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Forest Ecology and Management 227 (2006) 195–206
Forest Ecology and Management
www.elsevier.com/locate/foreco

Spruce beetles and forest ecosystems in south-central Alaska: A review of 30 years of research

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Abstract

From 1920 to 1989, approximately 847,000 ha of Alaska spruce (*Picea* spp.) forests were infested by spruce beetles (*Dendroctonus rufipennis*). From 1990 to 2000, an extensive outbreak of spruce beetles caused mortality of spruce across 1.19 million ha of forests in Alaska; approximately 40% more forest area than was infested the previous 70 years. This review presents some of the most important findings from a diversity of research and management projects from 1970 to 2004 to understand the biology, ecology, and control of this important forest insect, and the causes and effects of their outbreaks. We suggest that future research should examine the long-term effects of the spruce beetle outbreaks and climate variability on forest ecosystems in the region. Research into how different management actions facilitate or interrupt natural successional processes would be particularly useful.

Keywords: Alaska; Control; *Dendroctonus rufipennis*; Natural disturbance; Semiochemicals; Silviculture; Spruce beetle; Wildlife

1. Introduction

Boreal forests in much of interior and south-central Alaska have come under increasing stress because of a warming trend (Barber et al., 2000; ACIA, 2004) that has fueled outbreaks of forest insect pests and considerably altered forest ecosystems in the region (Werner, 1996). Chief among these insects is the spruce beetle which has caused extensive mortality of spruce from Alaska to Arizona during the last 20 years (Holsten et al., 1999). Outbreaks in Alaska have been concentrated in the south-central region with the Cook Inlet–Kenai Peninsula and Copper River Basin particularly hard hit by large-scale outbreaks (Fig. 1; Holsten, 1990). Approximately 847,000 ha of Alaska's spruce forest were impacted by the spruce beetle from 1920 to 1989 (Holsten, 1990). During this period, outbreaks rarely lasted more than 3 years or caused the loss of more than 60% of the commercial spruce [spruce with diameter-at-breast height (dbh) >22.9 cm] (Baker and Kemperman, 1974; Werner, 1978; Holsten, 1987a,b).

By the time the 1990s outbreak peaked in 1996, more than 930,000 ha had been infested (Fig. 2) with an estimated 30 million trees killed per year (U.S. Forest Service, 1997; Holsten et al., 1999). From 1990 to 2000 approximately 1,192,000 ha of forest in Alaska were infested by spruce beetles with approximately 429,000 and 275,000 ha infested on the Kenai Peninsula and Copper River Basin, respectively (R.E. Burnside Burnside, Alaska Division of Forestry, unpublished data; M. Rude, Kenai Peninsula Borough Spruce Bark Beetle Mitigation Program, unpublished data). More than 90% of the trees >11 cm dbh were killed by spruce beetles in many stands during this time (U.S. Forest Service, 1997). This massive outbreak was related to the relatively high densities of large-diameter spruce in an aging forest across the region and to a warming trend which increased spruce susceptibility to beetle attack and reduced the life cycle of many spruce beetles from a 2-to 1-year life cycle, thus increasing the number of maturing beetles in a given year (Werner and Holsten, 1985a,b). After 1996, spruce beetle outbreaks were on the decline and by the year 2003, active outbreaks affected approximately 37,000 ha (Fig. 2; U.S. Forest Service, 2004). The consequences of these outbreaks (e.g. value loss of wood products, the alteration of

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doi:10.1016/j.foreco.2006.02.050

