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THE RELATION OF INSECT ACTIVITIES TO FOREST DEVELOPMENT AS EXEMPLIFIED IN THE FORESTS OF EASTERN NORTH AMERICA¹

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HISTORY OF THE FOREST

The Primeval Forest. Some three centuries ago, when the French and English settlers were building cabins along the north Atlantic coast, the eastern part of North America was covered by a vast and almost unbroken forest. It extended from the prairies to the sea and from the south Atlantic coast to Hudson's Bay. It comprised hardwoods of many species with conifers on the uplands in the south and conifers with fewer species of hardwoods in the north. From the tales that have come down to us and the story revealed in the forest itself we can guess at its composition. White and red pine, usually mixed with balsam fir, spruce, and hardwoods extended over an enormous area in the New England and North Atlantic states, in the provinces of Nova Scotia and New Brunswick, and in the southern portions of Quebec and Ontario. White spruce, with red spruce in the far East, usually mixed with balsam fir and often with hardwoods, occupied parts of the same area, forming dense stands on the higher ground in Maine and Southern Canada and stretching in scattered forests into the extreme north beyond the Arctic Circle. Balsam fir occurred largely in mixed forests but also in pure stands on considerable areas of the higher slopes. Jack pine grew then, as at the present time, on sandy plains and ridges, but there is probably much more of it now than there was in the primeval forest. Larch or tamarac covered swampy areas throughout the entire region and although it did not occur in extensive forests its total quantity must have been enormous. Hemlock occurred mainly in mixed stands from Southern Ontario and Southern Quebec southward. Black spruce, then as now, grew in bogs and wet places and in addition, covered a vast belt of territory stretching across the area now known as Northern Ontario and Northern Quebec. Cedar grew in large quantity on moist ground about the margins of lakes and streams. The

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hardwoods were more abundant in quantity and more numerous in species in the southern half of the territory; they occurred in considerable quantities, nevertheless, northward throughout the Maritime Provinces and in the southern parts of Quebec and Ontario, but only the white birch and poplars extended beyond the black spruce belt into the extreme north.

In this ancient forest there were undoubtedly many changes from time to time. Fires set by Indians or caused by lightning no doubt swept off the mature timber on areas of considerable size with a resultant change in forest types. Insect pests, such as the spruce budworm and the hemlock looper, probably ravaged portions of the forest then, as they have done in later years over larger areas, and again changes in forest types must have been the result. In the mixed forests of pine, hardwoods, spruce and balsam, there was probably a rotation of dominant species. In the great black spruce areas of Northern Quebec and Northern Ontario, on the other hand, the conditions were probably much more stable; it is likely that a large part of that country has been covered with black spruce for many centuries and would continue so, unless interfered with by man, throughout this geologic age.

When the white man reached these shores, nevertheless, he entered a forest which, in spite of certain periodic or fortuitous changes, probably had acquired a considerable degree of equilibrium and could have maintained indefinitely its general characteristics. The development of the white man's civilization has resulted in the demolition of the forest on an enormous extent of its original area and has produced directly or indirectly an extensive deterioration in the remaining timber over almost all the territory south of the black spruce belt in Northern Quebec.

The Present Forest. The result of these changes may be summarized in a few words. The original virgin forest of red and white pine has virtually disappeared. There are, so far as I know, only three considerable areas of virgin white and red pine left, one in the upper drainage basin of the Ottawa River in Western Quebec, one in the Quetico district of Western Ontario and one in the Missisaga region of Algoma in Ontario. When the white and red pine were cut, they were usually replaced by spruce, balsam fir and hardwoods, with the result that the areas on which the young stands of these pines are now growing are only a minute fraction of the original pine forest.

The original stands of nearly pure white spruce have almost disappeared, except in the northern and less accessible valleys; but there is still a considerable quantity of virgin white spruce in mixed forests which was left when the pine was cut, and which is now being utilized. The finest virgin stand of white spruce remaining in the East is to be found in the alpine valleys of the Gaspé peninsula in the province of Quebec.

Cuttings and insect epidemics in mixed spruce-balsam forests have fre-

quently been followed by dense crops of balsam fir, with the result that on these areas the percentage of spruce has been greatly reduced while at the same time the balsam fir has increased in volume on an enormous extent of country, and it has replaced to a large degree the more valuable pine and spruce. Examples of the primeval balsam forest still remain in the higher or less accessible areas; one of the finest is to be found on an upland plateau in the extreme north of Cape Breton Island. Hemlock was utilized extensively in the past for tan bark and the old trees are found now chiefly about pleasure resorts. A splendid stand of virgin hemlock still remains uncut in the centre of Nova Scotia, north of Lake Rossignal, a perfect fairy land of forest beauty. Larch virtually disappeared from our Eastern forests as a commercial tree many years ago, swept away by repeated attacks of the larch sawfly. To-day, a younger crop of larch is growing on an area that is possibly somewhat reduced in extent. The great black spruce belt across Northern Quebec and Northern Ontario still exists, although greatly reduced in area by lumbering, by extensive fires and by settlement along the transcontinental railway. Jack pine will always remain on sites of poorer soil and its total volume has been greatly increased in recent years as the result of numerous fires and lumbering. Cedar has been cut out to such a degree that very little is left of commercial size in the northern and northeastern sections.

The hardwoods have undergone many changes, but they cannot be described here in detail. The species with a present high commercial value have been greatly reduced in volume throughout the Canadian zone, while in the mixed forests of the same region birch and poplar have increased greatly in volume as a result of fires and lumbering.

The magnitude of changes on so vast a scale may be appreciated better by considering the history of the forest on a particular area. The Ottawa River drainage basin comprises an enormous extent of country all of which was originally covered with forest. The upper or western portion is still a forested country although the greater part of it has been cut over several times for lumber or pulpwood; the lower portion is an agricultural section, with many scattered towns and villages. Furthermore, the nature of the original forest and the history of the lumbering operations on the area are recorded with some degree of accuracy. The history of the forest in the Ottawa Valley, therefore, should illustrate fairly well the general situation.

The Ottawa River drains an area of 35,416,000 acres, of which about 28,000,000 acres are, or were, productive forest land. The original stand of saw timber is estimated to have been at least 500 billion board feet (about 125 times the present annual cut in the whole of Canada). It is believed that at least one half of this timber (250 billion board feet) was white and red pine; 45% (225 billion feet) was spruce, balsam and other softwoods, and

5% (25 billion feet) was hardwood. The present stand is estimated to consist of not more than 10 billion feet of white and red pine, 5 billion feet of other softwoods, and 4 billion feet of hardwoods, a total of 19 billion board feet (1).

In addition, there are perhaps 40 million cords of softwood and 25 million cords of hardwood of smaller sizes suitable for pulpwood, ties, posts, fuel, etc., or the equivalent of a little over 50 billion board feet of all sizes. The records which are available indicate that during the last 120 years the amount cut for use has been between 35 and 40 billion board feet. The balance, some 410 billion feet, has been destroyed, chiefly by forest fires, land clearing, insects and fungi (1).

In effect, the forested area of the northeastern portion of North America has been reduced in extent to an enormous degree and the timber values have been largely dissipated on a great proportion of the forest land that remains. Instead of the big timber of the past, we have small trees, species of lesser value, thousands of miles of pure forest land on which repeated fires have exterminated all species of commercial importance, and, in general, a forest which is at best hardly holding its own against the agencies which are still operating to destroy it, and containing timber supplies which will probably be insufficient for the needs of the next generation.

Nevertheless, there is still a great quantity of commercial timber in Eastern North America and a large amount of young growth which, if protected, will be invaluable in the future. There is still a great forest, one that is well worth protecting, and one that will yield vast returns if it receives the care from this generation that it deserves.

