Death and Deterioration of Balsam Fir Weakened by Spruce Budworm Defoliation in Ontario[1]

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Part II. An Assessment of the Role of Associated Insect Species in the Death of Severely Weakened Trees.

Certain features of the seasonal history and habits of the insect species which breed in severely weakened and dead balsam fir trees in the Lake Nipigon region of Ontario have been dealt with in a previous contribution (*3*). For many years it has been recognized that some of these insects attack weakened trees before death is obvious, and therefore possibly contribute to tree mortality. Various interpretations of the importance of these insects in the death of the tree have been reached by previous investigators. Graham (*7*) suggested that some of the species hastened tree death during the spruce budworm outbreak in Minnesota during the early part of this century. Swaine *et al.* (11), who carried out the most intensive studies among the earlier investigators, concluded that only one species, *Monochamus marmorator* Kby., was capable of killing trees. Graham and Orr (*8*), in summing up what was known of these insects in 1940, stated: "There is considerable disagreement among forest entomologists as to the importance of these secondary agencies. Some attribute great importance to them, whereas others think that these species usually limit their attack to trees that have been defoliated so severely that they are doomed even without further injury."

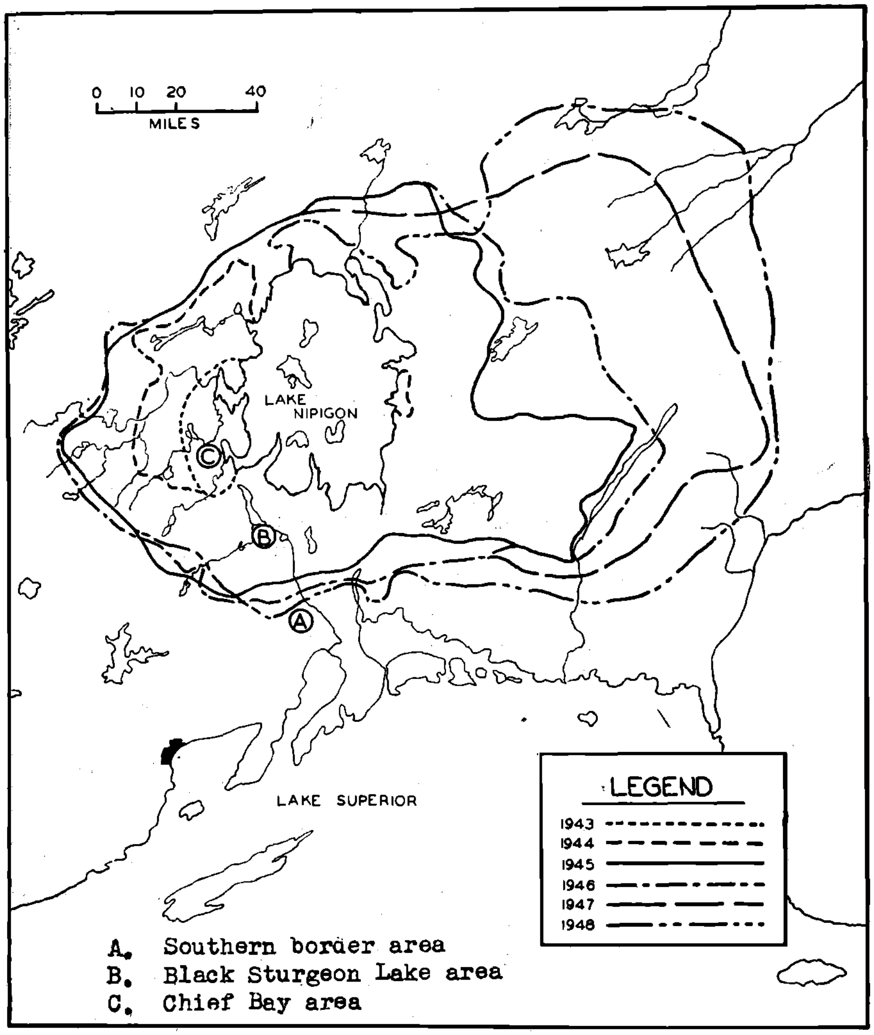

Fig. 1.—Map of Lake Nipigon region of Ontario illustrating yearly boundaries of heavy spruce budworm infestation (1943 to 1948, inclusive), and location of study areas.

The destructive spruce budworm outbreak in the Lake Nipigon region, which left large numbers of weakened, dying, and dead trees in its wake, provided an excellent opportunity to investigate the role of these insects in tree mortality. The studies were carried out during the period 1946-1951.

Plan of Study

The field investigations were carried out in the area west and southwest of Lake Nipigon, in northwestern Ontario, from the Black Sturgeon Lake Field Station (Fig. 1). This area falls within the Superior Section of the Boreal Forest Region, according to the classification of Halliday (*9*). The forest is characterized by white spruce associations with balsam fir, aspen, and white birch on the slopes and lower hilltops; by jack pine and white birch on the higher, more rocky portions; and by black spruce, tamarack, and some eastern white cedar on the lower, poorly drained portions. The area has been burned many times and the forest cover is consequently much fragmented. Fairly dense stands of balsam fir with some white spruce, frequently under a canopy of aspen of large size, were to be found throughout the area before the recent devastation by the spruce budworm. Shortly before this outbreak, the overmature aspen

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overstory began to break up rapidly. This breakup was possibly hastened by an outbreak of the forest tent caterpillar, *Malacosoma disstria* Hbn., which swept the area during the years 1936-1939.

A severe outbreak of the spruce budworm occurred throughout the Lake Nipigon region from about 1939 until 1948. It was first reported in 1943 (*1*), when heavy defoliation of balsam fir was observed in a comparatively small area on the west side of Lake Nipigon (Fig. 1). It was evident at that time that the outbreak had been in progress for some years since some mortality of balsam fir was recorded in the original report. The infestation increased in size each year, until in 1948 the area in which balsam fir had been heavily defoliated extended roughly 160 miles from east to west and 100 to 120 miles from north to south, completely surrounding Lake Nipigon (Fig. 1). In 1948 and 1949, spruce budworm populations dropped markedly, and by 1950 had reached a very low level.

