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FIRE AND INSECTS IN NORTHERN AND BOREAL FOREST ECOSYSTEMS OF NORTH AMERICA

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ABSTRACT

Fire and insects are natural disturbance agents in many forest ecosystems, often interacting to affect succession, nutrient cycling, and forest species composition. We review literature pertaining to effects of fire-insect interactions on ecological succession, use of prescribed fire for insect pest control, and effects of fire on insect diversity from northern and boreal forests in North America. Fire suppression policies implemented in the early 1900s have resulted in profound changes in forest species composition and structure. Associated with these changes was an increased vulnerability of forest stands to damage during outbreaks of defoliating insects. Information about the roles that both fire and insects play in many northern forests is needed to increase our understanding of the ecology of these systems and to develop sound management policies.

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INTRODUCTION AND OVERVIEW

Forest conditions in northern and boreal forests of North America are dynamic, continuously changing in response to disturbance within the limits set by climatic, physiographic, and edaphic factors. Both fire and insects are critical and intrinsic components of forest ecosystems, affecting species composition, nutrient cycling, and numerous other ecological processes. Interactions of fire and insects can delay or redirect forest succession and can have significant consequences for forest productivity and biological diversity.

Fire can affect insects by killing them directly or by altering soil properties, overstory or understory vegetation, tree density, or other aspects of their habitat (93, 97, 112). Many insects, particularly those that are associated with boreal and northern ecosystems where fire is frequent, have evolved their own strategies for surviving fire or recolonizing burned areas (29, 44, 112, 129).

Insect outbreaks can also dramatically affect the likelihood and severity of forest fire. Feeding by bark beetles, defoliating Lepidoptera, and other groups can alter the accumulation and distribution of fuels and vegetation. Insolation at the soil surface may increase, affecting moisture levels of fuels such as dead wood, fallen needles, or leaves and litter (97, 112). Tree mortality or dead tops resulting from insect attack determine the availability of fuels on the soil surface (e.g. dead wood and vegetation on the ground) and ladder fuels (i.e. vertically distributed dead wood). These factors play a large role in determining the risk of fire ignition, behavior, and intensity.

There is increasing recognition that fire suppression or control policies implemented early in this century have substantially altered forest composition, structure, and vulnerability to damaging insect pests (41, 53, 67, 134). As we struggle with definitions of old-growth forests, forest health, and related issues, it is imperative to realize that current forest conditions may differ substantially from conditions prevalent before European settlement or fire suppression (13, 27, 88, 91, 121). There is a need to evaluate associations between fire and insects, how these disturbances interacted historically, and how changes that have occurred in the past century have altered these interactions.

Interest in both reestablishing fire and using prescribed burning in many forest ecosystems continues to grow. Use of fire to enhance wildlife habitat, prepare sites for post-harvest planting, and accomplish other management objectives is becoming more common in many areas of the United States and Canada (20, 96, 157). Information on the response of insects to fire is needed to identify where burning can be used appropriately for control of insect pests and to assess impacts of fire on other guilds of insects and overall community diversity.

This review primarily addresses fire-insect interactions in boreal and northern forest ecosystems of Canada, Alaska, and northern or high elevation regions.
of the continental United States. This restriction results from space limitations and because most of our experience and expertise lies with northern or boreal forest ecosystems. We recognize that fire-insect interactions also play significant roles in many other forest, prairie, and chaparral ecosystems that are not addressed here.

**Fire Behavior and Intensity**

What are some of the different types or behaviors of fire that occur in forests? Pyne et al. (127) define wildfires as those ignited by lightning and other natural causes or unintentionally by human actions. In contrast, prescribed natural fires are allowed to burn in an approved area, although they are not ignited intentionally. Prescribed burning is the intentional ignition and knowledgeable application of fire to a specific area to accomplish predetermined objectives (157).

Fires can also be distinguished by their behavior and intensity. Surface fires burn through grass, shrubs, fallen limbs or logs, and needle and leaf litter on the soil surface. Crown fires are invariably ignited by surface fires and burn through the crowns of standing trees. Ground fires burn in subsurface organic fuels such as duff layers under Arctic tundra or taiga or in organic soils of swamps and bogs.

