A REVIEW OF THE IMPORTANT INSECTS AFFECTING THE SPRUCE - FIR FOREST IN THE MARITIME PROVINCES¹

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INTRODUCTION

This review of insects affecting the spruce - fir type in the Maritime Provinces of Canada is concerned only with the important enemies of spruce and fir. The white pine weevil, the larch sawfly, and other destructive insects that are confined to tree species of secondary importance in the spruce - fir type cannot be included. Also, of the long list of insects that occur normally on spruce and fir, the present account is limited to those that have either caused a significant amount of tree mortality in this area, or are believed capable of causing such mortality. Secondary insects like sawyer beetles, various barkbeetles, and shot-hole borers, are often important in trees weakened or killed by primary agents. As this type of damage has little relation to silviculture, beyond the implications of salvage, it is not reviewed. Also omitted are several defoliators, including sawflies of the genera *Neodiprion* and *Pikonema*, that sometimes become locally abundant but have no history of significant damage either here or in other parts of eastern Canada.

In a general treatment of forest insects, it is customary to describe the appearance of each species, its life history and feeding habits, and the nature of the damage to the host tree. As this information, supplemented by colored illustrations of both the insect and its damage, is readily available for all species to be reviewed (Swaine 1931 a, b, c; Balch 1932 b, 1936 a, b) it seems scarcely necessary to repeat it here. Instead, the available space will be devoted to the history of outbreaks and damage in the Maritime region; the epidemiology of each species, so far as it is understood to date; the silvicultural recommendations that have been made to reduce the vulnerability of the spruce - fir type to insect damage; and the possibilities offered by biological and chemical control.

The spruce budworm is among the major influences affecting the spruce - fir type, and it is also an insect that is receiving rather intensive study. This species will, therefore, be treated in some detail to illustrate how the nature of the forest may be a dominant factor in the population dynamics of an insect.

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The review of the epidemiology of the other species will be brief and will be based on comparisons with the budworm wherever possible. Concerted projects on the population behavior of insects in relation to forest type and silvicultural treatment are of comparatively recent origin and much fundamental work remains to be done on all species, especially under endemic levels of population.

The Maritime Provinces for present purposes include New Brunswick, Nova Scotia, and Prince Edward Island. The Forest Biology Laboratory at Fredericton, N.B., is the headquarters for forest insect research in this region. The functions and projects of the Forest Biology Division in general and of the Fredericton Laboratory in particular are described elsewhere (Forest Biology Division 1952, 1954). Reference is also made to the reports of the Forest Insect and Disease Survey, published annually by the Division; these reports have been consulted freely by the writer in describing the development of recent outbreaks in the Maritimes.

THE SPRUCE BUDWORM

Hosts

The spruce budworm, *Choristoneura fumiferana* (Clem.), feeds on balsam fir and on white, red, and black spruce in the Maritimes. Balsam fir suffers by far the greatest damage. It is reported in Ontario and recently confirmed in the Maritimes that mortality of mature trees of this species generally commences in the fifth year of severe defoliation. Complete or nearly complete mortality may occur eight years after the first year of severe defoliation (Belyea 1952). Understory trees and reproduction may be killed earlier through the dropping of larvae from overstory trees; enough of the smaller reproduction generally survives, however, to develop into an important constituent of the next stand (Vincent 1955). The mortality to spruce is lower and is generally related to the proportion of balsam in the stand (Craighead 1924; Turner 1952). There are records of local infestations that have persisted in pure white spruce stands for several years without causing appreciable mortality.

Outbreak History

The spruce budworm is a native insect, found only in North America, and its periodic outbreaks probably occurred long before the arrival of the white man. These outbreaks appear to be part of the natural cycle of events associated with the maturing of balsam fir. In New Brunswick, particularly, all foresters recognize budworm outbreaks as a major forest influence affecting stand history over extensive areas.

The history of outbreaks in this region is reviewed by Swaine and Craighead (1924), de Gryse (1947), and Greenbank (1956). Evidence of early outbreaks is provided by a suppression pattern in the growth rings of surviving trees, coinciding with the apparent destruction of a large proportion of the original stand. Although this type of evidence is somewhat circumstantial, our knowledge of the nature of budworm outbreaks and of other insect outbreaks within more recent years indicates very strongly that these earlier disturbances were spruce budworm outbreaks. Thus, there is evidence of outbreaks in at least some parts of New Brunswick commencing about 1770, 1806, 1878,

1912, 1949. In the periods between outbreaks, the budworm appears to become extremely scarce in New Brunswick. Evidence as to the extent of the early outbreaks and their effects on the forest is rather fragmentary. It is known that the outbreak of 1912-20 occurred throughout the greater part of New Brunswick (Fig. 1), and that it resulted in the death of some 20 million cords of fir and spruce, the most severe mortality occurring on the Miramichi drainage (Tothill 1922). In other sections of the Province, mortality was less severe. The outbreak that started in 1949 is still in progress and it is too early to predict what the eventual damage will be. This current outbreak originated to the northwest of the area severely damaged in the 1912 outbreak. Thus, although outbreaks may appear in New Brunswick at intervals of about 35 years, this does not mean that they originate in stands that are only 35 years old.

Outbreaks of similar proportions and damage have not been reported in the other Maritime Provinces, and there appears to be no evidence that Prince Edward Island or the mainland of Nova Scotia has suffered outbreaks that reached the tree-killing stage within recent decades. On Cape Breton Island, where balsam fir is generally a major component of the stand, an outbreak was recorded at about the same time as the 1912 outbreak in New Brunswick, and this was apparently followed by a more localized outbreak between 1924 and 1927 (Swaine 1933). During the present outbreak, localized areas of severe defoliation appeared on Cape Breton Island in 1951, and on the north-eastern mainland of Nova Scotia and on Prince Edward Island in 1953. In 1954 the infestation became more severe on Cape Breton Island but less severe on the Nova Scotia mainland and in southeastern New Brunswick. On both Cape Breton and Prince Edward Islands, the balsam is rather severely damaged by the balsam woolly aphid and it may require only a year or two of severe budworm defoliation to kill the trees. Another feature is that localized infestations of the budworm occur in pure white spruce stands in both places.

Epidemiology

The investigations of the 1912 outbreak in the Maritimes took place largely after the event. They provided information on the degree of damage and its relation to forest conditions, but not on the specific factors involved in the epidemiology of the insect. The outbreak of 1949 was anticipated, and in 1945 a co-operative project was initiated on the Green River Watershed in northwestern New Brunswick to study the epidemiology of the spruce budworm and its relation to forest management. With the exception of objects (Morris 1951 b) and methods (Morris and Miller 1954, Morris 1957) it would be premature to present results in detail until the outbreak is over. Two recent summaries of results are available, however, dealing with the whole Project (Morris *et al.* 1955) and with the population dynamics of the budworm (Morris *et al.*, *In press*). The present account is based on these summaries and on an earlier review by Prebble and Morris (1951).

