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Managing White and Lutz Spruce Stands in South-Central Alaska for Increased Resistance to Spruce Beetle

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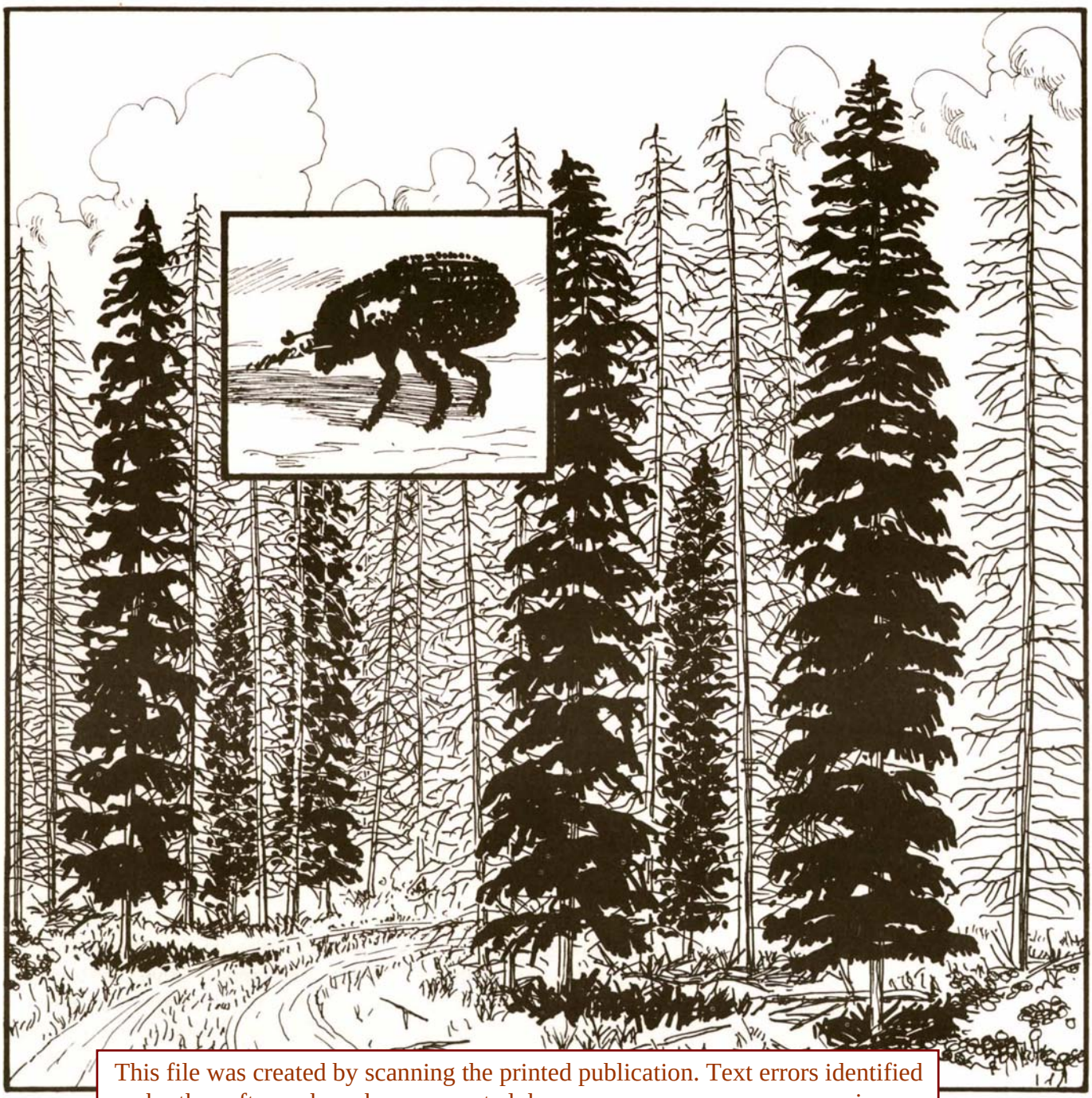

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Abstract

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Thinning is recommended for maintaining vigorous tree growth to minimize losses caused by spruce beetles *(Dendroctonus rufipenni* Kirby) and windthrow in residual stands of spruce in south-central Alaska. The anatomy of conifer stems, the variation in stem diameter growth, and the variability of tree response to wounding are discussed to explain why trees become vulnerable to attack by bark beetles. A working hypothesis, that beetle-attack patterns on the lower bole of trees have evolved to take advantage of the weak defense of a stressed tree, is presented as a rationale for maintaining vigorous tree growth.

Keywords: Thinning (-insect control, tree vigor, stand improvement, insect control, spruce, spruce beetle, south-central Alaska.

Summary

The spruce beetle *(Dendroctonus rufipennis* Kirby) is the primary tree-killing insect in Alaska and is prevalent south of the Alaska Range. Preferred hosts are white spruce *(Picea glauca* (Moench) Voss), Lutz spruce *(P.* x lutzii Little), and Sitka spruce (P. sitchensis (Bong.) Carr.). Black spruce (P. *mariana* (Mill.) B.S.P.) is rarely attacked.

Ornamental spruce and high-value trees in campgrounds and administrative sites can usually be protected from spruce beetle by lightly fertilizing annually and by watering during dry periods, or by applying insecticide to the trunk. These treatments are too costly for forest stands, so silvicultural treatments are required to maintain resistance to spruce beetle attack.

Clearcutting followed by natural or artificial stand regeneration is the logical alternative for overmature stands in areas where timber management is the desired objective and temporary denudation of the site is considered environmentally acceptable. In areas where watershed protection, wildlife habitat, and recreation or esthetics would be adversely affected by clearcutting in blocks as large as 10 to 15 acres (4 to 6 ha), smaller clearcuts and partial cuts may be used.

Mature stands that are lightly infested by spruce beetle or are not infested should be harvested to a residual basal area of 60 to 120 square feet per acre (14 to 28 m^2/ha) depending on site quality. Residual trees should be free from defects, firmly rooted and with vigorous crowns, and growing radially at a rate of about 1/2 to 1 millimeter or more in the last complete annual ring. Residual trees should be released from competition on at least three sides but not spaced so widely that substantial snowbreakage and windthrow are likely to occur.

Partial cutting can also be accomplished by clearcutting narrow strips of timber at right angles to prevailing winds, alternated with wider residual strips thinned according to principles mentioned above. Clearcut strips should be wide enough for skidders to pass, and residual timbered strip width should be twice the length of skidder cables so skidders can operate from outside the residual stand. Stands thinned in the manner proposed should be relieved of serious competition for soil moisture except during extreme droughts. Damage to residuals caused by harvesting will be minimized, and the stands should be comparatively windfirm.

Trees must be relieved from serious competition for moisture in late May and June if their resistance to spruce beetle attack is to be effective. Spruce beetles concentrate attacks in June in the lower tree bole which is farthest from the source of growth hormones and photosynthates produced in the crown. These materials are required with water for cambial cells to divide. Resistant trees respond initially to beetle attack with a copious flow of resin from existing resin ducts in the bark cortex, the phloem, and the xylem. Resin-producing cells surrounding these ducts must be hydrated to maintain positive resin pressure within the ducts and photosynthates are required for the cells to produce more resin when ducts are ruptured. Initial resinosus often causes beetles to abort their attacks.