DESTRUCTIVE AGENCIES

The destruction of timber has resulted chiefly from five causes; from the activities of the settler and lumberman, from fires, insects, fungi and from windstorms and heavy snow. The deterioration in the remaining forest has been occasioned through the change to less valuable timber species following fires, cutting, and insect outbreaks; through unhealthy conditions produced in the remaining stands by cutting, and through the effects of injury by insects and fungous diseases. In this connection, it should be noted that many of the more destructive forest insects in the country have been imported from Europe through the agency of man, and the injury they have caused must be charged against man's activities.

Insect activities. In this reduction of the original forest, insect life has played a very prominent rôle, and one that has become increasingly important during recent times. It is, however, only one phase of forest insect activity. Insects which are considered "primary" enemies feed upon some part of the living tree and are potentially destructive. Most of the primary species

cause little actual injury beyond an occasional severe pruning; some are notoriously destructive and periodically occur in great outbreaks, while other species, usually of little or no economic importance, suddenly appear in widespread infestations. A second great category of forest insects includes "secondary" enemies, since they attack only dying or dead trees or wood products. In so far as commercial values are concerned, some of these species cause a vast amount of loss—sawyer beetles and others in fire-killed timber and saw logs and in log buildings, for example, or powder post beetles in stored wood products. In so far as the health and wellbeing of the forest is concerned, however, the "secondary" species are of importance chiefly as scavengers and are either beneficial or neutral in their effect on forest development. It is probable that the activities of many secondary species are extremely beneficial to the forest in hastening the death of overmature and weakened trees and thus liberating the young growth and also in accelerating the destruction of the debris on the forest floor. It is obvious that the destruction of the debris is essential to the health and natural development of the forest, particularly in facilitating the growth of seedlings and in providing plant food and a moisture-retaining layer of duff over the forest floor.

The most impressive effect of insect activities in the forest is the destruction of timber wrought by great epidemics of the primary species. There might be recorded a long list of major pests which have contributed their considerable part towards the destruction of the primeval forest; but only a few of the most destructive species have been selected to serve as illustrations and they have been confined largely to those affecting coniferous trees.

The Spruce Budworm (*Cacoecia fumiferana* Clem.). Perhaps the most striking example of insect destruction in the forest is afforded by the great spruce budworm outbreak of the last generation, which extended eventually over an enormous territory including the state of Maine and all Eastern Canada from the Atlantic Ocean to Central Ontario south of the great black spruce belt. It did not spread down the North Shore of the Gulf of St. Lawrence, and for some unknown reason it missed the Gaspé peninsula; but it missed very little else in all that vast territory, where balsam fir was growing.

The ravages of the budworm during the last 20 years, in which such enormous quantities of timber were killed, probably constituted the most destructive forest insect outbreak that has ever been recorded. It has been estimated that in Eastern Canada alone more than 200 million cords of balsam and spruce were destroyed. The vast amount of this loss can be better appreciated by comparing it with the losses caused by fires. It has recently been estimated by one of our most competent foresters that fires have destroyed balsam and spruce in Eastern Canada during the last 20 years

to the amount of approximately 70 million cords (1). The spruce budworm alone destroyed three times as much.

The adult insect is a small brownish moth which appears in July and lays its eggs on the needles of fir, spruce and hemlock. The caterpillars which hatch from the eggs go immediately into hibernation in minute silken cases on the twigs. In the following spring they appear when the balsam and white spruce buds are opening and feed upon the buds and young foliage, avoiding the old needles until the young twigs are destroyed. Balsam fir and red spruce are injured most severely, white spruce usually to a lesser degree, and black spruce is usually immune from very serious defoliation. After two or three years of severe injury, the older stands of balsam and red spruce begin to die and in the overmature stands the mortality may attain more than 90%. The younger and thrifty stands of balsam fir are usually able to survive without serious injury and on this fact the recommendations for control are based.

During the last generation, lumbering, fires and insect outbreaks have resulted in augmenting to an enormous degree the original quantities of balsam fir, and this tree will have a very prominent place in the pulpwood industry of coming generations. In the forests of New Brunswick, for example, one effect of the spruce budworm outbreak was to increase the percentage of balsam fir from about 50% in the old stand which was killed to 85% in the young crop which is now growing up (2). If great areas of balsam fir are permitted to become overmature, another and even more destructive spruce budworm outbreak may eventually be expected. On the other hand, if the remaining overmature stands are utilized and the young balsam cut on a short rotation, the forest should become very largely immune to destructive budworm outbreaks.

The Larch Sawfly (Lygaeonematus erichsoni Hg.). The larch or tamarac sawfly is a most destructive enemy of the American larch. The larvae feed upon the foliage, which may be more or less completely destroyed, and then go into hibernation in silken cocoons on the ground beneath the trees. It is possibly a European insect which was brought into this country in some unknown way, probably more than 100 years ago. A reference to an insect defoliating larch, published by Audubon in 1835 and recording an outbreak which occurred 25 years before, may possibly refer to this insect (3). The species was apparently described from Massachusetts, under the name *Nematus notabilis* Cresson, in 1860, but it was not reported as a widely distributed and injurious insect until about 20 years later. In the years immediately following 1880, the sawfly developed into a tremendous outbreak extending throughout all Eastern Canada and the New England States from Nova Scotia and Maine to the Great Lakes. By 1890, nearly all the larch of commercial size

in Eastern Canada had died as a result of this attack. More recently, the outbreak has spread westward past the Great Lakes and north of the prairies into British Columbia and the Yukon, so that the sawfly now covers almost the entire range of the eastern larch.

The young stands of larch which have grown since the original outbreak occurred are now approaching commercial size. The sawfly has been varying in abundance on these young stands, but not to a destructive degree, and during the last few years its numbers have been greatly reduced. In the years 1911, 1912 and 1913, a European parasite of the larch sawfly (*Mesoleius tenthredinis* Morley) was imported into this country from Britain and distributed in several places in Eastern Canada and Manitoba. This parasite has become established and has recently been recovered as far as 200 miles from the place of liberation. An attempt has been made to spread the parasite more widely in Eastern Canada, but during the last 10 years there have been no larch sawfly outbreaks in Europe from which they could be obtained, and for the last two years there have been none in Eastern Canada.

How much the imported parasites have had to do with reducing the numbers of the sawfly cannot yet be determined. It is possible that native parasites may have recently become more effective.

The Larch Case-bearer (*Haploptilia laricella* Hb.). For the past three years another defoliating insect, also of European origin, known as the larch case bearer, has spread in a severe infestation on larch stands throughout the Eastern forest from Nova Scotia and Maine to Central Ontario. The needles are mined and killed by the small caterpillars and the outbreak has been so intense that in 1932 apparently most of the larch from New Brunswick to Algonquin Park in Ontario was almost completely defoliated. After the foliage has been destroyed by the caterpillars a second crop of needles is produced, and on this account previous outbreaks have not proven to be destructive. The present outbreak by the case-bearer, however, is apparently the most severe that has ever been experienced in this country, and it hardly seems possible that the trees could long withstand such severe attacks uninjured.

The Eastern Hemlock Looper (*Ellopiia fiscellaria* Guen.). In the years 1925 to 1928, defoliating caterpillars known as the eastern hemlock looper, destroyed a large amount of hemlock in Wisconsin, Minnesota and Central Ontario. In the Lake States the same species attacks balsam fir, and it has long been known as a destructive enemy of that tree on the island of Newfoundland. In Ontario, however, in so far as we know, the looper has confined its attacks to hemlock, and until recently this had apparently been the case in the province of Quebec. In the year 1928, extensive outbreaks on balsam occurred on the North Shore of the Gulf of St. Lawrence. The out-

breaks lasted for three years and disappeared. More than 100 square miles were affected in three large river valleys.

