1998

Fire and Insects in Northern and Boreal Forest Ecosystems on North America

Deborah G. McCullough

Richard A. Werner

David Neumann

Recommended Citation

McCullough, D., Werner, R. and Neumann, D. (1998). Fire and insects in northern and boreal forest ecosystems on North America. Annual Review of Entomology, 43: 107-127.

FIRE AND INSECTS IN NORTHERN AND BOREAL FOREST ECOSYSTEMS OF NORTH AMERICA[1]

Deborah G. McCullough

Department of Entomology and Department of Forestry, Michigan State University, 243 Natural Science Building, East Lansing, Michigan 48824-1115; e-mail: mccullod@msue.msu.edu

Richard A. Werner

USDA Forest Service, 308 Tanana Drive, Fairbanks, Alaska 99775-5500; e-mail: rwerner@polarnet.com

David Neumann

Department of Forestry, Michigan State University, 126 Natural Resources Building, East Lansing, Michigan 48824; e-mail: FORESTDN@aol.com

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.

[1]The US Government has the right to retain a nonexclusive, royalty-free license in and to any copyright covering this paper.

107

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.

FIRE ECOLOGY   Ecological effects of forest fires are highly variable, difficult to predict, and influenced by fire behavior, vegetation type, topography, climate, pre- and post-burn weather, and myriad other factors (82, 127, 157). Several reviews of ecological effects of fire are available and provide information related to specific factors or ecosystems (e.g. 5, 60, 62, 93, 127, 150, 157, 173).

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 occur 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).

FORESTS IN THE PACIFIC NORTHWEST, INLAND WEST, AND NORTHERN ROCKIES   An estimated 20 million ha in the Pacific Northwest and Rocky Mountains region is forested (21). Dominant vegetation reflects climatic and weather differences across the region. Major tree species include Douglas fir (*Pseudotsuga menziesii*), grand fir (*Abies grandis*), white fir (*Abies concolor*), noble fir (*Abies procera*), Engelman spruce (*Picea engelmanii*), western hemlock, ponderosa pine (*Pinus ponderosa*), lodgepole pine, western juniper (*Juniperus occidentalis*), western larch, and black cottonwood (21, 42).

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.), oaks (*Quercus* 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 northeastern states (78) and overwinter in the upper 5–10 cm of the forest floor. Emergence 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 emergence 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 affecting 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 wildfires 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 (*Paraclemensia 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 protection 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 harvests in spruce stands (137). Prescribed burning soon after harvest simultaneously reduced wildfire hazard and controlled populations of *Ips pini* (141) and *Dendroctonus 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 prescribed fire killed larvae of the wood-boring *Monochamus* spp. (Coleoptera: Cerambycidae) 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 buildups (146). Frequently, outbreaks are followed by intense wildfire that opens serotinous 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. fumiferana*) 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 biodi-
versity and long-term productivity of these ecosystems (161). In many north-
ern 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 di-
versity of insect taxa or feeding guilds. Werner (159) examined diversity of
forest-dwelling arthropods in six vegetation types in interior Alaska. Four tax-
onomic 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 as-
sociated 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 bee-
tles; 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 pro-
vided 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, preda-
tors, 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 successionally 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 popula-
tions 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 meso-
faunal groups after a controlled burn in a subarctic lichen woodland in Quebec.
Burning reduced the mite population by 50% and altered mite and collem-
bolan 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 peri-
odically 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 com-
position 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 sup-
pression 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 synchronic-
ity. 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.

**Visit the *Annual Reviews home page* at
http://www.AnnualReviews.org.**

Literature Cited

1. Aber JD, Melillo JM. 1991. *Terrestrial Ecosystems.* Orlando, FL: Saunders College Publ. Holt, Rinehart & Winston. 429 pp.

2. Agee JK. 1990. The historic role of fire in Pacific Northwest forests. In *Natural and Prescribed Fire in Pacific Northwest Forests,* ed. JD Walstad, SR Radosevich, DV Sandberg, pp. 25–38. Corvallis, OR: Oregon State Univ. Press

3. Agee JK. 1993. *Fire Ecology of Pacific Northwest Forests.* Washington, DC: Island

4. Ahlgren IF. 1974. Effect of fire on soil organisms. In *Fire and Ecosystems,* ed. TT Kozlowski, CE Ahlgren, pp. 67–72. New York: Academic

5. Ahlgren IF, Ahlgren CE. 1960. Ecological effects of forest fires. *Bot. Rev.* 26:484–33

6. Ahlgren IF, Ahlgren CE. 1965. Effects of prescribed burning on soil microorganisms in a Minnesota jack pine forest. *Ecology* 46:304–10

7. Aitchison-Benell CW. 1994. Responses to fire by taiga spiders. *Proc. Entomol. Soc. Ontario* 125:29–41

8. Amman GD. 1991. *Insect infestation of fire-injured trees in the Greater Yellowstone area. Gen. Tech. Rep. INT-398.* USDA For. Serv. Intermt. Res. Stn. 9 pp.

