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BUDWORM - CAUSED MORTALITY AND 20 - YEAR RECOVERY IN IMMATURE BALSAM FIR STANDS

by
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MARITIMES

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BUDWORM-CAUSED MORTALITY AND 20-YEAR RECOVERY

IN IMMATURE BALSAM FIR STANDS

by

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ABSTRACT

Budworm-caused tree mortality
and stand recovery over a 20-year
period following a spruce budworm,
Choristoneura fumiferana (Clem.),
outbreak were examined in an imma-
ture balsam fir, *Abies balsamea*
(L.) Mill., stand in northwestern
New Brunswick. Tree mortality
peaked in the sixth and seventh
year of the budworm outbreak and
showed high variability within the
stand, ranging from 18 to 80% of
the total volume per hectare.
There was no clear relationship
between volume loss and stand
characteristics, but mortality did
tend to have a strongly contagious
distribution in the stand. For
individual trees, the period of
defoliation was coincident with
greatly reduced diameter growth
and virtually no height growth.
Within five years of cessation of
defoliation, the crowns of surviv-
ing trees appeared fully recov-
ered, and diameter and height
growth were similar to that in
unaffected stands. Although
diameter growth showed a classic
response to the reduction in stand
density (thinning) and increased
substantially beyond predefolia-
tion levels, this growth was on
smaller trees (because of the
growth reductions during the
outbreak) and there were fewer
trees per hectare. Therefore, the
recovery in terms of volume per

RESUME

La mortalité des arbres provo-
quée par la Tordeuse, *Choriston-
eura fumiferana* (Clem), ainsi que
la régénérescence des peuplements
au cours des 20 années consécu-
tives à une infestation, ont été
étudiées pour un peuplement imma-
ture de Sapin baumier, *Abies
balsamea* (L). Mill., dan le
nord-ouest du Nouveau Brunswick.
La mortalité des arbres atteignait
son point culminant au cours des
sixième et septième années de
l'infestation par la Tordeuse et
présentait une grande variabilité
à travers le peuplement, allant de
18 à 80% du volume total à l'hec-
tare. Il n'y avait pas de rela-
tion évidente entre la perte de
volume et les caractéristiques du
peuplement, toutefois la mortalité
ne tendait pas à avoir une distri-
bution fortement contagieuse dans
le peuplement. En ce qui a trait
aux arbres, la période de défolia-
tion coïncidait avec une crois-
sance en diamètre fortement
réduite et l'absence virtuelle de
croissance en hauteur. En
l'espace de cinq années depuis la
cessation de la défoliation, les
cimes des arbres survivants
paraissaient complètement regéné-
rées, et la croissance en diamètre
et en hauteur était identique à
celle observée dans les peuple-
ments indemnes. Bien que la
croissance en diamètre ait mani-

hectare was poor, and only one plot had regained its predefoliation volume 15 years after defoliation ceased. Projection of stand development to age 75 years further suggested that on average, the plots which suffered budworm-caused mortality and growth loss would have only slightly more than one-half the projected volume without defoliation.

festé une réaction classique à la réduction de la densité du peuplement (éclaircie), et ait substantiellement dépassé les niveaux antérieurs à la défoliation, une telle croissance s'observait sur les plus petits arbres (ce, à cause des pertes de croissance au cours de l'infestation) et il y avait encore moins d'arbres à l'hectare. Par conséquent la régénérescence en termes de volume à l'hectare était médiocre et, 15 années après que la défoliation eut cessé, une seule parcelle a retrouvé son volume antérieur. La projection du développement du peuplement à 75 ans au-delà de son âge actuel laissait voir qu'en moyenne, les parcelles ayant souffert de mortalité par la Tordeuse et de perte de croissance auraient eu à peine plus de la moitié du volume projeté sans la défoliation.

INTRODUCTION

Historical records and tree-ring analyses have suggested that numerous, extensive outbreaks of the spruce budworm, *Choristoneura fumiferana* (Clem.), have occurred in the past over eastern North America. Vast areas of forest have been affected, but until recently the affected forest had little economic value. For various reasons, surveys of the impact of these outbreaks on forest productivity were at best patchy and imprecise, and thus any large-scale estimates of mortality losses must be viewed skeptically because of the lack of good survey and inventory data. However, to give a rough idea of the magnitude of these losses, the following estimates are presented: (1) at least 200 million cords of fir (*Abies balsamea* (L.) Mill.) and spruce (*Picea* spp.) killed in eastern Canada during the 1910's and early 1920's, equivalent to a minimum of 40 to 50% of the host trees present (Swaine and Craighead 1924); (2) 25-30 million cords killed in Maine during the 1909-19 outbreak (McLintock 1955); and (3) 17 million cords killed in northwestern Ontario from 1943 to 1955, or 58% of the host-tree volume (Elliott 1960). Tothill (1921) estimated that 7,967 million board feet (equivalent to approximately 5,200,000 cords) of fir and spruce died in New Brunswick from 1914 to 1921. This estimate was based on reconnaissance surveys and a 4% cruise of 460 square miles in Northumberland County, on which area 4% of the spruce and 75% of the merchantable fir (or 56% of the total fir) were dead.

Studies of the amount and rate of budworm-caused tree mortality are of two types: (a) annual assessment of mortality on permanent plots during and following an outbreak, and (b) a single, post-mortem analysis of mortality. Studies of the first type have been conducted for stands in New Brunswick from 1955-61 (Baskerville 1960, MacDonald 1962, Mott 1968[1]), in Quebec from 1948-52 (McLintock 1955), in Minnesota from 1957-66 (Batzer 1973), and are ongoing during a current budworm outbreak on Cape Breton Island (Magasi 1978, MacLean 1979). Examples of postmortem mortality studies include Craighead (1924, 1925), Turner (1952), Ghent *et al.* (1957), Blais (1958), and Hatcher (1964). Both types of study have shown a wide range of mortality in various stands, from approximately 33% to 100% of the number of merchantable trees.

The hypothesis that variability in budworm-caused tree mortality in forest stands is related to the structural characteristics of the stand at the time of initiation of the outbreak has been examined in at least a cursory fashion in a number of these studies. Craighead (1925) determined that tree vigor (as expressed by increment at dbh) at the time of defoliation was related to mortality, with more rapid growth rates associated with lower mortality; however, under severe defoliation the relation broke down, presumably because persistent severe defoliation will kill even vigorous trees. Craighead (1925) also examined mortality in relation

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[1] Mott, D.G. 1968. A study of mortality in balsam fir stands after attack by spruce budworm in northwestern New Brunswick, 1956-59. Contract Rep. 1, Marit. For. Res. Cent., Fredericton, N.B.

to density, basal area, and percentage balsam fir, but found no correlation. Turner (1952) determined that fir mortality was related to percentage fir in the stand and to actual basal area of fir considered independently of other species. Ghent et al.(1957) used a non-parametric rank correlation method to relate mortality, on a plot basis, to percentage of fir basal area and to actual fir basal area. Mott (1968) in a multiple regression analysis found that 'mean tree' basal area was the best of the 10 stand characteristics studied for explaining variation in fir mortality, and also noted a 'boundary-zone effect', with lower mortality in the zone between forest and clear-cut openings, possibly due to outward dispersal of small larvae and/or adults. Batzer (1969) also used mathematical techniques to select tree and stand characteristics related to mortality, and found that a combination of three stand attributes (percentage of basal area in spruce, percentage of basal area in non-host species, and total basal area of fir) explained 56% of the variation in mortality. Thus, mortality has been found to be loosely related to a variety of stand attributes, which generally include some measure of basal area.

Although several studies have examined tree mortality in budworm outbreaks in various regions, no published studies have followed stand recovery after the collapse of an outbreak, in terms of factors such as stand growth, species composition or productivity of the survivors. In the case of immature stands or under certain outbreak patterns, it is known that substantial numbers of trees may survive. How does the budworm affect the long-term stand producti-

vity in these cases? In this paper, budworm-caused tree mortality and stand recovery over a 20- year period following the outbreak are examined for 10 plots in northwestern New Brunswick. The early losses were summarized by Baskerville (1960) on the basis of an average for the 10 plots. The present paper provides some details of the variation in mortality among plots, as well as describing recovery.

METHODS

The work reported here was part of a cooperative program of entomological and forest research begun in the early 1950's on the Green River Watershed in northwestern New Brunswick. As part of that project, about 5400 ha were set aside and were neither protected from spruce budworm attack nor logged, so that insect and forest development in the absence of protection could be followed. This area, known as the Kedgwick Check Area (Morris 1963), was near the centre of the budworm outbreak that began in the early 1950's, and the forest received the full impact of an uncontrolled budworm outbreak.

