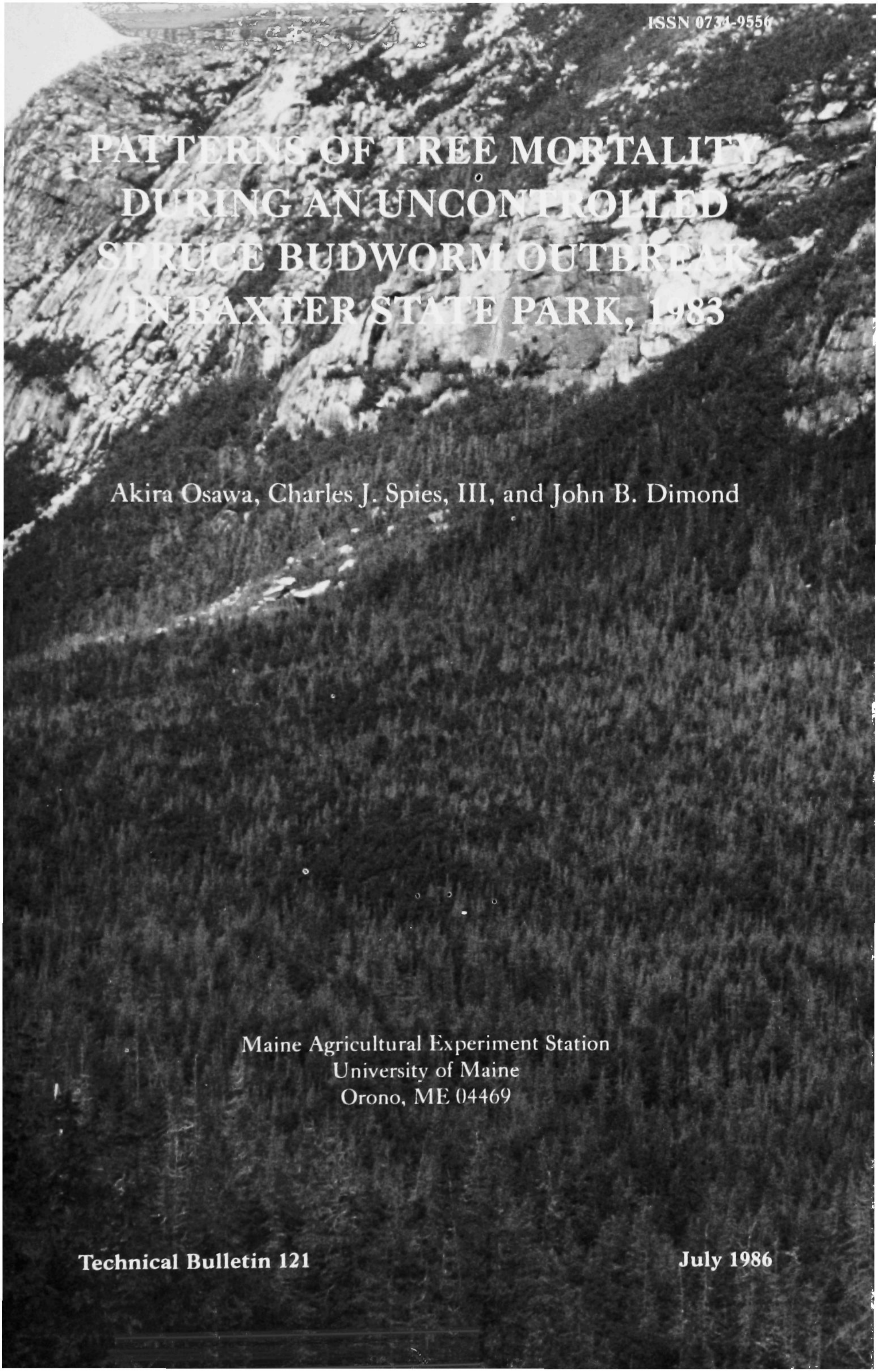

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Akira Osawa, Charles J. Spies, III, and John B. Dimond

Maine Agricultural Experiment Station
University of Maine
Orono, ME 04469

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Akira Osawa
School of Forestry and Environmental Studies,
Yale University
and
Charles J. Spies, III and John B. Dimond
Entomology Department
University of Maine

Maine Agricultural Experiment Station
University of Maine
Orono, ME 04469

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# ABSTRACT

A forest inventory of Baxter State Park, Maine was done during the summer and fall of 1983 to study the patterns of mortality in balsam fir (*Abies balsamea* (L.) Mill.) and in the red-black spruce complex (*Picea rubens* Sarg., *P. mariana* (Mill.) BSP. and their hybrids) during an uncontrolled spruce budworm outbreak.

In total, 6,953,000 $m^3$ (186 $m^3$/ha) of living trees were present, excluding the ones in hardwood forests. Spruce was the most abundant species with 61% of the total stem volume. The volume of trees that died during the outbreak was estimated as 4,647,000 $m^3$ (125 $m^3$/ha); 40% of the original quantity. Dead stem volume was 2,570,000 $m^3$ (68.9 m3/ha) for fir and 1,560,000 $m^3$ (41.8 $m^3$/ha) for spruce. They correspond to 77% and 27% of the original stem volumes in fir and in spruce, respectively.

Two mortality patterns were apparent. The fir mortality was consistently greater than that of spruce. The percentage mortality of spruce was always greater in the higher elevation zone (600 m to 870 m above mean sea level) than in the lower (below 600 m). Percentage mortality of fir and of spruce showed inconsistent patterns in relation to the proportion of hardwood species basal area and to the proportion of fir basal area in a stand. However, those mortality patterns tended to be pronounced when the overall tree mortality was relatively high. Except for the elevation, topographical factors (slope inclination, position on slope, and aspect) were not consistently related to the mortality. The tree mortality patterns could not be completely explained by multiple regression analysis, with 40% to 60% of variation of mortality remaining unexplained.

The hypotheses on the mechanisms producing the tree mortality patterns during a budworm outbreak were summarized and the observed tree mortality patterns were then interpreted according to those hypotheses. Most observed patterns could be explained by more than one hypothesis. It was suggested that complex processes were responsible for developing certain tree mortality patterns, and a deductive method based on the simple observations would not reveal the true mechanisms. As an alternative, an inductive method of controlled field experiments is recommended.

# INTRODUCTION

For at least the past two centuries, the spruce-fir forests of eastern North America have periodically experienced extensive damage by the spruce budworm, *Choristoneura fumiferana* (Clem.)(Lepidoptera: Tortricidae)(Baskerville 1975b, Brown 1970, Mott 1980). The insect reaches epidemic population levels at approximately 35-year intervals (Royama 1984), and kills much of the balsam fir (*Abies balsamea* (L.) Mill.) and, to a lesser extent, the spruce (*Picea*) species through defoliation. Unlike many serious insect pests, spruce budworm is native to North America, and is not found elsewhere (Miller 1963).

Outbreaks of this insect appear to be closely linked to the life-cycle of the host trees; mature forests of fir are destroyed by the budworm simultaneously over large areas. Forests of the same species then regenerate from the abundant seedlings that had become established prior to the budworm infestation. When the new generation of trees matures, the forests again become susceptible, and are destroyed. A regular pattern of fir-budworm-fir cycle seems to exist (Baskerville 1975b).

In regions where red spruce (*Picea rubens* Sarg.) co-occurs with fir in relative abundance, however, the effect of a spruce budworm outbreak on the alteration of the forest may differ from the effect on pure fir forests (Craighead 1924, Westveld 1946, Mott 1980, Seymour 1980). Appreciable numbers of codominant red spruce may survive budworm attack, and the forest may temporarily become more dominated by spruce after the epidemic. If this is the case, it presents an attractive option of modifying spruce budworm damage by silvicultural techniques (Seymour 1980, Mott 1980), if forests with large components of red spruce and relatively little fir can be created.

In the present spruce budworm outbreak, Baxter Park and surrounding regions first suffered heavy defoliation in 1972. Small acreages of insecticidal spraying in T5R10 and T4R10 were undertaken in 1973 and 1974, but thereafter it was ruled that spruce budworm control operations were contrary to the wilderness character of the Park. By 1983, mortality of balsam fir was virtually complete, accompanied by substantial damage to spruce. This provided a new opportunity to measure the impact of a spruce budworm outbreak on unprotected forests.

The objectives of the present study, therefore, were to estimate the volumes of living trees present in the Park and the quantity of spruce and fir that had been killed by the budworm. We also studied the patterns of tree mortality in relation to 1) the differences between host species, 2) species composition of stands, and 3) topographic factors of the site.

There is complication in studying the mortality of two spruce species, red spruce and black spruce (*Picea mariana* (Mill.) BSP.). Their hybrids commonly occur, and the distinction is ambiguous. Although the closeness of a genotype to each of the pure species can be estimated (Manley 1971), the method is not feasible for the rapid identification of many individuals in the field. Therefore, those spruce species were lumped and will be referred to as spruce throughout this report. Also, balsam fir will be referred to as fir, since there is only one fir species present in the region.

## ENVIRONMENTAL AND HISTORICAL SETTING OF BAXTER STATE PARK

### Location and Topography

Baxter State Park is located at 46 deg. N and 69 deg. W in north-central Maine, U.S.A. (Figure 1). It is about 180 km (110 miles) inland both from the Atlantic Ocean and from the St. Lawrence River. The topography is mountainous; Mt. Katahdin and the associated mountains cover roughly the southern two-thirds of the Park. The highest point, Baxter Peak, reaches an elevation of 1605 m (5,267 ft). Mt. Katahdin is the northern-most tall peak of the Appalachian Mountains, and the generally elevated area continues to the White Mountains of New Hampshire and the Green Mountains of Vermont. The northern one third and a small portion of the western part of the Park, however, are less mountainous. The area consists of rolling hills, lakes and moderately extensive wetlands. This less mountainous area is representative of much of the commercial forested area in northern Maine. The geology of Baxter Park was described in detail by Caldwell (1972).

### Climate and Vegetation

The climate of northern Maine is classified as Dbf (humid continental, cool summer, and constantly moist) by the modified form of the Koppen's scheme (Trewartha 1954). Detailed climatological information (U.S. Department of Commerce 1952, 1974) is available for Ripogenus Dam, Maine about 10 km (6 miles) west of the Park. The mean annual temperature is 4.6 deg. C (40 deg. F) and the mean annual precipitration is 1,052 mm (41 inches), much of it snow, distributed more or less evenly throughout the year.

Walter (1979) classified the general vegetation of northern Maine as being in the transition zone of type VI (nemoral broadleaf-deciduous forest) and type VIII (boreal coniferous forests). The forests in the area were similarly classified by Westveld (1956) as spruce-fir-northern hardwood forest.

### Fire and Logging History

Fire is not a major cause of disturbance in the forests of northern Maine. A cycle of 800 years was estimated as the period that any forested area is destroyed by fire (Lorimer 1977). However, relatively large areas of forest fire did occur in Baxter Park during the past century. The Great Wassataquoik Fire, the largest of known fires, occurred in 1903. It started in township

T6R10, swept through T6R9 and Pogy Notch in T5R9, and devastated the extensive area at the headwaters of Wassataquoik Stream (Ring 1903). Ring's (1903) data indicate that 80% of total area in T5R9, 60% of T4R9 and 40% of T6R9 were consumed by this fire. A separate fire developed in T3R9 about the same time, and approximately 3,200 ha (8,000 acres) of forests were burned (Ring 1903). These burns total about 18,000 ha (45,000 acres), 26% of the entire area of the Park. A large fire also occurred in 1911 in the western part of the Park, around Nesowadnehunk Field Campground in T4R10 (Anonymous 1911). In more recent years, about 1,400 ha (3,560 acres) of forest were burned by lightning fires in 1977 near the southern end of the

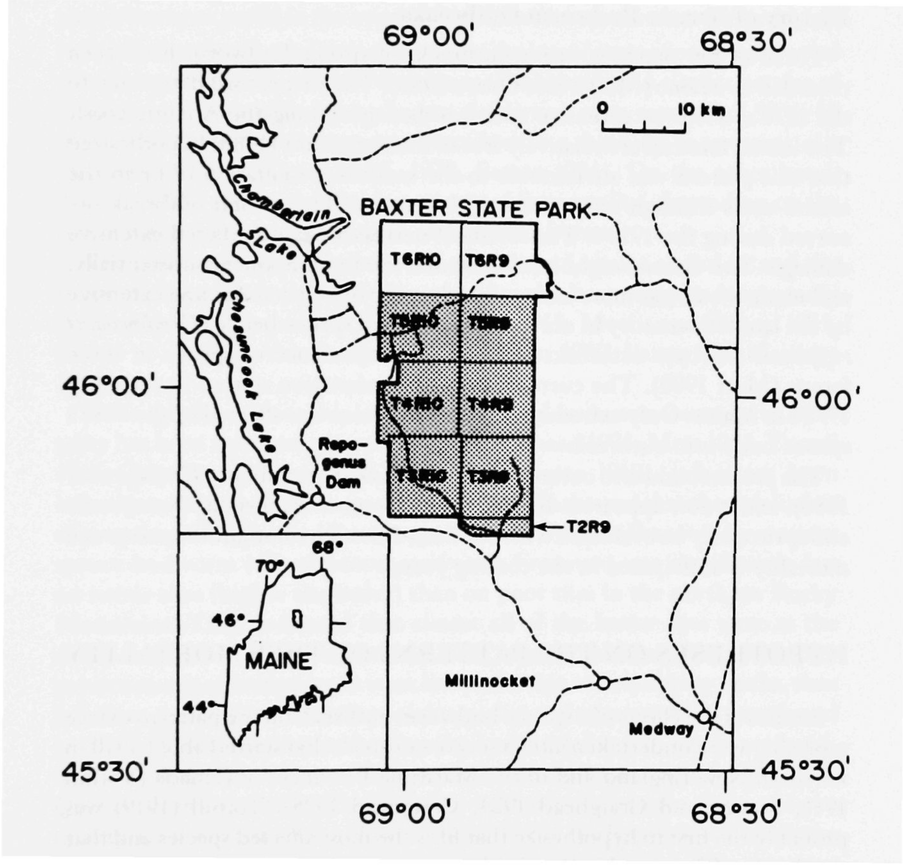

FIG. 1. Sketch map of Maine and vicinity of Baxter State Park. Township names and their boundaries in the Park are also shown. Forest inventory was carried out in all townships, except for T6R10 and T6R9 that contained forests which had been protected against the spruce budworm.

Park (Bowen 1977), after an extensive windthrow that occurred a few years previously.

The forests of the Park were logged from the mid 1800's until 1965 (Anonymous, no date). Since then, no trees have been cut commercially, except for some salvage cutting after a 1974 blowdown. The signs of lumbering operations, stumps and old logging roads, are seen in most parts of the Park. The lumbering has probably affected the structure of the present forest, especially the species composition. White pine, then large red spruce, were selectively harvested during the course of lumbering history (Smith 1972), and those species may be under-represented in Baxter Park today.

### History of Spruce Budworm Outbreaks

Three of the previous major outbreaks of spruce budworm have been recorded in Maine (Mott 1980, Osawa 1986). The first record dates back to the 1870's, when an extensive area was damaged along the Atlantic coast. The inland forests were relatively free of damage. Mott (1980) hypothesized that this pattern was attributable to the small representation of fir in the inland areas through most of the 19th century. The second outbreak occurred during the 1910's. The forests of northern Maine suffered extensive damage. Two factors might have increased the fir component substantially, and made the forests more susceptible; logging operations became extensive by the late 19th century in northern Maine, and spruce beetle (*Dendroctonus rufipennis* (Kirby)) outbreaks reduced the importance of spruce in those forests (Mott 1980). The current budworm infestation started in the early 1970's in Maine. Only extreme northeastern Maine was affected by the 1940's spruce budworm outbreak.

The present budworm outbreak in Baxter Park started about 1971 (Seymour 1980), and it now appears to be ending. Differences of mortality between fir and spruce may be evaluated with our data, although some additional spruce mortality is anticipated in the coming years.

## HYPOTHESES ON THE PATTERNS OF TREE MORTALITY

Studies of the effects of a spruce budworm outbreak on the patterns of tree mortality were undertaken after a severe outbreak that started about 1910 in northern New England and in the Maritime Provinces of Canada (Tothill 1919, Swaine and Craighead 1924, Craighead 1925). Tothill (1919) was probably the first to hypothesize that fir is the most affected species and that the degree of damage decreases with increasing mixture of other species in a forest. The higher mortality of fir than of spruce seems to be accepted by all investigators who have carefully looked at the difference between them (Craighead 1924, 1925, Westveld 1953, Seymour 1980, Mott 1980, MacLean 1980).

Craighead (1924, 1925) enlarged upon the observations of Tothill (1919) about mixed stands and postulated that mortality of fir and of spruce is smaller with increasing proportions of hardwoods in a stand, and that the mortality of spruce is greater with increasing proportion of fir. The association of increasing hardwood proportion and decreasing damage of host species was later suggested by a number of investigators (Blais 1958, Mott 1963, 1976, Batzer 1969, 1976, Seymour 1980, MacLean 1980).