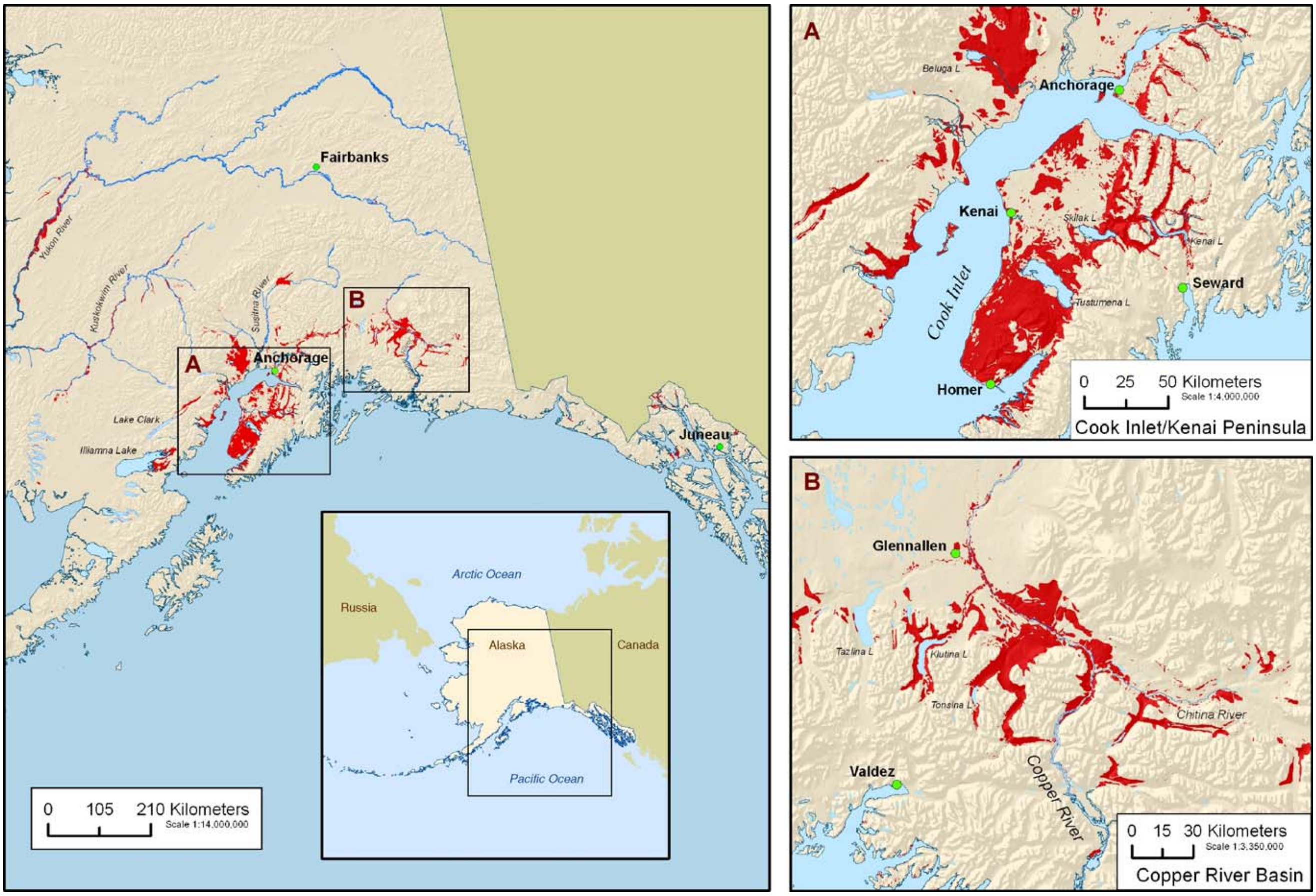

Fig. 1. Location of spruce beetle outbreaks in Alaska from 1980 to 2003. Outbreaks totaled 1,707,383 ha during this time and were concentrated in south-central Alaska in the (a) Cook Inlet–Kenai Peninsula (911,690 ha) and (b) Copper River Basin (303,068 ha). Not included in the map are small localized outbreaks recorded on the Seward Peninsula and Dall Island, Alaska.

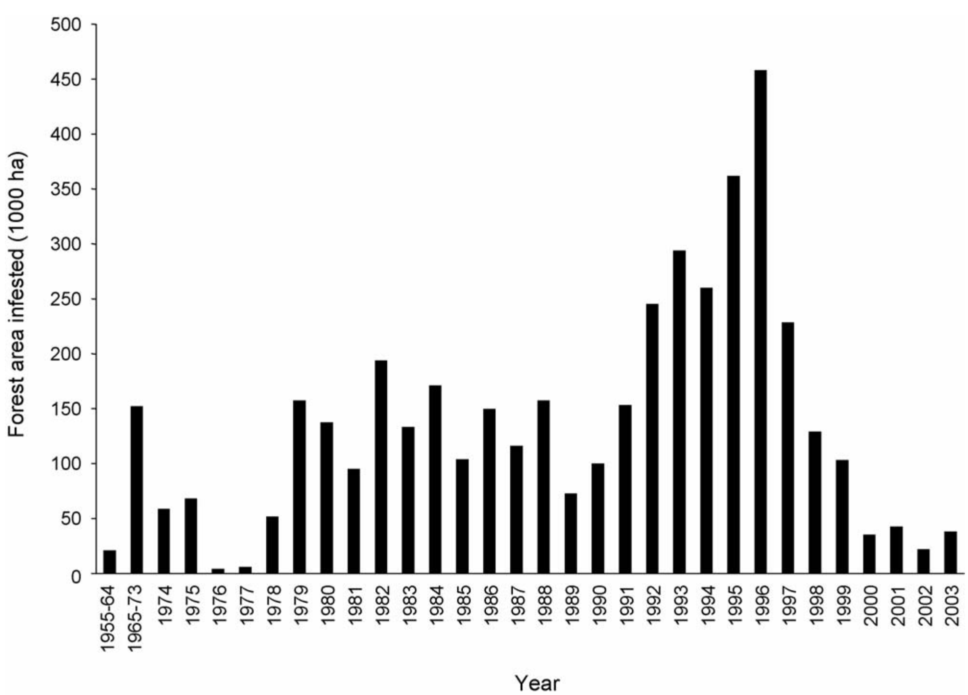

Fig. 2. Forest area (ha) infested by spruce beetles per year by time period in Alaska from 1955 to 2003. Data prior to 1974 are presented by time periods as annual estimates were not available.

wildlife habitat, hydrological changes, loss of aesthetic quality of landscapes, and a potentially greater threat to property and individuals from catastrophic fires and falling tree) became increasingly apparent.

Concern for abrupt changes in non-timber resources resulted in the formation of the Interagency Forest Ecology Study Team (INFEST) in 1995. Because of the magnitude of the 1990s spruce beetle outbreak, the decade resulted in a proliferation of research on the causes and effects of spruce beetle outbreaks on forest ecosystems in south-central Alaska. The results of these studies were presented in a 3-day INFEST sponsored symposium in February 2004, in Homer, Alaska. In this paper, we summarize the diversity of results from the various research and management studies that have been conducted on spruce beetles in south-central Alaska during the previous 30 years, not including the findings presented in the other papers in these conference proceedings.

2. Biology and ecology

The spruce beetle is distributed throughout all forested regions of Alaska where its life-history is tightly governed by temperature. Spruce beetles in Alaska exhibit facultative diapause and require either 1 or 2 years to mature. The rate of development varies with annual weather conditions (i.e. temperature and precipitation), geographic area, and elevation (Werner and Holsten, 1985b). The predominant pattern in south-central Alaska prior to 1980 was a 2-year-life cycle (Werner et al., 1977). From 1980 to 2003, however, more beetles matured in 1 year. This shift from 2- to 1-year-life cycles was considered a major factor contributing to exponential population growth during this period and is thought to have resulted from a trend in increasing temperature during the growing season (Werner and Holsten, 1985a; Barber et al., 2000). In contrast, the warm summers of interior Alaska usually result in 1-year-life cycles (Werner and Holsten, 1985a, b); however, cold winter temperatures limit beetle survival and thus likely population size in the region (see below).