Most of the data presented here come from ten 0.04-ha (0.1 ac) circular plots randomly located in an immature stand in the 8-ha entomological plot known as K-2 (see Morris 1963 figure 1.1 for plot location). These plots were established in 1956, and every tree was numbered and its position mapped. Records on each tree consisted of dbh, crown class, and defoliation by budworm. Defoliation of current foliage was visually estimated on a subjective scale, light (0-25%), moderate (26-75%), and severe (76-100%), based on the proportion of foliage

present compared to the amount that should have been present under undefoliated conditions. Trees were classed as dead only when the inner bark was dry and discolored on two sides of the stem. Total height was recorded for a sample of trees on each plot. The plots were measured annually from 1956 to 1961 during the period of peak mortality, and again in 1965 and 1970; five plots were also remeasured in 1975. For purposes of comparison, some data and relationships were drawn from twelve 0.01 ha (0.025 ac) plots, located near the entomological plot G-5 (Morris 1963), that were essentially unaffected by the budworm outbreak. These plots were in forest separated from the budworm outbreak by extensive clear cut areas, and, although budworm populations persisted in these stands, they never reached seriously damaging levels (Morris 1963). Of the 12 non-infested plots, four were in each of three stand density classes, with 2470, 7400, and 12350 stems per hectare. As in the plots damaged by budworm, all trees were numbered and mapped and individual tree records were maintained. These plots were established in 1955 and remeasured in 1960, 1965, 1970, and 1975.

RESULTS AND DISCUSSION

Initial Stand Conditions

The stands in the two study areas originated from advance growth that was present under the mature stand destroyed in the budworm outbreak of 1913-1919 (Vincent 1962, Baskerville 1975). They are even-aged, dating from release in the early 1920's, and are on excellent sites, all well-drained upland silty clay loams. These stands have sustained very little disturbance by man. Some

sawlogs were removed in the mid 1930's and early 1940's but cutting was limited to scattered large spruce that survived the 1913-1919 budworm outbreak. The logs were hauled out by horses in mid-winter, and consequently the disturbance to the stands was minimal.

In 1956, the stands in the Kedgwick Check Area were under intense attack from the spruce budworm, but they still maintained a continuous closed canopy. There was a scattering of overstory spruce that had survived the earlier budworm outbreak and had been too small to attract the attention of the sawlog cutters. However, the stands were distinctly single-story and apart from the dense canopy, the most striking feature was their apparent uniformity. Indeed, the plots were established to examine the impact of budworm in what appeared to be a uniform forest/budworm environment. Despite the remarkably uniform structural appearance of the stands, the sample plots displayed a rather wide range of density and species mixes (Table 1).

The 10 plots averaged 5620 stems per hectare of balsam fir, 540 stems of black spruce, *Picea mariana* (Mill) B.S.P., and 590 stems of white birch, *Betula papyrifera* Marsh. There were a few white spruce, *P. glauca* (Moench) Voss, in the stands, but in this report these trees are identified as "spruce" which should be considered black spruce. The basal area averaged 34 m^2 ha^{-1} and mean total volume was 162 m^3 ha^{-1} (Table 1).

Although the stands had suffered considerable defoliation by 1956, few trees had been killed according to records from the entomological plots and on-the-ground inspection.

Table 1. Mensurational characteristics of the 10 plots in 1956, before budworm damage

Plot No.	Density, stems ha^{-1}			Basal area, m^{2}ha^{-1}			Mean dbh, cm			Total volume, m^{3}ha^{-1}		
	Fir	Spruce	Birch	Fir	Spruce	Birch	Fir	Spruce	Birch	Fir	Spruce	Birch
71	4420	1240	490	30.2	5.8	0.5	9.3	7.8	3.5	144	26	1
72	5120	150	860	30.5	2.7	2.2	8.7	15.3	5.7	143	16	10
73	7980	670	640	39.0	4.5	0.9	7.9	9.2	4.2	174	23	3
74	4820	270	170	33.4	1.2	0.2	9.4	7.4	3.9	163	5	1
75	4620	840	1560	28.8	6.8	3.8	8.9	10.2	5.5	137	35	17
76	6130	370	520	37.4	3.2	1.1	8.8	10.5	5.2	176	17	4
77	3760	420	520	35.9	2.4	2.3	11.0	8.5	7.6	183	11	14
78	6350	540	440	39.4	4.4	0.8	8.9	10.1	4.9	185	23	3
79	5140	250	150	31.8	1.3	0.4	8.7	6.9	5.8	149	6	2
80	7910	670	540	38.1	2.8	1.0	7.8	7.4	4.9	169	13	4
Average	5620	540	590	34.4	3.5	1.3	8.9	9.3	5.1	162	18	6
Percent of total	83	8	9	88	9	3				87	10	3

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Defoliation History

Since the plots were located on an entomological sample area the budworm population history of the stands is well-established. Both population numbers and defoliation of current foliage were recorded annually by systematic surveys of the 8 ha stand. Data on budworm density from 1950 to 1960 for plots K-2 and G-5 have previously been presented (Morris 1963, fig. 33.1), and defoliation history for the stand as a whole is shown in Table 2. However, it was evident during the outbreak that there were substantial variations in defoliation on a local scale that would not be reflected in the estimate for K-2 as a whole (Morris 1963). Since this variation clearly would influence tree survival and stand development at the scale of the 10 small sample

Table 2. Defoliation history of the 8 ha stand containing the 10 plots

Year	Defoliation[1]
1948	0
49	0
50	20
51	45
52	91
53	98
54	98
55	34
56	92
57	48
58	2
59	2
60	2
61-75	0

[1] Defoliation expressed as a percent of the total new foliage on normal crowns.

plots, defoliation of each tree on these plots was assessed annually during the outbreak. Although the observer for this task was specially trained, analysis of the individual tree defoliation assessments from these visual estimates showed such inconsistencies as to preclude use of even an 'average' defoliation estimate for each plot.

While there were discernible variations in the intensity of defoliation throughout the 8 ha stand in which the plots were located, the overall picture was one of severe damage. By 1958, the tops of all trees in all plots were dead. From the air, the stand was a typical "grey area" of the type associated with extensive mortality. The budworm population in this area collapsed of its own accord in 1958. At that time the crown of every surviving fir and spruce tree showed a dead top and a degree of openness in the lower crown, depending on the intensity of defoliation. With the cessation of defoliation the trees were either unable to recover and died, or they showed incredible recovery of the crown and survived. The crowns that survived looked normal to the unpracticed eye by 1961, four years after the defoliation pressure ceased.

Budworm Impact on the Forest

On average, the plots lost 64% of the original fir trees and 14% of the original spruce trees to budworm-caused mortality (Table 3). The range was from 34 to 84% for fir and from 0 to 24% for spruce. The loss in terms of initial basal area averaged 53% for fir and 8% for spruce while the volume loss was 51% for fir and 8% for spruce (Table 3). These losses were such that the stands appeared truly devastated

Table 3. Total mortality from 1956-61 expressed as a percentage of the initial stand condition

Plot	Density stems ha^{-1} Fir	Spruce	Basal area m^{2}ha^{-1} Fir	Spruce	Total volume m^{3}ha^{-1} Fir	Spruce	Merchantable volume, m^3 ha^{-1} Fir	Spruce
71	73	24	59	7	56	4	53	1
72	84	17	81	1	80	43	80	45
73	78	22	68	6	66	4	63	2
74	34	0	25	0	24	0	24	0
75	44	12	21	2	18	2	14	1
76	67	20	52	4	5C	2	47	<1
77	74	18	68	13	7C	14	70	13
78	72	5	57	1	54	<1	51	0
79	67	10	71	2	70	1	71	0
80	48	15	32	8	29	8	25	7
Average	64	14	53	8	51	8	50	7

from 1958-60. The dense canopy had been greatly reduced by the loss of trees, as well as by defoliation of survivors, and, as the budworm population collapsed, the stands took on an open appearance with a distinct clumpiness to the surviving trees.

The most striking feature of the budworm-caused tree mortality was its high variability in what appeared to be a uniform stand. Plots within 50 m of one another showed the extremes of greatest and least mortality. This variability in percent fir mortality was not related to stand characteristics such as density or the proportion of fir in the stand over the range of these factors for the 10 plots (Fig. 1). It would appear that in uncontrolled outbreaks (5400 ha in the case of the Kedgwick Check Area) budworm-caused tree mortality overrides normal variations in stand dynamics resulting from density and

species mix. It was expected that the budworm would react to differences in stand character on the local scale and that this would, in turn, be reflected in tree mortality rates, but if the population did react to the forest cover, the pattern was not detectable. It appears that the local variability in budworm density (as evidenced by defoliation and mortality) is either a random phenomenon or the insect is reacting to a parameter of the forest that was not measured in this study.

