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Studies of the Balsam Woolly Aphid, *Adelges Piceae* (Ratz.) and its Effects on Balsam Fir, *Abies Balsamea* (L.) Mill.

by

R. E. BALCH

Young stand of balsam fir being killed by balsam woolly aphid at Springfield, N.B. Note red colour of trees that have died within the past year.

Department of Agriculture
Ottawa: Canada

CANADA
DEPARTMENT OF AGRICULTURE

Studies of the Balsam Woolly Aphid, *Adelges Piceae* (Ratz.) (Homoptera: Phylloxeridae) and its Effects on Balsam Fir, *Abies Balsamea* (L.) Mill.

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STUDIES OF *ADELGES PICEAE (RATZ.) (HOMOPTERA: PHYLLOXERIDAE)* AND ITS EFFECTS ON *ABIES BALSAMEA* (L.) MILL.*

By R. E. Balch

INTRODUCTION

The study of *Adelges piceae* (Ratz.) was commenced in Nova Scotia in 1931 as an attempt to explain a condition known as 'gout disease' on balsam fir, *Abies balsamea* (L.) Mill. This condition had been investigated by pathologists (14, 15) but its cause had not been discovered. A suspicion that the insect was responsible was confirmed by the experimental infestation of clean trees. It was found that the damage caused was of considerable economic importance and that nothing was known of the biology of the insect on this continent. Studies were therefore continued for a number of years, with the main purpose of determining the past history and the probable future status of this apparently introduced species as a forest pest in Canada. A brief summary of the more important results of this work up to 1933 has been published (3). The present paper describes these findings in more detail, with the addition of information obtained since that time.

The project was initiated under the direction of Dr. J. M. Swaine, then Chief, Division of Forest Insects, Entomological Branch, and considerable encouragement was received from him and later from J. J. de Gryse, Chief, Division of Forest Biology. Appreciation is also expressed to A. B. Baird, Head, Biological Control Investigations Unit, Division of Entomology, Canada Department of Agriculture, for the work done at the Dominion Parasite Laboratory, Belleville, Ont., in supplying colonies of introduced predators for liberation.

Acknowledgement is made to W. A. Reeks for his assistance in the preparation of the drawings and the correction of the manuscript. His reports on the work of the Forest Insect Survey in the Maritime Region were used in determining the recent spread and intensity of infestations. Dr. C. E. Atwood, now of the University of Toronto, made the measurements shown in Figure 38, and recorded most of the notes on native predators. L. E. Williams obtained the data for sample plots laid out since 1946 and drew the map and charts. Much of the field work was made possible only by the frequent assistance of Mrs. R. E. Balch. Thanks are due to Miss Evelyn Clark for her careful preparation of the typescript.

TAXONOMY

Adelges piceae belongs to the subfamily Adelginae, family Phylloxeridae, superfamily Aphidoidea. The Adelginae are characterized by unusually complex polymorphic life-cycles and an alternation of hosts. The primary host is always a spruce (*Picea* sp.), the secondary host another species of conifer. The typical species have at least five distinct forms, which will be referred to by the terminology used by Marchal (23) in Europe and by Annand (1) in his monograph of the North American species : —

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* Adapted from a thesis submitted in partial fulfilment of the requirements for the degree of Doctor of Philosophy in the New York State College of Forestry, Syracuse University, New York.

The *sexualis* is the wingless, bisexual form on spruce, the female of which generally lays a single egg near the buds. This gives rise to the *fundatrix*, a wingless, agamic form overwintering on the primary host. The fundatrix produces the *gallicola*, a wingless, agamic form that develops in a gall on a young shoot of the spruce. The gallicola generally migrates to the secondary host and is called *gallicola migrans*. In some species it remains on spruce and is called *gallicola non-migrans*.

The wingless, agamic descendants of the gallicola migrans may be of two types. Since they are confined to the secondary host they are called *exsules*, and continous paracyclic generations may occur, which are independent of the primary host. The *exsulis sistens* has three moults and is characterized by a period of diapause in the first stage after inserting its stylets. Its overwintering generation is called the *hiemosistens* ; its summer generation the *aestivosistens*. The *exsulis progrediens* has four moults and usually develops without a period of rest. The first instars of the exsules are called the *neosistens* and the *neoprogrediens*.

In the typical species with the full dioecious life cycle the exsulis sistens produces a winged, agamic form called the *sexupara*, which flies back to the primary host and gives rise to the sexualis.

In this bulletin the term *nymph* will be reserved for the penultimate stage of the winged forms (*alatae*), and all other immature stages will be referred to as *larvae*. They are considered to be larvae of the oligopod type rather than true nymphs.

The history of the nomenclature in Europe is as follows. In 1844 Ratzeburg (29) gave the name *piceae* to a species of *Chermes* producing abundant white 'wool' on the bark of *Abies pectinata* D. C. in Germany. In 1903 Nüsslin (25) described the exsulis, sexupara, and sexualis of *Chermes piceae* and reported migration to *Picea excelsa* Link., on which no eggs were produced. In 1907 Cholodkovsky (9) showed that there were two distinct species on fir : *Chermes piceae*, of which only wingless forms on fir were known, and *Chermes funitectus* Dreyfus, which migrated to *Picea orientalis* Carr. and had the complete pentamorphic life-cycle. He obtained specimens of *C. piceae* from Germany but could not find any in Russia. A gall caused by *C. funitectus* was obtained from the Caucasus Mountains. He also described swellings on *Abies nobilis* Lind. from Paris that he considered were caused by a variety of *C. piceae*. He thought he detected slight morphological differences and named it the variety *bouvieri*. About the same time Marchal reported similar findings regarding the separation of *C. piceae* and *C. funitectus* (23). Börner (5) referred both forms to *C. piceae* in his monograph of the group but later recognized morphological differences and named the form with the complete cycle *Dreyfusia nüsslini*. He rejected the specific name *funitectus*, as it had been described from *Tsuga canadensis*. Marchal pointed out that this was probably an error in the naming of the host but adopted Börner's name, as have most subsequent authors. Occasionally, however, the name *Chermes nordmannianae*, given to a species on *Abies nordmanniana* Spach by Eckstein (13) in 1890, is used by European authors (35).

The only discussion of the taxonomy of these two species in American literature is that by Annand (1), who pointed out that the characters used by Börner in separating the Adelginae into seven genera were often of specific rather than generic nature, some not being present in the adult. He arranged the species under *Adelges* and *Pineus*. The genus *Dreyfusia*, which contained only *D. piceae* and *D. nüsslini*, was therefore included in the new genus *Adelges*. This arrangement is followed.

There are a great many references to *A. piceae* and *A. nüsslini* in the entomological and forestry literature of Europe that will not be reviewed here. Confusion between the two species has resulted from the fact that the morphological differences are slight and can be recognized only after careful microscopic examination. Identification has often been based, quite unreliably, on whether the attack was found mostly on the stem or on the twigs. The presence of large numbers of exsules on the needles probably indicates the presence of *A. nüsslini* with reasonable certainty, but the progrediens of *A. piceae* may also occasionally be found on the needles.

The writer has relied mainly on the characters of the wax gland areas in the neosistens as described by Marchal (23). A large number of specimens from the Maritime Provinces, and small numbers from the states of Maine, New Hampshire, New York, and Oregon have been examined and all found to be *A. piceae*. The only specimens of *A. nüsslini* which he has seen were from British Columbia. He has found no infestations of the needles of balsam fir in eastern America, although occasional specimens of the progediens form of *A. piceae* have been taken.

Boas (4) thought that *A. piceae* and *A. nüsslini* were races of the same species, and Chrystal (10) was somewhat inclined to this opinion. The present studies indicate that only one species has become established in Eastern Canada and that it is identical, morphologically and biologically, with Marchal's *A. piceae*. If, as has been suggested by several European authors, *A. nüsslini* and *A. piceae* were biological races adapted to conditions on the twigs and trunk respectively, it might be expected that they would have appeared together in Canada.

DISTRIBUTION AND HOSTS

Because of the confusion between *A. piceae* and *A. nüsslini* there is some doubt about the distributions of the two species, but both appear to occur widely throughout Europe. Cholodkovsky (9) identified gallicolae from *Piceae orientalis* in Caucasia as *Chermes funitectus,* and Marchal (23) and Chrystal (10) showed that *Dreyfusia nüsslini* migrated to the oriental spruce, but not to the European spruce, *Picea excelsa.* It has been assumed the *A. nüsslini* originated in the Caucasian region and spread to Europe, losing its power of sexual reproduction as it got beyond the range of *P. orientalis.* It is possible, as suggested by Nüsslin (25), that *A. piceae* derived from *A. nüsslini* after it was separated from its primary host.

It is evident from the literature that both species have been present for many years in Germany, France, Switzerland, Denmark, and England, and severe infestations of *A. piceae* occurred in Norway and Sweden as early as 1913. Schneider-Orelli (32), on the other hand, gave good reasons for thinking that *A. nüsslini* was not introduced into Europe before the middle of the nineteenth century.

The first record from North America was made by Kotinsky (21), who identified collections from Brunswick, Me., in 1908, and from Mount Monadnock, N. H., in 1916. He recognized them as *A. piceae* from the characters of the neosistens. Kotinsky also referred to a species of *Chermes* collected by Felt on *Abies nordmanniana* imported from Europe in 1910, which he thought was probably *A. nüsslini* ; but as he examined only "old females" this identification is dubious. Swaine (40) reported *A. piceae* from Nova Scotia in 1929, stating that it appeared to be spreading but that its importance in Canada was not known, although in Europe it had not been considered serious unless accompanied by *A. nüsslini.* The neosistens of *A. piceae* was identified by the writer in 1932 from material collected in Maine and New Hampshire, and in 1934 from material taken in Fulton County, New York, by H. K. Henry. In 1935 MacAloney (22) stated that the species was generally distributed in stands of *Abies balsamea* throughout southern Maine, New Hampshire, Ver-

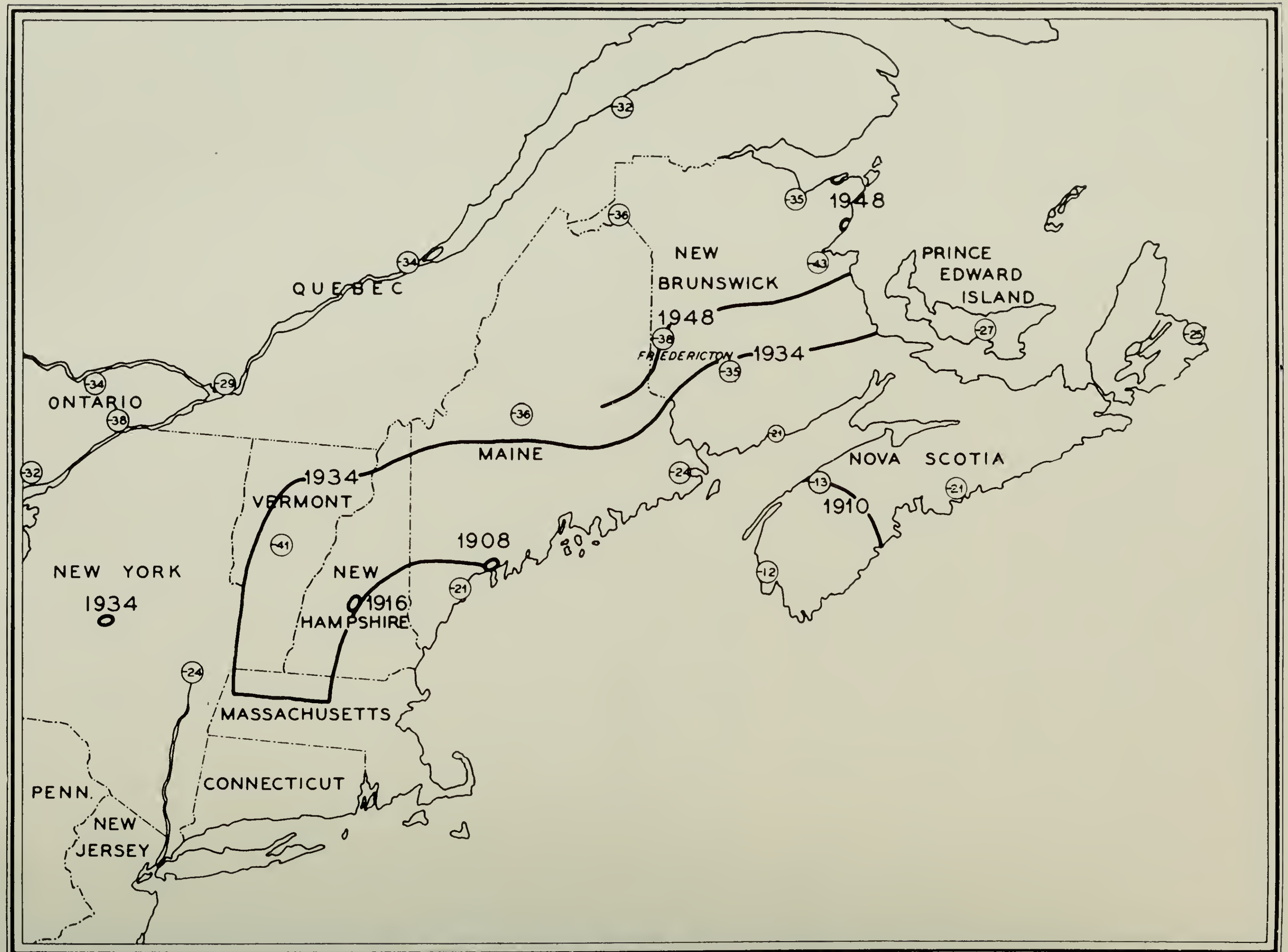

Fig. 1. Map showing limits of known distribution of *Adelges piceae* in 1934 and 1948, and some earlier records. Figures in circles are minimum recorded temperatures.

mont, and north-western Massachusettes. He reported an infestation from central New York and thought that scattered infestations probably occurred throughout the Adirondack Mountains. He was of the opinion that the insect had been established longer in the southern parts of the infested region in the United States.

Frequent surveys have been made in the Maritime Provinces of Canada since 1930. By that year the insect had become established throughout Nova Scotia and Prince Edward Island and along the southern coast of New Brunswick. Scattered outbreaks were found as far north as Shediac, Fredericton, N.B., and Vanceboro, Me., by 1933. During the following winter, severe weather conditions, which will be discussed later, greatly reduced the insect's numbers ; and little evidence of northward extension of the area of distribution was obtained for several years. Gradually new outbreaks appeared, however, which slowly extended the northern limit and demonstrated the general occurrence of the insect in southern New Brunswick. In 1948 a small local outbreak was found by W. A. Reeks of the Fredericton laboratory as far north as Grand Anse, on the south shore of Chaleur Bay in Gloucester County. The distribution up to 1948 is shown in Figure 1. In 1949 Mr. Reeks also observed infested trees over some 300 square miles in the Codroy Valley in south-western Newfoundland, and over a small area near St. John's on the east coast of the island. Material collected by him was identified as *A. piceae,* The condition of the trees indicated that the insect has been present in Newfoundland since 1940 or earlier.

As described below, information can be obtained regarding the age of an infestation by the analysis of surviving trees. By this method it has been established that the insect has been in western Nova Scotia since before 1910 and that it is of more recent occurrence in eastern Nova Scotia and Prince Edward Island. Infestations become progressively younger towards the north in New Brunswick.

The restricted distribution and the evidence of recent spread of the insect leave no doubt that it has been introduced into eastern North America from Europe. The date of introduction was probably before 1900, as it was already present in considerable numbers in Queen and Shelburne counties, Nova Scotia, by 1910 and was established in Maine by 1908. Apparently it was introduced at more than one point, and Felt's (21) record on imported nursery stock indicates the probable means. It is difficult to imagine how a sedentary insect of this kind could cross the Atlantic except on a living tree. As far as Canada is concerned there is no doubt that it first became established in southern Nova Scotia.

The presence of the insect in southwestern Newfoundland suggests that it was carried by air currents from Nova Scotia. The distance from Cape Breton Island is about 70 miles. It is shown below that the motile larvae can be carried in the air and, although the chances of dispersal and successful establishment over this distance appear small, it is possible that Newfoundland was reached in this way. There is evidence that another European species, *Stilpnotia salicis* L., has been carried from the mainland as a small larva. It appeared at several points in Newfoundland shortly after infestations became common in the Maritimes and its parasite, *Apanteles solitarius* Ratz., which was introduced to the United States from Europe in 1927, was also found to have reached the island. Since the parasite emerges from the 1st or 2nd stage larva it seems probable that it was carried by air in the young larvae of the satin moth, especially as the heavy-bodied female adult of its host rarely flies. It is also possible, however, that *Adelges piceae* reached the island on nursery stock, and this seems to be supported by its occurrence near the port of St. John's, where a number of European trees were planted a good many years ago.

There is no proof that *A. nüsslini* occurs in eastern North America, but both *A. nüsslini* and *A. piceae* have been found in western parts of the continent. Annand (1) has identified the two species from California. The writer found the neosistens of *A. nüsslini* in material collected by Dr. M. L. Prebble, Forest Insect Laboratory, Sault Ste. Marie, Ont., at Vancouver, B. C. Specimens of *A. piceae* were received from F. P. Keen, United States Bureau of Entomology, who collected them at Wilsonville, Oregon, and reported infestations on *Abies grandis* (Dougl.) Lindl. along the Willamette River from Portland to Corvallis. The fact that collections at Vancouver, B. C., and San Francisco, Calif., were made on European species of fir in parks suggests introduction on nursery stock.

It seems clear that outside the range of *Piceae orientalis*, the primary host of *A. nüsslini,* both species are confined to the genus *Abies,* all members of which probably serve as hosts. The writer has reared *Adelges piceae* successfully on *Abies pectinata, A. lasiocarpa* (Hook.) Nutt., *A. concolor* Lindl. and Gordon, *A. nobilis* Lindl., *A. grandis,* and *A. balsamea.* Chrystal (10) reports it on *A. cilicica* Carr., *A. cephalonica* Loudon, *A. forrestii* Craib, *A. pindrow* Spach, *A. firma* Siebold, *A. fraseri* Lindl., and *A. fraxoniana* Rehder and Wilson. Scheidter (31) found what he considered to be Cholodkovsky's variety *bouvieri* on *A. arizonica* and *A. sibirica.* Marchal reared *Adelges piceae* on *Abies nordmanniana* Spach. Thus species of *Abies* native to eastern and western North America, Europe, and widely separated parts of Asia have proved to be acceptable hosts.

Attempts to transfer the insect to *Pseudotsuga taxifolia* (Poir.) Britton at Fredericton, N. B., were unsuccessful.

DESCRIPTIONS

The following descriptions are based on microscopic examinations of living material, and of cast skins and whole insects cleared and mounted in Berlese's medium or balsam. The body contents were removed with warm lactic acid or cold potassium hydroxide. The former was more rapid, the latter more suitable for the less sclerotized specimens, which tend to collapse when placed in balsam unless carefully treated and hardened in absolute alcohol.

Sistens

No consistent difference was noted between the hiemosistens and the aestivosistens.