The rate of spruce beetle maturation is a function of the timing of dispersal, phloem temperature, and direct solar radiation to the bark surface during the early larval stages (Werner and Holsten, 1985a). A threshold temperature of 14 °C is generally required in late May and early June to trigger beetle emergence and flight, leading to early attack, oviposition, and hatch of first-instar larvae. A phloem-threshold temperature of 16.5 °C during the first- and second-larval instars has been related to the development of beetles with 1-year life cycles (Werner and Holsten, 1985a,b; Hansen et al., 2001). Fecundity and brood survival were found to be equivalent between beetles with 1- and 2-year life cycles (Hansen and Bentz, 2003). Summers with constant cloud cover and mean daily temperatures below 16.5 °C have been related to development of beetles with mostly 2-year-life cycles (Werner and Holsten, 1985b). Adult beetles with 1-year-life cycles typically overwinter underneath the bark of infested spruce, usually at the root collar, below snowline. Most beetles with 2-year-life cycles overwinter as fourth-instar larvae higher in the boles of infested trees (Werner et al., 1977).

Overwinter survival of spruce beetles depends on habitat selection and accumulated snow depth. If either larvae or adults select a phloem hibernaculum that is above snowline, survival is unlikely when minimum daily temperatures drop below −25 °C (Miller and Werner, 1987). Neither larvae nor adults are freeze-tolerant, so survival at low temperatures depends on changes in beetle overwintering chemistry and supercooling. Spruce beetles from interior Alaska have lower supercooling points (larvae −41 °C and adults −37 °C) because a higher accumulation of glycerol allows for lower lethal temperatures compared to other species of the genus *Dendroctonus* found at lower latitudes (Miller and Werner, 1987).

Adult beetles dispersed more commonly from areas surrounding the upper clear tree boles and lower live crowns with twice as many adults dispersing from unthinned versus thinned stands regardless of initial population levels (Holsten and Hard, 2001). Mark-release-recapture studies recovered adult spruce beetles from 90 to 600 m from the point of release in the direction of the prevailing winds (Werner and Holsten, 1997). Spruce beetles initially colonize only a few highly susceptible spruce within stands before soils completely thaw and the temperature threshold is reached to elicit mass dispersal by spruce beetles. As air and soils warm, the spruce adjacent to these initial points of attack are subsequently infested by emerging adult spruce beetles with spruce located further from the ''focus trees'' attacked at lower rates (Hard, 1987, 1989).

3. Host susceptibility and resistance

Spruce beetles colonize all species of spruce in Alaska; however, the susceptibility of trees to attack and subsequent mortality varies considerably and is related to the species of spruce, climatic conditions, rate of host growth, host tree chemistry, oleoresin flow rate, and occurrence of blue-stain fungi. Hosts include white spruce (*Picea glauca*), Sitka spruce (*P. sitchensis*), and Lutz spruce (*P.* × *lutzii*), the latter a hybrid of white and Sitka spruce (Werner et al., 1977). Black spruce (*P. mariana*) are rarely attacked. Spruce beetles typically colonize severely stressed or dying spruce (e.g. windthrown, fire damaged, logging and land-clearing slash). Live spruce weakened by drought, flooding, ice and snow damage, defoliation, root diseases, root compaction, high tree densities, or advanced age are also susceptible to attack (Hard and Holsten, 1985). Spruce beetle populations also experience periodic eruptions at 30- to 50-year intervals, during which they can kill most healthy mature spruce (Werner and Holsten, 1983; Hard and Holsten, 1985; Holsten, 1990).

Experimental studies on the Kenai Peninsula have shown that different species of spruce vary in their suitability in supporting spruce beetles reproduction with white spruce producing more progeny per adult spruce beetle than Sitka spruce, with Lutz spruce intermediate (Holsten, 1984; Holsten and Werner, 1990). In spite of these differences in suitability, stands of Lutz spruce have been more susceptible to frequent and severe spruce beetle outbreaks than stands of Sitka spruce, with white spruce stands intermediate in south-central Alaska (Werner et al., 2006). Several spruce beetle outbreaks have occurred in the Sitka spruce forests of southeast Alaska (Holsten, 1990; Schultz, 1996). However, outbreaks in southeast Alaska are of short duration as the cool summer temperatures and high precipitation usually limit the rate of spruce beetle development and growth in stands of Sitka spruce in coastal Alaska. Long-term monitoring and single-point-in-time plots have been established in a number of these localities in southeast Alaska (Eglitis, 1981, 1982, 1989; Schultz, 1996). Conversely cold winter temperatures limit survival of spruce beetles in white spruce stands of interior Alaska (Holsten and Werner, 1990). Thus, climate, host suitability, host susceptibility, as well as interactions among these factors may be important in influencing the incidence of spruce beetle outbreaks (Werner et al., 2006).

Large-diameter, slow-growing spruce were most susceptible to spruce beetle attack on both the Kenai Peninsula and Copper River Basin (Hard et al., 1983; Holsten, 1984; Hard, 1985, 1987, 1989; Doak, 2004), especially on north facing slopes where moisture stress was enhanced by low soil temperatures (Holsten, 1984, 1987a). Spruce that have low oleoresin flow rates, an important component of conifer defense against bark beetles, also are susceptible to beetle attack (Hard, 1985, 1987). Blue-stain fungi, which are transmitted by certain species of bark beetles (e.g. spruce beetles), can also weaken spruce resistance to spruce beetles by colonizing xylem tissues, interrupting the transport of water moving into the upper portions of the tree crown, and causing an energy-requiring chemical defense response in phloem tissues (Werner and Illman, 1994a,b; Werner et al., 2006; B. Illman, U.S. Forest Service, unpublished data). Several blue-stain fungi are associated with the spruce beetle, notably *Leptographium abietinum* (Reynolds, 1992). Other fungi recently cultured from spruce beetles from interior and south-central Alaska were *Ophiostoma piceae*, *O. ips*, and *O. olivaceum* (K. Haberkern, University of Wisconsin, unpublished data) and *Ophiostoma* species A, and *Pesotum* species F. (B. Illman, U.S. Forest Service, unpublished data). It is unknown whether any of these fungi are toxic to the spruce beetle or the host tree.

