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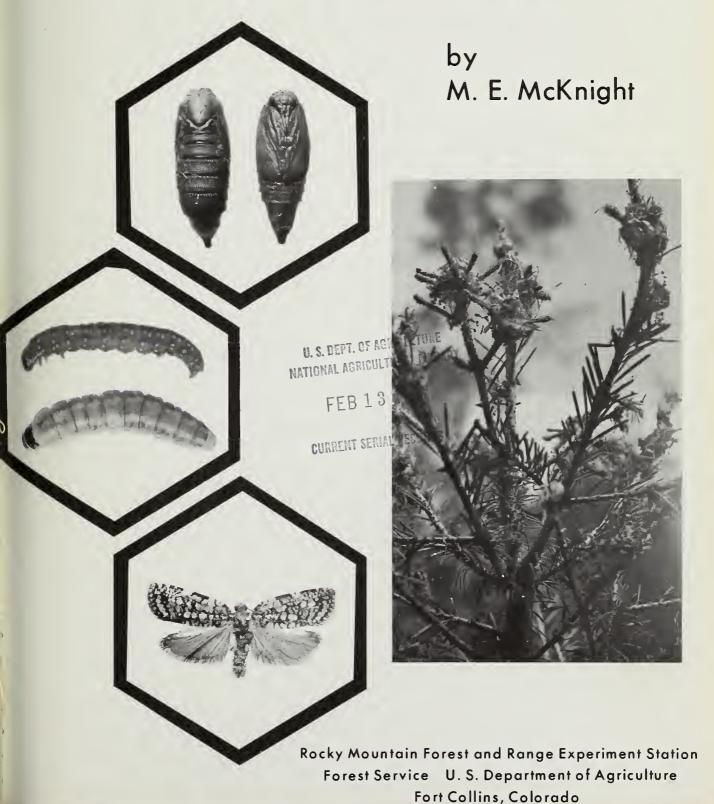
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A Literature Review of the
Spruce, Western, and 2-Year-Cycle Budworms

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Choristoneura fumiferana, C. occidentalis, and *C. biennis*

(Lepidoptera: Tortricidae)

by

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Covers 370 literature citations on the spruce (*C. fumiferana* (Clemens)), western (*C. occidentalis* Freeman), and 2-year-cycle (*C. biennis* Freeman) budworms through November 1967. Citations are also organized in a subject index.

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It is hoped that this review and subject index will help ento-mologists planning new research to distinguish between the areas that have been studied in depth and those that need further investigation. The subject index includes the published works ar articles of research nature that are obtainable through mast li-brary services. Popular articles and reviews that did not cantribute new knowledge generally ore not included. Unpublished office reparts that were not widely distributed or are not easily ob-tained ore not included.

Not all entries in the subject index ore reviewed in the text. However, the text reflects the state of knowledge of most of the subject areas.

It is recognized that the literature concerning the jock-pine budworm is accumulating rapidly. These works, other than those which contributed to the seporation of this species from the spruce budworm, are not indexed or reviewed.

INTRODUCTION

The statement "the spruce budworm is one of the most de-structive pests of the coniferous forests af North America," or its equivalent, oppeors often in the literature of forest entomalogy. The notoriety of the insect comes from its devastotion of millions of acres of balsom fir forests in Conodo ond northeastern United States, where millions of dollars hove been spent to protect the trees until they could be horvested. The western budworm, only recently recognized os distinct from the spruce budworm, hos been of greot concern to managers of the Douglos-fir forests of western United States. Here, too, millions of dollors hove been spent on chemicol control to prevent the devastotion thot wos expected from the history of spruce budworm outbreaks in Canada. Undoubtedly, the large-scale opplicotion of insecticides, DDT in porticular, to suppress epidemic populotions of the spruce bud-worm ond the western budworm contributed to the controversy over environmentol contaminotion by pesticides.

Outbreaks of the 2-year-cycle budworm have not had the economic impact of the other two species. Its principol hosts, Engelmonn spruce ond subalpine fir, are not under as intensive monogement os the hosts of the spruce budworm and the western budworm. Also, because of its 2-year cycle, the insect probobly hos less impact on the host tree. Outbreaks of this species moy have to be suppressed, howaver, when they impoir the esthetics of high-oltitude recreotion oreas.

The spruce budworm certoinly is omong the most studied in-sects in North America becouse of its greot economic significonce in Conoda. Its biology has been known since 1881; great expendi-tures of time ond money have been directed toward understond-ing its population fluctuotions, ond toward finding means of pre-venting ar minimizing its economic impact. Suppression of epi-demics of the western budworm hos been the mojor objective in western United Stotes, ond only in the past decade has ottentian been given to the couses of budworm outbreaks and their real effects on host trees ond forests.

TAXONOMY

The spruce budworm was named by Clemens in 1865 fram specimens collected in Virginia (Freeman 1953). In 1890, Packard described damoge coused by the insect to spruce and bolsam fir in Maine during the late 19th century. Pockard referred to the insect as <u>Tartrix</u> <u>fumiferona</u> Clemens. In 1869, Robinson described dork variants under the name <u>Tortrix</u> <u>nigridio</u> ond based his de-scription on specimens collected in Ohio, Pennsylvonio, and Mosso-chusetts. In 1913, Meyrick ploced the species in the genus <u>Harm-ologo</u> Myr., proposed by him for a group of primitive tortricid species from New Zealand. Forbes, in 1923, followed this system. The species hos since been ossigned to either <u>Archips</u> Hbn. or <u>Cacoecia</u> Hbn. by economic entomologists and toxonomists, until Freemon (1947o) transferred the spruce budworm from <u>Archips</u> Hbn. ta the genus <u>Choristoneuro</u> Lederer.

Grahom (1935) wos the first to point out thot the form of budworm feeding on pine was biologically distinct from that form feeding on spruce and balsam fir. He suggested that they be considered specificallly distinct. 8rown ond MocKoy (1943) osserted thot the jack-pine budworm should be designoted o subspecies, if not a seporate and distinct species. They presented as evidence differences in size, wing colorotion, geogrophicol distribution, host relotionships, life cycle dates, and mole genitolio.

MacKoy (1953) studied the larvoe of both species and found structural differences only in the heod. The heod capsule of <u>pinus</u> is usually lorger than thot of <u>fumiferona</u>, ond its length greater, in relation to its width. Also, late instar lorvae of <u>fumiferona</u> usuolly have dark heads and light prothorocic shields, whereos those of <u>pinus</u> usuolly have light heods and dark prothorocic shields. Early instar larvae of <u>fumiferono</u> ond <u>pinus</u> have heods and prothoracic shields of obout the same color, so color connot be used to separate the species.

Cox (1953) demonstroted thot the postclypeal index could be used to separote the two closely ollied species. The postclypeal index was defined as L/W, the width of the postclypeus ond the length of the medion dorsal line from the onterior morgin of the postclypeus to the terminotion of the odfrontal sutures. Cox also onalyzed the frequency distribution of the uncus widths of 100 adult moles of eoch species.

The morphologicol differences between the pupoe and egg masses were described by Compbell (Compbell, I. M., 1953). The eggs of <u>fumiferana</u> were laid in two to four rows, with on overoge of 19 eggs per moss. Balsom fir and spruce were preferred hosts. The eggs of <u>pinus</u> were olways loid in two rows with on average of 37 eggs per moss, ond jock-pine wos the preferred host.

Campbell reparted that newly formed male pupae of <u>pinus</u> ore yellow, while female pupoe ore green. The pupoe of both sexes of <u>fumiferono</u> ore initiolly yellowish to blue green. Stehr (1959) presented evidence thot this is o volid seporation. <u>C. pinus</u>

wos found to be sex-dimorphic, but not polymorphic os wos fumi-ferano.

Freeman (1958) stoted thot the two species will not hybridize in noture. They will, however, hybridize readily in coptivity. The mechonisms to which the integrity of the species has been at-tributed are ecologicol, temporal, and sexuol isolotion. In 1952, a locolized breokdown of the temporol borrier provided Smith (1954) on opportunity to evoluote the relative contributions of the three mechonisms to complete reproductive isolotion. With ecologicol isolation of larvoe ond moths, ond without temporol isolation of moths, successful matings still did not materiolize. It was concluded that sexual isolotion is the component of repro-ductive isolation which maintains the two species as mutuolly exclusive genetic systems.

The taxonomic stotus of the coniferophogous budworms of western North Americo has been in dispute for some time. Free-mon (1958) described budworm populations from British Columbio to Colifornio ond New Mexico (the "western complex") os ex-tremely voriable, porticulorly in wing maculation ond color. Some individuols ore olmost indistinguishable from reddish individuols of the jack-pine budworm, Choristoneuro pinus Freeman; others resemble groy voriants of the spruce budworm, C. fumiferono (Clemens). Powell, (1964), in Colifornio, found populations of the C. fumiferana group to be so closely reloted to the C. lomber-tiono (Busck) group os to be almost indistinguishoble on morpho-logicol bases.

In o recent series of popers, Freeman (1967), Stehr (1967), Horvey ond Stehr (1967), Harvey (1967), Campbell (1967), and Freemon and Stehr (1967) distinguished between ot least seven species of Choristoneuro on spruce, firs, and pines in western North Americo. All of these species ore now considered distinct from the eastern or spruce budworm, C. fumiferono, whose range is associoted with the Acadion, Greot Lokes-St. Lowrence, ond Boreal forest regions (terminology of Rowe 1959), or Northern and Boreal forest regions (terminology of the Committee on Forest Types 1954), and from two subspecies of C. pinus of the Northern, Boreal, and Central forest regions (terminology of the Committee on Forest Types 1954) of eastern North Americo.

The western budworm, C. occidentalis Freeman, is distributed from interior southern British Columbio ta Woshington, Oregon, Colifornio, Montono, Idaho, Colorodo, ond New Mexico (Stehr 1967) within the Montone forest region (terminology of Rowe 1959). Its ronge corresponds to thot of Douglos-fir, its principal host.

The distribution of the 2-yeor-cycle budworm, C.biennis Free-mon, is limited to the subolpine forest region (terminology of Rowe 1959) of Alberta, British Columbio, ond the Yukon Territory, and to adjacent portions of the Boreal forest region (Stehr 1967). In these regions, subolpine fir ond white spruce or western white spruce ore its hosts.

C. viridis Freemon, whose lorvoe ore green, occurs in north-eastern Colifornio and centrol Oregon on white fir and grand fir (Stehr 1967) in the white fir forest type (terminology of the Com-mittee on Forest Types 1954).

C. orae Freemon occurs in the northern part of the Coastal forest region (terminology of Rowe 1959) in British Columbio (Stehr 1967). Its hasts ore Sitko spruce ond omobilis fir.

Three distinct entities ore recognized in western pine-feeding populotions. These ore C. lambertiano (Busck) (C. lombertiono lombertiono of Powell (1964)), C. subretiniono Obr. (C. lamberti-ono subretiniona af Powell (1964)), ond on unnomed group. Stehr (1967) pointed out that the pines which ore hosts of the western pine-feeding species ore olso components of the Mantone forest

region. This emphasizes the close ecologicol relotionships of C. occidentolis to the western pine-feeding species.

BIOLOGY

Life Histories

The life histories of the spruce budworm ond the western budworm are not significantly different (Morris 1963o, Whiteside and Corolin 1961, McKnight 1967). The eggs are laid in masses on the needles of its host trees in midsummer. The eggs are green, imbricated, in one to five rows; the mosses, on the over-age, contoin 20 (spruce budworm) to 45 (western budworm) eggs. The egg mosses may be found on the foliage of small trees ond low-honging bronches in the understory, os well os throughout the crowns of the lorge trees of the stond.

Stairs (1960) described the embryology of the spruce bud-worm. The eggs hotch in about 10 days under normal conditions in the field. After o period of 1 or 2 doys in which they ore dis-persed over the tree and throughout the stond, the instor I lorvae spin hibernaculo in suitable sites, molt to the second instor, ond ceose further activity. Some lorvae undoubtedly hibernote on nonhost trees ond shrubs, but their distribution is best known on their host trees. On Douglas-fir, larvae of the western budworm are found on the branches from the needles to the bole, and on the bole from the top to the bottom; they ore most dense on the foliage ond bark of bronches of the lower crown, ond on the mid-crown bole (McKnight 1967). Few lorvae of the spruce budworm hibernote on the smooth-borked boles of balsom fir trees; most are found on the branches (Miller 1958). Mined buds moy be suitable sites (Botzer 1960) os are flower scors, bark scales, ond lichens.

The instor II larvoe emerge from their hibernacula in eorly Moy. April and Moy thermograph records indicote thot first emer-gence ot spruce budworm lorvae can be accurotely predicted to be 3,837 degree-hours obove a threshold temperoture of 2.5° C. (Bean 1961a), or soan ofter maximum daily temperatures reach 60° F. (Rose and Blois 1954). These lorvoe are subjected to dis-persal and they are distributed ogoin throughout the tree and stand.

