RELATION BETWEEN MORTALITY OF TREES ATTACKED BY THE SPRUCE BUDWORM (CACOECIA FUMIFERANA CLEM.) AND PREVIOUS GROWTH [1]

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INTRODUCTION

In a recent bulletin [3] reference is made to the local variation in mortality following spruce budworm defoliation. Several factors are considered as influencing the percentage of mortality, namely: Character of defoliation, available soil moisture, effects of severe winters, maturity, composition of the forest, and vigor of the trees.

But little data bearing directly on this last factor had been collected. In an earlier paper [4] the following quotation occurs: "The dying may be likened to a greatly accelerated natural thinning that takes place in a normal forest. It is suppressed or overmature trees that die first; younger stands suffer least."

In the first quoted bulletin [5] the writer makes the following statement: "The vigor of the stand at the time of the budworm attack largely determines the condition in which it will come through." The higher mortality in older forests as compared to younger forests is very striking, yet often spotted and by no means uniform; in second-growth stands, which suffer less, areas of high mortality are frequently found.

In comparing the rate of growth of trees dying on sample plots it was found that the slow-growing trees died first as well as those receiving heaviest defoliation, as illustrated by balsam in Table I.

A more detailed study of this feature was contemplated for the summer of 1922, but time did not permit its ful-

TABLE I.—*Radial increment in millimeters for 10-year period before budworm attack of trees dying at different periods*

[The first feeding occurred in 1918, the first mortality in 1920. Based on 2-acre plots containing over 350 trees, Lake Opasatika, Quebec]

	Summer 1920	Winter 1920–21	Summer 1921	Winter 1921–22	Summer 1922	Winter 1922–23
Increment in mm	8.2	10.5	10.9	11.7	14.0	15.4
Percentage of defoliation [a]	77	81	70	62	57	46
Average diameter, in inches	5.9	4.8	5.7	6.7	6.9	6.1

[a] Percentage of defoliation refers to old needles only at the end of the outbreak in 1921, or earlier in case of death. The new growth was completely destroyed each year from 1918 to 1921, inclusive.

[1] Received for publication April 22, 1924; issued June, 1925.

[2] This study was conducted by the writer as part of the 1923 program of work of the Division of Forest Insects, Dominion Entomological Branch, Ottawa, Canada.

The undertaking was greatly facilitated through the interested assistance of R. E. Balch and H. J. MacAloney, graduate students from Guelph College, Ontario, and the New York State College of Forestry, respectively. The collection of the data for Tables IV to IX and parts of Tables XII and XIII was made by the writer in person. On the remainder of the plots both the selection and tabulation were left entirely to the discretion of Balch and MacAloney. The compilation of the data was made by all three members of the crew. J. D. Tothill also assisted in taking some plots.

W. G. Wright, in charge of research work for the Dominion forestry branch, Ottawa, kindly assisted with suggestions concerning the tabulation of the data. E. N. Munns, Raphael Zon, and S. T. Dana offered valuable assistance through constructive suggestions on the preliminary manuscript.

This presentation represents a considerable condensation of the original manuscript, copies of which, with complete tables and data, are filed at the Bureau of Entomology and Forest Service, Washington, D. C., the Entomological Branch, Ottawa, and the New England Forest Service Experiment Station, Amherst, Mass.

[3] SWAINE, J. M., and CRAIGHEAD, F. C. STUDIES ON THE SPRUCE BUDWORM. Canada Dept. Agr. Bul. (n. s.) 37, 92 p., illus. 1924.

[4] CRAIGHEAD, F. C. BUDWORM INFESTATION VS. PULPWOOD PRODUCTION. 2. Amer. Paper and Pulp Assoc., Woodlands Sect. Ser. Proc., Ann. Meeting 2: 8–10, 1922.

[5] Footnote 3, Part II of this bulletin.

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fillment. During the summer of 1923 data on a series of plots in various forest types were taken near Bathurst, New Brunswick, and Metis Lake, Quebec.

The studies were concentrated on second-growth forests. Mature forests, where the mortality was much higher, were avoided, owing to the complication of other factors, such as periodic cuttings. It was also deemed advisable to put more time on the second-growth stands, since such results would be more directly applicable to forest conditions of the future.

EXPLANATION OF DATA

In the softwood forests one-tenth acre plots were used. It was found that this size suited the purpose better, since the variation in injury was quite local and spotted. The percentages of balsam, red spruce, and white spruce, and the basal area and average diameter are based on the total of softwoods only; the percentage of hardwoods is that of the total number of trees on the plot. The average diameter was computed from the basal area. All trees from 3-inch diameter breasthigh and up were tallied and all data computed on this basis. This naturally gives a low expression for average diameter.

The percentage of mortality was computed on the basis of number of trees rather than on volume or basal area. No volume tables were available for these small diameters, and it was thought that percentages by trees would give a better expression of the effects of defoliation on the plots, especially the suppressed ones. In cases where the injury is low, it would often be quite negligible if computed in volume.

All increments are expressed in millimeters, showing the radius for a 10-year period unless otherwise stated. In each plot a varying number of cores were taken at breastheight (by means of an accretion borer), depending on the percentage of the species and number of each dead. At least 10 cores from dead and living trees of each species were secured, or, if the number of trees in such classes was small, at least half were taken. No definite method of selecting trees was used; the plot was gone through and all trees taken as encountered selected from all diameter classes. In computing the average rate of growth for each species on the plot, averages were first obtained from the selected cores for both dead and living trees. These averages were multiplied by the total number of dead and living trees, respectively, added and divided by the total number of that species on the plot. On the first few plots the average rate of growth for each species was determined from dominant trees only, average-diameter trees, all trees or the method described. The variation between different plots as expressed by dominant trees and average-diameter trees was considerable, but that between the last two methods was so slight that the one involving less time was adopted.

The 10-year period previous to budworm attack was counted back from the enlarged ring produced by the defoliation. This is very marked on balsam. In spruce, where the enlargement is less pronounced, the year of budworm attack (previously determined for the region) can be counted back from the last ring formed, but this is not reliable for balsam, owing to the fact that two or three rings may fail to form on parts of the circumference and not show on the increment core. On dead or dying trees, both spruce and balsam, the enlarged ring must be utilized for orientation, since from two to four rings may fail to form previous to death.

CHARACTER OF BUDWORM DEFOLIATION [6]

A brief description of the character of the budworm feeding will help to explain certain results of the tabulated data. Previous investigations have shown that the severity of defoliation is the primary cause of death of the trees through inhibiting normal physiological functions.