Wellington et al. (1950) and Ghent (1958) described instances in which outbreaks of forest tent caterpillar caused deterioration of overstory hardwoods before the development of spruce budworm infestations on conifers which were originally subordinate in a suppressed crown class. The coniferous trees became exposed to the ovipositing budworm moths after the forest tent caterpillar outbreak, and they argued that the loss of protection by hardwood canopy was responsible for the damage to those conifers. A similar pattern of increased tree mortality by budworm defoliation after removal of 30 to 40 percent of hardwood canopy was described in a thinning experiment of a mixedwood forest (Crook et al. 1979, Batzer 1984). On the other hand, Turner (1952) reported variable patterns of fir mortality, depending on the crown class of fir trees growing in mixedwood forests.

The positive relationship between mortality of spruce and of fir and the proportion (or basal area) of fir in a stand has also been suggested repeatedly (Westveld 1946, Greenbank 1963c, Turner 1952, Morris and Bishop 1951, Ghent et al. 1957, Van Raalte 1972, MacLean 1980, Batzer and Hastings 1981).

Although the relationship of topography and budworm-caused tree mortality has been noted on a few occasions (Craighead 1924, Mott 1963, Terrell 1965, Terrell and Keefe 1965, Fauss and Pierce 1969), it has not been investigated thoroughly. Fauss and Pierce (1969) showed that the defoliation of overstory Douglas-fir (*Pseudotsuga menziesii* Mirb. (Franco)) by western spruce budworm (*Choristoneura occidentalis* Freeman) was significantly less on better sites (higher site index) than on poor sites in the northern Rocky Mountains. They indicated that almost all of the better sites were at the valley-bottoms near the waterways, and argued that moister and cooler environments of bottomlands were less preferable to ovipositing moths, thus less damage. Similar associations of site quality and tree mortality were found by Blais (1958), the better the site, the less mortality. On the other hand, McLintock (1955) did not find any relation between them in southern Quebec. It is important to note, however, that position on a slope and site quality are not synonymous. They may well be in the Rockies, but not in the forests where spruce and fir occur in eastern North America. The extensive lowland forest with abundant black spruce is usually excessively moist, and poor in site quality because of poor soil oxygenation.

Therefore, topographic factors themselves become independent variables, and should be investigated separately. It has been established by entomologists that the microenvironment plays an extremely important role in determining the behavior and survival of spruce budworm (Wellington and Henson 1947, Wellington et al. 1950, Mott 1963, Greenbank 1956, 1963). Also, topographical features affect the microenvironment of the site (Geiger 1965) and it is logical to seek some relationship between tree mortality and topography. Recently, Blais (1980) reported greater tree mortality at higher altitudes, but Turner (1952) and MacLean et al. (1984) did not find any strong correlation between mortality and site characteristics.

The following tree mortality patterns have also been suggested: (1) mature- and overmature-stands of fir receive more damage than immature stands (McLintock 1955, MacLean 1980); (2) mortality of understory fir is quite high in mixedwood stands (Swaine 1933, Turner 1952); (3) vigor of a tree at the time of defoliation is related to mortality (Craighead 1924, 1925, Morris 1946); (4) physiological age (flowering or non-flowering) of a tree significantly influences tree vulnerability (Blais 1958); and (5) amount of damage to individual stands is a function of cumulative defoliation (Blais 1958, Batzer 1973). These hypotheses were not tested in the present analysis, since we had no opportunity to measure the appropriate variables.

In summary, four general hypotheses on the patterns of tree mortality during an uncontrolled spruce budworm outbreak were tested:

1 Percentage mortality is greater in fir than in spruce.
2 Percentage mortality of fir and of spruce is smaller with increasing proportions of nonhost species.
3 Percentage mortality of fir and of spruce is greater with increasing proportions of fir.
4 Topographic factors such as position on slope, slope inclination, aspect, or altitude of the site are related to mortality patterns of fir and of spruce.

## METHODS

Stratified random sampling was used to estimate the basal area and the volume of living and dead trees in the Park. Several strata, representing different forest types and degrees of tree mortality, were distinguished using color infrared photography. The samples were taken in each forest type using square plots. In each plot, trees were sampled by variable plot sampling at ten randomly chosen points.

## STRATIFIED RANDOM SAMPLING

In 1982, color infrared photography at 1:80,000 scale was obtained for the Park, except for the two northern-most towns, T6R10 and T6R9. These towns are managed as the Scientific Forest Management Area and have been sprayed for protection from spruce budworm. The remaining six towns were divided into fourteen types based on the dominant tree species and by the health of the forest. Areas of dead trees and those of healthy ones appeared gray and red, respectively, on the infrared photography. The forests were first classified into four categories depending on the proportion of hardwood volume which was estimated by photo-interpretation. These are, 1) softwood type (S) having less than 25% hardwoods, 2) softwood-hardwood type (SH) with hardwood volume 25 50%, 3) hardwood-softwood type (HS) with hardwood 50 75%, and 4) hardwood type (H) having more than 75% hardwoods. Each type was further divided into four categories depending on the damage to the forest estimated with the photographs; gray (g), gray-red (gr), red-gray (rg), and red (r). The recognized forest types are shown in Table A1. All types designated as S, SH, and HS were included in the inventory; there were nine types in total. Hardwood type (H) and types lacking merchantable trees (rock and recent burns) were not sampled. The type-mapping and photography were done by the J. W. Sewall Co., Old Town, Maine.

Square plots of 50 m X 50 m (0.25 ha) were always used for the sampling in each forest type, because both shape and size of a plot may affect the accuracy of the estimated stand statistics (Greig-Smith 1983). The number of plots allocated to each type was determined by considering: 1) area of a type, 2) estimated standard deviation of fir and of spruce basal area in a type, and 3) accessibility of a particular stand. Accessibility strongly affects costs associated with sampling , and Snedecor and Cochran's approach (1967:p 523) was used in calculating the sample size. This procedure allowed us to maximaze the accuracy of the estimated stand statistics with the given resource that was available for the field survey. As accessibility was considered in stratification, each forest type was further divided into three accessibility classes, yielding 27 strata in total (nine forest types times three accessibility classes). Table A2 shows the allocation of the number of sample plots in strata. The more accessible the zone the higher the intensity of sampling, but the less the weighting of each sample. The areas of the forest types are shown in Table A3.

A total of 416 one-quarter-hectare plots was sampled. Locations were determined arbitrarily, but as randomly as possible, throughout the Park. The azimuth and distance to a sample plot were chosen using a random number table, and were located by pacing from an arbitrarily picked point. The distance was ordinarily less than 500 meters. Ordinarily, a line to the first plot was extended and a few plots were measured along that transect. When the prospective sample plot showed abrupt internal changes in species composition, tree density, or canopy height, the boundary was shifted slightly. If adjustment of the plot boundary did not make the stand condition relatively homogeneous, the plot was abandoned. Some clumping of sample plots resulted (Figure A1), due to establishing several plots at each locality.

## VARIABLE PLOT SAMPLING

Stand statistics were estimated in each 0.25 ha plot by a variable plot sampling technique (Dilworth and Bell 1976). The basal area and stem volume of living and dead trees were measured by species. A prism or an angle gauge with a basal area factor 2.5 or 5.0 $m^2$/ha was used depending on the stand condition. Ten sample points were located randomly within each sample plot. Ten points were used, because our preliminary data indicated that the number of prism points necessary to give 10% allowable error in the estimate of spruce and fir mortality by basal area in a 0.25 ha quadrat was less than or equal to ten (also see MacLean and Ostaff 1983).

The procedure for selecting the location of prism points was the following: (1) the coordinates of ten points in a 0.25 ha quadrat were determined by picking a series of two numbers from a random number table; (2) a map of the quadrat with ten points was prepared. Then straight lines were drawn between the points, marking the shortest route to travel to visit the ten points; (3) at each point on the map, the azimuth and the distance to the next point were calculated, and were indicated on the map, and 4) those three steps were repeated and 50 different maps were prepared, one of which was picked at random for each sampling.

At all sample points, basal areas of living and of dead standing trees were estimated with a prism or an angle gauge, by species. All trees that were taller than breast height and were judged as the sample trees were counted, regardless of their diameter at breast height (dbh). Two categories were used for living trees; relatively healthy (L1) and moribund (L2). However, they were lumped later in the analyses, since their distinction was somewhat arbitrary. A tree was considered recently dead of budworm attack if dead needles and dead fine twigs were present, or if recent sawyer beetle (*Monochamus* spp.) attack was evident. A dead tree was regarded as standing when there was no obvious disturbance of the root collar and a majority of the stem was present. Dead, but not standing, trees were also sampled. In this case, the distance between the sample point and where the tree was originally standing was measured. The dbh of the tree was also measured, and the plot radius of that tree was calculated for judging if it was to be sampled or not. A tree that had uprooted was categorized separately because such trees were unlikely to have died of budworm defoliation. Therefore, three classes of dead trees were used: dead standing (D1), uprooted (D3), and other (D2). The D2 included dead trees with broken stems. Trees in D1 and D2 categories were assumed to have been killed by the spruce budworm.

The procedure of Dilworth and Bell (1976:p 38) was used to adjust data from points in which some of the trees selected for sampling fell outside the boundaries of the 0.25 ha plot. Also, when there was appreciable slope inclination at the sample point, adjustments (Dilworth and Bell 1976) were made with a prism of basal area factor 2.5 $m^2$/ha to correct for plot area distortions due to slope.

The dbh and height of sampled trees were also measured at approximately one third of the sample points. Two heights, total height and the height to the four-inch-top (10 cm), were measured. The stem volume was then calculated, using the volume equations of Scott (1981). The volume-basal area ratio was calculated for each species and for each forest type.

The following information was also recorded for every 0.25 ha plot; (1) plot location, (2) date sampled, (3) forest type, (4) elevation (read from a topographical map), (5) aspect, (6) slope inclination, (7) position on slope, and (8) severity of budworm damage. The last three items were recorded by arbitrary scales of 1–5.

## CALCULATION OF STAND STATISTICS

The basal area and the stem volume of trees per hectare were calculated separately for each plot by species and as either living or dead of budworm attack. The standard error of the mean was also calculated for each. Then, stand statistics prior to the current spruce budworm epidemic were estimated. Estimates were also made of the basal area and the proportion of basal area that were killed during the budworm outbreak.

### Basal Area

The mean basal area of trees (G, $m^2$/ha) in each category was calculated by,

$$G = (k/n) \sum_{j=1}^{n} z(j) \qquad (1)$$

where k = basal area factor ($m^2$/ha) n = number of sample points in a 0.25 ha plot

z(j) = number of sample trees associated with the sample point j.

The basal area factor was either 2.5 or 5.0. The number of sample points was 10 in most cases, but some had fewer points for various reasons.

### Standard Error of the Mean Basal Area

The standard error of the mean in each basal area estimate (SE(a), $m^2$/ha) was calculated as,

$$SE(a) = (k/n)^{1/2}[(\sum_{j=1}^{n} z(j)^2 - (\sum_{j=1}^{n} z(j)^2)/n)/(n-1)]^{1/2} \qquad (2)$$

## Stem Volume of Individual Trees

The stem volume of an individual tree (v, $m^3$) was estimated by the volume equations of Scott (1981), which have a general form,

$$v = a + bD^c + dD^eH^f \tag{3}$$

where D = dbh outside bark (cm); H = bole length (m) to a 10 cm top; a, b, c, d, e, and f = parameters specific to tree species.

Since the parameters of Scott's original equations had the dimensions in English units, they were converted to metric units.

## Volume-Basal Area Ratio

We calculated the volume-basal area ratio (R, m) of each species in a forest type as,

$$R = (1/m) \sum_{j=1}^{m} \left(\sum_{i=1}^{z} v(ij)\right)/kz(j) \tag{4}$$

where m = number of sample points in a forest type where the stem volume of a species is measured and
v(ij) = stem volume of i-th sample tree of a sample point j.

## Stem Volume per Hectare

For each category of species, living or dead categories, and forest type, the mean stem volume per hectare (V, $m^3/ha$) was estimated as,

$$V = R\,G \tag{5}$$

## Standard Error of the Mean Stem Volume

The standard error of the mean (SE(v), $m^3/ha$) for each estimate of stem volume for a given forest type was calculated by,

$$SE(v) = R\,SE(a) \tag{6}$$

since the expression of stem volume per hectare (Equation 5) is a multiplicative coding of the basal area estimate.

## Stand Statistics Prior to the Budworm Outbreak

The stand statistics prior to the current outbreak of spruce budworm were estimated from the living and dead trees. Let G denote the basal area of a certain tree category before the outbreak. Also let G(L) and G(D) denote the living and dead trees currently present. The quantities g and d are further defined as the growth and mortality of basal area during the budworm epidemic. Then, we have,

$$G(L) = G + g - d \tag{7}$$

or, equivalently,

$$G = G(L) - g + d \tag{8}$$

If we could assume that the tree growth is very small, Equation 8 becomes,

$$G = G(L) + d \tag{9}$$

The exact quantity of trees that died during the outbreak is unknown. However, if we could assume that most trees that are dead at present were killed during the last decade, Equation 9 is approximately equivalent to,

$$G = G(L) + G(D) \tag{10}$$

For fir and spruce, the first assumption is probably reasonable. Their growth has been greatly suppressed by defoliation. However, we do not know what portion of dead stems were actually killed during the period; it is likely that some of them succumbed before the budworm epidemic for other reasons. Therefore, G(D) probably overestimates d. It means also that the original stand statistic estimated by Equation 10 is slightly overestimated.

The situation may be more serious among nonhost species. Their growth is rather accelerated during the outbreak because of the increased availability of light and other resources to surviving trees (Seymour 1980). Therefore, g is not negligible. As a result, the original stand statistic of nonhost species is an overestimate.

## Tree Mortality

The mortality of fir and of spruce was estimated from the quantity of dead and living trees. It was defined as the proportion of basal area that died during a budworm outbreak, and was estimated as,

$$M = G(D)/(G(L) + G(D)) \tag{11}$$

where M is mortality. In other words, mortality here is the probability that a unit of basal area is lost during the period. Uprooted trees were not included in the mortality calculation, because the cause of death is less certain, and the likelihood that it was from budworm damage was small.

The true tree mortality (M(t)) during a budworm epidemic would be,

$$M(t) = d/G = d/(G(L) - g + d) \tag{12}$$

And for fir and spruce, it can be well approximated by,

$$M(t) = d/(G(L) + d) \tag{13}$$

If the basal area of currently dead trees (G(D)) is not equal to the true quantity of trees that succumbed during the epidemic (d), those variables may be related as,

$$G(D) = d + e \tag{14}$$

where e is the basal area that died prior to the budworm outbreak. The sign of e would be positive. From Equations 11, 13, and 14, we have,

$$M - M(t) = eG(L)/((G(L) + G(D))(G(L) + G(D) - e)) \tag{15}$$

Since e is expected to be much smaller than both G(L) and G(D),

$$M - M(t) > 0$$

Therefore, the mortality estimate given by Equation 11 will probably be slightly overestimated.

The arcsine transformation was adopted in calculating mean mortality values to compensate for the departure of frequency distributions of sample plots among the mortality classes from normality. Whenever the mean tree mortality is presented, however, it is expressed on the original scale.

### Species Composition of the Forest

The species composition of a sample plot was expressed in two ways. In one approach, three categories of forest composition were distinguished depending on the proportion of nonhost species, by basal area, in a plot. They were: (1) softwood forest (less than 5% nonhosts); (2) softwood-hardwood forest (between 5% and 35% nonhosts); and (3) hardwood-softwood forest (greater than 35% nonhosts). The host species included fir, red-black spruce, white spruce, eastern hemlock (*Tsuga canadensis* (L.) Carr.) and white pine (*Pinus strobus* L.). Hemlock and white pine are not defoliated as much as the other host species, but were known to be attacked by the spruce budworm (Flexner et al. 1983, Talerico 1984) and were, therefore, regarded as the secondary host species. Both white spruce and hemlock were poorly represented in Park forests. All other species were considered as nonhosts, and consisted mostly of hardwood trees. Those categories of forests are somewhat different from the ones used in the forest typing, but appeared most useful and were used throughout the analyses.