Contrary to the general assumption that spruce budworm lar-vae always make their first attacks on buds or new needles, At-wood (1944) reported thot the larvae "almost invoriobly" formed mines in old needles of spruce ar balsam fir before attacking buds. McGugon (1954) found that most spruce budworm lorvae mine only one needle before ottacking buds, but o few larvae may enter buds directly, ond a few mine odditional needles. It was reported earlier thot larvoe of the western budworm mined Doug-los-fir needles prior to attacking the buds (Evenden unpublished). When swelling buds of the host are ovoiloble, ot first larvol emer-gence or loter, they ore attocked by instar II larvoe who feed on the developing needles within the bud. The flowers of bolsam fir are olso important food sources. Instar IV, V, ond VI larvoe are found on the new growth shoots in shelters loosely construct-ed of silk, green needles, deod needles cut off at the bose, bud scoles and frass. The larvoe spend most of their time in the shel-ter, but os the food is consumed instor V and VI larvoe move out ond establish new feeding sites ond shelters.

The anotomy of spruce budworm lorvae wos described by MocKay (1953) and McGugon (1954). Heod copsule width is o criterion commonly used to seporate the six instors. McGugon (1954), Bean and Botzer (1957), ond others hove tobuloted heod

capsule widths for the spruce budworm; Wagg (1958), McKnight (1967) and others for the western budworm. Bean (1958, 1959) showed that frass widths could also be used to determine the instars of larvae of the spruce budworm.

The sex of instar I, II, and III larvae may be determined by a technique utilizing heteropycnosis, the tendency of the sex chromosomes to remain compact and stainable during the resting stage. When the large silk (salivary) glands are stained by the Feulgen "squash" and temporary aceta-carmine smears, certain deeply staining bodies—the sex chromosomes— appear in the resting nuclei of female budworm larvae (Smith 1945). In instar IV and older larvae, the male gonads are seen as darkly pigmented bodies (McGugan 1955). This characteristic is altered by the presence of certain parasitoids that inhibit the development of the testes, however, so that sex of the last three instars cannot be distinguished.

The pupa stage lasts about 10 days in mid-July at the feeding site or inward nearer the main stem of the branch. The pupae of the spruce budworm were described by I. M. Campbell (1953).

Male moths emerge a few days earlier than females; the sex ratio is normally about 50 percent females. Predation of early developing male pupae of the western budworm by late developing female larvae and by larvae of Dioryctria reniculella (Grote) (Lepidoptera: Phycitidae) may significantly alter the sex ratio of that species (McKnight 1967). Campbell (1961) observed that, in captivity, male moths of the spruce budworm are capable of mating several times. He concluded that a shortage of males should not be considered a mortality factor in life table studies.

Morris (1948) first described a technique of trapping male moths of the spruce budworm by utilizing the natural sex attractant of virgin female moths. The technique has been used successfully in ecology studies of the spruce budworm in Canada (Greenbank 1963a) and the western budworm in Colorada (McKnight 1967). Investigations aimed at isolating, identifying, and synthesizing the sex attractant of the spruce budworm are in progress (Findlay and Macdonald 1966).

Relationships between the behavior of the spruce budworm moth and the distribution of its egg masses on its host trees were described in detail by Wilson (1962a, 1963, 1964a, 1964b), and Wilson and Bean (1963).

The external anatomy of spruce budworm adults was described by Freeman (1947b).

Mathers (1932, 1935) first described the life history of the 2-year-cycle budworm in British Columbia. Instar III larvae cease their activity in July of their first feeding season, and spin their second hibernacula (the first having been formed the previous fall). The following May the larvae emerge, continue feeding, and complete development.

Cool temperatures apparently are responsible for the selection and maintenance of populations with a second diapause at the higher elevations of Alberta and British Columbia. Shepherd (1961) correlated habitat temperature with developmental rates, and indicated that in most years the summer is too short and cool for 1-year-cycle budworm to succeed.

Diapause

During the period in which budworm larvae are entering diapause and for a period of varying length thereafter, they experience temperatures considerably higher than that which will induce them to emerge the following spring. Only a small percentage of the population emerges in the fall, however, and there is no evidence that these larvae survive the winter. Both temperature

and photoperiod appear to be involved in the inception and termination of diapause.

Cold storage in the laboratory can be substituted for the natural cold regime to which the budworm larvae would be subjected in the field. Harvey (1958) found that initial emergence of spruce budworm larvae at 21° C. that had been stored 6 and 14 weeks at 0° C. was greater when they were subjected to photoperiods of 15 and 18 hours than for photoperiods of 0, 12, or 24 hours. The greatest number of larvae eventually emerged when they were exposed to continuous light in comparison with all other photoperiods. The effect of continuous light was not observed after a storage period of 20 weeks.

The Absence of Diapause

Harvey (1957a) was able to develop a stock of nondiapause spruce budworm for laboratory cultures. The percentage of nondiapause larvae was 20.6 in the first generation, and 38.5 in the second. Values as high as 80 percent were obtained. The length of generation was 2 months, compared with 6 months for normal diapausing laboratory cultures.

Harvey (1957a) found that, in 62 percent of the spruce budworm families produced by matings of field-collected individuals, at least one larva could develop without diapause if subjected to long photoperiods while being held at 71° F. On the average, 3 to 4 percent of the instar II larvae of such progenies could forego diapause.

Selection over six generations yielded a strain that, when subjected to continuous light in the laboratory, was virtually free from diapause. The stock was reared for another six generations and still retained this characteristic.

Behavior of the nondiapausing larvae was normal during the period of hibernacula construction and molting, but the larvae then left the hibernacula and fed readily and developed normally. Mortality, mating success, and fecundity of this stock was not different from diapausing stock.

Harvey postulated that the ability to develop without diapause was determined by multiple genes; it was not sex linked but might be sex controlled to some extent.

Second Diapause

Second diapause has been observed in experimental rearings of the spruce budworm (Harvey 1961), the western budworm (Campbell, D. K. 1953), the jack-pine budworm, and C. orae as well as in rearings of the 2-year-cycle budworm in which it naturally occurs (Harvey 1967). Second diapause was not observed in C. viridis. There is evidence that second diapause is not under environmental control in the 2-year-cycle budworm where it occurs naturally. The fact that the incidence of second diapause has a genetic basis is considered support for the separation of the coniferophagous species (Harvey 1967).

Rearing Techniques

The budworm species are reared in large numbers with little difficulty in several laboratories. Stehr (1954) described the rearing sequence for the spruce budworm, which is followed for the other species as well. The method varies largely in the food source. Stehr (1954) used frozen shoots from balsam fir. Pitman (1963) coated Douglas-fir seedlings with agar for the western bud-

worm and C. viridis. Heron (1961) reared the jack-pine budworm and the spruce budworm on developing shoots of potted tamaracks.

Wellington (Wellington, Eunice F. 1949) described a satisfactory artificial diet for rearing the spruce budworm. It consisted of a suspension prepared from balsam fir foliage, an inhibitor of fungal growth, autolysed yeast, and agar. McMorran (1965) reported that one of the wheat-germ-based diets worked well for rearing the spruce budworm.

ECOLOGY

Weather

Temperature

Wellington and Henson (1947) summarized the effects of physical factors on the behavior of the spruce budworm. The instar I larvae, after emerging from the egg, react positively to light and move to the tip of the needle on which the eggs were laid. Crowding may cause many to drop on their silken threads. The larvae that fall may drop to a twig below, or they may be caught in vertical air currents and be carried above the trees. The larvae that drop to twigs below will again move to the periphery of the tree. Either event leads to dispersal.

If the larvae are shielded from the sun, they remain photopositive until they contact debris. Then a tactile response stimulates hibernacula construction. If the sky is clear and the larva becomes heated above the reversal temperature, it becomes temporarily photonegative and returns to the shade. If a larva emerges on an overcast day, it may spin its hibernacula where it could be desiccated by later hot, dry weather.

Emerging instar II larvae are strongly photopositive, and are attracted to the periphery of the tree, the area of most suitable food. They are again dispersed by the same mechanisms as in the previous fall. The larvae do not feed at temperatures less than 50° F., but direct sunlight may warm the foliage above air temperature and permit feeding. Since larvae feed in needles and buds at high humidities, some factor must counteract observed effects of low evaporation seen in later instars. Photic reversal, due to starvation or high body temperature (100° F. in instar VI), causes larvae to drop to lower levels. High temperature also causes movement to the interior of the tree. Vibration or flooding also causes dropping.

Adult females do not fly until they deposit one or two egg masses. Both sexes are subject to considerable dispersal. Males are photopositive when dark adapted, but quickly become adapted to any light intensity and become extremely sluggish. Dark-adapted females exhibit photonegative or compassing behavior. Light-adapted females are also sluggish. Neither sex is active until twilight.

Temperatures of habitats. —Wellington (1950a) reviewed the effects of radiation on the temperatures of insect habitats, and made significant measurements and observations. He concluded that the differences he observed between insect temperatures, or the temperature of their feeding sites on their food plants, and the temperature of the surrounding air were large enough to be considered in field studies. These differences are due to radiant heating in the day and radiant cooling at night. Spruce budworm larvae, in their webbed feeding tunnels, may be exposed to temperatures up to 8° C. above air temperature. The staminate flowers of white spruce are 5° to 8° C. above the temperature of vegetative buds in sunlight, and may be 10° to 14° C. above air temperature.

Internal temperatures. —Shepherd (1958) demonstrated, in laboratory studies, a direct relationship between the radiation intensity striking a larva and the excess of larval temperature over air temperature. He found that, in bright sunshine, larvae on overstoried spruce reproduction had an average temperature excess of 2.3° C., and larvae on reproduction in a stand opening had on average excess of 3.7° C. Wind and evaporation reduced the temperature excesses.

Temperature preference. —Wellington (1949a) found that spruce budworm larvae had no temperature preference as such. When he tested larvae in graded temperatures and rates of evaporation, he found that, below an upper limit of temperature, the larvae aggregated within specific ranges of evaporation regardless of where these ranges were placed within the temperature range. The upper limits of temperature beyond which the larvae did not travel when they were allowed to move freely in combined gradients of temperature and evaporation were: instar I larvae, about 28° C.; instars II and III, about 36° C.; instars IV, V, and VI, from 37° to 38° C. Below these upper limits, the larvae were indifferent to temperatures down to and including 10° C., the lowest temperature tested.

Effects of temperatures on hibernating larvae. —An unseasonal cold wave in Montana that lasted 7 days in November 1959, in which temperatures of -45° and -53° F. were recorded, appeared to have little effect on hibernating larvae of the western budworm (Terrell 1960).

In Ontario, the emergence of instar II larvae of the spruce budworm from hibernation was shown to be closely related to April and May temperatures (Rose and Blais 1954). Abundant emergence was observed after maximum daily temperatures had risen to 60° F., but temperature variations affected emergence. If the temperature rose suddenly to 60° F. from preceding low temperatures, emergence was delayed. If the rise was gradual, emergence followed almost immediately.

Laboratory studies by Bean (1961a) indicated that 2.5° C. approximated the threshold temperature that terminates diapause of hibernating larvae. By using this temperature as a base and calculating degree hours from thermograph records, it was possible to predict the approximate date of larval emergence in the field.

Effect of temperatures on feeding larvae. —In 1956, development of the spruce budworm in the Lower St. Lawrence and Gaspé regions was greatly retarded by below-normal temperatures in May, June, July, and August (Blais 1958c). A shortage of current growth forced the larvae to feed on old foliage, which retarded their development even further. At higher elevations, development was retarded to the point that some pupae and many eggs did not emerge before cold weather in the fall. In November, 13 percent of the pupae still had not emerged. Egg mass populations were high, but 53 percent were unhatched, 10 percent partially hatched, and 37 percent hatched. The eggs averaged only 11 per mass for 100 masses, in contrast to the usual 20 per mass for this area.

Prebble (1945) reported a general reduction in the level of spruce budworm populations on three districts in Ontario because of late spring frosts that killed new shoots on balsam fir and white spruce trees when the growth was well advanced and the budworms were feeding. He observed that the frosts froze many

larvae, and killed many more through destruction of the favored food. Also, insect parasites were very effective against the larvae that survived the damage by frost.

Evaporation Rate

Wellington showed that spruce budworm larvae showed preferences for specific evaporation rates regardless of where these rates occurred in the range of temperatures (Wellington 1949a). The larvae always congregated in the one preferred zone of evaporation rate, irrespective of temperature (Wellington 1949b).

The behavioral responses of the larvae to different evaporation rates have great survival value, as was pointed out by Wellington (1950b). Instar I larvae spin their hibernacula in their preferred zone. The turning reaction of instar II larvae keeps them away from situations of excessive moisture. The rate of evaporation inside the feeding tunnels of instar VI larvae is nearly identical to that of their preferred zone. When the tunnels are partially destroyed or consumed by feeding, the larvae move to a more favorable area. When the tunnels are flooded by rains and evaporation rates are low, the larvae react by dropping.

Shepherd (1959) studied the phytosociological and environmental characteristics of outbreak and nonoutbreak areas of the 2-year-cycle budworm. He concluded that the high mortality that keeps populations at a low level is partially attributable, directly or indirectly, to the high moisture conditions or low evaporation rates. The evaporation rates are determined not only by the weather systems but also by the habitats of the stands. The difference in evaporation rates between habitats increases with regional increases in evaporation, which results in a comparatively greater "release" of the budworm in the drier habitat.

Wind

Shepherd (1956) observed that a period of unusually strong wind reduced the number of instar V and VI larvae of the 2-year-cycle budworm on small Engelmann spruce and subalpine fir trees from 4 or 5 to 1 per 5-foot tree. An 81 percent loss was recorded from artificially infested trees.