The degree of defoliation of the spruce and balsam is chiefly due to the variation in development of the new growth, to the migratory habits of the larvae, and to the fact that the old foliage of spruce is not consumed by the larvae. For normal development, the young caterpillars require new foliage as food. They begin feeding at the time the balsam and white-spruce buds open. During epidemics their abundance is such that the new growth of balsam is consumed by the time the caterpillars are half grown; in the later instars they are able to subsist on the old needles and consume up to 100 per cent of these. White spruce furnishes a greater abundance of new growth, so that rarely do the larvae consume all of it before the needles harden. This hardening of the needles takes place about the time the caterpillars are half grown, causing

[6] For more detail see reference, footnote 3.

them to migrate in search of more succulent food. It is possible that slower-growing white-spruce trees putting out a less quantity of new growth are entirely defoliated of the current year's needles before they harden. Red spruce, the buds of which open 10 to 12 days later than balsam and white spruce (shortly before the larvae begin migrating), furnishes a second supply of succulent needles at a time when the larvae are most voracious; consequently much of it is consumed.

The density of the stand affects the degree of defoliation in that migrating larvae have a better chance of falling on other food before striking the ground, from which they can not regain the trees. As a result of this migrating habit of the larvae no trees, even balsam, standing in the open are defoliated of more than their new growth.

Higher percentages of balsam and white spruce encourage to a certain extent heavier defoliation on account of the greater supply of desirable food (early new growth), which enables the larvae to develop rapidly in their early stages.

Balsam is always more severely defoliated than white or red spruce, since the old needles are also consumed; consequently, the feeding is less uniform and offers an explanation for lack of correlation between mortality and rate of growth under conditions of severe feeding. White and red spruce are defoliated only of the new growth, white usually to a lesser degree than red, and both more uniformly than balsam. The amount of defoliation on the balsam sample plots at Lake Opasatika, Quebec, from 1918 to 1921 is shown in Table II.

Dominant trees, especially those highest in the stand, are less severely defoliated than those beneath, owing to the migrating habits of the larvae. Table III illustrates this feature on the balsam sample plots at Lake Opasatika. The figures apply only to old foliage, since all the new growth was consumed each year.

Thus the understory, which at the same time is composed of slower-growing trees, receives more defoliation. This does not apply to light outbreaks when, with abundance of food, the larvae do not migrate.

SECOND-GROWTH SOFTWOOD AND BUDWORM MORTALITY

Two widely separated areas were considered in these studies, centering about Bathurst, New Brunswick, and Metis Lake, Quebec.

The Bathurst plots were located about 15 to 20 miles south of Bathurst, on the Tabusintac drainage. The soil is of a light sandy character, formed from the millstone grit of the middle Carboniferous. It is fairly thin and subject to excessive drying out, except on the hardwood ridges, where it is much deeper and of a loamy character. It fairly well characterizes the Miramichi watershed, noted for its spruce forests.

The other series of plots were taken on the south shore of the St. Lawrence River near the height of land between the Metis and Patapedia Rivers, on a seigniory of Price Brothers at Metis Lake, Quebec. It is essentially a softwood region, only scattered yellow and white birch occurring, except on the tops of the higher hills. Some 40 years ago the area was very heavily cut over, so that the present stand averages about 75 years of age. A few older trees occurred on many plots. An attempt was made to secure the plots in more uniform younger growth and at the same time to select plots which showed higher mortality. Consequently, these figures are not quite typical of the area.

In the vicinity of Bathurst 40 plots were tallied in practically pure softwood stands. An attempt was made to group these by series conforming to site qualities, types, and age classes. Tabulation of 24 plots is given occurring on a 65-year burn representing three sites of the spruce flat type. The remaining plots were more scattered in

TABLE II.—*Percentage of trees in arbitrary defoliation classes*

Degree of defoliation	100	90	75	50	25	10
Percentage of trees in class	5.6	10.6	16.9	33.2	23.8	9.9

TABLE III.—*Percentage of defoliation by diameter classes*

Diameter breasthigh, inches	2	3	4	5	6	7	8	9	10	11	12
Number of trees	4	47	65	31	57	54	44	30	19	11	11
Average defoliation, per cent	54	77	66	64	51	46	42	29	28	28	14

various age classes up to 100 years and in jack pine and spruce swamp types. In general they conformed to the results here shown, but the number of plots on each condition was not sufficient to be conclusive, and consequently they are not included. Altogether, measurements were recorded from over 3,000 increment cores.

The defoliation on these plots was very severe, and all evidence indicates that it was quite uniform for the entire area.

The Metis plots, Tables X and XI, were chosen because of light budworm feeding for comparison with the heavy feeding in the Tabusintac area. The attack began in 1913. Although the percentage of balsam was high, the feeding apparently only lasted, with any degree of severity, for one year. This was reported from observations of the company officers who frequently visit the place during the summer. It is also further substantiated by the more rapid recovery, or greater increment for the 10-year period following defoliation, as compared to any other regions of Quebec and New Brunswick which have been studied. (See Table XVIII.)

The reason [7] for the light feeding, which is certainly due to the early dying out of the infestation, has been unexplained. It may have resulted from weather conditions. A similar state prevails eastward throughout the Gaspe Peninsula.

This series of plots was selected and tallied by Balch and MacAloney. The writer had previously visited the region on two occasions, but did not go over the present work. No attempt was made to segregate these plots by types or quality sites.

This region as a whole is characterized by preponderance of white spruce over red spruce.

TABLE IV.—*Composition of plots, Bathurst, New Brunswick*

No.	Balsam	Red spruce	White spruce	Hardwoods	Number of trees	Average diameter [a]	Basal area	Height	Largest trees [b]	
									Number	D. b. h.
	Per cent	*Per cent*	*Per cent*	*Per cent*		*Inches*	*Sq. in.*	*Feet*		*Inches*
7a	7.1	92.9	0	0	70	5.3	10.68	45	6	8
7	0.0	100.0	0	0	108	5.7	19.02	55	3	9
8	3.8	96.2	0	0	105	5.6	18.40	50	2	10
9	2.1	97.9	0	0	96	5.7	17.21	55	3	9
7c	13.2	86.8	0	0	106	5.9	20.31	60	2	10

[a] Includes trees 3 inches d. b. h. and over.
[b] The expression "Largest trees, d. b. h.," indicates the diameter class of the largest trees, and "Number," the number of trees in that class.

TABLE V.—*Radial increment in millimeters at d. b. h. from 1903 to 1912, inclusive, and mortality, of trees in plots of Table IV* [a]

No.	Dead spruce	Radial increment of spruce		
		Living	Dead	All
	Per cent			
7a	13.8	8.6	5.8	8.2
7	14.7	8.4	7.3	8.2
8	21.7	7.3	5.8	7.0
9	50.0	6.7	6.2	6.4
7c	49.0	5.5	4.4	5.0
Average	----------	7.6 (94)	5.8 (54)	6.9

[a] Figures in parentheses refer to number of measurements.