Forests in which spruce budworm outbreaks develop and gain momentum are characterized by a high content of mature or overmature balsam fir. The extensive outbreaks have occurred where such a condition was continuous, or

FIGURE 1:

Maritime areas severely infested in the spruce budworm outbreak of 1912 (after de Gryse (1947), with certain modifications based on more recent information for northwestern New Brunswick). In the cross-hatched area of most severe damage, even-aged balsam stands originating from the outbreak occupy over 50% of the land area (based on 1946 Miramichi cruise of New Brunswick Forest Service). Varying degrees of partial mortality, or of complete mortality in patches, occurred over other parts of the outbreak area, and in some areas severe mortality was followed by fire.

nearly continuous, over large areas. This importance of balsam fir to the development of sustained outbreaks is referred to very extensively in the literature on the spruce budworm in eastern North America. For confirmation in the Maritime region, it is only necessary to compare the hazard map published before the outbreak (Balch 1946) with the infestation maps published in annual reports of the Forest Insect and Disease Survey between 1949 and 1954 (Fig. 2). Also, the evidence of greatest damage from former outbreaks has been recorded mainly in the northern two-thirds of New Brunswick and in the highlands of Cape Breton, where many stands approach a monoculture of balsam fir. However, the phrase "and gain momentum" is an important qualification. Reference has already been made to the recent development and decline of high populations in southeastern New Brunswick and in northeastern Nova Scotia, where there was no extensive occurrence of mature balsam. A number of similar references can be made. Low-hazard stands on the lower Quisibis showed high populations as early as 1949, but these declined during the following three years, along with a number of adjacent infestations in Maine. Infestations that developed in stands of pure white spruce and persisted for rather long periods without spreading or gaining momentum have been reported in the Spruce Woods Reserve of Manitoba, and in Belle Isle, Newfoundland (first reported in 1942 and still persisting in 1954). Recent examples in the Maritimes occur on Prince Edward Island, at Strathlorne on Cape Breton Island, and at Cape George on the Nova Scotia mainland. These localized infestations on white spruce appear to be exceptions that are of limited importance, but from the epidemiological point of view they present a number of interesting features which deserve greater attention.

The nature of the forest areas where major outbreaks gain their momentum suggests that the budworm is favored by mature balsam as contrasted to young age-classes, by balsam as contrasted to spruce, by dense stocking of balsam as contrasted to open stocking, and by extensive areas of balsam as contrasted to isolated stands. These factors are receiving much attention, and work now in progress should provide a more complete picture of their quantitative role in budworm survival.

It is known, for instance, that mature flowering trees are more heavily populated by the budworm than non-flowering trees, especially in the earlier years of an outbreak, and that the opening staminate flowers encourage early establishment and rapid development of newly emerged larvae (Blais 1952). The bracts of the staminate flowers, which persist on the trees for many years, are also ideal overwintering sites. Moreover, equivalent populations cause greater defoliation on flowering trees because of the great reduction in foliage production brought about by the flowering process in balsam fir (Morris 1951 c). As flower production increases with relative height and crown exposure, however, it is not easy to distinguish the effects of these variables on budworm populations. The most dominant trees in the stand are preferred by ovipositing females (Morris 1955).

The importance of balsam in comparison to white spruce has been attributed to the fact that the new foliage of the latter completes its growth

FIGURE 2:

New Brunswick areas that received the highest hazard rating before the spruce budworm outbreak of 1949 (after Balch (1946)); areas where severe infestation had developed by 1951 (after Fredericton Laboratory, Forest Insect Survey); and areas to which severe infestation had extended by the end of 1954 (after Fredericton Laboratory, Forest Insect Survey). Note conformation between susceptible type of stands and early development of infestation. The Restigouche burn, in the centre of the area mapped as highly susceptible, contains patches of mature softwood that escaped the fire. These patches became infested, presumably through drift, only after the infestation had developed in the surrounding forest.

and hardens before larval development is completed, and also to the fact that survival is very low when larvae are forced to feed on the old foliage of spruce (Craighead 1924). Black and red spruce, on the other hand, initiate annual shoot growth so much later than balsam and white spruce that they provide unfavorable food for the early larval stages. In brief, then, the failure of budworm populations to gain momentum in pure, or nearly pure, spruce stands may be largely a matter of phenology and of the unsuitability of any but the current foliage of white spruce. Also, pure spruce stands in the Maritimes are generally of limited area and, in the case of white spruce, often confined to abandoned fields. Thus stand isolation, as discussed below, may be an additional factor. When spruce is mixed with mature balsam, however, it may suffer considerable mortality (Turner 1952).

The role of stand density and continuity in the development of outbreaks and in the degree of tree mortality is related to the dispersal habits of larvae and moths. Tiny larvae before hibernation in late summer and before feeding in the spring may spin silken threads and undergo a considerable amount of random dispersal through the action of air currents. The loss of larvae through failure to alight on a favorable host is very high, even in dense, continuous stands (Morris *et al.*, *In press*); in isolated stands or in stands where favorable host trees are widely scattered, it is higher still. Dispersal losses also occur in the later larval stages through the effects of foliage depletion, and in the moth stage through the effects of air currents and poor oviposition sites.

As forest composition is an important factor in the epidemiology of the budworm, any agency that brings about the susceptible forest type will be a contributing factor to budworm outbreaks. It has been postulated, for instance, that the lumbering activities of man have been important in creating susceptible forests. Although large spruce and pine trees were undoubtedly more common at one time in the Maritimes than they are now, there is adequate evidence that extensive areas of high balsam content occurred long before the activities of man became an important forest influence. The Green River area, for example, appears to have supported successive generations of even-aged balsam, which were removed after maturity either by wind storms or the budworm (Morris 1948 a). Only after forest fire has stand composition been altered appreciably in favor of spruce; so probably the most significant influence of man on forest composition in such an area has been the suppression of fires. Also, the evidence of outbreaks that preceded the influence of man, both in Ontario (Blais 1954) and in the Maritimes, makes it unnecessary to postulate any human influence. The influence of the budworm itself on forest succession is still being studied, but it is well known that balsam predominates in stands that have followed budworm outbreaks in New Brunswick. However, balsam also predominates in stands that have followed wind storms or clear cutting, and it has not yet been demonstrated effectively that the budworm gives rise to more balsam than other major forest disturbances, with the exception of fire. It is clear, therefore, that large areas of susceptible forest type can develop in the Maritimes quite independently of the influence of either man or the budworm. By their extensive nature, however, budworm outbreaks give rise to large areas of even-aged forest which mature simultaneously.

Flieger (1954) suspects that all the very large forest fires in this region have been made possible by the supply of dry fuel that accumulates on the ground after extensive insect damage. If this is so, and if in earlier times the fuel supply in the wake of budworm outbreaks was generally ignited by lightning, it is possible that budworm outbreaks were sometimes followed by a less susceptible forest than the one they destroyed.

Despite the importance of a favorable food supply to the development of outbreaks, there is adequate evidence to show that other factors must also be involved. For example, outbreaks do not inevitably develop as soon as balsam fir reaches maturity over large areas. Many stands in New Brunswick reached this condition at least two or three decades before the present outbreak. Swaine (1928) and Graham (1939) suspected that favorable climatic conditions for several successive years might be a necessary prelude to the development of budworm outbreaks. Evidence to support such a relation has been provided by Wellington *et al.* (1950) in Ontario and Greenbank (1956) in New Brunswick. During several years preceding both the 1912 and 1949 outbreaks, the climate of New Brunswick was characterized by decreasing numbers of low pressure centres and hence minimal storminess. Precipitation fell below normal, particularly in the month of June when most of the larval development takes place. It is known that dry, clear weather hastens larval development, as does the availability of pollen for food; the possibility that rapid development may have complex effects which encourage a relaxation of natural regulating factors or an increase in fecundity is being investigated. Although we cannot alter climate, three important conclusions stem from this relationship: (1) that a "climatic release" may generally be necessary before destructive populations develop, even where susceptible stands are available; (2) that climatic release may occur on a graduated time scale from Ontario to New Brunswick and may, therefore, provide an alternate explanation to moth dispersal for the apparent west to east spread of budworm infestations; (3) that it may be possible to predict future outbreaks in advance, depending upon the progress that is made with long-range weather forecasting. To avoid misinterpretation of the theory of climatic release, it must be emphasized that it is not necessary to postulate favorable climate throughout the course of an outbreak (Wellington 1954). Once a budworm population is released from its very low endemic level by several consecutive years of favorable weather, it appears that climate is no longer a major factor. Favorable climate between 1906 and 1910, and between 1944 and 1949, appears to have encouraged budworm populations in New Brunswick; in both outbreaks, however, the greatest momentum was reached and the greatest damage was done during a subsequent period of years in which the climate could generally be described as unfavorable to the budworm. This does not discredit the theory of climatic release; but it does indicate that the forester should not anticipate much help from climate in the control of budworm populations once they rise above their very low endemic levels.