It is not possible to say whether the differential mortality resulted from differential vulnerability from plot to plot within the stand and/or from random variations in the budworm population. If the budworm pressure was, in fact, the same from plot to plot then the results would indicate that there were factors of vulnerability that varied. However, in the more likely case (based on
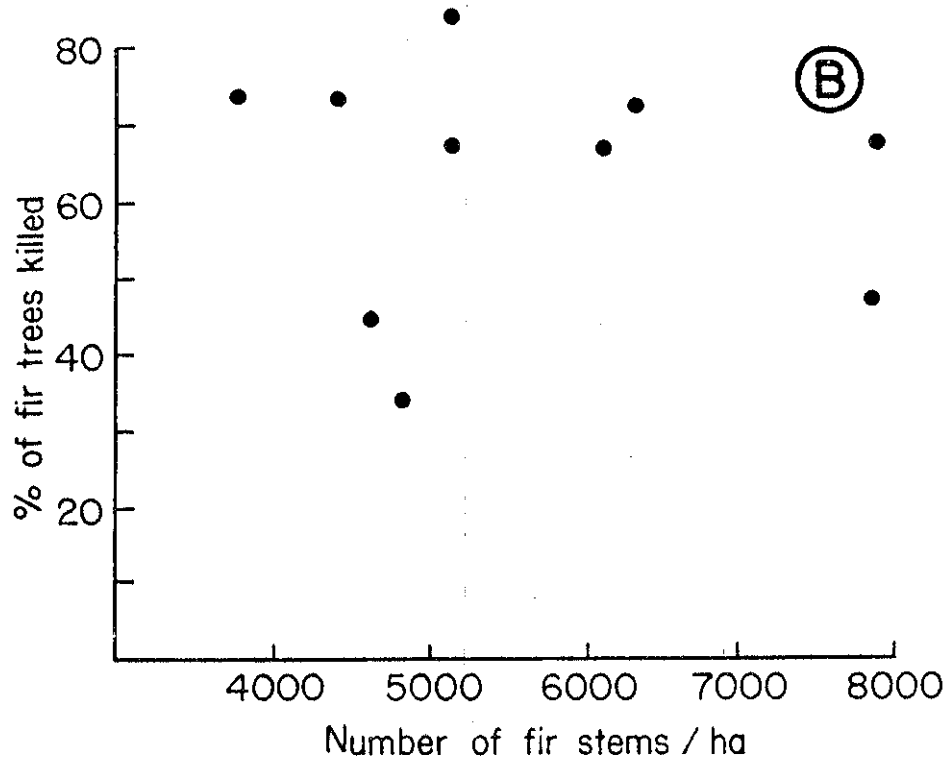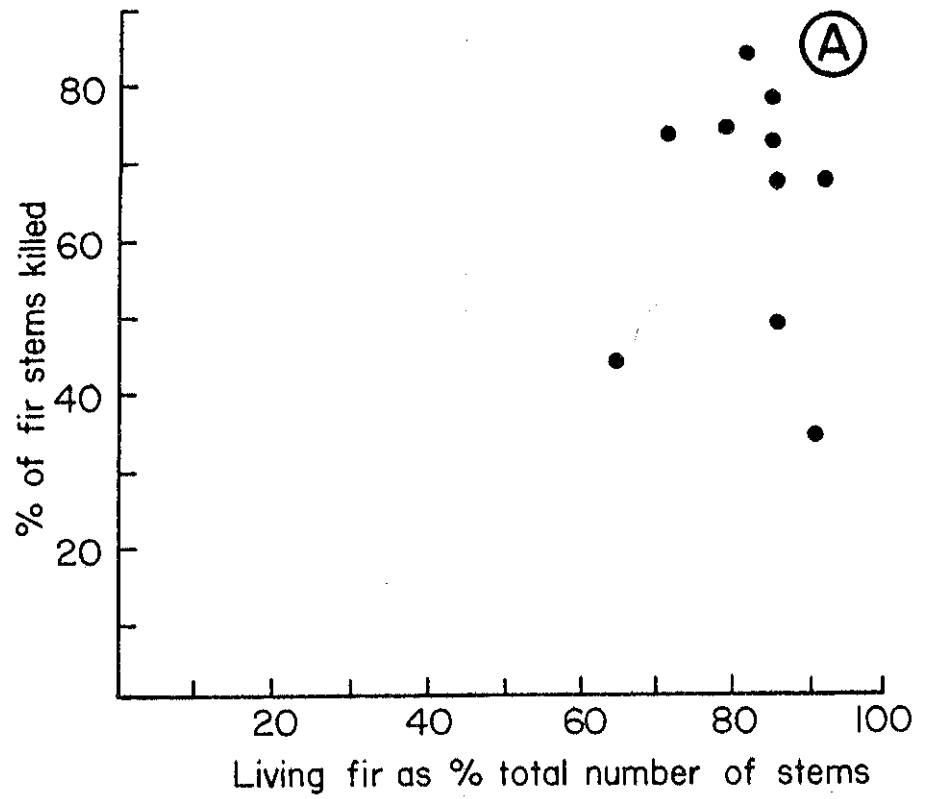
Fig. 1.   A — total fir mortality for the period 1956-61 related
to the proportion of fir in the stand.
B — total fir mortality 1956-61 related to density of
fir.

1956 1957

1958 1959

5m

1960 1961

● DOMINANT   + INTERMEDIATE
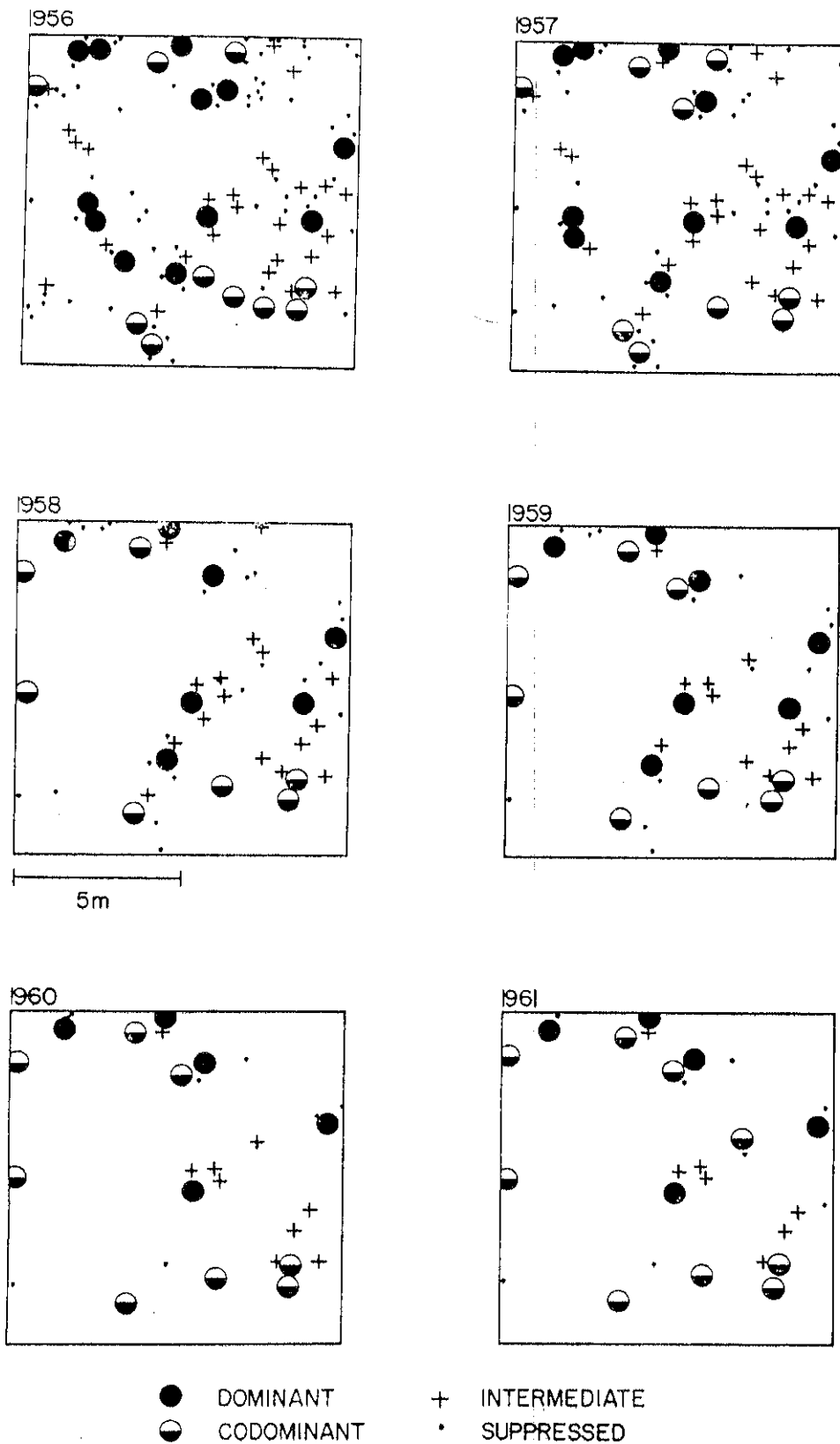◓ CODOMINANT   · SUPPRESSED

Fig. 2. Pattern of survival on a portion of a plot sustaining
average mortality during 1956-61. Yearly development
from age 35-40.