Climatic Release

Canadian workers proposed (Wellington et al. 1950) and later supported (Wellington 1952, Greenbank 1956, Pilon and Blais 1961), a theory that climatic release was a cause of outbreaks of the spruce budworm in Canada. The physical conditions ideal for budworm development are plenty of sunlight and dry weather (Greenbank 1963b). Dry conditions that provide more sunlight in the spring and summer and continued cold in winter are closely associated with polar continental air masses. The numbers of cyclonic centers passing through a given area may be taken as indices of the frequency of movements of these air masses. Wellington et al. (1950) made a survey of the outbreaks recorded in northeastern North America, and found a recurrence of several biological and physical phenomena in 3- or 4-year periods preceding known outbreaks. The outbreaks occurred during periods of decreasing or minimal numbers of the polar continental air masses.

In mixed stands of poplar and balsam fir in Ontario, heavy feeding by the forest tent caterpillar Malacosoma disstria Hbn., preceded spruce budworm outbreaks, and there were indications that a similar association might occur in western Quebec and in New Brunswick. Wellington et al. (1950) concluded that forest composition is a preparatory cause of outbreaks, but that relaxation of climatic control is the immediate cause of rapid population growth to the outbreak stage in susceptible foci.

Analysis of weather records supported this theory for outbreaks in Ontario (Wellington 1952), in New Brunswick for outbreaks which began in 1912 and 1949 (Greenbank 1956), and in Quebec for outbreaks between 1939 and 1951 (Pilon and Blais 1961).

Light

Wellington (1948) reported that spruce budworm larvae of all stages were at first positive to discrete light sources. Instar I and II larvae retained this reaction under all conditions; starved instar III larvae were indifferent to light; and starved instar IV, V, and VI larvae first performed light-compass reactions and then became photonegative. The larvae were photopositive when the digestive tract was distended, and exhibited light-compass reactions or become photonegative when the digestive tract began to empty. All the larval stages were photopositive to diffuse light.

Wellington et al. (1951) reported further that the basic light reactions of the spruce budworm larvae are related to their internal temperature. They react positively when cool but negatively when too hot. This was demonstrated in the field and in the laboratory, and to both discrete and diffuse sources of light.

Wellington (1948) found that adult spruce budworm moles were photopositive. Nonflying females were photonegative, and flying females performed light-compass orientations.

Edwards (1962) found considerably less activity in female than in male moths. Both sexes began flying in late afternoon, or several hours before sunset on a clear day. Males had two periods of peak activity, one immediately after sunset and another after midnight. They were not active after sunrise. Females reached a period of peak activity just prior to sunset.

Dispersal

The spruce budworm is susceptible to dispersal at three points in its life cycle. Instar I and II larvae, while seeking hibernation sites or suitable food, respectively, become dislodged from the foliage and drop on silken threads. They may be caught in air currents and carried short distances.

Batzer (1962) found that the average velocity of fall of instar II budworm larvae, when compared with the length of their silk threads, exhibited a negative exponential relationship that was highly significant. From this relationship, the dispersal distance can be estimated for any windspeed or height above the ground.

Yuill (1958) reported exploratory work which indicated that the migration of instar I budworm larvae could be studied with the aid of radioactive tracers.

Budworm moths may be carried considerable distances in air currents. Moth flights can be detected with light traps or attractants. Morris (1948) found mercury vapor lights to be more attractive than gasoline lanterns for spruce budworm moths. Of 54 spruce budworm moths taken in light traps in 1947, 77 percent were males. Male moths are more attracted to lights; fully gravid and spent females are sluggish and often incapable of flight.

Greenbank (1950) recorded a large flight of moths from a heavily infested area into the Green River area on July 28, 1949. The ratio of moths caught in traps to pupal population per tree was 10 in 1947 and 6 in 1948. In 1949, the ratio was 12 if this large flight is ignored, or 140 if it is taken into account. Females

constituted 20 percent of the cotch, and it was determined by dissection that they bore a meon egg complement of 70 eggs.

Light traps on forest lookout towers, supplemented by daily observation sheets, were found useful to detect large moth flights (Greenbank 1951). Large tanglefoot boards on the towers were also used. Light traps were not desirable in the forest stands because of the fire hazard and the frequent attention required. Virgin females, caged on tanglefoot boards, were found to be useful to trap males.

Greenbank (1957) concluded that, although spruce budworm populations were increasing in New Brunswick in 1947, the outbreak of 1949 was a continuation of the spread of high populations across Quebec to the west. He observed that if the invading moths are deposited in dense, mature, softwood stands, outbreaks soon develop. If the moths are deposited in young, open, or mixed-wood stands, the resulting high populations do not succeed unless replenished by other invasions.

Henson (1951) reported his analyses of 19 moss flights of spruce budworm moths. The mass flights always took place in the evening or early part of the night. The farther the point of deposition, the later at night the flight was observed. In some cases, the passage of a cold front followed deposition. In some cases, brief rain preceded the flight. The heavy evening flight was a response to decreasing light intensity, the number of insects in flight being directly related to the rate of decrease of light. The insects were carried by convective storms which preceded cold fronts. Prefrontal thunderstorms that caused a sudden reduction in light and also brought about pressure changes were responsible for initiation of mass flights.

A typical thunderstorm has a strong updraft in front of each cell, the wind blowing toward the storm. Insects drawn up into the storm may be tossed out at the top or sides of the cloud, deposited with rain in the central downdraft, or carried in the storm.

Flowering and Other Host Relationships

The flowering of balsam fir has frequently been cited as one of the major factors in the epidemiology of the spruce budworm in northeastern North America. In New Brunswick, flower production begins 20 to 30 years after the initial release of the tree, and increases directly with age, with respect to both the proportion of trees flowering and the intensity of flowering on individual trees (Morris 1951a). At Green River, flower and seed production is heavy every 2 years.

The growth of primary branch terminals, leaders, and annual rings is depressed in flowering years. The quantity of new foliage produced by balsam fir in flowering years is much less than in nonflowering years. The sections of the crown that produce the most staminate flowers also produce the greatest weight of foliage in nonflowering years.

Flower buds appear on current growth near the end of the growing season, and open the following spring. Female flowers are produced largely on the apical 5 feet, and male flowers on the next 10 feet. Flower production in the lower crown depends on light intensity.

Effect of Flowering of the Host on the Budworm

Jaynes and Speers (1949) observed in northern New York that spruce budworm larvae feeding on balsam fir with staminate flowers were slightly more developed than on balsam fir without such flowers. Moths from larvae fed on pollen showed no increase in fecundity, and no effect on the sex ratio was observed. In 1947, a year of abundant staminate flower production on balsam fir and spruce, the budworm population was reduced sharply. Blais (1952) found more spruce budworm eggs on the flowering trees than on nonflowering trees. The flowering balsam fir trees were found to harbor higher populations in the early larval stages, due to the presence of staminate flowers and flower cups. Larvae that fed partially on pollen developed more rapidly than larvae that fed exclusively on foliage. Pollen as a food did not appear to have any direct effect on survival or fecundity. Defoliation was more severe on flowering trees in the earlier stages of the infestation. As populations increased, however, wandering increased because of competition for food, which resulted in an overflow of larvae from flowering to nonflowering trees.

Other experiments showed that mortality was higher, development retarded, and fecundity reduced in insects forced to feed on old foliage in contrast with those that fed on current year's growth (Blais 1952). When budworm populations destroy all current growth prior to completion of the larval stage, the number of eggs per surviving female decreases; fecundity increases again when populations decline to where defoliation is not complete (Blais 1953). Gravid females reared on old foliage or collected from an area of complete defoliation were able to fly before ovipositing. This is in contrast to other observations that fully gravid budworm female moths were not able to fly until they had deposited one or more egg masses.

The "greenhouse" effect observed by Wellington (1950a) would help to explain why spruce budworm larvae on trees bearing staminate flowers develop more rapidly. The staminate flowers of white spruce are 5° to 8° C. above the temperature of vegetative buds in sunlight, and may be 10° to 14° C. above air temperature.

In Oregon, Carolin (1950) found the development of larvae of the western budworm to be the same on Douglas-fir trees with and without staminate flowers.

Shepherd (unpublished), in his studies of the 2-year-cycle budworm, reported on the variation in flowering of subalpine fir. He stated that, "The flowering on the outbreak area was double that on the nonoutbreak area in the preoutbreak period." However, there was only a small amount of flowering at any time. Most trees produced no flowers, and then only the favorable branches in the upper crowns of a few large trees produced flowers. Even in good years, less than 20 percent of these branches produced flowers. Thus, only a small percentage of the budworm population would be affected.

Other Host Relationships

Blais (1957) reported that spruce budworm larvae feeding on black spruce had a lower rate of development and a higher rate of mortality than those feeding on white spruce or balsam fir. This was attributed to the lateness in opening of the black spruce buds rather than to the inferior nutritional quality of the foliage. When staminate flowers were abundant on black spruce trees, development and survival of the insect was fairly similar to that on the other two species. The flowers provided adequate food during instars III and IV to permit the larvae to survive until the opening of the buds. The late opening of its buds explains the relative immunity of black spruce to severe spruce budworm damage.

Ghent (1958a) reported on his study of the relationship between the mortality of overstory trembling aspen to outbreaks

of the farest tent caterpillar and the spruce budworm. Wellington et al. (1950) had pointed out that forest tent caterpillar outbreaks in aspen regularly preceded outbreaks of the spruce budworm in balsam fir. In a mixed stand, anything that hastens the succession fram aspen to daminant canifers increases its susceptibility ta spruce budworm autbreak. Temporary defaliatian of the aspen has the same effect if the climatic canditions are ideal for a budworm outbreak.

Ghent faund that spruce budwarm autbreak near Lake Nipigan, Ontario, began in an area of decadent aspen stands, the remnants af which had been defoliated by the forest tent caterpillar just before the budworm outbreak. The initiatian of the spruce budworm papulation upsurge corresponded exactly with the periad of heavy aspen defaliatian. Flawering of balsam fir increased with aspen mortality. Ghent did nat suppart the suggestion (Wellington et al. 1950) that the farest tent caterpillar defoliation accelerated overstary eliminatian, and that the succession of coniferous campanent was thus hastened. He did not contradict the suggestion that the forest tent caterpillar defoliation extended the area af balsam fir and spruce susceptible to the budworm, but he did nat cansider the defoliation necessary.

The Basis for Feeding Preferences

Heron (1965) established that there is a chemosensory basis for the preferential feeding behavior of budworm larvae with respect to developing vegetative shoots, staminote flowers, and mature needles of white spruce. Staminote flowers are favored in part, because of their content of phagostimulants, sugors, and the amino acid L-proline. The consumptian of white spruce needles is limited by their content of the deterrent pungenin.

Budworm Outbreaks and Bark Beetle Outbreaks

The role of the western budworm as a predisposing factor for bark beetle autbreaks in western forests has often been assumed. It is mare than likely that the weakening effect of defoliation makes the host trees more susceptible to bark beetle attack. Apparently the point has never been tested, and therefore neither proven nor disproven.

Evenden (unpublished) noted that the incidence of Douglas-fir beetle, Dendroctonus pseudotsugae Hopk., increased in Cody Conyon on the Shoshone National Forest, Wyoming, in stands seriously defolioted by the western budworm, and that control operations ogainst the beetle were necessary in the fall of 1931.

Bedord (193B) used the following natation to record the presence of the western budworm on Douglas-fir: "The spruce budworm has killed many trees in the Rocky Mountain region by completely defoliating them. Epidemics of this insect are usually followed by epidemics af the Douglas-fir beetle, which attacks and kills mony odditional trees."

Thomas (195B) evaluated the role of bark beetles in mortality of spruce budworm-defoliated white spruce in the Lake Nipigon orea of Ontario. He reported that the increased supply of weakened and dying white spruce trees provided by the spruce budworm probably was a major factor permitting populations of the eastern spruce beetle, Dendroctonus obesus (Monn), to increase to destructive numbers from an endemic level. He indicated that outbreaks of this bark beetle may be a natural development in a spruce-balsam fir forest subjected to a severe outbreak of the spruce budworm.

Campbell (1958) defined fecundity as the number af eggs loid by a female that has been successfully inseminated; the numerical value of fecundity is actually the quotient af egg weight and egg mass. He demonstrated that these twa factars are determined by independent genetic systems. One system, acting during the larval period, determines the amount of body mass available for egg production. The other, acting during the pupal and adult stages, determines the weight of the eggs that are produced from that mass.

Campbell (1962) speculated that the reproductive potential of a budworm population depends on the relative frequency of two types of X chromosomes. One would determine small egg size, high fecundity, large body size, slow development rate, and low environmental resistance, and the other, large egg size, low fecundity, small body size, rapid development rate, and high environmental resistance. Campbell (1962) suggested that the X chromosomes produce these characteristics by determining different mitotic rates and consequently variations in the number and size af cells.

Studies of the fecundity of the spruce budworm have been approached by analyses of the pupal size-fecundity relationship in stands of different defoliation histories (Miller 1957). By sampling for mean pupal size, the expected fecundity should be estimated from regression equations appropriate to defoliation history. Changes in the quantity and quality of food available would be expected to change mean pupal size, mean fecundity, or the pupal size-fecundity relationship. The existence of area-specific or defoliation-history-specific regressions would enable the prediction of mean fecundity without elaborate fecundity trials.