The area of timber mortality was first mapped accurately in 1946, when balsam fir mortality was extensive. Following 1946, mortality became more severe and widespread, and by 1951 balsam fir had been killed over much of the area of the infestation. Within the same area, much of the white spruce was also killed.

In 1946, when studies began, spruce budworm infestations varying from very light in the south to very heavy with some mortality of balsam fir in the north, were available for study. Sample plots were established in the early summer of that year for the study of the influence of defoliation on tree vigor, and of the relationship of associated insect attack to tree condition. In the autumn of 1946 and the spring of 1947, additional plots were established for the more intensive study of weakened trees. The plots were representative of different intensities of spruce budworm infestation at that time, and each consisted of from 15 to 150 dominant and co-dominant balsam fir trees.

Severe defoliation of trees usually results in the reduction of radial growth, owing to a reduction in the photosynthetic production of the crown. Partial or complete destruction of the current year's foliage of coniferous trees usually must extend over more than one season before increment is severely affected, whereas reduction of increment in decidious trees often occurs immediately after removal of the leaves. The radial increment of balsam fir is progressively reduced by continued severe defoliation, and the measurement of this reduction offers one means of assessing the vigor of defoliated trees. Seasonal records of radial increment, measured at 7- or 10-day intervals throughout the growing season were maintained from 1946 to 1951 inclusive (or for as long as the trees remained alive) in 94 trees in sample plots throughout the study area. Measurements were made by means of a dendrometer (*4*). Special studies conducted in 1946, 1947, and 1948 showed that there was no consistent difference in total seasonal increment between different sides or different levels of the tree trunk below the crown (*2*). Measurements were therefore taken at breast height (4.5 feet) on the side of the tree that was most accessible. Defoliation by the spruce budworm also retards shoot development and causes the death of buds and shoots. This damage becomes more severe as defoliation is prolonged, and results in a further reduction of foliage and hence of radial increment. An appreciation of the severity and duration of defoliation and the reduction in number and vigor of buds and shoots, therefore, are other criteria of tree vigor. Consequently, weekly descriptions of foliage condition were made on study trees in conjunction with increment readings, in order that the succession of events leading to tree death might be appreciated.

Observations on the attacks of associated insects in the tagged trees were made at short intervals, and were co-ordinated with the knowledge of tree vigor based on crown condition and increment pattern.

The Influence of Defoliation on Tree Growth

In 1946, no dominant or co-dominant balsam fir trees could be found in the Lake Nipigon area which were not infested by the spruce budworm. It was therefore impossible to obtain radial increment records from trees completely unaffected by spruce budworm feeding for comparison with records from trees defoliated for varying lengths of time. However, at the southern border of the infestation, the spruce budworm population was very light, and the stands had suffered moderate defoliation for only one season. During 1947, the population increased in this area and heavy defoliation resulted. In 1948, the population declined to the 1946 level, again resulting in only moderate defoliation. In spite of the 1946 and 1947 defoliations, radial increment, as will be subsequently shown, was not affected until 1948.

In all other areas where increment studies were carried out, the trees had suffered heavy defoliation for several years before 1946, and radial increment was already affected.

Space does not permit the inclusion of increment curves for all study trees in the southern border area to illustrate typical seasonal radial increment in the area. Three representative trees have therefore been selected. The trees were approximately 8 inches in diameter, and occupied co-dominant positions in the stands. Increment curves for six growing seasons, 1946 to 1951 inclusive, are presented in Figure 2 *A*, *B*. *C*.

The construction of these curves, as well as others presented later, requires some explanation. Dendrometer records for the years 1948, 1949, 1950, and 1951 were all started at approximately the same time in the spring—May 11, 10, 12, and 14 respectively. However, in 1946, the year in which the sample plots were established, first records were not obtained until June 20, and in 1947 until May 29. First dendrometer records of 1949, 1950, and 1951 checked to within 0.003 inches with the final records of the preceding autumn, and the first records in the four years, 1948 to 1951, were followed by increases within 10 days. It would thus appear that the initiation of radial increment of balsam fir in the area under consideration occurs between May 10 and May 20, and that the initiation of increase is largely independent of seasonal weather—e.g., in 1949 and 1951 spring came relatively early in the area, and in 1950 relatively late, but the initiation of increment occurred at approximately the same time in all years. Similar results were obtained for a number of tree species in the more western part of the province during the same seasons (personal communication, A. H. Rose).

It is clear that early seasonal increment was not recorded in 1946 and 1947. Therefore, in constructing graphs of radial increment it has been assumed that increment before the first records in 1946 and 1947 was equal to the measured increment in the corresponding periods in 1947 and 1948. The 1947 curves are thus tied into the 1948 curves, and the 1946 curves into those for 1947. There is good evidence that such an assumption is correct and that the curves as constructed are reasonable. When discs were cut in 1949 from five trees adjacent to those illustrated in Figure 2, and the width of annual rings measured, the magnitude of increment in 1947 was found to be comparable to that in 1946 and, indeed, to that in 1945 and 1944 (Table 1). A decided decline in increment in 1948 was also apparent in the discs. Therefore, the increment pattern for the years 1946, 1947, and 1948 illustrated in Figure 2 *A, B, C,* corresponds very well to the pattern obtained from discs measurements for the same years.

It is apparent from Table 1 that increment was not affected by spruce budworm defoliation in 1946 and 1947. Since the increment in those two years was very similar in the three trees illustrated in Fig. 2 *A, B, C,* the weekly increases during 1946 and 1947 in each tree have been averaged, and a smoothed curve drawn to illustrate a "typical" seasonal pattern of radial increment in balsam fir in the study area (Fig. 2 *D*). The maximum rate of increase is reached soon after the initiation of increment in mid-May, and continues from approximately June 1 until August 12. Afer mid-August, it tapers off rather rapidly, and is practically ended by mid-

Table 1.—Width of Annual Rings (In Inches) Measured From Discs Measurements are Average of Four Radii

Tree Number	1944	1945	1946	1947	1948	1949
1	.076	.072	.075	.079	.060	.032
2	.060	.057	.057	.061	.050	.032
3	.104	.099	.084	.082	.030	.022
4	.102	.100	.096	.094	.060	......
5	.064	.060	.058	.056	.036	......

