

## Sequence of Trees Attacked by Spruce Beetles in a Mature Even-Aged Spruce Stand in South-Central Alaska

### Abstract

Spruce beetles (*Dendroctonus rufipennis*) concentrate early attacks on an initial tree, the "focus" tree, but later attacks occur on adjacent trees, "recipient" trees. The pattern of these initial and following attacks may provide a key for management approaches to deal with spruce beetle outbreaks. Thus, this study was done to determine timing and distribution of spruce beetle attacks among trees in an unmanaged even-aged spruce stand. Repeated observations on 9 plots, each containing 10 formerly uninfested spruce, revealed that the initially attacked trees ("focus" trees) were apparently moisture-stressed due to extensively frozen soils and rapidly warming air temperatures. Continued warm weather caused many more spruce beetles to emerge from hibernation and soils to thaw. Some newly emerged beetles attracted by odors from beetles already established in focus trees attacked the focus trees, but many attacked nearby unstressed trees ("recipient" trees). As a result, all focus trees and many recipient trees within 10 m of focus trees were killed. Furthermore, many recipient trees weakened by unsuccessful attacks were reattacked the following season. Knowledge of spruce beetle behavior that enables them to overwhelm the natural defenses of apparently unstressed trees in unmanaged stands should be useful to forest managers. Perhaps opportunities for spruce beetles to concentrate their attacks and kill clusters of trees could be reduced by partial forest harvesting to increase residual tree spacing. This should reduce competition among trees for soil moisture and should minimize stress at the beginning of the annual growth cycle when trees first become exposed to spruce beetle attack.

### Introduction

Spruce beetle (*Dendroctonus rufipennis* (Kby.)) adults emerge from hibernation sites beneath the bark of dead and downed spruce (*Picea* spp.) in May and June (Schmid and Frye 1977). The beetles then disperse by flight when ambient temperatures exceed 14.5°C (Werner and Holsten 1985a), and females begin to attack new hosts. Attacks, which usually begin during the early period of rapid host growth, flowering, and pollination, are concentrated in the tree's lower bole (Knight 1960, Gara and Holsten 1975, Werner and Holsten 1985b, Hard 1987).

Many, if not all, *Dendroctonus* species produce aggregation pheromones after successful female entry into the host. These pheromones attract both additional beetles that assist in killing the first-attacked or "focus" tree and other beetles that attack nearby resistant and nonresistant "recipient" trees. The phenomenon of rapidly shifting mass attacks among trees, which commonly overwhelms trees singly and consecutively, is called "switching" (Geiszler and Gara 1978). Switching behavior may be driven by particular threshold concentrations of aggregation pheromones or by specific combinations of aggregation and antiaggregation pheromones, but the mode of operation differs among bark beetle species.

Some species produce antiaggregation pheromones, which apparently operate at a shorter range than attractant pheromones (Geiszler and Gara 1978, Berryman 1982), and prevent adverse competition among beetle broods by controlling attack density on hosts. The mountain pine beetle (*D. ponderosae* Hopk.), however, apparently also uses antiaggregation pheromone to force beetle attacks at higher densities on surrounding recipient trees than on focus trees (Geiszler and Gara 1978, Geiszler *et al.* 1980, Raffa and Berryman 1983). This behavior has presumably evolved to overwhelm the defenses of resistant recipient trees (Borden 1982).

Spruce beetles produce frontalin as an aggregation pheromone (Borden 1982) and methylcyclohexenone (MCH) as an antiaggregation pheromone (Rudinsky *et al.* 1974). To investigate switching behavior by the spruce beetle, Ford (1986) artificially baited spruce with frontalin. Results of his tests were inconclusive because focus trees and surrounding trees were attacked almost simultaneously, presumably because they were engulfed in strong attractant pheromone plumes.

In this study, data gathered for other purposes (Hard 1987) were reanalyzed to determine whether a) switching of attacks from focus trees to recipient trees was evident in a spruce stand being heavily attacked by spruce beetles in the

absence of artificial baits, b) attacks on recipient trees were greater than on focus trees, and c) recipient tree diameter or sapwood growth rate differed as distance of recipient trees from focus trees increased.

### Study Area and Methods

The study area is near the junction of the Russian and Kenai Rivers at about 60°29' N, 149°58' W. Elevation of the site is about 130 m, slope ranges from 0 to 5 percent, and aspect is north. The stand that was monitored consisted of a virgin white spruce (*Picea glauca* (Moench) Voss) or Lutz spruce (*P. × lutzii* Little) stand about 135 years old at breast height (*bh*), but white spruce morphological traits predominated.