Sitka and Lutz spruce have several lines of defense of phloem tissues that inhibit feeding by spruce beetle larvae and colonization of potentially pathogenic fungi. If wounding occurs by initial beetle attack, the formation of periderm and resin act as an initial defense to further beetle colonization. If this defense is overcome by beetles and blue-stain fungi, increased production of toxic monoterpenes and antimicrobial stilbenes in the phloem tissues act as a second line of defense against beetles and blue-stain fungi, respectively (Werner and Illman, 1994a). Limonene and 4-allylanisole were the most toxic and inhibitory monoterpenes found in white spruce (Werner, 1995). In laboratory bioassays, stilbene aglcones deterred growth of the blue-stain fungi *L. abietinum* and feeding by spruce beetle adults and larvae (Werner and Illman, 1994b).

4. Effects on forest stands

Research quantifying the effects of outbreaks on forest stands in the region has noted some important similarities and differences between the more coastal forests of the Kenai Peninsula and boreal forests of the Copper River Basin. Early research prior to 1970 centered on descriptions and locations of outbreaks and estimation of stand volume loss (Holsten, 1990). For example, a severe 1970s infestation of the spruce beetle on the west side of Cook Inlet, Alaska, caused 65% mortality of white spruce >12.7 cm dbh. Birch (*Betula papyrifera*) became the dominant tree species in the residual stand following the beetle outbreak (Baker and Kemperman, 1974). Mapping spruce beetle infestations in Alaska through aerial surveys has accumulated over 40 years of spatial data on annual and cumulative areas infested by spruce beetle and other forest insects that has been archived by the State of Alaska (Alaska Department of Natural Resources, 1998 unpublished report).

Monitoring of infested forests in the Resurrection Creek drainage on the Kenai Peninsula has been particularly insightful into the longer-term effects of spruce beetles on both overstory and understory plant communities. Between 1976 and 1980, spruce beetles killed 29% of the white spruce accounting for 59% of the commercial spruce in a 4800 ha outbreak. Mortality was greatest in the larger diameter classes during the early part of the infestation, but smaller spruce were subsequently attacked as larger spruce were depleted (Werner and Holsten, 1983). After 16 years, 51% of the spruce >20 cm dbh had been killed representing nearly 90% of the commercial stand volume (Holsten et al., 1995). Tree species composition remained essentially the same after the outbreak, but both the size and density of spruce were substantially reduced. The number of understory plant species among infested stands also declined as two species, bluejoint (*Calamagrostis canadensis*) and fireweed (*Chamerion angustifolium*), soon dominated the affected sites. Over this same 16-year period, approximately 28 beetle-killed spruce per hectare fell, significantly increasing the fuel available for fire from an average of 6350 kg/ha before the outbreak to 31,752 kg/ha 20 years later. Cover by grasses, a fine flashy fuel, also rose considerably from <1% to > 50% (Schulz, 1995, 2003). Although an inventory of forest resources on the Kenai Peninsula showed that overall timber growth exceeded mortality (262 and 225 m^3, respectively) this balance varied spatially with mortality exceeding growth primarily on mature forest stands on the northern Kenai Peninsula (van Hees and Larson, 1991).

A widespread spruce beetle epidemic from 1989 to 1998 infested mature white spruce across nearly 243,000 ha in the Copper River Basin (National Park Service, 1999). Outbreaks there displayed some similar patterns of spruce mortality compared to those observed on the Kenai Peninsula, but important differences were also noted. Similar to the outbreaks on the Kenai Peninsula, spruce beetles in the Copper River Basin selectively attacked stands with high densities of white spruce >23 cm dbh and tended to avoid stands with greater densities of black spruce (Matsuoka et al., 2001; Doak, 2004). Spruce beetles substantially reduced basal area among stands in the region (Doak, 2004) by causing mortality of 71% of white spruce with dbh >23 cm, 43% of white spruce with dbh 16–23 cm, 11% of white spruce with dbh 2.5–15 cm, and 1% of black spruce (Matsuoka et al., 2001). Unlike beetle-killed Lutz spruce on the Kenai Peninsula, white spruce killed by spruce beetles in the cool and dry climate of the Copper River Basin were extremely resilient to rot following a 1930s outbreak and remained standing for more than 50 years (Werner et al., 1983a).

Responses by understory plant communities in the Copper River Basin were much different from those on the Kenai Peninsula, suggesting responses by plants to spruce beetle outbreaks may vary considerably with variation in climate, soils, and competitive interactions among species. Unlike on the Kenai Peninsula, grasses did not proliferate following mortality of overstory spruce. Fireweed was more abundant in heavily infested stands but was still rare in infested stands in the Copper River Basin compared to stands on the Kenai Peninsula. Shade intolerant alders (*Alnus* sp.) and crowberry (*Empetrum nigrum*); however, were more abundant in areas with heavy infestations in the Cooper River Basin, possibly in response to the mortality of the overstory trees (Matsuoka et al., 2001).

5. Management strategies

Strategies that have been developed and tested to manipulate populations of spruce beetles in Alaska (Werner et al., 1988) and manage stands following infestations include silvicultural treatments, cultural and biological control, treatment with approved pesticides, use of semiochemicals to attract or repel beetle flight and attack, and use of trap trees.