Extrinsic factors which may offect the fecundity of the spruce budworm directly or indirectly include food quantity, food quality, weather, disease, and the ovailability of oviposition sites (Miller 1963c). Of these, food quantity and quality have been studied in greatest detail by Canadian workers. Food quantity is a function of the density of the larval population and current foliage production. Food quality is a function of its age. Evidence was presented by Blois (1953) and Miller (1957) that a diet of 1-year-old and older foliage caused drastic reductions in fecundity. It is believed that, when spruce budworm populations are high and infestations are of several years' duration, larvae are forced to feed on greater proportions of older foliage and the fecundity of female moths is reduced.

A large complex of parasitoids is associated with the spruce budworm and the western budworm. The species complex differs in space and time, but the important elements are usually the some 12 to 15 species (McGugan and Blois 1959). The following authors have evaluated parasitoids in specific outbreaks: Wilkes et al. (194B) in British Columbia; Dowden et al. (1948) in New York and Colorado; Dowden and Carolin (1950) in New York; Jaynes and Drooz (1952) in New York and Maine; McGugan and Blois (1959) in Ontario; Carolin and Coulter (1959a) in Oregon; Blais (1960a, 1965a) in Quebec; and Miller (1963d) in New Brunswick.

In general, although parasitoids are always important mortality factors, their effectiveness is greatest only after anather agent, such as weather or starvation, has reduced the host population considerably (Miller 1963d). The presence of relative abundance

of alternate hosts greatly influence the nonspecific primary parasitoids, and hyperparasitism may reduce the effectiveness of primary parasitoids in the early stages of an outbreak (Carolin and Coulter 1959a).

The biologies of dipteran parasitoids (table 1) are well known (Coppel 1947, 1958; Arthur and Coppel 1953; Maw and Coppel 1953; Coppel and Maw 1954a, 1954b; Coppel and Smith 1957; Coppel et al. 1959; Dodge 1961b). Keys to the puparia (Ross

Table 1. --Summary of life histories of important dipteran and hymenopteran parasitoids of spruce budworm and western budworm

Species	Stage attacked	Stage killed	Pupation site	Overwintering habits	References
- - DIPTERAN - -					
Sarcophaga aldrichi Park.	Prepupae or pupae (Eggs or larvae deposited)	Pupae	Ground?	Puparium?	Arthur and Coppel (1953)
Phryxe pecosensis (Tns.)	Larvae Large larvae	Larvae or pupae	Ground?	Unknown "In some other host"	Maw and Coppel (1953) Dowden and Carolin (1950)
Madremyia saundersii (Will.)	Larvae Larvae (VI)	Larvae (VI) or pupae	Ground	As first or second instar larva	Coppel and Maw (1954b) Carolin and Coulter (1959a)
Omotoma fumiferanae (Tot.)	Larvae[1]	Pupae	Ground	Puparia Puparia	Coppel and Smith (1957) Coppel (1947) Carolin and Coulter (1959a)
Phorocera incrassata Smith	Larvae[1][2]	Pupae	In host pupal case	Unknown	Coppel (1958)
Ceromasia auricaudata Tns.	Larvae[1][2]	Pupae	Ground	As larvae in pupae of alternate hosts	Coppel and Maw (1954a)
Pseudosarcophaga affinis, authors	Late larvae or pupae[3]	Larvae, prepupae but usually pupae	Ground	Puparium	Coppel et al. (1959)
Aplomya caesar (Ald.)	Large larvae	Larvae or pupae		"In some other host"	Dowden and Carolin (1950)
Lypha setifacies (West)	Larvae	Larvae (VI)	Ground	Puparia	Wilkes et al. (1948) Coppel (1946) Carolin and Coulter (1959a)
- - HYMENOPTERAN - -					
Apanteles fumiferanae Vier.	Instar I and II	Instar IV or V	Cocoon on foliage	Eggs or larvae in host	Brown (1946a), Miller (1959)
Glypta fumiferanae (Vier.)	Instar I and II	Instars V and VI	Cocoon on foliage	Eggs or larvae in host	Brown (1946b), Miller (1960)
Phytodietus fumiferanae Rohw.	Late instar larvae	Feeds externally	Cocoon on foliage	In cocoon as mature larva	Coppel (1947), Wilkes et al. (1948)
Horogenes cacoeciae (Vier.)	Instar I and II (?)	Larva (V)		In host larvae	Coppel (1947), Carolin and Coulter (1959a)
Phaeogenes hariolus (Cress.)	Pupae	Pupae		As adult	Coppel (1947), Carolin and Coulter (1959a)
Ephialtes ontario (Cress.)	Pupae	Pupae		Mature larvae in host pupal case	Coppel (1947), Carolin and Coulter (1959a)
Meteorus trachynotus Vier.	Larvae	Late instar larvae[4]		In alternate host	Dowden and Carolin (1950), McGugan (1955)
Trichogramma minutum Riley	Eggs	Eggs	Egg	Unknown	Carolin and Coulter (1959a)

[1] Parasitoid does not develop until host pupates.
[2] Eggs are deposited on leaves and later ingested.
[3] Eggs deposited on or near host.
[4] Prevents host larvae from pupating.

1952) and to the adults (Coppel 1960) are available. Some of the hymenopteron species are well known also (Brown 1946a, 1946b; Coppel 1947, 1951; Dowden and Carolin 1950; Carolin and Coulter 1959a; Miller 1959, 1960; Miller and Renault 1963) and their life histories are summarized in table 1. Wilson and Bean (1964) keyed the hymenopterous parasitoids of the spruce budworm in Minnesota.

Trichogromma minutum Riley is the only recorded parasitoid of budworm eggs. It generally does not cause a high mortality, but Miller (1953) recorded parasitism as high as 48 percent in 1950 at Green River. Miller suggested two factors that appear to limit the effectiveness of Trichogramma. This species requires the presence of hosts other than the budworm prior to budworm oviposition. The abundance of alternate hosts will influence the number of budworm egg parasites. Also, the number of eggs deposited in each host egg (an average of 3.7 adults emerged from each parasitized host egg in 1950) limits the total number of host eggs that can be parasitized. This factor reflects characteristics of poor searching ability and high oviposition rate.

Thomas (1966) concluded that the influence of T. minutum on spruce budworm populations in Maine was small. Its activity did not show a trend during the budworm outbreaks, and its rate of attack was not related to the density of the host. Percent parasitism did not differ between quadrants or levels in the tree crowns. Miller (1953) found the percentage of spruce budworm eggs parasitized to be greater in the top half of the tree crown on a plot in a dense young stand with the lower crowns partially shaded.

Several factors have been found to affect assessment of the incidence of Apanteles fumiferanae and Glypta fumiferanae in hibernating budworm larvae. Unless these factors are taken into account, biased estimates of parasitism are obtained.

Jaynes (1954) removed branches from different heights on balsam fir trees in a medium infestation in Maine. All spruce budworm larvae that emerged from the branches were dissected. When the data were grouped by height of branch in feet from the ground, the percent parasitism by both Apanteles and Glypta increased with increasing height. When the data were grouped by portion of the crown from which the branches were removed, the parasitism by Apanteles was 14, 21, and 35 percent for the lower, middle, and upper thirds, respectively. Parasitism by Glypta was 6, 10, and 9 percent, respectively.

A second series of trees was sampled at the three crown levels, and the parasitism by Apanteles was 15, 20, and 27 percent for the lower, middle, and upper crown thirds. The means were significantly different (at the 5-percent level). It was concluded that parasitism at midcrown is a reliable indication of the average parasitism for the whole tree.

Dodge (1961a) conducted a similar study on infested trees, mostly Douglas-fir, in Montana. He found that parasitism of western budworm larvae by Glypta was significantly greater in the middle and upper crowns than in the lower crown. Combined parasitism was greatest in the midcrown, and limbs from this portion of the crown would give an exaggerated estimate of parasitism. He showed further that Glypta is more common in budworm larvae hibernating under bark scales, and that Apanteles was most common in larvae hibernating in the foliage. He concluded that a limb from the lowest wharl of vigorous branches would probably give the best indication of parasitism for the tree.

Lewis (1960) found other factors that affect assessment of parasitism by these two species. Apanteles was more efficient in attacking mobile spruce budworm larvae, and Glypta was more efficient in attacking larvae in their hibernacula. He also found that nonparasitized instar II larvae are strongly photopositive, while parasitized larvae are photonegative, or do not react at all to light. In addition, parasitized larvae emerge from their hibernacula as much as 7 to 10 days later than nonparasitized larvae. These factors could greatly bias the estimates of parasitism obtained by dissecting larvae that have been induced to collect in lighted vials placed in tight containers.

Lewis and other workers have observed increases in percent parasitism when measured when the budworms were in the bud-mining stage as compared to estimates based on dissections of hibernating larvae. He explains this as differential loss of parasitized and nonparasitized larvae. The less active parasitized larvae are less susceptible to dispersal loss, and since they leave their hibernacula later, the favored buds are more likely to be available for food.

Lewis also found no significant difference in percent parasitism on a 15-inch twig compared to the rest of the branch at either collection time.

Coulter (1954) reported that the parasitoids of hibernating budworm larvae, Apanteles and Glypta, survived aerial applications of DDT for budworm control in Oregon and Washington. Macdonald (1959) reported higher proportionate survival of Apanteles compared to Glypta in areas of New Brunswick sprayed with DDT from 1952 to 1958. He gave three reasons:

1. Apanteles emerge from the host earlier than Glypta and spin cocoons, and thus are relatively safe from poisoning.
2. Parasitized hosts are less likely to contact residual insecticide than are healthy, active larvae.
3. Well developed Apanteles larvae appear able to emerge from "knocked down" hosts; Glypta was not observed to do this.

Predators

Birds

Predation by birds has been cited as a natural control factor in several spruce budworm outbreaks. Their effect on population trend is not clearly understood, but their effectiveness against high budworm populations appears limited.

George and Mitchell (1948) attempted to calculate the extent of control exerted by insectivorous birds in a spruce budworm outbreak in New York. A systematic census in the Lake Clear area found the density of insectivorous birds to be three pairs per acre. The authors used 2.5 pairs per acre as the number of adult birds feeding chiefly or entirely on the budworm. These five birds and two nestlings per nest were present during the 40 days when the larvae were most susceptible to predation. The authors estimated that the adults would consume about 1,200 grams of budworms and the young birds, 750 grams, or a total of about 35,524 budworms. The budworm population was estimated at 500,000 to 1 million per acre. Thus, the degree of control would be only 3.5 to 7 percent. These calculations do not take into account the number of eggs and instar I and II larvae consumed in late summer, fall, winter, and early spring. Kendeigh (1947) estimated 4.3 percent control in Canada, where the spruce budworm population was estimated to be 376,000 per acre and the number of birds to be 3.19 pairs per acre. He referred to estimates of 13 percent control in 1918 in New Brunswick and 39 percent in British Columbia.

Predation by birds was studied in a Maine outbreak from 1949 to 1951 (Dowden et al. 1953). On one study area, an at-

tempt was made to shoot all birds observed during the critical period when the budworms were most susceptible to predation, and on two check areas birds were undisturbed. The percent reduction of budworms was 11 and 29 percent in 1949 and 1950, respectively, on the area where the birds were shot; 69,56, and 56 percent in 1949, 1950, and 1951 on check area number 1, and 48 and 71 percent in 1950 and 1951, respectively, on check area number 2.

Analysis of stomach contents of 826 birds showed that 21 and 40 percent of the food consisted of budworms in 1949 and 1950, respectively. Nearly all of the contents of stomachs from red squirrels collected in 1950 were insects; 51 percent were budworms (Dowden et el. 1953).

Mitchell (1952) presented a list of 45 species of birds from which the 826 stomachs were taken for analysis during a spruce budworm study in Maine in 1949-50. He obtained "average feeding pressure values" for each species by multiplying its resident population (pairs per 100 acres) by the average volumetric content of sample stomachs, and multiplying the product by the average percent budworm content. The feeding pressure values of 14 of the most important insectivorous resident birds, taken from his data, were:

	Feeding pressure
Bay-breasted warbler	3.36
Olive-backed thrush	2.36
Magnolia warbler	2.02
Purple finch	1.64
Robin	.92
Cape May warbler	.90
Blackburnian warbler	.48
Myrtle warbler	.46
White-throated sparrow	.33
Slate-colored junco	.26
Solitary vireo	.21
Tennessee warbler	--
Nashville warbler	--
Red-breasted nuthatch	--

The cedar waxwing was entirely a visitor, and no feeding pressure values could be calculated. The budworm occupied 89 and 84 percent of the volume of waxwing stomachs examined in 1949 and 1950.

It was concluded from these studies that birds were of little significance in an outbreak, but may play an important role in maintaining endemic populations.

Morris et al. (1958) and Mook(1963) found that some birds showed direct numerical response to budworm populations in New Brunswick. Three of these species were the bay-breasted, Blackburnian, and Tennessee warblers. Three other warblers showed an inverse response, probably due to competition from the three species showing a direct response. The predators were found to be of little control value during the outbreak.

A study of the feeding niches of three species of flycatchers, the western wood pewee, western flycatcher, and Hammond's flycatcher, revealed that these birds removed less than 1 percent of the available pupae and moths of the western budworm (Beaver 1967). Several other species of birds were observed taking budworms as prey, but their effects on the population are unknown.