Fire intensity (e.g., heat production per unit area) is largely determined by fuel accumulation, distribution, and moisture content. Fuel includes wood such as dead trees, logs, and slash (tree tops, branches, and other logging debris). Fine fuels include dead needles, leaves, and litter. In areas with a high accumulation of fuels, fires may burn hotter, move more slowly, and have more profound ecological effects than in areas with low fuel accumulation. Distribution and extent of fuels, wind, aspect (direction of slope orientation), topography, and other factors interact and affect fire intensity and behavior, typically creating a mosaic of post-fire conditions.

**Northern and Boreal Forest Ecosystems**

Historically, fire was a major influence on the species composition, diversity, and stability of many forest ecosystems in the northern United States and Canada (61). Records of fire frequency and descriptions of fire intensity and size were used to develop general classes of fire regimes for specific forest ecosystems (30, 62, 127). Fire regimes ranged from areas with rare or absent fires (e.g., coastal forests from the northwestern United States to Alaska) to regimes where severe fires occurred relatively often (e.g., pine forests in the Lake States and
many boreal forests). General characteristics of the ecosystems to which we refer in this review are briefly summarized here.

CANADIAN BOREAL FOREST The Canadian boreal forest covers 300 million hectares (ha) and runs in a continuous belt from Newfoundland north and west to the Yukon Territory. These forests vary according to climate, landform, and geology. Most forests have a history of repeated episodic disturbances from fire, insects, wind, pathogens, and timber harvest. These sources of variability have resulted in a complex and continually changing mosaic of forest conditions and successional development (58). Major tree species include spruce (*Picea* spp.), pine (*Pinus* spp.), balsam fir (*Abies balsamea*), western larch (*Larix decidua*), tamarack (*Larix laricina*), paper birch (*Betula papyrifera*), and quaking aspen (*Populus tremuloides*).

ALASKAN TAIGA AND COASTAL FOREST In Alaska, much of the northern boreal forest, also called taiga, is open slow-growing spruce interspersed with occasional dense well-developed forest stands and treeless bogs. Taiga forest extends from the Brooks Range southward to the coastal forests, east to the Canadian border, and west to a maritime tree line near the Bering Sea. Roughly 43 million ha of the total area of 139 million ha is forested (60, 69, 150, 151). Major tree species include white spruce (*Picea glauca*), black spruce (*Picea mariana*), tamarack, paper birch, quaking aspen, and balsam poplar (*Populus balsamifera*) (153). An additional 5 million ha of forested land occurs in coastal Alaska (69). Major tree species are Sitka spruce (*Picea sitchensis*), western hemlock (*Tsuga heterophylla*), black cottonwood (*Populus trichocarpa*), Alaska cedar (*Chamaecyparis nootkatensis*), and lodgepole pine (*Pinus contorta*) (152).


LAKE STATES AND NORTHEASTERN FORESTS This region includes forested land in the Lake States of Minnesota, Wisconsin, and Michigan and extending eastward to New England and Maine. Forested land ranges from lowlands, lakes, and bogs to rolling hills in the Lake States and includes the northern Appalachian Mountains in the eastern part of the region. A diverse array of hardwood species are found in this region, including beech (*Fagus grandifolia*),
paper birch, maples (*Acer* spp.), elms (*Ulmus* spp.), ash (*Fraxinus* spp.), and quaking aspen. Conifers are also well represented and include jack pine (*Pinus banksiana*), red pine (*Pinus resinosa*), eastern white pine (*Pinus strobus*), eastern hemlock (*Tsuga canadensis*), black spruce, white spruce, tamarack, balsam fir, white cedar (*Thuja occidentalis*), and eastern red cedar (*Juniperis virginiana*) (43, 126).

**USE OF FIRE FOR CONTROL OF INSECT PESTS**

Fire has long been used in agricultural and range systems to directly reduce populations of damaging insects or to alter habitat availability or quality, thereby indirectly reducing pest insect populations. In 1971, Komarek (80) reviewed many of these studies but noted the general lack of investigation regarding controlled burning to regulate forest insects.