In 1929, an airplane dusting operation was carried out on one infestation and the caterpillars were almost completely destroyed. The outbreak subsided in another valley in 1930 and in the third a year later. Cold, wet weather in early summer apparently was effective in destroying great numbers of the young caterpillars in the last two outbreaks, and may have been the chief influence in reducing the outbreak in those districts.

Bark-beetles. An extraordinary amount of injury has been caused in North American forests, particularly in the West, by the small beetles known as bark-beetles. Although many species of these insects occur in eastern forests only a few are of primary importance. The chief of these is the eastern spruce bark-beetle (*Dendroctonus piceaperda* Hopk.) which is now causing extensive injury in the Gaspé peninsula of Quebec.

The brown or black beetles, one-third of an inch long, breed only in the bark of spruce, chiefly in white spruce and red spruce. The vertical egg-tunnels, four to six inches in length, are cut between the bark and the wood on the trunk of the tree. In living trees the flow of sap is quickly checked and the death of the tree results very rapidly. Under normal conditions in the forest this species breeds in weakened or dying trees, in windfalls and in logs; but when their numbers become very great they readily attack and kill healthy trees and they have in the past destroyed large quantities of the finest white and red spruce in the eastern forests. Their outbreaks appear to have a certain periodicity, and we are now experiencing a series of attacks by this species in the forests of Quebec and in the Maritime Provinces.

The Balsam Woolly Aphis (*Dreyfusia piceae* Rtzb.). A species of bark infesting aphid, known as the European balsam woolly aphid, was imported from Europe into Eastern North America many years ago. It has been found affecting balsam fir in the Maritime Provinces and in several places in the Eastern United States, but it has increased most abundantly in Nova Scotia, New Brunswick and Maine. It is now spreading northward through New Brunswick and will possibly become distributed eventually throughout the balsam forests of Eastern North America. The insect is a minute plant louse with the body covered by white, wool-like, wax threads; it lives on the bark of the trunk or twigs and sucks the sap through the long slender beak which penetrates deep into the bark. When the insects are abundant, wool-like patches appear on the trunks of balsam fir, the only tree on which it occurs. This species kills the trees directly, but the most serious effect of its feeding occurs on young stands in which it produces a malformed growth, called the balsam gout, that may completely ruin or even kill the trees. In European forests this species is not considered to be of major importance, and it is evident that

the North American balsam (*Abies balsamea* (L.) Miller) reacts much more strongly to the insects' attack than do the European species, both in regard to the injury to the trunk and to the malformation of the young trees and growing tops. The form affecting the buds and twigs has been distinguished in Europe under the name *D. piceae* var. *Bowieri* Chol., and its effect on exotic species of *Abies* is said to be more serious than it is on native European species.

Certain species of agromyzids are being brought from Britain for distribution in the Maritime outbreak.

The European Spruce Sawfly. In 1930, a large area of white spruce in the Gaspé peninsula was found to be affected by a defoliating sawfly larva which was subsequently determined to be *Diprion polytomum* Hartig, a native of central and southern Europe where it is of but little economic importance. It is assumed that the insect has been introduced into this country sometimes during the past generation. Although so abundant in the Gaspé, this sawfly has never been recognized elsewhere in Eastern Canada, except that one specimen collected near Ottawa in 1932 is now believed to belong to this species. Several specimens were taken in Maine in 1931 and in 1932 and it was recorded from one other locality in the New England States in 1931.

Biological investigations, ground surveys and an aerial survey were carried out on the Gaspé outbreak in 1931. The infestation then covered the entire central area of the peninsula, with the severest degree of attack confined to the upland valleys of the interior. In 1932 the outbreak continued in severity in the central area and increased over a considerably extended range. In the most heavily infested valleys, the white spruce is now severely defoliated, with a noticeable retardation in growth extending over about four years. There is little doubt that much of the timber is badly weakened, although only a very few trees have yet been killed by the sawfly. There is every reason to expect that the outbreak will continue, although with less severity, in 1933, and the black spruce is now being attacked in some places as readily as is the white spruce. The larvae feed only on the old foliage, leaving the young twigs of the current year practically untouched, and this fact probably explains the ability of the trees to withstand the defoliation. The larvae hibernate in cocoons on the ground beneath the trees, and during the last two years considerably more than 50% of the cocoons have carried over the summer to the following year. This habit is of particular importance inasmuch as mice and shrews have thereby a continuous opportunity to feed upon the larvae. During the past two years these animals have destroyed more than 40% of the hibernating cocoons and they are at present the most important factor in control. Only a few parasitized larvae have been found.

Males are practically unknown, a fact which is probably significant in connection with the rapid increase of the outbreak.

During the past summer an effort was made to obtain parasites of this species in Central Europe and a supply will be available for distribution in the Gaspé outbreak in the spring of 1933. Inasmuch as native parasites have not yet attacked the sawfly, the introduction of the original parasites from Europe should prove to be beneficial; it is at all events the only forward step toward control that appears to be feasible at the moment. It has been determined that the sawfly succumbs readily to calcium arsenate and we have learned how to dust forests by airplane. When financial conditions become more favourable, airplane dusting may be employed to protect the most valuable stands.

The Black-headed Budworm. In the summer of 1929, a large area of balsam forest, some 200 square miles in extent, in the southern part of Cape Breton island, was found to be heavily infested with caterpillars of the black-headed budworm (*Peronea variaria* Fern.), a species with a method of feeding closely similar to that of the spruce budworm. The species had previously been exceedingly rare in Eastern Canada, only a few specimens having ever been collected. In 1930, some 500 square miles of territory were covered by this infestation; in 1931 the larvae were reduced to one-tenth of the number in 1930 and the infestation subsided at the end of the season; in 1932 it has practically disappeared.

The European Beech Scale (*Cryptococcus fagi* Barensp.). The European beech scale is a minute sap sucking insect covered with wool-like wax threads. It feeds on the bark of beech, whose trunks become covered with wool-like patches of the insects when the latter are very abundant. When followed by certain bark infesting fungi (*Nectria*) this species is very destructive to the American beech. It was introduced into Nova Scotia many years ago and has since spread throughout all parts of that province and throughout the southern part of New Brunswick, causing a very heavy mortality in beech stands. It occurs also in the New England States, although not yet in Quebec or Ontario. It will probably kill a large proportion of the beech in parts of Eastern North America where the species of *Nectria* which can follow it happens to be present.

The examples that have been presented include a few of the most injurious and more interesting of the major pests of the eastern forests, but the list could be extended to include many species, some of which, like the white pine weevil, are perennial in their depredations, whilst others spring into importance only at long intervals as the cause of extensive infestations.

Indirect Effects of Insect Injuries. An important effect of insect outbreaks is the reduction in the growth and health of the affected timber. Even

though little actual mortality be caused, an extensive infestation may result in an enormous unseen loss through the reduction of diameter and height growth in the timber as well as in an unthrifty condition of the stand. The present great outbreak of the larch case bearer can hardly fail to produce such an effect. Judging by investigations made in Maine, Connecticut and New Brunswick, the infestations of defoliating insects, *Bucculatrix canadensisella* Chamb., *Phyllotoma nemorata* Fallen, and *Fenusa pumila* Klug, on birch, which now extend from the Atlantic coast to the Great Lakes, have already produced both these results, particularly in the Atlantic coast region where the injury has persisted longest and has been most severe. The spruce budworm outbreaks caused an enormous loss in the reduction of diameter growth in stands which eventually recovered a fair degree of health.