Dispersal, or drift, is another important factor that may be responsible both for the initiation of new outbreaks and for great expansion in the areas of existing outbreaks. This occurs in the moth stage in late July or early

August, in the first larval instar in August, and in the second larval instar in May. Under certain conditions, many individuals of these stages of the budworm are borne aloft by rising air currents and may be transported many miles before they are ultimately deposited. The convective currents associated with the passage of cold fronts are often responsible for the mass transport of moths, and these so-called "flights" of budworm moths have been observed in towns over 50 miles from the nearest infestation (Henson 1951). The current outbreak in New Brunswick has provided very useful information on the role of moth dispersal (Greenbank 1957). Female moths generally predominate in mass flights and they may retain a sufficiently high proportion of their egg complement to be very effective in starting new infestations. Through moth dispersal, extensive sprayed areas often show higher egg populations than could be expected from the survivors of the spray. Also, although gradual increases in resident population were detected in the Green River area as early as 1947, there is evidence that the development of the outbreak to severe proportions was hastened by moth flight in 1949. From a silvicultural point of view, dispersal is very important for it often gives rise to severe defoliation and damage in stands that might otherwise escape. Although outbreaks develop and gain their momentum in susceptible types, they often spread into other types, particularly in the direction of the prevailing winds. Population studies in the Green River area have shown that fringe areas outside the main infestation may receive repeated invasions of moths (Morris *et al.*, *In press*). In Ontario it is reported that the collapse of a given outbreak occurs almost simultaneously in the centre and in the peripheral areas of spread, even when severe starvation is limited to the centre. This, also, suggests that peripheral areas and seemingly unsusceptible stands may owe their high populations to dispersal, and that they may no longer be able to maintain such populations when the momentum achieved in the more favorable stands has been dissipated through food shortage.

Biotic agents affecting the spruce budworm include many birds, small mammals, invertebrate predators, parasites, and diseases. These mortality factors, along with dispersal losses, are undoubtedly important in keeping budworm populations at a low level over the long period of years between successive outbreaks in a given area. As the budworm moth lays 200 eggs under favorable conditions, natural mortality factors must be effective enough to remove 99% of the individuals of each generation in order to prevent the population from increasing. This they can do at low populations, but once the balance is disturbed by several successive years of favorable climate and an abundant supply of the preferred food, biotic factors are unable to hold populations in check. Further, biotic agents have not generally succeeded in terminating budworm outbreaks until the effects of foliage reduction on starvation, fecundity, and dispersal have considerably reduced the population. Under these conditions, parasites and other natural factors may hasten the ultimate collapse of the population. In short, the historical evidence of repeated outbreaks does not encourage the view that the existing complex of biotic mortality factors is capable of preventing budworm population increases when such increases are favored by food supply and climate.

In severely infested check areas reserved from aerial spraying in New Brunswick, foliage reduction so far appears to be the most important factor contributing to a decline in budworm population. This operates through direct starvation, since early-instar larvae suffer high mortality when the new foliage is exhausted; through the greatly reduced fecundity of the individuals that are able to mature on older foliage; through increased dispersal losses in all larval instars; and through reduced oviposition, probably accompanied by a greater outward dispersal of moths. The possibility that some change may occur in inherent vigor of ageing populations is being carefully investigated, but definite evidence of such a change has not yet been secured (Miller 1957).

To summarize the main features in the epidemiology of the spruce budworm, the available evidence suggests that forest conditions, climatic release, and insect dispersal are the major factors leading to the development and expansion of outbreaks; foliage shortage is the major factor contributing towards their decline; and a complex of mortality factors appears to maintain long periods of extremely low populations between outbreaks, but these endemic periods have received no study to date.

Control

It is perhaps safe to say that no simple solution of the budworm problem through biological control should be expected. Although biotic control factors may be effective at endemic population levels, the budworm has repeatedly demonstrated its ability to escape from this level, when favored either by a temporary decline in the effectiveness of such controls or by suitable climatic and food relations, and to maintain high populations until the favorable food supply is exhausted. The problem of increasing the effectiveness of the biological control complex for a native insect is much more difficult than it is for an introduced one. However, with such a devastating insect as the budworm, no possibility should be overlooked. Studies are continuing on parasites, predators, and virus and fungal diseases, to learn their effectiveness at different population levels. Certain species of parasites from British Columbia are being introduced to the Maritimes, and parasites and diseases that attack related budworm species in Europe are being introduced to Canada. To date, these introductions have not shown significant results.

As balsam fir was not utilized extensively during the early logging period in the Maritimes, the early budworm outbreaks were of little economic consequence. This situation has been drastically changed by the rapid development of the pulp and paper industry in this region during the past thirty years, and by the suitability of fir as a pulpwood species. At the time the present outbreak developed in northern New Brunswick, pulpwood operations were well underway in this extensive area of mature balsam; thus, for the first time, the budworm became "man's competitor for the same wood pile" (Flieger 1954). This led to the initiation of aerial spraying in 1952 and to the annual expansions in the spraying program to 1957, in which year 5 million acres are scheduled for treatment (mainly re-spraying) in New Brunswick. This represents the first attempt to test aerial forest spraying on such a large scale for the control of the budworm under eastern conditions. As its ultimate effect

cannot be judged at the present writing, chemical control will not be discussed here in any detail. Briefly, the spraying in northern New Brunswick to date shows that it is possible to kill a rather high percentage of the budworm larvae and, by careful timing, to save a good proportion of the current foliage. The spraying has kept alive large areas of forest that, judging from the check areas available, would otherwise be in a dying condition (Webb, *In press*). Despite the high percentage kill, however, spraying leaves a residual population that is considerably higher than the normal endemic population of the budworm before its release. This residual, which is often augmented by insect drift, has shown itself capable of reaching serious proportions in the second or third year after spraying. If spraying is to keep trees alive, without indefinite repetition, it must therefore be postulated that the outbreak will eventually collapse through other factors; and in sprayed areas the important factor of foliage depletion is removed. The interactions between spraying and other mortality factors are receiving careful study, and any conclusions concerning the ultimate effects of spraying would be premature at this writing.

Over thirty years ago Craighead (1924) described the relations between forest conditions and budworm damage in New Brunswick and Quebec. Graham and Orr (1940) reached similar conclusions in Minnesota. More recently Turner (1952) presented the results of a more quantitative study of the same relationships following the recent outbreak in the Algoma forest of Ontario. His conclusions, very briefly, were that: (1) percentage mortality of fir increased with the basal area of fir per acre; (2) increasing fir mortality fairly consistently accompanied increasing relative height of fir; (3) in general the highest degree of fir mortality occurred in types where the softwood component was mainly fir - spruce, and was lower where the component was other species or mixtures of species; (4) fir mortality had a variable relationship to the percentage hardwood in the stand, but was generally decreased with increasing proportions of hardwood when fir was in the intermediate height class. All of these workers, and a number of others, have made silvicultural recommendations aimed at making stands less vulnerable to budworm damage. Space does not permit a detailed review of all these recommendations, and the reader may wish to refer to the summary presented by Turner (1952, Appendix E). Prior to the development of the present outbreak, Balch (1946) made recommendations concerning the spruce budworm and forest management in the Maritime Provinces, and Morris and Bishop (1951) showed that hazard maps could be prepared rapidly and inexpensively for large areas.