9. Amman GD. 1991. Bark beetle-fire associations in the greater Yellowstone area. In *Fire and the Environment: Ecological and Cultural Perspectives, Proc. Int. Symp. Gen. Tech. Rep. SE-69,* pp. 313–20. USDA For. Serv. Southeast. For. Exp. Stn.

10. Amman GD, Ryan KC. 1991. *Insect infestation of fire-injured trees in the Greater Yellowstone area. Res. Note INT-398.* USDA For. Serv. Intermt. Res. Stn. 9 pp.

11. Amman GD, Schmitz RF. 1988. Mountain pine beetle-lodgepole pine interactions and strategies for reducing tree losses. *Ambio* 17:62–68

12. Anderson L, Carlson CE, Wakimoto RH. 1987. Forest fire frequency and western spruce budworm outbreaks in western Montana. *For. Ecol. Manage.* 2:251–60

13. Arno SF, Sneck KM. 1977. *A method for determining fire history in coniferous forests in the mountain west. Gen. Tech. Rep. INT-42.* USDA For. Serv. Intermt. For. Range Exp. Stn. 28 pp.

14. Attiwill PM. 1994. Disturbance of forest ecosystems: the ecological basis for conservative management. *For. Ecol. Manage.* 63:247–300

15. Barney RJ. 1971. Wildfires in Alaska: some historical and projected effects and aspects. In *Fire in the Northern Environment Symposium,* ed. CW Slaughter, RJ Barney, GM Hansen, pp. 51–59. USDA For. Serv. Pac. Northwest For. Exp. Stn. 275 pp.

16. Beckwith RC, Werner RA. 1979. Effects of fire on arthropod distribution. In *Ecological Effects of the Wickersham Dome Fire Near Fairbanks, Alaska. Gen. Tech. Rep. PNW-90,* ed. LA Viereck, CT Dyrness, pp. 53–55. USDA For. Serv. Pac. Northwest Res. Stn. 71 pp.

17. Bergeron Y, Dansereau PR. 1993. Predicting the composition of Canadian southern boreal forest in different fire cycles. *J. Veg. Sci.* 4:827–32

18. Blais JR. 1983. Trends in the frequency, extent and severity of spruce budworm outbreaks in eastern Canada. *Can. J. For. Res.* 13:539–47

19. Bormann FH, Likens GE. 1979. Catastrophic disturbance and the steady state in northern hardwood forests. *Am. Sci.* 67:660–69

20. Brennan LA, Hermann SM. 1994. Prescribed fire and forest pests: solutions for today and tomorrow. *J. For.* 94:34–37

21. Brookes MH. 1996. *Disturbance and forest health in Oregon and Washington. Gen. Tech. Rep. PNW-381.* USDA For. Serv. Pac. Northwest Res. Stn. 105 pp.

22. Brose PH, McCormick LH. 1992. Effects of prescribed fire on pear thrips in Pennsylvania sugarbushes. *North. J. Appl. For.* 9:157–60

23. Buffington JD. 1967. Soil arthropod populations of the New Jersey pine barrens as affected by fire. *Ann. Entomol. Soc. Am.* 60:530–35

24. Carlson CE, Fellin DG, Schmidt WC. 1983. Western spruce budworm in northern Rocky Mountain forests: a review of ecology, insecticide treatments and silvicultural practices. In *Management of Second Growth Forests, The State of Knowledge and Research Needs,* ed. J O'Laughlin, RD Pfister, pp. 76–103. Montana For. Conserv. Exp. Stn., Univ. Montana, Missoula

25. Cerezke HF. 1977. Characteristics of damage in tree-length white spruce logs caused by the white-spotted sawyer, *Monochamus scutellatus. Can. J. For. Res.* 7:232–40

26. Clark JW. 1990. Twentieth-century climate change, fire suppression, and forest

production and decomposition in north-western Minnesota. *Can. J. For. Res.* 20:219–32

27. Covington WW, Everett RL, Steele R, Irwin LL, Daer TA, et al. 1994. Historical and anticipated changes in forest ecosystems on the Inland West of the United States. In *Assessing Forest Ecosystem Health in the Inland West. Am. For. Workshop,* ed. DL Adams, Spec. Publ. *J. Sustainable For.* 2:113–63

28. Dahl BM. 1971. Mortality of *Monochamus* larvae in slash fires. *Environ. Can. For. Serv. Bimon. Res. Notes* 27:12

29. Danks HV, Footitt RG. 1989. Insects of the boreal zone of Canada. *Can. Entomol.* 121:625–90

30. Davis KM, Mutch RW. 1994. Applying ecological principles to manage wildland fire. In *Fire in Ecosystem Management.* Train. Course, Natl. Adv. Res. Tech. Cent.

