periodic fires. Concerning cutting (mostly clearcutting), Hill, Metz and Farrier (1975) after citing somewhat contradictory results of several studies, indicate that mesofauna usually are decreased after cutting, and slowly return to normal after a number of years.

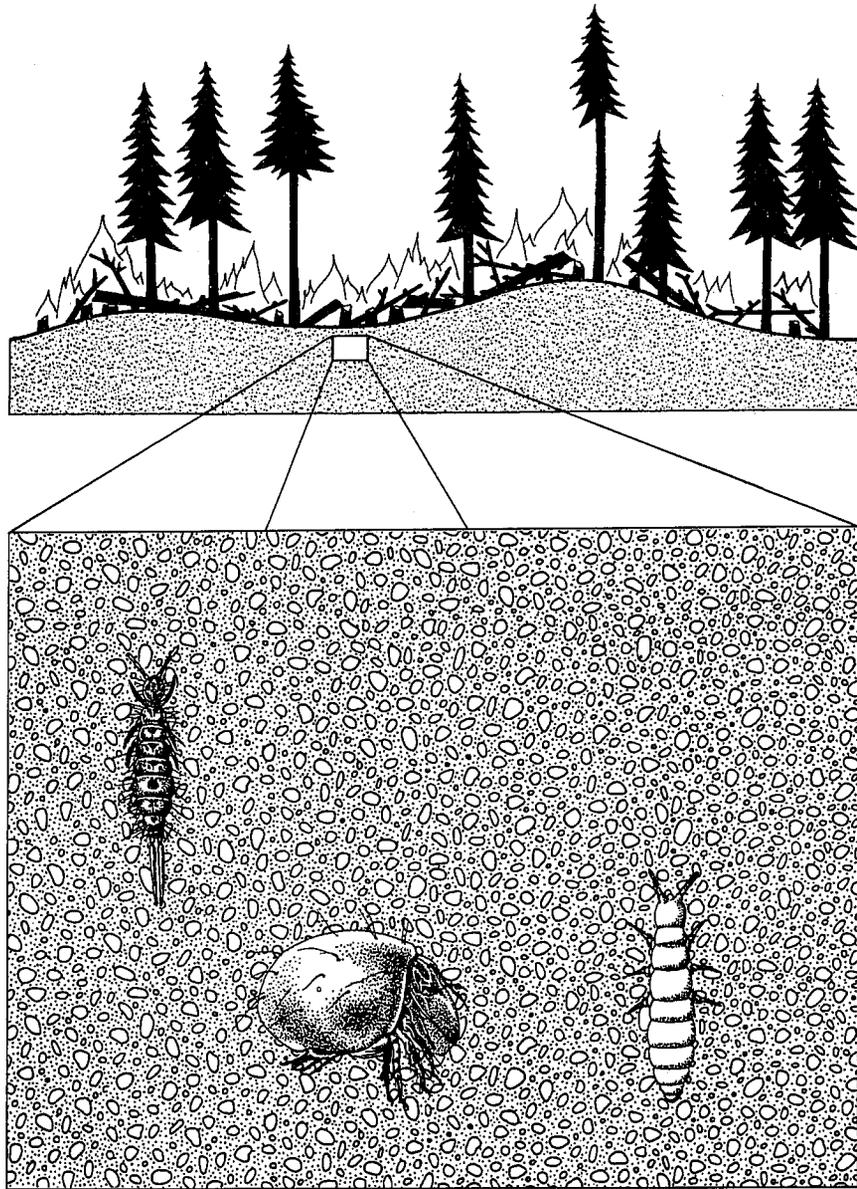


Figure 14.--Prescribed burning of forest residues under a shelterwood silvicultural system. Harvesting and silvicultural practices, as well as various residue management treatments, including prescribed fire, have differential effects on soil arthropods. Collembola and mites are the predominant groups of soil arthropods and most species are decidedly beneficial.