Before recommendations concerning forest management and budworm control can be examined effectively, it is necessary to distinguish between certain concepts that have been frequently confused in the rather extensive literature on the budworm. The first concept concerns the susceptibility of the forest to the development of severe infestations. This may depend on its content of balsam fir, the relative height and physiological condition of the fir with respect to flowering, the climate, and the size and degree of continuity of the susceptible type; in other words, all those factors that promote the release of the budworm population from its endemic level and its rapid attainment of pressure and momentum. Once an outbreak has gained the necessary momen-

tum in a susceptible forest, every stand within the outbreak area, and stands far outside it (particularly in the direction of the prevailing winds), are susceptible to attack through insect drift. Susceptibility, therefore, is a term that has real meaning only when applied to a large forest area. As stand factors are only part of the group of factors involved in susceptibility, we cannot define the susceptibility of an individual stand by measuring only the stand and tree factors. A mature balsam tree in the centre of Nova Scotia, or a small stand of such trees, may represent a highly susceptible type but may be relatively unsusceptible by virtue of location and isolation with respect to similar trees or stands. The dispersal loss of both larvae and moths may prevent infestations from developing. Similarly, in the outbreak area of northern New Brunswick, stands that are quite unsusceptible by virtue of their own characteristics may be susceptible to repeated invasion through drift.

In considering general susceptibility, therefore, it is necessary to think in terms of broad forest areas. It may be said, for instance, that northern New Brunswick represents a highly susceptible area while the mainland of Nova Scotia, in general, does not. This is supported by our knowledge of outbreak history and can be related to forest conditions in the two areas. By the same token, any study of susceptibility in relation to stand factors must be done on a broad basis and must include the survey of areas where the infestation did not develop as well as those where it did. Observations restricted to the interior of well-developed outbreaks give very misleading results because the role of stand factors may be completely obscured by drift. Such observations during the current outbreak in northern New Brunswick have led many foresters to question the premise that forest management can reduce susceptibility. Studies of susceptibility are greatly facilitated if the development of the outbreak from year to year is documented by means of a complete forest insect survey. The study of past outbreaks is useful, but is incomplete in that areas of light or of short-duration infestations cannot be detected by growth-ring measurements.

Vulnerability is a different concept and refers to the vulnerability of a stand to mortality after it has become infested. The studies of damage in relation to stand factors that were referred to at the beginning of this section were largely studies of vulnerability; that is, they were based essentially on the relative mortality in different stands after the outbreak had passed. As Turner (1952) has pointed out, many of the same stand factors may be involved in both susceptibility and vulnerability, and it is not easy to separate their effects. This applies particularly to stand age. It is probable that such factors as vigor and site influence vulnerability to a greater extent than susceptibility. After a given period of defoliation it is reasonable to expect higher survival of young stands unless the site is poor or the stocking is too dense. From its very definition, it is clear that vulnerability cannot be assessed on an absolute scale. The degree of mortality depends not only on vulnerability factors but on the duration and intensity of budworm attack, and no tree or stand is invulnerable if it is subjected to attack long enough. This was brought out very well in Turner's work; absolute vulnerability limits proposed by Balch (1946) and Westveld (1945), when applied to actual damage in Ontario, often proved to be excessively low or excessively high depending upon the momentum which

the infestation had achieved in a given area. However, the principles on which the vulnerability or hazard ratings were based proved to be sound. Studies of vulnerability are useful, therefore, in establishing the relative importance of different stand factors.

In recommendations for the reduction of susceptibility and vulnerability, distinctions have not always been made between those which concern silvicultural management and those which concern pre-salvage or salvage operations. Trees killed by the budworm are subject to windfall and to rapid decay (Basham 1951), and experience has shown that the salvage of any significant proportion of the dead wood after a budworm outbreak is not a hopeful possibility (Prebble 1951). It is reasonable to intensify operations and direct them into the most vulnerable stands when an outbreak is imminent. However, although some ten years of advance warning were given in New Brunswick before any tree mortality occurred in the present outbreak, it was not considered feasible to increase annual cuts beyond current mill capacity. Pre-salvage is not a substitute for long-term planning and management that includes consideration of the budworm as a permanent threat.

It has been noted above that major outbreaks develop and gain their momentum in areas like northern New Brunswick, where tremendous reserves of mature and overmature balsam fir have accumulated over extensive areas. Vulnerability, as well as susceptibility, is related to the basal area of fir per acre, and basal area is an expression of the amount of favorable foliage. When the supply of favorable foliage and flowers per acre is high, the chances of small larvae and moths being deposited in unsuitable situations during critical dispersal periods are reduced; the budworm mortality caused by non-specific parasites and predators is probably also reduced, because the diversity of such species and their concentration per individual budworm is not as great as in mixed stands. The basal area and the quantity of fir foliage per acre normally increase with the age of the fir; maturity, in its own rights, brings additional benefits to the budworm through increases in staminate flower production and relative height.

Greater utilization of fir is the main consideration, therefore, in the reduction of susceptibility to infestation development. This should result in a more normal distribution of age-classes in each management unit and the cutting of fir on as short a rotation as is economically sound. On what proportion of the whole region would such an age-class distribution have to be realized? This cannot be answered, but clearly the larger the proportion the better. The study of the current outbreak has revealed the potency of moth drift as a factor in epidemiology. An individual watershed under close management may be less vulnerable to extensive mortality, but if surrounded by a forest of the susceptible type, it will certainly be susceptible to infestation through drift. If factors of utilization and regulation promote an annual cut of fir that approaches the annual growth in northern New Brunswick, however, it is unlikely that future outbreaks could achieve the momentum of the present one. This conclusion seems rather safe when we compare areas where severe infestations have developed with areas where infestations have either not developed or have declined without reaching much momentum.

The reduction of budworm damage is, therefore, largely a matter of increased utilization of the forest, and particularly of balsam fir, over large areas. The silvicultural procedures by which this greater utilization and regulation of age-classes are achieved are probably not of primary importance so far as budworm control is concerned. In any case, as no extensive part of the susceptible type of forest in eastern Canada has been operated for pulpwood by methods other than clear-cutting, there is no way in which the relative resistance provided by different silvicultural practices can be appraised. Graham and Orr (1940) recommend that cutting be done in rather small blocks, so that each mature block is surrounded by blocks of recent cutting or of younger age-classes. Westveld (1946) and McLintock (1947), on the other hand, favor selective cutting methods to remove mature, heavily flowering fir trees from each stand on a cutting cycle of 20 or 25 years. Considering the importance of dispersal loss in certain periods in the life history of the budworm, there is much to be said in favor of any form of silvicultural management that provides for harvest cutting by small, well-distributed working units. This would take full advantage of the dispersal loss from mature units of the susceptible type into adjacent units of an unsusceptible type. Obviously, at any time, susceptible types of stands that have not reached the rotation age must be present on a proportion of the management area. As Flieger (1954) has pointed out, it is not realistic to recommend that fir be prevented from reaching maturity; it is realistic, however, to recommend that it be prevented from reaching maturity simultaneously over extensive, contiguous areas, and to predict that this can be achieved as age-class distribution becomes controlled by forest management rather than the natural processes that have removed overmature forests in the past. Present pulpwood operations used in the harvesting of a virgin watershed generally progress in an orderly manner from the bottom of the watershed to the top. Road construction and permanent improvements are written off against each year's cut, and it is not necessary to maintain a long road system during the early years of operation. Unfortunately, by this procedure, contiguous parts of the watershed will again mature simultaneously. A more diversified distribution of operating units would favor insect control. The large areas of even-aged balsam resulting from the 1912 outbreak will present particular problems in this regard as they reach operating age.