The secondary response of trees to attack is delayed and consists mainly of formation of wound periderm and more horizontal resin ducts in the phloem and bands of longitudinal resin ducts in the xylem adjacent to cambium above and below the beetle gallery. This formation of "traumatic tissue" and the production of additional resin inhibit survival of beetle larvae in the phloem and spread of water-blocking "blue-stain" fungus into the xylem.

Trees under moisture stress reduce photosynthesis and translocation of growth substrates to stem cambium. Supplies of these materials required for cambial cell division can be limited in the lower boles of trees with high-setting crowns in dense stands because of distance from the active crown and utilization by branch and stem cambial tissue farther up the bole. Shortage of growth substrates from the crown, in addition to reduced hydration of cambial cells, inhibits cell division, resin production in existing ducts, and formation of new resin ducts and resin in response to beetle attack.

Conversely, open-grown trees with long effective crowns are rarely exposed to moisture stress for extended periods except when flooded or during extreme droughts. Radial growth is comparatively rapid in the lower bole because requirements for cambial cell division are rarely limiting there. Such trees are typically more resistant to bark beetle attack unless they are suffering from some other physiological disorder such as infection by pathogenic root fungi.

We hypothesize that concentrations of spruce beetle attacks on the lower bole of spruce have evolved to take advantage of the limited response in the lower bole of the tree under moisture or nutrient stress. Apparently, requirements for rapid stem radial growth are the same as for vigorous primary and secondary resin responses to wounding in the stem cambium. Therefore, rapidly growing trees are more likely to respond vigorously to bark beetle attack than are slowly growing trees.

Contents

Introduction

The spruce beetle *(Dendrocfonus rufipennis* Kirby) is a major killer of spruce across Canada and from the southern Rocky Mountains to Alaska (Safranyik and others 1981, Schmid and Frye 1977, Werner and others 1977). Its primary hosts are Engelmann spruce *(Picea engelmannii* Parry exlEngelm) in the Rocky Mountains and white spruce *(*P.glauca (Moench) Voss) in Alaska. It also attacks the maritime species, Sitka spruce *(*P.*sitchensis* (Bong.) Carr.), and Lutz spruce *(P.* x *lutzii* Little), the hybrid of white and Sitka spruce which occurs extensively on the Kenai Peninsula (Copes and Beckwith 1977, Little 1953). Black spruce (P. *mariana* (Mill.) B.S.P.) may occasionally be attacked, but it does not support spruce beetle outbreaks and is also the least preferred host of spruce beetle in eastern Canada (Morris 1958).

Beetle outbreaks often begin where the is abundant breeding material such as dead or dying trees and slash (Schmid 1977). This material often results from fire, windstorms, land clearing, and logging. Live trees weakened by drought, flooding, defoliation, root disease, root compaction, or advanced age are also susceptible to attack by bark beetles. But outbreaks have begun in mature stands where these classical, preoutbreak conditions are absent. For example, Morris (1958) stated that in the Maritime Provinces of eastern Canada outbreaks often began in overmature stands, and beetles often concentrated their attacks on larger, slowly growing trees. In one large outbreak, 80 percent of trees killed were over 10 inches (25 cm) in diameter; and in another outbreak, before they were killed trees had been growing only 63 percent as fast as trees not attacked.

Knowledge about spruce beetle and its hosts, although far from complete, parallels much of what is known of other bark beetles and their respective hosts. We emphasize the defensive responses of a tree to wounding because they appear to be directly related to current growth rate (Pitman and others 1982) which can be manipulated through standard forestry practices. We also emphasize interactions between bark beetles and trees at the beginnings of outbreaks because they show how stands can be manipulated to prevent outbreaks in areas where high mortality of trees is not acceptable.

For stands that are not infested or are lightly infested by spruce beetle, we recommend procedures that should restrict future losses of trees to tolerable limits within accessible areas where wildfire, watershed protection, wildlife habitat, and the esthetic value of green stands are important public concerns.

Recommendations for Increasing Resistance of Spruce to Spruce Beetles

Vigor of high value spruce in campgrounds and administrative sites can usually be maintained by adequate watering during dry periods, by light applications of fertilizer at intervals of 1 to several years, or by spacing trees to reduce competition for soil moisture. If the sites are adjacent to dense spruce stands that harbor outbreak populations of spruce beetle, then tree boles of high value trees can be protected by annual or biannual applications of insecticide (Werner and others 1984). But such individual-tree treatments are expensive, and cost-benefit ratios are economical only for trees of very high value. Therefore, silvicultural manipulations are probably necessary to protect stands containing numerous trees from spruce beetle attack.

Pure spruce stands that are considered overstocked and mixed stands that are growing slowly as a result of apparent competition should be logged if high mortality resulting from spruce beetle attack is undesirable. If such stands are substantially more than a 120- to 150-year rotation age, depending on site quality (Eis and others 1982), clearcutting in 10- to 15-acre (4- to 6-ha) blocks followed by natural or artificial regeneration may be the most logical management option.

If timber production is not the selected management alternative, but maintenance of standing green timber for wildlife and watershed protection or esthetic purposes is desired, then partial cutting may be the appropriate management option even in stands well over 100 years old. White spruce is a relatively long-lived species and may live for 250 to 300 years on productive forest sites (Sutton 1969) and even for 500 to 1,000 years at high elevations and high latitudes (Giddings 1962). We have observed dominant spruce as old as 240 years at breast height (bh) with growth that had recently accelerated and that had recently survived spruce beetle attack.

When mature stands are thinned to reduce susceptibility of residuals to spruce beetle attack, all residuals must be released from competition to stimulate growth to measurable levels in the lower tree boles. Retaining some widely spaced individuals and clumps of closely spaced individuals defeats our purpose because the closely spaced individuals may elicit little if any growth response, and ability to survive spruce beetle attack will probably remain low. Natural clumps of trees with spacing wide enough that little or no competition exists among them will not require release.

Partial harvesting could also be accomplished by clearcutting narrow strips at right angles to the prevailing winds and then by releasing trees within the residual timbered strips. Residual timbered strips should be no wider than twice the length of a skidder cable, and clearcut strips bordered by expendable "bumper" trees should be just wide enough for harvesting machinery to pass. This procedure should provide windfirmness of residuals and should reduce damage to residuals from felling and skidding operations.

We propose that uninfested or lightly infested spruce stands selected for partial cuts to reduce susceptibility to additional spruce beetle attack have their basal areas reduced to 60-120 square feet per acre (14-28 m^2/ha) in the following manner:

1. Mark all spruce trees 14 inches (36 cm) or larger in diameter for removal regardless of growth rate.

2. Select and mark plainly for reference 10- to 12-inch (25- to 30-cm) diameter "leave" spruce trees that have straight stems free of defect, live-crown ratios of 40 percent or more, radial growth rates of 1 millimeter or more in the last complete annual ring at breast height, and that appear to be firmly rooted. When selecting trees for retention avoid trees with crowns confined to one stem quadrant or that are flat topped, and avoid trees growing on potentially moisture-stressing microsites (such as waterlogged depressions or small, sharp ridges or hummocks formed between former erosion channels). Some trees of these undesirable types located at strategic points along skidding trails should be designated as bumper trees to prevent damage to leave trees; they should be marked to be felled and removed last.

3. From the 8- to 10-inch-diameter (20- to 25-cm) codominants and intermediates around each of the initial selected leave trees, select additional smaller trees with the last complete annual ring 0.5 millimeter wide or wider and with well-formed crowns and sound stems. The lower radial growth rate of these smaller trees approximates the same percentage of basal area growth as of the larger leave trees. Make sure that each of the primary and the secondary leave trees will be released on at least three sides during harvest. Selection of residuals by growth rate should result in wider spacing and lower residual basal areas on unproductive sites than on productive sites.