When one considers the total mortality in the forest caused by the major insect enemies and, in addition, the depreciation in forest values caused by changes in forest composition following insect outbreaks, and the reduction in growth and health of the forest which has resulted directly or indirectly from insect damage, it becomes apparent that the effects of insect attack on the forests of Eastern North America have been tremendously injurious and that the prevention and control of injuries caused by forest insects constitute a problem of vital importance in forest protection.

INTERRELATIONS BETWEEN INSECTS AND THE FOREST ENVIRONMENT

The investigation of great forest insect outbreaks is continually extending our knowledge of the relations between the insects and their forest environment. An investigation of this kind may include within its scope the study of a large part of the forest complex, together with the climate and soil conditions of the district. The interrelations of the insects with any of the other components of the forest or their responses to climatic or other environmental factors may be intimately concerned with the progress of the insect epidemic, or, in a more general way, may affect the health or development of a portion of the forest itself. The present discussion of these relationships and of the factors which influence the economy of forest populations must necessarily be very brief, but some of the problems involved therein are of great interest and importance in any general consideration of forest development.

A thousand fascinating relationships exist between the insect fauna and the other life of the forest, between the insects and their host plants, their insect parasites and predators, the birds, mammals and other animal life and the fungi.

Insects and Their Host Trees. Some insects feed on only one or a few closely related species of trees, whilst others readily attack a wide range of host plants; some attack bark or wood only when it presents certain definite

physical or chemical characteristics and others appear to be much less particular in their choice; some species follow their host trees throughout the latter's range on the continent and other species are confined by climatic or other factors to a comparatively narrow area. The destruction of great quantities of a primary host in a region may result either in the virtual disappearance of an insect species or in forcing it to concentrate on secondary hosts.

Insect Parasites. The relations of forest insects to their parasites have received a great deal of study. Many attempts have been made to effect the control of introduced pests through the introduction of their native parasites. Successes and apparent failures have attended these efforts, but certain of the successful ventures have been so impressive that this method of establishing a natural control for introduced insects is being generally applied. In addition to the specific parasites of the introduced pest, it may sometimes be profitable to import the same species of parasite or even different species with suitable life-histories from other species of hosts. An interesting situation is now appearing in that parasites which were established in a district for the control of an imported insect are proving to be of service in checking the subsequent invasion of other species.

The utilization of native parasites through their multiplication and distribution for the control of outbreaks of native forest insects has received much less attention. Some extensive outbreaks of native defoliating caterpillars have evidently been controlled by parasites, and the possibility of utilizing parasites in such cases should be further explored; but in the case of many serious forest infestations the degree of parasitism has rarely become high enough to be considered of great importance. The effect of parasitism with many forest species is probably to check the multiplication of the host beyond the endemic condition and to lengthen the time between outbreaks.

Insect Predators. The insect population serves as a necessary food for birds and mice and even for fish in the lakes and streams. On the other hand, both birds and mice exert a certain, if usually minor, controlling influence on insect multiplication. Woodpeckers, for example, have destroyed as much as 90% of the broods of *Dendroctonus piceaperda* in small outbreaks. They are probably effective at times in controlling sporadic outbreaks and in hastening the decline of more extensive ones, although they are usually of little importance at the height of great infestations. Mice and shrews destroy large numbers of insects which hibernate in the debris on the ground surface. These animals have apparently been helpful, for example, in reducing some larch sawfly infestations and during the past two years they have destroyed approximately 40% of the hibernating larval cocoons of the European spruce sawfly in the Gaspé peninsula. Spiders, ants, wasps, syrphus flies, clerid

and carabid beetles, and others are sometimes of local importance in checking the increase of injurious forest species.

Forest Insects and Fungi. Forest insects and fungi have many interrelations. Insects are sometimes responsible for facilitating the invasion of the bark and wood which they attack, by species of parasitic fungi. Such a relation exists between *Cryptococcus fagi* Baren. and the *Nectria* which follows its attack on the bark of beech and which eventually kills the trees. On the other hand, entomophagous fungi and other organisms are sometimes effective in destroying many insects and may even become an important factor in the control of rather extensive outbreaks.

A very interesting association between certain bark-beetles and fungi causing blue stain in the trees attacked by the beetles has been brought to light recently on this continent by the studies of Dr. Craighead and Dr. Rumbold (4). It has been demonstrated both in Europe and in America that where they are introduced artificially into the inner bark and cambium the fungi are able to kill the trees without the aid of the beetles. It is probable also that some species of *Dendroctonus* would kill the trees without any assistance from the fungi. It remains to be proven whether the beetles or the fungi receive the greater benefit from this partnership. These studies have opened a field of great scientific interest and with possibilities of application in practical control.

It is apparent that the tunnels of bark and wood boring insects must aid in introducing the spores of wood rotting fungi into stumps, fallen trunks and other debris on the forest floor, but there is little exact information yet available on this subject.

A remarkable case of symbiosis exists between certain wood boring beetles, known as ambrosia beetles, and definite species of fungi, called ambrosia fungi, which invariably accompany the beetles in their tunnels, clothing the tunnel walls with a luxuriant growth of conidiophores during the time the larvae are developing. A few of these beetles attack living trees and are of some importance in the forest economy; *Corthylus*, for example, injures hard maple seedlings, and several species on this continent are injurious to commercial timbers. These fungi, therefore, upon which the beetle larvae are solely dependent for food, also play a definite part in the forest development.

The ambrosia beetles excavate slender tunnels deep into the wood of the trees they inhabit. The hyphae of the fungus penetrate the cut cells and the vessels for several millimeters and eventually stain the tunnel walls dark brown or black, but they cause no other injury to the wood. The forest of conidiophores which projects into the lumen of the tunnel, in the case of many species, serves as the sole food of the larvae and forms an important

food of the adult beetles. On the other hand, these species of fungi have been found only in the tunnels and in the alimentary canal of the beetles. A perfect case of symbiosis appears to have been established.

Shortly after the tunnels have been commenced, germinating thick-walled spores are found on bits of excrement on the walls of the tunnels, and the hypae, growing rapidly, produce vertical chains of conidia which ripen terminally as large thin-walled spores. These latter are distributed by the beetles over the tunnel walls as fast as the excavation proceeds and, germinating rapidly, they give rise to hyphae which speedily cover the tunnel walls with a dense forest of erect conidiophores like the pile on velvet. The thin-walled spores of the species I have studied go through the conidial cycle in drop cultures in about 60 hours. Within a very few days the production of thin-walled conidia ceases and thereafter only the thick-walled spores are produced. The latter will germinate, apparently, only after having passed some time in the alimentary canal of the beetle. Several genera and a considerable number of species of these fungi accompany the ambrosia beetles of North America, but none has yet been described. Many interesting relationships exist between different species of beetles and the particular food fungus which accompanies them. A somewhat similar fungus association is found elsewhere among insects, notably with certain gall-making species and in the coleopterous family *Lymexylidae*.

FACTORS INFLUENCING OUTBREAKS

One of the most important inquiries before entomologists to-day concerns the causes which influence the rise and fall of great insect outbreaks. Definite facts have been learned respecting the decline of a few insect epidemics in the forest, but too little is known of this subject as yet to justify much generalization.

Forest epidemics are usually well advanced before the entomologist has an opportunity to commence his studies. It has rarely happened that a great forest outbreak has been investigated throughout its full course, and it is partly owing to this situation that our knowledge of the factors affecting the rise of outbreaks is even more meagre than that of those causing the decline. There is much valuable information to be gained by an intensive environmental study of injurious species throughout the complete outbreak cycle, from the peak of one outbreak throughout the years until the peak and decline of the next.