## RESULTS

### Current State of the Forest

The quantity of living trees in the Park in 1983 was estimated by basal area and by stem volume (Table 1). The total values for the entire area of the Park, and the mean values per hectare were calculated for each tree species. *It should be noted, however, that trees in two northern-most towns, a sprayed area, and in hardwood stands are not included in those estimates.*

In total, 6,953,000 ±136,000 $m^3$ (245,500,000 ±4,800,000 $ft^3$) of living trees are currently present in all those forest types that were sampled. The standard error is indicated for each estimated mean. (The statistics are also given on a per hectare basis in Table 1.) In terms of basal area, the quantity of living trees is 1,059,500 ± 19,800 $m^2$ (11,400,000 ± 213,000 $ft^2$). The most striking feature of the forest composition in the Park is the high abundance of

**Table 1.** Basal area and stem volume of living trees[1] in Baxter State Park in 1983.

| Species[2] | Basal Area ($m^2$/ha) | Total Basal Area For All Forest Types (x$10^3m^2$) | Stem Volume ($m^3$/ha) | Total Stem Volume For All Forest Types (x$10^3m^3$) |
|---|---|---|---|---|
| *Picea rubens* & *P. mariana* | 16.84(0.45) | 628.4[3](16.9) | 113.4(3.1) | 4,230(110) |
| *Abies balsamea* | 3.38(0.19) | 126.0 (7.1) | 20.5(1.2) | 765 (44) |
| *Betula papyrifera* | 2.69(0.20) | 100.2 (7.6) | 14.4(1.2) | 538 (43) |
| *Acer rubrum* | 1.75(0.15) | 65.4 (5.6) | 10.8(1.0) | 401 (38) |
| *Betula alleghaniensis* | 1.17(0.15) | 43.5 (4.0) | 6.8(0.7) | 255 (25) |
| *Thuja occidentalis* | 1.05(0.15) | 39.1 (5.4) | 5.1(0.7) | 192 (26) |
| *Pinus strobus* | 0.97(0.12) | 36.1 (4.5) | 7.0(0.9) | 260 (32) |
| *Fagus grandifolia* | 0.37(0.10) | 13.6 (3.6) | 2.3(0.6) | 84 (24) |
| *Acer saccharum* | 0.30(0.08) | 11.2 (3.1) | 1.7(0.4) | 63 (17) |
| *Pyrus americana* | 0.16(0.04) | 5.9 (1.5) | 0.9(0.2) | 34 (9) |
| *Populus* spp. | 0.15(0.05) | 5.4 (1.8) | 0.8(0.3) | 30 (10) |
| *Picea glauca* | 0.13(0.09) | 4.9 (3.4) | 0.7(0.5) | 28 (18) |
| *Acer spicatum* | 0.12(0.04) | 4.5 (1.5) | 0.8(0.3) | 30 (10) |
| *Acer pensylvanicum* | 0.10(0.02) | 3.7 (0.7) | 0.6(0.1) | 23 (5) |
| *Tsuga canadensis* | 0.10(0.05) | 3.9 (0.2) | 0.5(0.2) | 20 (9) |
| *Prunus pensylvanica* | 0.04(0.01) | 1.5 (0.4) | 0.3(0.1) | 9 (3) |
| *Pinus resinosa* | 0.04(0.02) | 1.5 (0.8) | 0.3(0.2) | 11 (6) |
| *Fraxinus* spp. | 0.03(0.01) | 1.2 (0.4) | 0.2(0.1) | 7 (2) |
| *Alnus* spp. | 0.02(0.01) | 0.7 (0.3) | 0.1(0.05) | 4 (2) |
| All Living Trees | 28.40(0.53) | 1,059.5(19.8) | 186.5(3.6) | 6,953(136) |

[1] Trees in hardwood forests were not sampled, and are not included in this table.

[2] Five other species, *Ulmus americana, Quercus rubra, Ostrya virginiana, Betula populifolia,* and *Corylus* spp. were also observed. However, basal areas and stem volumes of those species were negligibly small.

[3] Standard error of the mean.

a few species. Twenty four species of trees were recorded within the boundary of the Park, but the four most common species constituted 85% of the total stem volume. (In some cases, species were not distinguished and only genera were recorded; e.g., *Populus, Fraxinus*. Therefore, the true number of tree species will be greater than 24.) The spruces are especially important. Spruce stem volume was estimated as 4,230,000 ± 110,000 $m^3$ (149,000,000 ± 3,880,000 $ft^3$). This alone represents 61% of the total stem volume in all forest types. Fir, white birch (*Betula papyrifera* Marsh.) and red maple (*Acer rubrum* L.) are also important. They constitute 11%, 8%, and 6% of total stem volume, respectively. However, the volume of fir decreased greatly during the current spruce budworm outbreak. Estimates of mean basal area and stem volume of trees in each forest type are summarized in Tables A4 and A5.

## Estimated Quantity of Dead Trees

The amount of trees killed during the budworm outbreak was estimated from the inventory data (Table 2). Stem volume of all trees, both living and dead, in the Park is 11,600,000 ± 160,000$m^3$. A volume of 6,953,000 $m^3$ has survived the budworm outbreak (Table 1) and the amount of trees of all species that have died during the outbreak was 4,647,000 $m^3$. This is 40% of the original volume.

The mortality patterns of fir and of spruce are different. The total stem volume of fir and of spruce (both living and dead) was 3,340,000 ± 100,000 $m^3$ and 5,790,000 ±160,000 $m^3$, respectively. Dead stem volume is 2,570,000 ±92,000 $m^3$ for fir and 1,560,000 ±91,000 $m^3$ for spruce. Therefore, 77% of fir volume and 27% of spruce volume died in the Park. When the proportion of dead trees is calculated by the total basal area, we have 76% for fir and 26% for spruce, almost identical to the figures for stem volume.

The stem volume of uprooted trees is small. The figures are 149,000 ± 16,000 $m^3$ for fir and 127,000 ±17,000 $m^3$ for spruce. Only 5% of dead fir and 8% of dead spruce were caused by windthrow.

## Patterns of Tree Mortality

Patterns of tree mortality were analyzed according to the suggested hypotheses described earlier. Two approaches were used. First, variation of tree mortality among host tree species, species composition of forest, and topographical factors were analyzed by nonparametric methods. Percentage mortality values were initially transformed by the arcsine transformation with the intention of using one-way- or multi-way-analysis of variance. However, our data showed that even the transformed values were not normally distributed (Kolmogorov-Smirnov test on pooled data for the entire Park, $p<0.01$, $n=402$ for fir and $n=416$ for spruce). Therefore, the Kruskal-Wallis and Brown-Mood tests were adopted. In the following analyses,

**Table 2.** Basal area and stem volume of living and dead trees[1] in Baxter State Park in 1983. The values are given by type of host to the spruce budworm.

| Tree Category | Basal Area (m$^2$/ha) | Total Basal Area For All Forest Types (x10$^3$m$^2$) | Stem Volume (m$^3$/ha) | Total Stem Volume - For All Forest Types (x10$^3$m$^3$) |
|---|---|---|---|---|
| *Abies balsamea* | | | | |
| Living and Dead | 14.35(0.43) | 537(16)[4] | 89.5(2.7) | 3,340(100) |
| Living | 3.37(0.19) | 127 (7) | 20.5(1.2) | 765 (44) |
| Dead | 10.98(0.38) | 410(14) | 69.0(2.5) | 2,570 (92) |
| Uprooted | 0.60(0.06) | 22 (2) | 3.9(0.4) | 149 (16) |
| *Picea rubens* & *P. mariana* | | | | |
| Living and Dead | 22.89(0.63) | 854(24) | 155.2(4.3) | 5,790(160) |
| Living | 16.84(0.45) | 627(17) | 113.4(3.1) | 4,230(110) |
| Dead | 6.04(0.35) | 224(13) | 41.8(2.4) | 1,560 (91) |
| Uprooted | 0.49(0.06) | 19 (2) | 3.4(0.5) | 127 (17) |
| Primary Host Species[2] | | | | |
| Living and Dead | 36.95(0.66) | 1,380(25) | 243.3(4.4) | 9,080(170) |
| Secondary Host Species[3] | | | | |
| Living and Dead | 1.29(0.15) | 49 (6) | 9.5(1.1) | 354 (42) |
| Nonhost Species | | | | |
| Living and Dead | 10.11(0.39) | 377(15) | 58.1(2.3) | 2,170 (85) |
| *Betula papyrifera* & *B. alleghaniensis* Dead | 0.89(0.06) | 34 (2) | 4.7(0.3) | 175 (12) |
| All Living and Dead Trees | 48.36(0.65) | 1,810(24) | 310.9(4.3) | 11,600(160) |

[1] Trees in hardwood forests were not measured, and are not included in this table.

[2] Primary hosts are *Picea rubens*, *P. mariana*, *P. glauca*, and *Abies balsamea*.

[3] Secondary hosts are *Tsuga canadensis* and *Pinus strobus*.

[4] Standard error of the mean

significant differences of the sample means were examined by those two tests, unless otherwise stated. Unplanned comparisons of tree mortality, such as Scheffe's and Ryan-Einot-Gabriel-Welsch Multiple F tests (SAS Institute, Inc. 1982), among different kinds of stands and sites were also done on the transformed values.

Second, we attempted to explain the variation of percentage mortality and the variation of dead basal area in fir and in spruce by multiple regression analysis. A few investigators (Mott 1968, Batzer 1969, MacLean 1980) have used multiple regression for the same purpose. Several site variables (slope inclination, position on slope, aspect, and altitude) were included in the regressors as well as basal area and stem volume of trees in the sample plots.

### Comparison Between Mortality of Fir and Spruce

The pattern of mortality distribution was not the same in spruce as it was in fir (Figure 2). More than 80 percent of the fir basal area was killed on more than half the plots. On the other hand, there were but few plots where the mortality of spruce exceeded 50 percent. In other words, the defoliation tended to thin the spruces but to kill most of the firs. Figure 2 shows that the frequency distribution of mortality percentages is negatively skewed (skewness = -0.99) in fir but positively in spruce (+1.14). Fir mortality was significantly greater ($p<0.01$) than spruce.

Furthermore, higher mortality of fir was found in virtually every town, both lower and higher elevation zones, and in almost every category of stands ($p<0.001$ or $p<0.01$) (Table 3).

### Comparison of Mortality by Species Composition of Forest

Fir mortality was nearly 100 percent in the softwood and the softwood-hardwood stands but less in the hardwood-softwood forests (Figure 3). The distribution curves of fir mortality again tend to be skewed to the left, whereas the ones of spruce tend to show the opposite skewness. In fir, the skewness of the mortality distribution curve becomes less pronounced with an increasing proportion of nonhost species. Although a majority of plots showed more than 90% mortality of fir in the softwood forest, the median was about 40% in the hardwood-softwood forests. On the other hand, the skewness becomes more emphasized with the increasing proportion of nonhost

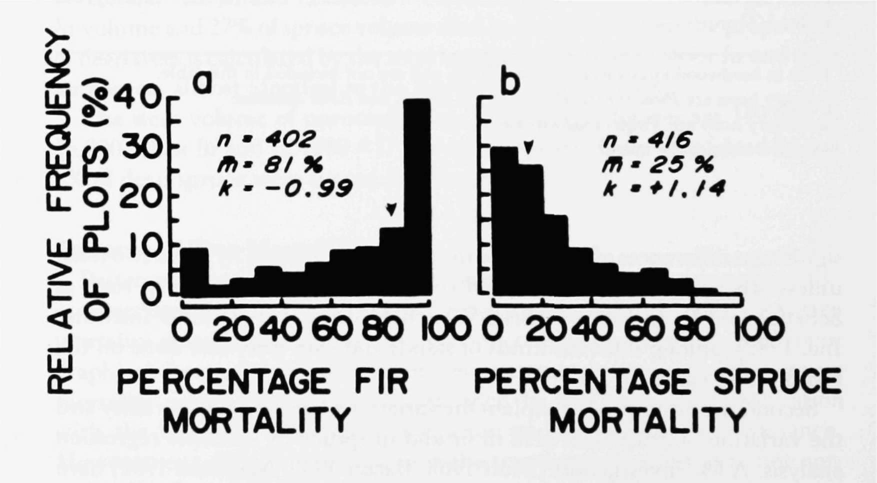

FIG. 2. Relative frequency distribution of percentage mortality in fir (a) and in spruce (b) for plots in Baxter State Park. Sample size (n), mean mortality ($\bar{m}$), and skewness (k) are indicated. Median is shown by a triangle.

**Table 3.** Comparison of mortality between fir and spruce in various areas of the Park and in forest types. The stands were divided by the proportion of fir in primary hosts and the one of nonhost species by basal area. The Kruskal-Wallis test was used. The significance levels are: * is 0.05>p>0.01, ** is 0.01>p>0.001, *** is 0.001>p, and ns is not significant.

| Area or type of stand from which samples were taken | | Chi-square value | significance | sample[1] size |
|---|---|---|---|---|
| Town | | | | |
| entire Park | | 386.62 | *** | 402(416) |
| T3R10 | | 93.29 | *** | 88 |
| T3R9 | | 83.29 | *** | 82 |
| T4R10 | | 105.08 | *** | 107 |
| T4R9 | | 9.84 | ** | 29 |
| T5R10 | | 106.25 | *** | 90 |
| T5R9 | | 1.70 | ns | 6 |
| Elevation Zone | | | | |
| below 600 m | | 349.87 | *** | 347(361) |
| between 600 m and 870 m | | 37.15 | *** | 55 |
| Forest Type[2] | | | | |
| less than 5% nonhosts | [1] more than 50% fir | 17.65 | *** | 14 |
| | [2] 30% - 50% fir | 21.15 | *** | 16 |
| | [3] 10% - 30% fir | 52.10 | *** | 43 |
| | [4] less than 10% fir | 36.21 | *** | 28(42) |
| nonhosts 5% - 35% | [5] more than 50% fir | 112.26 | *** | 92 |
| | [6] 30% - 50% fir | 76.42 | *** | 58 |
| | [7] 10% - 30% fir | 49.07 | *** | 40 |
| | [8] less than 10% fir | 4.12 | ns | 13 |
| more than 35% nonhosts | | 60.73 | *** | 98 |

[1] When the sample size for fir and for spruce differs, the one for spruce is indicated in parenthesis.

[2] Stands are categorized by proportions of nonhost species and of fir basal area among living trees.

species; in the case of spruce mortality, the median was about 30% in the softwood type, but it was close to 10% in the hardwood-softwood type. These results strongly support the hypothesis that mortality of fir and of spruce becomes smaller with increasing proportions of nonhost species.

The results of analyses for T4R10 will be presented separately from the ones for the entire Park in the following discussions, because topography and species mixture of forests in T4R10 approximate much of the commercial spruce-fir forest of northern Maine. Also, the tree mortality patterns appeared to be somewhat different among towns, which are arbitrary but convenient units for comparison.

As indicated in Table 4, tree mortality significantly differed ($p<0.001$) both in fir and in spruce among stands with varying proportion of nonhost species. The higher the proportion of nonhost species, the smaller was the mortality of both fir and spruce ($p<0.05$, Ryan-Einot-Gabriel-Welsch Multiple F test). This pattern was evident both in pooled data for the entire Park and in

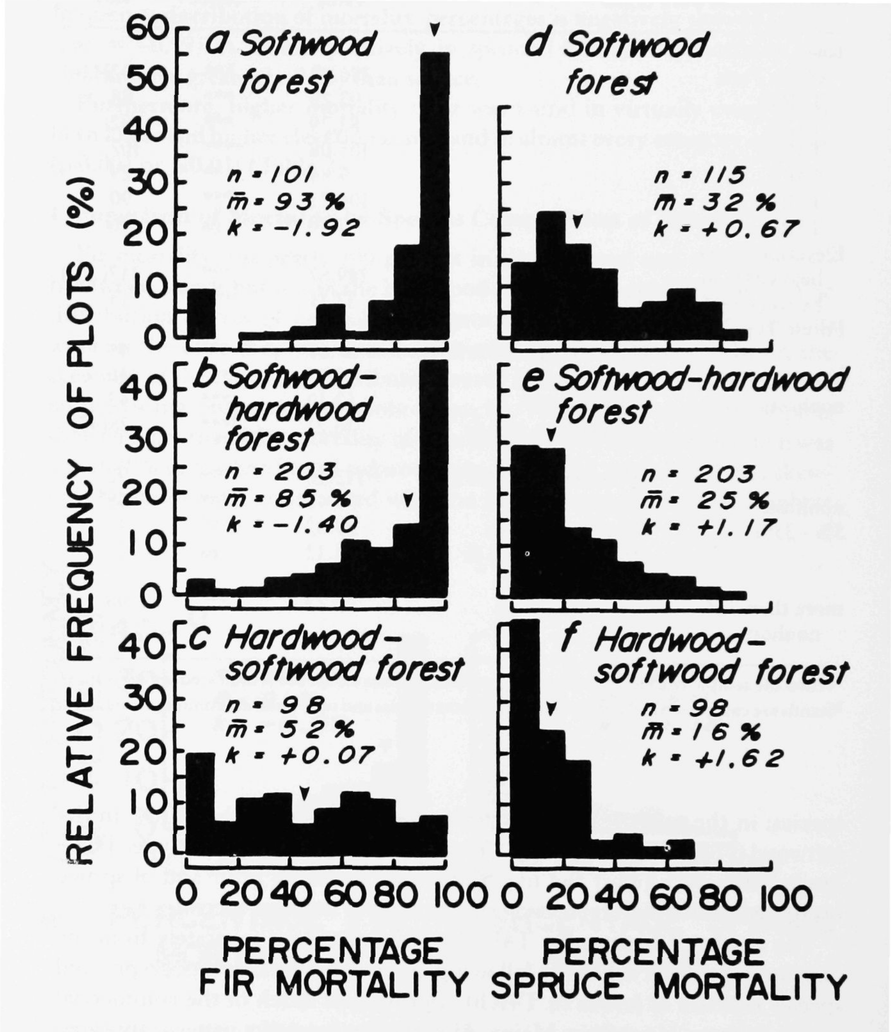

FIG. 3. Relative frequency distribution of percentage mortality in fir (a, b, and c) and in spruce (d, e, and f) for plots in three forest types.