5.1. Cultural control

Rights-of-way clearing for highway and powerline construction often results in large quantities of spruce slash and debris (Holsten, 1994a) which left untreated, can contribute substantially to an increase in spruce beetle populations (Schmid, 1977). In Alaska, recommended treatments have included burning, applying pesticides to, or removing slash to prevent increases in populations of spruce beetles (Hard and Holsten, 1991). However, techniques developed to suppress bark beetle populations in slash, debris, or infested piles of firewood in more temperate regions of North American have had variable results in Alaska's cooler climate. For example, bucking slash into short lengths (~2 m) was effective for restricting spruce beetle population increases in areas with hot, dry summers such as the southern Rocky Mountains (Mitchell and Schmid, 1973), but not during a field test on the Kenai Peninsula (Hard and Holsten, 1991). This method did not hasten drying of the inner bark or suppress spruce beetle populations on the Kenai Peninsula even though bucking stems into 0.61 m bolts and removing limbs is current policy for rights-of-way clearing in south-central Alaska. Removing limbs, however, did reduce attack density of beetles on felled spruce in areas with warm-dry summers where spruce beetle outbreaks are typically more intense (Hard and Holsten, 1991). Similarly, covering infested stacks of spruce firewood infested with spruce beetles with black or clear polyethylene sheeting did not raise inner bark temperatures high enough to reduce or kill populations of spruce beetles (Holsten and Werner, 1993), compared to uncovered stacks of firewood.

5.2. Silvicultural treatments

Land managers of forests susceptible to spruce beetle outbreaks should consider the use of silvicultural treatments to maintain vigorous tree growth and thereby minimize losses of spruce (Hard and Holsten, 1985) and the spread of spruce beetles. The first step in this strategy is to assess the amount of spruce mortality that would occur during an infestation (hazard; Holsten and Wolfe, 1979) with stands with moderate to high hazard the best candidates for treatment. The second step is to predict the probability that spruce stands will be infested by spruce beetles (risk) to help prioritize stands treatments. This assessment can be done using hazard and risk models developed for south-central Alaska that take into account stand attributes and spruce beetle population sizes (Reynolds and Holsten, 1994, 1996, 1997).

Thinning strategies are commonly recommended for many conifers, but primarily for stands approaching maturity or stands younger than rotation age (Shrimpton and Thomson, 1983). Mature stands that are lightly infested by spruce beetles or are not infested should be harvested to a residual basal area of 5.6–11.1 m^2/ha depending on site quality. Pruning of the lower 1/3 of the live crown of spruce is an alternative or complementary treatment to thinning that has been found to reduce by two times the number of successful spruce beetle attacks on slow, but not fast, growing spruce presumably by modifying the temperature, light intensity, humidity, and phloem moisture at this preferred location of attack (Hard, 1992). Pruning may be a particularly effective in protect slow growing spruce of high commercial or esthetic value.

5.3. Biological control

Competition from other bark beetles may interfere with development of spruce beetle populations (Werner and Holsten, 2002). For example, the presence of broods of *Ips perturbatus* and *Dryocoetes affaber* was the most important factor explaining mortality of spruce beetle larvae at two sites in interior and south-central Alaska (Whitmore, 1983). The small scolytids were found in 73% of bark samples with spruce beetles and accounted for more mortality of larval spruce beetles than dipteran (e.g., *Medetera* sp.) and coleopteran predators (e.g., *Rhizophagus dimidiatus*, *Thanasimus dubius*) and hymenopteran parasites (e.g., *Roptrocerus* spp. and *Dinotiscus* spp.) of spruce beetle (Whitmore, 1983; Gara et al., 1995). Thus, silvicultural treatments or semiochemicals (see below) that attract these less damaging species of bark beetles to stands could be tested and developed as a means of reducing populations of spruce beetles.

5.4. Chemical control

Reducing the number of spruce beetle adults that emerge from infested spruce is important in reducing the number of adults that can attack adjacent standing green spruce. Thus, several chemical insecticides have been tested in south-central Alaska with many protecting high-value spruce at campgrounds, administrative sites, and homes (Werner et al., 1986a). Results of tests generally indicate that numbers of spruce beetles can be reduced by 80% depending on the insecticide applied.

Prior to 1980, lindane was the only insecticide approved by the U.S. Environmental Protection Agency to protect spruce from attack by spruce beetles. Thus much research was directed towards testing the efficacy of insecticides (Werner et al., 1983c) that were less toxic to both humans and other taxa. Permethrin (0.25 and 0.5%), chlorpyrifos (0.5 and 1.0%), fenitrothion (1.0 and 2.0%) were tested and found to protect Lutz spruce from attack by spruce beetles briefly for 4 months with little and no measureable movement of insecticide residues into nearby soils and adjacent streams, respectively (Werner et al., 1984). Although these insecticides initially showed low LD_{50} (Werner et al., 1983c), permethrin was later found to have an adverse effect on aquatic organisms (Werner and Hilgert, 1992).

Werner et al. (1986a) found that carbaryl (1 and 2% Sevin SL) and lindane (0.5%) were extremely effective in protecting individual high value spruce. All three insecticide formulations provided 100% protection 16 months after treatment, and were 89–96% effective at the end of the third growing season following treatment (Werner et al., 1986b). Werner and Holsten (1992) later found that different formulations of carbaryl mixed with water or diesel varied in their remedial control of different age groups of spruce beetles. Sevin SL in water provided remedial control of emerged first-year and parent adults. Sevin 80S in diesel and Sevin SL in water provided remedial control of emerged second-year adults. Sevin 80S in diesel provided the best remedial control of larvae but not pupae. Treatments consisting of Sevin 4 oil in water, Sevin 80S in water, and diesel alone were not as effective in remedial control (Werner and Holsten, 1992). Application of pine oil (Norpine 65 and BBR-2; Werner et al., 1986b) and injection of three systemic insecticides (Shea et al., 1991) were found to be particularly ineffective in reducing attacks or preventing tree mortality by spruce beetles.

Persistence and movement of 2% aqueous carbaryl within soils of wet and dry sites was evaluated over a 485-day period after application in boreal (south-central Alaska), temperate (northwestern North Carolina), and Mediterranean (east-central California) forests (Hastings et al., 1998). The highest concentration of carbaryl were detected within the uppermost soil layers (upper 2.54 cm) of each site. Carbaryl persisted the longest on the North Carolina dry site. All sites, except the Alaska dry and North Carolina wet sites, had carbaryl levels exceeding 20 ppm in the uppermost layer of soil 90 days after application. The results of this study suggest that site-specific information related to local climate and soil types may be important factors in decisions regarding carbaryl for controlling bark beetles (Hastings et al., 1998).