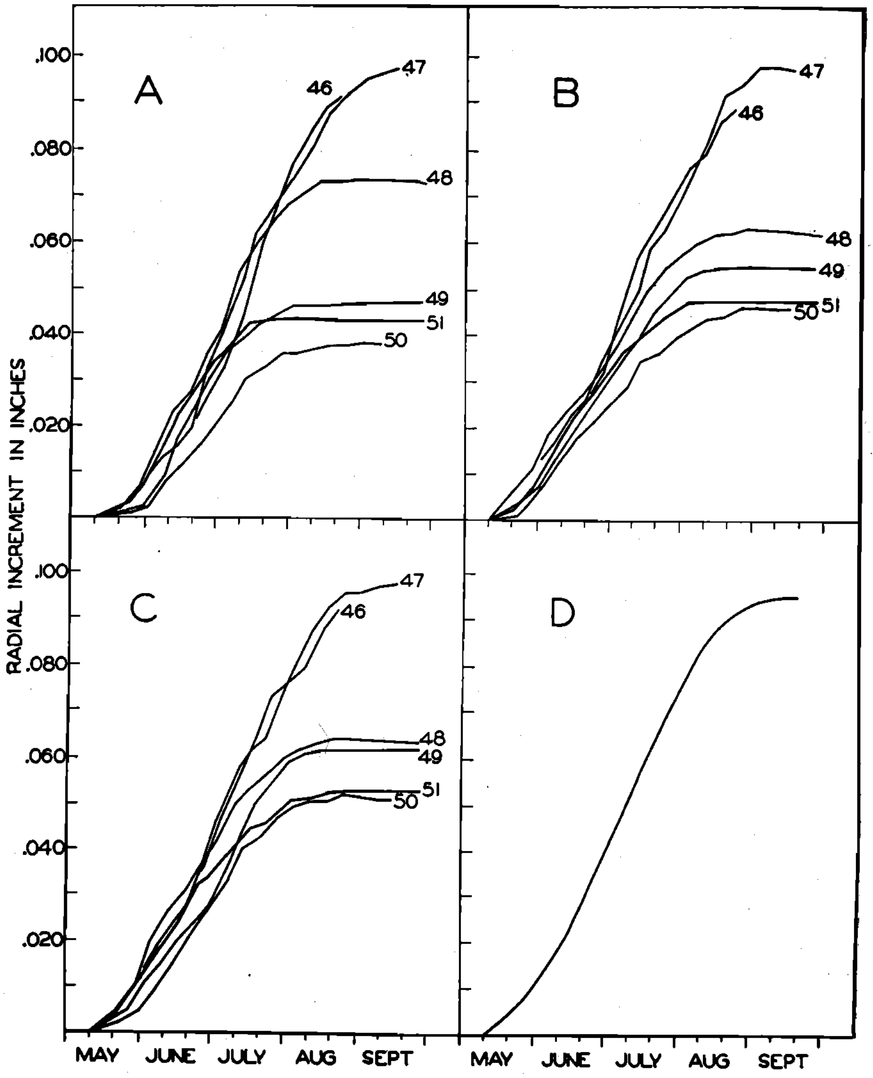


Fig. 2.—Curves illustrating seasonal radial increment of balsam fire in the Lake Nipigon region.

A, B, and C. Three trees in southern border area, 1946 to 1951, inclusive.

D. Smoothed composite curve representing "typical" pattern of radial increment. (Based on weekly average increment of three trees in A, B, and C, during 1946 and 1947).

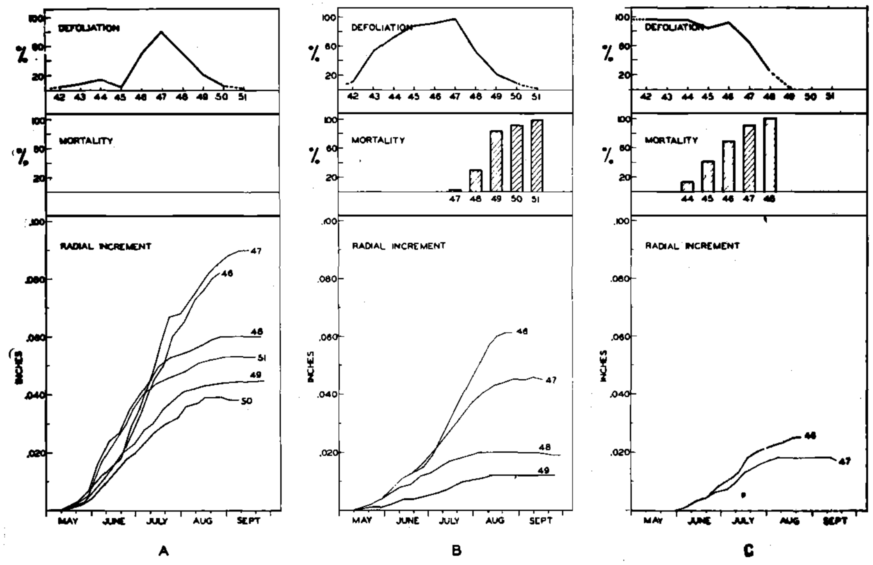


FIG. 3.—Records of defoliation, mortality, and average radial increment of balsam fir for three conditions of spruce budworm infestation in the Lake Nipigon region. A. Southern border area. B. Black Sturgeon Lake area. C. Chief Bay area.

September. This curve forms a basis of comparison for curves of trees defoliated for varying periods of time.

The suppression of radial increment in defoliated trees is very marked and is dependent on the severity and duration of defoliation. The sample plots established in 1946 and 1947 ultimately become representative of three different infestation conditions. In the north, at Chief Bay, defoliation occurred earliest and mortality of balsam fir had already commenced by 1946. At Black Sturgeon Lake, about midway between the centre and the southern border of the outbreak, defoliation occurred some years later and mortality did not commence until 1947, but ultimately was complete. The southern border area suffered only moderate defoliation for a short time, and no mortality resulted (Fig. 1). Average curves of seasonal radial increment have been drawn from dendrometer records of individual trees in sample plots for each of these infestation conditions for the six seasons 1946 to 1951, or for as long as the trees remained alive.