**Table 4.** Tree mortality in relation to proportion of nonhost species.

| | Entire Park | | | | Town T4R10 | | | |
|---|---|---|---|---|---|---|---|---|
| Nonhost Species Proportion by Basal Area | Mean[1] Balsam Fir Mortality (%) | Mean Red-Black Spruce Mortality (%) | Combined Fir-Spruce Mortality (%) | Sample Size | Mean Balsam Fir Mortality (%) | Mean Red-Black Spruce Mortality (%) | Combined Fir-Spruce Mortality (%) | Sample Size |
| less than 5% | 93 a[3] | 32 a | 48 a | 101 | 98 a | 40 a | 54 a | 45 |
| 5% - 35% | 85 b | 25 b | 51 a | 203 | 94 a | 37 a | 67 b | 35 |
| more than 35% | 52 c | 16 c | 36 b | 98 | 56 b | 14 b | 38 c | 27 |
| Chi-square value[2] | 104.67 | 34.41 | 14.60 | | 46.03 | 27.56 | 8.68 | |
| Significance[4] | *** | *** | *** | | *** | *** | * | |

[1] Mean mortality was calculated using the transformed value (arcsine transformation), then it was transformed back to the original scale.

[2] Two methods of nonparametric one-way analysis were used to test if the tree mortality was unrelated to the proportion of nonhosts in stands. The more conservative result between the Kruskal-Wallis test and Brown-Mood test is presented for each case.

[3] Result of unplanned comparisons among the means is indicated when tree mortality is significantly different among stands with varying proportions of nonhosts. The same letter represents that the means are not significantly different at the 5% level. Ryan-Einot-Gabriel-Welsch Multiple F test (SAS Institute, Inc. 1982) was used.

[4] Significance levels are: * is 0.05>p>0.01, ** is 0.01>p>0.001, *** is 0.001>p, and ns is not significant.

T4R10. At the level of the entire Park, 93% of fir was killed in the softwood forest, but mortality was only 52% in the hardwood-softwood forest. For spruce, the mortality values in the softwood type and in the hardwood-softwood type were 32% and 16%, respectively. However, the relationship between the proportion of hardwood and the mortality of fir and spruce is slightly more complicated than that, and tended to show some irregular patterns. When this hypothesis was tested separately for the remaining towns, it was often found that the factor which showed statistical significance for the whole body of data did not appear important in some of the individual towns (Table 5). In other words, while certain generalizations can be made, there is still much unexplained variation in mortality.

The hypothesis that the tree mortality is related to the proportion of fir basal area among the primary host species in a sample plot was also examined. The results are shown separately for the softwood type (Table 6) and for

**Table 5.** Tree mortality in relation to site characteristics and species composition.

| Source of variation | Entire Park | Town | | | | | |
|---|---|---|---|---|---|---|---|
| | | T3R10 | T3R9 | T4R10 | T4R9 | T5R10 | T5R9 |
| *Fir mortality* | | | | | | | |
| proportion of nonhosts | *** | ns | ns | *** | ns | ** | ns |
| slope inclination | ns | ns | ns | *** | ns | ns | ns |
| position on slope | ns | ns | ns | ns | ns | ns | ns |
| aspect of slope | ** | * | ns | ns | ns | ** | ns |
| altitude | ns | ns | ns | ns | ns | ns | ns |
| *Spruce mortality* | | | | | | | |
| proportion of nonhosts | *** | ns | ns | *** | ns | ns | ns |
| slope inclination | ns | | ns | ** | ns | ns | ns |
| position on slope | * | ns | ns | ns | ** | ns | ns |
| aspect of slope | ns | ns | ns | ns | ns | ns | ns |
| altitude | *** | *** | *** | * | ** | | [1] |
| *Combined fir-spruce mortality* | | | | | | | |
| proportion of nonhosts | *** | ns | ns | * | ns | * | ns |
| slope inclination | ns | ns | ns | * | ns | ns | ns |
| position on slope | * | ns | ns | * | * | ns | ns |
| aspect of slope | ns | ns | ns | ns | ns | ns | ns |
| altitude | *** | *** | *** | * | ** | | |
| Sample size | 402 | 88 | 82 | 107 | 29 | 90 | 6 |

[1] The samples did not contain high altitude plots, and the comparison could not be made.

**Table 6.** Tree mortality in relation to proportion of fir basal area in softwood forest type.

| | Entire Park | | | | Town T4R10 | | | |
|---|---|---|---|---|---|---|---|---|
| Proportion of Fir by Basal Area | Mean Balsam Fir Mortality (%) | Mean Red-Black Spruce Mortality (%) | Combined Fir-Spruce Mortality (%) | Sample Size | Mean Balsam Fir Mortality (%) | Mean Red-Black Spruce Mortality (%) | Combined Fir-Spruce Mortality (%) | Sample Size |
| more than 50% | 94 | 36 a | 71 | 14 | 98 | 52 a | 81 a | 6 |
| 30% - 50% | 93 | 45 ab | 62 a | 16 | 96 | 57 a | 71 ab | 8 |
| 10% - 30% | 92 | 38 ab | 47 b | 43 | 98 | 46 a | 55 b | 19 |
| less than 10% | 96 | 23 b | 27 c | 28 | 100 | 19 b | 23 c | 12 |
| Chi-square value | 4.99 | 19.88 | 33.31 | | 7.23 | 17.23 | 18.78 | |
| Significance | ns | ** | *** | | ns | *** | *** | |

the softwood-hardwood type (Table 7) forests. In general, spruce was killed much less frequently when fir was the minor component of the stands, but extensively in fir-dominated forests ($p<0.05$, Scheffe's test). On the other hand, fir mortality was so nearly 100% that it was unrelated to the abundance of fir. Both the softwood forest and the softwood-hardwood forest showed these patterns at the entire Park level, and the effect of fir proportion on the mortality of spruce was highly significant ($p<0.01$).

In T4R10, mortality patterns were somewhat different from the Park mean. The spruce mortality of softwood forests significantly differed ($p<0.001$) among plots with varying proportions of fir basal area; the higher the fir proportion, the greater the spruce mortality ($p<0.05$, Scheffe's test). However, this was not the case ($p=0.13$) in the softwood-hardwood forests. The irregularity of spruce mortality patterns as affected by the fir proportion was evident at the town level. Some towns showed no significant ($0.94>p>0.13$) influence of proportion of fir to the spruce mortality (Table A6).

The combined mortality of spruce and fir, on the other hand, was related to the proportion of fir ($p<0.01$). This pattern is, however, a result of the non-uniform distribution of fir and spruce among the categories compared and of the difference of mortality between them. Nearly all fir trees were dead in all plots, which contrasted to 20% to 45% mortality of spruce. Therefore, if there was more fir in a plot, the combined mortality of fir and spruce would become greater.

## Comparison of Mortality by Topographical Condition of Sites

Five topographic factors were considered in relation to tree mortality: slope inclination, position on slope, aspect, altitude, and town. Among them, altitude was the only variable that was found to be related to tree mortality consistently; there were more dead spruce trees in the higher elevation zone than in the lower zone. Figure 4 shows the relative frequency distribution of sample plots in each mortality class, using the pooled data for the entire Park. The distribution is presented separately for fir and spruce, and for the two elevation zones: below 600 meters, and between 600 m and 870 m. Negative skewness of the distribution was found in fir in both elevation zones because the mortality was so uniformly high. Table 8 shows that those two categories of fir mortality are not significantly different ($p>0.46$). On average, nearly 80% of fir basal area was lost during the budworm outbreak regardless of the altitude of the site.

The relative frequency curve of spruce mortality, on the other hand, was positively skewed in the lower elevation zone (Figure 4). Mean mortality was 22%. In the higher elevation zone, however, the pattern appeared to be different. The skewness was small (-0.08) and the mean mortality became greater (41%). The difference of mean mortality between the elevation zones is highly significant ($p<0.001$, Ryan-Einot-Gabriel-Welsch Multiple F test, Table 8).

**Table 7.** Tree mortality in relation to proportion of fir basal area in softwood-hardwood forest type.

| | Entire Park | | | | Town T4R10 | | | |
|---|---|---|---|---|---|---|---|---|
| Proportion of Fir by Basal Area | Mean Balsam Fir Mortality (%) | Mean Red-Black Spruce Mortality (%) | Combined Fir-Spruce Mortality (%) | Sample Size | Mean Balsam Fir Mortality (%) | Mean Red-Black Spruce Mortality (%) | Combined Fir-Spruce Mortality (%) | Sample Size |
| more than 50% | 86 | 32 a | 68 a | 92 | 100 | 45 | 77 a | 3 |
| 30% - 50% | 84 | 20 ab | 43 b | 58 | 94 | 22 | 48 b | 23 |
| 10% - 30% | 86 | 16 b | 28 c | 40 | 91 | 21 | 34 b | 9 |
| less than 10% | 67 | 17 b | 19 c | 13 | — | — | — | 0 |
| Chi-square value | 2.02 | 17.00 | 83.17 | | 3.90 | 4.05 | 11.60 | |
| Significance | ns | *** | *** | | ns | ns | ** | |

The relationship of tree mortality to elevation in T4R10 was similar to the entire Park (Table 8). Furthermore, all towns appeared to hold the same pattern (Table 5). Therefore, a hypothesis that percentage mortality of spruce during this budworm outbreak is related to and increases with altitude is strongly supported.

At the entire Park level, none of the tree mortality data was related to slope inclination ($0.46 > p > 0.17$; Table 9). However, a significant difference was found in T4R10 in all cases that were compared ($p < 0.05$). Fir mortality was greater on gradual slopes than on steeper ones ($p < 0.05$, Ryan-Einot-Gabriel-Welsch Multiple F test). Although the difference of the mean spruce mortality among the slope categories was not large enough for a significant difference ($p < 0.05$) to be detected, the tendency of greater mortality associated with less steep slopes was also apparent. The relationship between mortality and slope inclination was, however, not consistently found in other towns (Table 5).

Table 10 shows that, at the entire Park level, spruce mortality was different ($p < 0.05$) among positions on slope. There was tendency for greater mortality

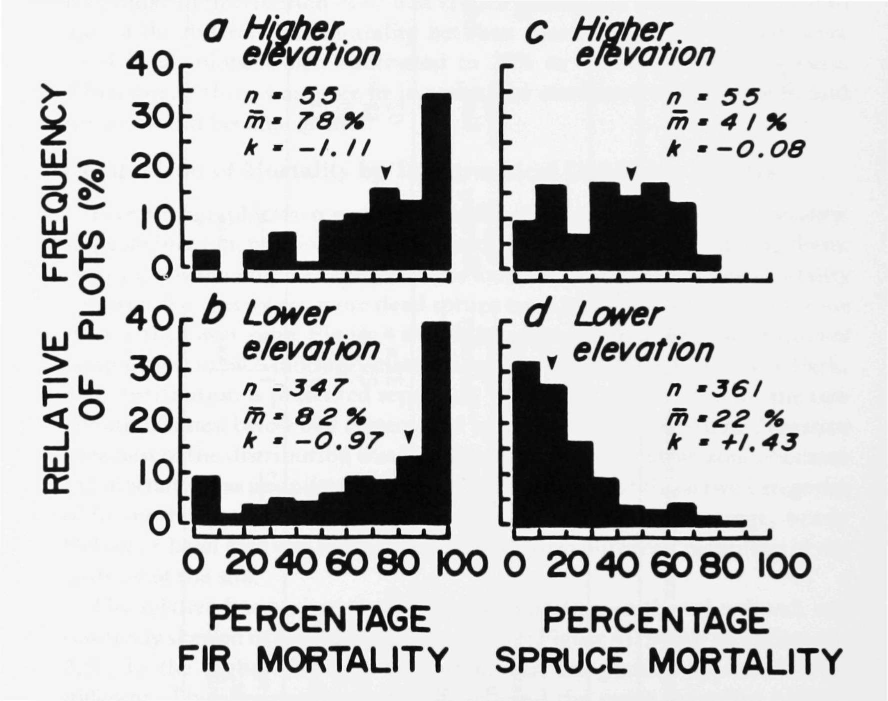

FIG. 4. Relative frequency distribution of percentage mortality in fir (a and b) and in spruce (c and d) for plots in two elevation zones.

**Table 8.** Tree mortality in relation to elevation.

| | Entire Park | | | | Town T4R10 | | | |
|---|---|---|---|---|---|---|---|---|
| Elevation Zone | Mean Balsam Fir Mortality (%) | Mean Red-Black Spruce Mortality (%) | Combined Fir-Spruce Mortality (%) | Sample Size | Mean Balsam Fir Mortality (%) | Mean Red-Black Spruce Mortality (%) | Combined Fir-Spruce Mortality (%) | Sample Size |
| below 600 m | 82 | 22 b | 44 b | 347 | 90 | 32 b | 53 b | 101 |
| between 600 m and 870 m | 78 | 41 a | 64 a | 55 | 95 | 51 a | 80 a | 6 |
| Chi-square value | 0.52 | 33.03 | 33.12 | | 0.02 | 5.49 | 8.01 | |
| Significance | ns | *** | *** | | ns | * | ** | |

**Table 9.** Tree mortality in relation to slope inclination. The result of unplanned comparisons among the means is also indicated when tree mortality is significantly different among the categories of slope inclination. The same letter represents that the mean values are not significantly different at the 5% level. Ryan-Einot-Gabriel-Welsch Multiple F test (SAS, Institute, Inc. 1982) was used. This test failed to detect differences in some cases.

| | Entire Park | | | | Town T4R10 | | | |
|---|---|---|---|---|---|---|---|---|
| Slope Inclination | Mean Balsam Fir Mortality (%) | Mean Red-Black Spruce Mortality (%) | Combined Fir-Spruce Mortality (%) | Sample Size | Mean Balsam Fir Mortality (%) | Mean Red-Black Spruce Mortality (%) | Combined Fir-Spruce Mortality (%) | Sample Size |
| flat | 87 | 24 | 45 | 91 | 98 a | 33 a | 52 a | 36 |
| less than 10 deg, but not flat | 80 | 24 | 48 | 220 | 92 ab | 41 a | 64 a | 48 |
| between 10 deg and 15 deg | 78 | 27 | 44 | 69 | 58 c | 15 | 36 a | 19 |
| between 15 deg and 30 deg | 70 | 27 | 36 | 15 | 66 bc | 13 a | 28 a | 2 |
| greater than 30 deg | 93 | 58 | 76 | 3 | - | | | 0 |
| Chi-square value | 3.57 | 5.22 | 6.38 | | 32.31 | 13.28 | 9.27 | |
| Significance | ns | ns | ns | | *** | ** | * | |

**Table 10.** Tree mortality in relation to position on slope.

| | Entire Park | | | | Town T4R10 | | | |
|---|---|---|---|---|---|---|---|---|
| Position on Slope | Mean Balsam Fir Mortality (%) | Mean Red-Black Spruce Mortality (%) | Combined Fir-Spruce Mortality (%) | Sample Size | Mean Balsam Fir Mortality (%) | Mean Red-Black Spruce Mortality (%) | Combined Fir-Spruce Mortality (%) | Sample Size |
| bottomland | 79 | 21 a | 41 a | 29 | 95 | 25 | 45 a | 10 |
| concave lower slope or somewhat poorly drained flat area | 82 | 20 a | 40 a | 87 | 94 | 24 | 41 a | 29 |
| midslope or better drained flat area | 81 | 24 a | 48 a | 215 | 89 | 37 | 62 a | 48 |
| convex upper slope | 78 | 36 a | 52 a | 63 | 79 | 38 | 59 a | 15 |
| on top of hill or ridge | 96 | 45 a | 66 a | 4 | 93 | 57 | 69 a | 3 |
| Chi-square value | 2.75 | 11.50 | 13.73 | | 5.67 | 6.25 | 14.35 | |
| Significance | ns | * | * | | ns | ns | * | |

at higher positions on slopes. On the other hand, this relationship broke down at the town level (Table 10 and Table 5). Fir mortality was consistently unrelated ($0.73>p>0.33$) to the position on slope at all levels (Table 10 and Table 5).

The relationship between tree mortality and aspect of slope is shown in Table 11. The pooled data for the entire Park indicated a significant difference ($p<0.01$) in fir mortality among aspects. The greater mortality tended to be associated with southern slopes ($p<0.05$, Ryan-Einot-Gabriel-Welsch Multiple F test). This association broke down at the town level (Table 11 and Table 5). On the other hand, spruce mortality was consistently unrelated ($0.68>p>0.14$) to the aspect of slope (Table 11 and Table 5).

There was a significant difference ($p<0.001$) in tree mortality among towns (Table 12). Two towns, T4R9 and T5R9, had less mortality of fir and of spruce than other towns.

Possible associations of tree mortality and topographical factors were also examined separately for each elevation zone (Tables A7, A8, and A9). An additional relationship between tree mortality and aspect of slope was found. In the lower elevation zone, percentage mortality of spruce was related to aspect ($p<0.05$). Northern slopes clearly showed smaller mortality than southern ($p<0.05$, Ryan-Einot-Gabriel-Welsch Multiple F test). A similar mortality pattern was found in fir in the higher elevation zone.