The causes behind the rapid increase or decrease of insect populations must usually lie in the field which has been termed, very aptly, the "environmental resistance." There are at present two great difficulties in dealing with this matter, one being our lack of knowledge of definite facts, and the

other that many of the factors may change very greatly from one outbreak to another and from one season to the next.

It is probably too early to make definite statements regarding the constancy of the factors in the biotic potential, but it is very apparent that those of the environmental resistance vary so greatly that it is useless to attempt an estimation of the total resistance in the case of a field problem from data obtained in a previous investigation.

Some forest species are probably held in check effectively by parasites and predators. Some outbreaks of forest tent caterpillars have been controlled by flacherie, and others by a combination of parasites and fungi. On many occasions native parasites and diseases have been among the most evident factors in controlling severe outbreaks of certain forest insects, and they appear to be responsible, in some cases in large measure, for producing the phenomenon of periodicity in connection with infestations.

Climate and Weather. The influence of weather and climate in regulating the distribution and the activities of insects is of great importance. Forests, in general, have climatic characteristics which differ in many respects from those obtaining in the open country. The work of Lorenz-Liburnau and others in Europe and that of Fernow and Zon in America has brought out many features of the forest climate which are gradually being applied to the study of insect life in the forest. Whilst the general effect of the forest cover is one of moderation and equalization of extremes, there are several phenomena peculiar to forest conditions which appear to have a special significance. Such are the reversal of temperature gradients in the spring and fall, the increased precipitation over forested areas, and the retention of humidity under the forest cover. This study is still in its infancy but it holds considerable promise for the explanation of such insect activities as the vertical distribution of species, migration into and out of the forest, and variations in life-history and habits.

Differences in light and in air circulation appear to have a marked effect on many species. In many instances, particularly in the study of boring species, the micro-climate requires thorough investigation. Undoubtedly, insects have become inured, to some extent, to many fluctuations in weather conditions, but these fluctuations are often sufficiently great to produce significant effects on density of population, local distribution, or modification of life activities.

Many outbreaks of defoliating caterpillars have apparently been controlled by cold, wet weather affecting the first few larval instars; or by heavy beating rains at the time of pupation, after the protecting foliage had been destroyed; or by starvation through exhaustion of the food supply; or by certain other conditions which have been fairly well established in the cases

of definite outbreaks. On the other hand, peculiar climatic conditions may favour the development of great insect outbreaks. The appearance of extensive bark-beetle infestations following periods of excessive dryness is a case in point.

Changes in Species Virility. The epidemic of the black-headed budworm in Cape Breton island, already mentioned, presented interesting features in connection with the cause of its decline. The outbreak was discovered in 1929 on some 200 square miles of territory. The infestation was so severe that the trees were reddened over a large part of this area, although an inspection of the same district in the previous summer had disclosed no such injury. It is evident that the outbreak developed with great suddenness and apparently in one season. In 1929 the eggs were extremely abundant, although the average number laid by the females was not ascertained. In 1930 the outbreak had spread over almost 500 square miles; but, although the moths were very numerous, they laid very few eggs either in the open or in the cages, the average per female being only about six in the several conditions under investigation. In 1931, the infestation was reduced to somewhat less than one-tenth the numbers of 1930, and parasites and disease destroyed the caterpillars so extensively that an average of less than one moth per tree was obtained on the areas studied. In 1932, the outbreak had disappeared and no trace of fresh defoliation could be found.

It is a temptation to speculate with even these meagre data. If the oviposition average in 1928 and 1929 had been 100 or more (which may very well have been the case since dissection showed the females to be capable of laying as many as 150 eggs and it is known that the oviposition in 1929, at least, was extremely heavy) the evident decrease in the oviposition of the females over a large extent of territory would explain the rapid decline of the outbreak. The weather conditions of that district during the spring months of 1927-1929 varied only very slightly from the normal and could hardly have affected oviposition to any marked degree.

The comparison by J. J. deGryse (unpublished report), of a large amount of carefully compiled data obtained during three years succeeding the peak of an outbreak of the maple leaf cutter (*Paraclemensia acerifoliella* Fitch) shows a yearly increase in the general debility of the strain. The eggs, although normal in the average number laid per female, showed a yearly decrease in the number hatching. The larvae showed a yearly increase in mortality while in the mine, a very definite yearly increase in the length of the second stage—and this in an increasing percentage of individuals—a similar progressive increase in the length of the third and fourth stages, with, as an ultimate result, a high percentage of mortality which appeared to be due solely to congenital weakness. This weakness was further manifested

throughout the life of the individual by a lack of ordinary activity, such as slow and irregular feeding.

The suggestion is made in a report (unpublished) by Norman Criddle and R. H. Handford concerning a recent outbreak of the Bertha armyworm (*Barathra configurata* Walk.) in Manitoba that the sudden termination of the outbreak appeared to be accompanied by a somewhat similar decrease in virility.

This insect, which had been of local annoyance in Saskatchewan for a number of years previous to 1927, began in that year to increase in Manitoba, and by 1929 it had become so abundant that large areas of sweet clover and flax were destroyed. Its activities at this time extended from Manitoba and North Dakota to British Columbia. Then, in 1930, after hatching in large numbers, the species suddenly dropped into insignificance. At the Treesbank laboratory, a study of the insect was being made at the time and a number of larvae were under observation, most of which had been reared from the eggs. The eggs proved to be mostly fertile and definite numbers of larvae were obtained and fed on sweet clover, one of their favourite food plants. They were reared under similar conditions to others which had reached maturity in 1929, yet despite every attention these larvae all perished. A few died in the first instar but most of them survived until the second or third stage. As they increased in age they steadily became more sickly, extended on beyond the period of normal moulting and finally died. This behaviour occurred not only in the laboratory but observations in the field showed that the larvae were behaving there in a similar manner and finally the entire outbreak collapsed. Scarcely a larva was present in 1931.

It should be added that while both parasites and diseases were present, these in combination did not account for more than 20% of the larvae. Thus the rapid subsidence of the outbreak seems to have been wholly due to a physical weakness in the larvae. Whether this weakness was brought about by weather or by some other factor or a combination of agencies was not determined.

The subject of virility of the strain is exceedingly complex and offers apparently a promising field for research. There is the possibility, particularly following the peak of an outbreak, of a subnormal sexual fertility appearing in either sex which may be disclosed by a reduction in the number of fertile eggs laid by the females, or a congenital weakness which may result in egg mortality and lengthening of the larval stages with greater susceptibility to disease and higher mortality. The same final results have evidently been caused by inclement weather conditions. The question of a reduction in the virility of bark-beetle broods during the latter part of an outbreak has been the subject of investigation recently by European workers, and data on the

same subject are being collected on this continent. A sudden increase in virility, on the other hand, may be a major factor in the sudden rise of some outbreaks.

Food Supply. The abundance of a suitable food supply is obviously necessary before a great insect infestation can develop, but vast supplies of the preferred host of an insect have existed for long periods before very extensive trouble of this kind has developed. Under such conditions, small outbreaks have occurred here and there over the forest during long periods and suddenly, from several distant points of origin, a series of outbreaks have developed and in some instances merged into a great infestation. This is, in effect, the history of the spruce budworm outbreak of Eastern Canada and Maine. There was unquestionably a vast food supply of balsam fir in the forest regions between the Atlantic Coast and Central Ontario. Extensive cuttings and fires during the previous generation had favoured the increase of balsam over the southern part of this area; but that could hardly be said of the northern portion, and it was in the north, between Lake Expansé and Lake Manawan, in northern Quebec, that the earliest outbreaks are supposed to have occurred.