Nine variable-sized plots, each consisting of 10 contiguous uninfested spruce 20 cm in diameter at breast height (*dbh*) or larger with a few hardwoods and beetle-infested spruce interspersed, were established in early May of 1985. Trees had not yet begun their annual growth cycle and beetles were still in hibernation. Upper and lower margins of a 0.5-m bark sample strip encircling the stem near *bh* were marked with twine for subsequent counts of beetle attacks on each sample tree. Thermocouples were installed at 20-cm soil depth in three randomly located sites on each plot for weekly soil-temperature measurements, and a recording hygro-thermograph was installed near the center of the study area for measuring ambient air temperature and relative humidity.

Beginning on 4 June 1985, bark sample strips on all 90 sample trees were examined for new beetle attacks at alternating 3- and 4-day intervals until 20 August. New attacks were marked with staples at each sample visit, and numbers of attacks were converted to attacks per square meter of bark sample surface for each tree and sample interval. Two short increment cores, one from the east side and one from the west side at *bh*, were removed from each sample tree in late September after growth had ceased. The juncture of heartwood and sapwood was marked on each core, and cores were then stored and frozen in labeled plastic drinking straws for laboratory measurement of individual ring widths. Percentage of sapwood basal area growth at *bh* in 1984, the year before attack, was computed as an indicator of tree vigor (Münster-

Swendsen 1987) and potential resistance to beetle attack (Waring and Pitman 1985). Cores were cross-correlated visually using "marker" rings to determine whether each tree had formed a new xylem ring at *bh* in 1985 because trees that are mass-attacked very early in the season are sometimes unable to develop even a portion of a new annual ring in the lower bole.

Approximate geographic center of each plot was marked and azimuth and distance to each sample tree were measured for preparation of plot maps. The tree or trees that were apparently attacked earliest on each plot and then mass-attacked most rapidly by spruce beetles were labeled as initial plot "focus trees." This procedure provided the best estimate of which trees were attacked first, but accuracy was limited by the 3- and 4-day sample interval. Concentric arcs or circles representing 5-m and 10-m distances from focus trees were drawn on each plot map for segregation of sample trees into concentric sample bands.

### Results

Spruce beetle attacks began on 14 June 1985 but did not increase rapidly until after 21 June (Figure 1a). Total attacks on all sample trees peaked on 2 July (Figure 1a), but attacks had begun from 1 to 2 weeks earlier on focus trees (Figures 1a and 2a).

Two of the nine plots each had two widely-separated focus trees that were apparently attacked simultaneously. One plot had two widely-separated focus trees that were not attacked simultaneously but were attacked earlier than surrounding trees. Remaining plots each had one focus tree. Heavy attacks on focus trees occurred as mean maximum air temperatures exceeded the lower threshold temperature for spruce beetle flight (Figure 1b). Mean soil temperature at the study site increased markedly above freezing (Figure 1c) after most focus trees were initially attacked (Figure 2a). Therefore, focus trees were successfully attacked during a period of apparent host-moisture stress, indicated by temporarily slowed tree expansion rates, that was widespread throughout the study area (Hard 1987). Soil moisture bound in still-frozen mineral soil was not available for increased transpiration by many trees exposed to low precipitation, rapidly increasing air temperatures, and slowly increasing soil temperatures.