Other insects

Thomson (1957) examined 400 pupal sites of the spruce budworm 3 days before adult flight began. Ants were observed to be of considerable importance in addition to the insects listed below:

	Number	Percentage
Whole pupae	327	81.8
Pupae attacked:		
By budworm (instar VI larvae)	10	2.5
By Coleoptera	9	2.2
By Dioryctria	23	5.8
By Syrphidae	2	.5
By unknown	29	7.2
Total	73	18.2

Warren (1954) described the relationship between Dioryctria reniculella (Grote), the spruce conewarm, and the spruce budworm. Under natural conditions, the two species compete, since both are defoliators of new growth. New foliage becomes scarce when defoliation is severe. A laboratory experiment indicated that predation of the budworm pupae by the conewarm greatly increased when only old foliage was supplied. No field observations were made. Predation of budworm pupae in 1948 when the conewarm populations were highest may have caused the reduction of budworm populations observed in 1949.

Liscombe and Lejeune (1949) reported that "hordes of dragonflies were observed preying on budworm larvae in 1948...."

Predation by solitary wasps including Ancistrocerus catskill albophalteratus (Sauss.), A. tigris tigris (Sauss.), and Rygchium leucomelas (Sauss.) was studied by Fye (1962). The peak nesting activity of the first generation of these species coincides with the late instars of the spruce budworm and other spruce-fir defoliators. The wasps provision their nests with paralyzed defoliator larvae.

Spiders and Mites

Morris (1948) reported predation of spruce budworm larvae and eggs by spiders.

By serological techniques, Loughton and West (1962) were able to assess spider and mite predation on the spruce budworm. Their results gave evidence of a functional response of spiders to fluctuations of spruce budworm populations (Loughton et al. 1963). The family Micryphantidae was the most important group because of their abundance, particularly Grammonota pictilis (O. P. Cambridge). The Theridiidae, web-spinners, were the most effective predators, based on the percentage found to have fed on the budworm. The Salticidae, hunting spiders, were important predators of all stages of the budworm. The Thomisidae were present in large numbers, but they were not as effective as the Micryphantidae.

Turnbull (1957) found members of the families Argiopidae, Theridiidae, Thomisidae, and Salticidae to be most abundant on Douglas-fir in an outbreak of the western budworm in British Columbia. The thomisids did not capture budworm larvae or moths. The argiopids and theridiids captured larvae occasionally, but they captured many budworm moths. The salticids captured larvae and moths, and probably exerted some control over the budworm population.

Diseases

Bird and Whalen (1949) reported the presence of viruses, fungi, bacteria, and a protozoan in a survey of pathogens present in spruce budworm populations of Ontario.

Virus Diseases

Bergold (1950) reported observations of electron micrographs of purified preparations of the viruses causing polyhedral diseases in the spruce budworm, the gypsy moth (Porthetria dispar (Linn.)), and the silkworm (Bambyx mori (Linn.)). He observed morphologically different forms which he described as stages of multiplication.

Quantitative infection tests found the spruce budworm to be highly resistant or immune to the virus (Bergold 1951). It was not determined whether this was because of low virulence of the virus or because the insect was resistant or immune due to previous sublethal infections. Bergold felt the latter to be more probable. The fact that a certain percentage of orally infected budworms developed into adults indicated some degree of immunity.

Two features of the life history of the spruce budworm have considerable influence on the transmission and dissemination of the virus. The feeding period is relatively short, but the time of infection to death is rather long (10 days). Healthy larvae do not have much time to become infected by contact with dead individuals before pupation. It was not known if transovarial transmission of the virus occurred. If it did, the infected instar II larvae would die in their hibernacula, and healthy larvae would not have an opportunity to come in contact with them.

Bird and Whalen (1954) reported that the budworm was susceptible to a second virus. The first, described above, is characterized by the formation of polyhedra within the nuclei of tracheal matrix, fat, hypodermal, and blood cells. The second is characterized by the formation of polyhedra in the cytoplasm of midgut cells.

The infectious nature of the cytoplasmic polyhedra was described. Larvae fed the polyhedra developed the disease within 72 hours. Many larvae survived, indicating that the disease was not particularly virulent, or that infected midgut cells sloughed off and were replaced.

Krywienczyk et al. (1958) reported that the polyhedral and capsular viruses of the spruce budworm belong to two serilagically distinct groups since no cross reaction occurs. This finding justified the previous distinction of the two groups based on differences in size and shape of the inclusion bodies, the morphology of the virus particles, and the developmental site of the inclusion bodies in the nucleus or cytoplasm. The capsular virus of the spruce budworm and of C. muriana (Hbn.) (the European counterpart of the spruce budworm) cross reacted strongly, but there was no cross reaction between the polyhedral virus of the spruce budworm and either capsular virus.

Bird (1958) found that the cytoplasmic or granulosis virus that he and Whalen (Bird and Whalen 1954) had described earlier could also infect fat, hypodermal, tracheal matrix, and blood cells. The virus develops in the cytoplasm of these cells, whereas the polyhedral virus develops in the nucleus of these same cells. He found that prior infection of a cell by one virus interferes with infection by the other (Bird 1959). To produce double infections, an advantage must be given to the granulosis virus either in time or infectious units. Adjacent cells are frequently infected with different viruses, but usually blocks of cells are infected with the same virus.

The development and characteristics of the polyhedrosis virus and the granulosis virus were studied further by Bird (1963, 1964) and Stairs (1964, 1965).

Stairs and Bird (1962) reported field tests against the budworm using both the nuclear polyhedral virus and the granulosis virus.

In both 1959 and 1960, all virus applications caused mortality, and no virus mortality was found on unsprayed trees. In 1960, mortality was greatest (61.5 percent) on trees sprayed with granulosis virus, but mortality was more rapid on trees sprayed with polyhedrosis virus. The authors pointed out that the practical use of the viruses depends on:

1. Development of efficient methods of virus propagation.
2. Knowledge of most efficient concentrations to apply.
3. Determination of the most susceptible stage of the insect.
4. Whether the viruses persist from year to year.

Associated Fungi

MacLeod (1949) reported that a 1948 survey of fungi that parasitize or grow in association with the spruce budworm, found Hirsutella sp. to be most frequently isolated from diseased larvae. Usually, there was no evidence of external mycelium. In 1947, however, diseased larvae had been coated with mycelium and had numerous long, black, rigid hairs. The drier conditions of 1948 were considered responsible for the difference.

Hirsutella sp., Empusa sp., Beauvaria sp., and Isaria sp. were considered the most important genera found in fungus-infected budworm larvae (MacLeod 1949).

Microsporidian Disease

Thomson (1955) found the protozoan of the spruce budworm to be a new species of the order Microsporidia, and for it he proposed the name Perezia fumiferanae, later amended to Glugea fumiferanae (Weiser 1958). In laboratory-reared insects, the principal site of infection is the cells of the midgut. The Malpighian tubules are frequently involved, and occasionally small areas of muscle tissue. In naturally infested (field collected) insects, the fat body, silk glands, epidermis, gonads, hind gut, and nerve tissue are also invaded. The difference is because laboratory-reared insects receive a large number of spores and die quickly, whereas naturally infected insects receive small numbers of spores, live longer, and the parasite spreads throughout the body. Thomson postulated that the parasite exerts its lethal effect in the midgut. Only the cytoplasm of the host cells is invaded. The disease produces no apparent external symptoms, even for several hours after death.

Thomson (1958a) described the epidemiology of the parasite. There are two methods of infection, oral and congenital. All infected females transmit the parasite to their offspring, and for practical purposes all the progeny of such females are infected. Infected males are sometimes capable of transmitting the parasite to a portion of their offspring. Congenital transmission is responsible for the passage of the parasite from host generation to generation. Incidence of the parasite increases by oral ingestion of spores, but the habits of host larvae restrict most transmission to the late larval instars.

Infection of the budworm by G. fumiferanae retards both larval and pupal development, and reduces pupal weight, fecundity, and adult longevity, these effects being more pronounced in female insects (Thomson 1958b). Thomson found no evidence that the parasite affects male fertility, mate choice, or the fertility of the eggs. The parasite causes some mortality, most of which occurs before the fifth instar. Among larvae infected orally, mortality seems to be related to the size of the initial dose. The

development and survival of the instar I larvae and the hibernating instar II larvae are not affected. Thomson suggested that most of the observed results were caused by reducing the insects' ability to assimilate food. Mortality, however, was believed to be due to the destruction of the midgut or Malpighian tubules.

Thomson (1960) measured the incidence of the parasite in hibernating budworm larvae for 5 consecutive years. A great budworm population reduction was observed the year that the incidence of the protozoan was 81 percent.

Neilson (1956) found the disease in spruce budworm adults collected at Green River in 1954 and 1955. As many as 42.6 percent of the collections were infected by Microsporidia. Some adults died soon after emergence from the pupal case. Some were so badly infected that they could not have mated or produced viable eggs or sperm. He pointed out that this may help to explain why, in some areas, fewer eggs are found than would be expected based on the number of empty female pupal cases.

The presence of microsporidian spores in the male moth seemed to have a greater effect on fecundity than when they were found in the female (Neilson 1963b). The presence of spores in the male or in both adults was thought to reduce fecundity appreciably. Egg deposition, including that of "healthy" pairs, in these experiments was much lower than observed by Thomson.

Neilson (1963b) suggested that Microsporidia have an adverse effect on fertility. He could not demonstrate significant differences between the life expectancies of infected and noninfected males or females.

It was observed that spruce budworm larvae infected by the microsporidian also could be parasitized by Apanteles or Glypta (Thomson 1958c). Prepared specimens of Apanteles and Glypta larvae from infected spruce budworm larvae showed large numbers of spores confined only to the gut, and they never invaded the tissues of the parasitoids. The parasitoid larva has a blind gut, and spores accumulate as they are ingested, being neither digested nor able to infect the parasitoid.

The parasitoid larvae emerging from the budworm were unable to complete development. Normally, the parasitoid larvae store food in their blind guts to last them through pupation. When the midgut was nearly filled with inert spores, not enough food could be stored and the parasitoid died of starvation.

Bacterial Diseases

Denton (1960b) found in laboratory and field tests that Bacillus thuringiensis Berliner was toxic to larvae of the western budworm when a sufficient amount of the pathogen was ingested. Adequate coverage of the pathogen over the foliage was difficult. Denton thought that dosages greater than those used with DDT would be necessary to achieve adequate control.

Aerial application of B. thuringiensis have demonstrated that it can cause considerable mortality of the spruce budworm, but not sufficient to consider its use in place of chemical insecticides (Mott et al. 1961, Klein and Lewis 1966).

Kushner and Harvey (1962) suggested that the antibacterial substances in the leaves that insects eat may play a direct part in protecting them against ingested bacteria, but not against bacteria injected into the hemolymph. The authors present evidence that an increase in antibacterial activity of foliage eaten, an increase such as may occur with increasing age of foliage, can render an insect more resistant to bacterial attack. The increased sensitivity of a bacterial strain to inhibitory substances in leaves is accompanied by lowered pathogenicity.

Spruce budworm mortality resulted when Bacillus cereus Frankland and Frankland was injected into the hemolymph, but not when it was fed to insects on balsam fir foliage (Kushner and Harvey 1962). Serratia marcescens Bizio caused mortality in budworms reared in the laboratory on balsam fir. This pathogen was not inhibited, in plate tests, by balsam fir extract or the gut contents of budworms that had been fed on balsam fir foliage. Smirnoff (1963a) demonstrated that B. cereus was more effective than B. thuringiensis at low temperatures which indicates that selection of strains to fit certain ecological conditions may be possible.

Associated Insects

Miller (1950) presented a key to some lepidopterous larvae associated with the spruce budworm in New Brunswick. The species keyed were Acleris variana (Fern.), Recurvaria sp., Dioryctria reniculella (Grote), Zeiraphera fortunana Kft., Clepsis persicana (Fitch), Archippus packardianus (Fern.), Z. ratzeburgiana (Ratz.), Eucordylea atrupictella Dietz., and Griselda radicana Wlshm.

SAMPLING BUDWORM POPULATIONS

Each of the life stages of the budworm—egg, hibernating larva, feeding larva, pupa, and adult—has been sampled. The techniques have necessarily differed if the sampling was for studies of population dynamics or for surveys to determine the status of the insect over large areas.

The long-term study of population dynamics of the spruce budworm in New Brunswick required a critical choice of sampling techniques. Morris (1955) described these techniques as follows:

"The universe for which each life table is prepared is a homogeneous forest stand. It is shown that a collection unit smaller than a whole branch, or its longitudinal one-half, is unlikely to be suitable for the measurement of absolute population. Intertree variance is the major source of population variance for the budworm, and for most other insects that have been studied intensively. Significant variance is also associated with crown levels, and the pattern of vertical distribution of the budworm is not predictable. The criterion of representativeness can be satisfied, however, by drawing samples from four crown levels in such a way that the intensity of sampling is equal in each level. The design found suitable for the budworm consists of proportionate sampling within the crown, stratified sampling by crown stories within the stand (with substrata, when necessary, according to host species or flowering condition), and cluster sampling within strata. Samples may be drawn from the same trees during successive budworm generations, and show correlations which appear to arise from the preferences of ovipositing adults."