[7] Heavy rainstorms at the time of opening of the buds and severe frosts, killing the new growth, have both been reported by Tothill and Craighead as causing high mortality in the budworm larvae.

TABLE VI.—*Composition of plots, Bathurst, New Brunswick*

No.	Balsam	Red spruce	White spruce	Hardwoods	Number of trees	Average diameter	Basal area	Height	Largest trees: Number	Largest trees: D. b. h.
	Per cent	*Per cent*	*Per cent*	*Per cent*		*Inches*	*Sq. in.*	*Feet*		*Inches*
3d	12.6	67.2	21.2	10.7	67	6.8	16.75	60	5	11
3c	4.8	75.0	20.2	1.2	84	6.8	20.49	60	2	11
3b	7.7	62.6	29.7	1.0	91	7.1	24.87	60	2	14
3a	30.2	52.4	17.4	1.5	63	8.0	24.17	70	1	15
9b	8.2	91.8	0	15.5	98	6.0	19.49	57	3	10
9a	5.8	94.2	0	8.4	87	6.1	17.77	55	2	10
6a	5.5	67.5	27.0	0	111	6.3	24.35	56	2	11
6b	1.2	67.4	31.4	11.9	89	6.1	18.20	56	3	10

TABLE VII.—*Radial increment in millimeters at d. b. h. from 1903 to 1912, inclusive, and mortality of trees in plots of Table VI* [a]

No.	Balsam, increment				Red spruce, increment				White spruce, increment				All spruce	
	Dead	Living	Dead	All	Dead	Living	Dead	All	Dead	Living	Dead	All	Dead	Increment
	P. ct.	*Mm.*	*Mm.*	*Mm.*	*P. ct.*	*Mm.*	*Mm.*	*Mm.*	*P. ct.*	*Mm.*	*Mm.*	*Mm.*	*P. ct.*	*Mm.*
3d	14.3	9.7	------	9.7	2.2	10.6	------	10.6	7.1	13.3	------	13.3	3.4	11.2
3c	50.0	7.0	------	7.0	3.2	10.6	6.0	10.4	35.3	11.4	4.6	9.0	10.0	10.3
3b	28.5	12.0	3.0	9.4	10.8	9.9	------	9.9	44.4	10.0	5.9	8.1	15.4	9.3
3a	100.0	------	9.2	9.2	15.1	9.4	7.2	9.1	36.4	8.9	6.0	7.8	20.5	8.8
9b	50.0	16.0	17.0	16.5	23.3	9.0	7.2	8.6	------	------	------	------	23.3	8.6
9a	100.0	------	7.7	7.7	40.3	9.0	6.2	7.8	------	------	------	------	40.3	7.8
6a	33.3	------	------	------	40.0	8.9	7.0	8.1	66.6	8.6	4.9	6.1	47.6	7.6
6b	100.0	------	------	------	41.7	8.8	5.5	7.4	53.7	10.0	2.7	6.1	45.4	7.0
Average	------	11.6 (12)	9.4 (16)	10.4	------	9.5 (118)	6.5 (54)	8.5	------	10.5 (40)	4.8 (29)	8.1	------	------

[a] Figures in parentheses refer to number of measurements.

TABLE VIII.—*Composition of plots, Bathurst, New Brunswick*

Plot No.	Balsam	Red spruce	White spruce	Hardwood	Number of trees	Average diameter	Basal area	Height	Largest trees (65 years): Number	Largest trees (65 years): D. b. h.
	Per cent	*Per cent*	*Per cent*	*Per cent*		*Inches*	*Sq. in.*	*Feet*		*Inches*
18	21.4	28.6	50.0	0	57	6.9	15.42	70	2	15
7b	53.2	42.0	4.8	26.2	62	6.0	12.78	65	1	12
17a	1.2	73.2	25.6	0	82	7.0	22.11	65	2	12
16	11.6	26.8	61.6	0	112	6.5	25.61	65	3	11
17	22.2	29.6	48.2	0	54	8.4	20.75	68	3	12
15	15.6	31.1	53.3	2	90	7.9	26.32	65	3	10
7	30.3	63.2	6.5	10.6	76	6.2	15.96	60	2	10
7a	39.5	51.1	9.4	2.3	86	6.5	19.97	61	2	11
14a	26.4	46.1	26.4	4.7	121	5.8	22.37	60	6	9
13	15.6	6.9	77.4	0	116	7.0	31.08	60	1	13
14	57.6	5.6	36.8	0	126	5.8	23.46	60	1	10

TABLE IX.—*Radial increment in millimeters in d. b. h. from 1903 to 1912, inclusive, and mortality in trees of plots of Table VIII* [a]

Plot No.	Balsam, increment				Red spruce, increment				White spruce, increment				All spruce	
	Dead	Living	Dead	All	Dead	Living	Dead	All	Dead	Living	Dead	All	Dead	Increment, all
	P. ct.	*Mm.*	*Mm.*	*Mm.*	*P. ct.*	*Mm.*	*Mm.*	*Mm.*	*P. ct.*	*Mm.*	*Mm.*	*Mm.*	*P. ct.*	*Mm.*
18	0	15.1	------	15.1	0	9.4	------	9.4	0	9.7	------	9.7	0	9.6
7b	64.2	11.7	7.8	8.9	3.8	9.1	13.0	9.3	33.3	12.7	2.0	9.8	4.8	9.2
17a	0		------	------	5.0	11.9	13.3	11.9	14.3	6.2	4.5	6.0	7.4	8.0
16	77.0	------	10.6	10.6	16.6	10.6	7.8	10.1	29.0	7.1	3.1	5.9	25.2	7.2
17	91.7	------	9.1	9.1	43.7	6.3	7.1	6.0	30.8	8.1	4.6	7.0	35.7	6.9
15	100.0	------	6.1	6.1	28.6	7.0	7.2	7.1	45.8	9.2	4.8	7.2	39.5	7.1
7	91.4	------	7.0	7.0	40.0	7.2	7.6	7.3	60.0	5.0	2.0	3.3	41.5	7.0
7a	97.1	------	9.7	9.7	52.3	6.9	6.6	6.7	50.0	5.0	2.5	3.7	52.0	6.3
14a	100.0	------	6.2	6.2	50.9	7.6	6.3	6.9	65.6	5.0	3.4	4.0	56.2	6.0
13	61.1	------	7.7	7.7	50.0	10.7	8.5	9.6	75.3	6.8	4.3	4.9	73.2	5.3
14	100.0	------	6.2	6.2	71.4	------	------	------	80.4	6.6	5.3	5.4	79.2	5.4
Average		13.5 (11)	7.4 (68)	8.3	------	8.9 (91)	7.5 (55)	8.3	------	7.5 (68)	4.2 (61)	5.9	------	------

[a] Figures in parentheses refer to number of measurements.