First instar (neosistens). — Length 0.35 to 0.47 mm. Body oval, flattened ventrally, moderately convex dorsally. On emerging from the egg light purplish-brown with red ocelli ; after inserting stylets gradually becoming almost black with a fringe of short, flattened wax threads around the margin of the dorsum and down the mesial line, and wax secretion outlining the segments (Fig. 13). Plates as in Figure 2, heavily sclerotized, with roughened surface and showing dark reticulations under transmitted light (Fig. 11). Wax gland areas on outer edge of marginal and inner edge of mesial plates distinctly defined, with pores irregular in shape, often overlapping and arranged in more or less triangular groups (never in clearly margined, rounded, or oval groups as in *A. nüsslini*) ; one ventral group of 5 or 6 pores between prothoracic and mesothoracic coxae (Fig. 3). Rostrum well developed, lying in a depression between coxae and reaching slightly beyond metacoxae. Stylets generally over four times as long as body.

Second instar. — Length 0.45 to 0.55 mm. Body broader and more convex dorsally than in first instar, purplish-black, gradually becoming covered with

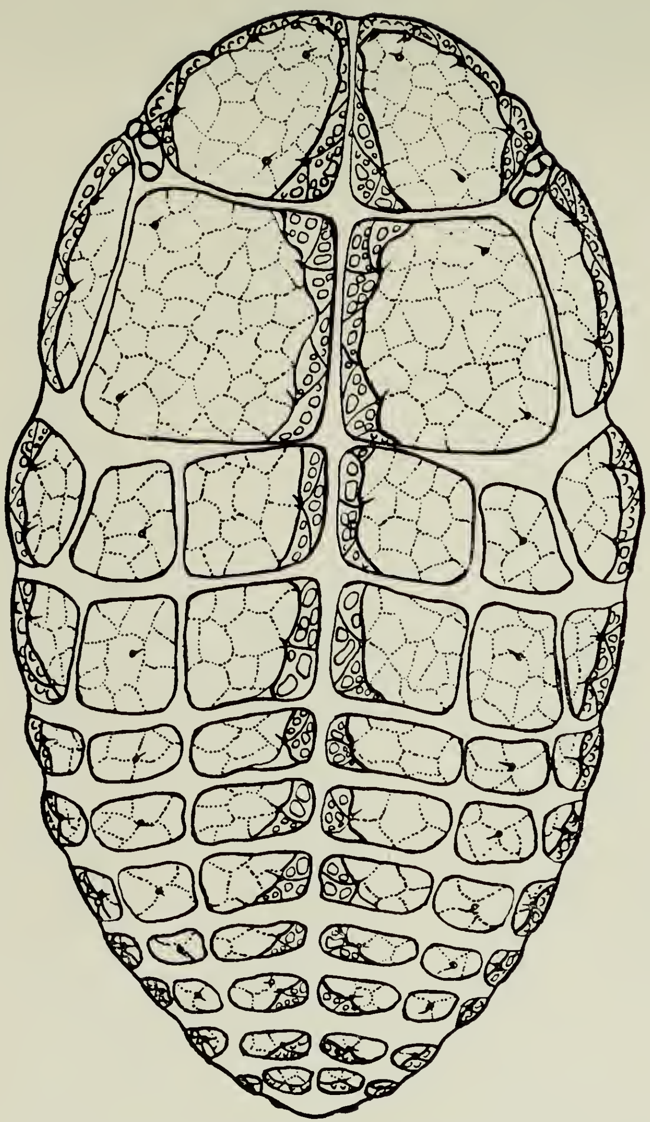

Fig. 2. Dorsal view of neosistens, showing plates and wax pores. X300.

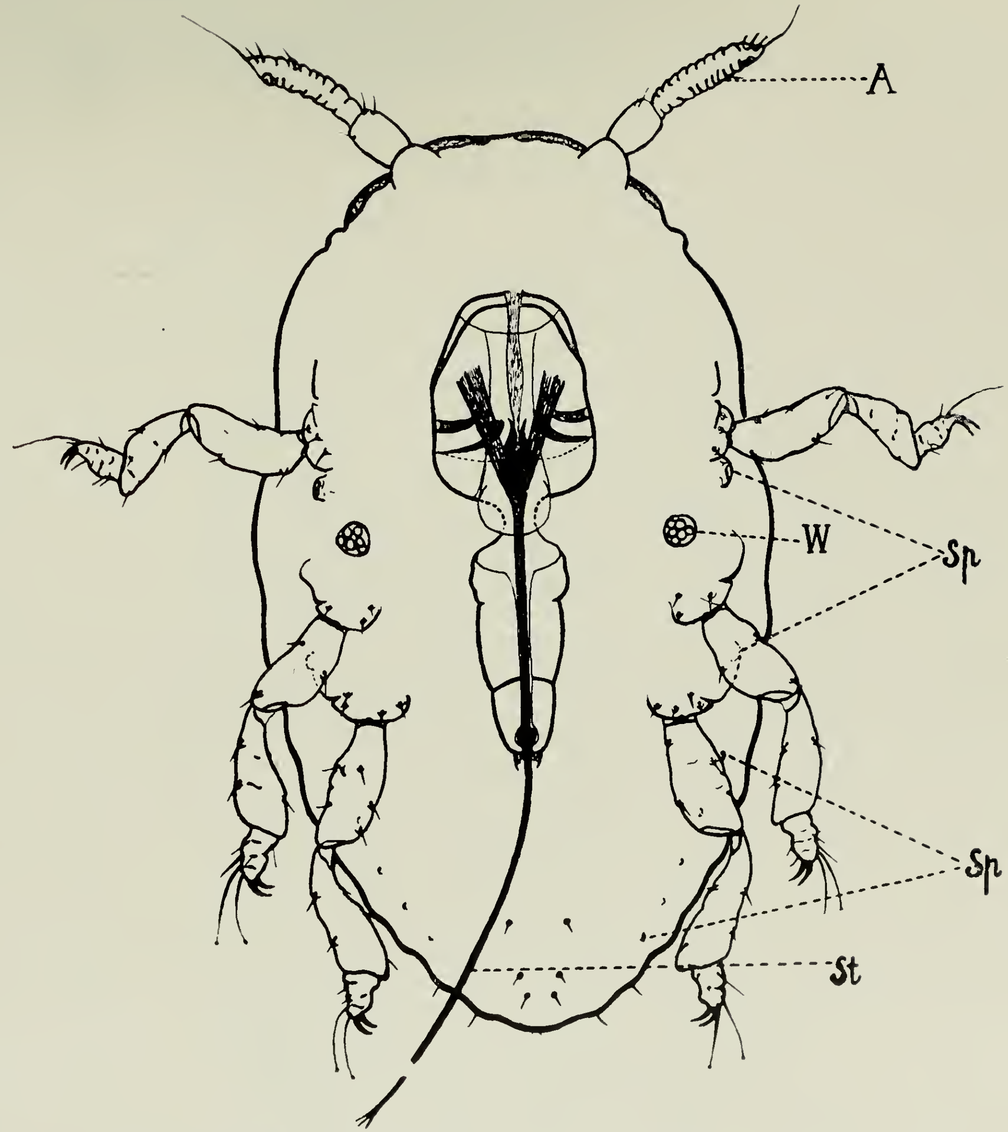

Fig. 3. Ventral view of neosistens. A, antenna; Sp, spiracles; W, wax pores; St, stylets. X300.

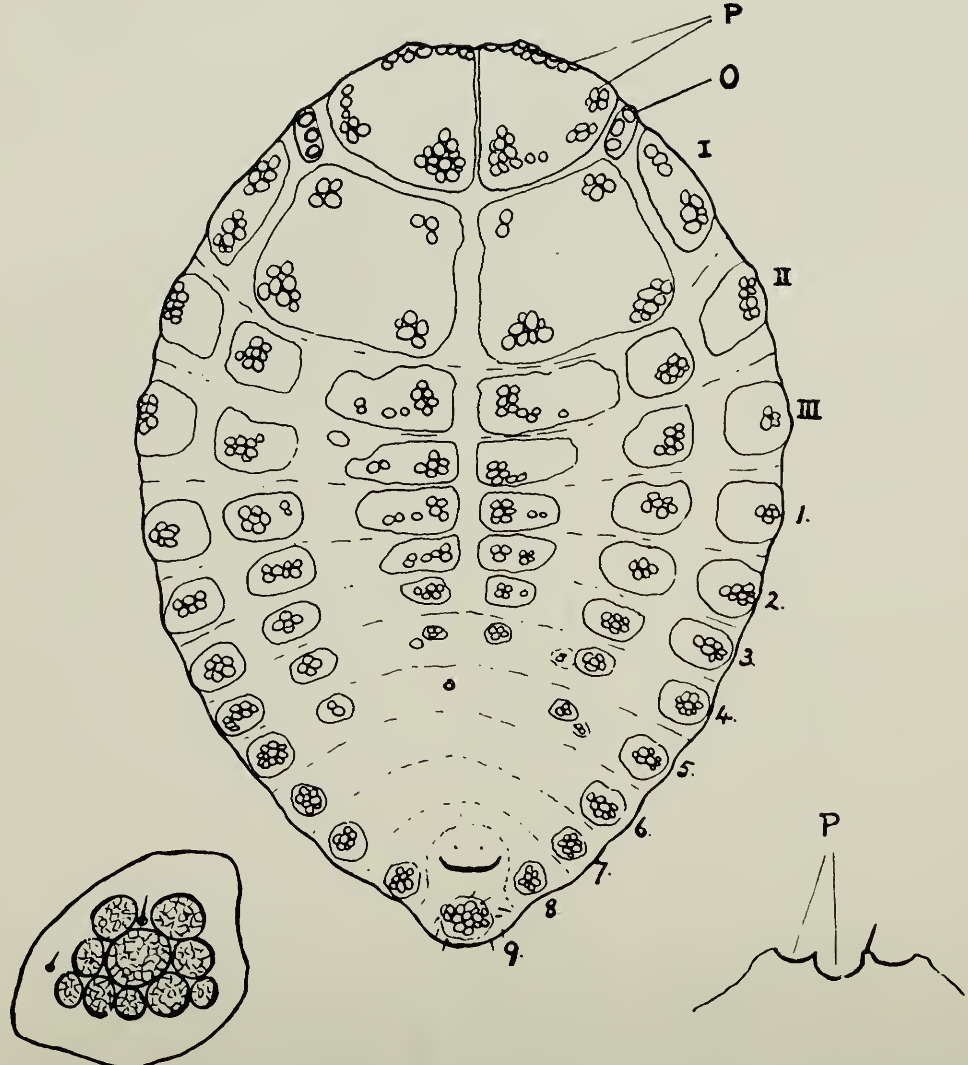

Fig. 4. Dorsal view of adult hiemosistens, flattened to show plates. P, pores; O, ocelli. Enlarged plate on left. Vertical section through pores on right. X160.

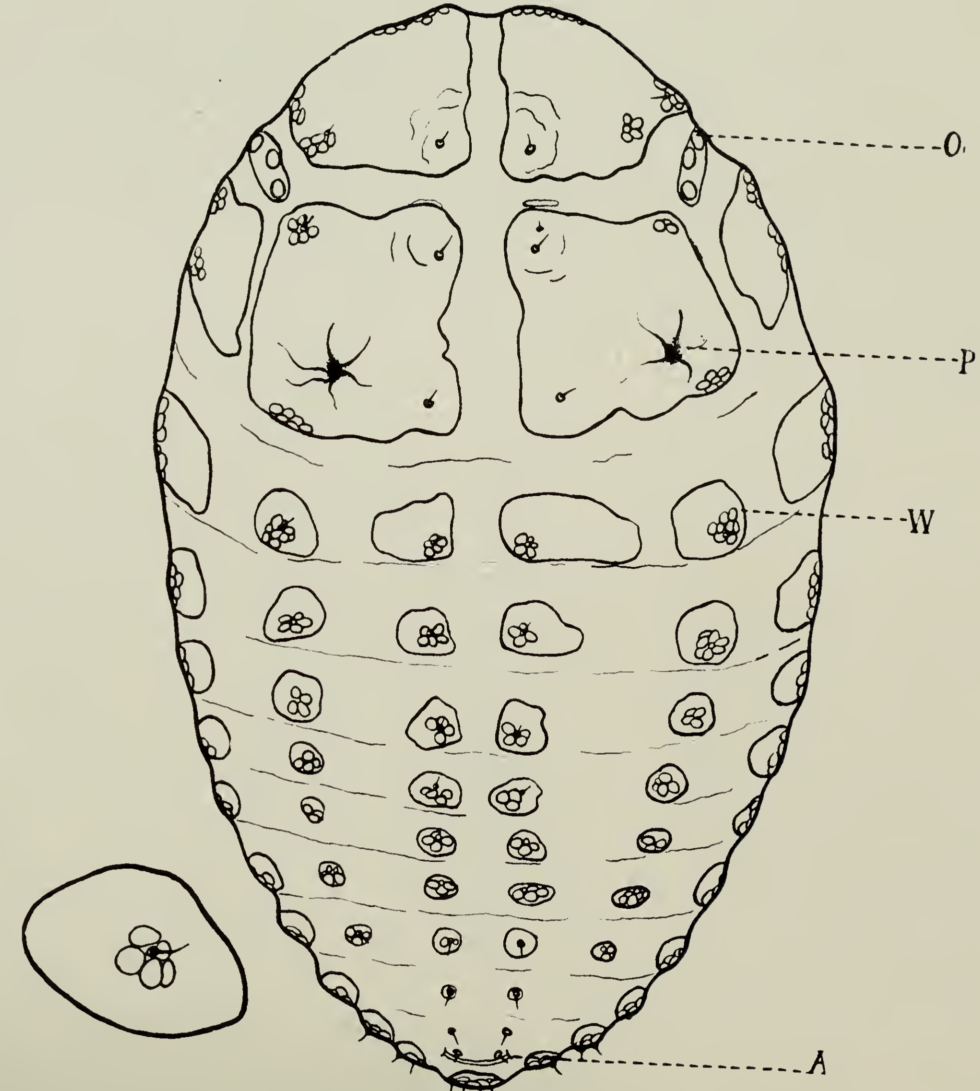

Fig. 5. Dorsal view of second instar aestivosistens. O, ocelli; P, pit; W, wax pores; A, anus. Enlarged plate on left. X300

long, curling wax threads. Plates less regularly rectangular and less heavily sclerotized, raised in centre like hummocks, gland areas flat. Pores more or less circular, arranged in groups around one or two setae and varying in numbers from 2 to 20, most commonly 6 to 10 ; largest groups on marginal plates ; mesial groups often absent on head and prothorax (Fig. 5). Antennae shorter, with third segment longer than first and second combined. Rostrum more slender, with stylets of same length as in first stage. Legs smaller.

Third instar. — Length 0.6 to 0.67 mm. Dorsum slightly more convex than in second instar. Antennae shorter, with third segment about as long as first and second combined. Plates and wax glands similar. Rostrum more slender and stylets about same length.

Adult. — Length 0.7 to 0.86 mm. Body almost hemispherical but longer than wide and slightly pointed toward posterior end, purplish black, becoming completely covered with long, slender wax threads. Plates of head and prothorax sometimes separate, sometimes divided only by a furrow ; a deep pit just behind the centre of the pronotal plates ; considerable variation in degree of sclerotization ; mesial plates often absent from fifth abdominal segment and both mesial and pleural from the sixth and seventh. Pore groups slightly larger than in third instar and present at mesial corners of head and prothoracic plates, varying in number and size of pores between individuals and on different sides of the same specimen, with up to 26 in a group (Fig. 12). Antennae and legs somewhat smaller than in previous stage. Rostrum and stylets similar. Ovipositor distinct. (Figs. 4, 6, 7, 8).

Progrediens Aptera

This form is rare but arises occasionally from the first eggs laid by the hiemosistens.

First instar (neoprogrediens). — Length 0.30 to 0.38 mm. Body narrower than that of neosistens, brownish-purple, lightly sclerotized ; plates less distinct ; no apparent gland areas or wax threads but body covered with slight waxy bloom. Stylets shorter, only slightly longer than body.

The intermediate stages were not examined microscopically. The second stage produces little or no wax but a moderate covering of threads appears in the third and fourth stages.

Adult (fifth instar). — Length 0.6 to 0.7 mm. Similar to adult sistens but less sclerotized, with plates and pores indistinct. Becoming covered with long, slender wax threads. (Fig. 9).

Progrediens Alata

This form is also rare, arising from the first eggs of some hiemosistentes. The first and second stages are similar to those of the progrediens aptera.

Third instar. — Lenght 0.6 mm. Body purplish-brown, with slight waxy bloom and short wax threads. Plates and pore groups similar to those of sistens but smaller, less sclerotized, and indistinct.

Fourth instar (nymph). — Length 0.75 to 1.06 mm. Cephalic and ocular plates strongly sclerotized and narrowly separated at median line. Thoracic and abdominal plates small, widely separated, irregular in shape, and often mesial and pleural abdominal rows lacking. Pores absent on head and prothorax, which are heavily sclerotized and roughened. Rostrum short, extending to bases of meso-coxae.

Adult. — Length 0.90 to 1.25 mm. Head and thorax purplish black, strongly sclerotized, generally without gland areas but sometimes with two on each

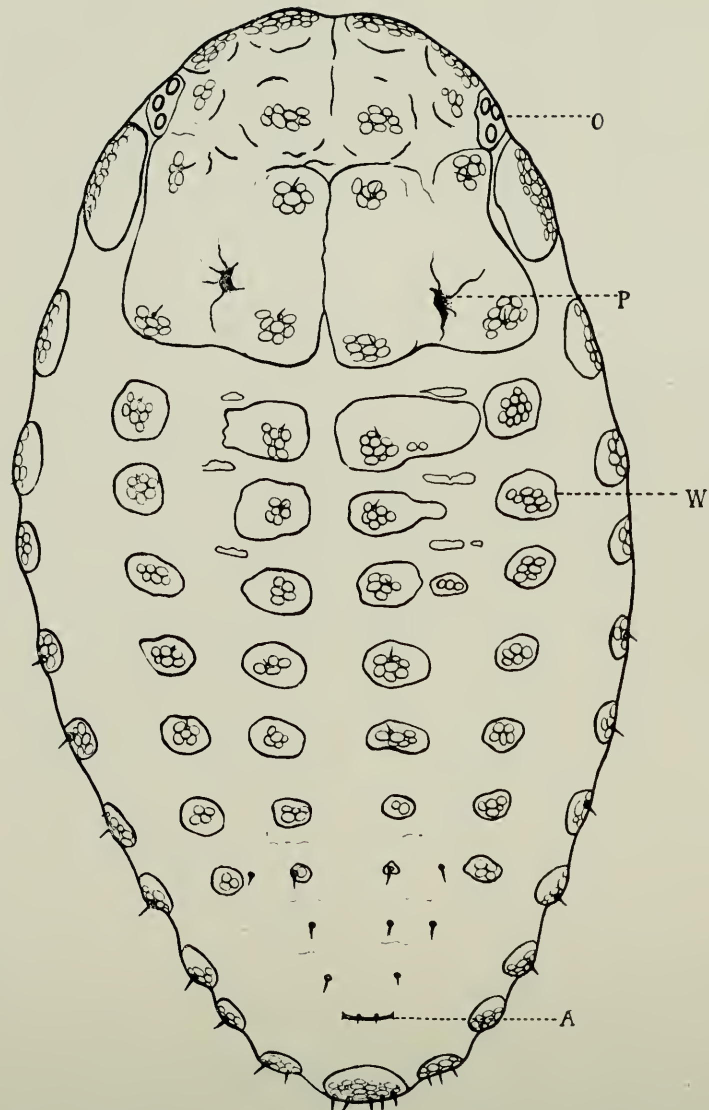

Fig. 6. Dorsal view of adult aestivosistens. O, ocelli; P, pit; W, wax pores; A, anus. Enlarged plate on left. X300.