Extensive sampling at the cost of considerable time and effort is justified to gain an accurate insight into the mechanisms responsible for population regulation. In survey sampling, precision must be sacrificed to sample many more locations to determine population status on much larger areas.

The methods described in the next sections were devised mainly for surveys.

Egg Masses and Eggs

Morris (1949, 1955) described a method to take unequal sizes of branches into account when sampling spruce budworm popula-

tions. The product of the length and the midpoint width of the foliated portion of each selected branch approximates branch surface area. Egg mass density was expressed as "egg masses per 100 square feet" of foliage examined. This method was used to compute the density of other life stages such as larvae and pupae.

Fettes (1951) used another method to eliminate variation due to the amount of foliage on the sample branches. An egg mass index was based on the number of spruce budworm egg masses per foliated twig of balsam fir. It was assumed that each twig presented comparable oviposition opportunities. Female moths had no preference for old or new foliage as oviposition sites.

Morris (1954) developed a sequential sampling procedure based on whole branches for spruce budworm egg mass surveys in Canada. Infestations were classified as light, moderate, or severe. Dowden and Carolin (1950) used 15-inch samples taken from the terminals of midcrown branches. Atwood (1944) used 18-inch samples in insect surveys in Ontario.

Wilson (1959) subdivided samples to reduce the amount of foliage examined for spruce budworm egg masses. The tips of the shoots were separated from the rest of the branch, and the numbers of egg masses on the tips were increased by 16 percent to obtain the total for the branch. The method could be used on any size branch from any portion of the crown, but it could not be used on branches with severe or complete defoliation.

The density of the egg population is usually expressed in egg masses, since it is quite time consuming to count individual eggs. Bean (1961c) counted the number of eggs in 45 egg masses from balsam fir in each of three stand conditions, and found a distributional pattern such that he thought the use of an average number of eggs per mass was undesirable in population studies. He presented a table based on the regression line showing the relationship between the number of eggs and egg mass length. Miller (1957) presented a similar table for converting counts of egg masses to counts of eggs.

In the western United States, the methods for sampling the western budworm on Douglas-fir were developed largely by Carolin and Coulter (1959b). They found that either the lower or middle crown thirds could be used for sampling the egg population. Two longitudinal half-branches from each of five trees in each plot were examined. The branch surface was computed by dividing by 2 the product of the foliated length and the width at the widest point of longitudinal half-branches. Egg mass density was expressed as "egg masses per 1,000 square inches of foliage" examined. Sampling errors, expressed as percent of the mean, were found to be similar for total number of egg masses per branch and number of egg masses per 1,000 square inches of foliage area. Fifteen-inch twigs were least useful as a sample of egg moss density (Carolin 1950). The number of egg masses per 1,000 square inches of foliage were significantly correlated with the number of larvae per 100 fifteen-inch twigs attacking the buds.

McKnight (1967) found 24-inch branches from the midcrown of Douglas-fir to be as useful as half-branches to estimate numbers of egg masses of the western budworm in Colorado.

Carolin and Coulter (1959b) found no significant differences between the density of new egg masses and the density of old egg masses the following year. Buffam and Carolin (1966) presented data indicating that trends could be determined with only 1 year's sampling by using old egg masses to represent the previous year's new egg masses. Terrell (1961b), however, contends that old egg masses do not represent an accurate index of the

preceding year's egg mass population due to the loss of many old egg masses during the first year.

Silver (1960), studying an outbreak of western budworm on Douglas-fir in British Columbia, did not consider egg mass density a reliable index of subsequent defoliation. Harris (1963) sampled 2-year-cycle budworm on subalpine fir and white spruce in British Columbia, and compared egg mass densities in different quadrants at three crown levels. Branch direction did not affect the counts, but significantly fewer egg masses were found on the lower crown third compared to the midcrown and upper crown. The 18-inch twig sample was found to be as satisfactory as the whole branch.

One purpose of determining egg mass density, particularly in survey work, is to predict the amount of defoliation that will occur the next season so that control activities may be planned. Webb (1958b) predicted defoliation of balsam fir by the spruce budworm by the following equation: probable percentage loss of new growth = $0.27X + 5.8$, where X = number of egg masses per 100 square feet of midcrown branch area. In sprayed areas the loss was about 9 percent less than predicted the first year after spraying.

Terrell (1966) presented a curvilinear relationship between the density of egg masses of the western budworm and subsequent defoliation of Douglas-fir.

Silver (1960) found the relationship between numbers of western budworm egg masses and subsequent defoliation of Douglas-fir to be improved when the data were grouped by age of outbreak.

Terrell (1961b) and McKnight (1967) presented regressions to convert c o u n t s of egg masses of the western budworm to counts of eggs.

Hibernating Larvae

Denton (1951, 1953) pointed out the advantages of being able to predict defoliation from counts of larvae forced from hibernation in the winter months or early spring before their natural emergence. When planning for control operations, it is desirable to be able to predict the need for control as close to the period of damage as possible. Predictions based on pupal or egg mass surveys the preceding summer do not include an estimate of overwinter mortality or fall dispersal. Counts of hibernating larvae made in the early spring are more realistic.

Miller (1958) showed that the collection of balsam fir foliage samples in the spring and sampling of the whole branch as a unit was an acceptable technique for population studies of the spruce budworm. Terrell (1959), working in Montana, caged field-collected bolts and collected the emerging larvae of the western budworm. He pointed out that a sampling program must consider these points:

1. Samples collected from north or south slopes yield higher populations than samples from valley bottoms.
2. Hibernating larvae are more numerous per unit of bark surface on tree boles than on limbs.
3. Five bole sections are required from each sampling point for an adequate sample.

Carolin (1950) concluded that hibernating populations of the western budworm on the trunk and limbs, when expressed on the basis of larvae per 100 square inches of bark surface, provide a reasonable index to subsequent feeding populations, on the basis of the branch whorl.

In presuppression surveys of the western budworm on Douglas-fir, Lindsten and Wright (1951) and Wright et al. (1952) used samples of branches as well as bale samples. Whiteside and Gruba (1955) used 15-inch pieces of branches.

McKnight (1967) worked out the proportional distribution of western budworm larvoe hibernating on Douglas-fir trees in Colorado. About 65 percent of the larvae were found on the branches and 35 percent on the bole. The stratum of the branches in the lower one-third of the crown contained the highest proportion of larvae, 27 percent.

Feeding Larvae

Larvae per new shoot or bud is the most appropriate index of larval density (Fettes 1951, Morris 1955) because budworm larvae prefer new shoots as food. Atwood (1944) used the 18-inch twigs to sample needle mining populations of the spruce budworm. Waters (1955) presented a sequential plan for classifying the densities of populations of spruce budworm larvae.

Two indirect methods of sampling lorval populations have been used. One is based on the assumption that the number of maggots of a group of dipterous parasitoids falling on a unit area of ground will be an index of the budworm populations on the tree above that area (Dowden et al. 1953; Bean 1957, 1958b). The other method makes use of the correlation of frass width, but not its length or volume, with the various larval instars (Bean 1958a, 1959). Field-collected frass can be used as an index of the percent of larvae in each instar present when the collection was made.

Fifteen-inch twigs have been used by western entomologists to sample populations of larvae of the western budworm on Douglas-fir (Carolin and Coulter 1959b). Cole (1960) calculated sequential sampling plans for precontrol sampling or appraisal survey and for postcontrol sampling.

Sampling Douglas-fir in Oregon, Carolin and Coulter (1959b) concluded that, to establish area-wide damage relationships, larval populations should be expressed on the basis of the number of larvae per 1,000 buds, rather than larvae per 100 fifteen-inch twigs. Using plot averages, they found the relationship of larval populations per 1,000 buds to percent defoliation of current growth to be highly significant.

Harris (1964) concluded that one 18-inch branch per tree, taken at midcrown, would suffice for showing year-to-year trends of larvae of the 2-year-cycle budworm.

Pupae

Fettes (1951) and Morris (1955) expressed the density of pupae in the same manner as larval populations. Western workers generally use the 15-inch twig to sample pupal populations.

Terrell (1961b) used the density of the pupal population as an index to the moth population by sampling after the moths have emerged and counting the empty pupal cases. He found that the moth population correlates with subsequent defoliation, but moth flight or the invasion of moths from other areas can make estimates of defoliation invalid.

POPULATION DYNAMICS

Morris (1963a) edited the long-awaited report of intensive population studies of the spruce budworm in northern New Brunswick during the period 1945-59. Life tables based on intensive sampling of populations on permanent plots, complemented by data on fecundity, natural and applied control factors, and dispersal, were constructed for consecutive generations in different forest types. A few years of observations on the endemic condition were obtained before the outbreak began, and now the studies of the endemic conditions following the outbreak are continuing. This research effort is recognized as the most significant contribution to our knowledge af the spruce budworm; the methods developed for the study and the techniques of dato analysis serve as examples often imitated by other students of population dynamics.

The findings of the many investigators would lose significance if a review of the entire report were attempted here. Their evaluations of natural mortality factors are cited throughout this review. The following summary, taken from Morris' (1963g) resume, should suffice to present the most significant findings in a general manner.

The.objective of the investigation wos to determine, and model mathematically if possible, the mode of action of the principal factors affecting the density of populations of the spruce budworm. Two study areas were involved: in one, the outbreak was allowed to run its course without disturbance; in the other, the effects of aerial application of insecticide (DDT) on the treated generation and subsequent generations were studied.

Analysis of survival.—In this analysis, the dependent voriable was survival rate, that is, the population density at the end of the age-interval compared to the population density at the beginning of the age-interval. Multiple regression techniques were used to express relationships between the survival of each age-interval and the independent variables found to be related significantly to it. These equations, submodels, were pooled to produce a model for survival of the entire generotion.

The first step in the analysis was to evaluate generation survival in terms of age-intervol survivals, and variations in survival with respect to time and place. Generation survival was found to be determined by the survival of the large larval interval (instars III-VI). Large larval survival and pupal survival were often closely related. Variations in large larval survival were associated mainly with time (generations). Variations in survival of the small larvae (instars I-II) were associated mainly with place (plots).

In the sprayed area, the insecticide treatment was the most important factor affecting survival in the treated generation and those immediately fallowing. Otherwise, in both study areas, population density and weather had the greatest effect on variations of survival with time (generations), and the density of balsam fir had the greatest effect on variations of survival with place (plots).

Key-factor analysis.—In this analysis, the number of large larvae in generation n+1 was used as the dependent variable. By regression analyses it was faund to be a function of the population density ond weather in generation n. The use of parasitism as a third independent variable did not improve predictability under epidemic conditions; it may be more useful in the endemic phase. As with other forest insects, key - factor analysis for the spruce budworm demonstrated that changes in population density are determined by only a few of the many regulating mechanisms.

Natural control factors.—Parasites and predators had negligible effects on survival rates during the outbreak period, but

their influence may be greater during the endemic phase. The incidence of disease was related to weather, but low virulence was a common feature of the pathogens. Among stand factors, stand microclimate seemed to be more important than the production of staminate flowers.

The population models developed for the epidemic situation indicate the relative importance of the different age-intervals and the variables affecting them.

With this stage accomplished, at least for the epidemic situation, critical study of various population regulating processes can now proceed. The models are already useful in that the effects of variables which can be manipulated by man can be predicted, and optimal procedures for outbreak prevention and suppression can be determined.

DAMAGE

Damage by the spruce budworm to balsam fir, its principal host, has been studied and documented extensively. Early workers noted that loss of needles was reflected almost immediately by reduction of the current annual ring (Craighead 1923, 1925). This effect on radial growth has been studied in detail (Mott et al. 1957, Blais 1958a) and used to date the occurrence of outbreaks.

Injuries caused by certain frosts can also produce characteristic "frost rings" (Bailey 1925) in balsam fir, alder, hazel, birch, cherry, and mountain ash. By cross checking the frost rings in spruce budworm hosts with those of other vegetation in the area, outbreaks may be more accurately dated.

During an outbreak in northwestern Ontario, defoliation was recorded yearly in certain stands from the beginning of the infestation (Blais 1958a). Radial growth measurements were obtained from increment cores taken at breast height from white spruce and balsam fir of merchantable size. The first year of radial growth suppression was calculated by comparing the growth of the spruce and fir with that of jack pine and red pine. Growth was generally suppressed in the second year at the earliest, and at the latest, in the fourth year of severe defoliation.

Ghent (1958b) found that satisfactory histories of spruce budworm outbreaks were recorded by damage to the main axis of seedlings caused by feeding of late instar larvae that dropped from the overstory.

Loss of Radial Increment

The characteristic increment reduction is a distinct loss to the forest manager. Craighead (1925) observed that, in trees that survived spruce budworm attack, the diameter growth for the 10-year period following the first year of feeding was only about one-half that of the preceding 10 years.

McLintock (1955) studied spruce budworm damage during a heavy outbreak in southwestern Quebec from 1944 to 1950. Increment cores from more than 100 trees showed a drop in increment in all trees beginning in 1 to 6 years, and most marked in 5 or 6 years, after the first defoliation. This drop continued for at least 3 years after defoliation ceased.