31. Dayton PK. 1971. Competition, disturbance and community organization: the provision and subsequent utilization of space in a rocky intertidal community. *Ecol. Monogr.* 41:351–89

32. De Grandpre L, Gagnon D, Bergeron Y. 1993. Changes in the understory of Canadian southern boreal forest after fire. *J. Veg. Sci.* 4:803–10

33. Evans WG. 1964. Infrared receptors in *Melanophila acuminata* De Geer. *Nature* 202:21

34. Evans WG. 1966. Perception of infrared radiation from forest fires by *Melanophila acuminata* De Geer (Buprestidae, Coleoptera). *Ecology* 47:1061–65

35. Evans WG. 1972. The attraction of insects to forest fires. *Proc. Ann. Tall Timbers Fire Ecol. Conf.,* 10:110–27. Tallahassee, FL: Tall Timbers Res. Stn.

36. Evans WG. 1973. Fire beetles and forest fires. *Insect World Dig.* 1:14–18

37. Fellin DC. 1980. A review of some relationships of harvesting, residue management, and fire to forest insects and disease. In *Environmental Consequences of Timber Harvesting in Rocky Mountain Coniferous Forests. Gen. Tech. Rep. INT-90,* pp. 335–414. USDA For. Serv. Intermt. For. Range Exp. Stn.

38. Fellin DC. 1980. Effects of silvicultural practices, residue utilization, and prescribed fire on some forest floor arthropds. In *Environmental Consequences of Timber Harvesting in Rocky Mountain Coniferous Forests. Gen. Tech. Rep. INT-90.* USDA For. Serv. Intermt. For. Range Exp. Stn.

39. Fellin DC, Kennedy PC. 1972. Abundance of arthropods inhabiting duff and soil after prescribed burning on forest clearcuts in northern Idaho. *Res. Pap. INT-162.* USDA For. Serv. Intermt. For. Range Exp. Stn.8 pp.

40. Fellin DG, Shearer RC, Carlson CE. 1983. Western spruce budworm in the northern Rocky Mountains: biology, ecology and impacts. *West. Wildl.* 9:2–7

41. Flieger BW. 1971. Forest fire and insects: the relation of fire to insect outbreaks. *Proc. Ann. Tall Timbers Fire Ecol. Conf.,* 10:107–14. Tallahassee, FL: Tall Timbers Res. Stn.

42. Franklin JF, Dyrness CT. 1988. *Natural Vegetation of Oregon and Washington.* Corvallis, OR: Oregon State Univ. Press. 452 pp.

43. Frelich LE, Reich PB. 1995. Spatial patterns of succession in a Minnesota southern-boreal forest. *Ecol. Monogr.* 65:325–46

44. Friend GR. 1995. Fire and invertebrates: a review of research methodology and the predictability of post-fire response patterns. In *Landscape Fires '93: Proc. Aust. Bushfire Conf., Perth, West. Aust., Sept. 1993. CALM Sci. Suppl.* 4:165–74

45. Frost F. 1958. Balsam wooly aphid and prescribed burning. *Nfld. Res. Comm. St. Johns Publ.* 1:19–35

46. Furniss MM. 1965. Susceptibility of fire-injured Douglas-fir to bark beetle attack in southern Idaho. *J. For.* 63:8–11

47. Furniss RL. 1937. Salvage on Tillamook Burn as affected by insect activity. *Timberman* 39:11–13

48. Gara RI. 1988. Interactions between fires, fungi, mountain pine beetles, and lodgepole pine in south-central Oregon. *Northwest Environ. J.* 4:355–58

49. Gara RI, Littke WR, Agee JK, Geiszler DR, Stuart JD, Driver CH. 1985. Influence of fires, fungi, and mountain pine beetles on development of lodgepole pine forest in south-central Oregon. In *Lodgepole Pine: The Species and Its Management,* ed. DM Baumgartner, RG Krebill, JT Arnott, GF Weetman, pp. 153–62. Pullman, WA: Wash. State Univ. Coop. Ext.

50. Gardiner KM. 1957. Deterioration of fire-killed pine in Ontario and the causal wood-boring beetles. *Calif. Entomol.* 89:241–63

51. Geiszler DR, Gara RI, Driver CH, Gallucci VR, Martin RE. 1980. Fire, fungi, and beetle influences on a lodgepole pine ecosystem of south-central Oregon. *Oecologia* 46:239–43

52. Geiszler DR, Gara RI, Littke WR. 1984. Bark beetle infestations of lodgepole pine following a fire in south-central Oregon. *Z. Angew. Entomol.* 98:389–94

53. Graham RT, Sampson RN. 1994. Silviculture, fire and ecosystem management. In *Assessing Forest Ecosystem Health in the Inland West, Am. For. Workshop,* ed. DL Adams, Spec. Publ. *J. Sustainable For.* 2:339–51

54. Hadley KS. 1994. The role of disturbance, topography, and forest structure in the development of the montane forest landscape. *Bull. Torrey Bot. Club.* 121:47–61

55. Hadley KS, Veblen TT. 1993. Stand response to western spruce budworm and Douglas-fir bark beetle outbreaks, Colorado front range. *Can. J. For. Res.* 23:479–91

56. Hall FC. 1977. *Ecology of natural underburning in the Blue Mountains of Oregon.* USDA For. Serv. Pac. Northwest Reg. *R6-Ecol.-79-001.* Portland, OR.11 pp.