In the long-leaf pine forests in the southeast, Heyward and Tissot (1936) compared fauna from "areas protected from fire for 10 years or longer and similar soils subjected to frequent fires." They found 5 times more mites and collembolans in the forest floor of the non-burned than the burned-over areas. In both the A₀ horizon and the upper 5 cm of mineral soil, mites and collembolans were 11 and 3 times more abundant, respectively, in the non-burned than in the burned areas. They also found that mites made up between 71 percent and 93 percent of the fauna in unburned soil, and between 30 percent and 72 percent in burned soil, depending on depth. Rice (1932) also found that mites and *Collembola* are reduced by burning.

Pearse (1943) hand sorted samples taken every 3 months from sites where litter had been burned over, raked off, or left undisturbed in North Carolina. His samples were 36 feet square (3.3 m²) and 6 inches (150 cm) deep. In all instances, he found the largest populations of both mites (90-95 percent) and collembolans (85-94 percent) in the forest floor and surface inch (2.54 cm) of mineral soil.

RESEARCH ABROAD

The majority of research concerning harvesting, residue, and fire management and soil mesofauna has been conducted by European (predominantly Scandinavian) researchers; one study is reported from Australia.

In Finland, Huhta and others (1967) found that the changes in the soil fauna as a result of clearcutting were not too significant. They found a decrease in the number of individuals, but the same species were dominant. The number of species, in fact, increased because of an influx of new species from surrounding areas. Huhta and others (1967) demonstrated that burning of the residues following tree harvesting was very destructive to all groups of soil animals, and that the soil and humus environment could be so changed that the reinvasion by soil fauna could be delayed. They found that many groups were permanently affected--oribatid populations were low for 7 years after burning--but they suspected that other animal groups might find conditions more favorable after the burning and would experience a more or less temporary population resurgence if the organic layer was deep enough to remain at least partly unaffected by the fire. In a later study, Huhta and others (1969) found the populations of some mites and *Collembola* to be greater in burned areas.

Burning has been shown to have some rather drastic effects on one family of mites--the Oribatidae. A year following the burning of residues on clearcut forests with thick, raw humus layers, populations of oribatid mites were greatly reduced (Karpinnen 1957), showed no signs of recovery 5 years after the burn, and were still at low levels 7 years after burning (Huhta and others 1967, 1969). The steep decline in oribatid mite populations following burning persisted. In deep layers of soil, oribatid populations were still below pre-burning levels 27 years after the burning (Karpinnen 1957).

In a more recent study of the effects of clearcutting, Huhta (1976) found that the biomass of soil invertebrates was at or even below original levels, 9 to 13 years after cutting.

Another Scandinavian investigator reported mites to be more numerous in unburned than in burned forests in northern Sweden, but ascribed the difference to normal population variation (Forsslund 1951).

In a study in Austria, mites were found to be less abundant in burned, than non-burned, areas (Jahn and Schimitschek 1950).

Following a wildfire in Australia, soil faunal populations in severely burned areas were reduced when compared to populations in lightly burned areas (French and Keirle 1969).

Summarizing essentially European research, Bell and others (1974) reported that all available research indicates that numbers of soil organisms (all biota) in general are greatly stimulated by cuttings. Often, in some Scotch pine, Pinus sylvestris, stands after both shelterwood and group selection felling, the stimulation increases with the intensity of the felling. However, the response of soil fauna to cutting, residue treatments, and fire treatments appears to differ from the response to cutting only, by all biota, as Bell and others have reported.

MESOFAUNA CAN SURVIVE SURFACE FIRES

Several investigators have reported that many soil-inhabiting animals can survive surface fires. In the Southeast, Heyward and Tissot (1936) indicated that even very hot surface fires rarely heat the underlying soil beyond 176° F to 194° F (80° C to 90° C) at a depth greater than 1/4-inch (0.62 cm) below the surface. According to Heyward and Tissot (1936), "...if either the animals themselves or their eggs were only 1/4- to 1/2-inch (1.2 cm) beneath the soil surface, they would stand in excellent chance of escaping harm during the fire."