observations at the time) that the budworm pressure was not constant from plot to plot, it seems most reasonable that the variable mortality was a function of variable budworm pressure (such as might result from uneven within-stand adult dispersal) and was unrelated to stand characteristics.

The variability of mortality throughout the stand occurred on a scale even smaller than the 0.04-ha plots. Within plots there were striking patterns of mortality with sequential mortality tending towards a contagious distribution. Thus, 'holes' developed in the stand as mortality progressed (Fig. 2). These holes tended to become larger and larger, leaving the surviving trees in an increasingly clumped configuration. However, once the budworm-caused mortality had ceased, the pattern of mortality in these stands was similar to that in non-infested stands (Figs. 3 and 4).

While there was wide variation in total mortality from plot to plot, the sequence of mortality in time showed the same pattern on all plots. The first dead trees were recorded in 1957 and budworm-caused mortality was thought to have been complete by 1961. On all plots the greatest mortality occurred in 1959, the year after the budworm population collapsed. In 1961, it appeared that all surviving stems had regained sufficient foliage to be subject only to normal density-dependent mortality and annual assessment on the plots was discontinued. Subsequent analysis of the 1961 to 1965 mortality data showed, however, that mortality in this period was still somewhat higher than would be expected, if compared with uninfested plots of similar density (Fig. 5). The pattern of mortality in the least affected

plot was not much different from that in a stand of similar density that was not subjected to budworm. The spruce mortality in absolute terms was too small to plot on Fig. 5.

In support of the conventional wisdom that fir is more vulnerable to the budworm than black spruce, about 64% of the fir trees died whereas only 14% of the spruce trees were killed by defoliation (Table 3). Again there was variation from plot to plot in the proportion of species dying but this could not be related to stand characteristics. There was also a definite pattern to the crown class of the trees that died. In general, dominant trees made up a smaller proportion of mortality than they did of the stand before it became infested, while suppressed trees formed a larger proportion of the mortality (Table 4). Mortality therefore altered the crown class structure towards a larger proportion of dominant trees, almost to the exclusion of suppressed trees. Further, the tendency was for the suppressed and intermediate trees to die first. Both the timing of death by crown class, and the change in crown class structure can be seen in Figure 2. In this figure, all the suppressed and intermediate trees surviving in 1961 are either black spruce or white birch. Not a single suppressed or intermediate fir tree survived beyond 1960.

The tendency for loss of suppressed and intermediate trees seems contrary to the fact that budworm tend to survive best in the upper portions of open-grown crowns (Morris 1963). The apparent paradox results from the fact that larvae dropping from the larger crowns land on the lower crown classes. Although the populations
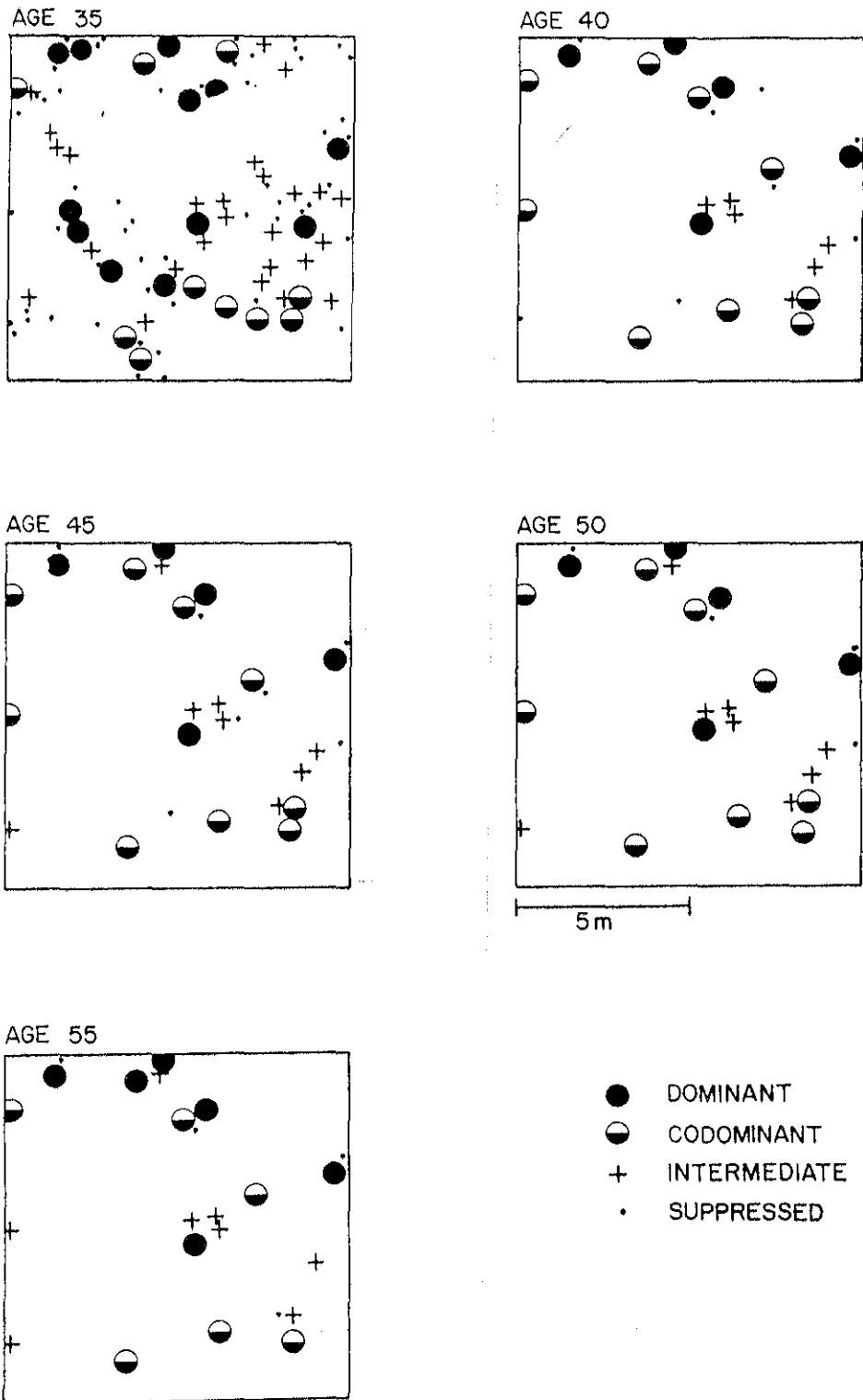
Fig. 3. Pattern of survival over a 20-year period for a portion of a plot sustaining average budworm-caused mortality between age 35 and age 40.