57. Hall FC. 1980. *Fire history—Blue Mountains, Oregon. Proc. Fire Hist. Workshop. Gen. Tech. Rep. RM-81,* pp. 75–81. USDA For. Serv. Rocky Mtn. For. Range Exp. Stn.

58. Hall JP, Apps MJ. 1995. Forest health monitoring in Canada: how healthy is the boreal forest? *Proc. Boreal For. Res. Assoc. Conf., Saskatoon, Sask.* 82:77–85

59. Harvey AE. 1994. Integrated roles for insects, diseases and decomposers in fire dominated forests of the inland western United States: past, present and future forest health. *J. Sustain. For.* 2:211–20

60. Heinselman ML. 1971. The natural role of fire in northern conifer forests. *Proc. Fire North. Environ. Symp.,* pp. 61–72. USDA For. Serv. Pac. Northwest Res. Stn.

61. Heinselman ML. 1973. Fire in the virgin forests of the Boundary Waters Canoe area, Minnesota. *Quat. Res.* 3:329–82

62. Heinselman ML. 1981. Fire intensity and frequency as factors in the distribution and structure of northern ecosystems. In *Fire Regimes and Ecosystem Properties: Proc. Conf. Gen. Tech. Rep. WO-26,* ed. HA Mooney, JM Bonnicksen, NL Christiansen, JE Logan, WA Reiners. pp. 7–57. Washington, DC: USDA For. Serv.

63. Hessburg PF, Mitchell RG, Filip GM. 1994. Historical and current roles of insects and pathogens in eastern Oregon and Washington forested landscapes. In *Eastside Forest Ecosystem Health Assessment, Volume III: Assessment. Gen. Tech. Rep. PNW-327,* ed. RL Everett. USDA For. Serv. Pac. Northwest Res. Stn. 72 pp.

64. Holland DG. 1986. The role of forest insects and diseases in the Yellowstone ecosystem. *West. Wildl.* 12:19–23

65. Holliday NJ. 1984. Carabid beetles (Coleoptera: Carabidae) from a burned spruce forest (*Picea* spp). *Can. Entomol.* 116:919–22

66. Holliday NJ. 1992. Carabid fauna (Coleoptera: Carabidae) during postfire regeneration of boreal forest: properties and dynamics of species assemblages. *Can. J. Zool.* 70:440–52

67. Holling CS. 1981. Forest insects, forest fires, and resilience. In *Fire Regimes and Ecosystem Properties. Proc. Conf. Gen. Tech. Rep. WO-26,* ed. HA Mooney, TM Bonnicksen, NL Christensen, JE Lotan, WA Reiners, pp. 445–63. Washington, DC

68. Huhta V. 1971. Succession in the spider communities of the forest floor after clearcutting and prescribed burning. *Ann. Zool. Fenn.* 8:483–542

69. Hutchison OK. 1967. Alaska's forest resource. *USDA For. Serv. Inst. Nor. For. Res. Bull. PNW-19.* 74 pp.

70. Jakubas WJ, Garrott RA, White PJ, Mertens DR. 1994. Fire-induced changes in the nutritional quality of lodgepole pine bark. *J. Wildl. Manage.* 58:35–46

71. Johnsen JO. 1983. Some effects of a moderate intensity prescribed understory burn on seed production and losses to insects in seral ponderosa pine in northern Idaho. *For. Abstr.* 44:716

72. Johnson EA, Fryer GI, Heathcott MJ. 1990. Influence of man and climate on frequency of fire in the interior wet belt forest, British Columbia. *J. Ecol.* 78:403–12

73. Kauffman JB. 1990. Ecological relationships of vegetation and fire in Pacific Northwest forests. In *Natural and Prescribed Fire in Pacific Northwest Forests,* ed. JD Walstad, SR Radosevich, DV Sandberg, pp. 25–38. Corvallis, OR: Oregon State Univ. Press

74. Kayll AJ. 1968. *The role of fire in the boreal forest of Canada. Petawawa For. Exp. Stn. INF Rep. PS-X-7.* Can. For. Serv., Chalk River, Ontario

75. Kelsall JP, Telfer ES, Wright TD. 1977. The effects of fire on the ecology of the boreal forest, with particular reference to the Canadian north: a review and selected bibliography. Ottawa, Ontario: Can. Wildl. Serv., Occas. Pap. No. 32

76. Kershaw KA, Rouse WR. 1976. *The impact of fire on forest and tundra ecosystems, Can. Dep. Indian Aff. North. Dev. ALUR Rep. 75-76-63.* 54 pp.