In summary, we observed the following eight patterns of tree mortality. The first two were found universally, or nearly so; the rest of the patterns were not consistently observed in all towns:

(1) higher percentage mortality in fir than in spruce;
(2) higher percentage mortality of spruce in the higher elevation zone than in the lower;
(3) lower percentage mortality of fir and of spruce with increasing proportion of nonhost species in a stand;
(4) higher percentage mortality of spruce with increasing proportion of fir in primary host species;
(5) in the lower elevation zone, higher percentage mortality of spruce on southern facing slopes than on northern facing slopes;
(6) higher percentage mortality of fir on southern facing slopes than on northern facing slopes especially in the higher elevations;
(7) higher spruce mortality at higher positions on slopes;
(8) in T4R10, higher percentage mortality of fir and of spruce on flatter sites than on steeper ones.

Table 11. Tree mortality in relation to aspect of slope.

| | Entire Park | | | | Town T4R10 | | | |
|---|---|---|---|---|---|---|---|---|
| Aspect of Slope | Mean Balsam Fir Mortality (%) | Mean Red-Black Spruce Mortality (%) | Combined Fir-Spruce Mortality (%) | Sample Size | Mean Balsam Fir Mortality (%) | Mean Red-Black Spruce Mortality (%) | Combined Fir-Spruce Mortality (%) | Sample Size |
| SE | 91 a | 30 | 54 | 29 | 97 | 40 | 63 | 7 |
| S | 83 abc | 29 | 51 | 55 | 92 | 36 | 59 | 11 |
| SW | 84 abc | 28 | 46 | 39 | 94 | 36 | 62 | 11 |
| W | 82 abc | 23 | 45 | 54 | 78 | 28 | 51 | 18 |
| NW | 74 bc | 25 | 47 | 45 | 87 | 26 | 52 | 9 |
| N | 76 abc | 19 | 39 | 49 | 86 | 25 | 52 | 13 |
| NE | 70 c | 21 | 41 | 32 | 74 | 36 | 59 | 6 |
| E | 75 abc | 26 | 47 | 49 | 99 | 41 | 50 | 5 |
| Flat Area | 88 ab | 22 | 43 | 40 | 97 | 30 | 47 | 16 |
| Chi-square value | 22.65 | 11.84 | 7.55 | | 12.65 | 8.58 | 3.86 | |
| Significance | ** | ns | ns | | ns | ns | ns | |

**Table 12.** Tree mortality in relation to region of the Park.

| Town | Mean Balsam Fir Mortality (%) | Mean Red-Black Spruce Mortality (%) | Combined Fir-Spruce Mortality (%) | Sample Size |
|---|---|---|---|---|
| T3R10 | 86 a | 28 a | 42 ab | 88 |
| T3R9 | 77 ab | 22 ab | 49 a | 82 |
| T4R10 | 91 a | 34 a | 55 a | 107 |
| T4R9 | 54 bc | 20 ab | 26 bc | 29 |
| T5R10 | 76 ab | 18 ab | 47 a | 90 |
| T5R9 | 35 c | 5 b | 12 c | 6 |
| Chi-square value | 55.62 | 36.72 | 46.21 | |
| Significance | *** | *** | *** | |

# DIFFICULTIES IN PREDICTING TREE MORTALITY FROM STAND CHARACTERISTICS AND TOPOGRAPHIC VARIABLES

An attempt was made to find linear models that could be used to predict tree mortality from stand characteristics and site variables which can be measured relatively easily. Percentage mortality of fir and of spruce was related to the 22 variables that were measured in more than 400 sample plots. Combined mortality of fir and spruce was also analyzed in the same manner. Three major classes of variables were used as regressors. The first group was the basal area, and its proportions of tree species and of host types in a sample plot. Second was the stem volume and its proportions in a plot. The third class was the variables that represent the topographic features of the site. The variables that were included in the multiple regression are shown in Table A10. The tree mortality data were analyzed in three groups: 1) pooled data for the entire Park, 2) by two elevation zones (below 600 m and between 600 m and 870 m), and 3) by towns.

Better models were selected from every possible linear model by two methods: the stepwise method and the maximum R-squared improvement technique. The stepwise method begins with no variables in the model, and adds a new regressor, one by one, that gives the greatest F statistic, which is not less than 0.5. The maximum R-squared improvement technique finds the model which gives the highest value of the coefficient of determihation for a given number of regressors (SAS Institute 1982).

After the better models were selected by the stepwise method and the maximum R-squared improvement technique, we further screened them according to our own rules:

(1) coefficient of a regressor has to be significantly different from zero at the 5% level, if there is reason, a priori, to believe that an independent variable affects tree mortality;

(2) coefficient of a regressor has to be significantly different from zero at the 1% level, if there is no reason, a priori, to expect that an independent variable affects tree mortality;

(3) the variance ratio for a model has to be significant at the 5% level;

(4) the coefficient of determination has to be greater than or equal to 0.3;

(5) sample size (number of 0.25 ha sample plots) is at least 25.

Fifty-five models remained in the total after this screening. Then, a model which gave the highest coefficient of determination was chosen in each group that was analyzed: entire Park, by elevation zone, and by town. The number of models (the "best" models) was reduced to 17. We did not find any model that satisfied our criteria in some groups.

The linear model which gave the greatest coefficient of determination (0.71) was for combined fir and spruce mortality in T4R10. Three regressors were included: total basal area of spruce, percentage of fir basal area in a plot, and sum of secondary host basal area (mainly white pine). For fir, the highest coefficient of determination (0.66) was found also in T4R10. The regressors included five variables: percentage of fir basal area among the primary hosts, percentage of spruce basal area among all trees, percentage of host species basal area among all trees, slope inclination, and position of a stand along a complex moisture gradient which was an additional variable used in the analysis. The location of a stand on this gradient was calculated by the Bray-Curtis ordination (Bray and Curtis 1957). Two end-points (stands) that were required for the calculation were an upland hardwood stand (plot 100, position on the gradient was set as unity) and a black spruce bog (plot 386, position on the gradient being zero). This ordination technique places each stand on an axis which represents the similarity (or dissimilarity) of a given stand to the two predetermined stands. According to our choice of end-points, this axis may approximate the drainage of the site.

The highest coefficient of determination (0.54) for spruce mortality was found in T4R9. Two independent variables, percentage of fir basal area among the primary hosts and slope inclination, were included. Among the 17 "best" models, the values of the coefficient of determination varied between 0.32 and 0.71, but a majority of them were between 0.4 and 0.6. In fact, at the entire Park level, the largest values of the coefficient were 0.40 and 0.58 for the models of fir mortality and of combined mortality of fir and spruce, respectively. We could not find models for spruce mortality that met our standard. MacLean (1980) showed, in his review of studies on tree mortality during spruce budworm epidemics, that the greatest value of the coefficient of determination of 0.56 was found by Batzer (1969). Our result is similar to Batzer's. The "best" linear models for the Park and for T4R10 are summarized in Table A10.

The multiple regression approach was of limited value. In general, about 40% to 60% of variation in tree mortality still remained unexplained (Table A10), even if we used topographic variables in addition to stand characteristics. MacLean (1980) suggested that the predictability of such models could be improved if annual defoliation level was recorded. We would like to point out, however, a problem of using multiple regression in studying tree mortality patterns during spruce budworm outbreaks. We indicated earlier that the percentage mortality data did not follow a normal distribution even after the arcsine transformation was applied. It is assumed in multiple regression that the dependent variable is independently and normally distributed (Sokal and Rohlf 1980). This assumption was violated in our data. The situation is especially serious when the mean tree mortality approaches either 100% or 0%, since the mortality distribution curves will be highly skewed in those cases, and the departure from normality becomes greatest. Our data fall in just such circumstances (See Figures 2, 3, and 4).

## DISCUSSION

### On the Irregular Tree Mortality Patterns

We have shown that there are two patterns that were consistently found in the Park: 1) fir mortality was greater than spruce mortality, and 2) spruce mortality was always greater in the higher elevation zone (between 600 m and 870 m) than in the lower (below 600 m). Beyond these points, the suggested mortality patterns held true in some cases, but not in others.

When data from the entire Park were pooled, both fir mortality and spruce mortality were related to the proportion of nonhost species in a stand (Table 4). Also, the higher the proportion of fir, the greater was the spruce mortality (Tables 6 and 7). Topographical factors also appeared to be related to tree mortality patterns at the entire Park level; spruce mortality seemed to be smaller on lowlands than on upper slopes (Table 10). Fir mortality was related to aspect of slope; it was greater on southern facing slopes than on northern slopes (Table 11). However, those relationships were not evident when each town was analyzed separately.

These apparently irregular patterns of tree mortality will be examined more closely, especially in two cases: 1) tree mortality in relation to proportion of hardwoods in the stand, and 2) tree mortality in relation to proportion of fir in the stand.

Figure 5 shows the relationship between the mean mortality of spruce (or fir) in a given town and the probability that the Chi-square statistic of the non-parametric test becomes either the calculated value or greater when the spruce (or fir) mortality is related to the proportion of hardwoods in a stand. No relationship between the spruce (or fir) mortality and the hardwood proportion is the null hypothesis being tested. In Figure 6, a transformed scale was used for this probability for ease of graphical presentation. The larger values of the transformed probability, -log p, suggest that an association of hardwood proportion and spruce (or fir) mortality is probably present. The results of two tests, Kruskal-Wallis test and Brown-Mood test, are shown.

Spruce mortality was related to the hardwood proportion only when the mean spruce mortality in the area was relatively high. The presence of hardwood cover did not affect spruce mortality when the mean mortality of spruce was smaller than ca. 30% (Figure 5a). A similar relationship existed also in fir mortality. The hardwoods seemed to affect the death of fir only when the mean fir mortality exceeded ca. 75% (Figure 5b).

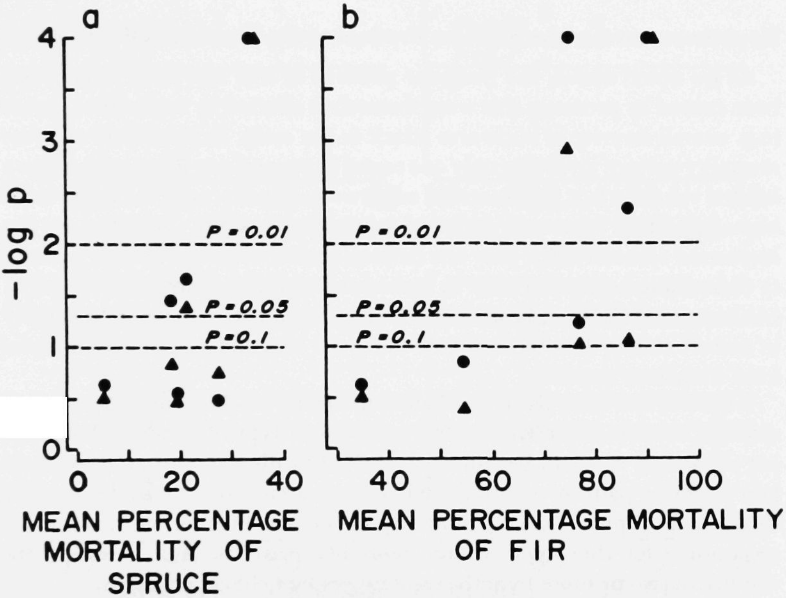

FIG. 5. Relationship between mean percentage mortality of spruce and of fir for plots in a given town and probability level of non-parametric one-way analyses testing the effect of proportion of nonhost species in a plot on spruce (a) and fir (b) mortality. Results of Kruskal-Wallis test (●) and Brown-Mood test (▲) are shown for each town. A transformed scale (− log p) of the probability level is used in the ordinate for ease of graphical presentation.

The mechanisms of these peculiar patterns are unknown. However, it might be related to the variable effects of hardwood cover on tree mortality, depending on the size of the affected trees. Turner (1952) noted that the fir trees of different crown classes showed different relationships between their mortality and the proportion of hardwoods in stands: no apparent effect of hardwoods on codominants, but either a positive or negative effect on the lower crown classes.

The relationship between the probability level and the mean spruce (or fir) mortality in the area is shown in Figure 6, for the null hypothesis: no association between spruce (or fir) mortality and the fir proportion among the primary hosts. In the softwood type, spruce mortality did not seem to be strongly related to the proportion of fir unless the overall spruce mortality in the area exceeded 40% (Figure 6a). The pattern was similar in fir, except that the effect of fir proportion became significant at ca. 90% fir mortality (Figure 6c). The mechanisms that caused those patterns are, again, unclear. The associations between the mortality of fir and of spruce and fir proportion were also irregular in softwood-hardwood forests (Figure 6b, d). The additional influence of hardwood cover might have created the complex relationships.

## Hypotheses on the Mechanisms Producing the Tree Mortality Patterns

As we noted above, the irregular patterns of tree mortality might have been caused by processes that were themselves affected by some other factors (e.g. overall severity of budworm attack in the area). Explanations of a tree mortality pattern involving only one causal factor and one effect seem to have limited value. In fact, we identified only two such patterns in the Park. If the higher elevation forests are excluded from the discussion, since they are less important commercially, only one definite pattern remains: greater mortality of fir than of spruce. This is in agreement with MacLean's (1980) review. (Although MacLean indicated another consistent pattern, greater mortality in mature stands than in immature ones, our data did not contain samples from immature stands.)

If the tree mortality patterns are determined by a web of causal factors, or if different mechanisms could operate on the same type of stands under different situations, it would become extremely difficult to understand how certain mortality patterns are produced. The necessary steps for understanding these complex processes are 1) identifying the possible mechanisms that are responsible for the observed tree mortality patterns, and 2) testing the validity of two or more hypotheses of causes by field experiments.

We summarize, in the following paragraphs, the hypotheses that have been suggested as causes of tree mortality patterns during an uncontrolled spruce budworm outbreak. Some hypotheses have been proposed as the mechanisms that explain specifically the susceptibility of trees to budworm attack, not the vulnerability to damage. However, we treat these collectively, since both might affect the likelihood of tree death during budworm outbreaks. A representative title is put on each hypothesis, so that it can be referred to easily in later sections.

*Phenology Hypothesis*

Synchrony of tree- and insect-phenology may determine tree mortality. Individual trees which break bud early enough in the spring to supply sufficient food for developing budworm larvae are presumed likely to succumb. This is primarily because the larvae develop and survive better with

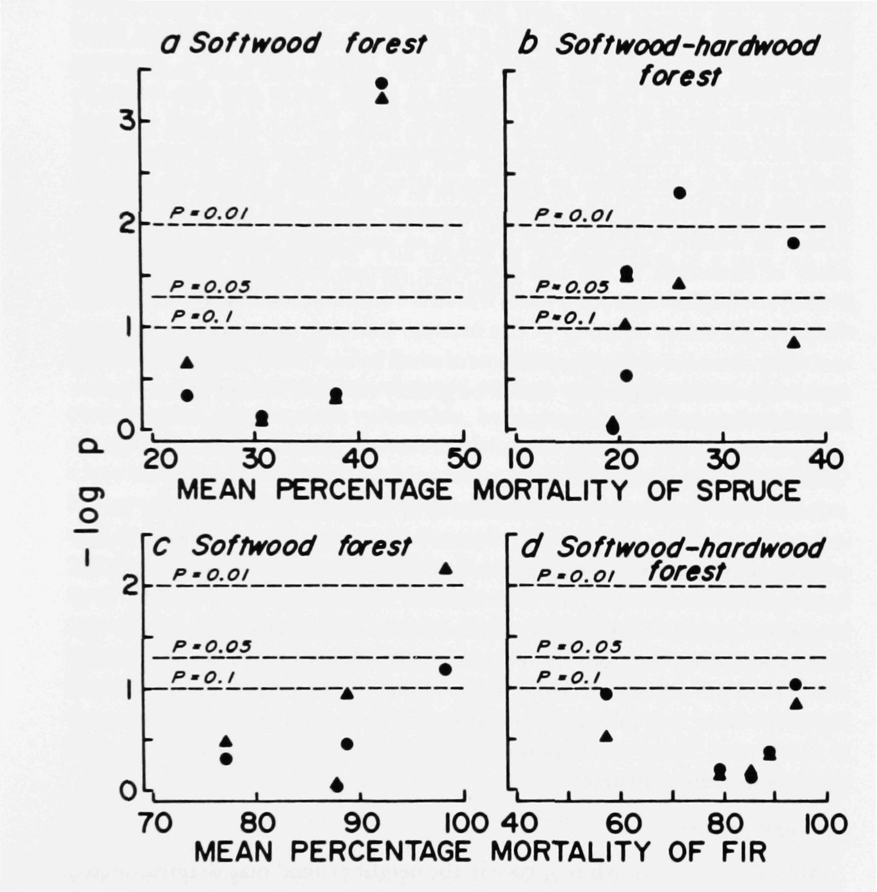

FIG. 6. Relationship between mean percentage mortality of spruce and of fir for plots in a given town and probability level of non-parametric one-way analyses testing the effect of fir proportion in primary host basal area on spruce (a and b) and fir (c and d) mortality. Results are presented separately for two forest types, softwood forest and softwood-hardwood forest.

current year's needles than old ones. It explains variation of tree mortality not only among host species, but also among individuals of the same species. Among host species, the higher mortality of early flushing fir and relative immunity of late flushing black spruce can be well explained. This hypothesis was proposed by Swaine and Craighead (1924) and reiterated by others (Blais 1957, Greenbank 1963b, Seymour 1980).