Other recommendations that have been made by various authors concern silvicultural methods to encourage a change in forest composition, so that balsam fir will become a less important component of future stands. Spruce has a longer life and greater stability, and its encouragement is obviously desirable. However, the practicability of such recommendations in northern New Brunswick is open to question. In this area, fir is an excellent pulpwood species that regenerates prolifically and produces a high volume per acre on a short rotation. Its discouragement by silvicultural means is of doubtful feasibility, unless fire becomes more generally accepted as a silvicultural tool. In regard to forest composition, however, it has been indicated above that mixed stands of hardwoods and conifers are more resistant to the budworm than are pure stands. The present forest of the Maritimes has very likely been rendered more susceptible to damage by the extensive dieback of birch, and

it appears that certain budworm outbreaks in Ontario have been preceded by extensive outbreaks of the forest tent caterpillar on poplar. There is a good reason, therefore, for the silvicultural encouragement of mixedwood stands wherever the site is favorable for such stands. Not only is the balsam component of mixedwood stands less vulnerable, but mixedwood and hardwood stands provide better isolation for the pure stands of softwood.

Assuming, then, that balsam fir will remain the major component of the forest over large areas in the Maritimes, it may well be asked what assurance can be given that the budworm problem will diminish as this forest comes under utilization and management. No positive assurance can be given, nor can we even define precisely what age of balsam would represent maturity, so far as the budworm is concerned, in a large forest under management. There is available for study no extensive area of boreal forest where management has been practiced long enough to provide a normal and diversified distribution of age-classes. Accordingly, all the available evidence supporting this premise is necessarily of an indirect nature. In the present review an attempt has been made to summarize this evidence, as revealed both by the bionomics of the insect and by the pattern of outbreaks, and it seems fairly strong. However, the extensive studies and control experiments in progress during the present outbreaks will undoubtedly increase our knowledge and influence our ideas about budworm control. What may be even more important is the information to be gathered by extending these studies through the endemic period after the outbreak. As we gain understanding of the population dynamics of the insect, our attempts to control it will become less empirical and it is even possible that new and fundamentally different methods of control will be revealed.

THE BALSAM WOOLLY APHID

Hosts

The balsam woolly aphid, *Adelges piceae* (Ratz.), is second only to the spruce budworm as an enemy of balsam fir in the Maritimes. In fact, if it proves itself capable of reaching high populations in northern New Brunswick, it may well become more consistently destructive and more difficult to control than the budworm. The present review of this insect is condensed very largely from the more complete account presented by Balch (1952). *A. piceae* attacks only firs of the genus *Abies*. Severe attack on the stem of the tree, easily recognized by the white "wool", may result in death in three years or less without any symptoms of "gout". Gout is caused by light to moderate attacks on the new shoots over a longer period. Persistent shoot attack results in the deformation of the crown and eventually in the death of the tree, through interference with shoot production. On Cape Breton, gouty trees with their reduced shoot production were killed by only two years' attack by the black-headed budworm in 1930 and the spruce budworm in 1954.

Outbreak History

The balsam woolly aphid was introduced to Nova Scotia from Europe about 1900, probably on nursery stock. It is now established throughout the whole of Nova Scotia and Prince Edward Island, the southern portion of New

Brunswick, a part of the northeastern United States, and two areas in Newfoundland. Figure 3 shows its distribution in the Maritime Provinces by the end of 1954, and there has been only a very slight northward extension since then. Spread has been most rapid near the coast. The advance of the insect into new areas is characterized by spotty and widely scattered infestations, which occur chiefly on the stems of the larger trees. As such infestations become more general in an area, they tend to coalesce while new, isolated infestations appear farther north. The usual sequence of events in a given stand is described by Balch:

"1. When the insect first becomes established in a stand it tends to multiply on the stems of individual scattered trees, which are often the larger trees with rather rough bark, or those with deep crowns. From these it spreads to other nearby trees.

"2. The population rises more or less steadily in the stand for a number of years, unless checked by unfavorable weather such as the winter weather of 1933-34. It finally reaches a peak at which a considerable number of the trees may be killed, or severely injured, by attack on the stems.

"3. The population then drops and remains at lower but considerably fluctuating levels. This period may continue indefinitely and is characterized by increasing evidence of twig injury, or 'gout', and gradual dying of some of the trees. It may be accompanied by partial or complete recovery of other trees."

Although the larger trees in a stand are generally infested first, smaller trees and reproduction often become infested and suffer severe mortality. Other effects of the insect include loss of radial growth and reduction in the quality of wood through the encouragement of "rotholz", which resembles compression wood. The destructive power of the insect in individual stands is revealed by plot studies of Balch (1952), Brower (1948), and the Forest Insect Survey (Ann. Rept. 1953). However, no satisfactory data are yet available on which to base an estimate of total loss for a given forest district.

Epidemiology

There appears to be no good evidence that the nature of the food supply, as represented by stand factors, is as important to the aphid as it is to the budworm. Brower observed in Maine that trees on thin soils or poorly-drained sites were the most severely injured and provided centres of infestation. Balch, however, while indicating the need for more intensive study of these factors, pointed out that some of the most severe infestations in the Maritimes have occurred on well-drained sites with relatively deep soil, in mixtures of softwoods and hardwoods as well as in pure softwood types. Further, although infestations develop most rapidly when balsam content is high, small forested areas surrounded by cleared land seem to be particularly susceptible. In a given stand, the death of the preferred trees is probably a factor stimulating both dispersal and population decline. Winged forms of the aphid are rare and probably do not reproduce. Dispersal results chiefly from the surplus population of motile larvae, which are carried by winds and air currents. The

FIGURE 3:
Distribution of balsam woolly aphid in the Maritimes in 1954 (after Fredericton Laboratory,
Forest Insect Survey).

presence of the insect in southwestern Newfoundland suggests that it was carried by air currents from Nova Scotia, a distance of at least 70 miles. No parasites attack the balsam woolly aphid, and native species of predators have proved themselves inadequate. To date, climate, as manifested by minimum winter temperatures, has been the important factor affecting the distribution and numbers of the aphid in the Maritimes. A minimum temperature of -32° F. in February, 1934, killed practically all the larvae above the snow line in central and southern New Brunswick. In 1948, however, a considerable proportion of the population survived temperatures of -30° F. and -31° F. Winter mortality is of prime importance and probably explains the more rapid advance of the infestation near the coast. Complete mortality above snow, however, occurred in only one winter since 1931 and its effect was mitigated by the protection afforded by snow to the larvae at the bases of the trees. Whether winter temperature will prevent severe infestations in northern New Brunswick or whether the insect will become adjusted to more severe conditions is an important question to be answered only by future developments. Balch (1954) believes that the insect is capable of establishing itself throughout the balsam - spruce forests of Newfoundland.

Control

Insects accidentally introduced to Canada from abroad often lend themselves to control through the introduction of effective natural enemies from the country of origin. The introduction of insect predators of the balsam woolly aphid from Europe to the Maritimes was started in 1933 and has been greatly intensified in the last few years. At least three of the species seem to be definitely established, and detailed studies are in progress to learn whether they are capable of exerting effective control under Maritime conditions (Clark *et al.* 1954). An important difficulty is that the twig attack leading to gout, which is responsible for much of the damage to balsam fir, does not occur on the native European hosts of the aphid. It is questionable, therefore, whether introduced predators will be able to prevent this type of damage.