Fettes (*6*) established percentage defoliation as a measure of spruce budworm population level and recorded the yearly defoliation history in each of these areas during a study of spruce budworm populations. Yearly figures of balsam fir mortality in the Black Sturgeon area were obtained during this study, and in the Chief Bay area from records of a permanent mortality plot, established in 1943 as part of the general program of the Forest Insect Laboratory, and located within one-quarter mile of the sample plots in a similar stand.

Radial increment, defoliation, and mortality of balsam fir are presented graphically in Figure 3 for the three infestation conditions.

The least severe defoliation occurred at the southern border of the infestation, where spruce budworm populations caused moderate to heavy defoliation for only three years, 1946, 1947, and 1948 (Fig. 3 *A*). Defoliation in 1946 and 1947 did not influence increment during those years, but the effect was apparently cumulative and a decided suppression occurred in 1948, even though defoliation in that year was lighter than in 1947. The examination of discs from other defoliated trees also indicated first suppression of increment occurring about two years after the first year of severe defoliation. Further suppression of increment occurred in the border area in 1949 and 1950. Increment for 1951 indicated some recovery. The foliage of the trees showed considerable recovery in both 1950 and 1951, and it is highly improbable that any mortality which could be directly attributed to defoliation will occur in the area.

At Black Sturgeon Lake (Fig. 3 *B*), the first severe defoliation occurred in 1943. Increasing populations of spruce budworm caused increasingly severe defoliation each year until 1948. In that year the population started to decline which continued in subsequent years. Radial increment was already suppressed by 1946; this was also confirmed by disc examination. It was further reduced later, reaching a very low level during the years of heavy mortality in the stand. Mortality of balsam fir first took place in the late summer of 1947, in the fifth year of severe defoliation, and was virtually complete in the area by 1951, eight years after the year of first severe defoliation.

At Chief Bay (Fig. 3 *C*), near the original centre of the infestation, foliage examinations in 1946 (*6*) indicated that severe defoliation probably started as early as 1941 or 1942. Accurate observations could not be made for earlier years owing to the prevalence of abnormal shoot growth resulting from prolonged defoliation. The first dendrometer records taken in the area in 1946 indicated that increment had been suppressed for some years. The last severe defoliation occurred in 1946, and the population dropped rapidly thereafter. Mortality of balsam fir first occurred in 1944 and was virtually complete in 1948. If it is assumed that the first mortality at Chief Bay took place in the fifth year of severe defoliation, as at Black Sturgeon Lake, the first year of severe defoliation at Chief Bay would be 1940. Similarly, if it is assumed that virtually complete mortality was achieved eight years after the first year of severe defoliation, as at Black Sturgeon Lake, 1940 is again indicated as the year of first severe defoliation at Chief Bay. It is therefore quite probable that the spruce budworm population reached a level sufficently high to cause severe defoliation of balsam fir in the Chief Bay area as early as 1940.

It will be noted in Figure 3 *A* and *B* that not only is the magnitude of increment affected by repeated defoliation of the tree, but that the growing period is also progressively shortened. A similar shortening of the growing period has been demonstrated in western Ontario in both balsam fir and white spruce defoliated by the spruce budworm, and in aspen defoliated by the forest tent caterpillar (personal communication, A. H. Rose). Cessation of increment in healthy balsam fir trees in the Lake Nipigon region did not occur until the first week in September, but in defoliated trees, as increment declined with successive years of defoliation, the date of cessation of growth was progressively earlier in the season (Fig. 2 *A*, *B*, *C*).

Changes in the crown of the tree resulting from spruce budworm defoliation are more obvious than changes in increment. Once established in the foliage, spruce budworm larvae feed almost exclusively on developing buds and on the needles of developing and full grown shoots of the current year's production. Fettes (*6*) estimated that the last five years foliage of a healthy balsam fir tree in the Lake Nipigon region constituted approximately 65 percent of the total foliage of the tree. After several years of severe defoliation the total foliage complement of the tree is therefore greatly reduced.

Since spruce budworm larvae feed extensively on developing buds and shoots in the early summer, heavy populations of larvae soon damage a large proportion of the shoots. Buds are commonly killed after one or two years of severe defoliation. In many instances new buds develop which in turn may be killed. However, some usually survive and create very ragged growth at the periphery of the branches. Severe feeding at the time of shoot development often results in complete killing of the shoot. In some cases the shoot of the previous years growth may also die, resulting in a dead twig.

After two or three years' severe defoliation, the terminal leader of the tree may also be killed. If the branches immediately below the leader are killed as well, which is often the case, a dead top results. By the time this happens, the upper part of the crown is almost devoid of foliage, and observation from the ground often gives the impression that the terminal 6- to 8-foot section of the tree is dead. Closer examination usually reveals that the top killing is actually less severe.

Other changes occur immediately before the easily observed evidences of tree death. If death takes place early in the summer, early bud development may be noticeably retarded. Early bud development is usually normal in trees whose death does not occur until later in the summer, but subsequent shoot development is much slower than in trees which survive. Consequently, at the time of death, the shoots are quite stunted. Immediately before death becomes obvious, the foliage may wilt noticeably.

Thus, it is possible by following the seasonal progress of radial increment and the changes which take place in the foliage during the period of severe defoliation or immediately after, to make an assessment of tree vigor, and to forecast impending tree death before definite signs of death are apparent.

The Role of Associated Insects in The Death of Balsam Fir

Death of a tree is not a clear-cut event, and the exact time at which it takes place is difficult to establish with available methods. It is easy to distinguish between a living balsam fir tree and an obviously dead one, and it is in these distinguishable differences that a criterion of death may be found. In the living tree the foliage is green, and the cambial layer when stripped away from the sapwood is milky white in color and, during the summer months, quite moist. In the obviously dead tree, whatever foliage is retained is reddish-brown in color, the cambial layer is dark brown, and, in trees dead for some time, dry and tight to the wood surface.