At least two factors appear to consistently contribute to the successful application of fire for insect control in forest ecosystems. First, if fire is used to incinerate insects directly, the insects must be in a vulnerable stage and location at the time of burning (16, 20, 38, 39, 110). Second, Miller (110) noted that fire was a significant evolutionary or ecological force in most ecosystems where burning for insect control was attempted. He also pointed out that burning must not result in unacceptable damage to residual vegetation. Success of insect control efforts is also affected by heat intensity, fire spread rate, and coverage, all of which can be affected by prescribed burning techniques (110). Finally, appropriate burning weather must occur during the insects’ vulnerable stage, a requirement that could limit the usefulness of this management tool in some cases (22, 109).

Burning has perhaps been used most successfully to control cone or seed-infesting insects. Miller (109) evaluated prescribed burning in northern Minnesota for control of *Conopthorus resinosae*, a cone-destroying insect that overwinters on the ground inside fallen shoot tips. Burning caused high beetle mortality and significantly reduced cone mortality from *C. resinosae*. Prescribed burning was a cost-effective control for a related species, *Conopthorus coniperda*, in a white pine seed orchard (156). Burning was also identified as a means to reduce damage by the acorn weevil (*Conotrachelus posticatus*) in red oak stands (174) and to control seed-infesting insects in ponderosa pine stands (71).

Prescribed burning was expected to substantially reduce populations of pandora moth (*Coloradio pandora pandora*), a native defoliator of ponderosa pine that spends about 14 months as a pupa on the forest floor (108). However, efforts to control pandora moth with prescribed burning met with limited success in stands where litter distribution was patchy (138, 139). Pandora moth larvae appeared to select pupation sites in open-canopy areas of stands, where fuel loads were relatively low (108). Pupae were less common where there was a
deep accumulation of litter, even though exposure to natural enemies or extreme
temperatures was presumably lower in these areas. Selection of pupation sites
in open areas may represent an adaptation to frequent low-intensity fire that
typified pre-European ponderosa pine forests (27, 108).

Pear thrips (Taeniothrips inconsequens) damage buds of sugar maple in north-
eastern states (78) and overwinter in the upper 5–10 cm of the forest floor. Emer-
gence of adults in spring is largely determined by soil temperature and must
coincide with bud burst of sugar maple trees in the area (79). Both spring and
fall burns reduced numbers of emerging thrips. Fall burns hastened adult emer-
gence the following spring, potentially disrupting phenological synchronicity
with maple bud burst (22). Reduced thrips populations following fire may have
resulted from direct incineration, elevated bacteria or fungal populations affect-
 ing thrips, or fire-induced changes in soil moisture, temperature, or chemistry
(4, 22).

Brose & McCormick (22) noted, however, that the long-term consequences
of introducing fire into sugar maple forests were unknown. Large-scale wild-
fires in northern hardwood forests are rare, and these sugar maple–dominated
ecosystems were once described as “asbestos forests” (14, 19). Simmons et al
(140) used prescribed burning to successfully control maple leaf cutter (Parac-
lemensia acerifoliella) and reported that there was no evidence of damage to
large sugar maple trees in the stand. Burning may be appropriate in a “sugar
bush” (stand of large trees managed for syrup production) situation where pro-
tection of mature trees is more important than survival of seedlings.

Burning has also been used successfully to reduce populations of potentially
damaging bark beetles (Coleoptera: Scolytidae) and wood-borers. In western
Canada, prescribed fire destroyed overwintering Dendroctonus rufipennis in
slash (e.g. branches, tops, and logging debris) and stumps following harvesting
in spruce stands (137). Prescribed burning soon after harvest simultaneously
reduced wildfire hazard and controlled populations of Ips pini (141) and Den-
droctonus ponderosae in stands of ponderosa pine (136, 170) and lodgepole
pine (144). Mitchell & Martin (113) identified possible uses of fire to control
damage by several western bark beetle species. Dahl (28) reported that pre-
scribed fire killed larvae of the wood-boring Monochamus spp. (Coleoptera: Cer-
ambycidae) in lodgepole pine logs in Canada. McRae (105) suggested that
fire could be used to eliminate favorable winter habitat of various insect pests
in Canada.