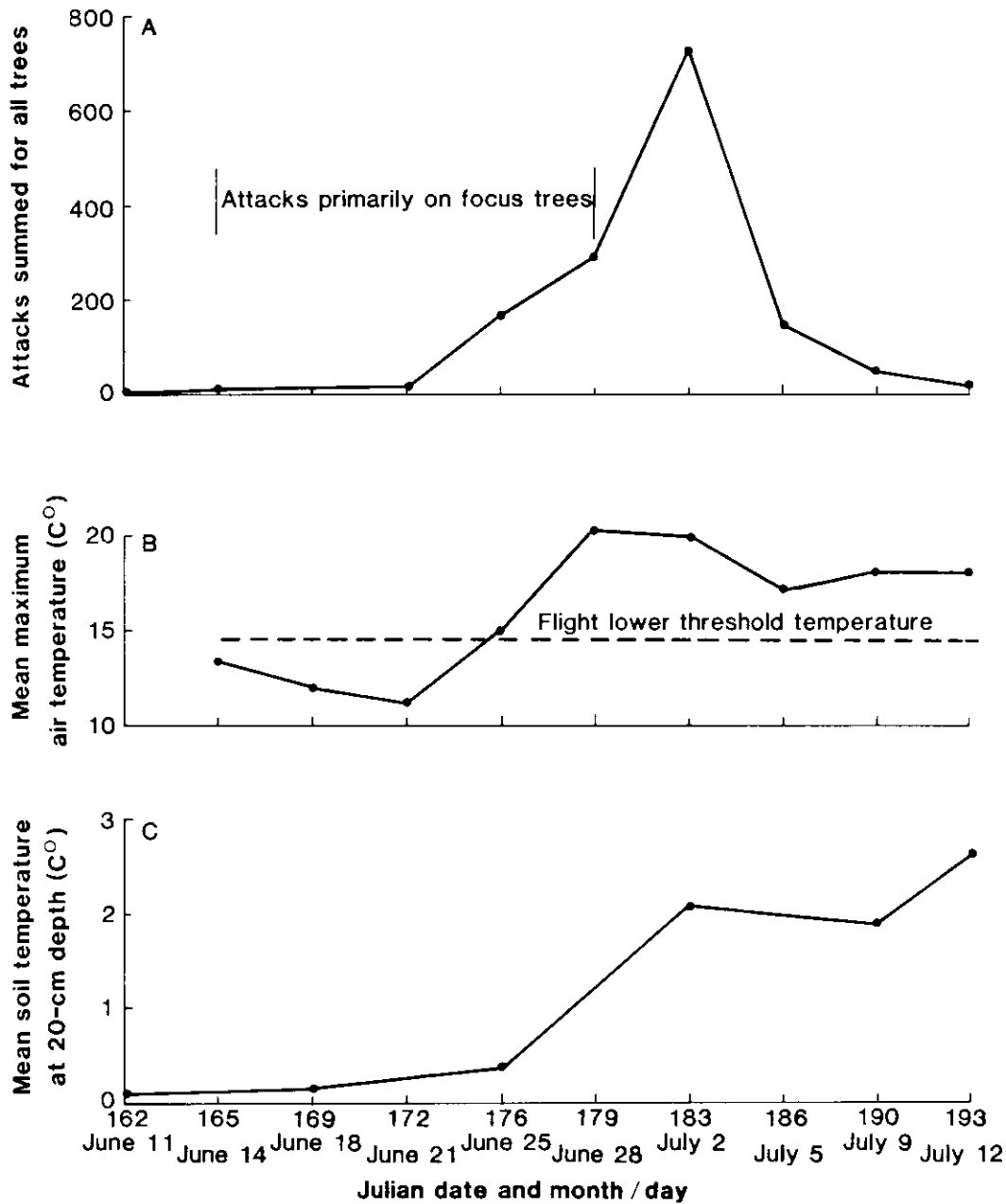


Figure 1. A. Spruce beetle attacks summed by sample interval for all sample trees. B. Mean maximum air temperature within the sample stand by sample interval. C. Mean soil temperature by alternate sample interval.

Mean Julian date when attacks were first observed increased from attack of focus trees to attack of trees in the outermost concentric sample band, but the greatest time delay of mean

initial attack between concentric samples occurred between focus trees and trees within the adjacent sample band (Figure 2a). All focus trees were killed, and mean percentage of recipient