77. Kimmey JW, Furniss RL. 1943. *Deterioration of fire-killed Douglas-fir.* Washington, DC: USDA Tech. Bull. 851

78. Kolb TE, McCormick LH, Simons EE, Jeffery DJ. 1992. Impacts of pear thrips on root carbohydrate, sap and crown characteristics of sugar maples in a Pennsylvania sugarbush. *For. Sci.* 38:381–92

79. Kolb TE, Teulon DAJ. 1991. Relationship between sugar maple budburst phenology and pear thrips damage. *Can. J. For. Res.* 21:1043–48

80. Komarek EV Sr. 1971. Insect control–fire for habitat management. In *Tall Timbers Conf. Ecol. Animal Control Habitat Manage.,* No. 2, pp. 157–71. Tallahassee, FL: Tall Timbers Res. Stn.

81. Koponen S. 1993. Ground-living spiders (Araneae) one year after fire in three subarctic forest types, Quebec (Canada). *Mem. Qld. Mus.* 33:575–78

82. Kozlowski TT, Ahlgren CE. 1974. *Fire and Ecosystems.* New York: Academic

83. Lenski RE. 1982. Impact of forest cutting on the diversity of ground beetles (Coleoptera: Carabidae) in the southern Appalachians. *Ecol. Entomol.* 7:385–90

84. Liebherr J, Mahar J. 1979. Carabid fauna of the upland oak forest in Michigan: survey and analysis. *Coleoptera Bull.* 33:183–97

85. Lindsey EG. 1943. Attraction of *Melanophila* beetles by fire and smoke. *J. Econ. Entomol.* 35:341–42

86. Lindtroth CH. 1969. Ground beetles of Canada and Alaska, parts 1–6. *Opuscula Entomol.* 20, 24, 26, 29, 33, 34, 35:1–1192

87. Loreau M. 1986. Niche differentiation and community organization in forest carabid beetles. In *Carabid Beetles: Their Adaptations and Dynamics,* ed. PJ den Boer, ML Luff, D Mossakowski, F Weber, pp. 465–87. Stuttgart: Gustav Fisher

88. Lorimer CG. 1977. The presettlement forest and natural disturbance cycle of northeastern Maine. *Ecology* 58:139–48

89. Loucks OL. 1970. Evolution of diversity, efficiency and community stability. *Am. Zool.* 10:17–25

90. Lucarotti CJ. 1981. Effect of fire and forest regeneration on mesofauna populations and microfungal species in lichen woodland soils. *McGill Subarctic Res. Stn. Publ. Meteorol.* 32:7–26

91. Lutz HJ. 1959. Aboriginal man and white man as historical causes of fires in the boreal forest, with particular reference to Alaska. *Yale Univ. For. Bull. 65*

92. Lynham TJ, Stocks BJ. 1991. Natural fire regime of an unprotected section of the boreal forest in Canada. *Proc. 17th Tall Timbers Fire Ecol. Conf., High Intensity Fire in Wildlands: Management Challenges and Options, May 1989, Tallahassee, FL,* pp. 99–109. Tallahassee, FL: Tall Timbers Res. Stn.

93. Lyon LJ, Crawford HS, Czuhai E, Fredririksen RL, Harlow RF, et al. 1978. *Effects of fire on fauna: a state-of-knowledge review, USDA For. Serv. Gen. Tech. Rep. WO-6.* 41 pp.

94. MacLean DA, Wein RW. 1977. Nutrient accumulation for postfire jack pine and hardwood succession patterns in New Brunswick. *Can. J. For. Res.* 7:562–78

95. Martin RE. 1989. Interaction among fire, arthropods and diseases in a healthy forest. *Natl. Soc. Am. Foresters Conf., Oct. 1988, Rochester, New York,* pp. 87–91. (Abstr.)

96. Martin RE, Dell JD. 1978. *Planning for prescribed burning in the inland northwest, Gen. Tech. Rep. PNW-76,* USDA For. Serv. Pac. Northwest Res. Stn. 22 pp.

97. Martin RE, Mitchell RG. 1980. Possible, potential, probable, and proven fire-insect interactions. In *Land-Use Allocation: Processes, People, Politics, Professions. Proc. Natl. Conv.,* pp. 138–44. Spokane, WA: Soc. Am. For.

98. Martin RE, Robinson DD, Schaeffer WH. 1974. Fire in the Pacific Northwest: perspectives and problems. *Proc. 15th Ann. Tall Timbers Fire Ecol. Conf.,* pp. 1–23. Tallahassee, FL: Tall Timbers Res. Stn.

99. McCullough DG. 1996. Fire and insects in jack pine ecosystems. In *Fire, Forest, Insect Interactions, Proc. North Am. For. Insect Work Conf., San Antonio, TX,* ed. RF Billings, TE Nebeker, p. 139. *TX For. Serv. Publ. 160.* 228 pp.