FIRE, INSECTS, AND SUCCESSION

Although major disturbances such as fire or insect outbreaks may appear to
be independent events, they are often causally related. Spatial or temporal
patterns resulting from disturbance may reflect synergism among disturbance agents (54) that act within limits imposed by physical characteristics of the landscape and ecological processes. Such interactions certainly occur in many northern and boreal forest ecosystems. Accumulation of fuels following insect outbreaks may determine extent and intensity of subsequent fire (145), or fire may predispose trees to subsequent attack by insects. Aber & Melillo (1:252) noted that disturbance by fire, insects, or other agents "is an intrinsic and necessary part of the function of most terrestrial ecosystems—a mechanism for reversing declining rates of nutrient cycling or relieving stand stagnation."

Episodic outbreaks of major defoliators in forests in the Rocky Mountains and Pacific Northwest may have served a similar and complementary role to that of surface fires in directing succession (67, 169). Western spruce budworm (Choristoneura occidentalis) and Douglas-fir tussock moth (Orygia pseudotsugata) feed on late successional Douglas fir and true firs, but not on seral pine species. Historically, both low-intensity outbreaks of defoliators and surface fires probably kept fuel accumulations low and prevented, or at least delayed, catastrophic stand-replacing outbreaks or fire (148). Evidence suggests that recent outbreaks of western spruce budworm and Douglas-fir beetle (Dendroctonus pseudotsugae) in Colorado effectively slowed the rate that Douglas fir replaced seral pines, taking a role analogous to that of frequent surface fires (55).

A series of studies near Lake Duparquet, Quebec, evaluated effects of spruce budworm (Choristoneura fumiferana) outbreaks on the dynamics and growth of balsam fir stands (114). In regions where fire cycles exceeded 200 years, spruce budworm outbreaks interrupted succession towards coniferous dominance, shifting sites back to earlier seral mixed deciduous forests (17). Gaps in the canopy of mature fir stands created by spruce budworm (123) resulted in soil litter accumulation and nutrient contents similar to younger stands. These gaps were associated with greater abundance of pioneer plant species and higher diversity of understory vegetation (32).

Insect outbreaks that are followed by fire can also effectively disrupt or redirect succession in forest systems. For example, interactions of mountain pine beetle (D. ponderosae), lodgepole pine, and fire largely determine composition of subsequent stands. Outbreaks of mountain pine beetle in senescing lodgepole pine stands result in large fuel buildsups (146). Frequently, outbreaks are followed by intense wildfire that opens serotinuous lodgepole pine cones, eliminates overstory vegetation, and exposes mineral soil. This situation returns the site to a vigorous young stand of lodgepole pine and ensures the continued role of mountain pine beetle (11). However, when no fire occurs after an outbreak, lodgepole may be replaced by ponderosa pine at low elevation sites or by Douglas fir at high elevation sites (4, 112).
In a similar relationship, jack pine budworm (*Choristoneura pinus pinus*) and fire are integral elements in the dynamics of boreal jack pine forest. Jack pine stands generally sustain a jack pine budworm outbreak at roughly 6- to 10-year intervals (155). In the absence of fire, seral shade-intolerant jack pine would likely be replaced by more shade-tolerant species (118). However, budworm defoliation typically results in dead dry needles cast off by larvae, some tree mortality, and “top-killed” trees, especially in overmature stands (102, 118). These conditions promote ground fires, which often become crown fires if jack pine canopies are contiguous (118). Fire opens serotinous cones and exposes a mineral seedbed, and a young, often dense, jack pine stand again occupies the site.

**Fires Predispose Trees to Insect Attack**

Studies of forest dynamics have demonstrated the importance of fire, insect outbreaks, and other disturbances such as windthrow in northern forest ecosystems (8, 9, 37, 41, 63, 64, 75, 113, 132). Fire can predispose surviving trees to attack by insects, particularly by phloem-boring bark beetles or wood-borers.