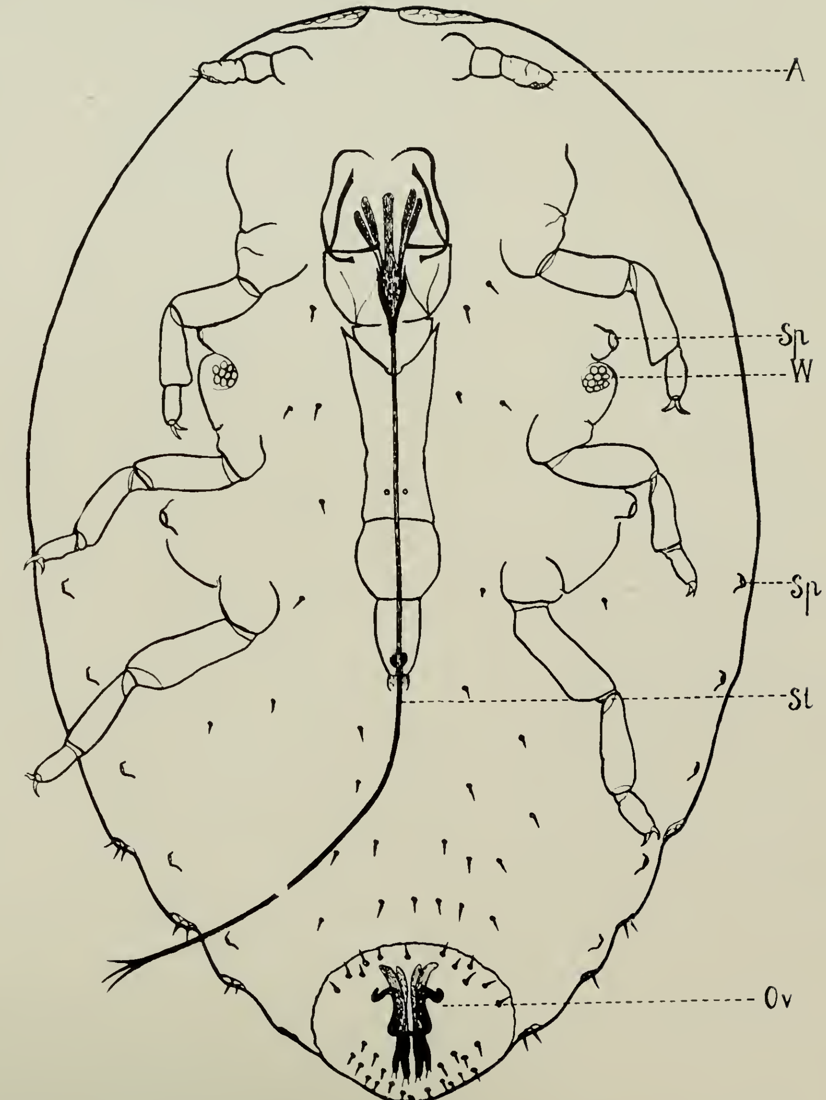

Fig. 7. Ventral view of adult aestivosistens. A, antenna; Sp, spiracle; W, wax pores; St, stylets; Ov, ovipositor. X300.

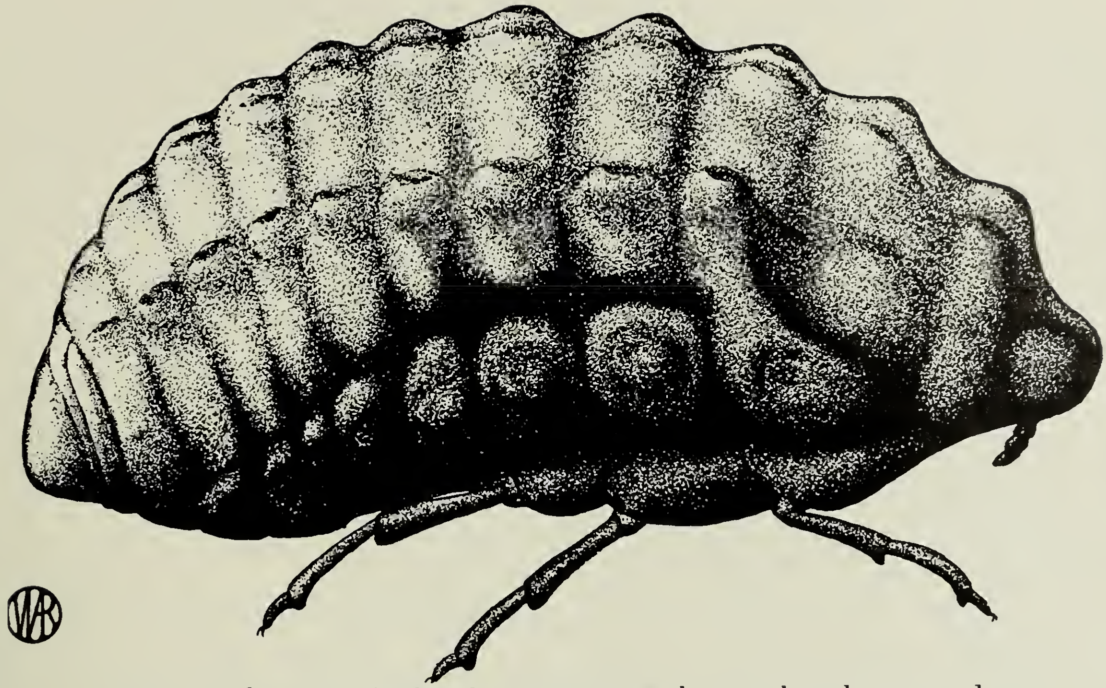

Fig. 8. Side view of adult hiemosistens with wax threads removed, uncleared. (Drawn by W. A. Reeks) X170.

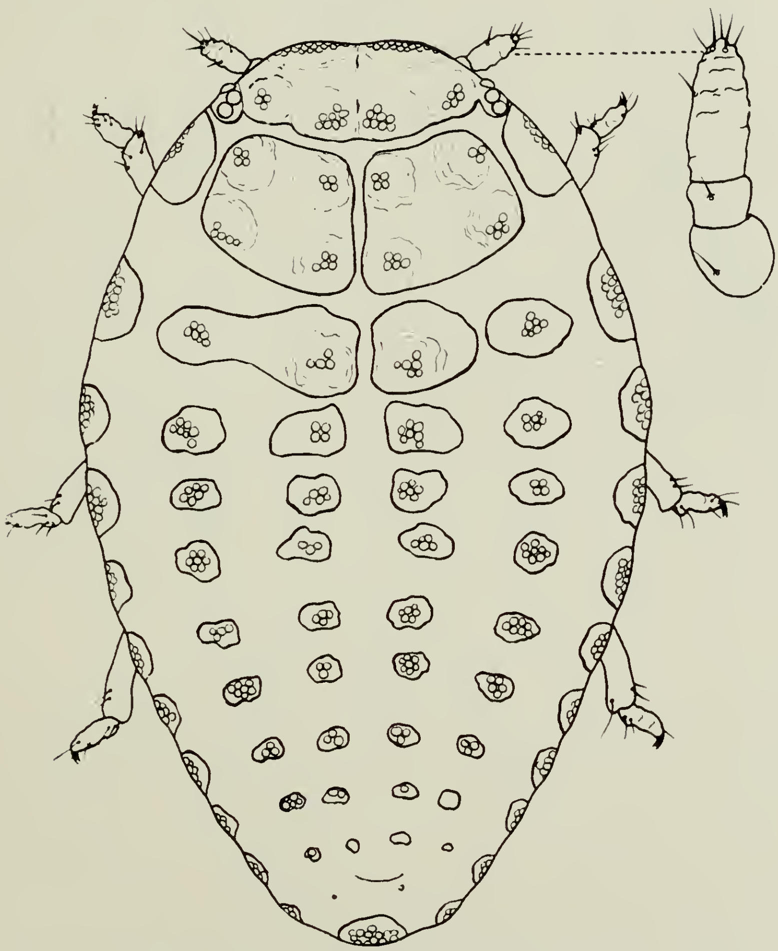

Fig. 9. Dorsal view of adult progrediens aptera. X300.

segment. Abdomen lightly sclerotized, without distinct plates, mesial and pleural pore groups small and sometimes missing, marginal groups larger on first and posterior segments, wax threads slender and relatively sparse. Antennae with 5 segments and rather small sensoria. (Fig. 10)

Fig. 10. Dorsal view of adult progrediens alata. X150.

LIFE-CYCLE AND SEASONAL HISTORY

The life-cycle was studied by infesting small potted trees with eggs of known origin. These trees, which were obtained from uninfested areas, were placed in the greenhouse or insectary and covered with cylindrical celluloid cages. The top of each cage was formed by a removable metal hoop over which was sewn a tightly stretched piece of cotton. The weight of the hoop ensured a close fit to the top of the cylinder. In all, 28 specimens of *Abies balsamea* and 4 of *Abies pectinata* were used between 1931 and 1933. Observations on the life-cycle and seasonal development were also made on artificially and naturally infested trees of all sizes, in the nursery and in the forest.

Dates of development are for the stages on *Abies balsamea* at Fredericton, in central New Brunswick. Climatic data for the locality are shown in Table I.

TABLE I.—AVERAGE MONTHLY PRECIPITATION, MEAN TEMPERATURE, AND SUNSHINE FOR FREDERICTON, N. B., 1913-46.

	Precipitation inches	Mean Temp. °F.	Sunshine hours
January	3.34	13.40	105.76
February	2.69	14.85	122.10
March	3.10	26.72	144.29
April	3.24	39.81	161.88
May	2.87	51.28	205.83
June	3.43	60.70	204.95
July	3.10	66.42	226.86
August	3.45	64.58	215.30
September	3.59	56.61	158.88
October	3.93	45.84	141.62
November	3.21	33.23	92.95
December	3.09	18.77	89.50

The sistentes occur on all parts of the bark from the ground to the new shoots. They show a preference for lenticels, crevices in the bark, callous tissue, nodes, old staminate flower scars, the bases of shoots beneath old bud scales, and the bases of buds. The only parts of the bark on which they cannot feed are where there is a layer of dead outer bark exceeding 1 mm. in thickness. They are found on trees of all ages. In severe infestations a few may settle on the needles but they fail to develop. The progredientes were found occasionally on the axes of young shoots, but they practically always go to the needles.

Hiemosistens

The insect overwinters only as a neosistens. Although all stages from egg to adult may enter the winter, and survive temperatures as low as 3° F., they all eventually die except the first instar. To overwinter successfully it must have inserted its stylets and reached the dormant condition, which is indicated by black plates and wax fringes (Fig. 13).

The first signs of feeding in spring are a swelling of the body and the appearance of a clear, sticky droplet of 'honey dew' at the anus. This has been observed as early as April 13, before there is any sign of swelling in the balsam buds. The time when development commences varies with the tree and between individuals on the same tree. Certain trees, generally those of most vigorous growth start growing earlier than others, and on these the insect tends to show the first signs of feeding. There may be, however, a difference of as much as 20 days between individual larvae on the same tree. Some have remained dormant until the third week in May.

The first observed moulting for the season was recorded on dates ranging from April 18 to 29. The larva then changes its form ; appendages are reduced in size and the body becomes covered with white wax threads. After two more moults it reaches the adult stage, which can be identified by the presence of the ovipositor. Adults were found as early as May 8, about 10 days before the buds burst, but some do not reach the adult stage before the end of May.

Oviposition commences after the adult is 2 or 3 days old and may continue for 5 or more weeks. Egg laying has been observed as late as July 13, but most of the adults die before the middle of July.

The hiemosistens is remarkably prolific considering the size of the egg, which is nearly half as long as the adult. One was observed to lay 5 eggs in 24 hours, and as many as 248 egg shells were counted in one egg mass. Fifty-two masses taken at random from twigs and stems after oviposition was completed averaged 96 per mass. The number of eggs per adult was larger on some trees than others, but there was no obvious correlation between the

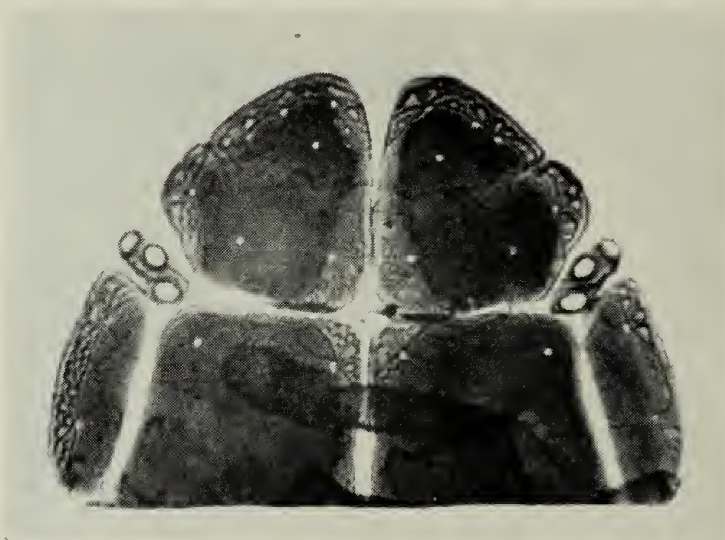

Fig. 11. Plates of head and prothorax of neosistens, showing wax pores and reticulation. X325.

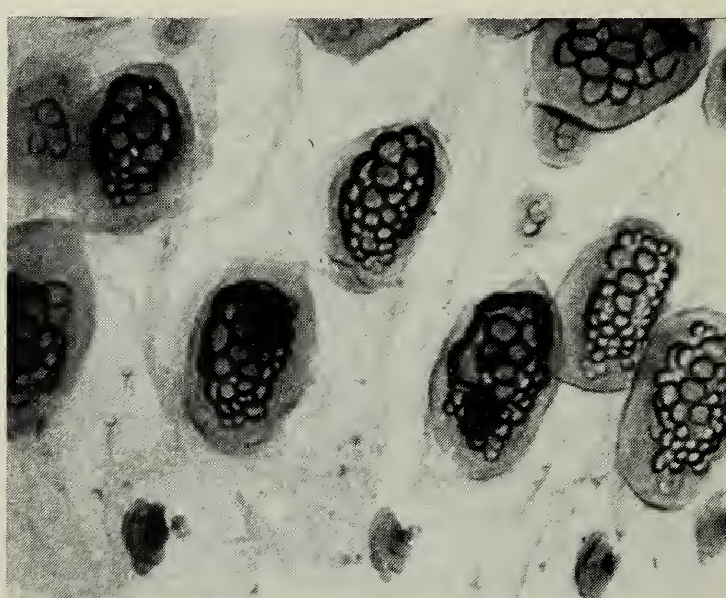

Fig. 12. Plates and wax pores of adult hiemosistens. Note spiracles below marginal plates. X325.

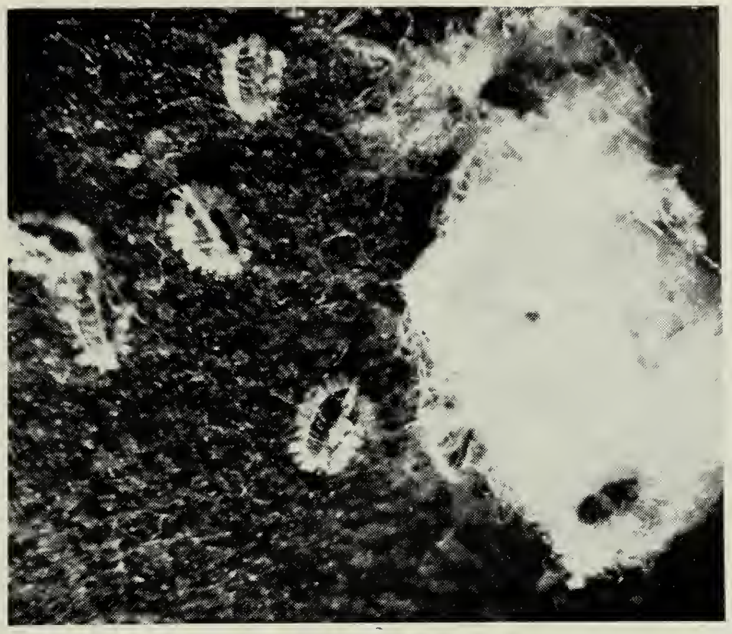

Fig. 13. Dormant neosistentes beside wax 'wool' of adult. X25.

number of eggs and the vigour of the tree, or the part of the tree attacked. In the greenhouse, egg masses were larger and development was more rapid on *Abies pectinata* than on *Abies balsamea.*

The incubation period is about 12 days but varies greatly with temperature. Hatching commences during the last week of May and continues until near the end of July. As oviposition continues for several weeks, and the eggs are attached to the bark by a silk thread, fresh eggs are added to the mass at one end and empty shells accumulate at the other. As many as 128 unhatched eggs were found in one mass on *Abies pectinata,* but this is unusual. If the period of incubation in this case were only 12 days, over 10 eggs were laid per day.

Aestivosistens

The offspring of the hiemosistentes are very similar to their parents morphologically and biologically. The newly emerged larvae are light purplish-brown and crawl rapidly. If feeding conditions are favourable they generally settle within a few hours and insert their stylets. Within 2 to 3 days they become black and produce marginal and mid-dorsal fringes of wax. They then go into diapause. Histological studies and experiments described below indicate that before resting they inject a salivary substance into the tree.

The resting period is variable. The shortest observed was 3 weeks, the longest 8 weeks. Thus there is a period about the end of July when the population consists entirely of dormant neosistentes (Fig. 17). Most of the aestivosistentes commence development during August, but some were found in the second stage at the end of September. Some fail to develop at all but it seems that these do not survive the winter.

The aestivosistens is somewhat less fecund than the hiemosistens. It was found with as many as 105 eggs, but the number probably averages less than 50. Oviposition occurs from mid-August until October, when it is brought to a gradual halt by low temperatures. The offspring are apparently all hiemosistentes, and no evidence has been obtained of a second generation of aestivosistentes as reported by Marchal (23). In the Maritime Provinces, a second generation would be unable to complete development before winter.

The multiplication of this species in Canada is dependent on these two generations of sistentes. There are two distinct periods, in May and August,

Fig. 14. A very heavily infested stem in August, covered with white wax 'wool'.