Because of their efficacy, carbaryl treatments are commonly used to protect most conifers from attack by *Dendroctonus* bark beetles, with one exception, the southern pine beetle (*D. frontalis*) (Zhong et al., 1994, 1995a, b). A review of the application of carbaryl treatments to protect conifers from attack by bark beetles in North American concluded that carbaryl was much safer, both environmentally and to human exposure, than most pesticides used in forestry (Hastings et al., 2001). Toxicological literature indicates that carbaryl is moderately toxic to humans and that adverse human and environmental effects are minimal if applied according to the label.

5.5. Semiochemicals

During the last 20 years, there has been increased interest to develop non-toxic, behavior modifying chemicals that prevent attacks or reduce attack densities of spruce beetles to below outbreak levels. Such chemical include synthetic attractant pheromones, anti-aggregation pheromones, inhibitors, repellents, or various combinations of these. Pheromones are chemicals used for intraspecific communication by insects such as bark beetles, and when combined with tree host chemicals are called semiochemicals (Borden, 1989). The use of pheromones for the control of bark beetles in Alaska has previously been discussed (Holsten, 1994b; Werner, 1994; Borden, 1995; Werner and Holsten, 1995).

Aggregation pheromones are potentially useful to attract spruce beetles to baited trees to either monitor spruce beetle population levels or trap and remove spruce beetles from isolated stands. Early research on spruce beetle pheromones in Alaska (Furniss et al., 1976, 1979) suggested that the attractant semiochemic was a combination of insect produced frontalin and/or seudenol and the host spruce terpene, alpha-pinene. Later studies (Werner, 1994; Borden et al., 1996) showed that attraction of semiochemical varied regionally with the ternary blend of host spruce alpha-pinene, and beetle produced frontalin and methylcyclohexenol (MCOL) very effectively in attracting spruce beetles in Alaska but not in British Columbia.

Methylcyclohexenone (MCH) is thought to be the primary anti-aggregation pheromone of both spruce and Douglas-fir (*D. pseudotsugae*) beetles (Kinzer et al., 1971; Rudinsky et al., 1974). MCH has been applied with much success in controlling Douglas-fir beetle outbreaks (Zogas, 2001); however, its has not been widely used on spruce beetles in Alaska. MCH from either bubble cap or bead formulation was non-efficacious as an anti-aggregate for spruce beetles in Alaska (Holsten, 1994b; Holsten and Werner, 1984, 1987; Holsten et al., 1992; Mask, 1995a,b; Werner, 1994; Werner and Holsten, 1995; Zogas, 2001), presumably because diffusion of the pheromone decreased with time and was not maintained at concentrations above the threshold needed during the beetle flight period (Holsten et al., 2001, 2002). MCH was only found effective on spruce beetles when released at a continuous metered dose through a disposable microinfusion pump developed by Med-e-Cell® (San Diego, CA) which has been found to be less temperature-sensitive than other diffusion release devices (Holsten et al., 2003).

Recently semiochemicals developed from synthetic pheromones have been successful in attracting competiting bark beetles, *I. perturbatus* and *D. affaber* to susceptible host spruce. The presence of these competitors significantly reduced spruce beetle attraction and brood development (Werner and Holsten, 2002). We recommend that application of these semiochemicals and the MCH pheromone should be further tested and developed to minimize colonization of forests by spruce beetles and thereby inhibit the initiation of a large-scale infestations.

5.6. Trap trees

Conventional trap trees are green spruce that are felled before beetle flight to attract beetles away from living, standing spruce and concentrate reproduction into areas where the trap trees, and the broods they contain, can be removed, or treated, prior to beetle emergence (Gibson, 1984; Bentz and Munson, 2000). A small, but successful trapping trial was conducted on the Chugach National Forest, Kenai Peninsula (Holsten, 1988). Once infested, these trap trees were successfully treated with fuel oil to kill all life stages of the spruce beetle under the outer bark (Holsten, 1989). Lethal trap trees are spruce that are treated with chemicals prior to, or at the time of felling. These trap trees kill attacking beetles or developing broods and eliminate the need for the removal of the trees. The use of lethal trap trees treated with monosodium methane arsenate (MSMA) was successfully tested in Canada (Gray et al., 1990) and Alaska (Holsten, 1985a,b, 1987b). Similarly, the use of preventive insecticides (e.g. carbaryl) along with attractant pheromones was tested in south-central Alaska for its efficacy as a standing lethal trap tree (Holsten et al., 1990; Shea et al., 1995). In all studies, two trap tree clusters per ha (three insecticide and treated trees baited with pheromone) were used. There were apparent differences in the number of newly infested spruce between treated and untreated control plots for 1 year. Carry-over treatment effects were less apparent the second year. Lethal trap tree strategies have not been used operationally in Alaska.

5.7. Utilization of beetle-killed trees

The value of beetle-killed spruce as commercial sawmill products is significantly reduced within 3 years of attack in south-central Alaska due to weather checking and sap-rots (Lowell, 1995; Lowell and Willits, 1998). Tests to evaluate the value of beetle-killed spruce as pulpwood (Werner et al., 1983a; Scott et al., 1996, 2000) showed that the dead spruce were still useful up to 50 years following tree mortality if they remained standing. The presence of sap rot decay is an important indicator of pulping efficiency and pulp quality. The value of beetle-killed spruce as house logs or firewood continues for many years.