100. McCullough DG, Kulman HM. 1991. Effects of nitrogen fertilization on young jack pine (*Pinus banksiana*) and on its suitability as a host for jack pine budworm (*Choristoneura pinus pinus*) (Lepidoptera:Tortricidae). *Can. J. For. Res.* 21:1447–58

101. McCullough DG, Kulman HM. 1991. Differences in foliage quality of young jack pine (*Pinus banksiana Lamb.*) on burned and clearcut sites: effects on jack pine budworm (*Choristoneura pinus pinus Freeman*). *Oecologia* 87:135–45

102. McCullough DG, Marshall LD, Buss LJ, Kouki J. 1996. Relating jack pine budworm damage to stand inventory variables in northern Michigan. *Can. J. For. Res.* 26:2180–90

103. McCune B. 1983. Fire frequency reduced two orders of magnitude in the

Bitterroot Canyon, Montana. *Can. J. For. Res.* 13:212–18

104. McRae DJ. 1994. Prescribed fire converts spruce budworm-damaged forest. *J. For.* 92:38–40

105. McRae DJ. 1996. Relationships between insects and fire in northern forests of Ontario. In *Fire, Forest, Insect Interactions. Proc. North Am. For. Insect Work Conf., San Antonio, TX,* ed. RA Werner, JR Meeker, p. 140. *TX For. Serv. Publ. 160.* 228 pp.

106. Metz LJ, Dindal DL. 1975. Collembola populatons and prescribed burning. *Environ. Entomol.* 4:583–87

107. Miller JM, Keen FP. 1960. Biology and control of the western pine beetle. *USDA Serv. Misc. Publ. 800.* 381 pp.

108. Miller KK, Wagner MR. 1984. Factors influencing pupal distribution of the pandora moth (Lepidoptera: Saturniidae) and their relationship to prescribed burning. *Environ. Entomol.* 13:430–31

109. Miller WE. 1978. Use of prescribed burning in seed production areas to control red pine cone beetle. *Environ. Entomol.* 7:698–702

110. Miller WE. 1979. Fire as an insect management tool. *Bull. Entomol. Soc. Am.* 25:137–40

111. Mitchell RG. 1966. Infestation characteristics of the balsam woolly aphid in the Pacific Northwest. *USDA For. Serv. Pac. Northwest. For. Range Exp. Stn. Res. Pap. PNW-35.* 18 pp.

112. Mitchell RG. 1990. Effects of prescribed fire on insect pests. In *Natural and Prescribed Fire in Pacific Northwest Forests,* ed. JD Walstad, SR Radosevich, DV Sandberg. Corvallis, OR: Oregon State Univ. Press

113. Mitchell RG, Martin RE. 1980. Fire and insects in pine culture of the Pacific Northwest. *Proc. 6th Conf. Fire For. Meteor., Proc. Natl. Convention,* pp. 182–90. Washington, DC: Soc. Am. For.

114. Morin H, Laprise D, Bergeron Y. 1993. Chronology of spruce budworm outbreaks near Lake Duparquet, Abitibi region, Quebec. *Can. J. For. Res.* 23:1497–506

115. Morris EV. 1967. Distribution and hosts of some horntails (Siricidae) in British Columbia. *J. Entomol. Soc. B. C.* 64:60–63

116. Mutch RW. 1970. Wildland fires and ecosystems: a hypothesis. *Ecology* 51:1046–52

117. Mutch RW, Arno SF, Brown JK, Carlson CE, Ottmar RO, Peterson JL. 1993. *Forest health in the Blue Mountains: a management strategy for fire-adapted ecosystems, Gen. Tech. Rep. PNW-310.* USDA For. Serv. Pac. Northwest Res. Stn. 14 pp.

118. Nealis VG. 1996. Population biology of the jack pine budworm. In *Jack Pine Budworm Biology and Management,* ed. WJA Volney, VG Nealis, et al, pp. 55–71. *Can. For. Serv. Info. Rep. NOR-X-342.* 158 pp.

119. Nealis VG, Lomic PV. 1994. Host-plant influence on the population ecology of the jack pine budworm, *Choristoneura pinus* (Lepidoptera:Tortricidae). *Ecol. Entomol.* 19:367–73

120. Niemala J, Langor D, Spence JR. 1993. Effects of clear-cut harvesting on boreal ground beetle assemblages (Coleoptera: Carabidae) in western Canada. *Conserv. Biol.* 7:551–61

121. Oliver CD, Ferguson DE, Harvey AE, Malany HS, Mandzak JM, et al. 1994. Managing ecosystems for forest health: an approach and the effects on uses and values. In *Assessing Forest Ecosystem Health in the Inland West. Am. For. Workshop,* ed. DL Adams, Spec. Publ. *J. Sustain. For.* 2:113–33

122. Ostaff DP, MacLean DA. 1989. Spruce budworm populations, defoliation, and changes in stand condition during an uncontrolled spruce budworm outbreak on Cape Beton Island, Nova Scotia. *Can. J. For. Res.* 19:1077–86

123. Pare D, Bergeron Y, Camire C. 1993. Changes in the forest floor of Canadian southern boreal forest after disturbance. *J. Veg. Sci.* 4:811–18

124. Parker DL, Stipe LE. 1993. *A sequence of destruction: mountain pine beetle and wildfire, Yellowstone National Park.* USDA For. Serv. Intermt. Reg. Misc. Publ.