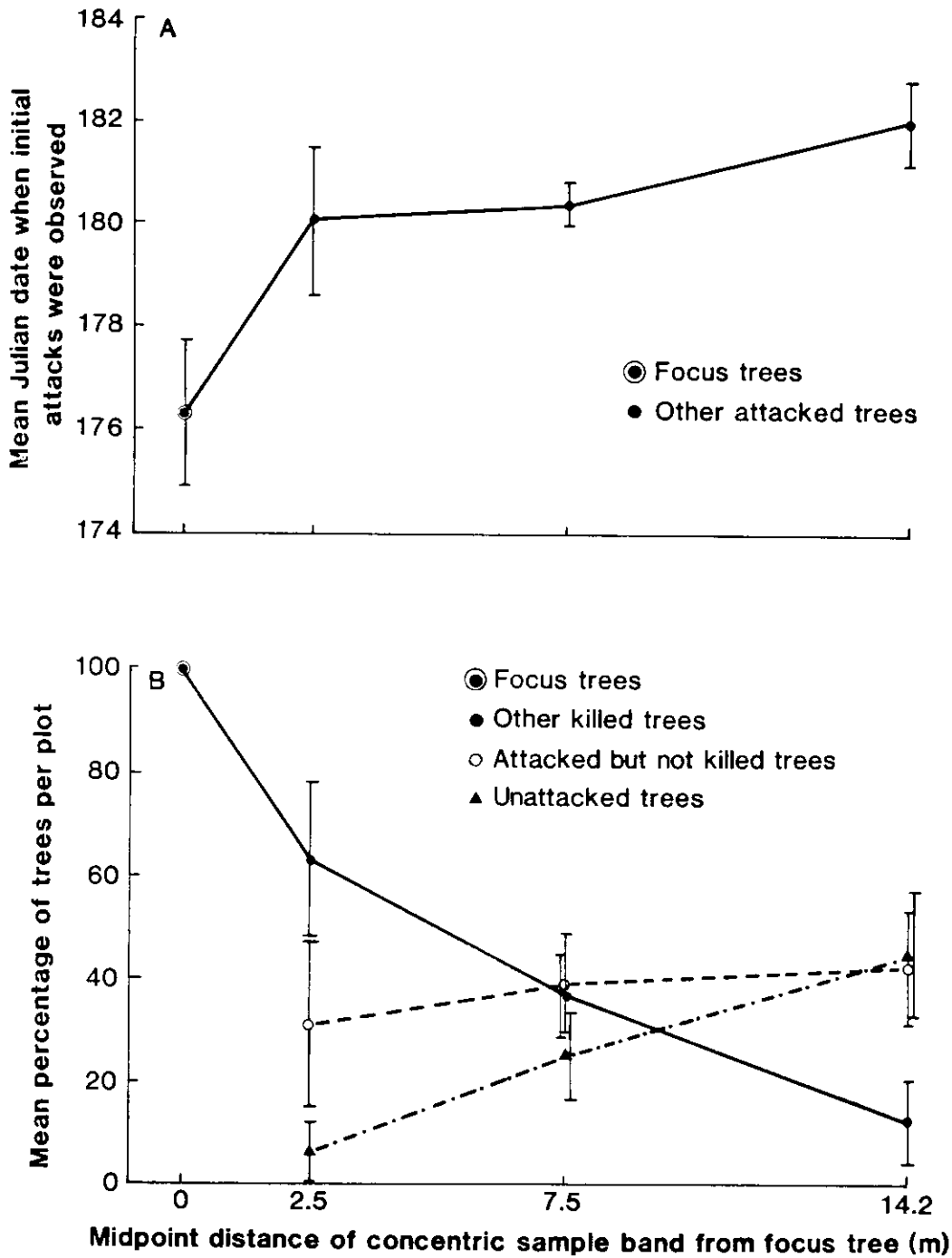


Figure 2. A. Mean Julian date when spruce beetle attacks were first observed on focus trees and on recipient trees in concentric sample bands. B. Mean percentage of sample trees that were killed, attacked and unkilld, or unattacked over mid-distance of concentric sample bands from focus trees. Vertical bars equal  $\pm 1$  standard error.

trees that were killed decreased as distance from focus trees increased (Figure 2b). Mean percentage of recipient trees that were attacked but not killed or trees that were unattacked increased as distance from focus trees increased.

Mean total numbers of attacks at *bh* and peak mean daily attacks decreased as the Julian date when attack densities peaked increased (Figure

3). Mean total numbers of attacks at *bh* decreased generally from focus trees to surrounding trees (Figure 4). Killed trees were usually attacked more heavily at *bh* than attacked but unkilld trees. Neither mean *dbh*'s of attacked trees nor mean percentages of sapwood area growth of attacked trees differed significantly as distance of recipient trees from focus trees increased (Figures 5a and b).