Fig. 15. Stem of tree showing moderately heavy infestation on basal 18 inches. Photo taken June 9, 1934, after all overwintering larvae had been killed above snow.

when new 'wool' appears in great quantities on the bark of heavily infested trees and gives them a characteristic grey or whitish colour. The insect is generally most numerous in the second generation, and infestations are therefore most easily detected during August and September. (See Fig. 14, and Table 2)

Progrediens

On some of the trees in the greenhouse that were infested with early eggs taken from twigs, a few larvae settled on the new needles. They were of the progrediens type, with short stylets which were inserted in the stomata. They began to develop immediately and had 4 moults. The great majority of these became alatae but about 5 per cent were apterae. Careful examination of several hundred small trees in the forest showed that these forms occurred very occasionally in small numbers : neoprogredientes between May 12 and 29, adults between June 12 and July 9.

When early egg masses were placed in vials for hatching, a few of the first to hatch were of the progrediens type, although the great majority of the masses produced only sistentes. Ten trees were infested with the first 5 to 12 eggs laid by a number of hiemosistentes. On 5 of these, eggs were used from the stems of large trees ; on the other 5, eggs from the twigs of small trees. One of the latter produced 32 progredientes alatae and 5 progredientes apterae. The others all produced only sistentes. In other experiments with some 70 artificially infested trees the progrediens form appeared occasionally, but only when infestations were started from early eggs obtained from twigs.

The progredientes alatae were not observed to lay any eggs. The adults left the needles, sometimes dropping to the bottom of the cage and dying in a few hours, sometimes crawling and occasionally flying for 1 to 2 days before dying. At different times as many as 250 were placed in cages with twigs of *Picea glauca* (Moench) Voss, *Picea excelsa*, and *Abies balsamea*. A few were attracted to the balsam fir and one inserted its stylets temporarily in a needle, but none was observed to go to the spruces.

The progredientes apterae usually settled on the undersides of the young needles, occasionally on the upper sides or on the axes. They remained at the same point and laid from 1 to 9 eggs, the average for 25 masses counted being 6.

Two abnormal specimens were found, apparently intermediate between the alata and the aptera. These had partially-formed wing pads, in one as long as the body, in the other much shorter. The antennae resembled those of the aptera but were longer and more wrinkled and showed a faint segmentation of the distal segment. Ocelli like those of the aptera and a small number of nymphal ommatidia were present. The ovipositor was like that of the aptera. One specimen laid 1 egg, the other 4. This may be a case of metathetely in the winged form (47).

It seems probable that the two types of progredientes are both exsules rather than that the winged form is the sexupara as indicated by Annand (1). This is supported by Marchal's (23) experiments in which the alatae settled on fir.

Twenty-five eggs from progredientes apterae were placed on a clean tree. They all produced aestivosistentes, which in turn produced hiemosistentes. The following spring because of heavy infestation there was no new shoot growth and progredientes were not observed, as they will not settle on old needles. A fresh tree was then infested with about 1,000 eggs from 24 of these sistentes, which were all descendants of progredientes. In June of the next year, counts of the offspring of the hiemosistentes on this tree showed 112 progredientes and 475 aestivosistentes. This is a very much higher proportion

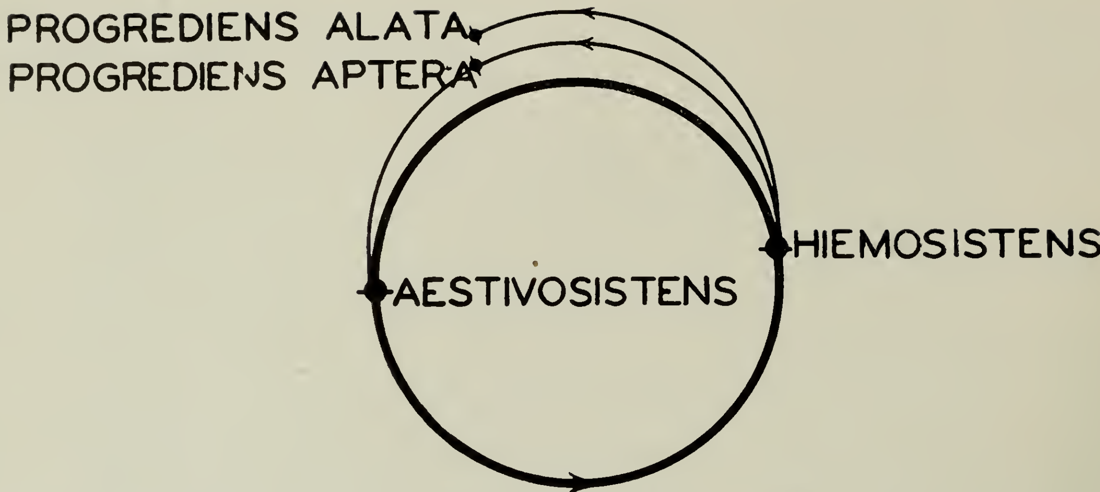

Fig. 16. Diagram of the life-cycle of *Adelges piceae* on *Abies balsamea* in Eastern Canada.

of progredientes than has been observed on any other tree and seems to indicate that the tendency to produce the progrediens type is inherited. The fact that the progredientes appeared only from mothers on twigs suggests that feeding conditions may influence the production of these forms. It may have been due, however, to the dependence of the progredientes on new needles. If they were produced on the stem of a large tree, they would have difficulty in reaching new shoots. Selective mortality resulting from their failure to survive would decrease the probability of their occurrence if the tendency to produce this form is inherited.

Discussion

The life-cycle on *Abies balsamea* in Eastern Canada is summarized in Fig. 16, and the seasonal history in Fig. 17. There is no migration to spruce

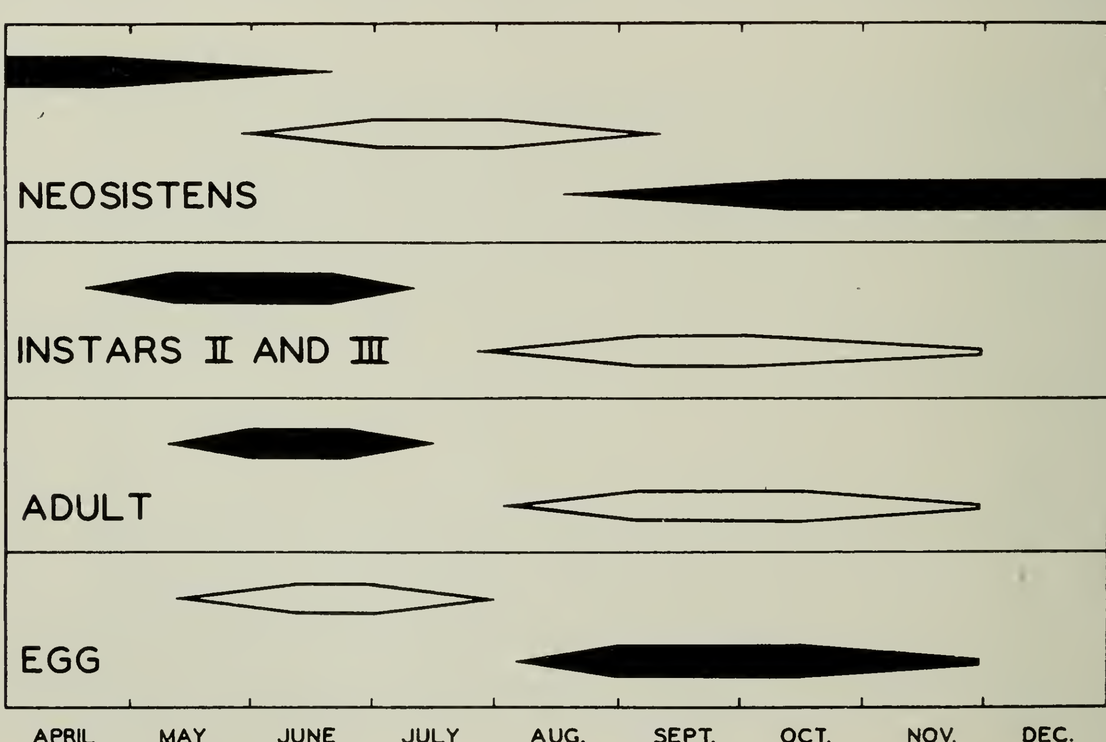

Fig. 17. Chart showing occurrence of the stages of the sistentes throughout the year in central New Brunswick. Solid black: hiemosistentes; outline: aestivosistentes. Based on earliest and latest records.

and therefore no sexual reproduction. The insect depends for its multiplication on two generations of sistentes that feed on the bark, twigs, or new shoots, but never on the needles. The winged and wingless progredientes are rare and their influence on population trends is negligible.

The life-cycle on *Abies pectinata,* as observed by Marchal (23) in France, differs in the following respects. Marchal records two generations of aestivo-sistentes. He describes the first as "d'une taille réduite et d'une faible fécondité", the second as "notablement plus fécond". The single generation in Canada appears to correspond with the second generation in Europe, rather than the first, which seems to have been completely lost. Another difference is that the second instar overwinters successfully in France whereas only the first instar survives the Canadian winter. Marchal's work also suggests that the progrediens forms are more numerous in Europe. It is probable that these differences have arisen as adaptations to climate, the reduction in the number of generations resulting from the shorter season in Canada, the failure of the second instar to overwinter from the low winter temperatures, and the rarity of the progrediens forms from winter mortality above the snow periodically limiting the population to the bases of stems at a distance from the new needles.

HABITS AND BEHAVIOUR OF SISTENTES

The following is a description of some of the habits and behaviour of the sistentes that have not been covered in the discussion of seasonal development and have a bearing on the spread and establishment of the insect and its effect on the tree.

Egg Stage

The eggs are attached to the bark behind the stationary adult by means of a silken thread. They are about 0.4 mm. long, oval, light purplish-brown, and covered with a slight wax bloom.

As the embryo develops the egg becomes orange-brown and the ocelli can be seen through the chorion as two dark reddish spots. Shortly before hatching the stylets become apparent as two distinct circular coils below the ocelli (Fig. 18). The head of the embryo is always at the end opposite the attachment of the thread.

The young larva emerges by splitting the chorion with its head. The shell of the egg remains attached to the bark as a flattened whitish object. The number laid by any one adult can be determined by counting the compact group of shells behind it.

Motile Larva

The young larva, or 'crawler', is very active and moves fairly rapidly over the bark, frequently touching the surface with its antennae. The track of one specimen was traced with a pencil on a piece of paper at a temperature of 70° F. At the end of 1 hour the track measured 21 inches.

Two hundred recently-hatched larvae were placed in 8-by-1 inch shell vials at this temperature. They were in constant, rapid movement whenever observed and at the end of 3 days approximately 25 per cent were still alive. A similar lot placed outside where temperatures ranged from 50° F. to 72° F. showed approximately 20 per cent still crawling after 8 days. It may be assumed that the motile larvae can crawl 100 feet or more under natural conditions.

When on suitable feeding sites many settle and insert their stylets within 2 or 3 hours. Some settle near their mother, but there is always a period of wandering after hatching. Some experiments were carried out to determine the factors influencing the distribution of the larvae on the tree.

When eggs from the stem of a large tree were placed at the base of the stem of a vigorous tree 2 feet high, the majority of the larvae went to the ends of the branches and many settled on the new shoots. In a similar experiment with a tree 6 feet high, the larvae crawled up the stems and a number reached the leader and new shoots, but the majority settled on the stem and branches. In the second generation, however, the new shoots became heavily infested. It had been noted that on many small trees in the forest infestations became heaviest on the leader and upper branches. This tendency to move upward might result from reaction to light or gravity, or from a preference for the type of tissue found in the upper parts of the tree.

A number of crawlers were placed in 8-by-1-inch shell vials at 70° F. One of these vials was completely darkened and placed on end for an hour. At this time over 80 per cent were in the upper half of the vial. Another was placed in moderate diffuse light away from the window of the laboratory. The majority found their way to the top and a similar proportion continued crawling in the upper half. The vials were reversed, with the same results. Another vial was darkened with black paper, except for the bottom inch, and placed in the same light ; the great majority remained in the lower 2 inches of the vial. The same results were obtained in stronger diffuse light near the window, but when the vial was placed in direct sunlight the larvae nearly all remained in the darkened portion. It was evident that there was a negative geotaxis but a stronger positive phototaxis in diffuse light. The reaction to strong direct sunlight, however, was negative.

Two small trees outside were half-covered with boxes from which one side had been removed, so that the north side of one and the south side of the other were in constant shade. Eggs were placed on the stems at the end of May. A number of progredientes appeared and all settled on needles outside the boxes. The first generation of sistentes showed a preference for the unshaded twigs, but in the fall both trees were fairly evenly infested over the whole crown, with a slightly heavier infestation under the boxes. The latter condition was probably due to higher survial as a result of protection from sun and rain.

In other experiments pieces of bark carrying eggs were tied on the stems of a number of fairly large trees. When hatching took place in sunny weather during early July, on stems exposed to direct midday sunlight, the crawlers sought the northerly side of the stem. It can be concluded that during clear weather in summer they will not settle on bark exposed to the midday sun. This could be due to a negative reaction to strong light or to the high temperatures at the surface of the bark.

These reactions to light and gravity guide the larvae upward and tend to keep the insect on the tree as long as it provides suitable food. However, they seem to be of less importance than the ability of the crawler to choose feeding sites where the cortical parenchyma is young and easily accessible. When trees that had been wounded on the stem were infested, the larvae settled on the callous growth as freely as on the new shoots. On trees with weak shoot growth, due to transplanting or previous infestation, they often showed a preference for the stem. On the older stems they settled first in the lenticels and in crevices formed by the splitting of the outer bark, where there was young parenchyma near the surface. A favourite site was under the old bud scales at the bases of the new shoots. Stereotropism may be involved, but the dominating factor determining the choice of site seems to be accessibility of parenchyma, with a preference for growing tissue.

As shown later, the feeding causes a proliferation of the parenchyma accompanied by a swelling of the twigs. The crawlers show a preference for these swollen parts, in which growth of the parenchyma has been stimulated by the salivary injections of other larvae.

Dispersal

During the period from 1931 to 1948 new infestations have been found over an increasing area in New Brunswick. The most advanced infestations were widely scattered and occurred chiefly on the stems of the larger trees. As these became more general in a district, new, isolated outbreaks appeared farther north. In the eastern part of the Province the present most northerly infestation, in Gloucester County, indicates a spread of as much as 5 miles per year. It has been less rapid in the west (Fig. 1).

Spread depends on dispersal followed by establishment. The rate is governed by such factors as weather and the occurrence of the host. It varies in different periods and regions. There is clear evidence, however, that the insect is being constantly dispersed from foci of heavy infestation and is sometimes transported considerable distances.

An example of local spread was studied near Fredericton, N.B., where a forest of some 3,500 acres was closely observed from 1932 to 1948. In 1932 only one small stand was noticeably infested. The following year a few infested trees were found about a quarter of a mile away. During the winter of 1933-34 all the larvae above the snow were killed, and no new infestations were found until 1937. During the next 10 years, however, infested trees gradually became more prevalent, at first scattered singly or in groups, later in larger groups. By 1948 the insect was present throughout the whole forest.

As the winged form is rare, and probably does not reproduce, dispersal must be dependent on the motile larvae or the egg. In other stages the insects are attached by their stylets, except just after moulting, and if moved are incapable of becoming established. It is possible that motile larvae and eggs occasionally become attached to birds, such as nuthatches, or to squirrels, but this is probably not an important means of dispersal. Because of their small size the young larva and the egg can be carried by wind. That this is the chief means of dispersal is indicated by the following experiments.

A number of traps were set up containing glass slides, 1 by 3 inches, smeared with a film of vaseline. The slides were held in an inverted trough of galvanized iron to which was attached a rudder that kept the slide facing the wind when the trap was suspended on a string. To reach the slide any windborne object would have to be travelling at an angle of not more than 30° to the horizontal. During the hatching period in September many young larvae and a few eggs were found on the slides that were hung within 10 feet of heavily infested trees. In 21 days a total of 422 larvae and 42 eggs were taken on 3 such slides. The number collected each day varied with the wind, from none in calm weather to as many as 58 following a day of rather high wind.

Traps of this kind placed in the stand at greater distances from heavily infested trees caught relatively few larvae. Only 4 were taken at 110 feet. It was evident that the insect was dispersed chiefly from trees on which the larvae were greatly in excess of the number that could find feeding sites, because of crowding and the dying of parts of the bark. Slides were also placed on the ground beneath large flat rocks at different distances from such trees. Large numbers were caught on those within 10 feet, much smaller numbers beyond that distance. Slides placed on top of the rocks showed that many were falling to the ground within the perimeter of the crown.

Larger traps were used to determine the distances such larvae might be carried outside the stand. These were glass plates, 10 by 12 inches, set at a 45° angle to the horizontal in boxes that gave some protection from rain and allowed the air to pass over the tops of the plates. In 1932 four were placed in clearings at different points of the compass from an infested stand, 50 to

75 feet from the edge of the stand. Between September 16 and October 8 the following were found on the plates : north, 3 larvae ; east, 7 larvae ; south, 23 larvae and 5 eggs ; west, 11 larvae and 5 eggs. In 1933 the 4 traps were placed in a field to the east of an infested stand at approximately 50, 120, 300, and 600 feet. They were examined and cleaned at intervals during June and August. Time did not permit of exact counts, but it was estimated that over 900 larvae and eggs were caught at 50 feet ; 86 larvae and 13 eggs were recorded at 120 feet ; only 4 larvae were taken at 300 feet and none at 600 feet. The prevailing winds were from the west. Several of the eggs but none of the larvae had wax threads from adults attached to them.

The capture of larvae on so small an area at 300 feet indicates that many are carried at least this distance by surface winds. Occasional grains of sand almost as large as the egg were found on the slides, and it was evident that this horizontal movement took place during the periods of strong winds. The relation of weight to surface area of the larva and the egg would be much less than that of the sand grains, and their buoyancy is doubtless sufficient to permit them to be carried to considerable heights when wind is accompanied by vertical air currents caused by sloping ground, convection or turbulence. As shown by Wellington (43), this would not be likely to result in transportation of a wingless insect over very long distances, but it is conceivable that so small an insect would often reach the 'plankton zone' and be carried at least several miles.

The prevailing summer winds in this region are from the southwest ; and the spread of *A. piceae* has, of necessity in recent years, been usually against them or across them (Fig. 1). The greater spread along the east coast of New Brunswick may be the result of prevailing wind direction. It is of considerable interest that the beech scale, *Cryptococcus fagi* (Baer.), a European species of similar size and habits, has had a very similar history of introduction and spread (16). The scale was introduced into Nova Scotia about the end of the last century, and its present distribution is very similar to that of *A. piceae.* Both insects illustrate the power of a small, wingless, parthenogenetic species to spread at a rate of several miles per year against the prevailing wind direction.

Successful establishment of air-borne larvae depends largely on their longevity, and their ability to travel in search of feeding sites after reaching a stand containing balsam. Experiments already described indicate that the motile stage can live over 8 days and crawl over 100 feet. It is probable that many drop on the ground after being carried in the air, but are capable of reaching the bases of trees within this distance.