4. Fell all the remaining trees except bumper trees in April, May, June, and early July; use chainsaws instead of tractor-mounted shears to minimize damage to the residuals; and allow the felled trees and logs to absorb beetles in the area.

5. Postpone skidding until after beetle flight, which occurs from late May through June, and after tree cambial activity has slowed inlmid-July to late July. This will allow for "capture" and removal of the beetle population, it will minimize skidding damage to residuals because bark will not "slip" as easily after cambial growth has slowed, and it will eliminate skidder-caused damage to soils when they are wettest.

6. Fell and remove bumper trees last.

7. Process or chemically treat logs at the mill before the next May to avoid local beetle infestations if there are spruce stands nearby.

If spruce are desired as residuals in mixed stands, the better spruce should be released in a similar manner by removing adjacent trees of the other species. Removing the better spruce and retaining the other species, which may be a management alternative, could essentially remove the site from spruce production permanently, however, unless it is clearcut and planted to spruce.

Based on what we have seen in natural stands with various growth rates and stocking levels, stands treated in the manner suggested should experience increased soil temperatures, increased soil-to-tree moisture flow, reduced internal tree moisture stress, and increased growth rates. As a result, modified stands should be substantially more resistant to outbreaks of spruce beetle, and the residual stand should be comparatively windfirm (MacDonald 1963). In addition, stand treatments can be partially paid for by sale of harvested saw logs, house logs, and firewood.

Relationship of Stand Stocking to Tree Growth and Bark Beetle Attack

Thinning to reduce tree losses caused by bark beetles is commonly recommended in cases of other conifer hosts, but primarily for stands approaching maturity or stands younger than rotation age (Shrimpton and Thomson 1983). Initially, residual trees may experience "thinning shock" before soils are recharged with moisture or before root systems have expanded because the crowns are exposed to more sunlight and air movement which may increase loss of water by transpiration (Whitehead and Jarvis 1981). This condition, although short lived, could temporarily increase susceptibility of residuals to bark beetle attack because of stress, but growth normally improves rapidly because of reduced tree competition.

Larsson and others (1983) thinned ponderosa pine *(Pinus ponderosa* Laws.) which resulted in increased growth of residuals and reduced loss of trees to mountain pine beetle *(D. ponderosae* Hopkins) attack. McCambridge and Stevens (1982) showed that Black Hills ponderosa pine stands thinned to less than 90 square feet per acre (21 m^2/ha) basal area experienced low mortality caused by mountain pine beetle, whereas mortality rates in adjacent unthinned stands continued.

Sartwell and Stevens (1975) reported similar results in eastern Oregon stands where ponderosa pine poletimber was thinned to basal areas of 117, 86, 62, and 35 square feet per acre (27, 20, 14, and 8 m^2/ha), but mortality caused by mountain pine beetle was higher in an unthinned plot with initial basal area of 173 square feet per acre (40 m^2/ha).

Mitchell and others (1983) reported that nine lodgepole pine *(P. contorta* Dougl.) stands in eastern Oregon, heavily thinned to an average basal area of 53 square feet per acre (12 m^2/ha), experienced an average of about 4 percent mortality from mountain pine beetle attack, whereas four stands lightly thinned to an average basal area of 117 square feet per acre (27 m^2/ha) averaged 21 percent. Unthinned stands with an average basal area of 191 square feet per acre (44 m^2/ha) experienced an average of 19 percent beetle-caused mortality. Low losses in heavily thinned stands were attributed to increased growth of residuals.

Belanger [n.d.] recommends that overstocked southern pine stands be thinned to basal areas of 80 to 100 square feet per acre (18 to 23 m^2/ha) to reduce risk of southern pine beetle *(D. frontalis* Zimmerman) attack, but that stands in areas subject to severe wind and ice storms should not be thinned too heavily. High winds and heavy snows are common causes of tree fall or top breakage of spruce (Van Cleve and Zasada 1970), particularly in south-central Alaska, so similar caution should be taken in Alaska stands to prevent loss of residual trees that would probably become breeding material for spruce beetle. Spacing trials of 50- to 60-year-old spruce in interior Alaska by University of Alaska personnel resulted in 45-percent breakage caused by snow in stands thinned to 16- by 16-foot (4.9- by 4.9-m) spacing; 25 percent in stands thinned to 12- by 12-foot (3.7- by 3.7-m) spacing, and 0 percent in unthinned stands.[1]

[1] Personal communication with John Zasada, Research Forester, Forestry Sciences Laboratory, 3200 Jefferson Way, Corvallis, Oregon 97331

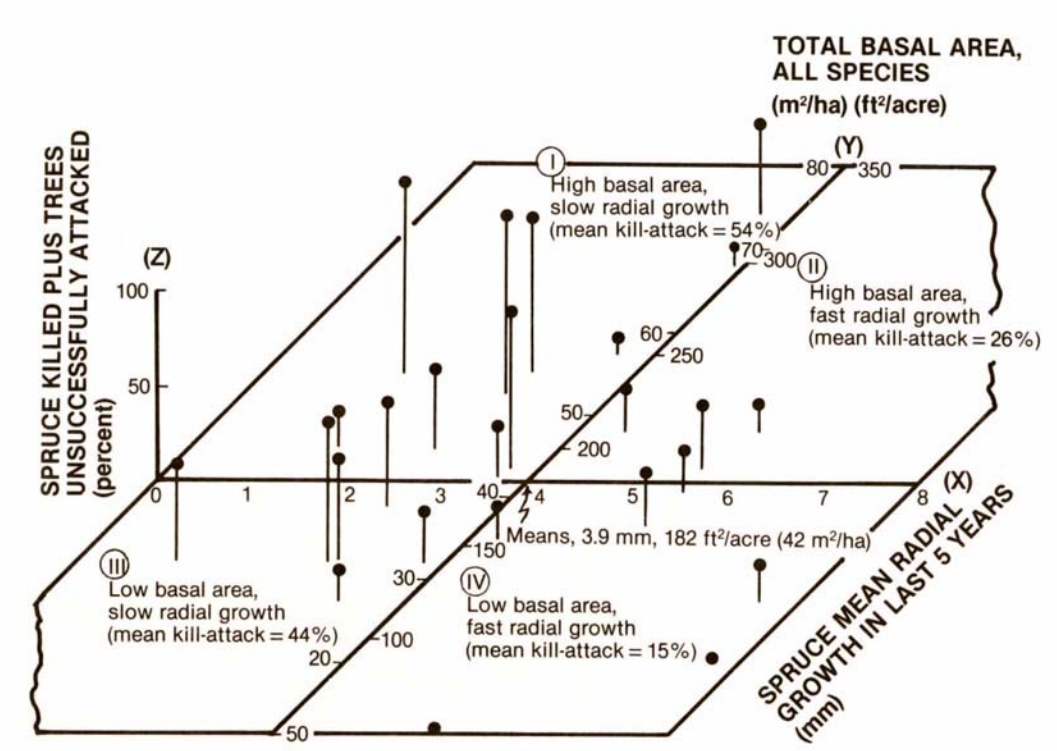

Figure 1 —Percentage of trees killed by spruce beetle and unsuccessfully attacked spruce (*z*) on 25 variable-radius plots during the early years of an outbreak versus mean radial growth of spruce (X) and total stocking of all tree species (Y) The graph is divided into quadrants based on intersection of the (X) and (Y) axes at their means. Vertical lines extending below plotted points indicate elevations of points above the (X,Y) plane

Frank (1973) determined that significant growth response in thinned 70-year-old white spruce required that residuals be released on more than two sides, and that the number of days that a tree grew during a season increased with degree of release. Trees released on three or four sides grew almost twice as rapidly the next 10 years as trees released on only one or two sides. Trees released on four sides started growth earlier and ceased growth later each year than trees released on three sides or less.