Color changes in foliage and cambium, therefore, constitute two criteria of tree death, the changes in either indicating a breakdown of the life processes of the tree. Color change of foliage proved to be difficult to employ in the field, and in many instances unreliable. It usually starts as a yellowing of the needles, sometimes considerably in advance of cessation of radial increment and cambial discoloration, but often not until after these other signs of death are evident. The fact that many trees which die after five or six years' defoliation have very little foliage left makes this a poor field criterion, for it is often difficult or impossible to determine from the ground, even with the aid of binoculars, whether the few remaining needles are green or brown.

Discoloration of the cambial layer, on the other hand, proved to be reliable and easily observed. It is first detected as a brown streaking, usually in longitudinal patches, when the bark is stripped away from the wood. Characteristically, it starts more or less evenly around the lower trunk, and spreads upward throughout the tree. Within three to four weeks from first streaking, the cambial layer is brown throughout the whole tree. In all trees studied, streaking of the cambium was followed by complete discoloration of the whole cambial sheath. Moreover, in all trees under critical study which died during the growing season, discoloration occurred *after* the cessation of radial increment. Discoloration of the cambium is probably not a precise indication of the time of tree death, but it is the first definite, easily observed · indication that the tree has reached a condition from which it cannot recover. It certainly indicates a grave disturbance to the vital processes of the tree, and probably takes place rather late

TABLE 2.—WINTER AND SUMMER MORTALITY OF BALSAM FIR IN PERMANENT SAMPLE PLOTS, LAKE NIPIGON AREA, 1946 TO 1951

Plot	Number of trees dying in each period											
	1946		1947		1948		1949		1950		1951	
	S*	W**	S	W	S	W	S	W	S	W	S	W
46–6	2	6 (3)	4	3 (2)								
47–6			6	10 (6)	4							
46–7		64 (35)	20	44 (24)	13	9 (0)						
47–9			3	19 (16)	20	8 (5)						
47–10				27 (22)	18	5 (3)						
46–4				2 (0)	2	5 (2)	3	3 (2)				
47–11			1	9 (2)	3	9 (4)	13	9 (5)	3	2 (1)	1	
Totals	2	70 (38)	34	114 (72)	60	36 (14)	16	12 (7)	3	2 (1)	1	

Total number of trees dying during winter period = 234 = 67 percent
Total number of trees dying during summer period = 116 = 33 percent
Total number of dead trees 350
* Summer period = May to September
** Winter period = October to April
Numbers in brackets indicate number of trees dying during winter period which had been attacked by *M. scutellatus* the previous autumn (see text).

in the chain of events which might encompass the "period" of death.

Therefore, in this study, death of the tree was presumed when the cambial layer became generally streaked with light brown near the base of the tree. This can easily be observed in the field by removing a small piece of bark with a sharp knife.

The radial increment pattern of the tree, particularly when known for two or three successive seasons, often gave information on impending tree death. Trees which showed very little or no increment in the early summer, when radial increment was normally beginning, invariably died during the following weeks. Cessation of increment prior to cambial discoloration may actually be the first definite sign of impending death in trees dying during the early part of the growing season. No evidence of trees failing to add new wood cells for two or even three years before death, as suggested by Swaine *et al.* (*11*), was found in the trees under close observation during the study. Subsequent work has established, however, that in some trees partial growth rings may be laid down, and in a very few cases, the outer ring may be completely missing at the base of the tree. In the latter case at least a partial ring can usually be found at the midpoint of the bole.

The majority of trees infested by associated insects were obviously dead at the time of initial attack, but at certain times during the year, apparently living trees were to be found in which one or more species were active. It is these latter species which are of most interest.

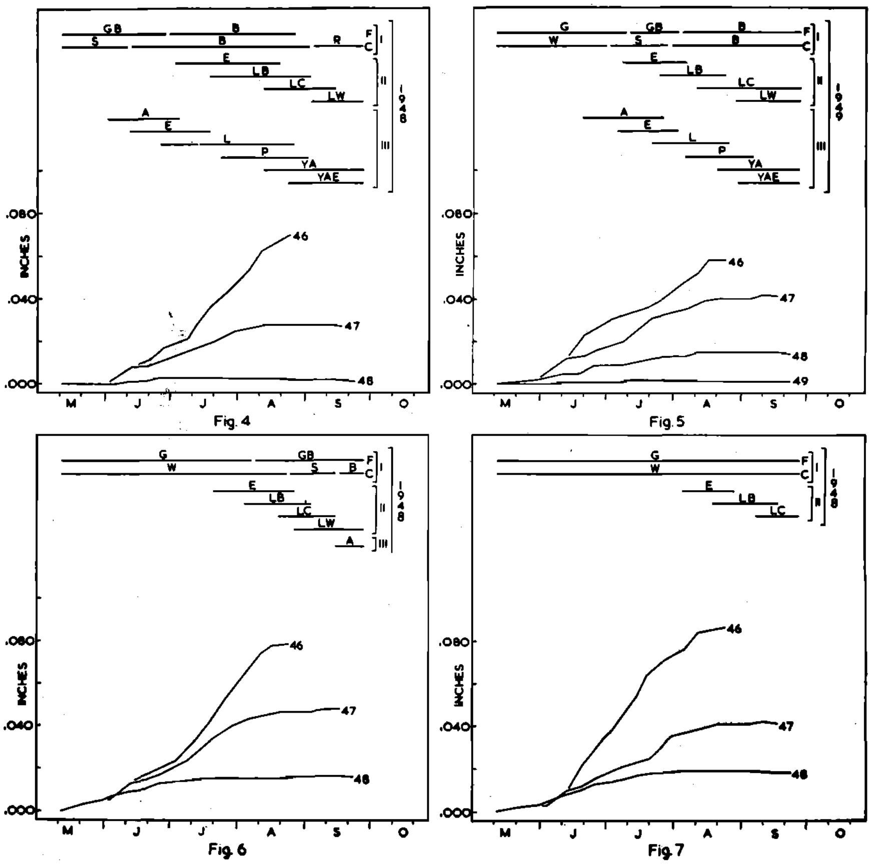
Some of the species may be immediately classified as playing no part in tree death on the basis of the time of attack. *Trypodendron bivittatum* Kby., *Serropalpus substriatus* Hald. and the siricids, *Sirex cyaneus* F., *Sirex* sp. (*noctilio* group, and *Urocerus albicornis* F. infested only dead trees. Some other species may be disregarded on the basis of their scarcity: *Monochamus marmorator* Kby., *Pissodes dubius* Rand., and *Tetropium cinnamopterum* Kby. *Pissodes dubius* Rand., and *Tetropium cinnampoterum* Kby. were scarce in the Lake Nipigon region during the years of this study, and observations on their activity in weakened trees were thus very limited. A few observations suggested that *T. cinnamopterum* confined its activity to dead trees, as recorded by Swaine *et al.* (*11*). These authors record *M. marmorator* and *P. dubius* as attacking living trees, and *M. marmorator* as being capable of killing trees which otherwise would have survived. Regardless of the ability of either species to contribute to tree death, because of their scarcity they must be regarded as playing no significant part in the widespread mortality of balsam fir during and immediately following the Lake Nipigon spruce budworm outbreak.