A recent study on an experimental area where clearcut logging slash exceeded 100 tons/acre, prescribed burned in late July, during hot, dry weather in the northern Rocky Mountains, showed that an extremely hot surface fire can generate temperatures as high as 300° F (149° C) at a depth of 5/8-inch (16 mm) (R. C. Shearer, personal communication). No doubt, most insects would have to have been deeper than 5/8 inch under the soil to survive such temperatures. However, because the intensity of heat varied, average and maximum temperatures at a depth of 5/8-inch in parts of the burn were considerably lower, and soil insects in these portions of the burn could have survived.

Reichert and Reeder (1972) found surface temperatures during fires in prairies to be between 120° C and 200° C, and the duration of lethal temperatures was short-- 70 to 140 seconds. Subsurface soil temperatures at 0.5 and 1.0 cm (16° C to 20° C) were virtually unaffected by the brief heating at the surface. Reichert and Reeder (1972) suggested that spiders below the soil surface are well protected from direct heating, and usually could escape heat damage.

Brown and Davis (1973) noted that the heating of soil by fires to a level lethal to living protoplasm usually occurs only close to the soil surface. They continue, "repeated fires can reduce the number of soil organisms near the surface, while increased average soil temperatures following burning can increase the number of organisms present." Coultz (1945) found that in the top inch of South African veld soil populations of a majority of the invertebrate species survived burning.

RESIDUES, FIRES, INSECTS, AND FOREST SUCCESSION

It is generally accepted that northern Rocky Mountain forests have evolved in the presence of repeated fires. The pattern of forest succession following fires in the northern Rockies has been defined as "...a sequential development of vegetation in which the more rapidly maturing and often shade-intolerant plants assume initial dominance, and, in turn, are dominated by taller, slower growing, and often more shade-tolerant species" (Lyon and Stickney 1976).

Natural fires have been a major influence on plant succession (Houston 1973). However, there is evidence that suppressing fires in areas managed for "naturalness" may be a serious disruption of natural processes (Mutch and Aldrich 1974). In Yellowstone National Park, a reduction in fire frequency through fire suppression has resulted in a greater expression of "climatic climax" vegetation, and forest succession has changed the relative abundance of species and increased the density and distribution of forests. Conifers have increased, but conifer succession could be returned to a more natural state if fire was either reintroduced (Houston 1973), or allowed to more nearly play its natural role; fire has always been present but its role has been seriously limited due to successful fire control (W. C. Fischer, personal communication). Early photographs in the Selway-Bitterroot Wilderness show numerous forest successional stages, attesting to the past incidence of fire, but more recent photos indicate "...a loss of lifeform diversity because of a gradual homogenous character resulting from fire suppression activities" (Davis 1977).

There is recent, growing interest in the natural role of fire as an influence on ecosystems, particularly in wilderness and other areas managed more for amenity values than for timber production. There is particular interest in the effect of periodic fires in maintaining stands of fire-dependent trees and in the diversity of the forest in general (Habeck and Mutch 1973). These interests are reflected both in the National Forest Management Act and in the revised Forest Service fire management policy, which has evolved from one of fire control to fire management (USDA, FS 1978b). The fire management policy allows that certain wildfires can be designated as prescribed fires if they burn under pre-selected conditions and in pre-determined areas--called fire management areas.

These interests and concerns, along with current fire management policies, have serious implications relative to forest residues and associated insect and disease interactions, to successional changes in our forests, and to our principal forest insect and disease problems in the northern Rockies. If we accept that natural ecosystems have evolved in the presence of fire and are at least partially dependent on fire for continued survival, we must also accept that animals, including forest insects, living in these fire-adapted ecosystems may also be adapted to the presence of fire (Clayton 1974). Hard (1974), in discussing northern coniferous forests in southeast Alaska, points out that the folly of indiscriminate control of all wildfire is analogous to the policy of "controlling" insect outbreaks, and says, "the lesson here is that it may not always be wise to attempt to control a factor that is an integral part of a natural system."