AGE 35

AGE 40

AGE 45

AGE 50

5m

AGE 55

⊛ .... DOMINANT

⊖ .... CODOMINANT
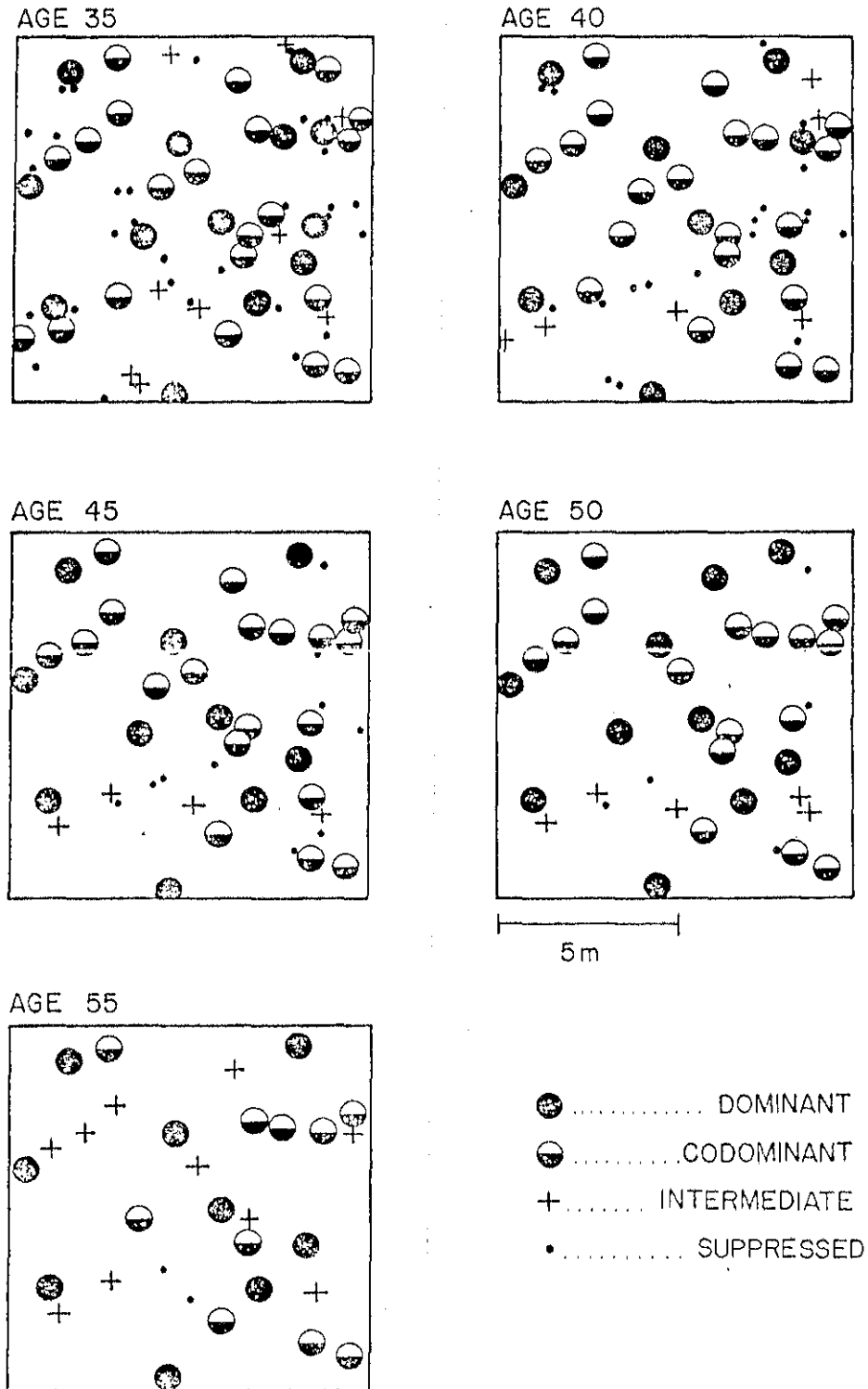
+ .... INTERMEDIATE

• .... SUPPRESSED

Fig. 4.   Pattern of survival over 20 years for a stand not affected
by budworm.

Table 4. The distribution of number of softwood stems and basal area per hectare by crown class for the initial stand and for the 1956-61 mortality

	Total	Domi-nant	Codom-inant	Inter-mediate	Sup-pressed	Over-story
		(percent of total)				
Initial stand	6165 stems ha^{-1}	17	17	26	39	1
Mortality	3970 stems ha^{-1}	12	14	27	46	1
Initial stand	37.9 m^{2}ha^{-1}	41	22	20	12	5
Mortality	18.7 m^{2}ha^{-1}	33	20	23	17	7

on the lower crown classes are less dense than on the dominant and codominant trees (Morris 1963) they are sufficient to defoliate and kill these weaker trees with smaller crowns.

The tendency for the budworm to kill smaller-than-average trees is also shown by comparing the mean diameter of trees that died (Table 5) with the initial mean diameter (Table 1). In every plot but one, the mean diameter of fir trees that died due to budworm feeding was smaller than the mean diameter of the stand before mortality began. While this difference was relatively small for fir, it was large for black spruce where the trees that died were on average much smaller than the average tree in the stand. An exception was plot 72, where one very large black spruce was killed giving an unusually large mean diameter of trees killed (Table 5).

Because of the differential pattern of mortality, the stand changed rather dramatically between 1956 and 1965 (Table 6). In terms of number of stems per hectare the average species mix changed as follows:

	Fir	Spruce	Birch
Proportion in 1956 (%)	83	8	9
Proportion in 1965 (%)	66	16	18

Table 5. The mean diameter breast height of trees dying from 1956-61.

	Mean dbh, cm	
Plot	Fir	Spruce
71	8.4	4.2
72	8.6	24.1
73	7.4	4.6
74	8.1	-
75	6.2	4.5
76	7.8	4.6
77	10.7	7.2
78	7.9	4.0
79	9.1	4.1
80	6.4	5.3

The change is consistent with higher mortality in fir than spruce. Further, in terms of canopy structure, the death of fir trees
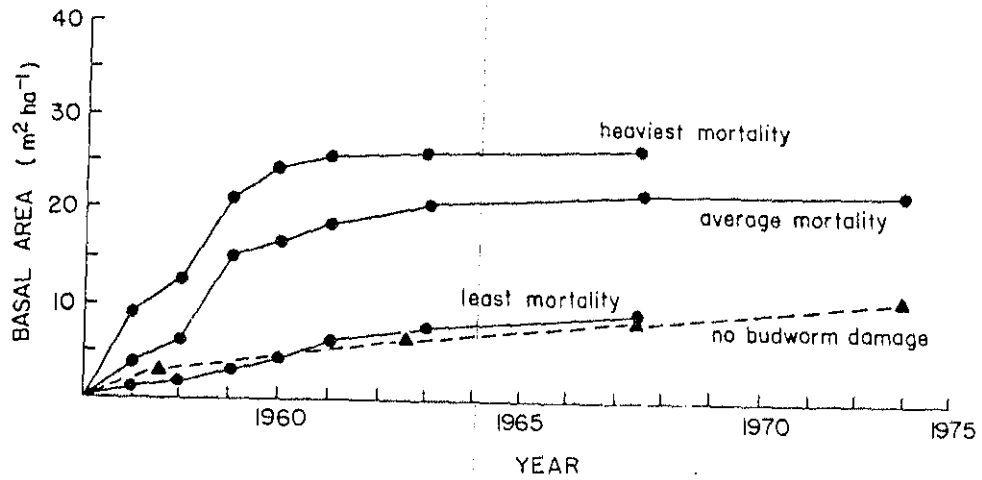
Fig. 5. Cumulative mortality of fir basal area on three plots subjected to budworm and one plot free of budworm damage.
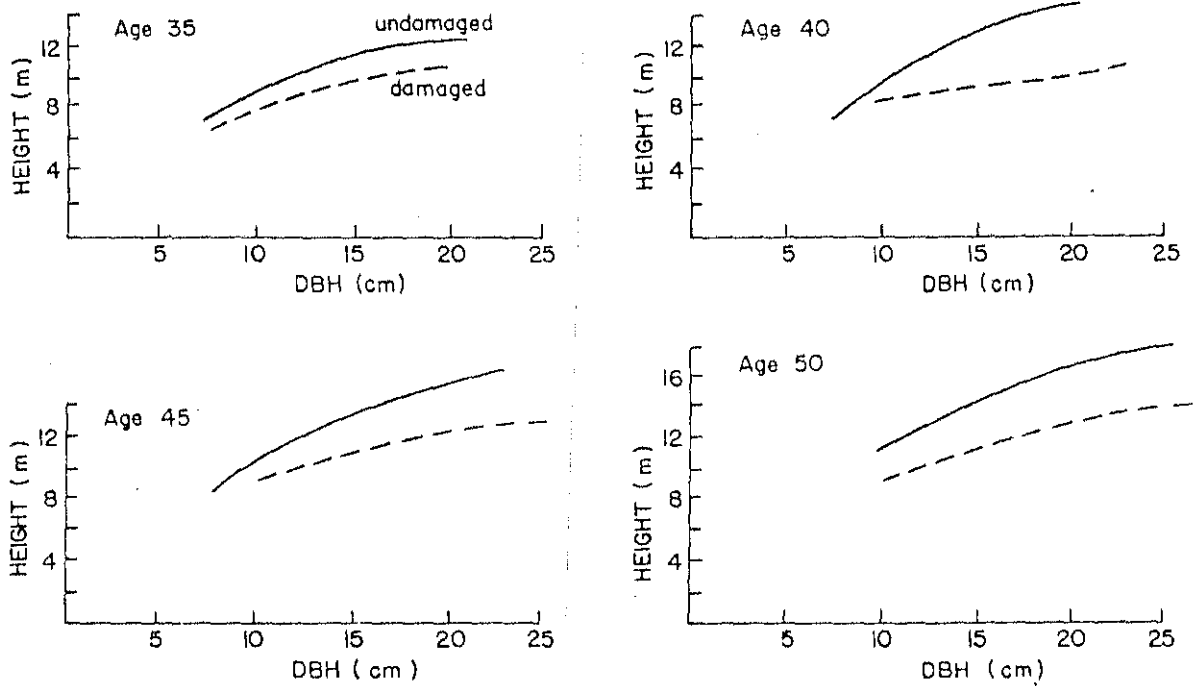

Fig. 6. The relationship of total height to diameter in the damaged and undamaged stands at four ages. The curves are means for all plots.