TABLE X.—*Composition of plots, Metis Lake, Quebec* [a]

Balsam	Dead balsam	Red spruce	Dead red spruce	White spruce	Dead white spruce	Hardwoods	Average number trees per plot	Average diameter	Average basal area	Average height	Average age, in years
Per cent	*Per cent*	*Per cent*	*Per cent*	*Per cent*	*Per cent*	*Per cent*		*Inches*	*Sq. in.*	*Feet*	
79.1	39.1	5.3	0	15.6	11.6	5.7	88.8	6.7	21.14	60	70

[a] Based on 33 plots.

TABLE XI.—*Radial increment in millimeters from 1903 to 1912, inclusive, and mortality of trees in plots of Table X. Plots averaged by groups in percentage classes* [a]

Dead	Balsam, increment			White spruce, increment			Red spruce, [b] increment
	Living	Dead	All	Living	Dead	All	Living
Per cent	*Mm.*	*Mm.*	*Mm.*	*Mm.*	*Mm.*	*Mm.*	*Mm.*
0 to 5	12.4	2.0	12.3	11.8	3.2	11.1	------
5 to 15	10.6	5.0	10.4	10.6	5.3	10.0	------
15 to 25	10.2	5.0	9.2	11.2	5.8	10.0	------
25 to 35	9.5	5.3	8.0	9.3	3.5	7.6	------
35 to 45	8.3	5.0	6.9	------	------	------	------
45 to 55	8.8	4.4	6.7	7.5	2.5	5.0	------
55 to 65	8.1	5.2	6.3	7.5	3.5	5.1	------
65 to 75	7.8	4.4	5.2	------	------	------	------
Average	9.0 (507)	5.0 (335)	7.4	9.6 (220)	4.3 (43)	8.8	8.4 (77)

[a] Figures in parentheses refer to number of measurements.
[b] Too few trees per plot to be considered.

From the data collected and from general observations made, certain conclusions are drawn concerning budworm mortality and silvicultural characteristics of balsam fir, white spruce, and red spruce. These, since they are based on limited areas, are presented as tentative and with the object of inviting criticism and further investigations from the foresters and entomologists familiar with the budworm infested regions. It is fully realized that with so many factors to consider it is practically impossible to make comparisons of conditions alike except for one factor and that the results brought out in this paper are largely suggestive rather than conclusive.

There is a certain correlation between vigor of the stands (as expressed by increment at breastheight) at the time of defoliation and budworm mortality such that it can be said the more rapid the rate of growth the lower is the mortality resulting from defoliation. This expression of the probable effects of budworm feeding is a more tangible quantity than any of the other factors heretofore considered, and should serve as a practical basis for preventive measures through proper silvicultural practices which maintain rapid growth.

There may be different minimum rates of growth, entailing immunity for different sites, types, and age classes, indicating the necessity of further investigation in conditions other than those discussed here.

All the data bearing on density and basal area were plotted with the assistance of E. N. Munns, but no correlation was found. Percentage of balsam in the mixture was likewise considered, but this bore no relation to the mortality of the spruce.

The correlation between rate of growth and mortality for balsam is not at all regular for the Bathurst series (figs. 1 and 2, Tables IV to IX), owing to the severe infestation in that region, resulting in complete defoliation of many trees. From 75 to 100 per cent defoliation will kill even very vigorous trees. The correlation for the white and red spruces is much more regular. These trees are more uniformly defoliated, only the new growth being eaten for three to four years; that for combined red and white spruce is still more regular, the explanation being doubtful unless it is because of the greater number of trees averaged. On the Metis area (Tables X and XI, fig. 2) the correlation between rate of growth and mortality for balsam is quite regular; that for white spruce shows very little correlation. Here the dead spruce trees are all small suppressed trees of the understory (see Table XVII, mortality by diameter classes) as compared with the Bathurst spruce and Metis balsam. In fact, so few spruces are dead that the entire mortality in these trees is considered to be that of a normal forest and gives a series of plots for contrast to conditions at Bathurst.

The diameter class tallies by species as well as by observation on the stumps of many felled trees indicate that

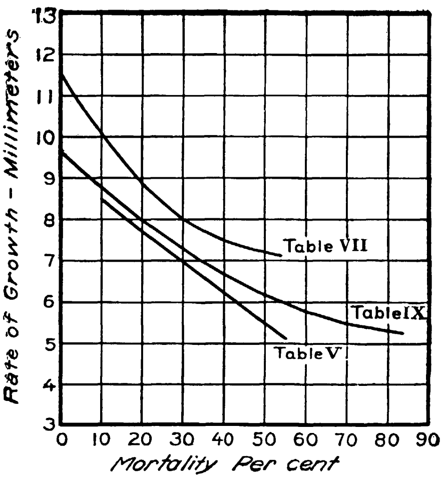

FIG. 1.—Diagram illustrating rate of growth of spruce and mortality resulting from spruce budworm defoliation as recorded in Tables V, VII, and IX

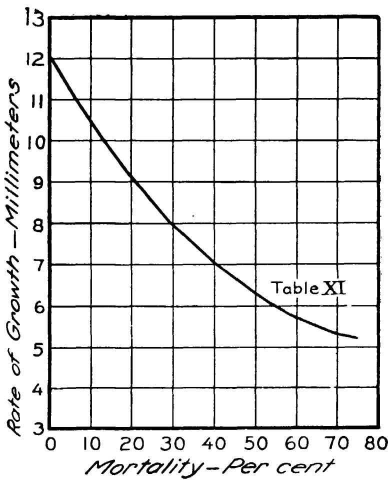

FIG. 2.—Diagram illustrating rate of growth of fir and mortality resulting from spruce budworm defoliation as recorded in Table XI

second-growth white spruce grows faster than either red spruce or balsam during the first 40 to 50 years, but after certain densities are reached its growth is retarded and it can not compete as well as red spruce. Considering the higher mortality of white spruce compared to that of red spruce in 60-year stands, the relatively lighter feeding (excepting the possibility that slow-growing trees may be subject to heavier defoliation) and the average slower rate of growth for dying trees, it may be considered that white spruce is more susceptible to budworm attacks than red spruce. This suggests that it should be encouraged only when good vigor can be maintained. Also a higher percentage of white spruce, like balsam, enhances heavier average defoliation of adjacent red spruce owing to the abundant food supply in the early feeding stages.