The most significant forest residue-fire-successional interactions with forest insects in the northern Rocky Mountains involve the mountain pine beetle and the western spruce budworm. The interaction of the role of fire, the succession of lodgepole pine, and the mountain pine beetle is very complex. In this region, light-medium fires and the mountain pine beetle are responsible for successional developments in lodgepole pine stands and for the maintenance of lodgepole pine as a widespread forest type (D. Cole 1978). Foresters trace the current mountain

pine beetle problem in the northern Rockies to catastrophic (stand replacement) fires of nearly a century ago. They (the fires) triggered the growth of large stands of lodgepole which are now about the same age over vast areas of western Montana, northern Idaho and in Yellowstone National Park (Kuglin 1980). At this time, an appreciable percentage of lodgepole pine stands, near and east of the Continental Divide in Montana, contain from two to several age classes, mainly because of the mountain pine beetle/fire history and severe conditions that excluded other species (D. Cole 1978) (fig. 15).

In many areas where natural fires have been suppressed, forest residues resulting from mountain pine beetle epidemics accumulate until hot fires occur. According to D. Cole (1978), "such fires are normally more destructive than ones that would have otherwise occurred if fires had not been suppressed, and they tend to perpetuate future extremes in the mountain pine beetle/lodgepole pine/fir interactions." Several opinions have been expressed that the bark beetle epidemics now rampant in the Rockies and Intermountain West may be a product of fire exclusion (Schwennesen 1979). In Glacier National Park, the mountain pine beetle epidemic took such a strong hold because fire suppression programs were so successful and trees that ordinarily might have burned are now mature and ripe for the beetles (Kuglin 1980).

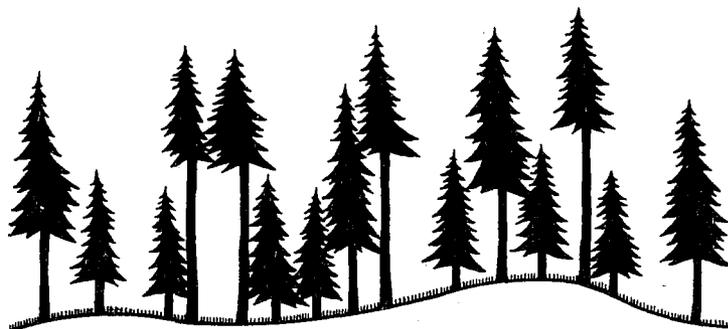


Figure 15.--Along the Continental Divide in Montana, an appreciable percentage of pure lodgepole pine stands contain from two to several age classes, mainly because of the mountain pine beetle-fire history and severe site conditions (D. Cole 1978).

Western spruce budworm infestations in the northern Rockies are influenced not only by the interaction of forest residues, fire and succession, but also by the interaction of the budworm and the mountain pine beetle. One recommendation for ameliorating the impact of the western spruce budworm is to return the more xeric Douglas-fir sites to pine (Williams and others 1971). However, in many young ponderosa pine stands, the mountain pine beetle not only kills many desirable crop trees and creates understocking in the stand, but also appears to be converting the stands from ponderosa pine to Douglas-fir (McGregor 1973). This succession could predispose such stands to be more susceptible to the western spruce budworm. The same successional situation can be created by silvicultural practices that harvest pine and favor Douglas-fir or the true firs.

In the spruce-fir stands infested with the eastern spruce budworm in the Maritime Provinces, fire is also involved in the successional relationships. In the absence of fire the budworm kills primarily shade-tolerant trees, and these species tend to regenerate. If fires occur often within the regeneration period, the shade-intolerant species regenerate instead, and these species are less preferred hosts of the eastern spruce budworm (Flieger 1970). Essentially, then, in eastern Canada, in the Lake States, and in other areas where the spruce budworm occurs, outbreaks may have been less prevalent in primeval times because fire may have curtailed the expansion of shade-tolerant climax species.

In the West, the fire-residue-insect-successional interaction also influences outbreaks of the Douglas-fir tussock moth. Forest managers and investigators have been concerned that fire exclusion in some coniferous forests may have increased the susceptibility to the Douglas-fir tussock moth by allowing the number of true fir understory components to increase (Kickert and others 1976). In studying the last two tussock moth outbreaks in Oregon and Washington, Williams (1978) found infestations most common in stands, where fire was excluded. There, fir stands developed under the pine and eventually dominated the site--a site ordinarily too dry for either Douglas-fir or true firs. Recently, research has begun to see if fire could, in fact, be used to reduce Douglas-fir tussock moth damage by preventing growth of susceptible Douglas-fir and true firs on sites more suitable to pine (Martin and others 1972).