Moulting and Renewal of Stylets

In the sistentes the mandibular and maxillary stylets are extremely long, sometimes five times as long as the body. The length varies between individuals but does not increase as the insect develops. The following measurements were made on specimens selected at random from the stem of a tree with a diameter of 8 inches. The length given is from the tip of the rostrum to the end of the stylets and indicates the depth to which they can be thrust into the bark.

Instar	Number	Range in mm.	Average in mm.
1	20	1.35 — 1.90	1.45
2	15	1.40 — 1.85	1.51
3	8	1.30 — 1.75	1.47
4	20	1.40 — 1.90	1.54

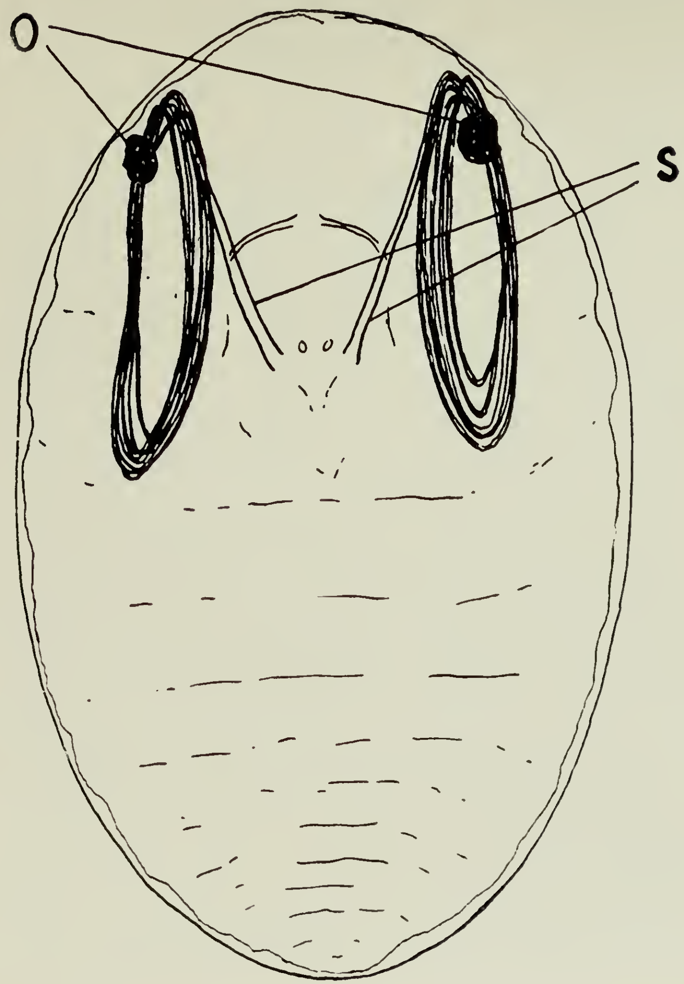

Fig. 18. Egg showing position of coiled stylets in developing embryo. O, ocelli; S, stylets. X250.

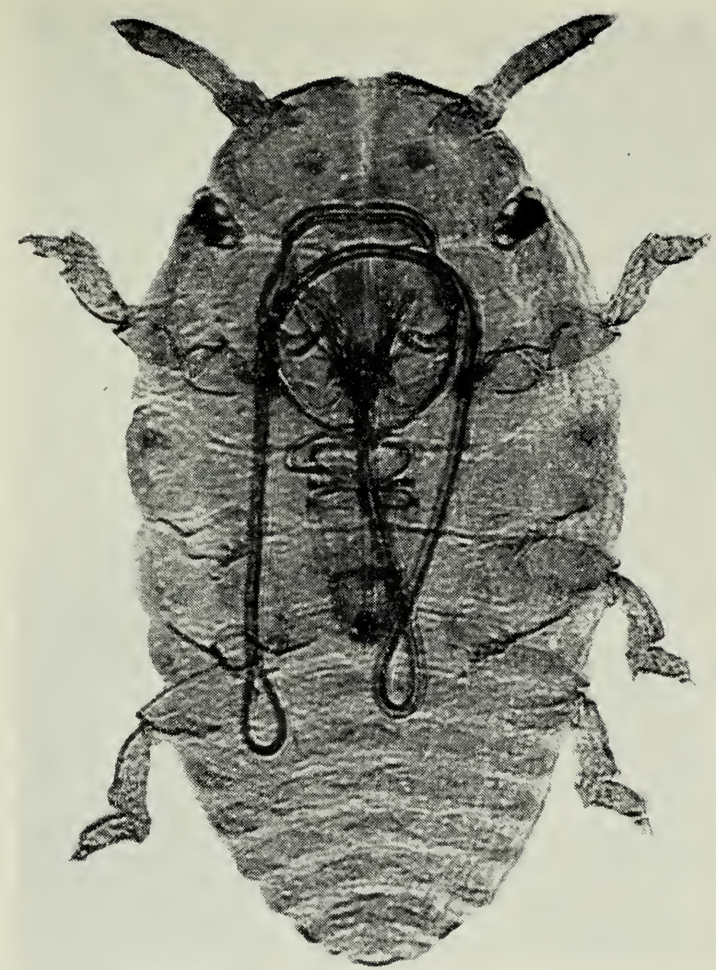

Fig. 19. Newly hatched neosistens showing stylets coiled within body. X240.

It was observed in 1931 that the stylets are completely renewed at each moult. Since the insect remains stationary during its development, three sets of discarded stylets, with the cast skins attached, are found inserted in the bark behind each adult. This has been found to be the case with all other adelgids examined and provides an easy means of identifying the instars.

In the embryo the stylets can be seen as two circular coils within the cephalic half, one on each side (Fig. 18). Each coil contains a mandible and a maxilla lying close together. Immediately after hatching they are uncoiled and united at the base of the rostrum to form a double-channelled tube, which is thrust out beneath the labrum through a groove in the labium. It is then looped back within the body, as shown in Fig. 19, where it lies presumably in a crumena. When the larva settles it thrusts the stylets into the cortex, generally to their extreme length.

The moulting of the larva is preceded by a partial withdrawal of the stylets. The skin then splits down the frontal median line from the thorax to the labium. It is gradually worked backward by movements of the body and legs until completely free. The old stylets, including the basal sclerites, are drawn from the base of the rostrum as the insect frees itself from the exuviae.

Immediately after moulting the new stylets are found coiled within the cephalothorax, much as in the embryo but with the tips united within the rostrum. They are apparently drawn into the labial groove as the old stylets are pulled out. The new instar is now free and capable of slow movement, but it almost invariably reinserts the mouth parts at the same spot, or slightly in front of it. In several cases it has been observed that before or during the process of insertion the stylets were extruded in a loop from beneath the tip of the labrum. It is not certain whether this is an invariable procedure ; if so, it is in contrast with the behaviour of the neosistens. The containing of the long stylets within the body is an obvious necessity for a motile larva, but not for the stationary instars.

Weber (42), in 1930, described the renewal of the stylets in several species of Hemiptera. Heriot (7) made similar discoveries independently and in 1934, showed how they were built up by coiled invaginations of hypodermal cells. According to Weber, species with long stylets may carry them in a crumena in the thorax, coiled in the preoral cavity, or looped outside the body. There is nothing in the work of either author to indicate that two methods may be used in different stages of the same insect.

Method of Feeding

Histological Studies. — Many sections were made of new shoots and bark in which the insect had been feeding. The most satisfactory results were obtained by using Carnoy's fluid as a fixative, embedding in paraffin, and staining with safranin and light green. The two stains gave a brilliant contrast between the stylet tracks and the plant cells. The following conclusions are drawn from the examination of this material (Figs. 20, 22).

1. The stylets are inserted intercellularly and seldom, if ever, penetrate the cell wall.

2. They pass through the epidermis or phellem into the cortex or phelloderm, and feeding takes place only in the parenchyma. In young shoots, however, the phloem is sometimes penetrated slightly.

3. The insertion of the stylets is accompanied by ejection of a salivary substance from the tip of the maxillae. This forms a sheath around the stylets that can be seen at the point of entrance and lining the path of the stylets. The substance occasionally flows into adjoining intercellular spaces.

Fig. 20. Transverse section of cortex of 1-year-old twig of *Abies balsamea,* showing stylets (S) inserted intercellularly and tracks (T) between cells. Note thickening of cell walls near stylets. X120.

Fig. 21. Transverse section of shoot of *Abies balsamea* at base of bud. Note pocket of enlarging cells, stylets tracks, and attraction of nuclei at T, also proliferation of surrounding tissue. X90.

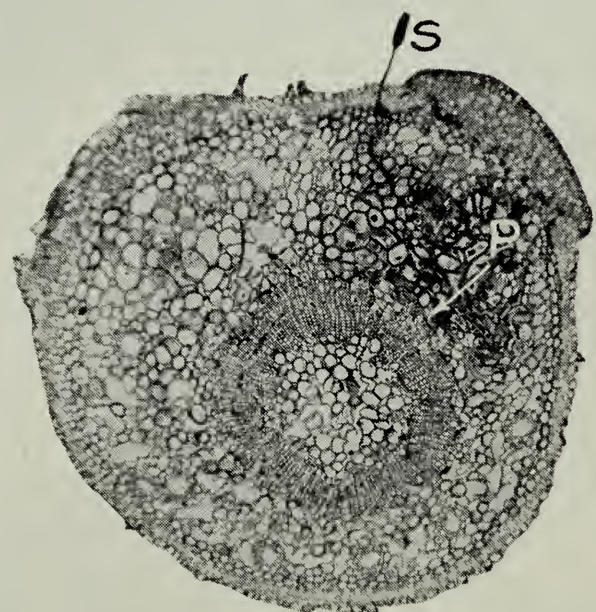

Fig. 22. Transverse section of 1-year-old shoot of *Abies balsamea* showing stylets (S) inserted at base of needle and interference with growth of phloem (P). X20.

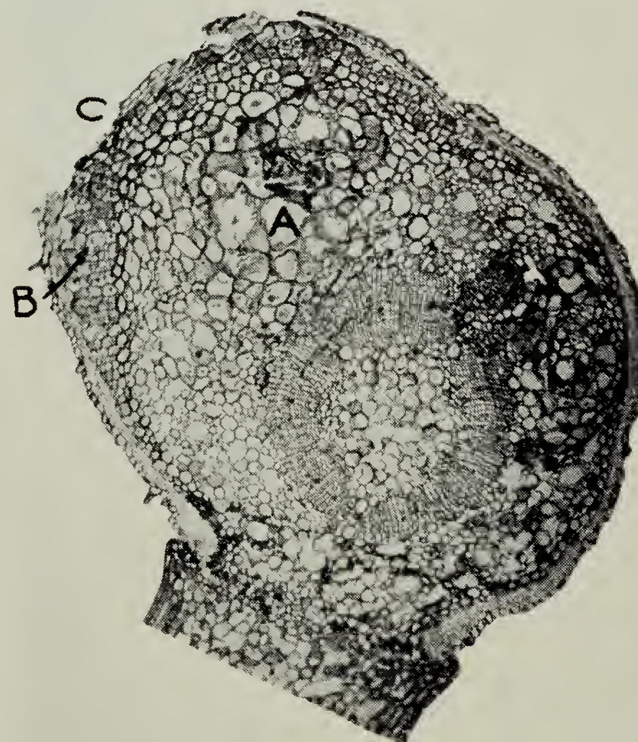

Fig. 23. Transverse section through swelling on 1-year-old twig of *Abies balsamea* infested in June. Sectioned in January. Note giant cells (A), proliferation from phellogen (B), and rupturing of epidermis (C). X20.

Fig. 24. Transverse section of 1-year-old twig of *Abies balsamea* showing ridges in cell walls of giant cells at A. X60.

4. The neosistens often inserts its stylets to their full length before entering diapause, and causes abnormal growth in the parenchyma and cambium before actual feeding commences. This stimulation occurs if the larva is removed before the end of its period of rest. It affects the cambium even in thick bark where the point of ejection is as much as 5 mm. from the cambium.

5. Feeding is carried out by repeated partial withdrawal and reinsertion of the stylets in a new direction. The tracks are branched so as to affect a roughly spherical pocket of cortical tissue.

Fig. 25. Transverse section of 1-year-old twig of *Abies pectinata*, infested in June, sectioned in January. Note pocket of enlarged cells at base of needle (N) and absence of proliferation. X60.

6. The direction of penetration is under the control of the insect and is not determined solely by the path of least resistance. Where the path is devious it is often jagged, indicating a trial-and-error method of probing.

Observations of stylet action. — The method by which long thread-like mouth parts of this kind are controlled is of great interest and until recently has been considered an "outstanding entomological mystery" (36). In 1930 Weber (42) showed that in several species of Hemiptera penetration was effected by an alternating protraction of the mandibles followed by protraction of the maxillae. Heriot (17) stated that this action was inadequate in the case of an aphid and a scale, and presented evidence that the stylets were inserted by means of successive short holds contrived by the joint action of the labrum and the labium. He showed that the scale lacked directional control and that this was compensated for by the length of the mouth parts. It was not possible to see the action of the stylets of *A. piceae* under natural conditions because of its small size and the fact that it is closely appressed to the plant. A few observations, however, throw some light on the question.

A number of first-stage larvae were lifted gently so that the stylets were partially drawn out of the bark and the larva was left supported by them. Invariably the larva began to wave from side to side. The body was thrown sideways with a jerky motion which was repeated about every 2 seconds. This suggested that the mandibular stylets, which are locked together by grooves to form a sheath for the maxillae and are capable of sliding upon each other, were being alternately protracted or retracted by the muscles at the base in an effort to reinsert or withdraw them. This was proved when the mandibles were partially separated by pressure with a fine needle. A loop was then formed alternately on each side as the larva continued its movements. As the distal ends of the mandibles were held in the bark and the insect had no purchase with its legs, their protraction or retraction would result in the above effects instead of insertion or withdrawal of the stylets.

When the adult was raised so that the greater part of the stylets was withdrawn, the body was too heavy to be supported and a rhythmic twisting or writhing of the mandibles resulted. If the adult was lifted a short distance, so that not much over 0.5 mm. of the stylets was exposed, it was capable of reinserting them if left in its normal position with the tarsi on the bark.

When the stylets were removed from the bark, slight rhythmic flexing was observed. When the tip of the stylet bundle was cut off, in some cases the remaining part was waved vigorously from side to side. This was thought to be due to the severed tips having become locked together as a result of the operation.

Attempts were made to observe the penetration of the stylets by placing newly hatched larvae on Petri dishes into which gelatin containing an infusion of balsam bark had been poured. A few appeared to settle, but when the plate was inverted and examined under the microscope only one was found to have extended its stylets. The maxillae were seen to be protruding a very short distance beyond the mandibles. Failure to sterilize the larvae and prevent contamination discouraged further attempts at artificial feeding, and it remains uncertain whether the tip of the maxillary tube precedes the mandibles during insertion. It is more probable that in the above case the stylets were being withdrawn.

A larva was observed shortly after hatching to have its stylets fully extended behind it. While it remained practically motionless the stylets were drawn into the body, the process taking about 15 minutes. Heriot (18) described similar behaviour in *Adelges abietis* (L.) and noted that the mandibles were retracted alternately a short distance, and then the maxillae.

When the mandibles were separated by pressure with a needle the tips were found to be smooth-pointed and curved inward.

The following conclusions were drawn.

1. The stylets are withdrawn by means of the retractor and protractor muscles at the base, aided by a clamping action in the groove of the labium or the heart-shaped process at its tip (Fig. 19). First one mandible is retracted a short distance, sliding on the other, with which it grooved. Then the other is drawn back, followed by the maxillae. The whole fascicle is then clamped in the labium while the bases are protracted, forcing the stylets into a loop within the crumena, or outside the rostrum, preparatory to a repetition of the process.

2. The reverse process is probably used to insert the stylets into the bark, aided by a dissolving action of the saliva on the middle lamella. It seems doubtful, however, whether the necessary force can be transmitted throughout the length of a tight, sharply bent, double loop such as is found in the young larva (Fig. 19). This would imply a remarkable freedom from friction in the grooves of the mandibles.

When the insect is inserting its stylets, the tip of the labium is turned downward under the centre of the body and the body is seen to move up and down. This suggests that another process is also employed and additional force is obtained by taking a short hold with the labium and thrusting the fasicle forward a corresponding distance.

3. The directing of the stylets is probably effected by advancing the tip of one mandible ahead of the other. As the tips are curved inward this would deflect the stylets away from the side of the advanced mandible. A partial rotation of the body, such as has been seen to take place, might facilitate the control of the thrust in almost any direction permitted by the cell walls.

4. As Weber (42) suggested, the nerves at the bases of the stylets give them a tactile sense and are also capable of transmitting chemical stimuli as the food is drawn up to reach the taste organs. Thus the obstruction of cell walls would be felt and the absence of satisfactory food detected, prompting the necessary withdrawal and redirection of the stylets.

NATURAL CONTROL

Population Trends

Direct attempts to measure populations had to be abandoned, because of the amount of work and the difficulties involved in quantitative sampling with this type of insect. The progress of infestations was followed, however, on 24 plots of 1 square chain, which were established at various points in Nova Scotia and New Brunswick between 1931 and 1933. The degree of infestation and condition of each tree were recorded annually for 3 to 8 years. General notes were made on other stands for as many as 15 years. The following conclusions were drawn regarding local population trends.

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

2. The population rises more or less steadily in the stand for a number of years, unless checked by unfavourable weather such as the winter weather in 1933-4. It finally reaches a peak at which a considerable number of the trees may be killed, or severely injured, by attack on the stems.

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

In other words, the first outbreak in a stand is generally the most severe, provided it is not checked by unsual weather. The local trend, which is determined chiefly by biotic factors, is subject to a regional trend which is determined chiefly by climatic factors. The regional trend in New Brunswick seems to have shown a peak between 1930 and 1933, and there were signs that another was developing about 1948.

Studies of the factors controlling population were preliminary in nature. A good deal of further work will be necessary before their complex interrelationships are understood, but a number of observations and experiments will be described to indicate some of the more important factors.

Biotic Potential

Since reproduction is by thelytokous parthenogenesis the potential rate of multiplication is not limited by the necessity of mating. As indicated above, the largest number of eggs observed from one adult was 248, but the average for the hiemosistens was probably not more than 100 and for the aestivosistens not more than 50. These are rough approximations, as the number varies greatly from tree to tree. They indicate a potential annual multiplication of X 5000 for an average population.

Some data were obtained in 1935 on the survival of offspring from individual hiemosistentes under optimum conditions. On May 23 a lightly infested tree, 9 inches in diameter, was chosen in a recently infested stand. Five adults were isolated by placing a ring of tree tanglefoot around each at a radius of 4 inches. The enclosed space was cleaned of all unhatched eggs and all stages except the first; the second and third were not separated. Previous attempts had shown that when smaller areas were enclosed many larvæ crawled into the tanglefoot. Some loss resulted from this, but it was reduced by freshening only the outer margin of the tanglefoot. The results are summarized in Table 2.