Balsam is the most susceptible under all conditions, since it is completely defoliated in heavy outbreaks. On the other hand, the Metis plots indicate, as well as certain Bathurst plots, that vigorous stands are more immune. Since balsam is a very fast grower, and reproduces abundantly and under adverse conditions, it might well be encouraged for the first 30 to 40 years. The only argument against it is that over wide areas it is considered the most important factor in giving impetus to an outbreak, though balsam is probably no more effective in this respect than is a mixture of white spruce and red spruce.

HARDWOOD MIXTURES AND BUDWORM MORTALITY

Two series of plots (Tables XII, XIII, XIV, and XV) were taken in hardwood mixtures. The object was to obtain some idea of the effect of budworm feeding on the free and overtopped softwoods in such stands. It has been held by several investigators that the mortality in hardwood mixtures is always considerably lower than in pure softwoods.

Two types were considered. Tables XII and XIII summarize 19 plots, totaling 3 acres, in a 60 to 65 year birch-poplar type on the same area as the softwood plots of Tables IV, VI, and VIII. Tables XIV and XV summarize 11 plots, totaling 3½ acres, in a northern hardwood type on the Bathurst area. This area has been subjected to periodic cuttings in the past. No white spruce occurred. The largest diameter for softwoods was about 20 inches. These plots were located on the top of a low ridge on the best growing site in the region.

Percentage expressions are the same as for previous plots except that total percentage of hardwoods is calculated on the basis of all trees on the plots. This expression was not considered a fair indication of the hardwood canopy, so the percentage of overtopped softwoods is used as indicating the amount of hardwood canopy. Two classes of softwoods were considered—overtopped, those whose terminals were under the softwood canopy, and free, those

TABLE XII.—*Birch and poplar type, composition of plots*

Balsam	Balsam, overtopped	Red spruce	Red spruce, overtopped	White spruce	White spruce, overtopped	Softwoods, overtopped	White birch	Poplar	Total hardwoods	Average number trees per 1/10 acre	Softwood, average diameter	Basal area, 1/10 acre
P. ct.	*P. ct.*	*P. ct.*	*P. ct.*	*P. ct.*	*P. ct.*	*P. ct.*	*P. ct.*	*P. ct.*	*P. ct.*		*In.*	*Sq. ft.*
34.2	39.2	50.3	38.6	15.4	32.0	60.7	70.7	29.3	24.2	70	6.3	15.34

TABLE XIII.—*Radial increment in millimeters at d. b. h. from 1903 to 1912, inclusive, and mortality of trees in plots of Table XII*

	Balsam, increment				Red spruce, increment				White spruce, increment			
	Dead	Living	Dead	All	Dead	Living	Dead	All	Dead	Living	Dead	All
	P. ct.	*Mm.*	*Mm.*	*Mm.*	*P. ct.*	*Mm.*	*Mm.*	*Mm.*	*P. ct.*	*Mm.*	*Mm.*	*Mm.*
Free	78.5	17.1	10.9	11.9	23.6	10.8	10.7	10 8	18.7	11.9	6.4	10.9
Overtopped	38.8	6.8	6.6	6.7	7.6	8.7	7.4	8.6	21.8	8.9	6.4	8.4
Average	228 trees			8.2	293 trees			9.5	117 trees			9.7

TABLE XIV.—*Northern hardwood type, composition of plots*

Balsam	Balsam, overtopped	Red spruce	Red spruce, overtopped	White spruce	White spruce, overtopped	Softwoods, overtopped	Yellow birch	Maple	Beech	Hemlock	Total hardwoods	Number trees, 1/10 acre	Softwood, average diameter	Basal area, 1/10 acre
P. ct.	*P. ct.*	*P. ct.*	*P. ct.*	*P. ct.*	*P. ct.*	*P. ct.*	*P. ct.*	*P. ct.*	*P. ct.*	*P. ct.*	*P. ct.*		*In.*	*Sq. ft.*
46.7	38.8	53.3	35.7	0	-------	59.7	20	15.3	64.7	0.4	27.4	32.2	6.8	7.20

TABLE XV.—*Radial increment in millimeters at d. b. h. from 1903 to 1912, inclusive, and mortality of trees in plots of Table XIV*

	Balsam, increment				Red spruce, increment			
	Dead	Living	Dead	All	Dead	Living	Dead	All
	Per cent	*Mm.*	*Mm.*	*Mm.*	*Per cent*	*Mm.*	*Mm.*	*Mm.*
Free	58.8	17.7	14.9	16.3	39.6	18.4	22.1	19.8
Overtopped	9.9	10.7	7.5	10.1	5.4	10.0	5.5	8.2
Average		206 trees		13.2		234 trees		14.6

whose terminals were above the canopy or standing in an opening in the hardwood foliage. Since no comparison of individual plots was contemplated, the tabulated data are a summary for all plots.

The mortality of four softwood series at Bathurst and Metis (Tables IV to XI) and two hardwood series (Tables XII to XV) is compared in Table XVI. The hardwood mixtures show considerably less mortality for white spruce and red spruce, though this is not so marked for balsam. If the percentages of mortality among the free and overtopped trees are compared, it is seen that the reduction in mortality is chiefly due to the overtopped trees.

In these series of plots the rate of growth for the overtopped trees is considerably lower than for free trees, so this factor would tend to increase mortality if it were not overbalanced by the protection offered by the hardwood canopy. The average rate of growth for the species of softwood trees in the hardwood series (Tables XII, XIII, XIV, and XV) is lower for balsam and higher for both red and white spruce than in the preceding softwood series.

In the northern hardwood type (Tables XIV and XV) the average rate of growth for all balsam (13.2) and red spruce (14.6) is considerably higher than for any other series of plots. Likewise the mortality of the overtopped softwoods is lower and shows a greater contrast to the free dead softwoods. The total mortality for balsam is lower than in the birch-poplar type (Tables XII and XIII), while that for red spruce is higher. It so happens that in these plots the rate of growth for the dead red spruce is higher than for the living. This discrepancy may be due to the method of tabulating free and overtopped trees, which does not properly group the trees according to the relative amount of defoliation. Balch recognized this, adding the following note on one plot:

> The free living red spruce are smaller than the free dead red spruce. The free living are in many cases partly overtopped, the free dead generally almost entirely free. Thus the percentage of canopy seems a greater factor than rate of growth.

These free living dead trees are thus subjected to a greater foliage exposure, and consequently to heavier defoliation, than those which survived and are partly overtopped, though classed as free because the terminal was free.