Van Cleve and Zasada (1976) fertilized and thinned 70-year-old white spruce in interior Alaska from 174 to 70 square feet per acre (40 to 16 m^2/ha) basal area. Soil moisture increased significantly, soil temperatures increased moderately, and basal area increment after 5 years was twice as high in thinned stands as in unthinned stands. There was no evidence of thinning shock, and growth accelerated the year after treatment.

Slowly growing mature spruce in heavily stocked stands near Summit Lake on the Kenai Peninsula had higher than average losses after spruce beetle attack (fig. 1). Stands growing faster than average (quadrants II and IV) had substantially lower spruce beetle attacks and tree mortality than slowly growing stands (quadrants I and III). The more heavily stocked stands shown in quadrants I and II sustained

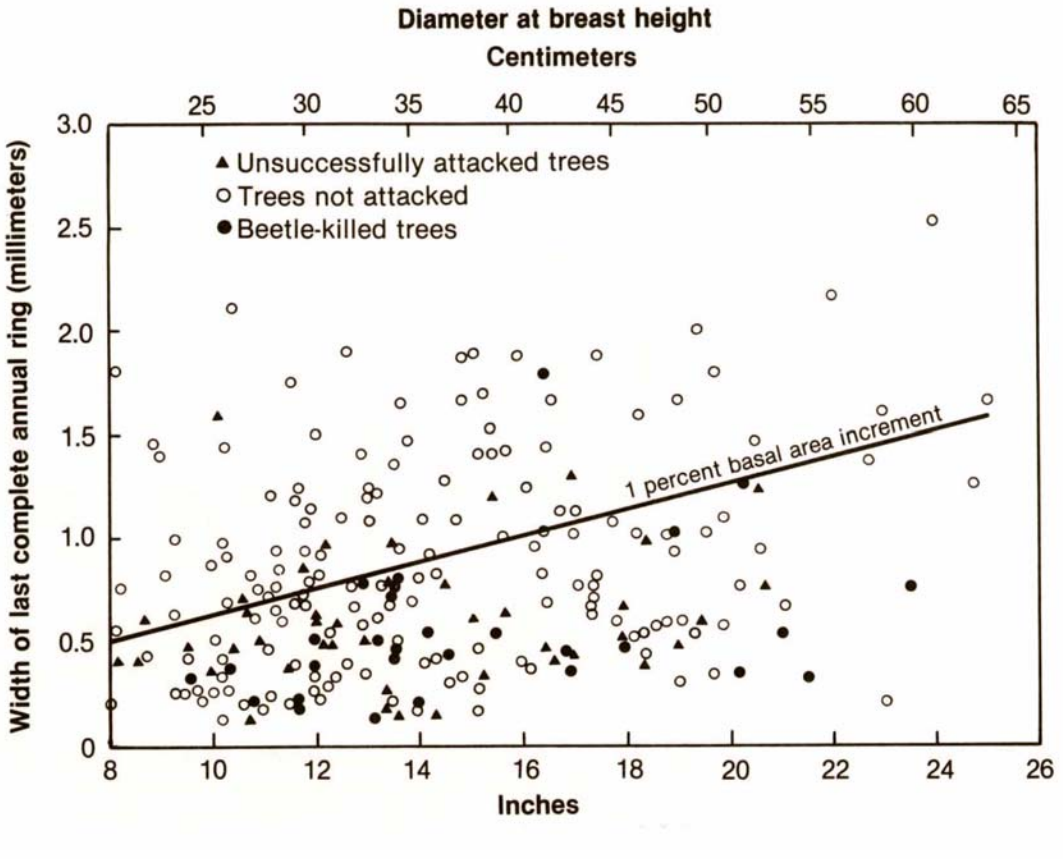

Figure 2.--Relationship of radial growth to diameter of trees in the year before spruce beetle attack, by tree condition class on the 25 variable-radius plots shown in figure 1. The ascending line intersects the ring width required for a tree of given diameter to grow at a basal area increment rate of 1 percent, if bark thickness is assumed to equal zero

greater average damage than did the more lightly stocked stands in quadrants III and IV which were growing at comparable rates to quadrants I and II, respectively. Damage caused by spruce beetles was highest in quadrant I in heavily stocked stands growing more slowly than average. Average attack and mortality were 10 percent less in lightly stocked, slowly growing stands in quadrant III, followed by greater reductions in quadrants II and IV.

These patterns of damage show that stands characterized by fast growing rates and low stocking levels (quadrant IV) were least susceptible to spruce beetle during early years of the outbreak, and that heavily stocked stands still growing rapidly (quadrant II) were less susceptible to attack than lightly stocked stands that were growing more slowly (quadrant III).

Growth in dense stands and in lightly stocked stands on very poor sites is often reduced because carbohydrates for stem growth are limited after demands for respiration and leaf formation are satisfied (Smith 1962). Limited carbohydrate reserves exemplified by slow radial growth may also reduce the ability of trees to respond defensively to spruce beetle attack. For example, when radial growth for the last complete annual ring of individual sample trees is plotted over tree diameter (fig. 2), it becomes readily apparent that basal area increment the year

before beetle attack was less than 1 percent of tree basal area for 57 percent of trees that were not attacked, for 80 percent of the unsuccessfully attacked trees, and for all but one of the killed trees.

Spruce Beetle Attack and Tree Response

To produce young the spruce beetle must kill its host tree, or a portion of the tree. Beetles can apparently sense stressed trees (Safranyik and others 1981), and in south-central Alaska they concentrate their attacks in June, which comprises the first half of the period of rapid cambial growth for interior Alaska white spruce (Gregory 1971). In some years, attack density peaks before soils have completely thawed,[2]/ and the cold soils'inay cause tree moisture stress (Kaufmann 1975) during initial growth.

The beetles carry spores of "blue-stain" fungi, and the trees are inoculated with these fungi during beetle attack. This fungal growth assists the beetles in killing the host by spreading into the sapwood, blocking the tracheids, and stopping water transport from roots to crown (Whitney 1982). Trees with only a portion killed by attacking beetles have a narrow vertical strip of killed cambium, called "strip kill" or "strip attack." They are not as abundant as trees killed outright by the bark beetles but are not uncommon during outbreaks.

Spread of blue-stain fungi in the bole is mainly radial and vertical (Safranyik and others 1975), and limited circumferential spread accounts for strip kills when only one side of a tree is successfully attacked. Stem vigor index is commonly less on the strip-killed side of the tree in lodgepole pine and often coincides with the side of the tree with spare crown (Pitman and others 1982).

Spruce beetles preferentially attack and kill large diameter trees that have been growing slowly at breast height (Hard and others 1983, Hard 1985, Morris 1958, Watson 1928). These trees are often dominants or codominants in well-stocked stands (Schmid and Frye 1976), but many uncrowded large diameter dominant and codominant trees still growing rapidly are attacked and not killed. Radial growth analysis of trees in the outbreak referred to by figures 1 and 2 shows that sampled trees of all classes grew more rapidly from 1967 through 1971 than from 1972 through 1978 (fig. 3). Trees killed in 1980 and 1981 grew slowly after 1973, and trees attacked in 1981 but not killed accelerated only slightly in growth after 1975. In contrast, unattacked trees larger than 9.5 inches (24.1 cm) in d.b.h. not only grew more rapidly than the others before 1973 but also accelerated more rapidly in growth after 1975.