For example, western pine beetle (*Dendroctonus brevicomis*) preferentially attacks old thick-barked ponderosa pine. But, because most old-growth ponderosa pine has been harvested, outbreaks of *D. brevicomis* now occur most frequently after wildfire (113). Trees scorched or wounded by fire are weakened and are less resistant to bark beetle attack. Beetle-caused tree mortality was found to be positively related to the percentage of crown scorched during a fire (95, 107). In many northern forest regions, wildfire has been followed by outbreaks of bark beetle species such as *D. ponderosae* (8, 9, 37, 47–49, 51, 52, 113, 124, 132), *D. pseudotsugae* (10, 46, 55, 77), *D. rufipennis* (10, 132, 162), and *Ips* spp. (10, 52, 160).

Species of buprestid and cerambycid beetles and other wood-boring insects frequently occupy recently burned roots and stems of conifers in western Canada and Alaska. Charred and uncharred areas of conifers have reportedly been infested with species of *Monochamus* (25, 28, 35, 36, 50, 113, 125, 130, 133, 149, 162, 165) and *Melanophila* (10, 35, 36, 86, 125, 162, 165, 167, 168). Wood-borers such as *Melanophila* spp. possess infrared receptors on their legs that enable the insects to orient directly to radiant heat from a fire (33, 34). Evans (36) estimated that *Melanophila* beetles could detect a glowing 20-ha fire at 5 km and a blazing fire at even greater distances. Many cerambycids, such as *Monochamus* beetles, are usually associated with trees that are injured, windthrown, or broken by snow and ice. However, several *Monochamus* beetles can orient to the smoke plume emitted by fires. They may infest partially burned conifers immediately after a fire, sometimes even while the burned trees are still smoking (50, 125, 130, 133, 168). Other species of insects that inhabit fire-killed trees
are horntails (Hymenoptera: Siricidae) (115), hardwood borers in northeastern hardwood forests (143), and cone borers of the genus *Ernobius* in cones of burned black spruce (166).

**Fire and Quality of Host Plants**

In addition to altering the abundance and spatial-temporal continuity of preferred host species, fire can also affect nutrient cycling and availability (e.g., 4, 59, 94). These effects, in turn, may consequently determine the quality of trees as hosts for plant-feeding insects (14, 135).

McCullough & Kulman (100) studied stands of young jack pine trees that regenerated following wildfire and similarly aged trees on nearby sites that regenerated after harvesting. Trees on the burned areas had lower foliar nitrogen levels and produced fewer pollen cones than trees on the unburned sites. Pollen cone production is associated with greater survival of early instars of jack pine budworm (*C. pinus pinus*) larvae (119). Caging experiments demonstrated that larval survival was related to foliar nitrogen concentration (100, 101). These data suggest that even when species composition does not change, ecological effects of fire may be long-lasting and affect susceptibility of stands to insect damage. Jakubas et al. (70) reported that insects and elk preferentially fed on lodgepole pine trees with burned bark in Yellowstone National Park. They attributed this preference to higher protein levels and lower concentrations of phenolics, monoterpenes, and resin acids in the burned bark.

**FIRE SUPPRESSION AND DYNAMICS OF INSECT OUTBREAKS**

Compelling evidence suggests that efforts to exclude or suppress fire in the United States and areas of Canada, sometimes in combination with timber harvesting, have altered the susceptibility of many forests to insect outbreaks or damage. These changes resulted largely from a shift in fire management policy that occurred around 1910 in the United States and much of Canada. Forest managers were widely encouraged to suppress and control forest fires where possible, and their enthusiastic efforts were remarkably successful (127). This emphasis on forest fire suppression arose from a complex interaction of social, political, and scientific issues around the turn of the century (127). Fire suppression activities were well organized by the 1930s, and by mid-century, nearly all wildfires of low and medium intensity were extinguished (2, 73).