Because spruce mortality currently exceeds recruitment in many spruce forests in the region, long-term subsistence harvest of white spruce for firewood and house logs may be affected in some local communities. Local demands for firewood and house logs were adequately supplied by beetle-killed spruce during the 1990s outbreak, but demand for live spruce will likely increase with time as beetle-killed spruce decay, fall, and become unsuitable for subsistence harvest. Based on a demographic model of a white spruce stand with 42% beetle-killed spruce in the Copper River Basin, such use of live spruce will expedite declines of white spruce (Loso, 1998).

By the mid-1990s lumber markets had expanded to accommodate a seemingly endless supply of beetle-killed spruce. The State of Alaska provided management guidelines for utilizing beetle-killed spruce on state and adjacent private lands in an attempt to accommodate forest managers and commercial interests (Alaska Department of Natural Resources, 1992, unpublished report). Because of limited access to State of Alaska resource areas on the Kenai Peninsula, most timber utilization on state lands was salvage harvest of dead spruce to supplement existing foreign and Western U.S. pulp chip markets.

5.8. Reforestation

Spruce beetle outbreaks can significantly alter stand composition and structure. On the Kenai Peninsula, plant diversity, including spruce regeneration, can also be reduced due to the competitive advantage of competing vegetation such as bluejoint and fireweed (Holsten et al., 1995). However this pattern of understory growth was not observed in the Copper River Basin (Matsuoka et al., 2001). Natural regeneration of Lutz and white spruce is often inadequate to meet reforestation standards due to the low persistence of seeds in soil, a sporadic seed production cycle, and inadequate site conditions for spruce seedling establishment (Cole et al., 2003). The effects of spruce beetle outbreaks and increased harvest activity in beetle-killed stands, has led to increased interest in enhancing spruce regeneration and juvenile growth to hasten reforestation. A recent study (Cole et al., 2003) has shown that both herbicide and mechanical site preparation increase white spruce height and basal diameters compared to untreated plots. Planted spruce seedlings have the greatest growth and survival where herbicide site preparation is undertaken (Cole et al., 1999). Planting stock is the most important factor in spruce growth and survival, with bare root transplant seedlings having the highest survival and growth rates 5 years after planting.

6. Impacts to non-timber resources

Comprehensive literature reviews on the spruce beetle in North America (Linton and Safranyik, 1988; Zogas and Holsten, 2002.) highlight the lack of research on the effects of spruce beetle outbreaks on non-timber resources. This area encompasses a diverse grouping of physical, biological, and social components of the forest ecosystems such as hydrology, wildlife and fish populations, carbon sequestration, and socioeconomic effects on communities within the affected areas. The effects of spruce beetle outbreaks have been assessed for only a few of these resources in south-central Alaska. For example, surveys of public perception of the impacts of the 1990s outbreak of spruce beetles showed: (1) wide agreement among those surveyed on the Kenai Peninsula that the scenic quality of landscapes declined along National Scenic Byways and forest management should be initiated, whereas, (2) disagreement on whether spruce beetle outbreaks damaged the scenic quality of backcountry areas and thus required management (Daniel et al., 1991; Eriksen, 1991; Kruse and Pelz, 1991; Orland et al., 1992; Flint, 2004). The impacts of spruce beetle outbreaks on wildlife populations was the most comprehensively researched non-timber resource and is discussed in detail below.

6.1. Impacts on wildlife populations

The effects of spruce beetle outbreaks and related tree mortality on wildlife populations in south-central Alaska were not seriously addressed until the 1990s outbreak. Resource managers realized practically no information was available to assess the effects of the outbreak or associated management prescriptions on wildlife populations in the region. As a result, a series of studies were conducted to assess short-term responses by avian and small mammal communities to the 1990s outbreak. These studies indicated that: (1) beetle-infested forests supported a diverse community of wildlife species, (2) spruce beetles influenced the structure of wildlife communities by altering both resource availability and relationships between predators and prey, (3) wildlife responses were highly variable with important differences observed between coastal and boreal forests on the Kenai Peninsula and Copper River Basin, respectively, and (4) salvage logging had more extensive negative effects on wildlife populations than the spruce beetle infestation alone.

The effects of the outbreak on wildlife populations were most apparent on species that rely on white spruce for food or nesting. For example, as levels of infestation increased, red squirrel (*Tamiascurius hudsonicus*) abundance declined, likely the result of losses of conifer seeds as a food source (Yeager and Riordan, 1953; Matsuoka et al., 2001; S. Boutin, University of Alberta, unpublished data). Also affected were several avian species that nest exclusively in conifers in Alaska, such as ruby- and (*Regulus calendula*) golden-crowned kinglets (*R. satrapa*), and Townsend's warblers (*Dendroica townsendi*) (Lance and Howell, 2000; Collins et al., 2001; Matsuoka et al., 2001). Similarly, marbled murrelets (*Brachyramphus marmoratus*), which nest in large conifers, may have had low rates of reproduction in coastal areas affected by spruce beetle outbreaks due to losses of nesting habitat (Kuletz et al., 1997).

Negative effects of outbreaks on spruce-nesting birds were more apparent in coastal forests on the Kenai Peninsula than in boreal forests of the Copper River Basin. This may have been because of the widespread use of beetle-killed spruce as nest sites by tree-nesting birds in the Copper River Basin (Matsuoka et al., 2001; Matsuoka and Handel, in press) and the faster rates that beetle-killed spruce decay, fall, and become unavailable as nest sites on the Kenai Peninsula (Werner et al., 1983a; Holsten et al., 1995). Woodpeckers, such as American three-toed woodpecker (*Picoides dorsalis*), which feed on the larvae of bark beetles (Murphy and Lehnhausen, 1998), appeared to increase briefly in numbers during outbreaks (Yeager and Riordan, 1953; Lance and Howell, 2000; Smith and Folkard, 2001), but likely decreased quickly in abundance as infestations abated and beetle larvae became scarce (Murphy and Lehnhausen, 1998; Matsuoka et al., 2001). Tree-nesting birds bred at lower densities in an infested forest that was clear-cut than infested stands that were left untreated (Lance and Howell, 2000; Collins et al., 2001). In the Copper River Basin, yellow-rumped warblers (*Dendroica coronata*), which nest exclusively in spruce (Matsuoka and Handel, in press), were particularly resilient within infested sites. They both selectively nested in beetle-killed spruce with no reduction in nest success (Matsuoka and Handel, in press) and commonly fed in beetle-killed spruce despite a decrease in arthropod abundance and biomass in beetle-killed compared to live white spruce (Rozell, 2004).