Fire, understory, and residue created by beetle attacks are also involved in the successional interactions of the western pine beetle and ponderosa pine. Weaver (1943) believed that fires, in combination with pine beetle attacks, frequently controlled the density, age classes, and composition of ponderosa pine stands. He also seems to have answered a question asked by land managers: "Would fire exclusion in ponderosa pine stands yield denser stands and more host material for bark beetles?" (Kickert and others 1976). Weaver (1951, 1955) indicated that as a result of fire exclusion, more intolerant white fir, incense cedar, Libocedrus decurrens Torr., and western larch increase and develop into densely reproducing stands that compete with the overstory pines for moisture, thus predisposing the overstory pines to bark beetle attacks.

In other situations, wildfires in forest residues created by beetle-killed pine have killed reproduction, changing the pine habitat to an aspen type. The pines eventually return, along with fir and spruce; the pines eventually are killed by the western pine beetle, leaving only the fir and spruce (Craighead 1925).

Another interesting fire-forest residue-successional interaction involves insects causing deterioration in fire-killed trees in the Pacific Northwest. Excessively dry or wet fire-killed trees do not attract insects. In a normally dry forest, recurring fires keep down regeneration, allowing fire-killed trees to become too dry. In normally wet coastal forests, fire-killed trees protected by the cover of a green forest are too wet for the deterioration causing insects; however, if recurring fires destroy the cover, the dead trees will dry out enough to become attacked (Kimme and Furniss 1943).

In a longleaf and slash pine, Pinus caribaea Morelet, forest in the southeast, the only known epidemics of engraver beetles, Ips spp., occurred in a stand that had not been burned annually for over 70 years. Transpiration by mixed hardwoods that in other areas had been removed by prescribed burning apparently weakened the pine, predisposing them to attacks by the engraver beetles (Komarek 1970).

The use of prescribed fire to disrupt normal succession patterns and control understory vegetation (Martin and others 1977) often has beneficial effects on forest insects, such as described above, with Ips problems in pine and aspen stands in the southeast. The use of fire in itself, besides reducing shrubs and herbaceous plants to increase tree growth (Martin and others 1977), has serious implications for forest insects. Fire exclusion could influence the incidence of parasitism in some cases by altering the species composition of flowering and fruit-bearing ground cover which is important as a food source for adult parasitoids, such as the ichneumonids. In other cases, fire exclusion could influence cone-seed or other "harmful" insects that spend part of their life cycle in the litter (Kickert and others 1976).

SOME MANAGEMENT IMPLICATIONS

Throughout this paper, I have described some of the interactions and relationships between harvesting, forest residues and fire management, and forest insects (to a lesser extent, diseases), particularly in the northern Rocky Mountains. I also have selected and described some classic, or at least representative, examples of some of these interactions. I will discuss three management implications of these varied interactions: management of forest residues, fire management, and silvicultural practices.

Management of Forest Residues

From the discussions above, it is apparent that forest residues constitute a habitat, substrate, and food for a wide variety of insect species--some "harmful", and some "beneficial"--as well as for a variety of decay organisms, many symbiotically associated with one or more insect species. In the northern Rocky Mountains and elsewhere, there are management implications associated with both natural and man-made residues that involve what we may call "harmful" insects.

NATURALLY CREATED RESIDUES

At least four significant natural factors create residues in the northern Rockies--insects, windthrow, fire, and diseases. I will discuss the first three.

Residues Created by Insects

Without a doubt, at this time the most serious and far-reaching management problem attributable to insect-created forest residues concerns the millions of dead lodgepole pine (standing and prone) killed by the mountain pine beetle.