The lower percentage of mortality of the softwoods in hardwood mixtures is entirely a matter of protection by the hardwood foliage. This protective effect is due to concealment of overtopped softwoods from the ovipositing moths and the lessened chance of migrating larvae falling on the softwoods.

The mortality among the free softwoods of hardwood mixtures is about the same or slightly higher for balsam than for the pure softwood. This substantiated many observations in the field where high mortality was observed, especially in older hardwood mixtures when the hardwoods were becoming decadent, and suggests that the conifers, after years of competition in hardwood mixtures, are even less resistant than those in softwood stands.

Some indication of the relative ability of these trees to withstand severe competition is obtained from the tables summarizing the hardwood plots (Tables XII, XIII, XIV, and XV) and that of the mortality by diameter classes (Table XVII), suggesting that white spruce is least resistant as indicated by the higher mortality of the overtopped trees of the birch-poplar type (Tables XII and XIII), and the higher percentage of mortality in the 3, 4, and 5 inch diameter classes of softwood types. The same tables indicate that balsam can withstand more competition than white spruce and that red spruce is the most resistant species.

MORTALITY BY DIAMETER CLASSES WITH SEVERE AND LIGHT DEFOLIATION

The following table of the tree mortality (Table XVII) of three series of plots tabulated by diameter classes is given to show the relative effects of different degrees of caterpillar feeding on the various softwoods concerned and how such feeding affects mortality in the larger and smaller tree classes.

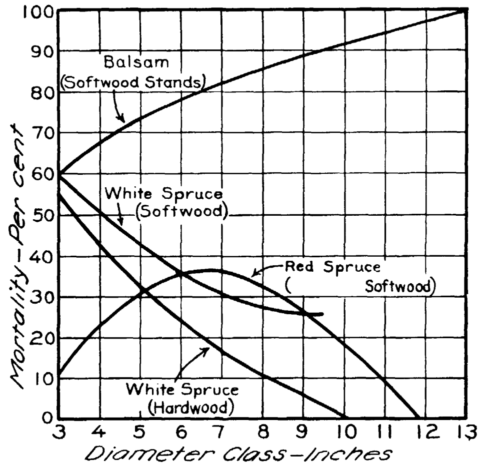

FIG. 3.—Mortality of spruce and fir in various forest types resulting from severe defoliation by the spruce budworm, shown by diameter classes. The white spruce (hardwood) are free

decreasing in the smaller and larger trees; in white spruce highest mortality occurs in the smaller-diameter classes, decreasing in the higher diameters.

Considering the same combination but with lighter feeding (fig. 4) as occurred at Metis, where the red and white spruce are very little affected (in fact, it might be questioned if

TABLE XVI.—*Percentages showing softwood composition before budworm attack and total mortality for each series of plots*

	Balsam		Red spruce		White spruce	
	Mortality	Composition	Mortality	Composition	Mortality	Composition
	Per cent	*Per cent*	*Per cent*	*Per cent*	*Per cent*	*Per cent*
Softwoods from Tables IV and V	5.2	66.2	94.8	29.8		
Softwoods from Tables VI and VII	9.5	59.5	72.1	22.1	18.4	40.6
Softwoods from Tables VIII and IX	27.4	60.2	33.3	27.9	39.2	37.3
Softwoods from Tables X and XI	79.1	39.1	5.3	5.5	15.6	11.6
Hardwoods from Tables XII and XIII	34.2	53.0	50.3	13.4	15.4	20.2
Free trees (alone)	60.8	78.5	61.3	23.6	68.0	18.7
Overtopped trees (alone)	39.2	38.8	38.6	7.6	32.0	21.8
Hardwoods from Tables XIV and XV	46.7	27.2	53.3	20.5		
Free trees (alone)	61.2	58.8	64.3	39.6		
Overtopped trees (alone)	38.8	9.9	35.7	5.4		

Considering the mortality of the three species of trees concerned by diameter classes and under conditions of heavy defoliation (fig. 3) (such as is represented by softwood stands of Tables VIII and IX) it is shown that in balsam mortality is relatively high in all classes, but increases with diameter; in red spruce highest mortality occurs in the middle-diameter classes, mortality in these two species can be attributed to other than natural thinning), we find that in balsam greatest mortality occurs in smaller-diameter classes, decreasing with larger diameters; in red spruce all mortality occurs in low-diameter classes below 6 inches; in white spruce all mortality occurs in low-diameter classes below 6 inches.

Considering mortality in the hardwood plots, Tables XII and XIII, where defoliation was severe on the free trees and relatively lighter in the overtopped trees, it is shown that balsam mortality of free trees is similar to that in softwoods (as illustrated in fig. 3); among the overtopped trees it falls quite regularly from the smaller diameters to the higher. Red spruce mortality among the free trees is similar to that of softwood stands (as illustrated in fig. 3); among the overtopped trees it falls quite regularly from the smaller diameters to the higher. White spruce mortality among the free trees falls rapidly as diameter increases and is lower than white spruce in the softwoods; among the overtopped trees the mortality falls similarly to that of red spruce, although it is higher in all diameters.

It might be assumed that the correlation drawn between rate of growth and mortality is not conclusive from the fact that the position of the tree in relation to the crown influences the amount of defoliation (intermediate and suppressed trees receive relatively more defoliation in severe epidemics), and degree of defoliation is no doubt the most important factor causing death. In other words, may not the higher mortality of slower-growing trees be a result of their position?

This is clearly not the case with balsam, which is subject to heavy defoliation, since greater mortality occurs as diameter increases, and there was found to be no correlation between rate of growth and mortality for such heavily defoliated balsam.

With red spruce receiving severe defoliation both in pure softwoods and free trees in hardwood stands the greatest mortality occurs between the diameter classes 6 and 8 inches, which trees in these 60-year stands would be largely either dominants or codominants.

In the case of white spruce receiving heavy defoliation, greatest mortality does occur in the lower-diameter classes 3, 4, and 5 inches, and here it is impossible to decide how much of the mortality is due to position, suppression, or budworm defoliation. In hardwood stands (Table XVII) greater total mortality occurs in the overtopped trees, which receive less defoliation, than in the free trees. On the other hand, with lighter feeding, mortality in all species is greater in the lower-diameter classes, which, of course, on the whole are slower-growing trees, but here again in balsam, which receives more defoliation, the mortality persists well up into high-diameter classes (both in softwood stands and overtopped trees in mixed hardwood stands) where many of the trees in softwood stands would be dominants and codominants.

It is not intended to argue that position does not have a certain effect on mortality, yet it seems impossible this long after the budworm feeding to determine just what weight can be attributed to it.[8] Referring to Table I, it will be seen that there is little difference in the average diameter of trees dying over a three-year period, while rate of growth and percentage of defoliation show regularly increasing or decreasing values in respect to time of death.