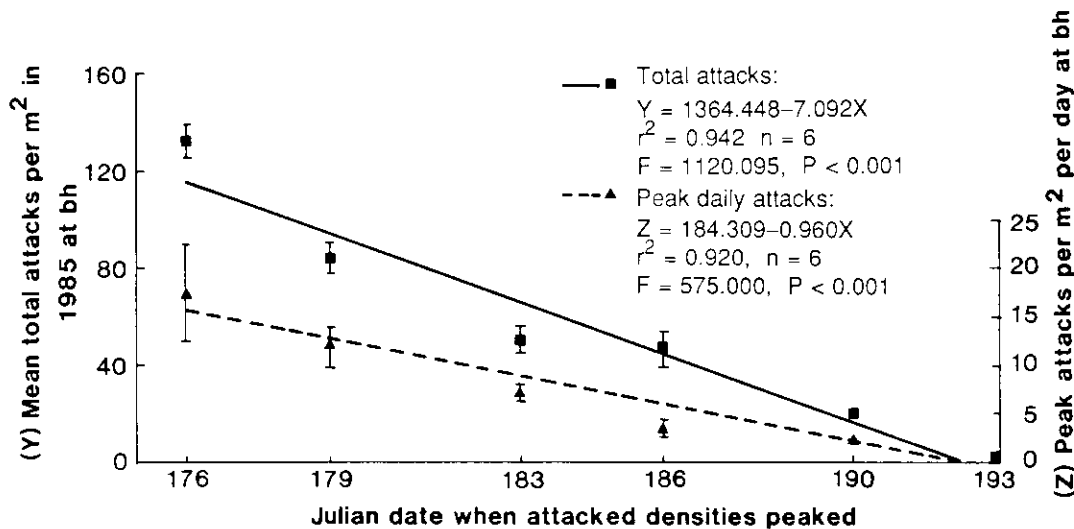


Figure 3. Mean total spruce beetle attacks in 1985 (Y) and peak mean daily attacks (Z) relative to Julian date when attack densities peaked. Vertical bars equal  $\pm 1$  standard error.

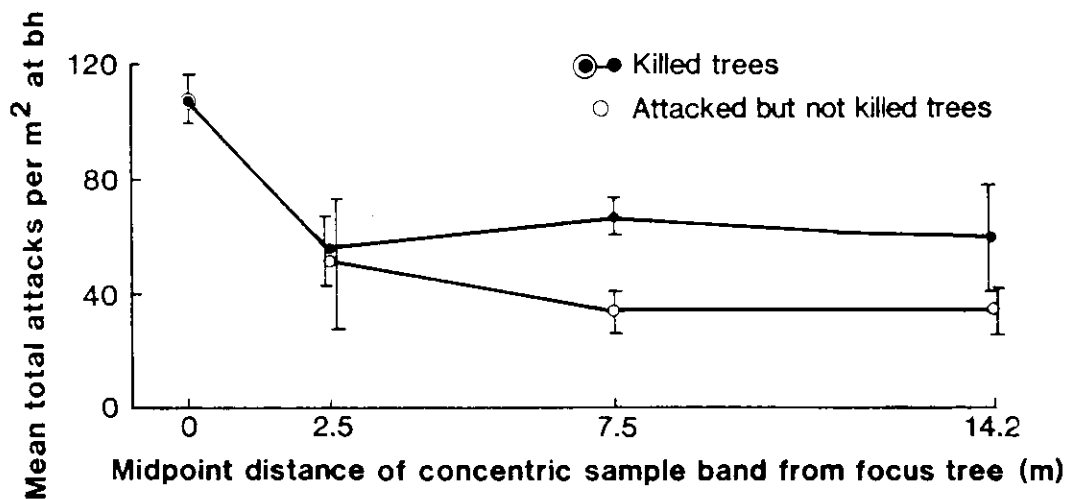


Figure 4. Mean total numbers of spruce beetle attacks per square meter on focus trees and on trees in concentric sample bands. Vertical bars equal  $\pm 1$  standard error.