### *Crown Exposure Hypothesis*

It has been suggested that height and exposure of the crown to the sun determine the tree mortality. The most favorable oviposition site of budworm moths is near the tops of tall, well exposed trees, which also provide more favorable microclimates for survival of large larvae (Mott 1963, Seymour 1980). Budworm larvae are also known to prefer warm and dry microclimates (Wellington et al. 1950, Greenbank 1956, 1963c); tall, well exposed trees provide just such conditions. Overmature fir forests, which were recognized as highly susceptible to budworm attack by Balch (1946) are another example that create such microenvironments. Shepherd (1959) has demonstrated in western Canada, that there is an association between the occurrence of outbreaks in the two-year-cycle spruce budworm (*Choristoneura biennis*) and high evaporation rates, which are accompanied by warm and dry climates. Excessive opening of the canopy, however, may reduce the tree mortality, because of the dispersal loss of small larvae (Mott 1963). According to this hypothesis, mortality would be greatly reduced in host species growing under hardwood overstories.

### *Hardwood Shield Hypothesis*

It has been postulated that abundance of nonhost trees, ordinarily hardwoods, may reduce mortality of host trees. Mortality of small larvae associated with inter-tree dispersal is greater when nonhost species are present. This hypothesis was advocated by Mott (1963) and by Seymour (1980). It is important to note that the Crown Exposure Hypothesis differs from the Hardwood Shield Hypothesis. Presence of hardwoods in the neighborhood rather than the physical overtopping of conifers by a hardwood canopy is the key in the latter, but presence of overtopping hardwood overstory is essential in the former. These two hypotheses are not mutually exclusive and may or may not operate concurrently.

### *Epicenter Hypothesis*

Abundance of fir or white spruce in the neighborhood may determine tree mortality. This hypothesis works in two ways: 1) in stands of primarily fir, red spruce, and black spruce, spruce mortality may be determined by the abundance of fir in a stand. Increase of budworm density is enhanced by the presence of fir, because it is a more favorable host, and the larvae migrate to nearby spruce trees (Greenbank 1963c, Mott 1980), 2) in stands primarily of fir and white spruce, fir mortality may be determined by the abundance of white spruce in a stand. White spruce is more resistant to excessive defoliation because of its rapid shoot growth. Defoliated stands of white spruce harbor budworm populations which are otherwise dispersed out to find a better oviposition site (Greenbank 1963c).

### *Hybridization Hypothesis*

Mortality of the red-black spruce complex may be determined by the proportions of black or red genes in the trees. Red spruce may be more vulnerable than black spruce (which is itself an hypothesis), and a hybrid of the two may have intermediate mortality. It has been shown by Manley and Fowler (1969) that the extent of defoliation by budworm larvae is correlated with the degree of introgression in the red-black spruce complex; the closer an individual tree approximates red spruce, the greater the severity of defoliation. If spring phenology of hybrid spruce is intermediate of the two spruce species, this hypothesis could be thought of as being synonymous with the Phenology Hypothesis. The degree of hybridization of a tree can be estimated by Manley's (1971) hybrid index.

### *Energy Budget Hypothesis*

A tree with a lower level of stored energy or a higher level of energy consumption may be more vulnerable, because of the greater probability of energy exhaustion. This hypothesis explains two patterns of tree mortality: 1) a tree with large root biomass, thus greater level of stored carbohydrate, may be less vulnerable than the one with smaller root biomass. Therefore, trees on well drained sites, with deep roots, are probably less vulnerable than those on poorly drained sites (Seymour 1980); 2) greater exposure of a tree to the sun may make it more vulnerable, because of its higher rate of maintenance respiration. Abundance of fir, which tends to die first during a budworm infestation, may leave the residual trees more exposed, and more vulnerable (Seymour 1980), providing a positive feedback mechanism.

### *Foliar Nutrition Hypothesis*

The concentrations of nutrient elements in foliage of a host tree might determine budworm-caused tree mortality. Higher nutrient levels in foliage may enhance the build-up of budworm populations, which cause extensive defoliation and tree death. Nitrogen might be an important element. White (1969, 1974, 1976) suggested the role of foliar nitrogen level on the development of insect epidemics. He has repeatedly found good correlations between water status of the host plants, which may influence the foliar nitrogen level, and the increase of insect population densities. Potential importance of foliar amino-acids in the dynamics of spruce budworm was also proposed by Kimmins (1971).

However, the details of the importance of different nutrients and of the processes involved in determining budworm growth and survival are still unknown. Research in this direction was initiated only recently (Mattson et al. 1983, Montgomery and Czapowskyj 1984, Robinson et al. 1984).

### Expected Tree Mortality Patterns Under the Proposed Hypotheses

No single mechanism is likely to explain all of the mortality. However, it is useful to summarize what mortality patterns are expected to be found under each hypothesis.

Under the Phenology Hypothesis, mortality would be greater in fir than in spruce; the earlier the bud-break of a tree, the higher the mortality. Tree mortality will be lower on poorly drained sites, where the soil is wetter and cooler, than on well drained sites, where the soil dries and warms more quickly. Phenology of spruce budworm may be controlled by air temperature (Morris and Bennett 1967), but soil temperature might also be important in tree phenology (Hickin and Vittum 1976). This may create a discrepancy between insect- and bud-phenology on poorly drained sites, and may make the trees on poorly drained sites less vulnerable.

If the Crown Exposure Hypothesis is applied, we would expect to see either of two patterns: first, the taller and more exposed the tree crown, the higher the mortality, although the presence of excessively large crown gaps might reduce the tree mortality. Second, when a host tree is overtopped by hardwoods, mortality would be low. However, presence of non-overtopping hardwoods in the neighborhood would not affect the mortality of a host tree. The Hardwood Shield Hypothesis suggests the following pattern: mortality of a host tree is low when hardwood is abundant in the neighborhood. It is not important whether or not the hardwood is overtopping a host tree.

The Epicenter Hypothesis could cause two possible mortality patterns. First, spruce mortality would be higher when fir is more abundant in the neighborhood. Second, fir mortality would be higher when white spruce is more abundant in the neighborhood. If the Hybridization Hypothesis is accepted, we would expect that the closer the genotype of a hybrid is to red spruce, the higher the mortality. The Energy Budget Hypothesis offers three possible patterns. First, tree mortality would be lower on well drained sites than on poorly drained sites, because of the greater root biomass. Second, tree mortality would be higher in more open stands than in denser ones. Third, mortality of spruce is probably higher when fir is more abundant because of the large extent of crown gaps and resultant penetration of sunlight to the remaining trees after the death of fir. The maintenance respiration of spruce would be increased by the raised stem temperature.

The Foliar Nutrition Hypothesis suggests that tree mortality would be related to the site quality, especially the nutrient status. As a special case, effects of fertilization on budworm-caused damage might also be predicted. Since the level of foliar nutrients in a spruce-fir forest is expected to increase significantly after applying fertilizers (Mahendrappa and Salonius 1982), tree mortality might be accelerated.

### Interpretation of Observed Tree Mortality Patterns.

A review of the hypotheses on mechanisms that are causing tree mortality patterns during a budworm outbreak, presented at length, now allows us to discuss the possible mechanisms of the observed patterns with alternative explanations. We will show that all but one pattern could be explained by more than one hypothesis.

#### *Explanation of Observed Patterns*

Two patterns of tree mortality were observed consistently; higher mortality of fir than of spruce, and greater spruce mortality at the higher elevation zone than at the lower. The first pattern could be explained by the Phenology Hypothesis, because of the earlier bud break of fir than of spruce species (Swaine and Craighead 1924). This hypothesis is the only one that satisfactorily explains the difference in mortality between fir and spruce.

The role of staminate flowers in the dynamics of spruce budworm populations was once proposed; abundant pollen may enhance the larval survival and adult fecundity (Blais 1952), thus the difference in flowering condition among individuals and species may explain the variation of defoliation and tree mortality. However, this hypothesis was rejected by Greenbank (1963b) based on the careful observations in northwestern New Brunswick. The effect of pungenin, a feeding deterrent substance, was also suggested as a process for lower vulnerability of spruces (Strunz, et al. 1986). However, this hypothesis has not been well established.

Four mechanisms could explain the second pattern of tree mortality, the association between altitude and spruce mortality. They are the Epicenter Hypothesis, the Hybridization Hypothesis, the Foliar Nutrition Hypothesis, and the Soil Acidification Hypothesis. The fourth one considers a possible cause of tree mortality other than the spruce budworm. The Epicenter Hypothesis is possible, because there is a significantly higher percentage of fir basal area in the higher elevation zone (between 600 m and 870 m) than in the lower (below 600 m) ($p<0.001$, $n=346$ in the lower zone and $n=55$ in the higher). The Hybridization Hypothesis should be considered, because spruce trees at the well drained sites of higher altitude may be closer to pure red spruce than the ones in lower altitude. The Foliar Nutrition Hypothesis may be responsible, because the soil on moderately inclined mountain sides will invariably be better drained than the flat lowlands. Better drainage may make the foliar nitrogen level of spruce in the higher zone greater than in the lower zone (Gagnon 1964). It is worth noting that the consistent pattern of high spruce mortality at higher elevation zones was also reported in the

Green Mountains of Vermont (Siccama, et al. 1982) where spruce budworm outbreaks did not develop in the recent past. Acid precipitation might have an influence on tree vulnerability through soil acidification (Ulrich, et al. 1982). It is easy to visualize that a tree which has been weakened by acid precipitation is likely to die with little defoliation by the spruce budworm. Therefore, soil acidification is another possible factor creating greater tree mortality at higher altitudes.

Two mechanisms, the Crown Exposure Hypothesis and the Hardwood Shield Hypothesis, could be used to explain the association between a high proportion of nonhost species and low percentage mortality of fir and of spruce. When the proportion of hardwood species in a stand increases, it becomes more likely that the Hardwood Shield Hypothesis will operate. At the same time, the chance of a host tree being overtopped by a hardwood canopy increases, so the Crown Exposure Hypothesis is also possible.

There are five ways of explaining the higher spruce mortality with increasing fir proportion in a stand; Epicenter Hypothesis, Energy Budget Hypothesis, Phenology Hypothesis, Hybridization Hypothesis, and Foliar Nutrition Hypothesis. The first two hypotheses are directly related to the quantity of fir in a stand. The other hypotheses require an additional assumption: that the proportion of fir in a stand and the drainage of a site are correlated. Although a type of vegetation may not be determined by the site condition alone, there is evidence to support this assumption at least in some areas of the Park.

We estimated the site drainage in selected sample plots (plots 376 to 394). A list of site indicator species which was developed by Thorpe (1983) for the western part of the Park was used for estimating the drainage. Thorpe categorized the sites into several groups depending on their ecotypes by considering drainage condition, soil type, and vegetation, and the site indicator species (herb- and shrub-species) were listed under each category. We assigned weight to each indicator species; the smallest weight to the plants that occur in poorly drained sites, and the largest to the ones in well drained sites. A drainage index was calculated for each stand, by the weighted average ordination technique (Whittaker 1967). The index was defined as the weighted average of the relative frequencies of indicator species, which were recorded at ten sample points in each plot. Therefore, the greater the drainage index, the better the soil drainage. The proportion of fir basal area in a stand and the drainage index were positively correlated ($r=0.69$, $n=19$).

The Phenology Hypothesis may be the mechanism explaining greater mortality with increasing proportion of fir, if the bud bursting tends to be accelerated at better drained sites where fir is usually abundant. The Hybridization Hypothesis becomes plausible, if the genotype of a spruce tree approximates pure red spruce on well drained sites. The Foliar Nutrition

Hypothesis is related to soil drainage, and the association between the proportion of fir and spruce mortality may be explained directly.

Three hypotheses could explain, in the lower elevation zone (below 600 m), the higher spruce mortality on southern facing slopes than on northern slopes: Phenology Hypothesis, Energy Budget Hypothesis, and Foliar Nutrition Hypothesis. Phenological events of plants in the spring may occur earlier on south facing slopes than on north facing slopes, because of the warmer climate (Geiger 1965). Snow may remain on the ground until later on northern slopes, and bud break of spruce may be delayed sufficiently to reduce the feeding damage by the budworms (Phenology Hypothesis). Also, the warm climate of southern slopes could make the maintenance respiration of a spruce tree greater than on north slopes. Therefore, even if the extent of defoliation is held constant, spruce on a south slope may have higher probability of death (Energy Budget Hypothesis). Similarly, the soil moisture level may be lower on warm, south facing slopes than on cool, north facing slopes. This could make the concentration of foliar nitrogen or other nutrient elements greater on a south slope than on a north slope (Foliar Nutrition Hypothesis).

We also observed that higher mortality of fir occurred on south facing slopes than on north facing slopes. The same mechanisms that were proposed for explaining the variation of spruce mortality among aspects could be used; Phenology Hypothesis, Energy Budget Hypothesis, and Foliar Nutrition Hypothesis.

Three mechanisms could explain the greater spruce mortality on higher positions on slopes; Foliar Nutrition Hypothesis, Phenology Hypothesis, and Hybridization Hypothesis. Better drainage may be associated with a higher position on slope. Furthermore, the better the drainage, the higher the level of nitrogen (and other potentially important nutrients) in the foliage, and eventual tree mortality (Foliar Nutrition Hypothesis). Also, it may be warmer near the hill-top than in the lowlands, if the altitudinal difference of those sites is small. Therefore, the warmer climate of upper slopes may enhance bud development and may make a spruce tree more susceptible (Phenology Hypothesis). The higher spruce mortality at upper slopes could also be explained if there are more trees that approximate pure red spruce near the hill-top (Hybridization Hypothesis).

A highly significant relationship between slope inclination and the mortality of fir and of spruce was observed in T4R10 (Table 9). The greater tree mortality was associated with flatness of the site. There are two ways to explain this pattern: Crown Exposure Hypothesis and Hardwood Shield Hypothesis. In T4R10, there was a highly significant difference in the proportion of nonhost species among categories of slope inclination ($p<0.001$, $n=110$); the steeper the slope, the more nonhost species. Therefore, the higher tree mortality on flat areas could be a result of a smaller proportion of nonhost species at those sites (Crown Exposure Hypothesis and Hardwood Shield Hypothesis).

It is important to note that the opposite of this tree mortality pattern may be realized under the following mechanisms: Phenology Hypothesis, Hybridization Hypothesis, Energy Budget Hypopthesis, and Foliar Nutrition Hypothesis. We may suppose that there is an association between greater slope inclination and better drainage. Therefore, the higher tree mortality on a flat site could be translated as the greater mortality at a poorly drained site. All those hypotheses are counter-supportive of this pattern; poor drainage may be associated with cooler climate, thus later bud break, which tends to reduce budworm feeding (Phenology Hypothesis). Poor drainage may be related to the genetic proximity of spruce to pure black spruce, which is relatively immune to budworm damage (Hybridization Hypothesis). Maintenance respiration of a tree might be relatively small on poorly drained (thus cool) sites, which might make the tree death less probable (Energy Budget Hypothesis). Foliar nitrogen level might be lower at poorly drained sites than at well drained sites. Therefore, the tree mortality might be relatively small there (Foliar Nutrition Hypothesis). The tree mortality pattern that we found in T4R10 suggests that, at least in this town, abundance of nonhost species tended to be quite important in the outcome of mortality patterns.

### *Problems in Interpreting the Patterns*

In interpreting the observed tree mortality patterns, we have repeatedly referred to the possibility that the variation of one factor is associated with the change of another; those variables are not always independent of each other. For example, when the proportion of the nonhost species varies among sites, such variables as slope inclination, position on slope, drainage, and proportion of fir basal area, may also show directional change. Identification of true mechanisms becomes more difficult when independent variables are correlated. A tree mortality pattern may be caused by a factor X, but X may also cause Y to change, frequently but not consistently. If this is the case, it may appear to us that Y is causing the observed tree mortality pattern. An analysis of the mortality pattern may show that there is significant association between tree mortality and factor X, as well as between the mortality and factor Y. Therefore, analysis of pattern alone may not reveal the mechanisms which are truely responsible.

An example of dependency in variables and difficulty in interpreting the observed tree mortality patterns will be presented in the following. We took 19 sample plots (plots 376 to 394) in a relatively small area in the western part of town T4R10 (area A, see Figure A1). All plots were located on flat or slightly inclined slopes, all within about 1,600 m (one mile) of each other. Importance of nonhost species was very small in every stand; they were classified as softwood forest or softwood-hardwood forest. However, the proportion of fir basal area varied considerably. The relationship of tree mortality and six variables was analyzed; drainage index, percentage of fir basal area in primary hosts, percentage of fir basal area in a plot, percentage of nonhost species in a plot, fir basal area, and spruce basal area. The mortality of fir, spruce, and the combination of the two, were examined separately. The result is summarized in Table 13.

Two significant relationships were found in spruce mortality. First, percentage mortality differed depending on the drainage index. The linear regression of untransformed mortality data on drainage index appeared to be highly significant ($p<0.001$), and 88% of variation in spruce mortality was explained by this single variable (Figure 7). It should be noted that the $R^2$ value of 0.88 is far better than any of the values that we found in the multiple regression analysis in which the drainage index was not included.