Table 6. Mensurational characteristics of the plots in 1965 after
cessation of budworm-caused mortality

	Density, stems ha^{-1}			Basal area, m^{2}ha^{-1}		
Plot	Fir	Spruce	Birch	Fir	Spruce	Birch
71	1038	865	469	12.9	7.6	1.6
72	667	124	791	7.3	2.3	5.0
73	1606	494	568	16.4	6.6	1.7
74	2669	247	124	30.8	1.5	0.3
75	2224	692	1260	27.5	9.4	4.7
76	1952	272	395	21.7	4.1	2.3
77	865	346	395	14.0	3.2	3.2
78	1507	494	445	18.8	7.1	1.9
79	1507	247	99	10.8	2.1	0.7
80	3608	519	395	29.3	3.9	1.8
Average	1764	430	494	18.9	4.8	2.3
Percent	66	16	18	73	18	9

resulted in a substantial improvement in the relative crown position of birch trees. In 1956, most of the birch trees were of intermediate crown position, and appeared to be dying out of the stand. In the plots not subject to budworm attack, the birch content did decline sharply over the study period. By contrast, the birch only declined from 591 stems per hectare to 494 stems in the attacked plots. There was a similar, although less dramatic improvement in the crown position of the black spruce as a result of the differential survival of the species.

For both fir and spruce, the loss of a number of trees of smaller - than - average diameter resulted in an increase in the mean diameter of the surviving stand even without any diameter growth.

Recovery of the Stands to the Present

In most respects, the stands have recovered remarkably well from the damage inflicted by the budworm in the 1950's. In 1978, casual observation of the stands described above would not detect the past damage. The dead trees have fallen to the ground and are largely decayed. The crowns of surviving trees are completely filled out and appear normal. The stands are more open than those that were not damaged in the 1950's, but the major difference is that the trees are substantially shorter than in the undamaged stands (Fig. 6).

Stem analysis of individual trees has indicated that the stands had comparable tree heights before defoliation began in 1951 (Fig. 7). By 1956 the trees in the damaged stands were slightly
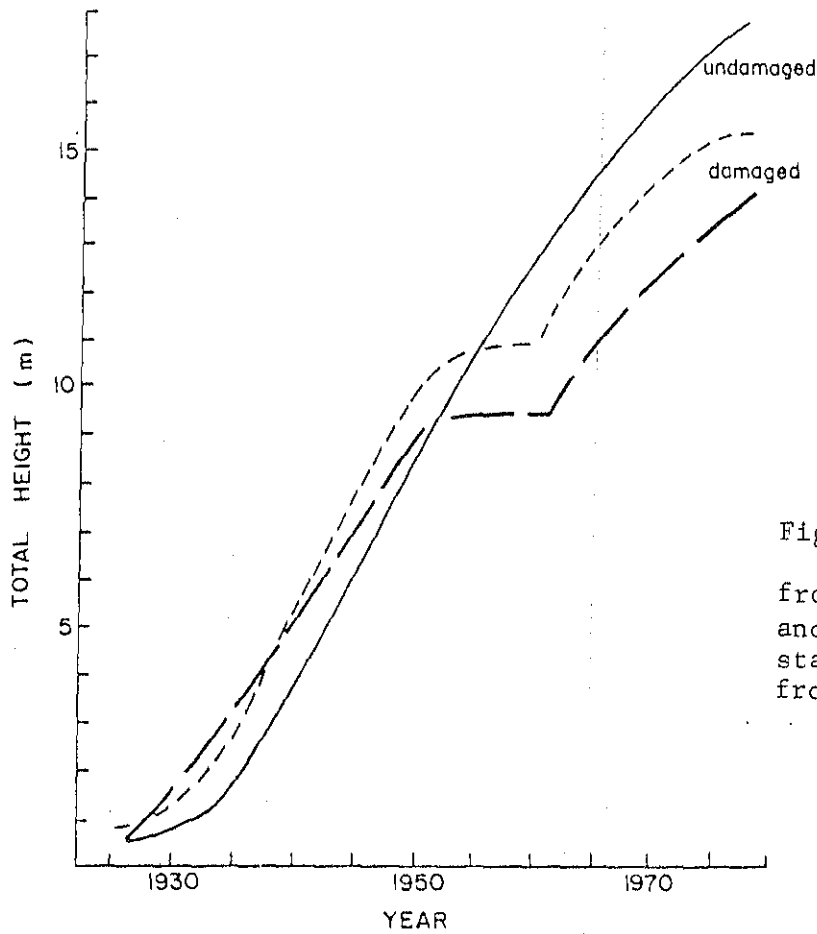
Fig. 7. Development of height over time for two trees from the stand damaged by budworm and one tree from the undamaged stand. The effect of defoliation from 1950 to 1958 is clear.
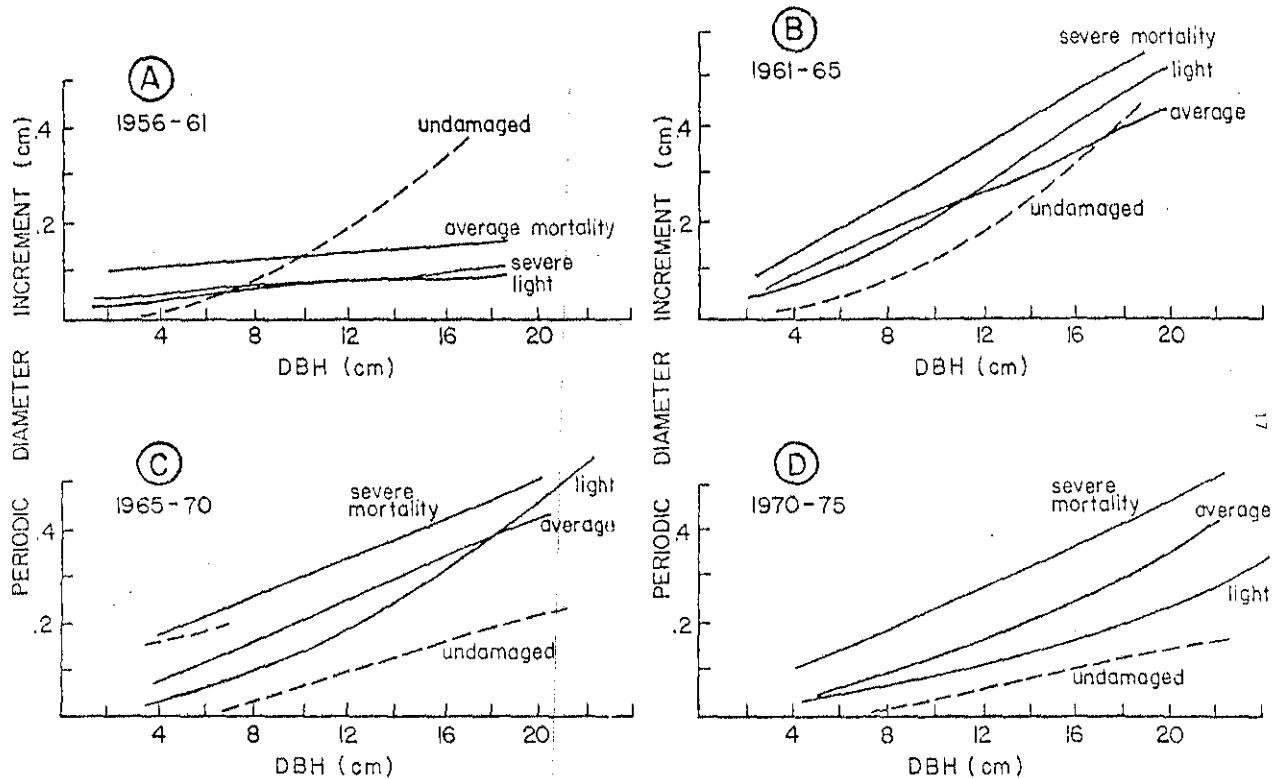