By the mid-1980s, successful application of fire suppression policies had dramatically altered fire regimes in many forested areas of the United States and parts of Canada. For example, McCune (103), using tree-ring analysis, concluded that fire frequency, size, type, and origin changed radically in western
Montana. As a result of fire suppression activities, fire cycles increased from 55–70 years before 1911 to 7500 years after 1911. Data from Minnesota showed similar drastic increases, with a pre-1910 fire cycle of ca 47 years increasing to a fire cycle of 2000 years (60, 103). Lynham & Stocks (92) reported that fire periodicity of 60–100 years occurred in the boreal forest of east-central Canada before European settlement. Fire suppression since 1900 has increased the fire periodicity to 500–1000 years in this region. Blais (18) also noted that immense areas in the boreal and transition zone of eastern Canada burned annually up until 1920, when fire suppression policies were instituted. Of course, in some northern forest sites there has been little change in fire cycles because of naturally long fire intervals (131) or weather patterns or inaccessible terrain that surmounted fire suppression efforts (14, 72).

Structure of forest stands has changed remarkably in many northern forests where fire frequency has been drastically reduced. For example, in some ponderosa pine forests, average tree densities have increased from 9 trees per ha in presettlement times to more than 300 trees per ha today (27). These changes are also associated with increased canopy closure and more accumulation and continuity of vertical and surface fuels (97). Species and landscape diversity in Pacific Northwest forests have also decreased (3, 64, 98, 117). Increased amounts of litter, coarse woody debris, and altered species composition were associated with fire suppression in northwestern Minnesota (26).

These striking changes in fire regimes appear to have profoundly altered dynamics of important native forest defoliators such as western spruce budworm (C. occidentalis). Major patterns emerge upon review of dendrochronology studies conducted in several western states. Since fire suppression began in 1910, there has been a notable increase in abundance and spatial continuity of tree species preferred by western spruce budworm such as Douglas fir, white fir, and spruces (12, 54, 55, 103, 147). These species are more shade tolerant than seral ponderosa pine, a non-host of the budworm that dominated these areas when frequent surface fires occurred. Selective logging of pine likely exacerbated this situation in some areas (55). Fire suppression has also increased tree density, and stands are more likely to be multi-layered than even-aged. Mortality of dispersing budworm larvae is lower in these stands, and young or low-vigor trees typically sustain high defoliation and mortality during outbreaks.

Associated with these changes in forest composition and structure are consistent increases in synchronicity and duration of western spruce budworm outbreaks (12, 24, 40, 54, 55, 103, 147, 148). Tree mortality and overall intensity of outbreaks has also increased in this century. Swetnam et al (148) observed that it was unlikely that tree mortality rates of 80%, recorded during the most recent budworm outbreak, could have been sustained historically.
Analysis of Douglas-fir tussock moth (O. pseudotsugata) outbreaks reveals similar patterns. At high elevations, a dynamic tension exists between Douglas fir/true firs and ponderosa pine. When fire regularly occurred, sites were likely to be occupied by thrifty stands of ponderosa pine (56). After fire control was initiated, seral ponderosa pine stands shifted to climax stands of shade-tolerant Douglas fir and true firs, the favored hosts of tussock moth (113, 169, 172). Williams (171) estimated that periodic prescribed burning in these sites would have resulted in a 53% decreased risk of tussock moth outbreaks. Other studies similarly reported that tussock moth outbreaks were more common and severe in drier stands originally occupied by ponderosa pine than in sites with higher moisture or nutrient levels that were historically dominated by spruce fir (112).

Fire suppression also appears to affect spruce budworm (C. funiferana) dynamics in central and eastern Canada and the northeastern United States. Spruce budworm is the primary defoliator of balsam fir and white spruce, and outbreaks are viewed as periodic natural occurrences in this ecosystem (14, 18, 122). Since fire suppression was initiated in 1920, spruce budworm outbreaks in eastern Canada have occurred at shorter intervals, are more widespread, and result in more mortality, especially of white spruce, than before 1920 (18, 104). This rise in outbreak frequency, area, and intensity was attributed to several factors, including selective logging of white pine and insecticide applications that perpetuated development of vulnerable fir or spruce-fir forests (18). At the same time, fire suppression reduced abundance of pioneer species, such as aspen, birch, jack pine, and black spruce, that previously formed a mosaic and interrupted continuity of balsam fir–spruce stands. Blais (18) also noted that in northwestern Ontario, where relatively little fire suppression or logging occurred during this century, frequency of spruce budworm outbreaks had not changed.