Williams (1963, 1966, 1967) in Oregon found that external symptoms, the bases of damage classes, were related to radial and height increment losses in hosts of the western budworm. Radial increment was most sensitive to budworm feeding, particularly at midcrown. Radial increment in the most serious damage classes was reduced more than 41 percent in grand fir but only

about 13 percent in Douglas-fir. The radial increment of Douglas-fir increased during the later stages of the outbreak, while that of the grand fir and Engelmann spruce was still declining.

Loss of Height Increment (Top Killing)

Top killing is a characteristic of prolonged outbreaks. Schmiege (1961) reported top killing as high as 78 percent in some areas in the Lake States.

In Montana, larvae of the western budworm severed terminal shoots of young western larch, creating trees with multiple leaders and crooked boles (Fellin and Schmidt 1967).

Silver (1960) commented on the ability of Douglas-fir trees to sustain severe defoliation by the western budworm and remain alive. In an infestation in British Columbia, numerous trees had all of their buds killed, lost over 90 percent of their needles, and yet no trees on the study plots were killed. Top kill was common, but usually only one or a few years' terminal growth was killed back. Branch tips were killed, but heavy adventitious budding made recovery rapid. Radial growth began to improve the year after the first year of light defoliation.

Williams (1963, 1966) did not observe top killing of Douglas-fir in Oregon. The competitive position of grand fir was greatly reduced because of top killing, but that of Douglas-fir increased relative to grand fir and Engelmann spruce.

Rootlet Mortality

Swaine et al. (1924) reported that, during the spruce budworm outbreak of 1912 to 1920 in New Brunswick, all rootlets and roots less than 2 millimeters in diameter were dead 6 months prior to the death of severely damaged balsam fir trees. Redmond (1959), by sequential sampling, found that when the defoliation of new shoots was greater than 70 percent, rootlet mortality was greater than 30 percent. When the loss of current growth reached 100 percent, rootlet mortality soon exceeded 75 percent. When the defoliation of young trees diminished or ceased, rootlets were immediately regenerated, but the trees were unable to survive a recurrence of defoliation severe enough to kill these new rootlets. Mature trees were less able, and overmature trees were unable, to regenerate new rootlets after 4 or 5 successive years of total defoliation of new shoots.

Stillwell (1960) reported progress on a study, initiated in 1957, to determine the relationship between rootlet recovery and foliage recovery. In 1950, 20 percent of the current foliage was lost, 40 percent in 1951, and 100 percent from 1952 to 1955; but very little after that year. Rootlet samples were taken in 1957, 1958, and 1959, and the degree of mortality was determined by the sequential sampling plan devised by Redmond (1959). By 1959, rootlet recovery in 43 of 47 trees appeared to be normal. It was concluded that rootlet recovery lagged behind foliage recovery by 3 years.

Tree Mortality

During a spruce budworm outbreak in the early 1900's in Quebec, Ontario, New Brunswick, and Maine, Craighead (1923) observed that all trees that were 75 to 100 percent defoliated died 1 to 2 years later. No trees that were less than 25 percent defoliated died.

Mortality of balsam fir generally begins in the fifth year of severe defoliation by the spruce budworm (Belyea 1952b, Blais

1958b, Baskerville 1960). In the spruce budworm outbreak in southwestern Quebec between 1944 and 1950, the first mortality was observed in 1948 and the first heavy mortality in 1949 (Mc-Lintack 1955). In the overstory, there was little difference in mortality in the d.b.h. classes 4 to 5 and 6 to 8 inches, but from 9 inches upwards, mortality was about 10 percent higher each year than in classes below 9 inches. Dominant and intermediate trees sustained heavier losses than overtopped (but not suppressed) trees. Mortality was heavier among trees suffering heavy than among those suffering medium or light defoliation, and in trees with short crowns than in those with large crowns. No consistent relationship was found between site quality and mortality, but there appeared to be higher mortality on poorly drained sites.

Craighead (1925) stated that, in hardwood types, the immunity of softwoods was proportional to the protection of the hardwood overstory. The percentage mortality of dominant softwoods in mixed stands was as high as in pure softwood stands. Turner (1952) found that where fir was of intermediate height, fir mortality decreased with increasing proportions of hardwoods. Where fir was understory, fir mortality increased with increasing proportions of hardwoods; the fir was possibly more susceptible with increased shade. Where fir was codominant, the proportions of hardwood did not affect fir mortality. In general, increasing fir mortality accompanied increasing relative height of fir. Within all localities of generally high fir mortality and in most of the broad cover types studied, the percentage mortality of fir increased with the basal area of fir per acre.

Effects on Regeneration

The spruce budworm was observed to feed in and on white spruce cones and in preference to foliage (Tripp and Hedline 1956). LeBarron (1944) reported that insects were the chief cause of early mortality of jack pine and black spruce seedlings. The spruce budworm was observed to feed on the tops of the seedlings.

Ghent et al. (1957) concluded that trends of forest succession that develop after a spruce budworm outbreak are determined on a regional basis. If the site and climate are favorable, either spruce or balsam fir may increase in proportion following an outbreak. Apparently neither has greater competitive abilities in all circumstances.

An early effect of defoliation in balsam fir is the cessation of female flower production (Ghent 1958b). During an outbreak, seedlings are not released, because larvae that drop from the overstory feed on them. Seedling height increases immediately following the period of peak budworm populations and when overstory mortality begins.

Deterioration of Defoliated Trees

Belyea (1952a) found the following species of insects attacking severely weakened or newly dead balsam fir trees:

Order COLEOPTERA

Family Cerombycidea

Monochomus scutellatus (Say)—the white-spotted sawyer beetle
Monochomus mormorotor Kby.—the balsam sawyer beetle
Tetrapium cinnamopterum Kby.—the four-eyed spruce borer

Family Curculionidoe

Pissades dubius Rand.—the balsam weevil

Family Scalytidae

Pityokteines sparsus Lec.—the balsam bark beetle
Trypodendron bivittatum Kby.—the spruce ambrasia beetle

Family Melandryidae

Serrapalpus substriatus Hald.

Order HYMENOPTERA

Family Siricidae
Sirex cyaneus F.
Sirex sp. (noctilio group)
Uracerus albicarnis F.

Of these, only two, Pityakteines sparsus and Monachamus scutellatus, were abundant. They were observed to attack the trees before death, but their activity was such that no damage was done before the tree died (Belyea 1952b).

On the Green River watershed, balsam fir with forked tops, marked crooks, and slight sweeps or crooks were felled and dissected to relate the size of buried leaders to the extent of decay resulting from the 1912 to 1920 spruce budworm outbreak (Stillwell 1956). All of the trees with forked tops and marked crooks, but none of the trees with slight sweeps or crooks showed decay entering through budworm injury. Buried leaders of one-half inch diameter or larger were always seats of origin for decay. Those smaller and younger were not.

Boshom and Belyea (1960) found the general pattern of deterioration to consist of a relatively sudden invasion by insects at or near the time of apparent tree death. This was followed by a more gradual fungal invasion, which completely replaced the insects after 2 years. Evidence indicated that bark beetles, sawyer beetles, and weevils carry deteriorating fungi from dead balsam fir to dying or newly killed trees, and that the development of sap rot is related to sawyer beetle activity.

Stillwell (1962) reported that the rate of deterioration by decay is more rapid in balsam fir trees killed by insects than in trees killed by fire or windthrow. Two years after death, decay caused mainly by Stereum chailletii penetrates one-half inch, but is not present in windthrown or fire-killed trees. Wood wasps, Sirex juvencus (L.) and Urocerus spp., may introduce S. chailletii into the sapwood of trees weakened by budworm defoliation. Another species, Xeris spectrum (L.) also oviposits in balsam fir but lacks the specialized sacs in which the fungal strands of S. chailletii are carried and does not transmit the organism.

Moisture content is another factor influencing the rate of deterioration. In contrast to fire-killed and windthrown trees, trees killed by the spruce budworm remain standing, the bark loosens slowly, and the moisture content remains high enough for decay to develop.

Aerial Surveys

The airplane has been used as a platform from which to detect and delineate budworm outbreaks since 1923 (Swoine et al. 1924) when F. C. Croighead made observations on defoliation

by the spruce budworm. Research to improve aerial surveys is relatively recent. Heller et al. (1952) reported that defoliation as light as 15 percent of current growth could be detected by aerial reconnaissance. The use of an operation recorder for recording defoliation intensities was described. Waters et al. (1958) compared the relative accuracy of aerial observation and aerial photographic interpretation in assessing damage by the spruce budworm. Aerial observation was more accurate at detecting light defoliation, less expensive, and possible under a wider range of weather conditions. Aerial photographic interpretation was more reliable for quantitative appraisal of top killing and tree mortality. These authors stressed the importance of supplemental ground surveys for correct interpretation of aerial observations.

Heller and Schmiege (1962) were able to relate degrees of defoliation as observed from the air with numbers of spruce budworm larvae causing the damage. The midcrown was established as the optimum location for sampling balsam fir for defoliation. They used a quantitative method of estimating defoliation similar to that used by Fettes (1951).

Aerial surveys, utilizing aerial photographic interpretation (Weber 1964) as well as operation recorders (Gardiner and Prielipp 1964), have been useful in estimating timber losses caused by the spruce budworm.

Estimating Defoliation

It is generally agreed that estimates of defoliation are useful indices of past budworm activity (Fettes 1951, Terrell 1961b). An estimate of current defoliation is not a valid means of predicting the trend of the outbreak, however (Terrell 1961b).

Fettes (1951) and Terrell (1961a) reported methods of estimating current defoliation from collected branch samples. Fettes trained observers to grade any new growth shoot according to one of 13 standards, corresponding to categories of percent defoliation. Terrell (1961a) found a curvilinear relationship between the number of undamaged shoots of Douglas-fir and the percent defoliation by the western budworm. McKnight(1967) presented a similar curve for estimating defoliation of white fir as well as Douglas-fir.

Carolin and Coulter (1959b) found that visual estimates of percent defoliation on individual trees, based on field glass estimates for each crown third, were related to the density of population of western budworm larvae on Douglas-fir trees. Their method of weighting the estimates for each crown third by the proportional amount of foliage in each improved the relationship. Other workers have found that field glass estimates for only the midcrown do not differ from estimates based on weighted estimates of each crown third. Carolin and Coulter found that damage estimates based on shoot tallies for the middle crown third were not closely related to larval densities on the trees, but gave better estimates of defoliation and bud killing for the plot than did field glass estimates. The incidence of bud killing was not directly related to the population level or to percent defoliation.

Silver (1960) used field glass estimates to determine current defoliation on Douglas-fir in British Columbia. He used unpublished data showing that current growth constitutes 20 to 30 percent of the total foliage on a tree to estimate total defoliation.

BIOLOGICAL CONTROL

Heimberger (1945) suggested that biological control of the spruce budworm in New Brunswick and Maine be approached through the population genetics of the budworm, and the use of its parasitoids and their interactions with balsam fir and other hosts. He considered the budworm to be biologically "young" in relation to its environment because it requires long periods to achieve high population pressures sufficient to cause outbreaks. He believed the budworms of other spruce and pine species in other regions to be "mature," and advocated the introduction of "mature" parasitoids of "mature" budworms for biological control.

Tothill (1923) used an early version of the life table to compare the natural control factors of the spruce budworm in New Brunswick with those of the western budworm in British Columbia. Because the western outbreaks collapsed and Phytodietus fumiferonae was abundant there, he urged that introductions be made into New Brunswick where outbreaks persisted. This parasitoid and three other species from British Columbia as well as 13 species from Europe were released in eastern Canada (Wilkes 1947). None of the European species was recovered, Blais (1960a) recovered one specimen of Ceromasia auricoudata, and Wilkes and Anderson (1947) recovered a few specimens of Phytodietus fumiferonae. The failure of these biological control efforts apparently is related to the scarcity of knowledge of their environmental requirements (Miller 1963d).

Stoirs and Bird (1960) described an occurrence of unusual parasitism of spruce budworm where "foreign" parasitoids were important. Instar II larvae transferred from a natural infestation in Ontario to Sault Ste. Marie, were placed on small balsam fir trees near an adjacent stand of sugar maple, white oak, white birch, balsam fir, and white spruce. The natural budworm populations at Sault Ste. Marie were very low. Parasitism of the transferred larvae was high. Of the recovered Ontario larvae, 10 percent were killed by Apanteles and Glypto and 55 percent by Clinocentrus sp., normally a rare parasitoid of spruce budworm and not found in the original budworm population in Ontario. Its natural host was probably Argyrotoxo semipurpurona Kft. which was epidemic on oak in the adjacent stand at Sault Ste. Marie.

SILVICULTURAL CONTROL

Spruce budworm control by forest management was recommended for balsam fir stands as early as 1923 (Tothill 1923). Craighead (1923) made three recommendations for control of epidemics:

1. Diversified types to break up continuous canopies of balsam fir.
2. Utilization of hardwoods to encourage mixed softwood-hardwood types.
3. Short rotations of all balsam fir mixtures and pure spruce in the vicinity of balsam fir.

Heimburger (1945) was convinced that an artificial change in species composition "preferably by almost completely eliminating balsam fir" would be unsuccessful, and discussed the value of tolerant hardwood barriers and their location by biogeographical considerations.

There was an obvious need for standards to estimate the susceptibility and vulnerability of any given stand to budworm attack. Pulpwood operators needed to know which stands were in immediate danger and which were relatively safe so they could plan their cutting operations. Foresters and entomologists were interested in detecting areas that would be particularly susceptible and serve as foci for outbreaks. Balch (1946) present-

ed a map showing the relative susceptibility of different areas in the Northeast with recommendations for management. Morris and Bishop (1951) described a method of rating forest areas from aerial photos.