Indirect effects of the outbreak on understory communities of wildlife were highly variable. In particular, northern red-backed voles (*Cleithrionomys rutilus*), an important prey species for many avian and mammalian predators, showed different responses to outbreaks with populations negatively affected in the Copper River Basin and positively affected on the Kenai Peninsula. Voles in the Copper River Basin showed consistent declines in abundance, reproduction, and recruitment as levels of spruce beetle infestation increased, presumably due to decreases in the abundance of mycorrhizae, a major food source of voles (McDonough and Rextad, 2005). In stands of white spruce on the Kenai Peninsula, populations of voles (i.e., adults, pregnant and lactating females, and juveniles) were highest in infested stands, intermediate in uninfested stands, and lowest in clear-cut areas. Low population levels of voles in harvested sites were likely the result of ground scarification, proliferations of bluejoint grass following logging, and a decrease in vole foods such as berries and mycorrhizae. Differences in vole abundance were not found among mixed coniferous-deciduous forests with various levels of infestation and harvest treatments (Williams, 1999). Unlike voles, masked shrews were found almost exclusively on harvested sites on the Kenai Peninsula (Williams, 1999), likely because of the dense ground cover required by this species (Banfield, 1974) that was provided by bluejoint reed grass.

Birds that nest in the forest understory or are associated with shrub habitats in Alaska appeared to benefit from the outbreak in the Copper River Basin. Ground and shrub-nesting birds, such as hermit thrush (*Catharus guttatus*), orange-crowned warbler (*Vermivora celata*), blackpoll warbler (*Dendroica striata*), and Wilson's warbler (*Wilsonia pusilla*), were all more abundant in heavily compared to lightly infested stands. These increases in avian abundance were related to increases in understory alders available to concealed nests from predators (Matsuoka et al., 2001) and to decreases in the abundance of red squirrels, a major nest predator (Willson et al., 2003; Matsuoka and Handel, in press). The benefits associated with nesting in infested forests were most apparent among dark-eyed juncos (*Junco hyemalis*) whose nest success was 10 times greater in heavily compared to lightly infested stands. Predation of junco nests was extremely high in lightly infested stands suggesting that red squirrels may have immigrated to these stands from nearby infested sites where the larger cone-producing spruce had been killed by spruce beetles (Matsuoka and Handel, in press).

Higher densities of understory-nesting birds were not observed in infested stands on the Kenai Peninsula because of the lack of dense shrubs in infested areas. However, understory-nesting-birds and birds associated with disturbed areas in other portions of their range were clearly more abundant on a clear-cut salvage harvest site. Species such as alder flycatcher (*Empidonax difficilis*), American robin (*Turdus migratorius*), yellow warbler (*Dendroica petechia*), blackpoll warbler, dark-eyed junco, savannah sparrow (*Passerculus sandwichensis*), white-crowned sparrow (*Zonotrichia leucophrys*), golden-crowned sparrow (*Z. atricapilla*), Lincoln's sparrow (*Melospiza lincolnii*) and song sparrows (*M. melodia*) were all either more abundant or observed exclusively on harvested sites with an abundance of deciduous seedlings and alders compared to infested stands (Lance and Howell, 2000).

7. Conclusions

The ecology, impacts, and management activities associated with a large spruce beetle disturbance have led to increased forest-related research in south-central Alaska. As evident in the previous sections, 30 years of research on spruce beetles in the region has provide insight into: (1) climatic conditions that trigger increased reproduction and dispersal that lead to eruptions of spruce beetle populations to outbreak levels, (2) short-term effects of outbreaks on forests and associated plant and animal communities, (3) land use practices to avoid that result in infestations by spruce beetles; (4) silvicultural and chemical measures that control local infestations, mitigate the negative effects of outbreaks, enhance reforestation, and prevent future infestations from occurring. Many important issues, however, remain to be addressed regarding the long-term effects of spruce beetle outbreaks on forest ecosystems in the region.

Emphasis should be placed on developing landscape-level models for land and natural resource managers in south-central Alaska (Ross et al., 2001) to assess the consequences of different management scenarios for mitigating for the negative effects of spruce beetle outbreaks. Future research on spruce beetles in the region should be focused on verifying, improving, and broadening the predictive capabilities of such models. In particular, further research should take an interdisciplinary approach to assess the long-term, landscape-level effects of spruce beetle outbreaks and related management prescriptions. Research should address not only forest regeneration and succession of plant and animal communities, but also hydrology, water resources, quantities and qualities of fuels, and the economies of affected communities in the region (Ross et al., 2001). Such studies should carefully measure how climate change, invasive species, and other disturbances further modify successional trajectories, trophic relationships, and susceptibility of areas to future outbreaks of spruce beetles. These studies will be important not only in better understanding how management activities hasten or interrupt natural processes of succession, but also in helping achieve landscapes that are both ecologically viable and more resilient to disturbance from future outbreaks of spruce beetles.

Acknowledgements

We thank all of the presenters at the symposium, a changing Alaskan ecosystem: effects of spruce beetle outbreaks and associated management practices on forest ecosystems in south-central Alaska, for both sharing with us their knowledge and stimulating discussions on how a tiny insect changed the face of south-central Alaska. We are particularly grateful to Hans Buchholdt, Alaska Division of Forestry, for development of the map of our study area and to William van Hees and Michael Shephard, U.S. Forest Service, and two anonymous reviewers for many helpful suggestions on improving earlier drafts of this manuscript.

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