Damage by other guilds of insects also has increased as a result of fire suppression. Frequent fires in dry areas of the Pacific Northwest formerly prevented invasion of fire-resistant ponderosa pine stands by thin-barked lodgepole pine. Although mountain pine beetle (D. ponderosae) prefers lodgepole pine, it will frequently attack ponderosa pine when it grows in mixed or adjacent stands. Since fire suppression was implemented, mixed stands have become more common and risk of ponderosa pine mortality from mountain pine beetle has increased (112).

In western Oregon, fire exclusion, combined with logging practices, has resulted in replacement of seral Douglas fir at low elevations by the more shade-tolerant Pacific silver fir (Abies amabilis). This situation has led to increased damage to fir by balsam woolly adelgid (Chermes piceae) (111, 112). Notably, as early as 1958, Frost (45) advocated prescribed fire in balsam fir stands to alter overstory composition as a means of indirectly reducing damage from balsam woolly adelgid.
FIRE AND INSECT DIVERSITY

Information on the effects of fire on abundance and diversity of insects in northern forests is needed to formulate management strategies to sustain biodiversity and long-term productivity of these ecosystems (161). In many northern and boreal forests, disturbances such as fire or insect outbreaks maintain mosaics of forests varying in species composition, age class, and structure (2, 15, 17, 27, 53, 57, 60, 74, 76, 116, 134, 153). Periodic disturbance was noted as an essential factor in perpetuating long-term stability and species diversity across landscapes (14, 61, 89).

Several studies have examined effects of fire on insect abundance and diversity of insect taxa or feeding guilds. Werner (159) examined diversity of forest-dwelling arthropods in six vegetation types in interior Alaska. Four taxonomic classes representing 94 arthropod families were collected from herb, shrub, and tree levels in undisturbed stands before a prescribed burn. Only 15% of these arthropods were present immediately after the fire. In Wisconsin, abundance and diversity of insect feeding guilds were surveyed using pitfall trapping and sweepnetting for two summers in young jack pine stands that had regenerated after either wildfire or clearcut harvesting (99). In the burned areas, jack pine regenerated densely, limiting understory vegetation diversity. Predatory, sap-feeding, and foliage-feeding insects were more abundant on the clearcut sites, while ants were more abundant on the burned sites.

Effects of fire on species diversity of bark beetle, wood-borer, and related groups were evaluated in studies in Alaska. Species diversity of scolytids associated with white spruce stands were monitored in three sites with latitudes ranging from 60°37′ to 68°15′. Fire cycles ranged from 100–200 years, and 20–27 species of scolytids were collected at each site (163). Both fire frequency and scolytid species diversity were related to cumulative seasonal degree days in the three areas. Another project evaluated long-term effects of fire in Alaskan white spruce stands on species diversity of bark beetles and wood-boring beetles; populations of scolytid, buprestid, and cerambycid beetles were monitored at 1-, 5-, and 10-year intervals after burning and timber harvest on floodplain and upland white spruce sites (162). Fire removed most of the host trees normally inhabited by scolytid and cerambycid beetles. However, the scorched trees provided habitat for the buprestids _Melanophila accuminata_ and _Buprestis nuttalli_ the first year after burning. Partially burned spruce at the perimeter of severely burned areas provided habitat for a diverse assemblage of beetles, including six cerambycid species and eight scolytid species. Beetle populations and diversity remained high for up to 5 years after the fire, then decreased as hardwood stands replaced spruce in the burned areas (162).

Despite the potential importance of carabids as indicator species, predators, or saprophages (85, 120, 128), relatively few studies have evaluated the
Response of ground beetles (Coleoptera: Carabidae) to fire in northern forests. Response of carabid beetles to fire or other disturbances may be determined by plant species composition, vertical distribution of plants within communities, and habitat complexity (161, 164). Leibherr & Mahar (84) theorized that carabid beetle abundance and diversity should be higher in more successional advanced and structurally diverse forest stands. However, if interspecific competition determines the structure of carabid beetle assemblages (83, 87), then beetle diversity should decrease in the absence of fire or other disturbance as competitively superior species exclude inferior competitors (31, 142). Size of the pool of potential colonists may also govern carabid response to fire or other disturbance (66).