TABLE 2. — DEVELOPMENT AND SURVIVAL OF OFFSPRING OF 5 HIEMOSISTENTES ON STEM OF LIGHTLY INFESTED TREE.

	Hiemosistentes	Aestivosistentes				Hiemosistentes	
	Adults	Eggs	I	II+III	Adults	Eggs	I
May 23	5	15					
June 2	5	98					
June 15	5	167	P*				
June 24	5	185	P				
July 4	3	102	P				
July 20	0	21	P	12			
Aug. 4			P	76	38	P	
Aug. 17			P	117	175	P	P
Sept. 1			?	42	260	P	P
Sept. 13			?	18	288†	P	P

* Present, not counted.
† Including dead.

The number of offspring reaching the adult stage was almost 60 per parent, and ranged from 41 to 75. The mortality occurred chiefly in the first stage. Some got into the tanglefoot and others failed to develop. The high survival was attributed to protection from the weather by a heavy crown, absence of predators, lack of competition, and a favourable condition in the tree. That the tree was a favourable individual was indicated by the rapidity with which it became heavily infested the following year.

Climatic Factors

High temperature. — No evidence was found that mortality results from high air temperatures in shade. In 1935 a temperature of 100° F. was recorded at Fredericton, but none of the stages appeared to suffer any direct injury. The average annual highest is 91° F.; the highest on record is 101° F.

There is, however, high mortality on the south side of stems exposed to the sun. Often part of the south side of such stems is free of 'wool' while the rest is covered. Several experiments were carried out to determine whether this was the effect of the sun.

Experiment 1: On July 28 an infested tree, 12 inches in diameter, with its south side fully exposed by a cutting, was selected. Two circular shields were fitted around the stem, one 4 feet above the other, so that they jutted at 45° and protected an area beneath them from rain. One was of canvas and gave shade from the sun; the other was of transparent celluloid.

Beneath the canvas the larvae settled down and developed on all sides of the tree. Beneath the celluloid relatively few larvae settled on the south side, and these all died before developing.

Experiment 2: On June 14 the stem of a heavily infested tree, 7 inches in diameter, was cut into sections 18 inches long. These were placed as follows:—

(a) In the open, leaning to the north at 45°.
(b) In the open, lying horizontally north and south.
(c) In the open, standing vertically.
(d) Same as (b), but shielded from the sun.
(e) Same as (c), but shielded from the sun.
(f) Protected from rain and sun.

After a clear, calm day, with a maximum air temperature of 75° F., the sections were examined. Sections (a) and (b) showed all stages dead over one third of the surface on the side facing the sun. On section (c) a number of eggs had been killed, but those that were shaded by wax threads or lichens were living and later hatched; there was no significant mortality among the adult or larvae. The remaining sections were unchanged.

The following day, after a heavy thunderstorm, observations were made of the effects of the rain. On sections (a), (b), and (d) the 'wool' was matted down and most of the eggs had been washed off the upper third. On the vertical sections (c) and (e) the 'wool' was matted somewhat on all sides, uncovering many of the eggs; and some of the eggs had been broken from their silk threads and washed downward.

This experiment was set up again on the evening of June 23. June 24 was clear and calm, with a maximum temperature of 78° F. By 1.00 p.m. all eggs on the south quarter of sections (a), (b), and (c) were darkened and shrivelled and other stages appeared dead.

Experiment 3: On June 21, a clear day with a strong breeze and a maximum temperature of 74° F., two sections of an infested stem were placed horizontally in the sun. One was fully exposed to the breeze, the other sheltered by two walls. Examination at 3.00 p.m. showed that practically all stages were dead on the top of the sheltered log, but there was little sign of mortality on the log exposed to the wind.

Experiment 4: Four small trees in the nursery were given varying degrees of protection from sun and rain, as follows:—

(a) A large sheet of glass horizontal above the tree.
(b) A cage with sides of fine wire screening and top of factory cotton.

(c) A box, with a wide slit down one side, covering the north half of the tree.
(d) Uncovered.

These trees were infested on June 2 by placing, on a lower branch, bark carrying many eggs. During the season a moderate infestation developed on (a), but it was largely confined to the undersides of the branches and parts shaded from the noon sun. A heavy infestation developed over the whole of (b). On the uncovered part of (c) a light infestation occurred on the undersides of the branches. On the covered part a moderate infestation of larvae was present on all sides of the branches when the box was removed on June 19. By September this tree was infested lightly on the stem only. The uncovered tree developed a light infestation, chiefly on the stem and the undersides of shoots and branches.

Experiment 5: A large number of motile larvae were placed on sheets of cardboard, one covered with white paper, the other with black. The sheets were exposed at right angles to the rays of the sun on June 23 at 3.30 p.m., in clear, calm weather. In less than 10 minutes all those on the black paper were dead. On the white paper the larvae were very active, but none died within an hour.

This experiment was repeated on July 12 between 11.00 a.m. and 12.30 p.m. On the white paper the larvae crawled rapidly for 40 minutes and 1 died. On the black paper, in 10 tests, all the larvae stopped moving within 10 seconds and some in 4 seconds. One lot was given only 8 seconds exposure and none survived. It was évident that death was caused by the high temperature at the surface and this was much higher on the black surface, which absorbed the heat of the sun.

Attempts were made to measure the temperature on the surface of the paper and different parts of the bark of trees exposed to full sunlight. A thermocouple of fine iron and constantin wire was used with a Leeds and Northrup potentiometer. The junction was shaded with a small paper shield and moved forward over the surface while readings were made. The method probably does not give accurate temperatures, but the following results permit comparisons between diferent surfaces.

Surface	Air movement	Air temperature	Maximum temperature on surface
Stem	Slight	80° F.	125° F.
Stem	Strong	65° F.	87° F.
Twigs	Slight	80° F.	102° F.
Black paper	Slight	86° F.	130° F.
White paper	Slight	86° F.	109° F.

From the above experiments and from observations on naturally infested trees the following conclusions are drawn.

1. Mortality from high temperatures occurs only on surfaces exposed to direct sunlight.

2. All stages may be killed where the midday sun strikes the bark during summer, in clear, calm weather. First stage larvae and eggs are more susceptible than later stages, which are partially protected by their covering of white 'wool'.

3. Death results from the high temperature at the surface of the bark. The darker the surface and the larger the area the higher the temperature.

Death is least likely to occur on new shoots because of their small area and light colour.

4. Protection is afforded over most of the stem by the shade of the crown. It is also found on the undersides of twigs and branches, beneath old bud scales, in bark crevices, and beneath mosses and lichens on the stem.

Rain. — On the upper sides of branches and the more exposed parts of stems, rain mats down the wax threads of the last three instars and sometimes removes them entirely. This may contribute to mortality from direct sun. Heavy rain also washes some of the eggs from the tree.

In periods of wet weather first-stage larvae are often covered with a film of water for a day or more, particularly when they lie in crevices. To test the possibility that this caused mortality, 2 pieces of stem infested with the first instar were immersed in water for 2 and 6 hours respectively. They were placed in an incubator at a relative humidity of 100 per cent. After 24 hours they were still wet. They were then allowed to dry and were incubated, with an untreated check, at 90 per cent R.H. A week later 100 larvae were examined from each piece and classified as living or dead. The number dead was 38 in the lot soaked 6 hours, 32 in the lot soaked 2 hours, and 41 in the check ; there was no evidence of mortality attributable to the water. *Adelges piceae* appears to be well protected from drowning by its wax secretions.

Low temperature. — Samples of infested stems were brought into the laboratory at various times during the winter to determine the insect's ability to survive low temperatures. If the bark was left attached to a piece of wood 6 by 8 inches and 2 inches deep, and placed in an incubator at a temperature of 70° F. and a relative humidity of over 90 per cent, feeding and development occurred for about 10 days before mortality resulted from the drying of the bark.

One sample brought in on November 29, after a minimum temperature of 30° F., showed that representatives of all stages were still living. A few eggs hatched and several adults resumed oviposition. A later sample brought in after —5° F. had been recorded showed that all stages were dead except the neosistens. The minimum lethal temperature for all stages except the overwintering first instar is probably close to 0° F.

The percentage of the wintering sistentes that survives the winter varies considerably from year to year. It is not easy to estimate, as those that die during the winter cannot always be differentiated from those that die in the summer or fall. In fact it is sometimes difficult to distinguish the living from the dead until spring development takes place. This is best done after incubation for a week. If the larvae are then lifted with a needle under a dissecting microscope they generally show some movement if still alive.

Some estimates of winter mortality were made in the spring for 6 years by counting only those larvae that had a sufficiently fresh appearance to indicate they had probably been alive in the fall. It is important to avoid trees on which mortality may have occurred because the bark had become unsuitable for feeding as a result of heavy infestation. The estimates ranged from 20 to 100 per cent. Although the data were of dubious significance, except in the latter case, they corresponded fairly well with subsequent observations of the amount of infestation developing on the trees.

Samples taken at Fredericton on February 20, 1934, indicated that all the larvae above the snow were dead. A minimum temperature of —32° F.

had been recorded on February 17 and 18. The following June, examination of many trees in central and southern New Brunswick showed that no fresh 'wool' had appeared above 2 feet from the ground, and generally not above 18 inches. This was about the average depth of snow around the bases of the trees. Near the coast where winter temperatures were less severe, there was some survival above the snow. It should be noted that the depth of snow around the bases of the trees is often less than the general depth, as it tends to be reduced by the combined effects of wind and higher temperatures near the stems.

It was concluded that the insect could not survive temperatures below approximately —30° F. In 1948, however, a considerable part of the population survived temperatures of —30° F. on February 5 and —31° F. on February 10. Samples taken in the spring by N. R. Brown (7) showed a mortality of 82 per cent above and 51 per cent below the snow. It may be that the population has become more resistant to low temperature, through natural selection among the descendants of those that survived the severe winter of 1933-4 under the snow. The lethal minimum is probably close to —32° F., but it is doubtful whether a difference of 1° is sufficient to explain the difference in mortality during the two winters. It is more likely that the effect of minimum temperatures is dependent on other factors such as length of exposure, humidity, or air movement. Lack of equipment capable of producing sufficiently low temperatures prevented experimental studies of these factors.

It may be concluded that winter mortality is of prime importance in limiting the rate of multiplication and that it is closely related to minimum temperature. Complete mortality above snow, however, occurred in only one year between 1931 and 1948. Its effect was mitigated by the protection afforded by snow to a small part of the population at the bases of the trees.

Studies of permanent sample plots between 1934 and 1938 showed that on some trees the population built up rapidly from below the snow line. On one tree 50 feet in height the larvae had spread 35 feet up the trunk by the fall of 1934, although the great majority were within 6 feet of the ground. By 1936 scattered trees were heavily infested and these began to die in 1937.

The effect of severe winters such as that of 1933-34 is to confine the population to the lower parts of the trees and encourage attacks on the stems. This probably accounts in part for the more frequent occurrence of such attacks toward the interior of New Brunswick and the more general occurrence of attacks on the twigs near the coast. Winter mortality may also affect rate of spread and partially explain the fact that the insect became generally distributed first in areas within about 25 miles of the coasts of the Maritime Provinces and the State of Maine. However, it has not prevented severe infestations developing as far west as Greenville, Me., and Northfield, Vt., where minimum temperatures of —36° F. and —41° F. have been recorded. Table 3 shows minimum temperatures and snowfall for a number of points in the Eastern Provinces. It indicates that some of the lowest temperatures occur within the present area of establishment. It also shows that near the coast temperatures do not drop to —30° F. south of Chatham. Snowfall is generally highest and the snow cover deepest at the points where temperature is lowest. It is sufficient to prevent the distribution of *A. piceae* from being limited to coastal regions. In Fig. 1 are shown minimum temperatures recorded at stations inside and outside the area of distribution.

TABLE 3. — MINIMUM TEMPERATURES AND SNOWFALL AT VARIOUS LOCALITIES IN EASTERN CANADA AS RECORDED BY THE METEOROLOGICAL DIVISION, DEPARTMENT OF TRANSPORT, OTTAWA.

STATION	Length of record Years	Average annual lowest ° F.	Lowest 1933-1934 ° F.	Lowest on record ° F.	Average annual snowfall Inches
Charlottetown, P.E.I.	65	−13	−19	−27	113.0
Annapolis, N.S.	25	− 6	−11	−13	74.8
Halifax, N.S.	75	− 8	−12	−21	70.8
Sydney, N.S.	69	−11	−23	−25	79.9
Yarmouth, N.S.	59	0	− 8	−12	80.0
Chatham, N.B.	50	−26	−34	−43	107.3
Fredericton, N.B.	67	−25	−32	−35	95.5
Saint John, N.B.	56	−13	−21	−21	71.1
Quebec, Que.	72	−23	−32	−34	123.7
Montreal, Que.	55	−18	−29	−29	112.3
Ottawa, Ont.	65	−24	−34	−35	82.0
Morrisburg, Ont.	..	....	−38	....	....
Woodstock, N.B.	..	....	−38	....	....
Edmundston, N.B.	..	....	−36	....	....

Biotic Factors

The percentage mortality caused by winter temperatures and other climatic factors may be high and periodically reduce the population to a low level. It is not, however, dependent on the density of the population ; and, as Nicholson (24) has shown, the level to which animal populations rise is controlled in the long run by the biotic, or density-dependent, factors. In the absence of other biotic factors that are capable of effective control, increasing as the insect population rises, the upper limit of the population must be determined by intraspecific competition and starvation. In the case of *A. piceae* this is accompanied by severe injury and generally followed by the death of the host.

The biotic factors that operate prior to this stage of over population are therefore of particular importance in economic control. The Adelginae appear to be free from attack by parasitic insects, and no evidence of parasitism of this species was found. Predacious insects are the most effective natural enemies. As the native species were evidently inadequate several European species were introduced, as indicated below.

NATIVE PREDATORS. — Between 1932 and 1934 studies were made of the native species found attacking *A. piceae* on plots near Fredericton, N. B. The following is a list of those that could be identified. The identifications were obtained through the assistance of Systematic Entomology Unit, Division of Entomology, Department of Agriculture, Ottawa.

Trombiidae : A small orange-red mite was frequently found feeding on the second to fourth instars, during June. It was very occasionally numerous enough to kill about 25 per cent of the insects on some trees. Adults were not taken.

Hemerobiidae : Three species were found occasionally. One was identified as *Hemerobius stigmaterus* Fitch.

Miridae : *Psallus piceicola* Kngt. was found feeding on another species of *Adelges* and was successfully transferred to *A. piceae*.

Anthocoridae : One specimen of *Tetraphleps canadensis* Prov. was seen feeding on eggs.

Coccinellidae : *Anatis quindecimpunctata* Oliv., *Cleis picta* Rand., and *Coccinella monticola* Muls. were taken occasionally. *Chilocorus bivulnerus* Muls. was found more frequently, also at Gagetown and Oak Bay, N. B. This species is very numerous on trees heavily infested by the beech scale, *Cryptococcus fagi* (Baer.), which often occurs in the same stand with *A. piceae. C. bivulnerus* shows a strong preference for the scale. It is sometimes heavily parasitized.

Syrphidae : Syrphids were very common on infested trees in 1932 and 1933 and were undoubtedly the most important group among the natural enemies. Their effectiveness was limited by heavy parasitism, particularly by an unidentified ichneumonid. They were seldom found on any but fairly heavily infested stems, where they became numerous only about the time that the injury to the tree was already severe. Their presence is indicated by a ragged appearance of the 'wool' on the trees. The following notes were made on 3 species.

Metasyrphus lapponicus (Zett.). Possibly an American form of this European species. Fed also on other species of *Adelges*. Not numerous but of fairly general occurrence. Two generations. Adults emerged in late June and between September 5 and October 4.

Metasyrphus wiedemanni (Johns.). Fairly common on heavily infested trees. Adults emerged during last week of August. Larvae mottled grey, brownish, or pinkish above, olive grey below ; each abdominal segment with two more or less prominent tubercles which become less conspicuous toward maturity ; not distinguished from *M. lapponicus*.

Syrphus torvus O. S. More common than the other species. Overwinters as an egg. First instar present middle of May, mature larvae first week in June, adults in early July. Fed mainly on adults but occasionnally on eggs and larvae of *A. piceae*. Egg 1 mm. long, elongate oval and thicker at one end, greyish-white ; surface covered with regularly placed excrescences consisting of a stem and an enlarged flattened end with the flat sides facing transversely and connected by an irregular reticulation of the chorion. Mature larva black and orange above, olive green to grey below, without prominent tubercles.

In the study of this predator a cage of close-meshed wire was placed around a heavily infested stem 7 inches in diameter. It was erected on May 13, enclosing 4 feet of the stem, on which many young larvae of *S. torvus* were present. By June 8 the larvae had consumed all of the host within the cage, except those of the first instar, and were found in considerable numbers at the bottom. Outside the cage syrphids were then scarce and the predation was only slight. This indicated that the syrphid was numerous enough to destroy all of its host except the neosistens, but outside the cage this was prevented by natural enemies. These natural enemies were not determined. Parasitism outside the cage did not seem to be sufficient to explain the result. Chicadees and nuthatches were often found feeding on infested stems and it is thought they were eating the predacious larvae, but proof was not obtained.

Octhiphilidae : *Leucopis americana* Mall. was common but not numerous. The larvae are generally found burrowing beneath the matted 'wool' of the host, where they feed on the second to fourth stages. There are at least 2 generations, adults appearing during the latter part of June and about the end of August. Puparia were found on the bark in winter. This species is parasitized fairly frequently by *Pachyneuron altiscum* How.

Neoleucopis pinicola Mall. was taken only occasionally. Adults occurred during the second week of July.

Introduced predators.—*Leucopis obscura* Hal. was referred to by Tragardh (41) as an important predator in Sweden. In 1933 it was introduced from

Europe through the Dominion Parasite Laboratory, Belleville, Ont., and 1,628 adults were liberated near Fredericton. Another colony of 396 was liberated near Gagetown, N. B.

The Fredericton liberations were made in June in a small stand where there were a number of heavily infested trees. On August 5 a large number of adults were seen flying about several of these trees. In September larvae were numerous, and during November one tree showed an average of 9 puparia per square foot on the lower stem. During the following winter all were killed above the snow, as well as the host. Most of them survived, however, below the snow ; and during the next few years the predator became very numerous, outnumbering all the native predators combined and largely replacing the native syrphids and *L. americana.*

During 1936 further liberations were made of adults reared from puparia taken from trees at Fredericton. Colonies were put out at the following points in New Brunswick : Jemseg, Burton, New Maryland, French Lake, and Geary. In 1941 colonies were placed at Fortune Bridge, P. E. I., and near Liverpool, N. S.

Recoveries have been made over an increasingly large area, and studies by N. R. Brown (7) in 1947 and 1948 show that *L. obscura* has established itself throughout most of the area in which *A. piceae* occurs. In 14 years it has spread more than 150 miles from the nearest point of liberation. This is a remarkable case of rapid dispersal and successful establishment. There can be little doubt that the species was not present in North America before its introduction in 1933. G. E. Shewell, Division of Entomology, Ottawa, pointed out that it is so markedly different from all known American species, and yet so clearly a member of the genus, that there is no possibility of its being present in collections under another name. If present before 1933 it could hardly have failed to be represented in earlier collections. It was not found during 1931 and 1932 but became numerous at points of liberation immediately after 1933.