125. Parmelee FT. 1941. Longhorned and flat-headed borers attacking fire-killed coniferous timber in Michigan. *J. Econ. Entomol.* 105:795–806

126. Petrides GA. 1958. *A Field Guide to Trees and Shrubs.* Boston, MA: Houghton Mifflin. 431 pp.

127. Pyne SJ, Andrews PL, Laven RD. 1996. *Introduction to Wildland Fire.* New York: Wiley & Sons. 769 pp. 2nd ed.

128. Refseth D. 1980. Ecological analyses of carabid communities: potential use in biological classification for nature conservation. *Biol. Conserv.* 17:131–41

129. Richardson RJ, Holliday NJ. 1982. Occurrence of carabid beetles (Coleoptera: Carabidae) in a boreal forest damaged by fire. *Can. Entomol.* 114:509–14

130. Richmond HA, LeJeune RR. 1945. The deterioration of fire-killed white spruce

by wood-boring insects in northern Sa-skatchewan. *For. Chron.* 21:168–92

131. Romme WH. 1982. Fire and landscape diversity in subalpine forests of Yellowstone National Park. *Ecol. Monogr.* 52:199–21

132. Roovers LM, Rebertus AJ. 1993. Stand dynamics and conservation of an old growth Engelmann spruce-subalpine fir forest in Colorado. *Nat. Areas J.* 13:256–67

133. Ross DA. 1960. Damage by long-horned wood borers in fire-killed white spruce, central British Columbia. *For. Chron.* 36:355–61

134. Rowe JS, Scotter GW. 1973. Fire in the boreal forest. *Quat. Res.* 3:444–64

135. Rundel PW, Parsons DJ. 1980. Nutrient changes in two chaparral shrubs along a fire-induced age gradient. *Am. J. Bot.* 67:51–58

136. Safay RE. 1983. Intensity of bark beetle attack following prescribed understory burning in seral ponderosa pine stands in northern Idaho. *For. Abst.* 44:720

137. Safranyik L. 1978. Spruce beetle mortality in stumps following an operational broadcast burn. *Pac. For. Res. Cent. Bimon. Res. Notes* 34:7–8

138. Schmid JM, Parker DL. 1989. Fire and forest insect pests. In *Effects of Fire in Management of Southwestern Natural Resources, Tucson, AZ, Nov. 14–17, 1988,* pp. 232–33

139. Schmid JM, Thomas I, Rogers TJ. 1981. *Prescribed burning to increase mortality of pandora moth pupae. Res. Notes RM-405.* USDA For. Serv. Rocky Mtn. For. Range Exp. Stn.

140. Simmons GA, Mahar J, Kennedy JK, Ball J. 1977. Preliminary test of prescribed burning for control of maple leaf cutter (Lepidoptera: Incurvariidae). *Great Lakes Entomol.* 10:209–10

141. Smith D, Mrowka R, Maupin J. 1983. Underburning to reduce fire hazard and control *Ips* beetles in green thinning slash. *Fire Manage. Notes* 44:5–6

142. Sousa WP. 1979. Disturbance in marine intertidal boulder fields: the nonequilibrium maintenance of species diversity. *Ecology* 60:1225–39

143. Stickel PW. 1934. Forest fire damage in the northeast. I. Bark beetles and fire damaged hardwoods. *J. For.* 32:701–3

144. Stock AJ, Gorley RA. 1989. Observations on a trial of broadcast burning to control an infestation of the mountain pine beetle, *Dendroctonus ponderosae. Can. Entomol.* 121:521–23

145. Stocks BJ. 1987. Fire potential in the

146. Stuart JD, Agee JK, Gara RI. 1989. Lodgepole pine regeneration in an old, self-perpetuating forest in south Oregon. *Can. J. For. Res.* 19:1096–104

147. Swetnam TW, Lynch AM. 1989. Tree-ring reconstruction of western spruce budworm history in the southern Rocky Mountains. *For. Sci.* 35:962–86

148. Swetnam TW, Wickman BE, Paul HG, Baisan CH. 1995. Historical patterns of western spruce budworm and Douglas-fir tussock moth outbreaks in the northern Blue Mountains, Oregon, since A.D. 1700. *Res. Pap. PNW-RP-484.* USDA Pac. Northwest. Res. Stn. 27 pp.

149. Tethill JD. 1924. Injury to fire-killed lumber in New Brunswick by the softwood borer. *N. B. Land Dep. Annu. Rep.* 63:86–87

150. Viereck LA. 1973. Wildfire in the taiga of Alaska. *Quat. Res.* 3:465–95

151. Viereck LA. 1975. Forest ecology of the Alaska taiga. *Proc. Circumpolar Conf. North. Ecol.,* pp. I-1–I-24. Ottawa, Ontario: Can. Nat. Res. Counc.