Although the woolly covering gives protection to the insect, insecticidal sprays will give good control on ornamentals if applied with thoroughness and force in the spring (Brower 1948; Balch 1952). Under forest conditions chemical control would be difficult.

Considering the wide variety of stands in which infestations have developed there is as yet no good reason to suppose that damage can be prevented by silviculture or management, except through the reduction of the balsam content where feasible. As initial infestations obtain their impetus on the larger trees, however, it has been recommended that salvage and control can be combined by cutting all merchantable balsam as soon as a stand is noticeably infested. An attempt is being made in Newfoundland to eliminate spot infestations by a system of cutting and burning. Factors other than tree size are also involved, and one of the salient features of new infestations is the heavy attack on some trees in contrast to the absence of attack on neighboring trees. More detailed investigations of both tree and stand factors in relation to susceptibility and vulnerability may provide results of interest to the silviculturist.

THE EASTERN SPRUCE BARKBEETLE

Hosts

The eastern spruce barkbeetle, *Dendroctonus piceaperda* Hopk., attacks white, red, and black spruce, in that order of preference. All the important outbreaks have developed on white spruce, which is by far the preferred host. Limited infestations have occurred on large red spruce in localized areas in Nova Scotia. In a small outbreak at Frater, Ontario, in the 1920's, black spruce was immune to attack under natural conditions (Watson 1928). After the severe Gaspé outbreak of 1930-34, cruise lines in the affected area showed 47% mortality to white spruce, by volume, but only 6% mortality to black spruce in the same stands; pure stands of black spruce were not attacked (Balch 1942). It would appear, therefore, that black spruce is not completely immune, but is unlikely to suffer very serious mortality. Infested trees usually die in one year, losing their foliage by the first winter following the attack. Unsuccessful attack sometimes occurs on vigorous trees, in which the beetles are drowned out by the copious flow of pitch.

Outbreak History

Swaine (1924) refers to an extensive outbreak that occurred throughout a large part of New Brunswick and Maine, and in southeastern Quebec, during the years 1897 to 1901. More than a billion feet of spruce were estimated to have been killed in Maine and New Brunswick. Since that time no extensive outbreaks have occurred in the Maritimes. From time to time small localized infestations have been reported on white or red spruce in Nova Scotia, where stands of large spruce are more common than in New Brunswick. Spruce that has reproduced on abandoned fields seems particularly susceptible. Some rather severe outbreaks have occurred north of the Maritimes, in the Gaspé Peninsula. Of these, the major one occurred between 1930 and 1934, and the damage has been described by Gobeil (1941) and Balch (1942). The greater susceptibility of the Gaspé to this insect has been attributed to the frequent blow-downs, which provide ideal breeding material, and to failure to utilize the large white spruce before it becomes overmature. It is also very likely that the 1930 outbreak was aided by the extensive defoliation caused by the European spruce sawfly.

Epidemiology

A suitable food supply, as represented by weakened or fallen trees, is the prime factor in the epidemiology of the spruce barkbeetle. It belongs to a group of insects that may be called "secondary-primary". Under normal conditions it is secondary; that is, it breeds in windfalls and slash, and standing trees that are weakened from overmaturity or injury. When, however, the beetle has increased to large numbers, through a temporary supply of this preferred breeding material, it may become primary and kill trees that are in any condition. The supply of breeding material may be provided by blow-downs, fires, lumbering operations, insect defoliation, or simply by the overmaturity and decadence of the spruce in a given area. The most extensive and severe outbreaks appear to have been associated with overmaturity, while lumbering operations or blow-down have generally given rise to localized

attack of limited severity. Watson (1928) reports that this insect seldom breeds in timber, either standing or fallen, that is less than five inches in diameter, and that the stumps of freshly-cut spruce are not very productive breeding places. The slash from pulpwood operations, therefore, would not provide much breeding material, but the larger tops and culled logs left in lumbering operations might.

Once the surplus population of beetles has developed, the kind of trees attacked may depend largely on the momentum achieved by the outbreak. In small infestations, the beetles often confine their attack to the largest and less vigorous trees; at the height of severe outbreaks, when 50% or more of standing trees may be affected, some of the most vigorous trees in a stand may be attacked and killed. Even under these latter conditions, however, there is still a decided preference for the larger and less vigorous trees. Of the white spruce killed in the last Gaspé outbreak, 80% were over 10 inches, D.B.H.; and those attacked at Frater were growing, on the average, only 63% as fast as those that were not attacked.

Other factors involved in epidemiology, and particularly in the reduction of surplus populations, are described by Watson (1928). Parasites and predatory insects appear to be of very limited value. Woodpeckers are the most important predators and, in controlled experiments, were capable of finding and consuming over 98% of the insects under the bark. Woodpeckers prefer to work on standing trees, and they do their most effective work during the winter months; this is one reason why fallen trees, which may be protected by snow in the winter, are the most effective breeding places for the barkbeetle. Watson reports that woodpeckers are attracted to a barkbeetle outbreak from surrounding districts; if this is so, they are probably more effective in controlling localized outbreaks than large, extensive outbreaks. When barkbeetle populations are high, the overcrowding of the broods in the preferred trees and the resulting competition of the larvae for food is another factor of natural control. Also, when only vigorous trees remain to be attacked, the chances of the tunnels being drowned out by copious resin flow are greater.

Control

Clearly, from what is known of the epidemiology of the eastern spruce barkbeetle, the prevention of serious outbreaks is a matter of utilization and management. Balch (1942) writes, "Serious outbreaks would be unlikely to occur in forests managed on a short rotation of 100 years or less. When our last virgin stands have been cut, and all our spruce forests are managed on such a rotation, we may expect the spruce barkbeetle to become a minor pest, of importance to those who want to grow full-sized trees for large logs, or in park preserves. That, in fact, is its present status throughout a good part of the Maritime Provinces where stands of large spruce have become comparatively scarce." It seems improbable, therefore, that future outbreaks of a very severe or extensive nature will be experienced in the Maritimes. For the localized infestations that occur from time to time, control can be combined with salvage if the infested trees are cut in the winter and the logs placed in water, or peeled and the bark burned, before the beetles emerge in the spring (Swaine 1924).

THE EUROPEAN SPRUCE SAWFLY

Hosts

The European spruce sawfly, *Diprion hercyniae* (Htg.), can successfully attack all species of spruce in the Maritimes, but is favored by white spruce. In contrast to the spruce budworm, the sawfly has a decided preference for the old foliage as opposed to the current year's growth. This preference is particularly marked on red and black spruce, and in areas like the Gaspé where the sawfly has only one generation per year; under these conditions, new needles are rarely eaten until the old foliage is completely exhausted. The new needles of white spruce may be fed upon towards the end of the larval period, however, with the result that this host is subject to more rapid defoliation and mortality. The killing of trees over any large area by this insect tends to be a gradual process, particularly in one-generation areas. In the Gaspé outbreak, tree mortality started seven years after severe feeding and reached its peak (about 10% of total stand killed annually) five years later (Reeks and Barter 1951). Loss of all the old foliage and 75% or more of the new foliage was generally necessary before death occurred. Comparable records are not available for the two-generation areas in New Brunswick or three-generation areas in the northeastern States, for the outbreak collapsed before there was any important tree mortality in these areas.