Recently, Senator John Melcher (Montana) sponsored a controversial bill to encourage better utilization of forest residues. The bill would encourage the sale of wood residues left after harvesting, all of which would be hauled to a central collection yard and sold. Melcher's bill was prompted by the fact that many western forests are infested with the mountain pine beetle. Melcher has said, "that wood should be harvested now so we can get on with forest regeneration." He has emphasized that there are markets for dead trees, and "I believe the Forest Service should expedite the harvesting of these trees before rot, wind, or fire further diminish their value" (Hodges 1979). "Beetle-killed lodgepole can be harvested for several years but there is substantial devaluation" according to Jack Usher, former Timber Management Chief in the Northern Region of the U.S. Forest Service (Kuglin 1980). Dead lodgepole produces sawlogs with splits, and the beetles also stain the wood with a fungus which reduces the value.

The harvest-salvage of mountain pine beetle-created residues in lodgepole pine forests may have far-ranging resource management implications. Although the Forest Service is in some areas responding to the problem by accelerating timber harvest to salvage beetle-killed timber and making uninfested stands "beetle-proof", "this means more roads, more clearcutting and more complaints from environmentalists" (Kuglin 1980). On the positive side, foresters say that the beetle "epidemic gets rid of old trees and permits regeneration of other species, opens meadows which provide elk and deer forage and even provides housing for snag-nesting birds" (Kuglin 1980).

Residues Created by Windthrow

Should Melcher's bill pass and become law, its effect on forest management plans in the Northern Region would be similar to that created by the thousands of acres of Engelmann spruce that were windthrown and relegated to residue and to subsequent infestations by the Engelmann spruce beetle in the northern Rockies in 1949. I have discussed the residue utilization, biological, socio-political, and forest successional aspects of this Engelmann spruce beetle problem, as well as other implications in the Rocky Mountains of windthrown Douglas-fir, Engelmann spruce, and ponderosa pine. I have also discussed some of the entomological and management implications of windthrown timber in the Pacific Northwest.

Although at this time there are no serious, widespread insect problems associated with forest residues caused by windthrow, any future windthrow-created residues will have even more significant forest insect management implications because of the economics of residue utilization, and current markets for forest residue.

Residues Created by Fire

The most important management implication related to fire-created residue concerns the prompt salvage, or harvest, of fire-killed or fire-weakened trees. The early removal of these trees is necessary for two reasons. Fire-killed or fire-weakened trees are more likely to be attacked by a variety of wood borer species; subsequent riddling of wood and the associated deterioration-causing fungi can rapidly degrade these trees for lumber and other products. In one sense, woodboring species are very beneficial in that they are the primary fragmenters in the natural cycling process that transforms residues into humus and soil. It is

only when wood borers compete with man for material having economic value that they become "harmful." Because of a drier climate, neither the borer nor the associated deterioration problem is as acute in the northern Rockies as in the Pacific Northwest.

The second reason for promptly removing fire-weakened trees is to prevent the buildup of bark beetle populations that often spill over to attack and kill green trees in surrounding forests. Oftentimes, the speed at which fire-killed or fire-weakened trees need to be removed is determined not only by the species of insect involved, but also by the tree species involved. The problems of insects in fire-killed or fire-weakened trees is of increasing importance since more prescribed burning is being done in partial cuttings (W. C. Fischer, personal communication). Fischer (In Press) discusses in detail the fire management implications of bark beetle problems in ponderosa pine stands.

RESIDUES CREATED BY MAN

Although usually not as serious or widespread as residues created by natural factors, man at times has created management problems for himself in the form of residues generated by harvesting or thinning operations. With some conifers, particularly ponderosa and lodgepole pines, managers need to be aware of potential problems with engraver beetles and to pay particular attention to weather conditions and the time of year when thinning or harvesting creates residues.

Entomologically speaking, there is still some disagreement, and apparently always has been, concerning the hazards of forest residues in attracting large numbers of tree-killing insects--often serving as a breeding medium for some pest species--and the use of prescribed fire in managing those residues. We have already pointed out some of the varying philosophies of using prescribed fire to manage residues in the late teens and early 1920's. Recently, Mitchell and Sartwell (1974) pointed out that according to some and in some regions, the threat of outbreaks posed by insects breeding in residues is generally overrated. They went on to say:

"Conclusions are that certain residues in Douglas-fir and ponderosa pine often create serious pest problems that should be considered in residue management programs. But the beneficial aspects of insects associated with residues may have more significance to man's objectives in the long run."