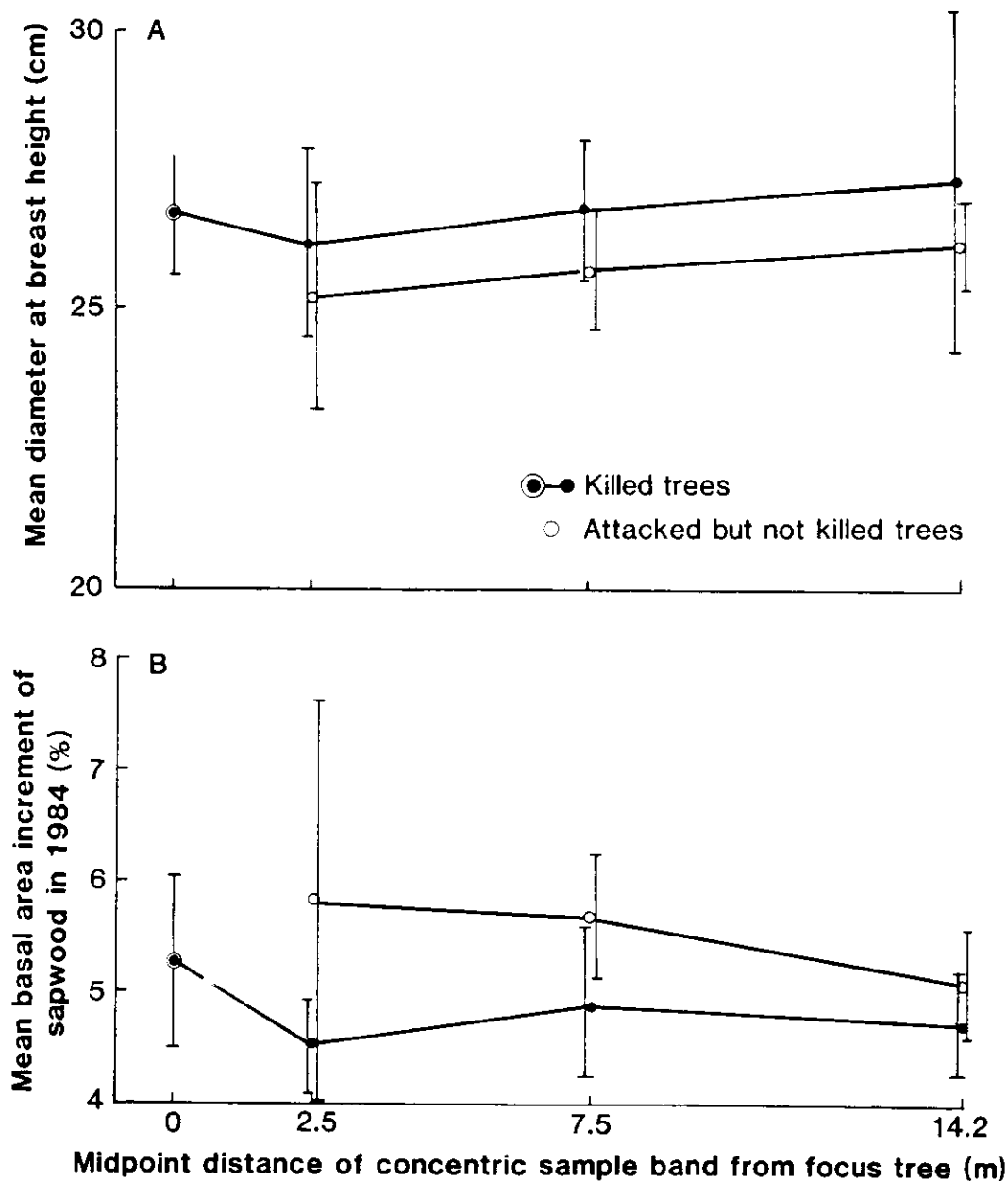


Figure 5. A. Mean *dbh*'s of focus trees and attacked trees on concentric sample bands. B. Mean percentages of sapwood basal area increment of focus trees and attacked trees on concentric sample bands. Vertical bars equal  $\pm 1$  standard error.

The ratio of width of xylem ring formed in 1985 to width of ring formed in 1984 decreased as number of beetle attacks at *bh* increased (Figure 6). Narrow xylem rings formed in heavily attacked trees may reflect earlier interruption of radial growth compared to growth in lightly at-

tacked and unattacked trees because some photosynthates normally used for respiration and stem radial growth are used for tree defense instead.

Reduced ratios of attacked trees paralleled reductions in bole expansion rates after tree attack by spruce beetles (Hard 1987). Many of the