Outbreak History

As the name implies, the European spruce sawfly is an introduction from Europe. The time of its introduction to Canada is not known; when first discovered in the Gaspé in 1930, a large outbreak had been in progress for several years. During the next ten years, the insect was reported throughout the Maritimes and over large areas in Quebec, Ontario, and the northeastern United States; it also reached Newfoundland. In New Brunswick populations reached the epidemic level in 1936, particularly in various stands in the central and southern districts where spruce was an important component of the forest. In the other Maritime Provinces, infestations never reached the severe level. The peak of the outbreak occurred in 1938 and populations declined very rapidly throughout the outbreak area in 1939 and 1940. Since that time, no appreciable defoliation has been caused by the sawfly. Significant tree mortality was restricted to the Gaspé, where it approached 11½ million cords.

Epidemiology

The behavior of the sawfly in Canada was perhaps typical for a species that is introduced to a new country without its natural regulating factors. Parasites and diseases native to Canada did not attack it effectively (Balch 1939). Small mammals destroyed a proportion of the cocoons (Morris 1942) but this mortality was not great enough to prevent the population from increasing. Insect predators destroyed only a small number of cocoons (Morris 1951 a). The sawfly has a high fecundity, and its multiplication and survival in the absence of effective natural enemies was further encouraged by its habits of parthenogenesis and diapause (Prebble 1941). Stand factors appear to be of limited importance in the epidemiology of this insect. The most extensive infestations occurred in mature stands of white spruce, and the old trees of

this species were generally the most severely defoliated. Considerable areas of young white spruce were heavily attacked, however, both on abandoned pasture lands where it grows in pure stands, and on old burns where it is mixed with and sometimes overtopped by hardwoods. Also, pure black spruce slopes in the Gaspé, although more resistant than white spruce, suffered a mortality of 43% by volume. For both white and black spruce, the percentage of stems killed increased directly with diameter.

Control

The European spruce sawfly is not an important pest in the countries from which it originated. A large program of parasite introductions from these countries to Canada was initiated in 1934 and by 1938 some of these parasites began to have significant effects on the sawfly population in New Brunswick. In the same year, however, a polyhedral virus disease appeared in the field and this disease was introduced, in all probability, along with the parasite shipments. It was very largely the disease, in the following two years, which brought about the collapse of the sawfly populations throughout the outbreak area (Balch and Bird 1944; Morris 1949 a). Studies of the sawfly have been continued on a reduced scale in the post-outbreak period. Seven species of the introduced parasites have established themselves and, along with the disease, have been effective in keeping sawfly populations at an endemic level (Reeks 1953; Bird and Elgee 1957). Unless some unexpected relaxation of the present complex of biological control should occur, there will be no need to consider additional control measures against the European spruce sawfly.

THE BLACK-HEADED BUDWORM

Hosts

The black-headed budworm, *Acleris variana* (Fern.), feeds on balsam fir and on all species of spruce in the Maritimes. Like the spruce budworm, it is greatly favored by balsam fir and extensive outbreaks have developed only in forests where this host is predominant. Also like the spruce budworm, it feeds on the new foliage. When the new foliage is exhausted, large larvae feed on the old foliage of balsam but not on the old foliage of white spruce. Red and black spruce are only lightly attacked. As tree mortality has followed a black-headed budworm outbreak only on Cape Breton Island, where the trees were already severely weakened by the balsam woolly aphid, it is not known how many years of severe attack by the budworm alone would be required to kill a tree. Larvae of the black-headed budworm emerge later in the spring than those of the spruce budworm, at the time when the buds of balsam are opening. Therefore, since there is no damage through bud mining as there is for the spruce budworm, it seems safe to assume that some five years of severe attack would be required to kill dominant and codominant trees. As in the case of the spruce budworm, however, understory trees may be killed earlier through the dropping of larvae from the overstory.

Outbreak History

The first known outbreak of this insect in eastern Canada was reported on Cape Breton Island in 1929. This outbreak reached a peak in 1930 (Fig.

4) and in that year the late-larval instars suffered severe mortality from natural factors. In 1931 the population collapsed and no significant defoliation occurred (Balch 1931, 1932 a). Thus, there were only two years of severe defoliation: 1929, when mature balsam trees lost practically all their new foliage; and 1930, when they lost their new foliage and 10% to 30% of their old foliage. White spruce, where mixed with balsam in the severe part of the outbreak, lost most of its 1929 and 1930 foliage, but pure stands of white spruce lost only part of this foliage.

The next outbreak covered a much greater area. Figure 4 shows the areas in the Maritimes where defoliation was most noticeable; however, in this same period, population increases were detected throughout New Brunswick, Nova Scotia, Prince Edward Island, and parts of Quebec, Maine, and Newfoundland (Forest Insect Survey, Annual Report 1948). The history of this outbreak followed very closely that of the earlier one on Cape Breton. The first noticeable defoliation over any extensive area occurred in 1947, and in 1948, which was the peak year, the late larval instars suffered severe natural mortality (Morris 1949 b). In 1949 the collapse of the population was general over the Maritimes, except for two isolated areas in Cape Breton where high populations continued for another year or two (Fig. 4). Mature balsam suffered the greatest loss of foliage and in many stands white spruce suffered only a 10% loss, even when mixed with balsam. No trees of any species were killed and no important loss of radial growth occurred. The disfigurement of Christmas trees in localized areas was the only economic effect reported.

Epidemiology

The role of stand factors in the epidemiology of the black-headed budworm, although they have not received the same attention, appear similar to their role in the epidemiology of the spruce budworm. The outbreaks show the same conformation to Maritime areas of high balsam content (c.f. Fig. 2, Fig. 4), and the greater defoliation suffered by mature balsam has been apparent in both outbreaks. It is possible that climatic release may also be involved, although the effect of climatic factors on this species has not been studied. The outbreak that reached its peak in 1930 developed during what was a notably dry period in the Maritimes. Population studies on the Green River Watershed reveal that significant increases over the endemic level of black-headed budworm populations started at least as early as 1946 (Morris 1948 b). The outbreak that reached its peak in 1948 developed, therefore, during the same dry period that appeared to encourage the present outbreak of the spruce budworm.

In the relative efficiency of the natural control complex at high populations, however, the two budworm species show great differences. Outbreaks of the spruce budworm are very destructive because natural control factors do not generally regain their effectiveness until populations are severely reduced by foliage exhaustion. Outbreaks of the black-headed budworm have not been destructive because natural regulating factors have effectively reduced high populations. In 1930 and 1931, the most important of these factors appeared to be disease, parasites, such predators as stinkbugs and spiders, and the

FIGURE 4

Outbreak history of the black-headed budworm in the Maritimes, showing years of peak infestation (1930 area after Balch (personal communication)); 1948 area after Fredericton Laboratory, Forest Insect Survey (Ann. Rept. 1948). Areas classed as "moderate" and "severe" on the original maps have been combined under "moderate".

possible failure of moths to deposit their full egg complement (Balch 1932; Prebble 1933). In 1948 and 1949, disease was not observed in the Green River area but native parasites caused a very high degree of larval mortality.

Control

If future outbreaks of this insect behave like the past two, there will be no need to consider control measures for any extensive areas. In limited areas where balsam is grown for Christmas trees, aerial or ground spraying may be necessary to preserve the appearance of the new foliage. It may also be helpful to isolate such stands from stands of mature balsam. There is no assurance, of course, that future outbreaks will always collapse so rapidly and the possibility of sustained outbreaks, which could approach the destructiveness of spruce budworm outbreaks, cannot be ignored. The place of forest management in the protection of Maritime forests from extensive spruce budworm damage has been outlined above; the same type of management will undoubtedly reduce the chance of extensive damage from the black-headed budworm.