In spite of its success in becoming established in large numbers, *L. obscura* has not given adequate control. This appears to be due in part to the fact that it does not feed on the egg or the neosistens ; many of the adults destroyed have already laid a number of eggs ; also, it becomes numerous only on trees that are already heavily infested and severely injured. Its failure to establish itself on lightly infested trees is the result of the limited searching ability of the larvae, a characteristic of predators as a group that makes them generally less effective than parasites, as pointed out by Smith (38). Its success in maintaining its population at a high level is probably due to the fact that it does not cause a severe reduction of the numbers of its host except on trees where they would be reduced eventually in any case by the injury to the bark. Hence it feeds chiefly on the surplus population, and new infestations develop as a source of food for subsequent generations.

The native parasite *Pachyneuron altiscum* attacks this predator, emerging from the puparium. Reeks (30) recorded 9 per cent parasitism in 1943 and Brown (7) 25 per cent in 1947. This species also attacks *L. americana.* It may be the first indication that native enemies will eventually increase the environmental resistance to *L. obscura,* bringing it closer to the status of a native insect.

It seems, nevertheless, that *L. obscura* has been very useful in checking the dispersal from heavily infested trees by reducing the number of eggs laid and of larvae produced in the final stages of attack. This reduction may often be sufficient to enable trees to recover. If this species were aided by other predators that attacked the egg and the neosistens, control might be effected at a lower level of host population and the killing of trees prevented. Other enemies are being sought in Europe by the Biological Control Investigations

Fig. 26. Infestation on smooth-barked stem showing concentrations at the rings of rough bark at nodes and at lenticels.

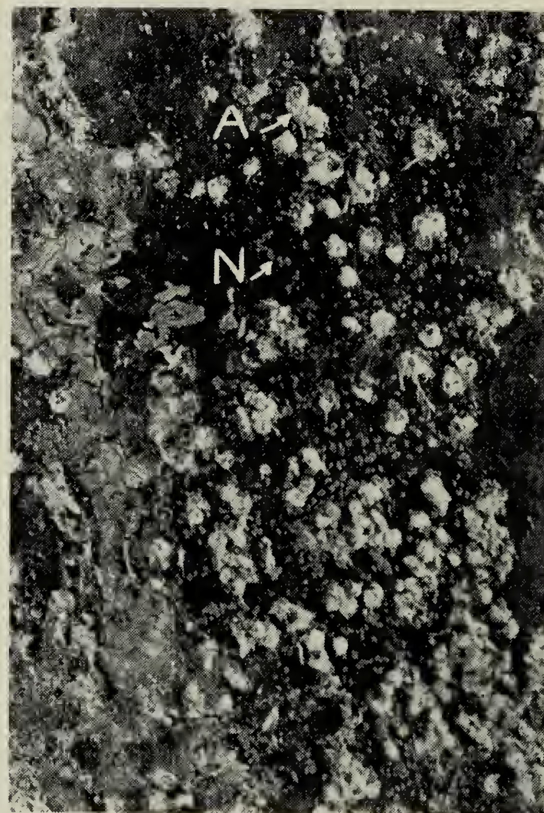

Fig. 27. Piece of infested bark showing neosistentes (N) on smooth bark after crevices have been occupied by previous generations of adults (A). X2.

Unit, Division of Entomology, Canada Department of Agriculture, through the Commonwealth Bureau of Biological Control.

The larvae, puparia, and adults of this species can be distinguished easily from *L. americana*. Its characters and habits have been partially described by Reeks (30) and Brown (7).

Liberations of other predators, obtained from England, have been made but none of these have been recovered and it appears that they did not survive the winter.

Exochomus quadripustulatus L.

Fredericton, N. B. — 1935 — 400 adults
" N. B. — 1936 — 1,450 "
" N. B. — 1937 — 7,864 "
Gagetown, N. B. — 1936 — 1,300 "

Hemerobius nitidulus Fabr.

Fredericton, N. B. — 1935 — 810 eggs

Hemerobius stigma Sch.

Fredericton, N. B. — 1935 — 1,331 eggs
" N. B. — 1937 — 2,177 "

Disease. — A pink fungous growth is often found on dead individuals of the second to fourth stages. It may possibly be the primary cause of death but does not appear to be of major importance and has not been studied.

The tree as a factor.—The power of multiplication of the insect is affected by the external conditions of the tree, and by the feeding conditions within the bark. The former are largely a matter of the amount of protection afforded from climatic factors and are related to the form and size of the tree. The latter are due to qualities of the bark tissue that may be inherent in the individual tree, or may vary with the age and condition of the tree. It is not always easy to determine whether external or internal conditions are responsible, but there is considerable evidence that some trees are more favourable to the multiplication of the insect than others.

It has been observed that in newly infested areas the insect first becomes numerous on the stems of particular trees. These are often the larger trees, or those with branches growing well down the stems. This was noticeable on the sample plots in New Brunswick. On the plots in Nova Scotia, where the insect had been present for a longer time, the infestation was more generally distributed in the stand although there was considerable variation in its intensity on different trees.

In 1933 a study was made of the balsam on 2 tenth-acre plots in a stand near Fredericton, which had become infested only a few years previously. The trees were classified according to the degree of infestation on the stem. Two increment cores were taken from opposite sides of each tree and the radial increment was measured for the period 1925 to 1929, as an indication of rate of growth before attack. Table 4 shows that the trees that had developed the heaviest infestations were, in general, the larger ones in the higher crown classes. All the dominant trees were heavily or moderately heavily attacked.

It is also shown that the trees that had become heavily, or moderately heavily, attacked were growing considerably faster than those that were still lightly infested or showed no signs of infestation. This seems to indicate that vigour of growth in the tree favours the multiplication of the insect. These faster-growing trees, however, were also the large trees, with more crevices in the bark and deeper crowns. It is likely that the protection from weather afforded by these characteristics was of major importance. It may be concluded, however, that at the age of this stand, approximately 50 years, a high rate of growth does not constitute a factor of resistance to the insect's powers of increase and may favour it.

Table 4. — Classification of trees on 2 plots at Fredericton, N.B., according to attack on stem in 1933, showing average diameter at breast height, percentage in each crown class, and rate of growth before attack.

	Infestation, 1933			
	Heavy	Medium	Light	None
No. of trees	24	29	13	19
Av. D. B. H.	9.0	7.5	6.4	5.4
Range D.B.H.	6–12	4–10	3–9	3–7
% dominant	38	7	0	0
% codominant	33	28	54	37
% intermediate	29	41	31	37
% overtopped	0	24	15	26
Av. radial increment 1925-9 in mm.	1.7	1.4	0.6	0.5

The results of the following attemps to produce artificial infestations provide further evidence that trees vary in their resistance to the survival and multiplication of the insect.

1. In experiments to determine the cause of 'gout', 15 small trees in the open were equally infested in June, 1932. A fair number of adults developed during the summer and initial symptoms of 'gout' were produced. On all but

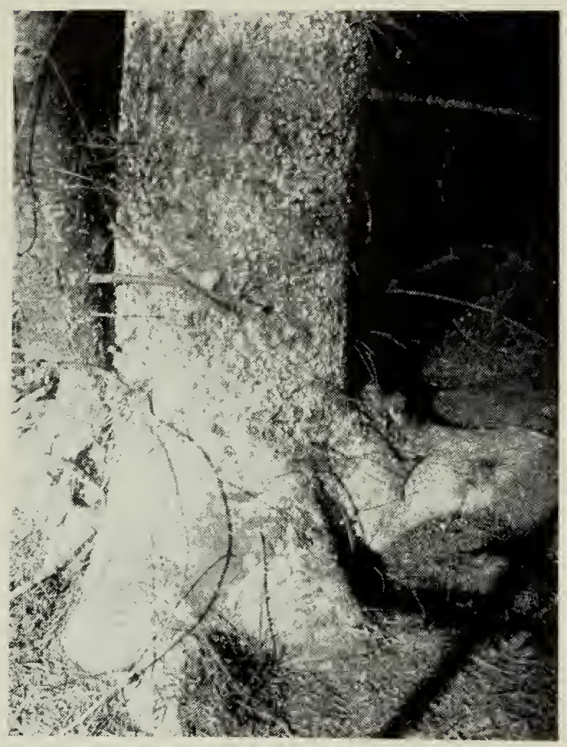

Fig. 28. Base of tree showing heavy infestation extending to surface of ground.

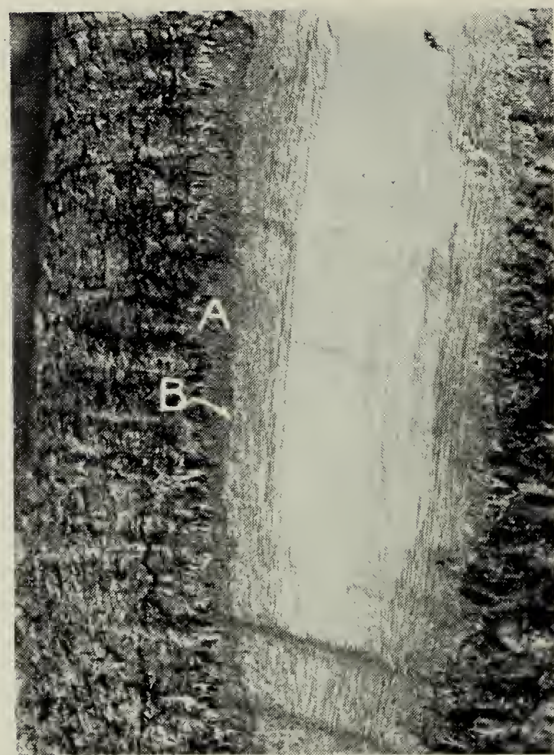

Fig. 29. Blaze on a stem that has been heavily infested, showing a superficial layer of dead bark (A) and underlying purple layer of cork cells (B).

2 of the trees, however, the infestations had completely, or almost completely, disappeared by the end of the second summer, and the trees recovered their normal appearance within the next few years. The other 2 trees were heavily infested the second summer and died a year later. These trees were noticeably bushy but otherwise similar in size, age, and vigour of growth.

2. On all small trees infested in the nursery and left unprotected, the infestations died out within 2 or 3 years, with the two following exceptions. These two trees were infested shortly after being planted in the spring, one with 30, the other with about 500 eggs. The former produced only 1 adult in the second generation, and it laid no eggs. The latter produced 10 adults in the second generation, but their offspring did not survive the winter. Two years later the trees, which had overcome the shock of planting and were now growing well, were each reinfested with approximately 1200 eggs. Moderately heavy infestations developed that year. The following year they increased until by fall the stems were almost covered, and both trees died during the winter. The greater success of the second infestations may have been due to the greater initial population, or to the improved vigour of the trees.

3. Six codominant trees, from 6 to 8 inches in diameter, were found to have suffered little injury although the surrounding trees in the stand had almost all been killed by severe attack. Several large pieces of bark covered with eggs were placed at the base of each tree. A fair number of larvae settled on the lower parts of the stems, but only a small number became adults and these produced few eggs. The infestations died out the following year.

4. Ten codominant trees, from 7 to 9 inches in diameter, were selected in an uninfested stand and infested in a similar manner. Larvae settled on all the trees. On 6, relatively few adults developed and in 2 years the infestation died out. On the other four there was a greater survival of larvae, the adults

were more prolific, and the infestation had become heavy on the lower stem in 2 years.

5. An attempt was made to infest the smooth internodal bark on the stems of 4 young trees 3 inches in diameter. About 9 inches of the internode was insolated by rings of cotton wool above and below, and pieces of bark with many eggs were tied between the rings. A large number of larvae settled on the stem, but except for a very few they crowded under the cotton. The cotton was removed after 10 days. Only a few of the larvae developed, and the next year the trees showed no signs of the insect.

From these results, and from observations of natural infestations, it is concluded that the survival of the larvae and the reproductive rate of the adults are controlled in part by conditions within the tree, in part by the degree of protection afforded on the surface of the tree. In general the larger, rough-barked trees with well-developed crowns favour the insect and provide the starting points for outbreaks in newly infested areas. Once an outbreak develops, the variation in the resistance of the trees becomes less apparent, as it is overcome by the excess of population.

The tree may show resistance to injury after it has become rather heavily infested, by laying down a secondary periderm below the tissue that has been killed by the feeding. In this way considerable areas of the bark may become covered by a layer of dead tissue that prevents the larvae from inserting their stylets into the parenchyma below. This most often occurs where the bark is fairly thick, but small areas may be cut off in this way on twigs. The ability of the tree to provide itself with this protection depends on its vigour and the fraction of the tree that is heavily infested. The cork cells of the periderm of balsam fir are reddish-purple and can be easily recognized beneath the hardened superficial layer of dead tissue (Fig. 29).

Conclusions

The following is a summary of conclusions concerning natural control. They are presented as a basis for more intensive investigations.

1. *Adelges piceae* has a high biotic potential because of its fecundity and its parthenogenetic method of reproduction. Because of the absence of wings in the reproductive forms, dispersal is limited and infestations build up locally, causing an irregular or spotty distribution of outbreaks.

2. Biotic factors, being dependent on the density of the host population, are of chief importance in determining the ultimate level of population within a stand and therefore the destructive capacity of the insect. The most important is the resistance of the tree, or its varying suitability as food and shelter. This factor becomes most apparent after the first period of outbreak has killed the more susceptible trees, or increased their resistance.

Insect predators provide the only other major biotic factor. Their value is limited by their dependence on a high level of population and failure to attack the first instar. Although they increase rapidly with a rising host population, they do not prevent its continued rise on susceptible trees until the trees are severely injured. The death of the trees, or of the bark, then causes the complete mortality of the remaining larvae except for a relatively small number of 'crawlers' that reach other trees.

3. Climatic factors are of chief importance in influencing the rate at which the population reaches outbreak proportions and the rate at which the insect spreads. The most important is winter temperature. This would prevent establishment throughout much of the range of the host in Eastern Canada if it were not for the partial protection of snow. It produces irregular periodic fluctuations in the population over large areas, and slows up the spread to the north and west.

Fig. 31. Tip of crown of tree suffering from 'gout'. Infestation has died out. One branchlet had grown normally for 3 years, then died (A). Another is still living (B).

Fig. 30. End of branch of *Abies balsamea* showing typical swellings caused by *Adelges piceae*.

Fig. 32. Stem of small tree showing swellings at lenticels where *Adelges piceae* has been feeding.

Sun and rain limit the survival on exposed portions of the tree, and their value depends on the size and crown depth of the trees in the stand.

4. The effectiveness of natural control can be increased by removal of the susceptible trees or by introduction of additional natural enemies. Predators would be more likely to succeed if they were active forms with high searching ability in the larval stages and capable of destroying the first instar and the egg. Parasites would probably have greater searching ability than predators, but none is known to attack the Adelginae.

EFFECTS ON THE TREE

'Gout Disease'

For some years before 1930 an abnormal condition of balsam fir had been noticed in many parts of Nova Scotia. It was referred to by Faull (15) as 'gout disease', a name that has come into general use. Attempts to discover the cause had been unsuccessful and it was thought to be due to a virus.

Symptoms. — The external symptoms consist of swelling and distortion of the twigs and smaller branches. This appears in varying degrees over the crown but is generally most noticeable in the top. The branchlets are thickened and irregularly twisted, often turned downward at the ends (Fig. 30). The swelling is frequently more noticeable at the nodes and around the buds, which are sometimes almost enclosed in a knob of tissue. The stem may taper rapidly toward the top. The tip of the crown is often flattened or bent, sometimes umbrella-shaped, and in typical cases is dead (Fig. 31).

When the affected branchlets are sectioned, small purple pockets of tissue will usually be found embedded in the outer bark at different points. It will also be seen that the swelling is due to abnormal thickness of both the bark and the xylem.

Cause. — It was difficult to detect any signs of insect activity on the affected parts until examinations were made of twigs that showed the symptoms in an early stage. It was then found that *A. piceae* was often present. As familiarity with the insect increased, the remains of dead first-stage larvae were discovered on nearly all specimens, often under the old bark scales. Later the stylets could be detected in the bark on specimens from which the bodies of the insects had disappeared.

To determine whether *A. piceae* was responsible, a number of small, clean trees were infested with eggs in August, 1930. The following year small swellings were found on the 1930 growth wherever larvae had settled, and similar swellings developed on the new shoots during the summer, always beneath the larvae. The tendency of the insect to settle at the bases of the buds and under the bud scales at the bases of the new shoots seemed to explain the more frequent swellings at the nodes. During the next 3 years those trees which were vigorous, and on which the insect maintained a moderately high population, developed twisted, swollen branchlets.

A great many naturally infested trees were also cut and examined, or tagged and kept under observation. The following is a summary of the conclusions regarding the processes by which 'gout' is produced.

1. A stimulation of the growth of the bark and the wood occurs over a small area at the point of insertion of the stylets.

2. This stimulation results even if the neosistens dies without developing further. Swelling was observed when the dormant larva and its stylets had been removed 3 weeks after it had settled and before it showed any signs of feeding. The abnormal growth is generally somewhat greater, however, where the larva has completed its development to the adult stage.

Fig. 33. Young trees showing various stages of injury to twigs. Tree on far right shows very little injury. Note short, drooping shoots, dead twigs, and dead leaders on other trees.

3. Distortion results from the uneven stimulation of growth, particularly at the bases of new shoots and at the nodes of branchlets.

4. The swollen appearance is due not only to the stimulated growth in the bark and wood but also to the fact that infested buds often fail to open, or produce only short shoots. Thus elongation of the branchlet ceases and diameter growth increases.

5. The greater the vigour of the part attacked the greater the response to the salivary injections of the insect. Hence leaders and topmost branches generally show the most striking symptoms.

6. The amount of swelling is dependent also on the degree of infestation. It is greatest when the number of larvae is sufficient to produce the maximum reaction, and not sufficient to inhibit growth by the toxic effect of their injections or the exhaustion of food materials.

7. Striking symptoms of 'gout' may result from an infestation averaging not more than 10 larvae per shoot, if it persists for a number of years. Typical 'gouty' trees are generally the result of a moderately heavy attack for 2 or more years which inhibits the growth of most of the buds. This is followed by lighter attacks, which continue to discourage new shoot growth but are not sufficient to cause rapid death of branches.