During the previous century, a series of budworm outbreaks, some of them of considerable size, had occurred in the forests of Maine, New Brunswick and Southern Quebec, but there are no records for that period from Northern Quebec and Northern Ontario. There was an immense amount of balsam fir in the Gaspé peninsula and along the North Shore of the Gulf of St. Lawrence, yet the budworm outbreak did not develop in either place. The extensive upland plateau in northern Cape Breton island has carried a pure stand of balsam, probably for countless ages, and yet, although the budworm occurs in that stand and has even been reported as rather abundant at times in the northern portion, no budworm outbreak of any importance has left any record of its occurrence.

The hemlock looper is a common insect in the forests of New Brunswick and Nova Scotia; both balsam fir and hemlock occur there abundantly, and the climatic conditions are probably more favourable there than in Newfoundland or on the North Shore of the Gulf; nevertheless no important outbreaks of this insect have been reported from the Maritime Provinces for many years.

The food supply, such as extensive pure stands or rich mixtures, is a pre-requisite for an outbreak, and under our forest conditions such stands are constantly in danger, but the cause of the outbreak must be sought elsewhere.

The Influence of Forest Types. The abundance of forest insect epidemics in recent years has been ascribed sometimes to the alterations in forest types which have resulted from man's activities. On this continent so much injury

has occurred in virgin stands and in both mixed and pure stands which have resulted from cutting operations, that the planted and managed forests of Europe have been looked on with envy in the past in the belief that they were less susceptible to insect attack. On the other hand, European forests have suffered so severely from insect depredations that foresters and entomologists in Central Europe formed the opinion that their insect troubles were due largely to their artificial and managed forests and for a time they thought with envy of our virgin stands and mixed forests as being immune from great insect outbreaks. Large areas of forest containing only one or two species are considered to favour the development of outbreaks by certain insects and, other things being equal, it will probably be best to encourage the growth of mixed forests in so far as management can effect it. It should be noted, however, that overmaturity of the stand has been responsible for much of the mortality during recent insect outbreaks in pure stands, and, also, that there has been some evidence that insects which usually inhabit pure stands by preference may be able to adapt themselves readily enough to the conditions in a mixed forest. There is probably little reason to have much confidence in the general immunity of any type of stand, although certain types certainly have an advantage with respect to particular insect species.

A rather peculiar case of natural protection has occurred in a larch forest north of Belleville in Ontario. This forest is more than a mile long and nearly as wide, and is composed mainly of larch growing in a wet alder swamp. The water table is at the ground level throughout the year, except for a short period in midsummer, and for that reason larch sawfly cocoons have probably not been able to hibernate successfully. The trees vary in age in the main stand from 90 years to 216 years, and consequently they have escaped completely the larch sawfly outbreaks. A similar case has been reported from Eastern Manitoba and Graham has referred to other instances observed in the Lake States.

Groups of Outbreaks. It is somewhat peculiar that several or many outbreaks of the same species of insect sometimes arise at nearly the same time on widely separated areas. The spruce budworm outbreaks have already been mentioned. The outbreak of the black-headed budworm (*Peronea variana*) in Cape Breton island, was paralleled by an outbreak of the same species on the coast of British Columbia and in parts of Western United States. The series of outbreaks by the hemlock looper at nearly the same time in the Lake States, Ontario, and the North shore of Quebec, already described, and recent outbreaks of the Douglas fir tussock in Western United States and British Columbia afford other striking examples.

The eastern spruce bark-beetle (*Dendroctonus piceaperda*) appears in outbreaks, periodically, from the Atlantic Coast to Northern Alberta. Two

such periods of infestation are recorded and several others are to be inferred from the older records. In the last instance outbreaks occurred in the Gaspé peninsula, Nova Scotia, New Brunswick, Central Ontario, Manitoba and in Northern Saskatchewan, all within a few years of each other. At the present time there is an extensive outbreak in the Gaspé peninsula and smaller infestations in parts of Nova Scotia, although for the previous few years there had been no outbreaks reported. If history repeats itself in this instance, we shall discover outbreaks of this beetle in Ontario, Manitoba and Saskatchewan within the next two years.

For the last few years there has been an unusual abundance of various sawfly species in Canadian forests. The larch sawfly was increasing in the East until two years ago and has since declined; the spruce sawfly of the Gaspé is a new occurrence; there have been three hitherto unknown species of jack pine sawflies concerned in an extensive outbreak in Central Ontario and a new species had just before been recorded defoliating jack pine in Minnesota; the fir sawfly occasioned the most extensive outbreak ever recorded in Canada for that species in the Sault Ste. Marie district in 1930; an undescribed species of sawfly has been defoliating hemlocks in Queen Charlotte islands for the last two years; and a considerable number of other species might be added to the list. Climatic conditions in these widely separated regions are so diverse that they could hardly favour the development of the same insect at so nearly the same period of time, and in any case, how shall we explain this extraordinary plague of sawflies?

Periodicity. Certain of our well-known forest insects have appeared in extensive outbreaks at more or less regular intervals. The tent caterpillars, the fall webworm, and the birch leaf skeletonizer will serve as examples. During the last 40 years, extensive outbreaks of the birch leaf skeletonizer have occurred in the forests of Eastern Canada at intervals of almost exactly 10 years, and have lasted approximately three years before subsiding. In the case of some insects, the parasites, predators and diseases appear to play a part in maintaining this periodicity; with others the outbreaks may be dependent on the development of a new food supply, either through growth or by the overthrow of timber in windstorms, or by other causes which may present a measure of real or apparent regularity.

A striking correlation has been shown by Criddle (5) to obtain between sun spot maxima and the greatest abundance of both grasshoppers and grouse on the Canadian prairies during the last 40 years. The possible relation between the sun spot phenomena and insect abundance is evidently deserving of a much wider investigation than it has yet received.

No combination of the known agencies appears to be sufficient to explain all the phenomena involved in the development of groups of outbreaks and

periodicity, and it is possible that there is some factor influencing the rise of great insect outbreaks that has not yet been discovered.

In the whole field of Entomology there is probably no subject of deeper scientific interest or of greater practical importance than the general question of the causes underlying the appearance and progress of great insect epidemics. Hidden among its secrets are the possibilities of forecasting outbreaks and taking measures for their prevention or mitigation, predicting their progress and providing for control or salvage, and laying intelligent plans of management for obtaining a measure of insect immunity.

The factors involved and their interrelations are manifold. Any component of the forest may be concerned in the matter, as well as various influences from without. The study will draw upon all the resources of Entomology—Taxonomy, Morphology, Biology, Bionomics—and extend into other sciences, but it is primarily a study of the forest environment. If every opportunity is taken to prosecute the study of forest insect bionomics, the gradual accumulation of data eventually may enable many of these problems to be solved.

Variation in Habits. Variations in the factors of the environmental resistance are able to effect significant changes in the habits of the same insect species. A few interesting examples of varying habits have been met with in recent investigations and many others are recorded here and there in the literature. Referring again to the spruce budworm, it was found that throughout the greater part of the eastern outbreaks the larvae hibernated in tiny silken cases on the twigs, and, appearing in the following spring at the time the buds of the balsam fir and white spruce were opening, they killed a large percentage of the buds and the new shoots before the latter had time to develop. This was a marked characteristic of the species everywhere, except in the island of Cape Breton. In that interesting country, the budworms emerged from hibernation after most of the buds had burst and the shoots had commenced to lengthen, with the result that the new shoots grew to nearly their normal length, the buds for the ensuing year developed normally at the tips, and the larvae merely stripped off the needles leaving the new twigs completely bare of foliage. Under these conditions the outbreak lasted apparently for about 15 years, instead of dying out in about 3 years, partly through starvation of the caterpillars, as had happened elsewhere.