Fig. 8. Periodic annual diameter increment plotted on diameter for an unaffected plot and for three plots representing severe, average, and light budworm-caused mortality.

shorter, for an equivalent diameter, than the undamaged trees at the start of the study, because there had already been some top killing of the trees by 1956 and heights were measured to highest living leader. Figure 6 shows that, despite full recovery of the crowns, 20 years after the budworm attack (age 50), the total height of the trees in the damaged stands remains 3 to 4 m less than in the undamaged stands. Budworm defoliation typically begins at the top of the crown, and therefore moderate defoliation will result in the death of the leader and loss of one year's height growth. Persistent defoliation will result in the virtual elimination of height growth for several years (Fig. 7). With severe defoliation the problem is exacerbated, as not only is the leader prevented from developing, but the top of the tree can be gradually killed back, resulting in an actual reduction in total height. Thus, although after defoliation has ceased, height growth continues and the crown begins to recover, the limitation of height growth during the period of defoliation results in a loss of total height. In 1978 virtually every softwood tree in the study plots exhibited bole deformity of the type reported by Stillwell (1956) for trees surviving a budworm outbreak.

The recovery of fir crowns after the budworm population collapse in 1958 was startlingly fast. Trees either refoliated rapidly, with near full retention of each year's foliage until a full crown was established in approximately four years, or the tree just withered and died. The latter phenomena is probably related to the rootlet response noted by Redmond (1959) and Stillwell (1960). Defoliated trees that had

the capacity to regenerate roots and foliage recovered rapidly. Those that had retained some foliage, but which had suffered such extensive root die-back that the root system could not recover quickly, died as the recovering crowns outstripped the damaged root systems.

Under defoliation stress, some diameter growth continues as long as the tree survives, although at a reduced rate. The reduction in diameter growth can result in a reduced size for a given age, but, unlike the effects on height, defoliation can never make the diameter smaller. The pattern of diameter growth recovery is shown in Figure 8. Figure 8A shows the relationship of diameter growth to tree size for the period of most intense defoliation and mortality, 1956-61. Plots that suffered light, average, or heavy mortality showed minimal diameter growth for trees of all sizes during this period of intense stress. By comparison, an undamaged plot of similar density showed a normal diameter growth pattern substantially greater than in the damaged plots.

In the period following the heavy mortality, 1961-65, diameter increment on the damaged plots exceeded that on similar sized trees on an undamaged plot of the same preoutbreak density (Fig. 8B). Diameter increment recovered as rapidly as the crowns within five years of the population collapse. Following mortality, intertree competition in the stands was reduced, and those plots which had suffered the heaviest mortality showed the greatest diameter increment (Fig. 8B, C, D). This effect became more pronounced over time and, for the period 1970-75 (Fig. 8D), the greatest diameter growth was on

the plot that suffered the most mortality, followed by plots with average mortality, least mortality and those unaffected by budworm. That is, the trees damaged by budworm are now growing in normal open-grown stands and diameter growth shows the density-dependent relationships that one would expect.

The individual trees that survived the budworm outbreak fully recovered both height and diameter growth within five years of the budworm population collapse. Despite this, the recovery of stands on a per hectare basis has been disappointing. By 1975, only two of the 10 plots had recovered in terms of total volume per hectare to the predamage level (Table 7). That is, despite the complete recovery of height growth, and the increase in diameter growth of individual trees, 15 years after the budworm population collapse the total volume per hectare was less on most plots than it had been before mortality occurred. The increased growth per tree was not sufficient to offset the loss per hectare. By contrast, the total volume per hectare in the undamaged stands has increased

Table 7. The actual accumulation of total volume (m^3ha^{-1}) on the damaged and representative undamaged plots and forecasts of total volume at age 75.

	Total volume, m^3ha^{-1}					Projected to	Projection from age 35 without budworm damage	
Plot	Age 35	Age 40	Age 45	Age 50	Age 55	Age 75	Age 55	Age 75
71	170	90	104	131	161	222	392	480
72	158	38	49	65	*	107	400	494
73	197	87	118	150	178	343	324	371
74	168	130	168	204	*	284	406	500
75	172	154	196	228	*	317	398	488
76	194	107	135	170	*	410	348	390
77	194	76	97	123	145	208	446	545
78	208	110	133	167	194	273	348	397
79	155	51	63	87	115	231	398	492
80	182	135	161	*	*	254	328	372
1/	159	225	283	342	362	583		
2/	181	238	291	330	370	515		
3/	208	256	318	362	390	489		

* Plot not remeasured.
1/ Undamaged plot of low initial density.
2/ Undamaged plot of medium initial density.
3/ Undamaged plot of high initial density.

dramatically over the same period despite the lower growth per tree in these stands (Table 7).

Recovery of total volume in the damaged stands is being limited in two ways. First, the volume growth of individual trees is not as great as it would be in trees that had not sustained damage. The loss of several years height growth as evidenced in Figures 6 and 7 means that some 3 to 4 m of bole is 'missing' from the average tree. This missing length would now be near the base of the crown where maximum radial increment is laid down. Thus, the loss of height growth in the 1950's has made the trees in the damaged stand less productive in terms of volume growth simply because of the absence of a substantial portion of the base upon which volume growth occurs (Fig. 9). The two trees depicted in Figure 9 had similar annual volume growth up to the time of the budworm outbreak about age 28 years. The defoliation drastically reduced annual volume increment on the affected tree. The figure also shows that in at least two of the years of the 1950's outbreak, the trees in the unaffected plot were, in fact, affected. Further, the defoliation in both areas that began about 1970 (age 50) has again reduced volume growth on both trees. Note that both the reduction in volume increment and recovery occur rapidly with little or no delay. The second limiting factor is that of stocking. It is apparent that, for all but the least severe mortality levels, budworm-caused mortality reduced the stand density to below full stocking. While it is possible that continued rapid growth of the individual trees will eventually result in trees of sufficient size

to give full stocking again, this will be dependent on the amount and nature of the budworm-caused mortality sustained. The question of full stocking is a major issue that will be addressed in a separate paper making fuller use of the undamaged plots.

Projected Future Development of the Stands

Stands of the age described here are now nearing maturity and already form a substantial portion of the annual harvest in New Brunswick. This class of stands is extensive in area (N.B. Forest Inventory, 1958) and thus it is of interest to speculate on their probable development over the next 20 years as they mature and are harvested. Predictions for each plot were made using a simple mensurational model based on performance of the 12 undamaged plots during the 1955 to 1975 period. As a mensurational model, it assumes that growth relationships that have existed over the past 20 years will persist over the next 20 years. The relationship of total volume to number of stems per hectare was strongly linear for each plot with the slope depending on the initial volume/density condition. Stand projections were obtained by estimating the survival of stems per hectare from a regression and then reading volume per hectare from an extension of the 20-year volume/density relationship for the plot. Survival for the past 20 years was closely related to density (number of trees per hectare) and this relationship was used to forecast future survival.