Thus, the bark beetle, *Pityokteines sparsus* Lec., and the sawyer beetle, *Monochamus scutellatus* Say, were the only species associated with dying balsam fir trees in the Lake Nipigon region which were both abundant and known to attack trees before death was obvious. The role played by each of these species will be discussed separately.

Pityokteines sparsus Lec.

Table 2 records the time of death of all trees dying in study plots throughout the course of this study. Approximately two-thirds of all mortality occurred during the winter months. Most of the trees infested with *P. sparsus,* therefore, were dead before being infested. Regardless of the aggressiveness of the species, then, it could not have contributed to the death of more than one-third of the vast number of trees that died after severe defoliation, during and immediately following the spruce budworm outbreak.

The earliest seasonal attacks by the newly-emerged adults of *P. sparsus* were in obviously dead trees, most of which had died during the previous winter. Infestation at this time was almost always heavy. Figure 4 represents graphically the sequence of events in a tree attacked in this manner. The tree died during the winter of 1947-1948 after at least five years' severe defoliation. Judging by the radial increment curves, the tree had reached a low level of vigor by the end of the 1947 growing season. The tree was alive in late



Figs. 4 to 7.—Graphic representation of sequence of events in balsam fir trees attacked by *Pityokteines sparsus* Lec., and *Monochamus scutellatus* Say.

The curves at the bottom of each figure represent cumulative radial increment for the years indicated. The short, lettered lines in the upper part of each figure represent tree condition and insect development for the year indicated.

The two series of lines bracketed at the right by I, indicate tree condition: those labelled at the right by F for foliage (G = foliage green; GB = foliage partially browned; B = foliage brown; no line = foliage dropped from tree), and C for cambium (W = cambium white; S = cambium streaked; B = cambium brown; R = cambium rotten.

The series of lines bracketed at the right by II represent the developmental stages of the sawyer beetle, *M. scutellatus* (E = presence of eggs; LB = larvae hatched and mining in bark; LC = larvae mining in cambial region between bark and wood; LW = larvae entered and tunneling in wood).

The series of lines bracketed at the right by III represent the developmental stages of the bark beetle, *P. sparsus* (A = attack, cutting of nuptial chamber and commencing brood galleries; E = presence of eggs; L = larvae hatched and mining; P = pupae formed; YA = young adults formed and feeding in inner bark; YAE = young adults emerged from host tree).

September 1947, but dead on May 10, 1948, by which time the foliage had completely discolored and the cambium was generally streaked. On June 2, the tree was heavily attacked by *P. sparsus*. The activity of this species could in no way have contributed to its death. Practically all trees dying during the winter or early spring were infested in this way, the only trees escaping attack being those which apparently died so early in the winter that the bark and cambium were too dry by spring to be attractive to the beetles.

Shortly after the earliest attacks in dead trees, *P. sparsus* attacked trees which were apparently still living. Initial attack was lighter than in the dead trees described above, and was usually confined to the lower parts of the trunk. Figure 5 illustrates the sequence of events in one tree, representative of a total of 23 trees under close observation which were attacked in this manner during 1947, 1948, 1949, and 1950. The tree had been severely defoliated for five or six years prior to attack, and was located in the same plot as the tree illustrated in Figure 4. On May 10, 1949, when first examinations of the year were made, the tree was apparently alive; the remaining foliage was green and the cambium white and normal in appearance. By the third week of May, it was noted that bud development was retarded. Radial increment curves indicated severe suppression for several years preceding death. The curve for 1949 indicated very slight swelling, but examination of discs from the tree failed to reveal any wood cells.

When the first bark beetle eggs were observed, the cambium had started to discolor generally, and the tree was classified as dead. Close examination of the tree at this time showed that each bark beetle attack consisted merely of a nuptial chamber approximately one-quarter-inch in diameter and the beginnings of one or more brood galleries, each not more than one-eighth or one-quarter-inch in length. The injury to the cambial sheath was thus very slight, and the attacks were not sufficiently numerous to girdle the tree. It is therefore difficult to see how the activity of the beetle adults during a period of only 10 to 14 days could have actively contributed to the death of the tree, and it is concluded that the tree was dying at the time of attack. Kraemer (*10*) has suggested that changes in osmotic pressures in the stem and bark of the tree resulting from weather and injury by other insects to the branches and foliage may produce conditions attractive to *Pityokteines* beetles in *Abies alba* Mill. The vitality of the tree discussed above was very low before attack, as evidenced by the failure of the tree to add new wood cells, and by the retarded development of the vegetative buds. Although trees attacked in this manner were not common, similar events were observed in all trees so attacked.

No trees attacked by this species, when examined in detail, ever showed evidence of previous unsuccessful attacks, and no trees which had not been defoliated for a number of years and in obviously weakened condition were ever observed being attacked while still apparently living. Thus it appears that some change prior to death makes the tree attractive to the beetles.