In the cold, wet spring climate of that region, the cold and humid air conditions apparently retarded the development of the larvae without affecting so greatly the growth of the buds, so that a large proportion of the shoots were well started before the larvae appeared.

This outbreak disappeared finally under rather unusual conditions. Throughout our studies of the spruce budworm, parasites were found usually

to play a minor role. In the Cape Breton outbreak, however, as in a few other localities, the parasites were rather more numerous than usual, and in 1927 the parasitism suddenly increased to more than 80% and the outbreak disappeared.

On a high plateau in northern British Columbia, some 3000 feet above the sea, a spruce budworm outbreak has been in progress for a considerable number of years in a forest composed of mountain balsam and Engelmann spruce. In that cold, wet climate, with frequent heavy rains throughout the summer, the budworm larvae develop in the first season of feeding to only the third or fourth stage without causing much defoliation, and go back to the twigs at the end of the season, spin a second hibernating cocoon, and pass the second winter therein. In the following spring they attack the foliage vigorously, causing a noticeable defoliation, and complete their course of development. The eggs are laid in the normal way and in the following year the larvae reach only the third or fourth stage as before.

There is in this case a two-year life cycle with noticeable defoliation appearing in the alternate years. The trees were not being killed by the budworm and the outbreak had apparently lasted for a considerable period of time.

The mountain balsam bark-beetle, *Dryocoetes confusus* Sw., is killing the timber in that forest rapidly and it exhibits a peculiar habit in cutting a second egg-tunnel as an extension of the first without the labour of excavating a new entrance hole, a habit which may also be related to the climate.

Throughout the province of Quebec and the Maritimes the spruce budworm injury occurred chiefly in pure stands of balsam and spruce. In mixed stands of hardwoods and balsam, the defoliation appeared mainly on the balsam tops which projected above the crown cover of hardwoods and, as a consequence, mixed stands were considered to be largely immune from severe budworm injury. They appeared to be so in Quebec and the Maritimes; but when the budworm outbreak developed later in Central Ontario, the balsam fir beneath hardwoods in mixed stands was destroyed to a very high degree. It is therefore far from certain that mixed stands of hardwoods and conifers will be immune against future budworm invasions.

In all the infestations which have been studied in Eastern Canada, the spruce budworm fed chiefly upon balsam fir and spruce and rarely fed at all on the foliage of jack pine. In the Lake States, however, there is a budworm which is considered to be the same species that feeds by preference on the needles of jack pine, and in Wyoming there is another which prefers the foliage of lodgepole pine. In one section of the Cape Breton island outbreak, the spruce budworm showed a preference for swamp spruce, which was being

killed by the defoliation, although clumps of balsam fir in the same stand were but slightly injured.

The white-marked tussock is a common enemy of elms and other deciduous trees and is found occasionally feeding on balsam fir and larch. In 1928 and 1929 two outbreaks of this insect occurred in Nova Scotia on balsam fir in which the trees were heavily defoliated over an area of many acres in each case.

The food preferences of insects have been completely changed under pressure in experimental work, and there is some reason to assume that the same result may have been produced under natural conditions in the forest.

Host Selection. A very definite preference in the selection of their hosts is exhibited by many forest insects. In fact, many species breed normally in only one or at most a very few species of trees, and this preference is so strongly fixed that they can be forced to breed in other hosts only under pressure of very unusual circumstances. In the case of insect species which have only a few closely allied host trees it has sometimes been assumed that the individuals which had bred on one of the host species showed a distinct preference for the same species either for food or for the purpose of oviposition. This assumption often appears to be a logical one and has not been without the support of evidence in a number of cases. It cannot, however, be accepted yet as an established principle that has general application. The habit of each insect species requires to be studied in that regard on its merits, and there is some reason to suspect that certain species will exhibit considerable variation in the strength of their preference. The difficulties that may be met with in studying this subject are exemplified by the case of the mountain pine beetle (*Dendroctonus monticolae* Hopk.), in lodgepole pine and yellow pine in Western North America. Workers in California and Oregon have held the view that an outbreak of this species occurring in a lodgepole pine forest was not likely to spread into a neighbouring stand of yellow pine for the reason that the beetles, having bred in lodgepole pine, would almost certainly attack only that tree, at least until the lodgepole stands were destroyed. Naturally, there was evidence to support this view.

On the other hand, workers in British Columbia have long been convinced that in the forests of that province outbreaks of the mountain pine beetle have on numerous occasions developed in lodgepole forests and have spread down the slopes and into the yellow pine stands below. It is difficult to obtain conclusive proof under field conditions, but a study of the development and extension of these outbreaks in British Columbia, extending over a period of many years, has convinced entomologists there that outbreaks of these beetles in lodgepole pine spread readily enough into yellow pine in the neighbourhood.

Experimental work with large cages has disclosed no evidence of any decided host selection. Infested lodgepole pine logs were enclosed in cages with an equal number of freshly cut lodgepole pine and yellow pine logs, and infested yellow pine logs were treated in the same manner. Several of these cages were employed in each of three successive years. In no instance was any preference shown. The beetles which emerged from yellow pine or from lodgepole pine went in approximately equal numbers into the yellow pine and into the lodgepole pine logs provided in the cages. It should be noted that this beetle breeds readily enough in cages of the type employed in the experiments, and there is, therefore, little reason to suppose that the caged conditions distracted them from the exercise of any normal preference.

It seems probable that the distinct differences in the course of outbreaks by this beetle, which have been noticed between those in southern British Columbia and those occurring in Oregon and California, may be paralleled by distinct differences in the matter of host selection.

Individual Selection of Trees. The evident selection exerted by the insects for individual trees or for trees in a definite condition of health is another matter of the greatest importance. It is well known that even at the height of a severe outbreak certain individual trees may be more or less completely exempt from injury. Many examples of this individual immunity have appeared in the course of investigations, and it has sometimes been suggested that immune races of trees might be propagated from these individuals with great advantage to forestry.

It is well known that most species of bark-beetles, even those which at times cause the most destructive outbreaks, select at normal times trees in a weakened or dying condition. *Dendroctonus piceaperda* Hopk., which breeds in the bark of spruce, normally selects for attack only the over-mature, weakened or dying trees, windfalls or logs. Under normal forest conditions, the species exerts a very definite selection for bark in a weakened or dying condition. When, however, the species has increased to enormous numbers, as often occurs in extensive windfalls or in great quantities of large slash left in cuttings, and a destructive outbreak develops, the beetles attack with apparent freedom all conditions of trees in the stand, excepting the small diameters of less than six inches. In one instance, it was found that 13% of the trees which were killed by the beetles had previously been growing as fast as any in the stand, 20% had been making the average diameter growth for the whole stand, and the remainder had been growing more slowly than the average.

It has frequently happened in Eastern Canada that an outbreak of this species killed approximately 50% of the larger spruce in an infested valley and then died away. Is it possible that the beetles are exerting any selection

in their attack on the trees during the height of an outbreak, or that there is any reason why they attack that 50% and not the other?

Up to the present time the investigations of entomologists on this point have not been conclusive. It appears that resin production has little to do with the matter, all degrees of resin flow being exemplified in the trees which are killed. Also the rate of growth does not appear to be related in white spruce with the production of resin.