The spruce beetle concentrates its attacks on the lower tree bole (fig. 4) (Knight 1960), as does the mountain pine beetle on lodgepole pine (Klein and others 1978, Rasmussen 1974). The first-arriving mountain pine beetles ("pioneers") attack the lower boles of lodgepole pine. If the pioneers are successful in entering the tree, they emit odors that attract other beetles; the attacks spread around the initial attack site and then up the bole (Berryman 1982). When attack densities reach a critical level, the beetles emit different odors or the tree ceases to exude resin; this signals that the tree is colonized and new arrivers are repelled (Raffa and Berryman 1983). Therefore, newly arriving beetles may attack nearby trees instead (Geiszler and Gara 1978).

[2]/ Spruce beetle attack relative to host phenology and host vigor index. Unpublished report by John S Hard on file at the Institute of Northern Forestry, Fairbanks, Alaska 99775-5500

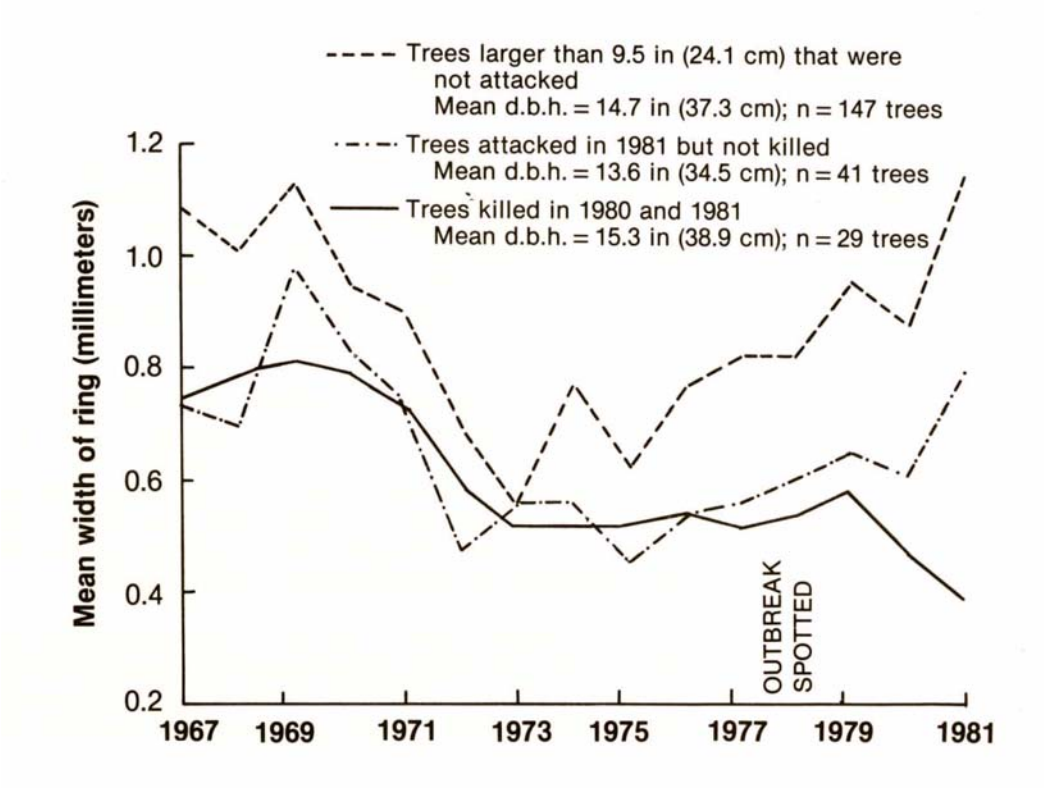

Figure 3 —Mean annual radial growth at breast height from 1967 to 1981 by tree condition class. Deflection of radial growth in the final year for trees killed by spruce beetle is probably caused by trees dying before the end of the growing season

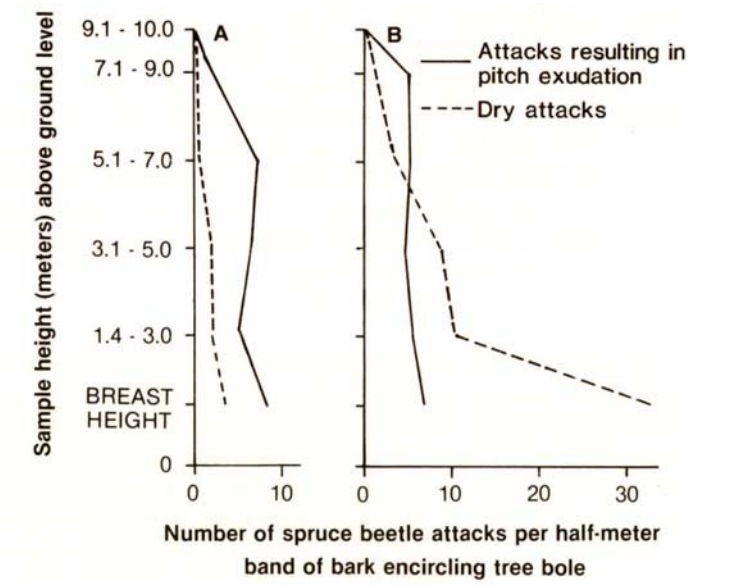

Figure 4—Height distribution of spruce beetle attacks below live crown in 1984 in a 100-year-old densely stocked stand. A. Unsuccessfully attacked trees (n = 48). B. Killed trees (n = 16).

The initial pattern of attack on the lower bole of pine is partially due to the deep bark fissures that aid entry by the attacking beetles through the thick lower bark (Safranyik and Vithayasai 1971, Shepherd 1965). In addition, the lower bole is often below the snow line which affords protection for bark beetle broods from lethally low temperatures during extremely cold winters and from predation by woodpeckers (Schrnid and Frye 1977). Perhaps the lower bole can also be considered the "Achilles heel," especially of slowly growing trees, because attacking beetles may have less chance of being repelled there by defensive reactions of the host. Attack densities were fairly uniform along the boles of unsuccessfully attacked spruce in an outbreak in Alaska, and most attacks resulted in a resinous response from the host (fig. 4). Conversely, killed trees were attacked most heavily on the lower bole, and most attacks there were nonresinous whereas the majority of attacks in the upper bole still elicited a resinous response.

Horizontal phloem resin ducts proliferate near bark wounds, (and some spruce respond to attack with a profuse flow of resin from an already existing network of vertical ducts in the bark cortex outside the phloem and horizontal unconnected ducts in the phloem and xylem rays (Thomson and Sifton 1925). Spruce also form tangential bands of longitudinal xylem resin ducts or "traumatic tissue" at the cambium adjacent to the wound.

Resin formed in the epithelial cells of parenchyma tissue is secreted to areas between the cells which forces them apart to form an elongated, cylindrical, resin-filled cavity called a resin duct. The duct widens quickly and may reach maximum diameter before adjacent tracheid walls are completely developed.