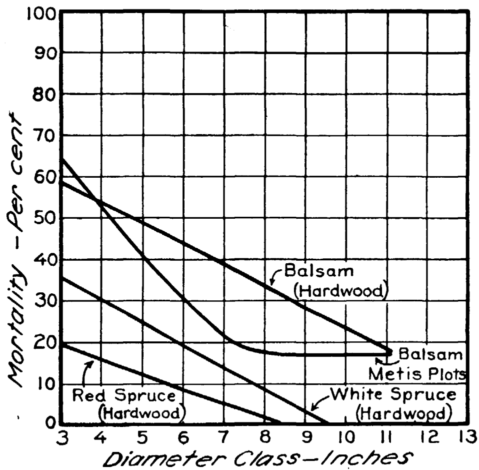

FIG. 4.—Mortality of spruce and fir in various forest types resulting from light defoliation in hardwood mixtures by the spruce budworm, shown by diameter classes. The balsam (hard wood), red spruce, and white spruce are overtopped

COMPARISON OF RADIAL INCREMENT OF SOFTWOODS BEFORE AND AFTER BUDWORM ATTACK

These series of measurements (Table XVIII and fig. 5) were taken to compare the rate of growth of partially defoliated trees before and after the budworm attack. The trees were selected promiscuously over the areas on which the foregoing plots were taken. Only dominant or codominant trees

[8] The degree of feeding on individual trees could not be determined at the time of this study.

TABLE XVII.—*Mortality by diameter classes (in percentages)*

SEVERE FEEDING

Tree species and association	3	4	5	6	7	8	9	10	11	12	13
Balsam:											
Softwoods of Tables VIII and IX	40	71	75	83	79	96	83	67	0	100	0
Free trees in hardswoods, Tables XII and XIII	50	62	82	79	70	93	79	92	90	83	100
Red spruce:											
Softwoods of Tables VIII and IX	19	9	36	39	33	32	29	7	11	0	0
Free trees in hardwoods, Tables XII and XIII	20	31	23	22	36	26	20	14	0	0	0
White spruce:											
Softwoods of Tables VIII and IX	48	60	56	12	32	32	21	32	21	0	0
Free trees in hardwoods, Tables XII and XIII	------	54	24	30	17	13	0	0	0	0	0

LIGHTER DEGREES OF FEEDING

Tree species and association	3	4	5	6	7	8	9	10	11	12	13
Balsam:											
Softwoods of Tables X and XI	55	71	48	33	19	21	16	21	18	0	0
Overtopped trees in hardwoods, Tables XII and XIII	30	37	49	44	42	30	18	29	------	------	------
Red Spruce:											
Softwoods of Tables X and XI	0	25	3	0	0	0	0	0	0	0	0
Overtopped trees in hardwoods, Tables XII and XIII	57	11	8	9	12	8	0	0	------	------	------
White spruce:											
Softwoods of Tables X and XI	39	35	24	3	0	0	0	0	0	0	0
Overtopped trees in hardwoods of Tables XII and XIII	33	29	33	17	18	8	0	0	0	------	------

TABLE XVIII.—*Rate of growth before and after budworm attack*

FROM SPRUCE FLAT TYPE, BATHURST, NEW BRUNSWICK

	Balsam				Red spruce				White spruce			
	10 years before	5 years before	10 years after	Number of trees	10 years before	5 years before	10 years after	Number of trees	10 years before	5 years before	10 years after	Number of trees
	Mm.	*Mm.*	*Mm.*		*Mm.*	*Mm.*	*Mm.*		*Mm.*	*Mm.*	*Mm.*	
Living [a]	19.9	9.2	11.0	85	12.2	5.7	7.2	88	12.3	5.6	6.5	89
Dead [b]	12.2	5.4	-------	199	9.3	4.4	-------	192	5.5	2.2	-------	133

FROM NORTHERN HARDWOOD TYPE, BATHURST, NEW BRUNSWICK

	Balsam				Red spruce				White spruce			
Living	18.9	10.4	12.5	90	19.8	10.0	13.0	116	-------	-------	-------	-------
Dead	18.7	9.9	-------	63	16.6	9.6	-------	76	-------	-------	-------	-------

FROM METIS LAKE, QUEBEC

	Balsam				Red spruce				White spruce			
Living	11.5	5.3	7.8	16	-------	-------	-------	-------	-------	-------	-------	-------

[a] From trees which recovered.
[b] From trees which died in 1922 from effects of defoliation

were bored. For this reason they can hardly be used to express the rate of growth of the regions as a whole so well as can the plot increments.

On the softwood plots the rate of growth for the 10-year period following first feeding (i. e., including 4-year feeding period and 6 years' recovery) was only about one-half that of the previous 10 years, while in the northern hardwood type this increment was about two-thirds the previous 10-year period. This may be due to greater ability of the trees to recover in the latter type, though possibly the trees scattered through these hardwoods were not so severely defoliated. These figures, as do previous tabulations, show that the white spruce dying from defoliation was growing at a slower rate than the red spruce which died.

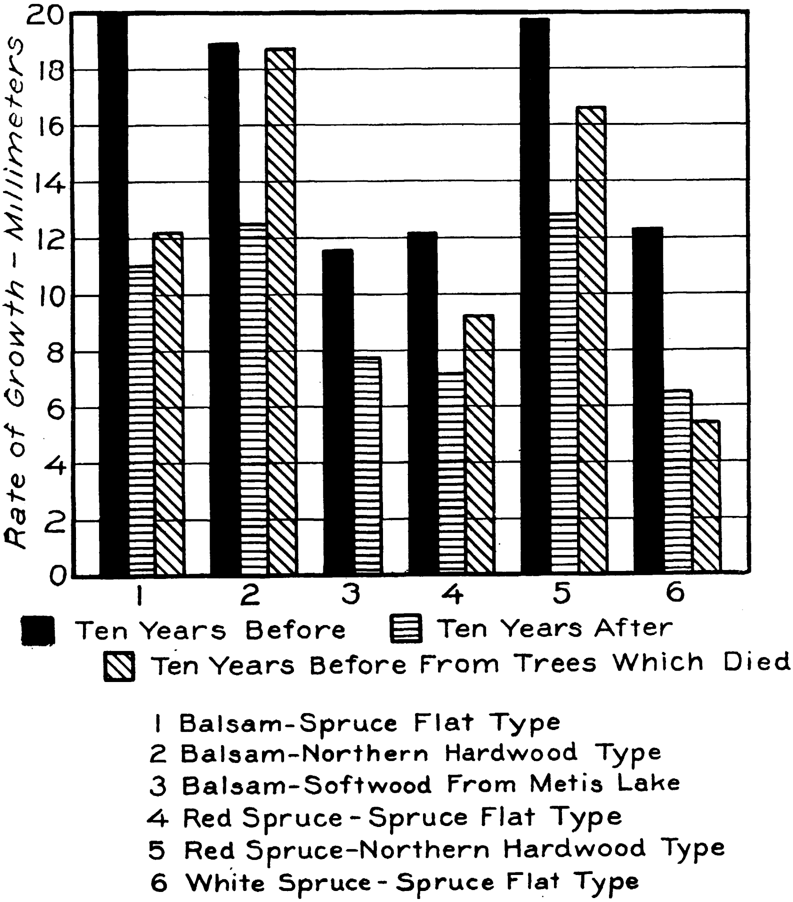

FIG. 5.—Diagram showing rate of growth of spruce and fir, occurring in various forest types, for the 10-year periods preceding and following spruce budworm defoliation