THE EASTERN HEMLOCK LOOPER

Hosts

Outbreaks of the eastern hemlock looper, *Lambdina fiscellaria fiscellaria* (Guen.), have occurred in hemlock forests in Ontario and in the Lake States. Outbreaks of what is possibly another sub-species have occurred in balsam forests in Newfoundland and Quebec. The present review is concerned only with the form of the hemlock looper that occurs on balsam fir. Balsam fir is by far the preferred host of this form and outbreaks have occurred only in forests that were very predominantly composed of this host tree. Under epidemic population levels, spruce and many other species including hardwoods may be fed upon, but mortality is generally restricted to balsam. The small larvae in the spring feed on the opening new shoots of balsam and later the larger larvae feed readily on the old foliage. This is in decided contrast to the feeding habits of other defoliators that have been discussed above, and often results in the complete defoliation of balsam fir in one season. This is hastened by the wasteful feeding habits of the larvae. Outbreaks are often sudden and severe; many trees in a stand may lose over 90% of their total foliage in the first season and such trees die during the ensuing winter.

Outbreak History

The hemlock looper has no recorded history of outbreaks in any of the Maritime Provinces. However, as it is always found rather commonly on balsam throughout the Maritimes, and as destructive outbreaks have occurred as close as the Gaspé, the possibility of outbreaks in this region cannot be ignored. The history of the hemlock looper in Newfoundland shows that there have been four periods of heavy attack in various parts of the Island since 1912 (Carroll 1956); these were approximately 1912-15, 1920-25, 1930-35, 1947-55. In any one period, localized outbreaks tend to develop independently in different localities and to exist for about three years. The first outbreak was reported on the mainland of eastern Canada in 1928 on the north shore of the St. Lawrence between Pentecost and Bersimis (Watson 1934). Here, also, the

defoliated areas were very irregularly distributed, patches of completely defoliated forest being surrounded by stands that were practically untouched. About 100 square miles in three different valleys were affected. This outbreak subsided in 1929-30. In 1948, similarly localized outbreaks appeared on the northeastern coast of the Gaspé, killed a high proportion of the infested stands in one year, and subsided in 1949-50.

It is of particular interest to observe that during the 1928-30 outbreaks in Quebec, populations of the hemlock looper high enough to cause noticeable defoliation were recorded in Nova Scotia (Balch 1931). They subsided in 1931 without causing damage. Again, during the 1948-50 outbreaks in Gaspé, higher than usual populations were recorded during the population work on the Green River Watershed, and throughout the Maritimes by the Forest Insect Survey. This suggests that the hemlock looper increases in numbers almost simultaneously throughout large areas in eastern Canada, but only succeeds in reaching tree-killing epidemics in localized spots. These spots may vary in size from a few acres to several square miles.

Epidemiology

The epidemiology of this species is only imperfectly understood at present, but detailed work is in progress in Newfoundland. The available evidence to date suggests that stand factors are very important, with respect to both the content and maturity of balsam fir. The description of a recent outbreak in Newfoundland, for example, shows that severe defoliation was restricted to areas in which the balsam was 120 to 150 years old, and comprised 90% of the stands; near the periphery of the outbreak the balsam content dropped to 60 or 70% (Forest Insect Survey, Annual Report 1953). Carroll (1956) concluded " . . . all the severe attacks commenced in stands containing over 70% balsam fir. An increase in the spruce content of a stand seems to have resulted in a corresponding decrease in susceptibility to attack".

The chronological agreement is suggestive between: (1) the 1928-30 and 1948-50 hemlock looper outbreaks, (2) the 1929-31 and 1947-49 black-headed budworm outbreaks, (3) the 1949-? spruce budworm outbreak; particularly since outbreaks in one area seem to be accompanied by less conspicuous population increases over much wider areas. Similar agreements have been observed between outbreaks of these same insects in the west (Prebble 1951). The relationship of the eastern hemlock looper to climate has not yet received detailed study. Watson (1934) suspected that the decline of the north shore outbreak was related to wet weather; on the other hand, starvation, disease, and parasites have been important factors in the decline of recent Newfoundland outbreaks.

Control

The spotty areas of severe infestation do not spread and coalesce, as do the epicentres of spruce budworm or black-headed budworm outbreaks. This facilitates direct control or salvage. Chemical control may be practical, providing incipient outbreaks can be detected early enough and spraying can be done before the trees are already fatally defoliated. Aeroplane dusting was tested

successfully in hemlock stands in Ontario in 1929, but the outbreak was already declining in that year (de Gryse and Schedl 1934). Where the individual outbreaks are accessible and restricted in size, the clear-cutting of the infested stands may be more practical (Watson 1934). From the long-term point of view, forest management aimed at the reduction of large areas of overmature balsam should reduce the chances of any extensive mortality.

DISCUSSION

The six most important insects of the spruce-fir type in the Maritimes have been reviewed. These six species fall naturally into three groups. The first group includes native "secondary-primary" insects, of which our only example is the eastern spruce barkbeetle. Outbreaks in the Maritimes in recent years have been relatively unimportant, because spruce stands are generally being utilized before they become overmature.

The second group consists of introduced species and includes the European spruce sawfly and the balsam woolly aphid. The Maritime forest, because of its position, is generally the first forest in Canada to suffer the effects of such introductions. A logical control procedure is the introduction of natural enemies of the pest from the country of origin. This has been so successful for the sawfly that it has been reduced to the status of a native, endemic species. It is to be hoped that the balsam woolly aphid will yield to similar importations before it becomes established in the extensive balsam forests of northern New Brunswick.

The third group contains three native defoliators—the spruce budworm, the black-headed budworm, and the hemlock looper. It has been seen that these three have a number of things in common, such as the chronological relationships between outbreaks, as discussed under the hemlock looper; and the relation of infestation development to areas where mature and overmature fir has accumulated (Figs. 1, 2, 4). There seems good reason to believe that such species will diminish in importance as the extensive virgin fir stands of northern New Brunswick come under utilization and management. In the northern plateau of Cape Breton, where the poor form and quality of the fir do not encourage utilization, periodic outbreaks of one or more of these species may cause only aesthetic losses. Stand factors are of considerable importance in the epidemiology of these defoliators. At the same time our treatment of epidemiology, however brief, has been designed to show that many other factors are also involved and that any simplified explanation for insect outbreaks should be viewed with caution. It is not likely, then, that insect problems in the spruce-fir forest will disappear after normal age-class structure and more diversified distribution of operating units have been obtained. However, the problems will be smaller and more amenable to direct control and salvage than the problem presented by the present budworm outbreak.

Little has been said and, indeed, little could be said, about the relative merits of different silvicultural systems in reducing the vulnerability of the spruce-fir type to insect damage. The entomologist is handicapped by the fact

that silvicultural management has not yet been practiced on any large scale in this forest type. The general principles involved in the cultural control of forest insects, as well as they are known to date, have been discussed by several authors (Swaine 1933; Balch 1935; Graham 1951, 1952; Prebble 1951) and need not be reviewed here.

Chemical control is another subject on which little has been said in the present review. This is also as it should be, for the Maritimes are now in the middle of the most extensive chemical control experiment that has ever been conducted against a forest insect. The conditions under which this experiment is being conducted are as difficult as any that are ever likely to be encountered, for the outbreak has achieved a momentum and extent that could not be repeated in managed areas. So if the spraying does not succeed in terminating the outbreak in the extensive areas under treatment, it will not mean that chemical control will have no place in the more limited infestations that would be expected in a managed forest. On the other hand, if the outbreak should collapse as a direct or indirect result of repeated spraying, the large areas of mature balsam that aid infestation development will still exist. Spraying, therefore, is unlikely to provide a permanent solution to the problem, while indiscriminate spraying may create many new problems of its own (Graham 1951; Pickett *et al.* 1946; Solomon 1953). Forest management seems likely to remain the essential basis for the prevention of extensive mortality.

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