In terms of the impact of residue management on beneficial organisms, our concerns at the present time seem to be 1) the relative merits or drawbacks of removing all or most forest residues from a site, either mechanically or by prescribed fire, particularly in terms of impact on forest soil biology; and 2) how silvicultural treatment, superimposed on residue treatments would affect insect and disease relationships.

Most research has shown that fires reduce the populations of most soil and forest floor fauna, the majority of which are generally beneficial. Complete utilization, or removal of residue by prescribed fire, both act indiscriminantly and nonselectively on beneficial organisms. The disruption of beneficial arthropods would have potential long-term consequences on all phases of residue decomposition and nutrient cycling; these consequences should be considered in residue management

plans. Since fire, too, is a decomposing and nutrient cycling agent, the need for decay and nutrient cycling organisms could be diminished for a short period of time following fire.

The decimation of beneficial insects could be prevented, or at least ameliorated, if burning were done so that patches of material could be left, from which the burned areas could be repopulated. Partial utilization and/or light burns under a partial cutting, shelterwood, or selection prescription, may achieve the manager's objectives as well as provide more optimum conditions for beneficial forest insects and fungi.

Fire Management

Our past preoccupation with attempting to suppress all wildfires may have had some subtle, but serious, influences in predisposing some of our northern Rocky Mountain forests to insect and disease infestations, through the disruption of natural fire, insect, and disease, successional processes.

Recently, researchers have expressed concern and have attached considerable importance "...to the problem of genetic response of plants to changes in natural fire frequency and the form taken by adaptations to fire to sustain species diversity and ecosystem stability" (Kickert and others 1976).

Howe (1974) presents examples of how some trees and shrubs cannot assume their natural ecological roles in the absence of fires because of mechanisms that have developed specifically in response to the selection pressure of fire. One possible adaptive mechanism (though perhaps less obvious than others) concerns the control of native insect and disease pests, which may prevent the development of strong genetic resistance in trees. "That is," Howe (1974) states, "fire may have consistently removed the selection pressure of an insect or disease pest before enough host generations were exposed to it to build genetic resistance."

"Forest protection" usually and historically encompasses fire, insects, and diseases. It appears that our past wildfire control policy, though necessary to prevent serious economic loss, may have predisposed forests to insect and disease problems, the other two targets of our forest protection efforts. The implications for management are that the diversity of ecosystems as a result of past wildfires has been gradually replaced by more homogenous forests because of fire suppression activities.

D. Cole (1978) suggests that a deliberate program of fire management and prescribed fire can be instituted to moderate the mountain pine beetle-lodgepole pine-fire interaction cycle. His premise is that both wildfire and prescribed fire management plans can be developed to use fire to "create a mosaic of regenerated stands within extensive areas of large timber that have developed." D. Cole (1978) believes that prescribed fires can create these ecosystem mosaics more effectively than wildfires. With the recent change from fire control to fire management, managed wildfires will be, in fact, prescribed fires.

Silvicultural Practices

Five years ago, one researcher summed up the implications of silvicultural practices on insect and disease problems; in my opinion those implications are equally applicable today. The discussion that follows is essentially from Hard (1974).

The forest manager's current, most realistic approach to insect and disease management in virgin stands, based on biological and economic considerations, may be to do nothing to suppress widespread outbreaks. Perhaps we should let outbreaks run their course, but establish a flexible harvesting policy that permits salvaging good quality timber in damaged areas and converting non-productive old growth to more productive even-aged stands (Hard 1974). In their most recent plan for the management of the western spruce budworm in the Northern Region, resource managers have, in fact, selected the alternative of "current management" (interpreted by some as "do nothing") in many western budworm-infested forests (USDA, FS 1977).

Silvicultural practices and other stand manipulations are a desirable alternative in averting potential pest problems. However, "since many of the requirements and limiting factors for the potential pest species are as yet unknown, effective silvicultural practices cannot always be prescribed" (Hard 1974).