The Metis Lake plots (Tables X and XI) unfortunately (due to misunderstanding) were based on too few trees to make fair comparisons possible.

SUGGESTED APPLICATION

The recent widespread series of budworm epidemics in eastern Canada and northeastern United States, coming as they did at a time when the softwood supplies of these regions are becoming depleted and when considerable interest in putting the forests on a sustained-yield basis is being manifested, will no doubt stimulate more intensive forest practices. At all events, the budworm is an ever-present menace to the growing of spruce and fir in these regions and must be given due consideration in the application of any silvicultural systems.

Our knowledge of how budworm outbreaks originate and the factors necessary for their phenomenal increase and spread is so meager that any recommendations for the prevention of future outbreaks are only speculative. When outbreaks do occur, we can hope for little relief from direct control measures, though prompt salvage of the defoliated material will greatly reduce the total losses.

With such limited possibilities of prevention or control before us, the only alternative is to keep the future forests in a condition least susceptible to the effects of defoliation. It is believed that the present study indicates that this can be accomplished by maintaining thrifty and vigorous stands.

This result can only be secured in natural stands by judicious cuttings to reduce the density and promote more rapid increment in the individual trees. As an example, in second-growth stands, such as those under consideration, varying from 20 to 50 cords per acre at 40 to 50 years of age, it would certainly be practical to make a pulpwood cutting when competition becomes so severe as to induce high mortality from defoliation. Such an operation should remove from 5 to 10 cords per acre, so as to make it profitable, and it should be conducted with the idea of maintaining trees of better quality.

The selection of the trees for thinning should be governed by the following considerations:

Remove all the balsam possible to the smallest possible diameter limit, since it is most susceptible to budworm defoliation, promotes heavy feeding, and may be an important factor in originating outbreaks. Any balsam that is left should be single, thrifty, dominant trees. Groups of balsam should never be left.

Remove all inferior red and white spruce and those that will not gain dominance by the time the next logging operation is contemplated.

Between doubtful red spruce and white spruce favor red spruce, since it better withstands adverse conditions and is a more persistent grower. The presence of red spruce is least effective in promoting severe budworm defoliation.

These thinnings should induce reproduction and, judging by the effect of bud-worm thinnings, this regeneration may be largely balsam. However, by removing practically all of the balsam and by breaking the soil litter through logging, possibly a high percentage of spruce can be secured.

If the stands are being managed for pulp wood, 10 to 20 years later, after reproduction is established, clear cutting should be adopted. In this case the new crop could again be mixed with balsam.

If saw material is desired later, pulpwood thinnings should be made to reduce density and promote more rapid growth, following the same selection as before but favoring red spruce still more because of its quality of persistent growth.

Balsam and white spruce should only be grown on the better sites. On these balsam is sufficiently immune to budworm feeding up to 40 years to leave a well-stocked stand, though several years' increment will be lost and the rotation lengthened.

In the spruce swamp type, where reproduction is very good and balsam practically negligible, some form of selection system is advocated which would aim to remove mature and less thrifty trees, giving room for younger trees which grow more rapidly. Further study is needed in this type to determine the causes of periodic cycles of rapid growth in older stands and the conditions favoring rapid growth observed in younger stands following fires.

Any recommendations in hardwood mixtures are dependent on the possibilities of utilization of the hardwoods. Since hardwoods are only a protection to the softwoods while the latter are overtopped, and since once the softwoods gain dominance the mortality of balsam from the budworm is as high or higher than in pure softwoods, even greater care will be necessary to handle these mixtures successfully.

In the birch and poplar type, which is a transitional stage in the formation of the spruce flat type, the hardwoods should be regarded as purely a shelter, and the earlier the conifers are liberated the better.

In the yellow birch and northern hardwood types, where the softwoods grow very rapidly and where practical conversion to a softwood type will probably be an impossibility, efforts should be made to utilize or dispose of as much of the hardwoods as possible to liberate higher proportions of softwoods.

In hardwood mixtures balsam is most susceptible as a free tree and white spruce as an overtopped tree, which demands early cutting of free balsam and early liberation of overtopped white spruce. The spruces, particularly white spruce, should always be favored in preference to balsam.

Mature softwood types were not studied in detail, though it is believed methods involving clear cutting with the object of securing more uniform second-growth stands in compartments of varying ages are more desirable. The history of these northern forests in the past has been largely the history of burns, the resulting second growth producing relatively more budworm-resistant forests, with lower percentages of balsam. There may be a lesson in this, suggesting periodic clear cutting, a case somewhat analogous to the better results secured by periodic renewal of coppice forest by seedling trees.

Diversified forests, both as to age classes and types, will aid in lowering the momentum of budworm outbreaks and result in less general and disastrous devastation.

These recommendations are not to be considered as applicable to the Laurentian region. The entirely different silvicultural characteristics of the spruce of this region, the great difficulty of securing spruce reproduction, and the prolificness of balsam will demand different methods.

SUMMARY

The study herein reported indicates that there is a definite correlation between the mortality occurring in spruce and fir stands (from spruce budworm defoliation) and the rate of growth of these stands prior to attack. The more rapid the rate of growth as expressed in diameter increment the lower the resulting mortality under equal conditions of feeding. This relation between the effects of budworm feeding and previous vigor is a more tangible quantity than any of the other factors heretofore considered and should serve as a practical basis for preventive measures through proper silvicultural practices which maintain rapid growth.

A comparison of the rate of growth of trees surviving budworm attack shows that the diameter growth for the 10-year period following the first year of feeding is only about one-half that of the preceding 10 years.

It was found that in hardwood types the immunity of softwoods was proportional to the protection of the overstory of hardwood foliage. The percentage of mortality among dominant softwoods in mixed stands was as high as in pure softwood stands.