The trees attacked late in the season by newly-emerged *P. sparsus* adults of the first brood of the season, which cut feeding galleries and overwinter therein (*3*), were invariably dead trees. Figure 6 illustrates such an attack in a representative tree on September 13, 1948, approximately one month after the tree was classified as dead.

Monochamus scutellatus Say

Adults of this species were found to oviposit in four different classes of balsam fir trees in the study area. The earliest attacks, soon after mid-July, were made in trees which died during the previous winter, in which the cambium and bark were still moist (Fig. 4). The trees had almost always been infested earlier the same season by *P. sparsus.*

Oviposition also followed earlier attacks by *P. sparsus* in apparently living trees (Fig. 5). It will be noted, however, that the cambium had already started to discolor by the time the first *Monochamus* eggs were laid, and by the time the first larvae were mining in the combial area, the trees had been obviously dead for some time.

In neither of the above cases could the activity of this species have contributed to tree death.

Comparatively few trees dying during the summer months were attacked by *M. scutellatus* without having been previously infested by *P. sparsus.* Figure 6 illustrates the sequence of events in one of the eight study trees attacked in this manner. Initial *M. scutellatus* oviposition took place on July 20, 1948, when the foliage was still green and the cambium white and unstreaked. By August 3 some eggs had hatched and the larvae were mining through the bark. First mining in the cambial area was observed August 18. First streaking of the cambium was observed August 12, and by August 18 it was extensively discolored. It is obvious that no damage was done by the borer larvae before the tree showed definite signs of death. Some radial increment was recorded during May and June, 1948, and this was confirmed by examination of discs after death of the tree. However, cessation of increment occurred about June 25, almost six weeks earlier than in trees in the same plot which survived the summer of 1948 (Fig. 3*B*), and approximately one month before first oviposition by *M. scutellatus* was observed. Buds burst normally in this tree in late May 1948, but by mid-June the new shoots had developed to less than half the size of shoots in trees which survived the summer. By mid-July the new shoots showed signs of wilting. There were, therefore, definite indications in radial increment and shoot development that serious changes had taken place in the tree before death became obvious. These changes apparently make such trees attractive to the beetles.

Later in the summer, from late July to early September, a fourth class of balsam fir trees was attacked by *M. scutellatus.* These trees differed considerably from those already described. The sequence of events in a representative tree is illustrated in Figure 7. The tree produced foliage similar to that of trees in the same area which were not attacked in the late summer, and the radial increment records show that it put on considerable wood in 1948. Oviposition, first noted about August 2, was light, and most of the eggs were deposited around old branch scars and at the edge of small wounds in the bark. Many empty egg slits were found. These conditions were usual in trees attacked at this time; in many, very few eggs were actually laid, most of the slits being empty. This tree did not show obvious signs of death soon after attack, as did the trees represented in Figure 6, but was still alive in late September when the last seasonal observations were made. Death occurred during the winter.

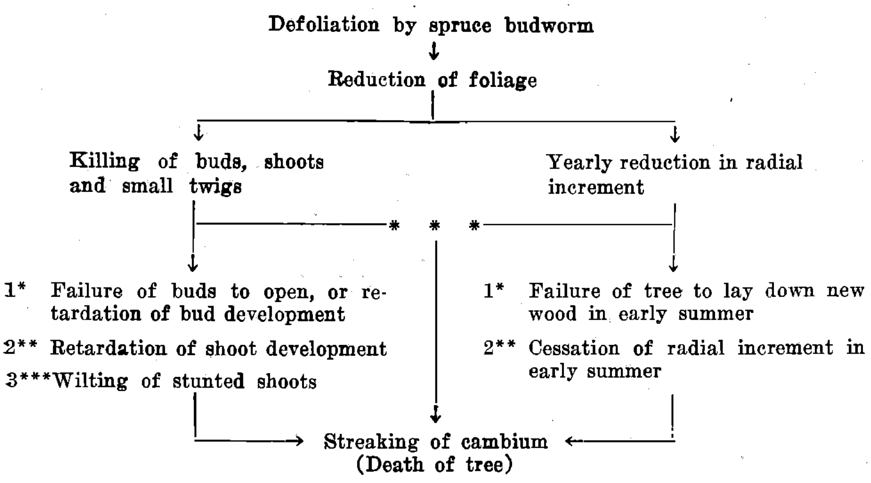
Severe suppression of radial increment was apparent in the tree during the summer of attack, and oviposition took place just after cessation of increment. The larvae succeeded in boring through the bark and mining in the cambial layer only to a limited degree by the middle of September. No larvae had entered the wood by the date of the last examination, September 20.

Approximately 60 percent of all trees that died during the winter period, or 40 percent of all trees that died in study plots were attacked by *M. scutellatus* in this manner (Table 2). Of 81 trees attacked in the late summer of 1947 and still apparently living in late September 1947, 72 were dead by early May 1948. The nine trees which survived the winter had been attacked very lightly the previous autumn, and all died during early June 1948, after infestation by *P. sparsus.*

During late May and early June, 1949, four of the seven trees which had been attacked in late July and August 1948 (Table 2), and had died during the intervening winter, were cut, and samples consisting of 1-foot blocks at 8-foot intervals along the trunk were examined before and after barking. In samples from all trees, *M. scutellatus* egg slits were numerous, but few had contained eggs. Many of the larvae that had hatched died after boring about half way through the bark. No larval activity in the cambial area could be found in samples from two of the trees. In samples from the other two, some larvae had succeeded in mining to a limited degree between the bark and wood, densities of 2.2 and 1.5 mines per square foot of wood surface being recorded in the two trees. No individual mine was larger than one square inch, and in very few had the larvae entered the wood. Tunnelling into the wood might have taken place in the spring, for the larvae were active when the examinations were made. Little or no damage was therefore done to the four sample trees by the beetle larvae.