Bands of vertical ducts become dispersed above and below the wound but are usually confined to the same annual ring in spruce. These ducts may reach more than 2 feet (60 crn) in length and generally increase in number with cambial age. The increase is probably due partially to an increased number of injuries incurred by the lower tree stem, but the proportion of functional thin-walled epithelial cells surrounding resin ducts is higher in outer rings of the lower bole, and for a given wound size the number of traumatic resin ducts formed tends to increase as ring width increases (Bannan 1936). This occurs probably because a wider band of active cells in the cambial zone and a greater number of cambial cell divisions occur in spruce with wide annual rings (Gregory and Wilson 1968, Gregory 1971).

Vite (1961) believed that trees became susceptible to bark beetle attack when transpiration from the crown and water absorption into the tree were unbalanced, which resulted in decreased turgidity of epithelial cells lining the resin ducts and in reduced exudation of resin. Wounded white spruce seedlings formed resin ducts only when cambial cell division was occurring and formation ceased when radial growth ceased because of moisture stress; density of resin ducts formed in seedlings relieved of moisture stress was lower than in seedlings that were never moisture stressed (Safranyik and others 1981). Turgid epithelial cells in fully hydrated trees exert pressure on the duct so resin is forced out into the wound when the duct is damaged (Bannan 1936). Therefore, even if the initial response of a tree is inadequate to prevent the attacking beetles from laying eggs, larvae and blue-stain fungi will probably encounter newly formed ducts in the cambium or additional ducts in the phloem and may be killed by heavy resinosus if stem tissues are fully hydrated.

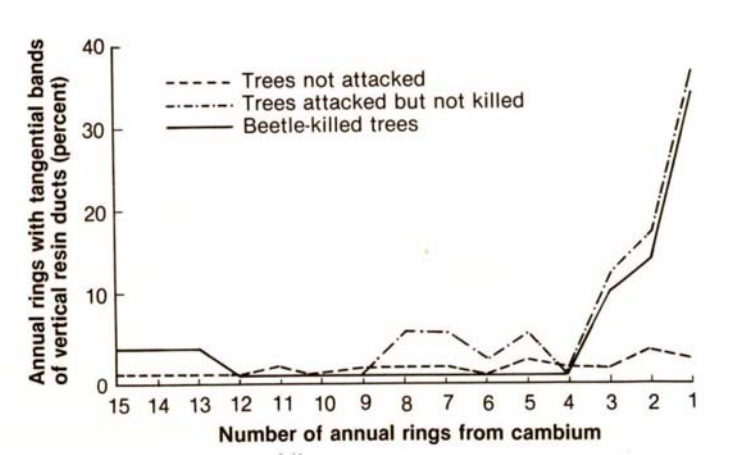

Figure 5.- Percentage of "traumatic" resin ducts in spruce increment cores by tree damage class and annual ring Cores were collected in 1981 from an area on the Kenai Peninsula where a spruce beetle outbreak appeared in 1978

Berryman (1976) showed that in lodgepole pine, resin ducts in the bark cortex increased in density and size with height on the bole but that they occurred abundantly as far down as the root collar on younger trees. Beetles attacked a longer section of bole in nonresistant trees, and limited resinosus followed the attack, whereas more abundant attacks concentrated near the base of the tree were required to kill resistant trees.

The disparity in spatial arrangement of attacks between nonresistant and resistant trees suggests that beetle behavior has also evolved to take advantage of a gradient of tree response to attack. Metabolic activity tends to be lowest near the base of tree stems (Larson 1962, 1963), and rate and seasonal duration of radial growth in suppressed pine were greater in the upper stems than in the lower stems which emphasizes recurrent deficiency in metabolites in lower stems (Kozlowski 1964). Metabolic activity that contributes to resinosus is apparently not constant along the bole because inoculation of resistant lodgepole pine at various stem levels with blue-stain fungus resulted in an increased response up to 18 feet (5.5 m) and a diminished response higher up (Reid and Shrimpton 1971).

Tangential bands of traumatic resin ducts seen in increment cores extracted from trees attacked by spruce beetles indicate that some trees are attacked repeatedly before they are finally killed (fig. 5). Traumatic resin ducts first appeared in significant numbers in the eighth annual ring from the cambium, which probably coincides with the beginning of spruce beetle attacks on live trees within that particular infestation.

Effects of Reduced Water and Growth Substrates on Stem Diameter Growth

Stemwood is composed primarily of longitudinal cells called tracheids. Water is transferred between tracheids through thin-walled, membranous connections called pits that are normally concentrated on the radial, overlapping tracheid surfaces (Zimmerman 1983). In heartwood the pits have become aspirated or closed to the passage of water and the tracheids are occluded (Brown and others 1949). The sapwood is the primary pathway for transport of water from roots to crown (Kozlowski 1968), so the cross-sectional area of the sapwood is proportional to tree crown size (Grier and Waring 1974).

Each annual ring is composed of early wood and late wood. Transition from production of early wood to late wood, associated with cessation of shoot elongation and reduced production of growth hormones, begins annually in the lower bole (Larson 1962, 1963). Water is transported within the sapwood mainly through the large-diameter early wood tracheids; the smaller diameter, thick-walled tracheids in the late wood, which have fewer and smaller pits than early wood tracheids, are essentially nonconductors (Whitehead and Jarvis 1981, Kozlowski 1968). Natural aspiration or functional sealing of pits within the early wood tracheids increases from the cambium toward the heartwood in many conifers, so water transport is concentrated in the outermost sapwood rings, the zone of least resistance (Kozlowski 1971).

Carbohydrates and growth hormones produced in the foliage, necessary for cambial cell-division in the stem, are transported downward from the foliage through sieve cells in the phloem between the cambium and bark cortex (Crafts and Crisp 1971, Zahner 1963). The portion of phloem actively involved in translocation is a very narrow band of cells and is only a fraction of a millimeter thick (Abbe and Crafts 1939). Its sieve cells must be mature for rapid translocation of growth substances to occur (Crafts and Crisp 1971), and they are functional for only two seasons in spruce (Gregory 1971). The number of phloem cells formed radially from the cambium each season is a constant proportion of the number of xylem cells formed (Gregory 1971, Grillos and Smith 1959); therefore, narrower xylem rings are accompanied by narrower annual phloem rings as radial growth slows.

The primary cause of reduced tree growth is diminished water supply to the crown (Whitehead and Jarvis 1981). During transpiration, water vapor is drawn through closeable leaf pores called stomata to the atmosphere and is replaced by water stored in branches and stem. During normal and dry weather, except in very humid geographic areas, the loss of water through transpiration exceeds water uptake almost daily, but the leaf stomata close at night and the tree is recharged with moisture through the roots if soil moisture is available (Kozlowski 1968) and soil temperatures are high enough.

Soil temperatures below a critical threshold of about 1 °C for Sitka spruce and about 7.5 °C or Engelmann spruce cause low root conductivity of water and reduced water potential within the tree (Whitehead and Jarvis 1981, Kaufmann 1975). We do not know the critical soil temperature for white spruce, but soil temperatures below 10 °C resulted in increased resistance to waterflow in white spruce (Goldstein and others, in press) and reduced root elongation (Tryon and Chapin 1983). Root moisture flow is affected by the increased viscosity of water at low temperatures and by the permeability of root membranes, which varies by temperature and species (Kramer 1983).

If soil moisture is not available because of (a) low soil temperatures in the active root layers, (b) lack of recharge through precipitation, or (c) excessive competition among trees and ground vegetation during normal weather, then even the most vigorous trees will experience stress from internal water deficits. When moisture stress occurs, the leaf stomata close during daylight hours and photosynthesis is slowed. All land plants experience internal moisture stress periodically even when soil moisture is near field capacity, and in most regions soil moisture is rarely optimal during the growing season (Kozlowski 1968).