Many peculiar vagaries in the matter of selection come to light in the study of trap-trees in bark beetle control. One incident will serve for illustration. An apparently healthy spruce, 10 inches in diameter was felled on June 15, 1932, and left lying on the ground. One week later only a few beetles of *Dendroctonus piceaperda* had entered the bark of the felled tree, but in the meantime a great swarm of beetles had attacked a healthy, 13 inch spruce standing nearby. Both trees had been retarded by sawfly defoliation for the previous four years. Cases such as this appear to suggest that under certain conditions individual trees may exert a definite attraction.

It is probable that the attraction which dying bark exerts on these beetles under normal conditions must be associated with chemical changes in the trees, presumably in the cell sap. Researches on the chemical changes which occur normally in trees from month to month throughout the season, and in trees which are slowly or rapidly declining in vigour should yield invaluable results.

There are many such problems in the forest which lead directly into the fields of biochemistry and plant physiology. Their solution will be achieved only through co-operation in research.

Reaction of Trees to Insect Attack. The reaction of the trees to the insect attack is a matter of the greatest interest and a problem that abounds with difficulties. In the case of species which normally attack trees that are unthrifty but to all appearances still alive, it is sometimes a matter of dispute whether the insects have actually killed the timber or whether they have merely selected trees which had already been weakened by other causes beyond the point of recovery. The attack of the balsam weevil (*Pissodes dubius* Rand.) on weakened balsam fir is a case in point. The broods of this species are invariably developed in trees which are unthrifty and which are making little or no diameter growth.

The broods develop to maturity only in trees which die rapidly shortly after the attack. If the infested tree does not die the larvae succumb when only partly mature. Unless the larvae are able, through the effect of their tunnels cut in the inner bark, to kill the weaker trees, it is evident that the females often make grievous mistakes in their selection. The beetles of this species excavate feeding punctures freely in the bark of healthy trees and,

during a recent investigation in New Brunswick there appeared evidence that the effect of these feeding punctures, made over a period of years, may weaken trees to such a degree that eventually the broods can develop to maturity in the bark.

Insect Populations. The so-called population studies, in which an attempt is made to follow accurately the numbers of the species throughout the full course of its development, have achieved very interesting and practical results. In many cases, no doubt, the results have been much more interesting than practical, but the value of these studies is unquestioned. The very thoroughness with which the investigation must be planned and conducted through all its stages to completion ensures the best opportunity for obtaining the most essential data, and for discovering obscure habits and associations of the insects. The estimation of the original egg population, the larval population in each instar, the pupal population and finally the adult emergence, conduct and oviposition, together with the mortality in each life stage and the causes of it, serve as a background on which a most complete investigation of the insect and its associations can be built.

The studies on bark-beetle populations in Europe made recently by Seitner, Golovyanko (6) and Iljinski (7) are excellent examples of a study of this kind directed to a practical end, in those cases, the determination of the number of trap trees required to absorb all the beetles that would be produced per unit area. The formulae that were developed no doubt represented the conditions met with in the outbreaks that were investigated, but the results of investigations of this sort cannot yet be applied generally to forest outbreaks. They must be made, in great part at least, on each individual infestation. Many such studies will be required on any insect species, representing many varied conditions, before much generalization can be made.

Forest Insect Biologies. There is a great need for more general knowledge of forest insect biologies. In the Cerambycidae and Buprestidae, not even the host tree is known for a number of the species, and in the case of these and many other forest insect groups there is an astonishing lack of information on the biologies of even some of the commoner species. In the general field, there is very little advance to be found in the literature since the time of Packard's 5th Report and Felt's Park and Woodland Insects. A great deal of information has been obtained, it is true, but the greater part of it has not yet been published. This is one field in which the young investigator can make sure and valuable progress.

The practical importance of studies in insect habits may be illustrated by reference to the generations and broods of bark-beetles. Until very recently, it had been assumed that many common species of these beetles, *Dendroctonus*, *Ips*, *Pityogenes*, and others, exhibited annually a series of over-

lapping generations. Through a series of careful investigations it has been shown that most of the bark-beetles in Canadian forests have, at most, only one generation each year, but that many species produce two distinct broods each season and in some cases even more. The same females cut one tunnel in early summer, lay the complement of eggs, feed for a short time and then emerge and cut a second tunnel elsewhere and deposit a second batch of eggs. The progeny from the first tunnel emerge early in the following summer; that from the second tunnel may emerge late in the following summer or may carry over in the bark until one year later, making a two-year life-history for the late season brood.

The same females of *Polygraphus rufipennis* Ky. have produced as many as three such broods in one season and lived over the winter to produce a fourth brood in the following season. Some species of northern origin, *Dendroctonus johnsoni* Sw. and *D. rufipennis* Ky., for example, have normally a two-year generation. It is possible that in the southern part of the continent some species may have more than one generation each year; but it has not been found to occur in the Canadian forest in either the East or in British Columbia. The fact that the parent beetles normally emerge shortly after the first tunnels are completed and enter other trees has an important significance in connection with control measures.

Overcrowding the brood sticks in cages has resulted in inciting a species which has normally only one brood per season to cut three separate tunnels and lay three batches of eggs. *Dendroctonus* species habitually overcrowd many of the trees they attack, but it is not yet known what effect this habit may have on the number of broods produced in the open.

It has also been learned that many species of bark-beetles belonging to the genera *Ips*, *Orthotomicus*, *Trypodendron*, and others, have the habit of leaving the brood trees during fine days in the late autumn and going into hibernation in the moss or under the litter beneath the tree. It seems an extraordinary habit for these beetles, but proves to be rather common in a number of genera. In the case of *Ips pini* Say and *Ips calligraphus* Germ., the majority of the young brood hibernate on the ground and a smaller portion cut food tunnels in the tops of dying trees. It appears that these few beetles in the tops have been able in the past to deceive us into a belief that burning the trees was sufficient for control and have sacrificed themselves for the benefit of the main population which was safely hidden under the litter.

The bionomics of forest insects is now receiving much greater attention than ever before, and a considerable amount of data on this subject has already been accumulated. Unfortunately, only a small proportion of it has appeared as yet in the literature. Ecological studies require this collection of data in large amount, and its subsequent collation and study occupy a

great deal of time. Unless the results of the research together with the significant data are published, a large part of the benefit which should accrue is lost and much valuable time is wasted. Researches of this kind are perhaps as difficult as any in the field of Entomology and are usually of little value unless directed by well-trained and experienced investigators.

Twenty years ago the criticism was made, and with reason, that entomologists were paying too little attention to the bionomics of the insects they studied; today the criticism is being made by many economic entomologists that the schools have been paying too little attention to the fundamentals of entomology. It goes now without saying that every young entomologist should receive a sound training in the principles of bionomics, but it is surely quite as important that he have a thorough grounding in the classification, structure and general habits of the organisms which are to be the subject of his future investigations. When one considers the frequency with which undescribed species or unknown species appear in the course of our investigations, the difficulty in obtaining any reliable identification of collections in many important insect families, the paucity of our entomological literature on taxonomy—except in a few favoured groups—during the past half generation, and the not too hopeful prospect for young taxonomists to take over the load from those few stalwarts who are now bearing it for us so nobly, there is a tendency to hope for a revival in the study of the “three R’s” of Entomology, Taxonomy in association with Anatomy and Biology.

In concluding it may be said that the major forest problems include so many interrelations between various components of the forest complex that they can be dealt with successfully only by co-operative researches in several fields of science. The investigation of a forest insect outbreak may lead directly into research in silviculture, in mycology, in biochemistry, in plant physiology, and no one knows how much higher mathematics may be needed to deal with the data that may be accumulated in its course. It is a satisfaction to know that entomologists are realizing the need for this co-operation with other scientific men, for, without any doubt, therein lies the greatest hope for the solution of our most difficult problems.

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