It was agreed that an accumulation of mature balsam fir was necessary for a spruce budworm outbreak, and cutting practices were recommended to remove such accumulations (Westveld 1946, McLintack 1947). Management plans and risk-rating systems for selective cutting were presented by McLintock (1948, 1949) and Westveld (1954) for the Northeast. Bean and Batzer (1956) and Graham (1956) devised risk-rating systems for use in the Lake States. Batzer (1966) found that individual tree characteristics were not determinants of risk of damage by the spruce budworm in Minnesota. In general, stand age, site index, staminate flowering, and basal area were not significantly related to defoliation, top killing, and tree mortality.

CHEMICAL CONTROL

Insecticide Evaluation

Aerial applications of insecticides for budworm control were made as early as 1929 (Swaine 1930). Calcium arsenate dust was applied at rates of 30 to 40 pounds per acre against the spruce budworm. Lead arsenate, applied with ground equipment against the western budworm in Cody Canyon, Shoshone National Forest, Wyoming, was not much more effective than natural control on untreated trees (Evenden, unpublished).

Orr and Wygant (1945), using a large power sprayer in Colorado, found that DDT at 0.5 pound or more per 100 gallons of water or about 2.5 pounds or more per acre caused almost complete mortality of the western budworm on Douglas-fir and spruce, and was nearly as effective on pine. The best results were obtained by spraying just before the larvae left their hibernacula, but applications during feeding periods gave satisfactory results. Adult moths were readily killed by DDT. None of the lead arsenate formulations were as satisfactory as DDT.

Brown et al. (1947) tested 15 organic insecticidal compounds for their direct contact toxicity to larvae of the pale western cutworm (Argrotis orthogonia Morr.), the flax bollworm (Heliathis ononis (Denis and Schiff.)), and the spruce budworm. The compounds, dissolved in a benzene-kerosene mixture, were applied at graded concentrations in a spray tower. The pyrethrins, gammexane, and DNOC were among the four most toxic compounds to all three species. DDT was highly toxic to flax bollworm and spruce budworm. Rotenone and toxaphene were moderately toxic to all three species.

In screening tests in the laboratory, Hurtig and Wenner (1953) found instar V and VI spruce budworm larvae to be highly susceptible to very small doses of DDT. A formulation of 3 percent DDT plus 1 percent pyrenone (piperonyl butoxide plus pyrethrins) was as toxic as a 10 percent DDT solution. Pyrethrins alone were highly toxic. Lindane, aldrin, and chlordane were relatively ineffective. Schradan (OMPA), a systemic, was translocated to new shoots on test twigs but it was nontoxic to the larvae.

Instar II larvae of the spruce budworm were extremely susceptible to minute amounts of DDT applied as a contact insecticide (Hurtig and Rayner 1953a). DDT-oil solutions on dormant foliage remained toxic for about 1 week.

The DDT-pyrenone formulation in solvent (Velsicol AR-50) and fuel oil was evaluated further against instar VI larvae (Hurtig and Rayner 1953b). It was found that the primary solvent could be eliminated without significantly reducing the toxicity. How-

ever, applications with fuel oil alone would alter the physical characteristics of the spray with effects on atomization and evaporation. No evidence was found that the piperonyl butoxide was a synergist for DDT, but it may have enhanced the joint toxic action of DDT and pyrethrin. Replacement of pyrethrins with allethrin produced formulations of low toxicity.

The dosage-mortality relationships of DDT, parathion, endrin, and pyrenone were determined against instar VI larvae (Rayner and Hurtig 1953a). DDT was relatively ineffective on the basis of contact action alone; large increases in dose gave small increases in mortality. Parathion was the most toxic of the chemicals tested. About 30 times more DDT than pyrenone, and about 40 times more DDT than parathion was needed to kill 50 percent of the test larvae in 48 hours. Endrin was relatively nontoxic. Testing of malathion was recommended.

Deposits of DDT on foliage were compared with topical applications for toxicity to instar VI larvae (probably 2-year-cycle budworm) by Rayner and Hurtig (1953b). Deposits on foliage equivalent to 2.25 pounds of DDT deposited per acre were not as effective as similar deposits applied directly to larvae. After 48 hours, larvae with these deposits placed on foliage with similar deposits suffered 81 percent mortality; larvae with only the topical applications (not on treated foliage) suffered 78 percent mortality. Because aerial applications of DDT at 1 pound in 1 gallon per acre gave deposits on trees of only 0.2 pound per acre, the authors suggested that the high mortality of larvae in field tests was the result of a strong repellent effect, not necessarily lethal, of the DDT. These authors were convinced that aerial applications of DDT should be applied to the instar II larvae rather than to the instar VI larvae, the most DDT-resistant instar.

In 1953, Elliott et al. (1954) compared BHC and an organic phosphate with DDT in hand sprayer, mist blower, and aerial tests. DDT at 1 pound per gallon and applied at 1 gallon per acre, produced the best results. The choice of solvents appeared to be of little or no importance in terms of spruce budworm mortality.

Smith (1954) reported tests in New Brunswick to compare four insecticides with DDT for small ground-spraying projects. The tests indicated that malathion was almost as effective as DDT, and since it also killed mites it was considered a suitable substitute for DDT for use on shade trees. Lead arsenate was only moderately effective, and both aldrin and dieldrin gave poor results. Fettes (1960) tested malathion and other chemicals for aerial forest spraying. DDT at rates of 1.0, 0.5, and 0.25 pound per gallon per acre was more effective than malathion, DDD, Korlan, or Sevin. Secrest and Thornton (1959) found DDT to be superior in laboratory tests involving DDT, BHC, aldrin, dieldrin, and endrin at normal and quarter strengths.

Reducing the dosage of DDT from 0.5 to 0.25 pound per acre in 0.5 gallon, did not reduce its effectiveness against the spruce budworm, but it was less toxic to fish and aquatic insects (Fettes and Randall 1962).

Malathion was shown to be effective against the western budworm when compared with DDT in a pilot control test in southern Colorado in 1962 (Wilford unpublished).

Randall (1962) reported laboratory tests involving the systemic insecticides dimethoate, menazon, and phosphamidon. As measured by mortality of spruce budworm larvae, dimethoate and phosphamidon were effectively translocated in white spruce seedlings. In aerial tests, Fettes and Randall (1962) found phosphamidon to be effective against the spruce budworm with less hazard to fish. Nagel (unpublished) demonstrated that both dimethoate and DDT prevented damage by larvae of the western budworm to buds on Douglas-fir of Christmas-tree size. Dimethoate was

as effective as D D T at twice the emulsion concentration. The translocation of dimethoate was not demonstrated because of late application, but the larvae were killed by wetting the needles. In northern New Mexico, dimethoate was equally effective against instar V larvae of the western budworm when applied at dosages of 4 ounces or 8 ounces in 1 gallon of water per acre (McKnight unpublished). Neither dosage was effective against larvae in the bud-mining stage.

Aerial Spraying Techniques

Control of the budworm by aerial application of insecticides is a complex operation involving several agencies, many individuals, much equipment, and large forest areas. Precise timing of the application is necessary to obtain the desired results, and cooperation among individuals and agencies is of great importance. General treatments of the history, techniques, and problems of aerial spraying for budworm control include those by Balch (1952), Webb (1955a, 1955b, 1958a, 1959), Blais and Martineau (1960, and Webb et al. (1961).

The development of the technique of aerial application of insecticides to control the spruce budworm was largely a cooperative effort between United States and Canadian investigators (Webb 1960). Some differences have evolved, however, perhaps due to the variations of the budworm species involved and their corresponding differences in host forests and outbreak behavior. In the United States, spraying was generally recommended early in the outbreak to prevent tree mortality where it might occur within 1 or 2 years, and to minimize reinvasion by also spraying buffer zones of lighter infestations. In Canada, the policy was to spray only in areas where another year's attack would seriously threaten the life of trees. This policy requires precise recognition of the ability of trees to survive; considerable respraying of reinfested areas must be accepted.

Differences in techniques lie largely in dosage and timing of spray application. In the United States, the objective was maximum population reduction, and 1 pound of DDT per acre was the standard dosage applied late in the feeding period. In Canada, the emphasis was on saving the current foliage crop, and spraying was started earlier in the season. Dosages of 0.5 pound, and later, 0.25 pound of DDT per acre were used successfully in terms of tree protection.

The persistence of a small, localized outbreak in Quebec provided an opportunity to test the idea that suppression of a local outbreak would prevent its spread. The outbreak was finally brought under control by the combined effects of 3 years of spraying with DDT and natural control factors (Blais 1961b, 1963). Suppression of the incipient outbreak was not as successful as hoped because of dispersal of instar I and II larvae, and unusually favorable conditions for survival in the early part of the operation.

Although aerial applications of insecticides were made against the spruce budworm as early as 1929, the techniques were not perfected until DDT came to wide usage. After the apparent success of operations in Ontario against the spruce budworm (Stewart 1949), Eaton et al. (1949), demonstrated the effectiveness of DDT sprays applied by airplane and helicopter against high populations of the western budworm in Oregon. Excellent control was obtained with both 1 pound of DDT in 1 gallon of fuel oil per acre and 2 pounds of DDT in 2 gallons of fuel oil per acre. Control was unsatisfactory when 0.5 pound of DDT in 1/2 gallon of fuel oil per acre by helicopter was used. Also, 1-pound applications by helicopter gave lower, but satisfactory, mortalities than

did the applications by plane. The sprays were applied when the larvae were actively feeding on the foliage.

Davis et al. (1956) tested different atomizations, dosages, and stages of spruce budworm development to determine the best combination of factors. They concluded that maximum kill would be attained if treatment was made when most of the larvae were in the instar IV and V. The minimum dosage of DDT for maximum kill was 1 pound of DDT per acre. A spray of medium atomization (150 microns mass median diameter) gave the most consistently effective results.

Davis et al. (1957) described tests conducted in 1956 in Montana and Idaho to determine if the spray height for large planes could be raised from the 200-400 feet that was being recommended. Six blocks of 2,500 to 6,000 acres each were sprayed, 2 at 250 feet, 2 at 500 feet, and 2 at 750 feet. Lowest variability in budworm mortality and greatest insecticide deposit were obtained at 750 feet. These results prompted a more critical evaluation of the 750-foot height in 1957 (Davis et al. 1958) on a 30,000-acre area. Low budworm mortality (average 89.1 percent) was attributed to low intensity of infestation, late application, and irregularities in flight line spacing and deposit distribution. Due to this marginal control, the adoption of the 750-foot height was not recommended.

Bean (1961b) suggested that balsam fir shoot elongation be used for timing aerial spray programs for spruce budworm control in the Lake States. However, Bean and Wilson (1964) found temperature summation methods to be more accurate for predicting the peak of the third instar.

Terrell (1956) presented criteria by which an observer in a small plane could judge the adequacy of aerial spray applications. On the ground, dyed oil-sensitive cards are usually used to judge spray coverage. The screening effect of surrounding trees should be considered when the cards are set out (Maksymiuk 1963a). Budworm mortality cannot be predicted from the insecticide deposits recorded on the cards (Maksymiuk 1963b).

Himel and Moore (1967) presented evidence that mortality of larvae of the western budworm was caused largely by the insecticide in spray droplets 50 microns or less in diameter. Because about 95 percent of the spray applied to forests by current methods consists of droplets larger than 50 microns, most of the lethal portion of the drop spectrum is ineffective.

Fettes (1958) urged that techniques for spraying forests be studied more intensively, rather than rely on methods developed for spraying croplands. More toxicological studies are needed to better define dosage-mortality relationships for forest insects. The meteorological aspects, particularly air currents and temperature gradients, of aircraft spraying over forests should be investigated.

Side Effects

The application of DDT to large forest areas has been considered a possible hazard to insectivorous birds. George and Mitchell (1947), after laboratory and field tests, concluded that if nestlings were fed both treated and untreated insects, they would not die. If the dosage of insecticide was sufficient to cause complete mortality of the budworm larvae, some nestlings would probably die due to poisoning or a combination of poisoning and weakness because of lack of food. Blais and Parks (1964) saw no evidence of ill effects of DDT to evening grosbeaks, which were of importance in controlling the spruce budworm in an outbreak in Quebec.

Mony young solmon were killed in 1957 on Voncouver Islond ond in New Brunswick ofter opplications of DDT ot rotes of 1 pound ond 0.5 pound per acre, respectively (Fettes 1960, Fettes ond Rondoll 1962). Ide (1956) reported that opplicotions of 0.5 pound of DDT per acre in New Brunswick mode streoms defi-cient in the kinds of insects fed upon by solmon in unsproyed streams. Larger numbers of insects emerged from sproyed streams but with smoller volume becouse of the scorcity of lorger species, porticularly caddis flies.

DDT applied ot 1 pound per ocre in the Yellowstone River droinoge reduced the numbers of streombottom invertebrotes immediotely ofter the sproy (Cope 1961). They recovered to neor normol numbers within o year in most streams, but the species composition was altered. No mortolity to fish wos observed. DDT wos found in trout 85 miles below the sproy oreo, ond fish token more thon 2 years ofter spraying contoined DDT.

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