For each of the 10 plots a forecast was made of the probable development from two initial conditions: (1) the stand at age 35
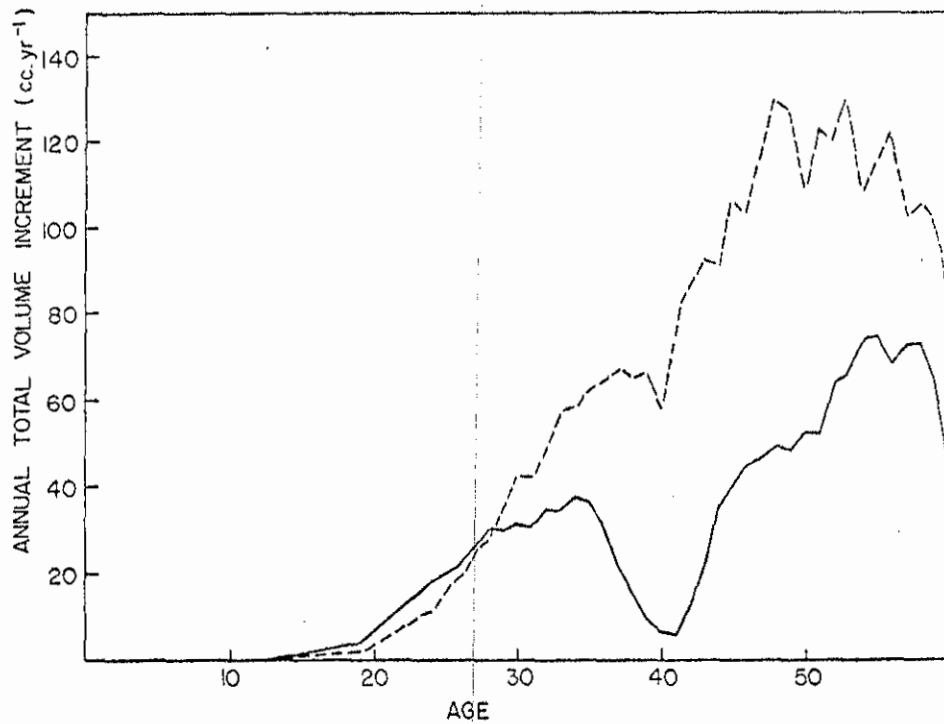
Fig. 9. Annual volume growth for a tree unaffected by budworm (broken-line) and for a tree suffering severe defoliation 1952-61 (solid line).
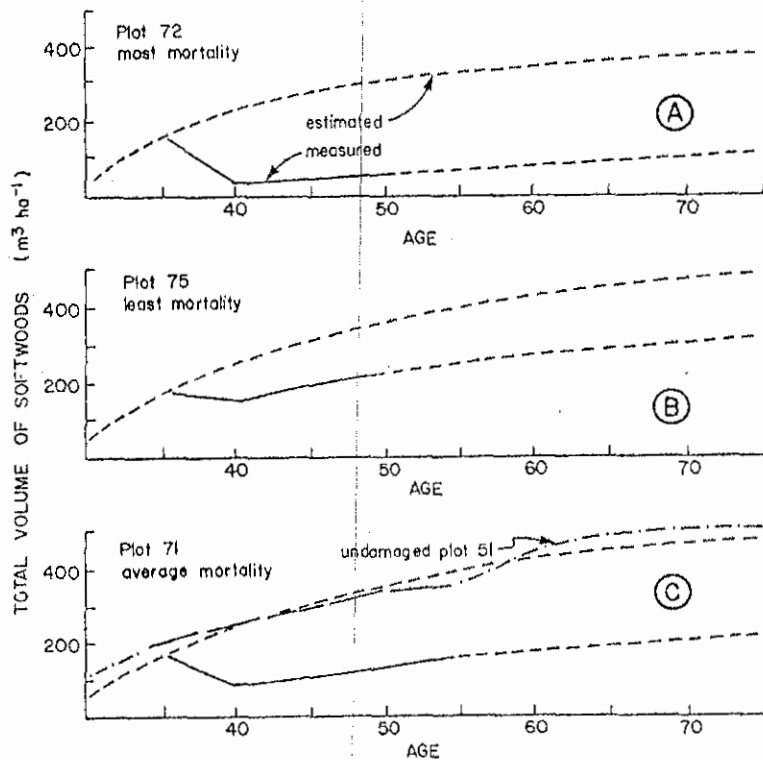

Fig. 10. Actual and simulated performance of several plots. A. The plot with highest mortality showing actual growth age 35-50, simulated growth after age 50, and simulated growth after age 35. B. Plot with least mortality. C. Plot with average mortality and an undamaged plot.

with no damage from budworm and, (2) the stand at age 55 as it had survived the budworm outbreak. These forecasts indicate several interesting points. Only one plot (number 76) showed an expected growth to a higher total volume by age 75 than it would have had without budworm damage (Table 7). All the other plots are predicted to have substantially less volume at age 75 than they would have had without damage from budworm.

The forecast pattern of development of total volume for three characteristic plots is shown in Figure 10. Figure 10A shows the expected development of the plot that suffered the greatest mortality. It is clear that the mortality in the late 1950's reduced the stocking in this plot to a level that makes recovery of total volume per hectare impossible despite exceptional growth per tree. At age 75 this plot is expected to have only 20% of the standing crop it would have had without budworm damage. The plot with the least mortality (Fig. 10B) is forecast to reach a much greater volume than the previous plot, but it still will reach just 65% of the volume it might have had at age 75 without budworm damage. The forecast development for the plot with near 'average' mortality, along with the actual and forecast development of a non-infested plot with similar initial stand conditions are shown in Figure 10C. At age 75 the average plot is forecast to have 45% of the volume it might have had without budworm damage.

All of the forecasts for damaged plots suggest open understocked stands at age 75. In fact, the forecasts range from 530 to 2200 stems per hectare with a total volume range of 107 to 410 m^3ha^{-1}. There were, until recent-

ly, large areas of softwood forest in the Green River and Kedgwick areas that developed following a budworm outbreak in the 1880's. These stands had suffered the 1913-19 budworm outbreak as dense immature stands (Morris 1963, Baskerville 1975). Virtually every stem in these stands showed evidence of deformity at about 10 m from the ground and stem analysis revealed this to be the loss of leaders during the 1913-19 outbreak (Stillwell 1956). Further, there was a strong feeling that these stands were understocked (Vincent 1955). A review of data for such 75-year-old stands (1965 data) indicated a range of 500-2500 stems per hectare and 170-350 m^3 per hectare. The forecast development for the damaged stands in this study is similar to those that have had similar damage in the past.

CONCLUSIONS

The loss in this stand, due to budworm-caused mortality during an uncontrolled budworm outbreak, was distributed in time in a manner similar to that described in the literature, peaking in the sixth and seventh year of defoliation as the budworm outbreak collapsed. In spatial terms, these losses showed high variability within the stand. Budworm-caused mortality ranged from 18 to 80% of the total volume per hectare on the 10 plots within a stand of about 8 ha in area. Although the plots showed variation in stand structure there was no clear relationship between the extent of this volume loss and characteristics of the stand. Mortality tended to occur in distinct patches spreading over time and thus to have a strongly contagious distribution. Almost all trees in these patches were

killed. The variation in mortality from plot to plot was thus related to the extent to which such patches occurred in each plot. Furthermore, because of the contagious pattern of mortality, plot size strongly influences the range of mortality in the data, and the detectability of a relationship between that mortality and predefoliation stand conditions.

The spatial variability of mortality has important implications for the study of stand vulnerability to budworm attack. Our data suggest that within-stand variability is high and apparently not related to stand characteristics. If this is a common occurrence, then conventional large scale, between-stand, sampling to establish the characteristics of stand vulnerability could easily lead to an artifact. Extensive sampling might lead to statistically significant relationships between mortality and average stand conditions. However, the interpretation of these conditions as the parameters of vulnerability, to be used silviculturally to reduce vulnerability, could well be erroneous if the mortality is not functionally related to average conditions.

Further exploration of the concept of vulnerability, particularly with reference to its silvicultural application, which will occur at the within-stand level, should address the causes of spatial variation, rather than simple statistical expressions of averages over large areas. Since these causes are related to some functional budworm/stand interaction it would appear that the nature of these functional relationships must be understood before sensible silvicultural prescriptions for reducing stand vulnerability can be prepared.

The depression of growth in individual trees was coincident with the period of defoliation, and with cessation of defoliation, the recovery of the surviving trees was swift and complete. That is, in neither case was there a detectable lag in the response. During the period of defoliation diameter growth was greatly reduced, and height growth virtually ceased. In fact, most surviving trees were slightly shorter after the outbreak collapsed than before because the tops had been killed back.

Within five years of the cessation of defoliation, the crowns of the surviving trees appeared fully recovered, and diameter and height growth were similar to that in unaffected stands. Diameter growth showed a classic response to the reduction in stand density (thinning), increasing substantially beyond predefoliation levels. Although individual trees showed good recovery of growth rate, this growth was on a smaller tree because of the growth reductions during the outbreak and there were fewer trees per hectare. As a result, the recovery in terms of volume per hectare was not complete. Only one plot had regained its predefoliation volume some 15 years after defoliation ceased.

A projection of development to age 75, on the assumption that the existing density-dependent mortality and growth-rate relationships persist for 20 years, shows that only one plot would reach the volume it would have had at that age without mortality caused by budworm. The range was from 22 to 105% of the projected volume without defoliation, averaging 60%. The damaged stands will be more open than unaffected stands, with larger trees (on average), but the stands will be substantially

understocked. Based on these projections, it appears that while these immature stands have recovered remarkably from the effects of intense uncontrolled defoliation, they will yield only slightly more than one-half of the projected volume at maturity.

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