Examination of standing trees in the spring of 1948, 1949, and 1950 revealed similar conditions. It is,

TABLE 3.—PROGRESSIVE CHANGES IN BALSAM FIR TREES RESULTING FROM PROLONGED SEVERE DEFOLIATION BY THE SPRUCE BUDWORM



* In trees dying in early summer
** In trees dying in mid or late summer
*** In trees dying during winter

TABLE 4.—RELATIONSHIP OF ATTACK BY ASSOCIATED INSECT SPECIES FOR WHICH RELIABLE INFORMATION IS AVAILABLE TO SEASON OF TREE DEATH, AND TREE CONDITION

Season of tree death	Insect attack in relation to tree condition			Remarks
	Tree injured beyond recovery. Attack By *P. sparsus* *M. scutellatus*	Tree newly dead. Attack by: *P. sparsus* *M. scutellatus* *S. substriatus* Siricids	Tree dead, bark partially dried. Attack by: *T. bivittatum*	
Summer	XX	XXX		Attack during summer of death
Winter		XXX		Attack during summer following death
Winter			XX	
Winter	X *M. scutellatus* only. Attack in late summer before death.	XX Attack in summer following death		

X Light attack by species listed at head of column.
XX Medium attack by species listed at head of column.
XXX Heavy attack by species listed at head of column.

therefore, difficult to see how the activity of the borer larvae in these trees during the autumn and winter actively contributed to tree death, particularly in view of the fact that many trees died during the same periods after late summer infestation in which the young larvae died before reaching the wood surface. Again it must be presumed that some change preceding death made the trees attractive to the ovipositing beetles in the late summer. Certainly the beetles were selective, since they attacked only trees which died either during the winter or very early the following spring.

Therefore, the weight of evidence presented herein supports the conclusion that the activity of *M. scutellatus* in severely weakened trees was truly secondary in the Lake Nipigon region, during and immediately following the severe spruce budworm outbreak.

Discussion

The progressive changes which take place in balsam fir trees from the time of first severe defoliation by the spruce budworm until the time of death are summarized in Table 3. Although some variation was observed, events generally followed this pattern in the area under study. It is evident that serious changes took place in the trees before the first discoloration of the cambium, the criterion of death used in this study for assessing the aggressiveness of associated insect attack. Failure of buds to develop in the early summer, retardation of bud and shoot development, wilting of shoots, failure of the tree to lay down new wood cells in early summer, and cessation of increment early in the growing season, all represent serious disturbances in the physiological processes of the tree. These considerations, therefore, suggest very strongly that cambial discoloration may actually be a rather late manifestation of tree death. If this is so, the conclusion reached that the activity of neither *P. sparsus* nor *Monochamus scutellatus* contributes to the death of weakened trees is strengthened.

The relationship of associated insect attack to season of tree death and tree condition is summarized in Table 4. The time of year at which a tree died governed the complex of associated insect species which infested it. Trees which died during the winter were infested by all or nearly all of the associated species the following summer, if the bark and wood were sufficiently moist. If the bark and wood were partially desiccated by early summer (presumably if death occurred during the early winter), conditions were suitable for attack by only one species, *Trypodendron bivittatum.* In cases of severe desiccation, trees often escaped infestation by any species. Most of the trees which died during the winter in the Lake Nipigon area were sufficiently moist the following spring to be attractive to at least some of the associated species. Trees which died during the summer were almost always infested by all of the associated species, except *T. bivittatum.*

The species of associated insects

encountered during this study were the same as those recorded by Swaine *et al.* (*11*) in eastern Canada (*Serropalpus barbatus* Schall. = *S. substriatus* Hald.), with the exception of the three siri-siricids, *Sirex cyaneus, Sirex* sp. (*noctilio* group), and *Urocerus albicornis*. The earlier workers made no reference to these species, which were fairly abundant in newly killed trees in the Lake Nipigon region.

Only four species of associated insects attacked trees before their death was obvious. For two of these, *Pityokteines sparsus* and *Monochamus scutellatus,* it has been shown that even though they infested weakened trees in number, their activity was such that no real damage was done to the trees before death was obvious. Little can be said at this time regarding the remaining two species, *Monochamus marmorator* and *Pissodes dubius,* owing to their scarcity in the Lake Nipigon region during the period under study. It has been suggested by previous workers (*5, 11*) that both of them became more numerous and aggressive some years after the subsidence of the spruce budworm outbreak, when they are said to be capable of attacking and killing apparently living trees. Craighead (*5*) suggested that at this time *P. dubius* and possibly *M. marmorator* actively kill trees in which foliage growth has recovered, but in which radial growth has never recovered from the severe suppression of the outbreak years. Some evidence has recently been found in western Quebec that *P. dubius* may kill balsam fir trees that survive the outbreak period, and put on good foliage growth for three or four years, but whose radial growth never recovered. Sufficient time has not elapsed in the Lake Nipigon region to establish whether or not a similar situation will prevail.

While attack by the two most abundant species, *P. sparsus* and *M. scutellatus,* never occurred except in trees which were already beyond recovery, the fact that attack did take place can serve as a basis for prediction regarding the fate of the tree. For example, late summer attack by *M. scutellatus* in apparently living trees can be regarded as definite indication of impending death during the following winter or early spring. These might be important considerations in possible salvage operations in spruce budworm outbreak areas.

Conclusions

1. Mortality of balsam fir commenced in the fifth year of severe defoliation by the spruce budworm in stands in the Lake Nipigon region where balsam fir was an important constituent. Complete or nearly complete mortality of trees was attained eight years after the first year of severe defoliation.
2. Changes in the foliage and radial increment of severely weakened balsam fir trees prior to death indicate that the criterion of death employed during this study—the streaking of the cambium—is probably a conservative estimate of the time of tree death.
3. Ten species of bark- and wood-inhabiting insects (associated insects) were found to attack either severely weakened or newly dead balsam fir trees. Of these, only two, *Pityokteines sparsus* and *Monochamus scutellatus,* were abundant and were observed to attack trees before death was obvious. However, they played no part in tree mortality, for their activity in the tree before death was such that no real damage was done to the tree before death was obvious. Two other species, *Monochamus marmorator* and *Pissodes dubius,* were so scarce in the area that little accurate information on their aggressiveness could be obtained. They were in some cases observed to attack apparently living trees, but were so rare in the area that their contribution to widespread tree mortality could only have been negligible. All other species attacked only newly killed trees.

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