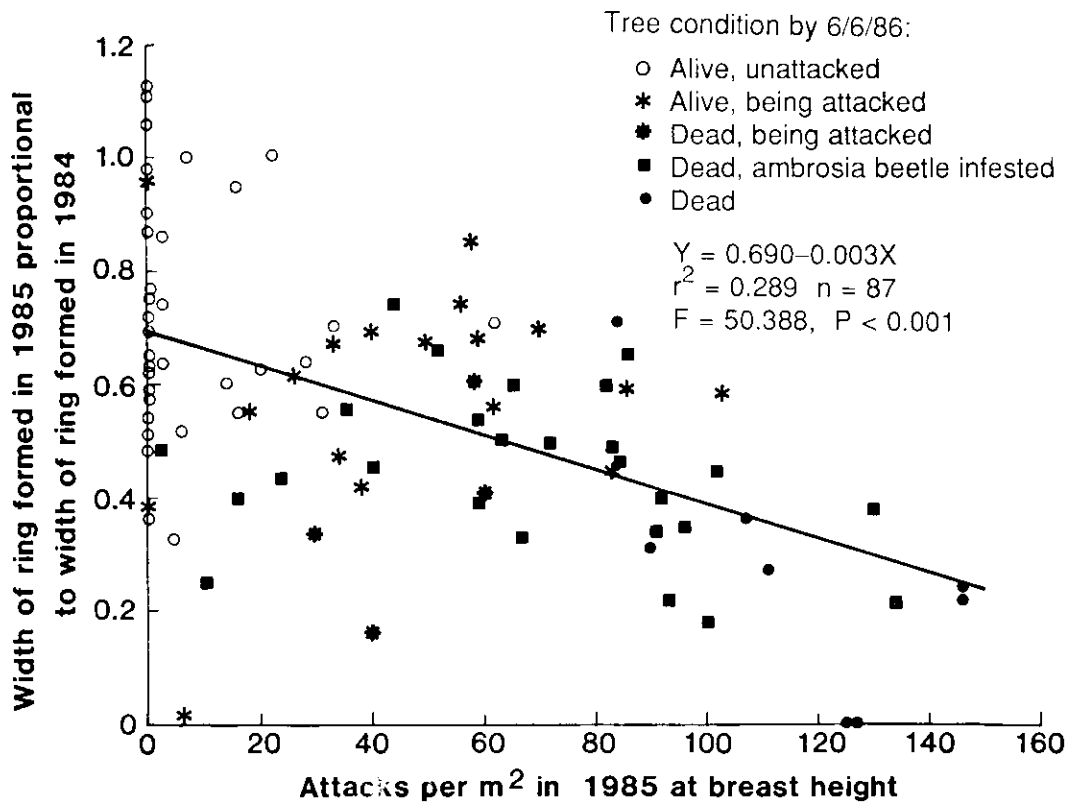


Figure 6. Width of xylem ring formed in 1985 proportional to width of xylem ring formed in 1984 relative to spruce beetle attacks per square meter in 1985.

trees that died during the winter of 1985-86 were attacked by ambrosia beetles (*Trypodendron* sp.) in the late spring of 1986, whereas many trees that survived 1985 spruce beetle attacks were reattacked by spruce beetles in 1986.

### Discussion

The few trees attacked first appeared to serve as foci for attacks on nearby trees. Attacks continued on focus trees after recipient trees were attacked, however, and mean total attacks on recipient trees were less than on focus trees. Apparently, the "repelling model" of switch attack behavior characteristic of mountain pine beetles (Geiszler *et al.* 1980) is not characteristic of the spruce beetle because higher attack rates did not occur on surrounding resistant trees. The "threshold model," first termed by Geiszler *et al.* (1980) to label descriptions of switching by the southern pine beetle (*D. frontalis* Zimm.) (Coster

and Gara 1968, Gara and Coster 1968), appears to be more characteristic of the spruce beetle.

Spruce beetles concentrate attacks in localized areas around focus trees, presumably because strong attractant pheromone plumes form around focus trees. Nonresistant trees are often killed, but less concentrated attacks in apparently resistant trees may convert them to a less resistant state for attack the following year. This appears to be an effective but less aggressive manner of colonizing resistant hosts than that used by the mountain pine beetle (Geiszler and Gara 1978, Raffa and Berryman 1983).

Tree survival appears to depend primarily on attack density, and attack density appears to depend largely on early occurrence of initial attack, rapidity of mass attack, and length of time that a tree undergoes attack. Neither *dbh* nor percentage of sapwood basal area increment of recipient trees appeared to differ as distance from focus trees increased.

Artificial baits or artificially high concentrations of bait that could cause abnormal beetle behavior were not used in this study. Factors that control spruce beetle switch-attack behavior could have been obscured, however, by the twice-weekly sampling regime.

Further studies using a shorter sample interval are needed to clarify the antiattractant func-

tion of MCH. Details of its role in the switching of attacks by spruce beetles from focus trees to recipient trees remain unclear.

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