Notwithstanding these unknowns, the manager's goal in insect and disease management in intensively managed stands should be prevention, and, if necessary, suppression. As Hard (1974) has said, "Probably the least expensive approach in the long run, environmentally as well as monetarily, is to anticipate pest problems and attempt to forestall them through cultural manipulations of the forest and natural control factors."

There are several elements of silvicultural practices that have implications in resource management. Two of them are 1) insect and disease resistance and 2) changing forest insect problems.

INSECT AND DISEASE RESISTANCE

In some respects, knowledgeable harvesting can replace pests and fire in accomplishing desired genetic turnover. Pest resistance can be encouraged through prescribed fire management procedures that promote consumption of infested residue while protecting potentially resistant trees. Where non-infested residues have accumulated in sufficient quantity (Harvey and others 1979), they represent an opportunity for increasing fiber production from our forests. Therefore, through intelligent harvesting, prescribed fire, and residue management, we have an opportunity to increase productivity of our forests and possibly raise the pest resistance level of second- and third-generation forests.

Accumulation of resistance can also be enhanced through planting resistant stock and protecting this resistant stock from wildfire. Geneticists and managers must realize, however, that in accepting pest-resistant strains or increased productivity of genetically improved varieties, we are substituting artificial for natural evolution, and because of this artificiality, we must watch for unforeseen problems in the future. Until we know more, extensive plantings of an improved or resistant strain should be avoided, and some mix of varieties maintained, even if growth potential or pest resistance is sacrificed (Shea 1971).

Insects, diseases, and their host trees have evolved together for centuries, each responding to changes in the other. Though antagonistic to individual trees, insects and diseases may be beneficial to the virgin forest ecosystem, acting not as intruders, but as a natural, and necessary component of the system.

As more virgin forest is harvested and converted to managed stands, what once were only potential insect and disease pests may become real pests for a variety of reasons, primarily because of increased competition with the forest manager for a resource in which he is investing time and money and expects maximum return (Hard 1974).

One might concur with Heinselman (1970) that fires have destroyed many old forests and kept a significant proportion of each region in young stands, and that these young stands are less susceptible to certain insects and diseases. However, it is equally important to point out that young, intensively managed stands are much more susceptible to some pests than are old-growth forests.

Young, intensively cultured forests differ markedly from the natural forests. Therefore, it is not surprising that new insect and disease problems are arising. In the past, managers have focused their attention primarily on pests that kill trees; now and in the future, we must place greater emphasis on pests that reduce growth or predispose trees to other damaging agents (Shea 1971).

RESEARCH NEEDS

The most significant and widespread forest insect problems in the northern Rockies at this time are the western spruce budworm and mountain pine beetle. Nearly all of our entomological research efforts and a sizeable silvicultural research effort is being directed toward these two pests. The entire spruce budworm effort, and a sizable portion of the mountain pine beetle research, is entomologically-silviculturally oriented. The research needs for these two insect species are, compared to the overall insect research effort, relatively well-covered.

Two other areas related to residue and fire management merit additional research: forest floor and soil arthropods, and insects affecting regeneration.

With respect to forest floor and soil arthropods, we need information on 1) specific habitat requirements, life histories, and interspecies relationships of key faunal species or groups; 2) group systematics; 3) roles and importance of groups in nutrient cycling and conversion of residue to humus and soil; 4) influence of physical factors on reinvasion and reproduction rates in burned areas; 5) effects of various residue management and silvicultural practices; and 6) the ways in which soil, litter, or residue can be treated to reduce or ameliorate the impact of "harmful" insects or disease organisms that complete at least a portion of their life cycles in one or more of these substrates.

We know very little, in some cases nothing, of the role forest insects and diseases play in the management of young forests of seedlings, saplings, and pole-sized trees in the northern Rocky Mountains. If we wish to minimize damage and losses caused by these agents in young coniferous stands, where much of our forest management effort is directed, more research must be devoted to the study of the biology, ecology, and impacts of insects and diseases affecting forest regeneration.

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