Water absorption by the roots can also be impeded if soils are waterlogged (Whitehead and Jarvis 1981, Zahner 1968). Trees are tolerant of waterlogged soils during dormancy, but actively growing root tips are very sensitive to the resulting anaerobic conditions in waterlogged soils (Coutts and Philipson 1978).

Most growth responses responsible for (a) amount and quality of photosynthates and growth hormones, (b) level of cambial activity, (c) period of tracheid growth and expansion, and (d) rate of upward waterflow through new tracheids in the current-year early wood adjacent to the cambium are governed by atmospheric conditions, transpiration rates, and variations in available soil moisture (Zahner 1963). Furthermore, moisture stress that affects grodh in the current year may have a lag effect on the next year's growth because bud formation in the current year predetermines the number of needles that will be formed on shoots the following year (Kozlowski 1971). Thus, photosynthetic capacity of the next year's shoots can be diminished even if weather conditions are optimal for growth. Spruce may carry several consecutive years' complement of needles, but the greatest photosynthetic production occurs late in the season in current-year white spruce needles and throughout the season in needles 1 year old (Clark 1961).

Scattered trees in open stands usually have comparatively wide, fully active crowns, pronounced stem taper, and few self-pruned dead branches. They experience little or no competition from neighbors; and if roots are healthy, they incur serious moisture stress only during flooding and severe droughts or when air temperatures are warm and soils are very cold or are actually frozen. Trees in dense stands usually have longer, more-cylindrical boles with comparatively more dead lower branches and relatively short live crowns (Farrar 1961, Larson 1963). Much of the lower live crown is partially shaded by neighboring trees, and photosynthesis is concentrated in the upper exposed crown portions. In addition, soils are usually colder during the growing season in dense stands because sunlight is reduced at the forest floor and thick layers of undecomposed organic debris insulate soils from ambient air temperature.

For radial growth to begin in the spring, growth hormones as well as food substances must be present in the stem cambium because cell division will apparently not begin if only food substances are present. After bud break, which initiates growth hormone production, cambial activity proceeds down the bole more rapidly in open grown trees with long effective live crowns and continues longer at breast height than in trees with short, high-setting crowns in dense stands (fig. 6A).

Growth hormone requirements for cambial activity are less in the smaller total cambial surfaces of short upper branches than in longer lower branches, so the highest growth hormone levels along the stem cambium often occur near midcrown because of surplus hormones from the upper crown. Therefore, the annual sheath of newly formed stemwood is often thicker near midcrown (fig. 6B). In some years, an annual ring that can be measured at the base of the live crown may be discontinuous or even nonexistent at breast height because growth substances are completely consumed by cambium farther up the stem. Under these circumstances cambium at breast height (fig. 6A) remains alive but dormant (Brown and others 1949). In years with better growing conditions growth substances are transported in greater quantities to the lower bole, and a wavelike increase of radial growth moves down the tree to form a wider annual ring at breast height (Larson 1962).

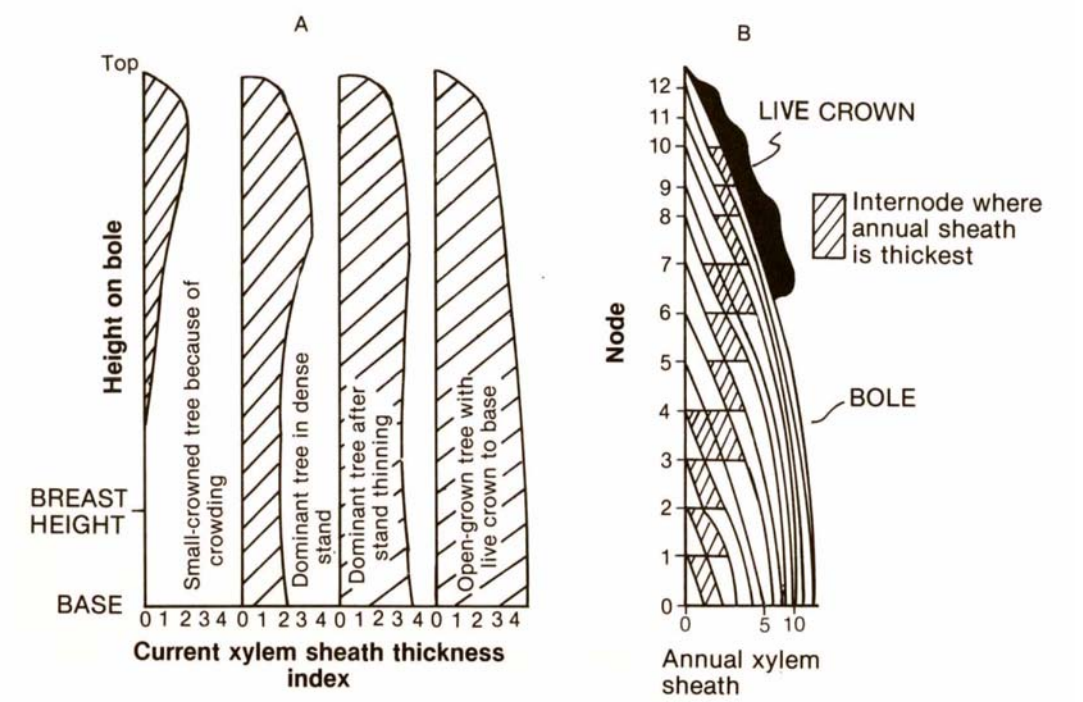

Figure 6 —Diagrams with expanded horizontal scale of hypothetical tree xylem sheath growth patterns. A. Vertical variation in width of annual sheath controlled by stand closure and size of effective crown (after Farrar I961).B . Change in vertical position of widest part of xylem sheath relative to tree age and unfoliated length of bole (after Smith and Wilsie 1961)

Generally, good growing conditions shift the location of maximum radial growth down the stem, and unfavorable growing conditions shift the position of maximum radial growth up the stem closer to the source of growth hormones and photosynthates (Larson 1963). The position of minimum radial growth below the live crown is shifted accordingly. For example, Shrimpton and Thomson (1983) sectioned mature lodgepole pine in stands infested by mountain pine beetle to reveal radial growth patterns along the stems in the 15-year period before cutting. Location of minimum radial increment for a given year varied from one-tenth to six-tenths of stem height, but the mean height of minimum increment occurred at about one-fifth of stem height and the modal height of minimum increment was at about one-seventh of stem height.

Ultimately, mature trees will die if they are growing so slowly that growth substances produced by the crown are inadequate to support cambial activity in the lower bole. A similar process of senescence is responsible for self-pruning of lower branches in shaded crowns. Less and less live foliage remains on shaded branches and is concentrated near the branch tips. Fewer growth substances are produced to support cambial growth at the base of the branch which is far removed from the source within the foliage. Ultimate death of the basal branch cambium occurs (Larson 1962) because growth hormones and photosynthates produced in higher branches are available for the stem cambium below them but not for the cambium of lower branches. This explains why callous tissue grows over branch scars flush with the stem but not over the ends of branch stubs projecting from the stem.