Results of studies examining fire effects on abundance of carabid beetles are equivocal. Holliday (66) trapped lower numbers and fewer species of carabids on burned sites compared to unburned sites in boreal black spruce and trembling aspen stands in Manitoba. Reduced abundance of carabids following fire was also recorded in Minnesota jack pine stands (4). In contrast, more coleopterans were observed on burned plots sampled both 1 and 2 years after wildfire in Alaskan black spruce stands than on unburned plots (16). Carabid abundance was also significantly greater in plots burned biannually than in unburned plots in mixed pine stands in Michigan (D Neumann, unpublished data).

Research conducted in northern and boreal forests suggests that fire has little effect on carabid species diversity, but species composition may change. Holliday (66) observed no difference in species evenness or richness between burned and unburned spruce stands when carabids were sampled over a 10-year period following wildfire. He attributed this lack of change in diversity to rapid changes in plant taxonomic and spatial diversity. However, some carabid species are attracted to fires in forests; for example, Evans (35) identified three pyrophilous species belonging to the genus Agonum that do so. Holliday (65) observed two of these species, A. obsoletum and A. quadripunctatum, following wildfire in boreal spruce stands and classified a third, Harpalus laticeps, as pyrophilous after observing it exclusively on burned sites. Length of site occupation by pyrophilous species varied from a few weeks to several years (65).

Spider communities were sampled in recently burned and undisturbed black spruce bogs and jack pine ridges in Manitoba (74). Some pioneer spider species traveled up to 30 m to colonize burned areas. Other species that required phytophagous prey, high amounts of litter, abundant vegetation, or high humidity were found only on undisturbed sites. Several species were eurytrophic and apparently not affected by the disturbance. Koponen (81) listed spider species found mainly in burned areas in Quebec; response of most species to disturbance was similar to that observed in Manitoba (7).

Fire may also affect soil organisms involved in decomposition and nutrient cycling, particularly those in the upper humus or litter layers not protected by...
insulating effects of soil (90, 113). High-intensity wildfires reduced populations of Collembola in pine stands in California (158) and in pine barrens in New Jersey (23). Density of Acari and Collembola were reduced by logging and further reduced by slash burning in stands dominated by cedar and hemlock in British Columbia (154). However, neither logging nor burning caused total mortality of any group, and populations were able to rapidly reinvade disturbed areas. Lucarotti (90) identified changes in mite, Collembola, and other mesofaunal groups after a controlled burn in a subarctic lichen woodland in Quebec. Burning reduced the mite population by 50% and altered mite and collembolan species composition; however, it did not reduce Collembola abundance. Studies in other ecosystems have generally reported declines in Collembolan abundance following fire, although duration of the population reduction varied (7, 39, 68, 106). Species diversity may increase, however, in sites burned periodically but not annually (106). Prescribed fire in Minnesota jack pine stands caused an immediate reduction in soil microbial numbers and activity, followed by a sharp increase after rain fell later in the year (6). In the third year after burning, most microbial populations approached pre-burn levels.

SUMMARY

Fire and insects are intrinsic and often synergistic components of many northern and boreal forest ecosystems in North America. Interactions of fire and insects can delay or redirect succession, affect nutrient cycling, and alter species composition and diversity. Episodic outbreaks of defoliating species can affect the likelihood of fire ignition, fire behavior and intensity, and resulting post-fire species composition. In some cases, insect outbreaks can mirror or complement ecological effects of fires. Fire can predispose trees to attack by bark beetles or wood-boring insects, may influence abundance or species diversity of many insect groups, and may affect quality of foliage for plant-feeding insects. In some situations, prescribed burning can successfully control insect pests that spend part of their life cycle in a vulnerable stage on the ground. Fire suppression efforts initiated around the turn of the century have profoundly altered species composition and structure of many northern forests. These changes are associated with greater vulnerability of stands to damaging insect pests and often dramatic increases in outbreak intensity and spatial-temporal synchronicity. An increased understanding of the ecology of fire-insect interactions is needed as we identify strategies to manage forest pests, enhance forest health, and maintain biological diversity in northern forest ecosystems.
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