Second, spruce mortality was related to the fir basal area ($p<0.01$). Now, is the quantity of fir in a stand causing the variation of spruce mortality, or is it drainage of a site that is causing the tree mortality pattern? We do not know. In fact, Figure 8 shows clearly that basal area of fir and the drainage index are indeed related.

Table 13 also shows the relationship between tree mortality and the variables that were measured in 14 sample plots located in a relatively small area near Kidney Pond, T3R10 (area B, Figure A1). Area B differed from area A in two ways; the proportion of nonhost species was generally greater, and the range of drainage was very small. Table 13 indicates that spruce mortality was not related to any of the variables ($p>0.3$). Drainage index could not be used as an independent variable, because of its small range in area B. The comparison of mortality patterns in areas A and B seems to suggest that it was drainage index, not the basal area of fir, that was important in determining the spruce mortality. However, we do not know which is the cause without a controlled experiment.

Fir mortality, on the other hand, was not related ($p>0.08$) to the variables that were analyzed. Almost all fir trees were dead in area A; if the fir mortality is plotted against an independent variable, the slope of the regression line will be zero regardless of the choice of a variable. The fir mortality in area B was generally small, and we were unable to find a relationship that was significant. This result supports the finding of Baskerville and MacLean (1979) that fir mortality is unrelated to the quantity of fir or its proportion in a plot (Baskerville and MacLean used tree density instead of basal area for calculating mortality).

Another problem that may arise in the interpretation of observed tree mortality patterns is the fact that the proposed hypotheses of the mechanisms are often not mutually exclusive. For example, both the Crown Exposure Hypothesis and Hardwood Shield Hypothesis are related to the quantity of

**Table 13.** Tree mortality in relation to several variables in area A and in area B. The Chi-square value and the significance (in parenthesis) are given for each comparison.

| | area A | | | | area B | | | |
|---|---|---|---|---|---|---|---|---|
| Independent Variable | Balsam Fir Mortality | Red-Black Spruce Mortality | Combined Fir-Spruce Mortality | Sample Size | Balsam Fir Mortality | Red-Black Spruce Mortality | Combined Fir-Spruce Mortality | Sample Size |
| Drainage Index | 2.92<br>(ns) | 12.91<br>(***) | 9.00<br>(**) | 19 | | [3] | | 14 |
| Percentage Balsam Fir Basal Area in Primary Hosts | 0.35<br>(ns) | 2.75<br>(ns) | 2.46<br>(ns) | 19 | 1.30<br>(ns) | 0.00<br>(ns) | 5.20<br>(*) | 14 |
| Percentage Balsam Fir Basal Area in Plot | 0.35<br>(ns) | 2.75<br>(ns) | 2.46<br>(ns) | 19 | 1.08<br>(ns) | 1.07<br>(ns) | 8.07<br>(**) | 14 |
| Percentage Nonhosts Basal Area in Plot | - | | | 19 | 0.21<br>(ns) | 0.00<br>(ns) | 2.39<br>(ns) | 14 |
| Balsam Fir Basal Area | 0.39<br>(ns) | 10.67<br>(**) | 5.95<br>(*) | 19 | 1.30<br>(ns) | 0.00<br>(ns) | 5.20<br>(*) | 14 |
| Red-black Spruce Basal Area | 0.00<br>(ns) | 0.62<br>(ns) | 0.00<br>(ns) | 19 | 0.29<br>(ns) | 0.11<br>(ns) | 2.60<br>(ns) | 14 |

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[1] The observed values of each variable were divided into two levels, higher and lower, so that each contains approximately equal number of samples. Then tree mortality of two groups were compared by Kruskal-Wallis test and Brown-Mood test The more conservative result of the two was presented.

[2] Location of area A and area B is shown in Figure A1.

[3] The range of a variable was too small and the comparison could not be made.

nonhost trees in a stand. Two mechanisms might work at the same time. Likewise, the Phenology Hypothesis, Hybridization Hypothesis, and Foliar Nutrition Hypothesis could all operate together to produce an observed mortality pattern. Therefore, the investigation of the causes of tree mortality may require study of dominance of each mechanism in developing a particular pattern.

The range of a certain mechanism in operation is also important. We may expect that some mechanisms could be responsible for producing a tree mortality pattern only within a certain range of the environmental factor. For example, we may predict the pattern along the gradient of soil drainage according to two processes: 1) tree mortality increases with increasing drainage (Foliar Nutrition Hypothesis), 2) tree mortality decreases with increas-

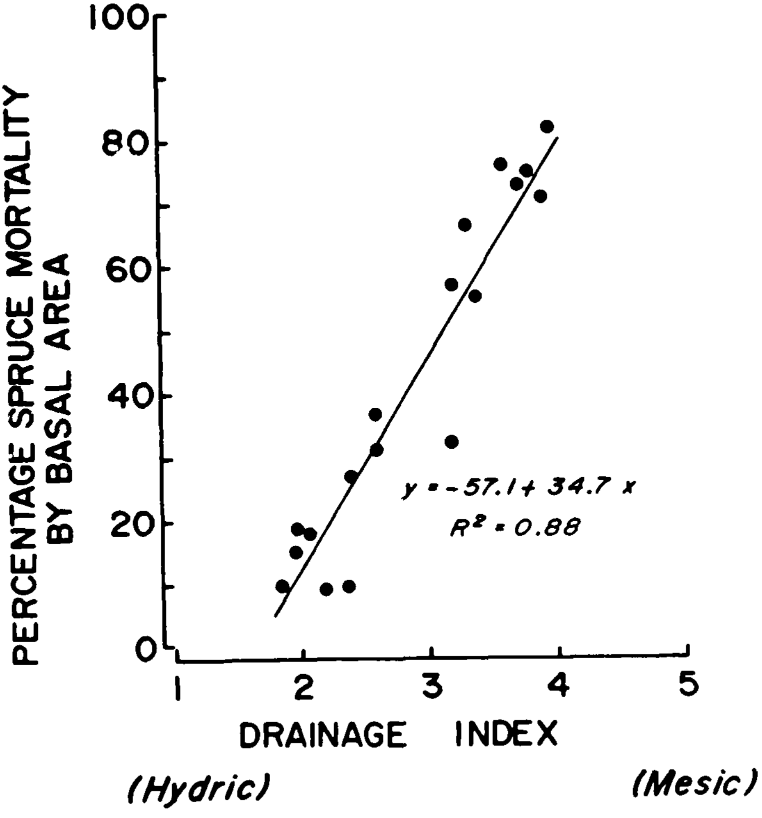

FIG. 7. Percentage mortality of spruce in area A in relation to the drainage index which was calculated by the weighted average ordination using Thorpe's site indicator species.

ing drainage, because proportion of nonhost trees increases accordingly (Crown Exposure Hypothesis or Hardwood Shield Hypothesis). We observed in the Park that both predictions could be correct. The first mechanism is probably responsible toward the wetter end of the drainage gradient, and the second toward the drier end. Therefore, it becomes important to determine the range within which a possible mechanism might operate.

One of the most important limitations is related to factors that operate on a scale much larger than the size of plots used. All variables of tree mortality and stand characteristics were measured in 0.25-ha quadrats. They do not reflect the factors that might be found outside the plots. Therefore, if tree mortality of a plot is affected by those outside factors, the mortality pattern

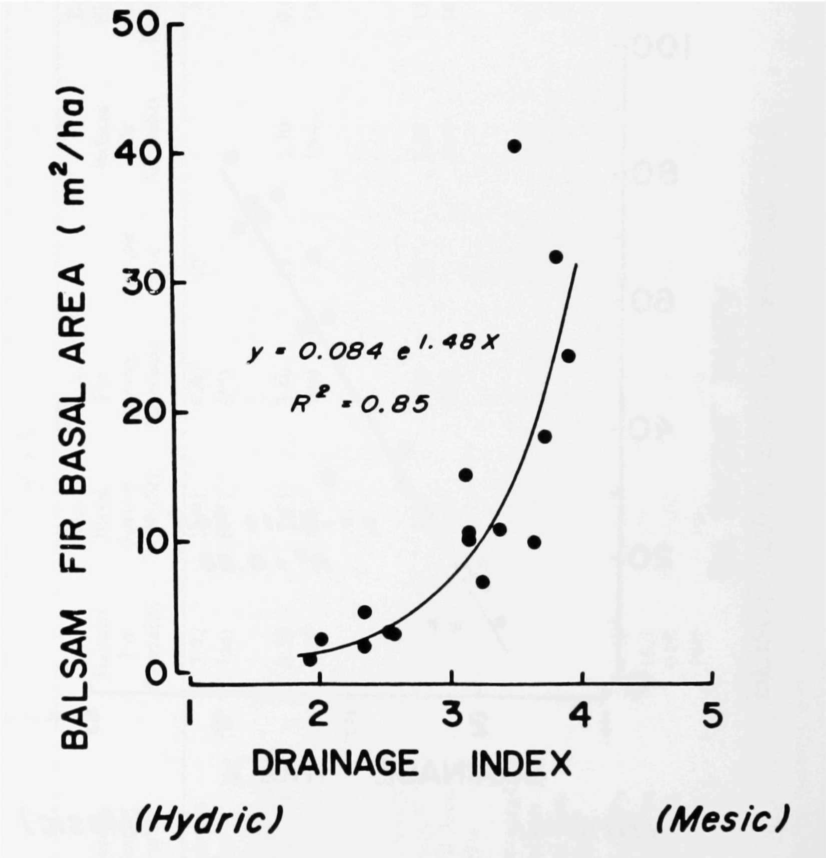

FIG. 8. Relationship between basal area of fir and the drainage index in area A.

could not be explained successfully. Mott (1963) showed that the involuntary dispersal of budworm larvae among stands is important in the development of an outbreak. Therefore, the spatial relationship of a stand to the heavy outbreak area, and the structural characteristics of neighboring forests may be extremely important in determining the level of tree mortality in a given plot.

Baxter Park presents a peculiar problem that further complicates the interpretation of the tree mortality patterns. A large mass of mountains is situated in the south-central part of the Park, and there is no reason to assume that the presence of high mountains did not affect the patterns of tree mortality. Dispersal of adult moths would have been affected by it. Thus, the mountains themselves might have created a gradient of susceptibility in forests which would not otherwise be present. The inter-town variation of tree mortality noted above may, at least in part, be a result of some mountain mass effect. In general, mortality of trees was greater on the western, or windward, side of the Park, than on the eastern side.

In summary, the following problems were reviewed in interpreting the observed tree mortality patterns:

(1) the measured variables, with which the tree mortality patterns are to be explained, are probably not independent of each other. Therefore, cause-and-effect relationships may not be established by the simple observational approach;

(2) the proposed hypotheses on the mechanisms that are producing tree mortality patterns are often not mutually exclusive. Therefore, there is usually more than one possible mechanism which can explain an observed pattern;

(3) there may be a limited range within which a given mechanism of tree mortality might function. Therefore, understanding of tree mortality patterns may require the knowledge of the ranges associated with the proposed mechanisms;

(4) there are important factors which affect the tree mortality patterns of the sample plot, but were not considered in our investigation: spatial relationship of forests and mountain mass effect.

It is difficult to understand the mechanisms producing the tree mortality patterns during an uncontrolled spruce budworm outbreak by a deductive approach based on empirical observations. There are many possible processes and they may interact with each other. An alternative is an inductive approach which utilizes controlled field experiments for elucidating the causes.

## Suggestions for Controlled Field Experiments

In natural communities of plants, such as forests, many factors that affect the dynamics of plant populations vary simultaneously. Therefore, when observations from those natural communities are taken, we may be looking at an outcome of the effects of many factors acting at the same time. It may be difficult to establish any causal relationship. However, when we are faced with a serious damaging agency, e.g. spruce budworm, we would like to know the mechanisms that are determining the mortality patterns of trees as well as the dynamics of the pest populations. Once the crucial factors are understood, it may become possible to formulate a control technique that could successfully be used to reduce the damage. Therefore, the understanding of the mechanisms is of importance.

An inductive approach could be applied to elucidate the causes of tree mortality patterns. The hypotheses of mechanisms that are causing the observed mortality patterns should be formulated first. Then, the field experiments should be designed so that some possible hypotheses could be ruled out. In the field experiments, one factor would be varied among treatments, and the other factors will be allowed to fluctuate in unison throughout the treatment blocks. The last step is the actual execution of the field experiments.

During the past two outbreaks of the spruce budworm and the current one in eastern North America, a great deal has been learned about the relationship between this insect and the forests (Swaine and Craighead 1924, Morris 1963, Seymour 1980, MacLean 1980, and others). A number of hypotheses on the mechanisms that control susceptibility and vulnerability of forests have been proposed and we have summarized those hypotheses. Therefore, the first step of the inductive method has already been accomplished. Although Platt (1964) demonstrated the power of this approach, and emphasized the importance of its systematic use, it seems that most foresters have forgotten that this method is available. In the discussion of possible forest management strategies against spruce budworm, Craighead (1924:p82) wrote:

> "In fact, from a review of the literature treating the management of spruce, it is evident that considerably more experimental work is needed before satisfactory methods will be evolved."

Numerous experimental studies on the effects of chemical insecticides and biological control techniques on budworm dynamics have been conducted (Klein and Lewis 1966, Kettela et al. 1977, Dimond and Morrison 1978, Blais 1979, Dimond and Spies 1980, Dimond et al. 1981, and many others). On the other hand, it seems that there are only a few studies that demonstrated, experimentally, the effect of insecticides on the marked reduction of tree mortality during a budworm outbreak (Batzer 1973, Seymour 1980). Experimental studies of the relationship between stand or site characteristics and tree mortality during the budworm outbreak are also few. We have encountered three papers that investigated the effects of regular silvicultural treatments on the defoliation intensity by spruce budworm (Batzer 1967, Crook et al. 1979, Roberts and Chow 1977). The results of those studies are suggestive of certain mechanisms of the patterns of tree mortality. However, they could not be used to exclude some of the proposed hypotheses on tree mortality. Batzer's (1984) work seems to be the only experimental investigation that is providing information on the causal mechanisms of tree mortality patterns.

Sixty years have passed since Craighead (1924) called attention to the need of experimental work in developing successful silvicultural control techniques. Time is probably ripe for initiating field experiments to understand what causes the observed patterns of tree mortality during the spruce budworm outbreaks; however, for conducting the experiments, it may be necessary to await a new budworm outbreak.

## CONCLUSIONS

1. Baxter State Park had a total of 6,953,000 cu m (187 $m^3$/ha) of living tree stems in 1983, excluding the hardwood forest and the two northern towns, of which 85% was represented by the four most dominant species, spruce, fir, white birch, and red maple. The proportion of each species to the total volume was 61%, 11%, 8%, and 6%, respectively.

2. The stem volume of trees that have died during the current spruce budworm outbreak was estimated as 4,647,000 cu m (124 $m^3$/ha), 40% of the original volume. Dead stem volume was 2,570,000 cu m (69 $m^3$/ha) for fir, and 1,560,000 cu m (42 $m^3$/ha) for spruce. The overall mortality of fir and of spruce were 77% and 27% by volume, respectively. Minor portions of fir and spruce had been uprooted; 5% and 8%, respectively, of the total stem volume that was dead.

3. Eight patterns of tree mortality were identified. Two patterns were found regularly, both in each town and in pooled data of the entire Park. Other patterns were found in some towns but not in others.

4. The two patterns that were regularly found are: a higher percentage mortality of fir than spruce, and a higher percentage mortality of spruce in the higher elevation zone (between 600 m and 870 m) than in the lower zone (below 600 m).

5. The following patterns of tree mortality existed for the Park area as a whole but did not clearly exist in each of six separate town areas: (a) lower percentage mortality of fir and of spruce with an increasing proportion of nonhost species basal area; (b) higher percentage mortality of spruce with increasing proportion of fir basal area; (c) higher spruce mortality on south-facing slopes than on north-facing slopes at the lower elevation zone; (d) higher percentage mortality of fir on south-facing slopes than on north-facing slopes; (e) higher spruce mortality on higher positions on slopes than on lower, and

higher percentage mortality of fir and of spruce on flatter sites than on steeper sites.

6. We were unable to confirm the generally accepted hypothesis that lower mortality of fir and of spruce is associated with an increasing proportion of nonhost species in a stand. This hypothesis first appeared in Tothill (1919) and was supported repeatedly (Craighead 1924, 1925, Wellington et al. 1950, Blais 1958, Ghent 1958, Mott 1963, 1976, Batzer 1969, 1976, Seymour 1980, and Witter et al. 1984). In our study, the hardwoods seemed to be affecting the tree mortality in T4R10 of which topography is similar to the majority of the commercial spruce-fir forest region in northern Maine. However, the relationship broke down in most towns of the Park. This irregularity leads us to suspect that the presence of nonhost component plays a limited role, especially when the overall damage by the budworms is not severe.

7. Multiple regression analysis was unsuccessful in relating tree mortality to the structural characteristics of forests and to the topographical variables. In general, 40% to 60% of variation in tree mortality remained unexplained. Moreover, our tree mortality data tended to violate the normality assumption of linear regression even after the mortality values were transformed by the arcsine transformation.

8. The hypotheses on the mechanisms producing the tree mortality patterns during a spruce budworm outbreak were summarized. Seven hypotheses were identified: the Phenology Hypothesis, the Crown Exposure Hypothesis, the Hardwood Shield Hypothesis, the Epicenter Hypothesis, the Energy Budget Hypothesis, and the Foliar Nutrition Hypothesis.