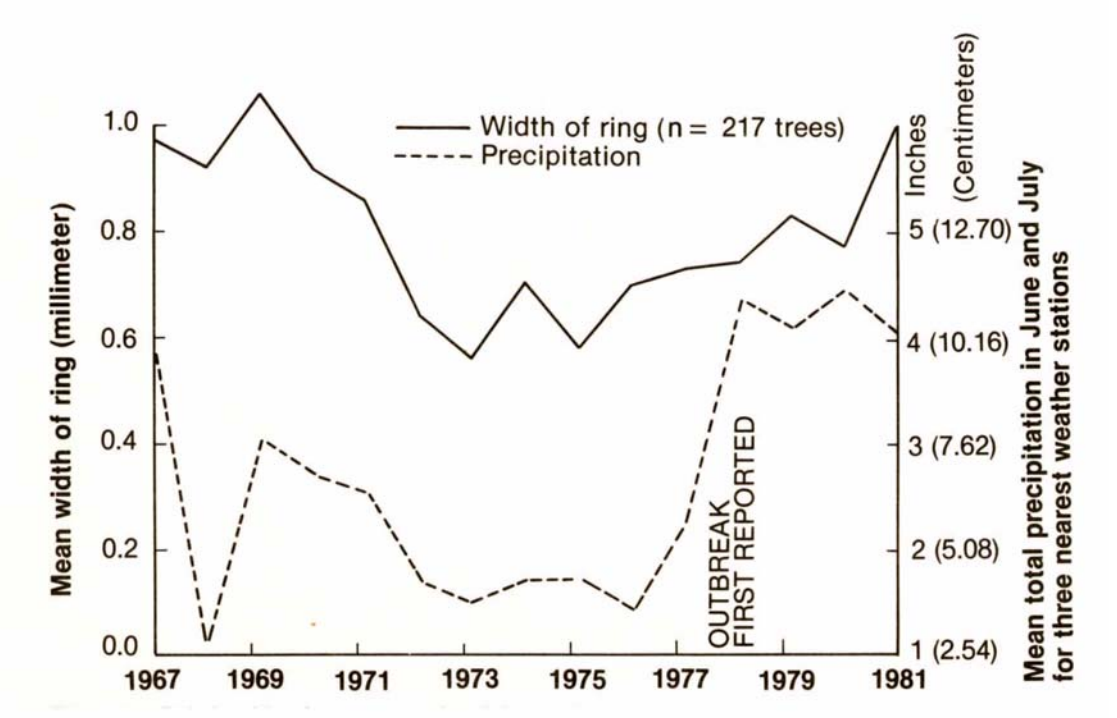

Figure 7 —Relationship of mean annual radial growth at breast height for all sample trees in figure 3 to average total precipitation during June and July at Cooper Lake, Moose Pass, and Kenai Precipitation records for 1977 and 1978 were not available for Cooper Lake and Moose Pass, so those points represent Kenai only Precipitation in 1980 and 1981 is for Cooper Lake and Kenai, only

Water is also required for cambial cell division to begin after dormancy. Cambial zone cell division begins first in the partially differentiated cells at the inner margin of the cambial zone adjacent to the last-formed late wood of the previous growing season rather than in the initial cambial cells (Bannan 1962). Normally, pits are concentrated on the radial surfaces of tracheids, but horizontal ray tracheids and concentrations of pits (called growth-ring bridges) on the tangential surfaces of the last-formed late wood tracheids in the previous annual ring provide avenues for water to the cambial zone before fully functioning early wood tracheids are formed in the new ring (Zimmerman 1983).

Seasonal radial growth is not continuous. It proceeds intermittently during the growing season and is partially dependent on cambial zone hydration because water deficits in cambial regions reduce growth substantially (Kozlowski 1964). Clark (1961) showed that photosynthesis in white spruce diminished as soil moisture decreased from field capacity to the wilting point, and Fraser (1962) stated that soil moisture deficit in June and July had a greater inhibiting effect on growth of white spruce in Ontario, Canada, than at any other season because most growth occurs then. Similarly, tree growth was correlated with precipitation on the Kenai Peninsula during June and July for 1967-81 (fig. 7).

Trees in stagnated overstocked stands under continuous or pronounced repeated moisture stress suffer reduced vigor, apparently as follows: Current annual xylem and phloem rings formed in the lower bole are narrower than adjacent rings because of reduced photosynthesis in the crown which reduces translocation of growth hormones to the lower stem (Kozlowski 1964). As a result, water transport capability through the xylem is diminished, as is translocation capability of growth substances from the crown through the fewer functional sieve cells in the narrow phloem. Thus, a vicious cycle may begin because further reduced water transport may ensue, followed by reduced photosynthesis and translocation of growth substances to the lower bole and roots.

Reduced radial growth in the lower bole, which appears to create a hydraulic constriction, may be similar in effect to the constrictions that occur at branch bases in some conifers because of reduced tracheid size (Ewers and Zimmerman 1984, Zimmerman 1983); but relative conductivity of water increases toward the tops of some trees and is partially attributed to faster growth rates along the upper stem (Larcher 1983, Whitehead and Jarvis 1981). In contrast, Zimmerman (1**983)** states that conifer tracheids normally become longer and wider with increased stem diameter, and they also increase in size from the crown to the lower bole These trends can be reversed, however, as radial growth slows. For example, tracheid length in white spruce shortens as ring width narrows to less than 2 mm (Bannan 1963, 1967)**,** especially in outer rings narrower than 0.5 mm of mature trees (Bannan and Bindra 1970). Shortened tracheid length results in more cell walls and pits for water to penetrate in a vertical column of given length. This condition may further reduce the conductivity of water (Zimmerman 1983), especially in the lower boles of slowly growing trees.

Whitehead and Jarvis (1981) hypothesize that stand flow resistance of water from soil to crown within stands of comparable leaf surface area is inversely proportional to the number of stems in the stand, that fall in water potential between soil and crown depends on flow rate and flow resistance within individual trees, and that flow resistance in individual trees depends mainly on sapwood basal area and relative conductivity of sapwood tracheids. The ratio of early wood to late wood is greater in the lower bole of trees with large crowns than in trees with short, high-setting crowns (Larson 1962). Thus, water conduction is typically more efficient in the lower boles of trees with large crowns because of their proportionally wider bands of large-celled early wood and wider sapwood.

It follows that of two fully stocked stands, one densely stocked with medium diameter stems bearing small crowns and one with comparable basal area but less densely stocked with fewer large diameter stems bearing large crowns, there will be less moisture-flow resistance in individual trees of the latter stand and less chance of within-tree moisture deficits. Large diameter spruce in such stands should be resistant to spruce beetle as long as the site is not overstocked and trees continue to grow vigorously.

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Hard, John S.; Holsten, Edward H Managing white and Lutz spruce stands in south-central Alaska for increased resistance to spruce beetle Gen Tech. Rep PNW-188. Portland, OR U **S** Department of Agriculture, Forest Service, Pacific Northwest Forest and Range Experiment Station; **1985.** 21 p.

Thinning is recommended for maintaining vigorous tree growth to minimize losses caused by spruce beetles *(Dendroctonus rufipennrs* Kirby) and windthrow in residual stands of spruce in south-central Alaska. The anatomy of conifer stems, the variation in stem diameter growth, and the variability of tree response to wounding are discussed to explain why trees become vulnerable to attack by bark beetles A working hypothesis, that beetle-attack patterns on the lower bole of trees have evolved to take advantage of the weak defense of a stressed tree, is presented as a rationale for maintaining vigorous tree growth.

Keywords: Thinning (-insect control, tree vigor, stand improvement, insect control, spruce, spruce beetle, south-central Alaska

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