152. Viereck LA, Little EL Jr. 1972. *Alaska Trees and Shrubs.* USDA Handb. 410. 265 pp.

153. Viereck LA, Van Cleve K, Dyrness CT. 1986. Forest ecosystem distribution in the taiga environment. In *Forest Ecosystems in the Alaskan Taiga: A Synthesis of Structure and Function,* ed. K Van Cleve, FS Chapin III, PW Flanagan, LA Viereck, CT Dyrness, pp. 22–43. New York: Springer-Verlag

154. Vlug H, Borden JH. 1973. Soil Acari and Collembola populations affected by logging and slash burning in coastal British Columbia coniferous forests. *Environ. Entomol.* 2:1016–23

155. Volney WJA, McCullough DG. 1994. Jack pine budworm population behaviour in northwestern Wisconsin. *Can. J. For. Res.* 24:502–10

156. Wade DD, Debarr GL, Barber LR, Manchester E, MacIver DC. 1989. Prescribed fire—a cost effective control for white pine cone beetle. *Proc. 10th Conf. Fire For. Meteorol.,* ed. H Auld, R Whitewood, pp. 117–21. Dry Branch, GA: USDA For. Serv. Southeast For. Exp. Stn.

157. Weber MG, Taylor SW. 1992. The use of prescribed fire in the management of Canada's forested lands. *For. Chron.* 68:324–34

158. Wenz JM. 1976. *Implications of wildfire and pesticide applications on forest*

soil microarthropod populations in northWeastern California. PhD diss. Univ. Calif., Berkeley. 103 pp.

159. Werner RA. 1983. Biomass, density, and nutrient content of plant arthropods in the taiga of Alaska. *Can. J. For. Res.* 13:729–39

160. Werner RA. 1988. Recommendations for suppression of an *Ips* perturbatus outbreak in interior Alaska using integrated control. In *Integrated Control of Scolytid Bark Beetles: Proc. IUFRO Working Party 17th Int. Congr. Entomol. Symp.,* ed. TL Payne, H Saarensmaa, pp. 189–96. Vancouver, BC: Va. Polytech. Inst. State Univ. Press

161. Werner RA. 1996. Forest health in boreal ecosystems of Alaska. *For. Chron.* 72:43–46

162. Werner RA. 1997. Effect of ecosystem disturbance on diversity of wood borers and bark beetles (Coleoptera: Buprestidae, Cerambycidae, Scolytidae) in white spruce ecosystems of Alaska. *Environ. Entomol.* In press

163. Werner RA, Holsten EH. 1984. Scolytidae associated with felled white spruce in Alaska. *Can. Entomol.* 116:465–71

164. Werner RA, Meeker JR. 1996. Fire/forest/insect interactions. *Proc. North Am. For. Insect Work Conf., San Antonio, TX,* ed. RF Billings, TE Nebeker, p. 136. *TX For. Serv. Publ. 160.* 228 pp.

165. Werner RA, Post KE. 1985. Effects of wood-boring insects and bark beetles on survival and growth of burned white spruce. In *Early Results of the Rosie Creek Fire Research Project–1984,* ed. GP Juday, CT Dyrness, pp. 14–16. Fairbanks, AK: Agric. For. Exp. Stn. Univ. Alaska. Misc. Publ. 85-2

166. White RE. 1983. A new species of *Ernobius* (Coleoptera: Anobiidae) injuri-ous to spruce. *Proc. Entomol. Soc. Wash.* 85:557–59

167. Wickman BE. 1964. Attack habits of *Melanophila consputa* on fire-killed pines (Coleoptera: Buprestidae). *Pan-Pacific Entomol.* 40:183–86

168. Wickman BE. 1964. Freshly scorched pines attract large numbers of *Arhopalus asperatus* adults (Coleoptera: Cerambycidae). *Pan-Pacific Entomol.* 40:59–60

169. Wickman BE. 1978. A case study of a Douglas-fir tussock moth outbreak and stand conditions 10 years later. *Res. Pap. PNW-244.* USDA For. Serv. Pac. Northwest For. Range Exp. Stn. 22 pp.

170. Wickman BE. 1990. *The battle against bark beetles in Crater Lake National Park: 1925–34. Gen. Tech. Rep. PNW-259.* USDA For. Serv. Pac. Northwest Res. Stn. 40 pp.

171. Williams JT. 1978. *Management implications from timber type evaluation of Oregon and Washington tussock moth outbreak areas.* MS thesis. Univ. Wash. 66 pp.

172. Williams JT, Martin RE, Pickford SG. 1980. Silvicultural and forest management implications from a timber type evaluation of tussock moth outbreak areas. *Proc. 6th Conf. Fire For. Meteorol.,* pp. 191–96. Washington, DC: Soc. Am. For.

173. Wright HE Jr, Heinselman ML. 1973. Introduction. In *Ecological Role of Fire in Natural Conifer Forests of Western and Northern North America,* ed. AL Washburn, JS Creager, pp. 319–28. *Quat. Res.* 3:317–513

174. Wright SL. 1986. Prescribed burning as a technique to control insect pests of oak regeneration. In *Prescribed Burning in the Midwest: State-of-the-Art,* pp. 91–95. Stevens Point, WI: Univ. Wisc.