9. Expected tree mortality patterns were identified for each proposed hypothesis. Then, the observed mortality patterns were interpreted according to those expected patterns. The greater mortality of fir than of spruce was expected by the Phenology Hypothesis. On the other hand, there are several ways of explaining the other patterns. There may be two reasons for this complication; apparent dependence of some variables with which the tree mortality patterns are to be explained, and the fact that the proposed hypotheses are often not mutually exclusive. Simple observations could not reveal which one of the proposed mechanisms is responsible for the observed tree mortality patterns. Use of controlled field experiments is recommended as an alternative.

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**Table A1.** Photo forest types in Baxter State Park.

| Forest Type | Description[1] |
|---|---|
| Sg | Softwood, gray |
| Srg | Softwood, reddish gray |
| Sgr | Softwood, grayish red |
| Sr | Softwood, red |
| SHg | Softwood-hardwood, gray |
| SHrg | Softwood-hardwood, reddish gray |
| SHgr | Softwood-hardwood, grayish red |
| SHr | Softwood-hardwood, red |
| HS | Hardwood-softwood |
| H | Hardwood |
| Shrub | |
| Rock | |
| Bog | |
| Burn | |

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[1] The following definitions were used by Sewall Co. for different stand composition expressed by the proportion of stem volume that was estimated by the aerial photographs: Softwood (S) = more than 75% softwood, Mixedwood (SH) = between 50% and 75% softwood, Mixedwood (HS) = between 50% and 75% hardwood, and Hardwood (H) = more than 75% hardwood. For each stand, four colors were distinguished in the infra-red photographs: gray, reddish gray, grayish red, and red. The gray corresponds to stands with many dead stems, and red to the ones with healthy trees.

**Table A2.** Number of sample plots taken in each forest type by accessibility class.

| | Forest type | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| Accessibility Class | Sr | Srg | Sgr | Sg | SHr | SHrg | SHgr | SHg | HS | Sum |
| I | 22 | 6 | 12 | 19 | 4 | 6 | 23 | 3 | 6 | 101 |
| II | 14 | 10 | 9 | 9 | 1 | 2 | 4 | 4 | 3 | 56 |
| III | 38 | 49 | 33 | 52 | 15 | 3 | 25 | 9 | 31 | 255 |
| Sum | 74 | 65 | 54 | 80 | 20 | 11 | 52 | 16 | 40 | 412 |

**Table A3.** Area of forest types in hectares in Baxter State Park. The types are delineated by species composition and degree of tree mortality, using infra-red aerial photography taken in late fall of 1982.

| Forest type[1] | T3R10 | T3R9[2] | T4R10 | T4R9 | T5R10 | T5R9 | All towns |
|---|---|---|---|---|---|---|---|
| Sr | 2,452 | 2,558 | 1,195 | 982 | 422 | 447 | 8,056 |
| Srg | 1,318 | 654 | 195 | 1,376 | 1,115 | 40 | 4,698 |
| Sgr | 429 | 1,282 | 661 | 597 | 1,347 | 137 | 4,453 |
| Sg | 866 | 1,081 | 3,571 | 832 | 928 | 188 | 7,466 |
| SHr | 270 | 1,282 | 77 | 353 | 342 | 211 | 2,535 |
| SHrg | 134 | 130 | 0 | 166 | 407 | 0 | 837 |
| SHgr | 579 | 178 | 348 | 155 | 1,519 | 92 | 2,871 |
| SHg | 0 | 168 | 1,404 | 23 | 30 | 35 | 1,660 |
| HS | 373 | 814 | 988 | 875 | 1,302 | 356 | 4,708 |
| Subtotal | 6,420 | 8,146 | 8,439 | 5,358 | 7,412 | 1,506 | 37,281 |
| Hardwood forest or Nonforested area | 3,011 | 4,607 | 1,250 | 4,358 | 2,539 | 8,794 | 24,258 |
| Total of town | 9,431 | 12,753 | 9,689 | 9,716 | 9,951 | 9,999 | 61,539[3] |

[1] The definition of each forest type is given in Table A1.

[2] This includes portion of town T2R9.

[3] This excludes two towns, T6R10 and T6R9. Total area of the Park is 81,350 ha.

**Table A4.** Basal area of living trees in each forest type.

| Forest type | Basal area ($m^2$/ha) | | | | | | Total basal area for the forest type |
|---|---|---|---|---|---|---|---|
| | Fir | Spruce | Primary hosts | Secondary hosts | Nonhosts | All Trees | ($x10^3m^2$) |
| Sr | 1.41 | 28.55 | 29.96 | 2.69 | 2.89 | 35.54 | 286.3 |
| Srg | 1.58 | 24.05 | 25.63 | 2.63 | 5.24 | 33.50 | 157.4 |
| Sgr | 5.96 | 13.26 | 19.23 | 0.32 | 6.28 | 25.83 | 115.0 |
| Sg | 2.69 | 11.15 | 13.91 | 0.19 | 1.18 | 15.28 | 114.1 |
| SHr | 6.03 | 15.61 | 23.14 | 0.22 | 14.92 | 38.28 | 97.0 |
| SHrg | 6.00 | 11.78 | 17.89 | 0.33 | 11.39 | 29.61 | 24.8 |
| SHgr | 4.02 | 15.83 | 19.97 | 0.31 | 8.96 | 29.24 | 83.9 |
| SHg | 4.66 | 8.09 | 12.75 | 0.22 | 13.87 | 26.84 | 48.5 |
| HS | 4.45 | 7.30 | 11.78 | 0.17 | 16.87 | 28.82 | 135.7 |

**Table A5.** Stem volume of living trees in each forest type.

| Forest type | Stem volume (m$^3$/ha) | | | | | | Total stem volume for the forest type |
|---|---|---|---|---|---|---|---|
| | Fir | Spruce | Primary hosts | Secondary hosts | Nonhosts | All Trees | (x10$^3$m$^3$) |
| Sr | 6.1 | 185.4 | 191.5 | 17.8 | 14.0 | 223.3 | 1,799 |
| Srg | 7.8 | 158.7 | 166.5 | 19.8 | 24.4 | 210.7 | 990 |
| Sgr | 40.5 | 97.2 | 137.8 | 2.4 | 41.5 | 181.7 | 809 |
| Sg | 20.1 | 81.0 | 101.6 | 1.7 | 16.6 | 119.9 | 895 |
| SHr | 25.3 | 97.3 | 130.5 | 1.4 | 74.2 | 206.1 | 522 |
| SHrg | 34.8 | 69.9 | 105.4 | 2.6 | 72.8 | 180.8 | 151 |
| SHgr | 22.8 | 114.9 | 138.5 | 2.4 | 61.5 | 202.4 | 581 |
| SHg | 28.9 | 53.2 | 82.1 | 1.1 | 85.7 | 168.9 | 280 |
| HS | 30.2 | 48.6 | 79.0 | 1.1 | 116.4 | 196.5 | 925 |

**Table A6.** Tree mortality in relation to proportion of fir basal area in primary host species. The comparisons were made by town for two forest types. The more conservative result of two tests, Kruskal-Wallis and Brown-Mood, was presented.

| | Softwood forest | | | | Softwood-hardwood forest | | | |
|---|---|---|---|---|---|---|---|---|
| Town | Balsam Fir Mortality | Red-Black Spruce Mortality | Combined Fir-Spruce Mortality | Sample Size | Balsam Fir Mortality | Red-Black Spruce Mortality | Combined Fir-Spruce Mortality | Sample Size |
| T3R10 | ns | ns | ns | 28 | ns | * | *** | 52 |
| T3R9 | ns | ns | ns | 9 | ns | ns | *** | 63 |
| T4R10 | ns | *** | *** | 45 | ns | ns | *** | 35 |
| T4R9 | -[1] | | - | 1 | ns | * | * | 17 |
| T5R10 | ns | ns | ** | 18 | ns | ns | ** | 35 |
| T5R9 | | - | | 0 | | - | | 1 |
| Entire Park | ns | ns | ns | 101 | ns | * | ** | 203 |

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[1] Sample size was too small to allow comparison.

**Table A7.** Tree mortality in relation to topographical factors in different forest types at the lower elevation zone (below 600 m).

| Source of variation | Mortality of: | All forest types | Softwood forest | Softwood-hardwood forest | Hardwood-softwood forest |
|---|---|---|---|---|---|
| Slope inclination | Fir | ns | ns | ns | ns |
| | Spruce | ns | ns | ns | ns |
| | Combined fir-spruce | ns | ns | ns | ns |
| Position on slope | Fir | ns | ns | ns | ns |
| | Spruce | ns | ns | ns | ns |
| | Combined fir-spruce | ns | * | ns | ns |
| Aspect of slope | Fir | ns | ns | ns | ns |
| | Spruce | * | ns | ns | ns |
| | Combined fir-spruce | ns | ns | ns | ns |
| Sample size | | 331 | 89 | 151 | 91 |

**Table A8.** Tree mortality in relation to topographical factors in different forest types at the higher elevation zone (between 600 m and 870 m).

| Source of variation | Mortality of: | All forest types | Softwood forest | Softwood-hardwood forest | Hardwood-softwood forest |
|---|---|---|---|---|---|
| Slope inclination | Fir | ns | ns | ns | ns |
| | Spruce | ns | ns | ns | ns |
| | Combined fir-spruce | ns | ns | ns | ns |
| Position on slope | Fir | ns | ns | ns | ns |
| | Spruce | ns | ns | ns | ns |
| | Combined fir-spruce | ns | ns | ns | ns |
| Aspect of slope | Fir | ** | ns | ** | ns |
| | Spruce | ns | ns | ns | ns |
| | Combined fir-spruce | * | ns | * | ns |
| Sample size | | 52 | 6 | 40 | 6 |

**Table A9.** Tree mortality in relation to aspect of slope in two elevation zones.

| | Elevation below 600 m | | | | Elevation between 600 m and 870 m | | | |
|---|---|---|---|---|---|---|---|---|
| Aspect of Slope | Mean Balsam Fir Mortality (%) | Mean Red-Black Spruce Mortality (%) | Combined Fir-Spruce Mortality (%) | Sample Size | Mean Balsam Fir Mortality (%) | Mean Red-Black Spruce Mortality (%) | Combined Fir-Spruce Mortality (%) | Sample Size |
| SE | 90 | 28 ab | 47 | 25 | 97 ab | 43 | 85 a | 4 |
| S | 82 | 30 a | 50 | 50 | 92 abc | 19 | 64 ab | 5 |
| SW | 83 | 28 ab | 46 | 33 | 100 a | 26 | 71 ab | 1 |
| W | 80 | 18 b | 39 | 46 | 94 ab | 55 | 80 a | 7 |
| NW | 74 | 18 ab | 42 | 33 | 71 cd | 47 | 59 ab | 10 |
| N | 78 | 18 b | 38 | 41 | 56 d | 26 | 41 b | 7 |
| NE | 68 | 16 b | 35 | 27 | 77 bcd | 45 | 69 ab | 5 |
| E | 80 | 20 ab | 45 | 36 | 60 d | 41 | 53 ab | 13 |
| Flat Area | 88 | 22 ab | 43 | 40 | | | | 0 |
| Chi-square value | 15.01 | 16.55 | 8.63 | | 24.14 | 8.57 | 14.26 | |
| Significance | ns | * | ns | | ** | ns | * | |

**Table A10.** The "best" linear regression models of percentage tree mortality for the entire Park and for T4R10. All the mortality values and the proportions were calculated by basal area. The basal area and the stem volume represent the values per hectare.

| Tree mortality | | Coefficient | [Regressor] | F | R$^2$ |
|---|---|---|---|---|---|
| | | | **Entire Park** | | |
| Fir mortality | = | −0.187 | | 41.54 | 0.40 |
| | | +0.564 | [Fir proportion in primary hosts] | | |
| | | +0.817 | [Proportion of all host species in stand] | | |
| | | +0.0401 | [Total basal area of spruce] | | |
| | | +0.0304 | [Total basal area of fir] | | |
| | | −0.0351 | [Total basal area of all hosts] | | |
| | | +0.00376 | [Total stem volume of secondary hosts] | | |
| Combined fir-spruce mortality | = | +0.0553 | | 128.45 | 0.58 |
| | | +1.105 | [Fir proportion in stand] | | |
| | | +0.00719 | [Total basal area of spruce] | | |
| | | −0.0143 | [Total basal area of primary hosts] | | |
| | | +0.00170 | [Total stem volume of primary hosts] | | |

Table A10. The "best" linear regression models of percentage tree mortality for the entire Park and for T4R10. All the mortality values and the proportions were calculated by basal area. The basal area and the stem volume represent the values per hectare.

| Tree mortality | | Coefficient | [Regressor] | F | $R^2$ |
|---|---|---|---|---|---|
| | | | **T4R10** | | |
| Fir mortality | = | −0.728 | | 37.31 | 0.66 |
| | | +0.766 | [Fir proportion in primary hosts] | | |
| | | +0.987 | [Spruce proportion in stand] | | |
| | | +1.935 | [Proportion of all host species in stand] | | |
| | | +0.790 | [Position on complex moisture gradient (between 0 and 1)] | | |
| | | −0.0785 | [Slope inclination (degrees)] | | |
| Spruce mortality | = | −0.119 | | 27.28 | 0.46 |
| | | −0.0137 | [Total basal area of fir] | | |
| | | +0.967 | [Fir proportion in stand] | | |
| | | +0.00130 | [Total stem volume of secondary hosts] | | |
| Combined fir-spruce mortality | = | +0.0467 | | 76.79 | 0.71 |
| | | +0.00424 | [Total basal area of spruce] | | |
| | | +0.0577 | [Total basal area of secondary hosts] | | |
| | | +1.148 | [Fir proportion in stand] | | |

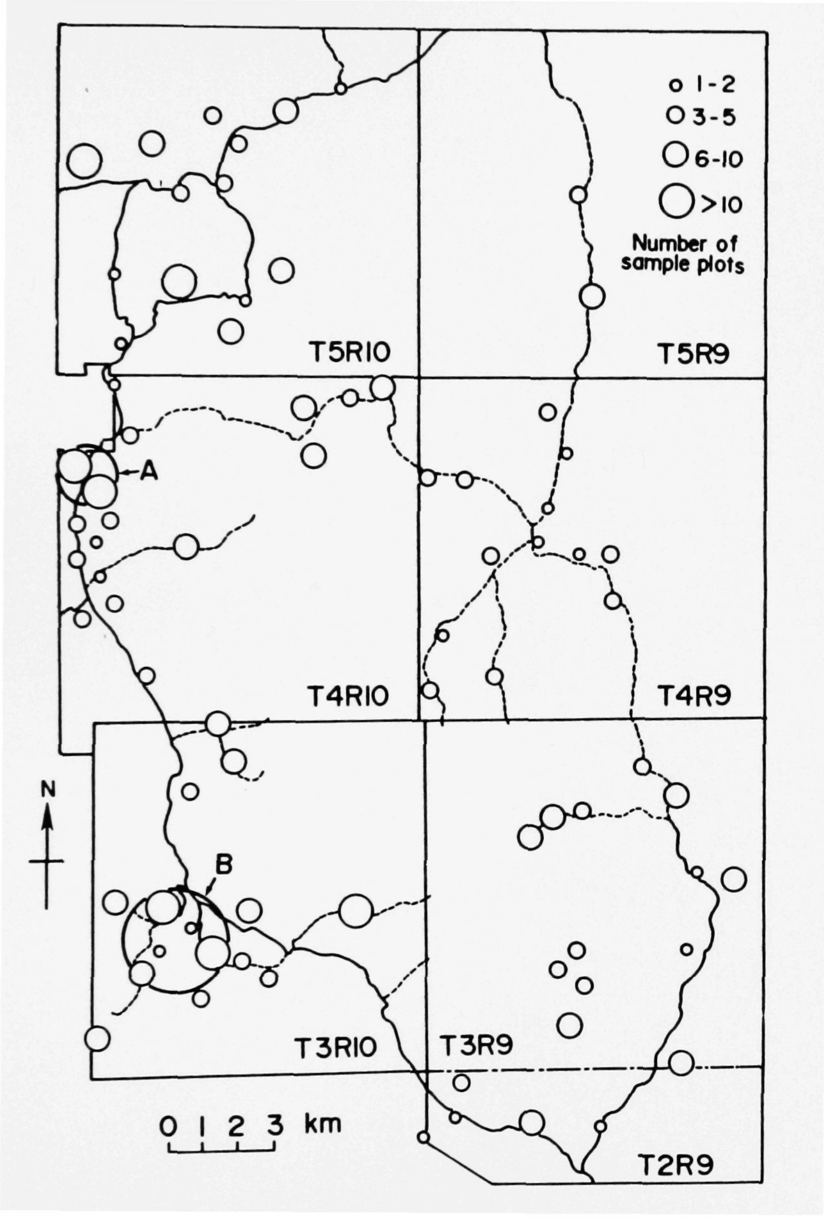

FIG. A1. Location of one-quarter-hectare quadrats that were sampled in Baxter State Park. Solid line and broken line indicate automobile road and hiking trail, respectively. The positions of area A and of area B are indicated by larger circles.