8. The extremely rapid taper of the stems of many trees is caused by persistent moderate infestations of the tip of the crown preventing height growth, while light to moderate infestations of the stem stimulate diameter

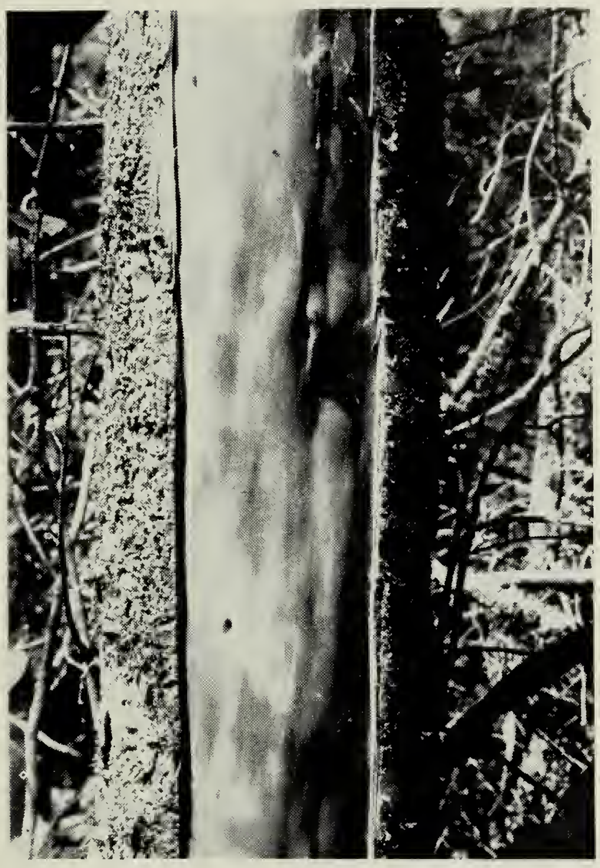

Fig. 34. Stem of tree showing dark blotches on surface of wood, caused by light infestation hidden under lichens.

growth. Such attacks are more common near the coast than inland, where winter-killing periodically destroys the insect on all parts of the tree except the base of the stem.

9. A branch on which all bud growth has stopped will commence to die in about 2 years, the ends dying first. A relatively small number of growing buds will, however, keep a branch alive and permit it to recover if the infestation ceases. Trees die from 'gout' when the twigs are attacked for a number of years and new shoot growth is almost entirely stopped.

Production of Abnormal Wood

Lumbermen in western Nova Scotia say that balsam fir not only grows poorly but also produces "boxy" wood. By this they mean that the wood is hard and brittle and boards sawn from it tend to warp and split. It was noticed also, before these studies were commenced, that in most parts of the Province when the bark was removed from a balsam tree the surface of the wood generally showed areas, or blotches, of a dark reddish-brown colour (Fig. 34). This abnormal colour was often most noticeable under patches of lichens on the bark. It has been responsible for the rejection of pit props on the grounds that they were suffering from "chemical stain".

These conditions are the result of infestation by *A. piceae,* although the presence of the insect is seldom noticed, especially as it may occur chiefly under lichens. In fact, its presence in small numbers can be more quickly determined by looking for the blotches than for the insect.

In the small trees that were infested to study the cause of 'gout', the xylem rings produced after infestation were irregularly enlarged and reddish-brown in colour. To get a clearer picture of the cause of this, two larger trees,

Fig. 35. Section of the base of a branch of a 'gouty' tree showing many irregular rings of 'rotholz' caused by persistent infestation on underside of branch.

about 3 inches in diameter, were lightly infested in June so that isolated larvae could be marked on the smooth bark of the stem. The following June faint dark blotches or broad longitudinal streaks were visible on the surface of the wood beneath most of the points where they had settled, even though many had not developed.

On June 19, 1934, two similar trees were heavily infested over a definitely restricted area of the stem by placing eggs between two bands of cotton wool 9 inches apart. The cotton was tied around the stem with string, and "tree tanglefoot" was applied to the bark outside the strings to make sure that no larvae settled beyond them. A third tree was similarly banded but not infested. The larvae became established in a continuous line just inside the strings and were scattered over the bark between, about one to the square inch. Only a few developed beyond the first stage ; these were under the cotton wool, and no offspring were produced. On June 9, 1935, the trees were examined. Between the bands the surface of the wood was dark, contrasting with the pale normal colour above and below. One tree had been growing at the rate of 4 mm. radial increment per year, the other at about one-fifth of this rate. The faster-growing tree showed much darker wood between the bands than the other. The dark colour extended about half an inch below the bottom band in the slower-growing tree and 3 inches in the other, but ceased fairly abruptly at the line of the upper bands. Sections of the wood demonstrated that the dark colour was due to abnormal thick-walled tracheids in the outer part of the 1934 ring. This ring was distinctly larger beneath the bands, where the larvae had been most numerous. The 1935 ring consisted of a few layers of normal spring-wood tracheids through which the dark 1934 wood was easily seen. No abnormal growth had occurred on the uninfested tree.

The annual rings of many hundreds of trees in various stages of infestation were examined. Studies were made of sections and increment cores of tagged trees on which the degree of infestation had been recorded for 4 years. In all cases where there was a detectable infestation, however light, the dark wood

Fig. 36. Section of stem of tree that was infested for 7 years. Dying of outer bark prevented further attack and 2 small rings of normal wood (A) have been added since. Bark died to Cambium at B.

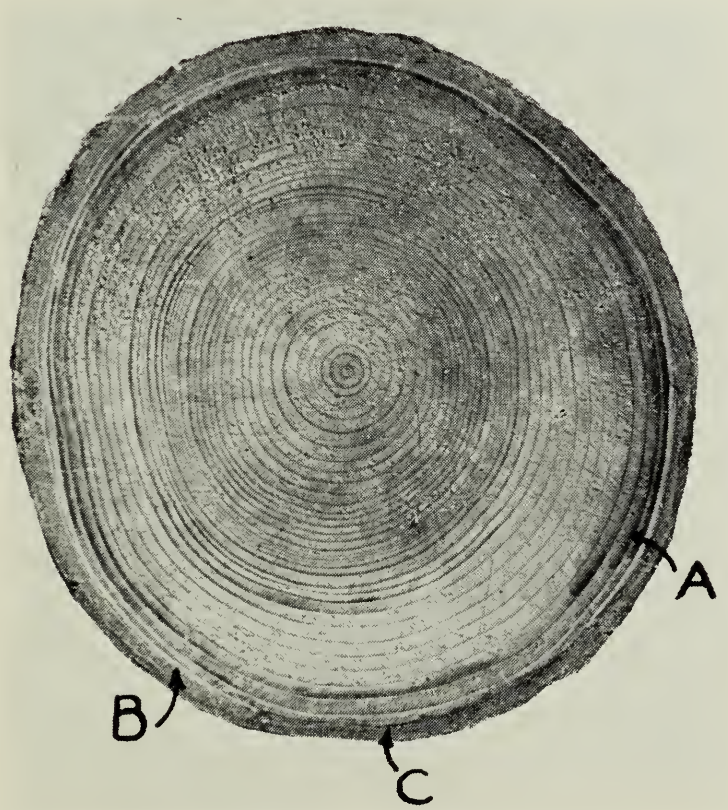

Fig. 37. Section of stem of tree killed by 4 years of infestation. Note 'rotholz' (A) and partial outer ring of light wood (B) put on after outer bark died. Bark died to cambium at C.

was present. Moderate to heavy infestations were invariably associated with enlarged rings composed chiefly, or entirely, of dark, hard wood. The amount of such wood varied with the degree and length of the infestation, and the vigour of the tree. A typical rapidly developed infestation on the stem of a tree of average vigour generally resulted in 2 or 3 enlarged rings of the abnormal wood followed by 1 or more very small rings, depending on the rate of dying (Fig. 37). If the tree survived and further attack on the stem was prevented by the dying of a superficial layer of the bark, the subsequent rings were of normal colour (Fig. 36). Trees that had suffered from persistent light to moderate infestation of the stem might show many years' growth of abnormal wood, varying in degree and distribution with the degree and distribution of the infestation (Fig. 35).

On stems where the insect had been killed during the winter of 1933-4, the 1934 ring often showed dark wood on the inside and normal wood on the outside, as though the usual positions of the spring and summer wood had been reversed.

The following conclusions are drawn.

1. A substance contained in the saliva, or produced in the cortical tissue by the action of the saliva, diffuses from the point of insertion of the stylets and affects the cambium, even in thick-barked trees.

2. The area of cambium affected by a single neosistens extends basipetally as much as 15 mm., tangentially only 2 or 3 mm., and hardly at all acropetally.

3. This substance stimulates cell division in the cambium and causes the production of tracheids with thickened cell walls and a dark, hard, brittle wood. This is similar in appearance to 'compression' wood, but can be distinguished from it by the irregularity in the width of the rings, by its occurrence on all sides of the stem or branch, and by the fact that it often occupies the whole depth of the ring. The dark colour is most noticeable when the wood is fresh, or wet.

4. This reaction of the cambium is dependent on the vigour of the tree and the intensity of infestation. The greatest amount of abnormal wood is produced in fast-growing stems that are moderately infested. Heavy infestations tend to exhaust the materials available for growth and produce a toxic effect through the large amount of salivary substance injected.

5. The aestivosistentes do not affect the growth of the following year. The injections of the hiemosistentes affect the tracheids laid down the following spring.

Total Effect on Growth

The effect on the growth of the tree depends on the distribution and severity of attack. A heavy stem attack may kill the tree within 1 or 2 years. Lighter attacks affecting all parts of the tree may persist for many years, causing varying degrees of 'gout' and a much slower process of dying.

The history of infestation on any one tree can be fairly accurately determined from the abnormal dark wood in the annual rings. Measurement of the rings and height growth will show how the tree has reacted to the attacks. Ten trees of various sizes were studied in this way. The method and general results are illustrated by a graphical description of the largest of these trees (Fig. 38).

This tree showed the characteristic rapid taper and 'gouty' top. It was growing in a balsam-spruce stand at Clyde River, N. S., that had originated from clear cutting about 1880. Because of the thinness of the stand it had not suffered from competition. When it was cut in August, 1933, it was dead, but its condition and the presence of eggs of *Monochamus* sp. indicated that it had been living in 1932.

The height and diameter outside the bark of each internode of the stem were measured down to 40 inches from the base. The internodes were then sectioned at their centres and dated from the 1932 ring. A section was also taken at 20 inches from the base. Measurements of the annual rings were made on 4 radii of each section, and the presence of the dark wood was noted. The dates, lengths, and diameters of internodes are shown in Table 5.

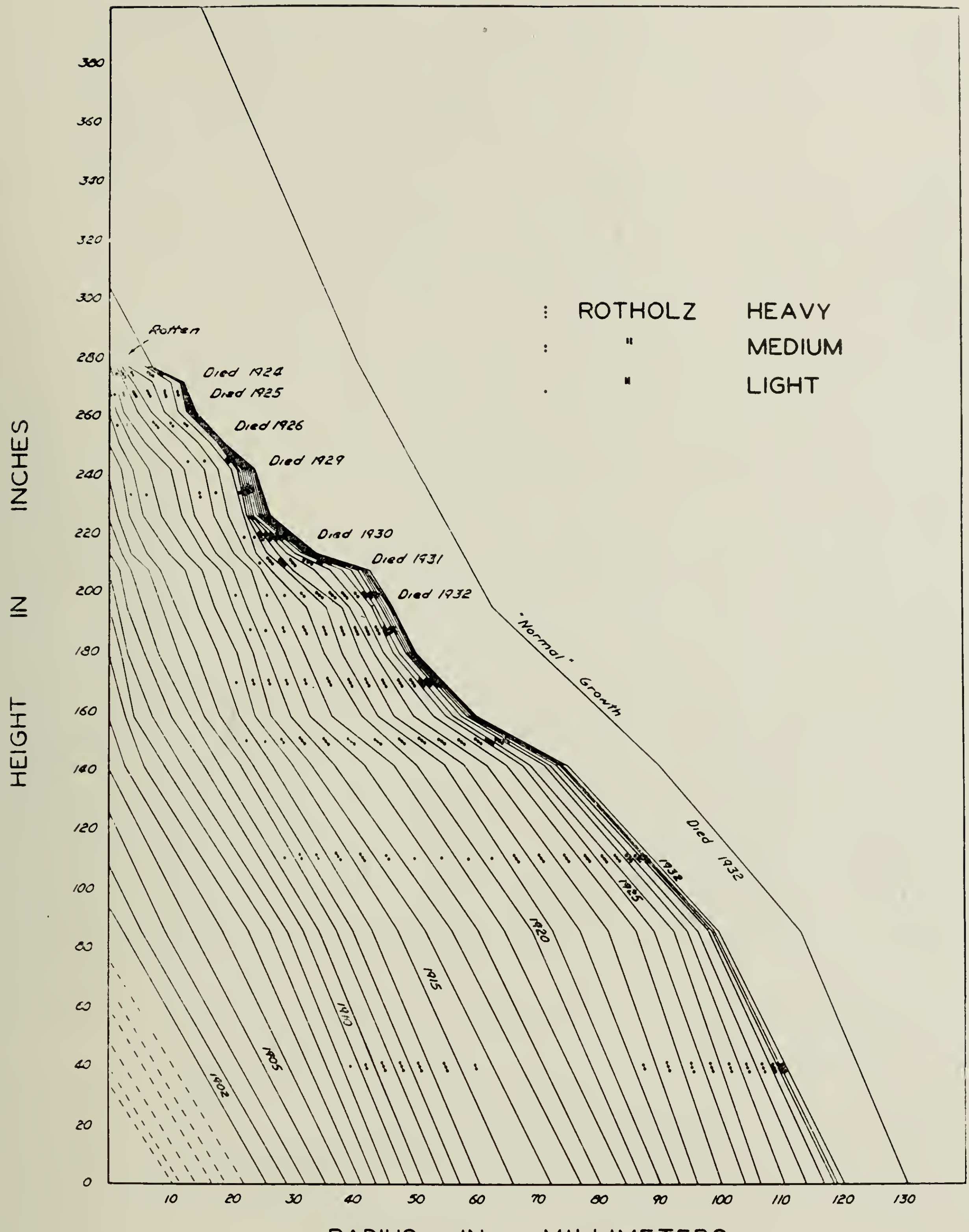

Fig. 38. Graph of annual height and diameter measurements of typical 'gouty' tree at Clyde River, N.S., showing occurrence of 'rotholz'.

The annual radial growth, height growth, and occurence of the abnormal wood ('rotholz') are shown in Fig. 38.

The graph shows that the first infestation occurred about 1910 on the lower part of the stem. This increased and gradually moved up the stem, reaching the top of the tree by 1915. The top remained infested until it began to die, about 5 years later. The attack was considerably reduced on the lower stem between 1916 and 1921, but in subsequent years it became general over

Table 5. — Measurements of internodes of 'gouty' tree at Clyde River, N.S., that died in 1932.

Year of Growth	Height in inches	Diameter outside bark in inches
*1924	1.2	0.1
1923	2.0	0.1
1922	2.2	0.2
1921	1.5	0.3
1920	1.5	0.5
1919	3.0	0.6
1918	8.0	0.9
1917	5.5	1.1
1916	6.5	1.4
†1915	9.5	1.7
1914	11.0	2.2
1913	10.0	2.5
1912	15.0	3.6
1911	12.0	4.0
‡1910	7.5	4.3
1909	12.5	4.5
1908	15.5	5.2
1907	21.0	6.7
1906	17.0	7.3
1905	15.0	7.5
1904	18.0	7.7
1903	14.0	8.5
1902	9.0	8.7
1901	9.0	8.8
1900	9.0	9.1
1899	8.0	9.2
1898	10.0	9.4
1897	10.0	9.7
1896	6.0	9.7
1895 to 1883?	40.0	9.6 to 10.8

* Leader died.
† First attack on leader.
‡ First attack on stem.

the tree. Probably at no time was the infestation heavy enough for the white 'wool' to be very noticeable, except to the trained eye.

The tree was about 25 years old and growing fast when it became infested. It had been putting on about a quarter of an inch of diameter and 14 inches of height for 10 years. After the infestation became established in the top, height growth was rapidly reduced and ceased within about 5 years. Diameter growth, on the other hand, continued at a somewhat accelerated rate during this period, and for a longer period in the lower stem. Reduction in diameter growth began in 1921, occurring first in the top and later in the lower part of the stem. The extreme tip commenced to die about the same time. By 1924 some 2 feet of the stem was dead and by 1931 this had increased to 8 feet. The following year the whole tree died after being infested for 24 years.

At time of death the tree was 50 years old, 26 feet high, and 9.7 inches in diameter at breast height. If the average rate of growth for the period 1900 to 1909, just prior to attack, had been continued until 1932, the tree would have been 44 feet high and about 10 inches in diameter. In the graph the 'normal' growth is shown as calculated from an average for the period prior to 1920, when reduction in diameter growth began to appear. For the lower stem this may be open to some objection, as it includes some enlargement of rings that may be attributable to stimulation of growth by the first attacks of the insect.

This tree is a fair sample of many in western Nova Scotia. It illustrates the reasons for the unpopularity of balsam fir in the area. On an average site the species is capable of reaching pulpwood size, or small sawlog size, at 50 years of age. When infested by *A. piceae*, however, it may die before it reaches this size, or become a tree of poor form and quality, useless for lumber and of low value for pulpwood because of high lignin content. The cause is seldom recognized.

A very different result is produced by heavy attacks on the stem, which occur more frequently in newly infested areas. There is a brief period of stimulated ring growth followed by 1 or 2 years of reduced growth and sudden death. No distinct signs of 'gout' appear. Examples of this type of attack were common near Fredericton in 1933, and the effect on ring growth was studied.

Two increment cores were taken from opposite sides of 20 dominant or codominant trees that had recently died from heavy stem attacks. They all had red or yellow foliage, and dry or discoloured cambium. The last 10 rings were measured and the amount of abnormal wood in each ring, on the basis of the colour of the moistened cores, was noted. There was a good deal of variation in the results, as may be expected from cores, which provide only small samples of the growth of the stem ; but the general pattern of growth was sufficiently uniform to warrant a summary presentation in Table 6. The cores were all taken in September, 1934 ; but as the trees were dead the rings could not be dated with certainty. All were known to have been heavily infested in the spring of 1933 and died the following winter or summer. In some cases the last ring was very small and may have been laid down in 1934.

Table 6 indicates that the majority of the trees showed the first signs of infestation 4 years before death and became heavily infested 1 year before death. In the typical case there were 2 enlarged rings followed by 1 small ring. This illustrates the rapidity with which trees are killed when conditions are favourable to the insect.

Table 6. — Average widths of last 10 rings and occurrence of abnormal wood on 20 mature trees killed by heavy attack on stems. Based on 2 cores per tree.

Width of ring in mm., commencing with last	No. of cores showing abnormal wood			
	None	Light	Medium	Heavy
0.7	2	15	12	11
2.6	0	2	18	20
1.9	5	13	9	13
1.6	16	19	5	0
1.5	39	1	0	0
1.5	40	0	0	0
1.7	40	0	0	0
1.6	40	0	0	0
1.5	40	0	0	0
1.6	40	0	0	0

The effect of *A. piceae* on the growth of the tree varies infinitely, according to the type and degree of infestation that the resistance of the tree and the action of the other control factors permit. It may persist for many years in such small numbers that the damage is negligible ; it may cause varying degrees of 'gout' and loss of growth ; it may kill trees slowly, or rapidly.

Histological Studies

The effects of the feeding processes of the insect on the cell structure of the tree were studied by sectioning twigs and pieces of bark that had been infested for various lengths of time. Short lengths of new shoots and 1- or 2-year-old twigs were fixed in Carnoy's fluid, dehydrated with butyl alcohol, and embedded in paraffin. Serial sections, 10 microns thick, were made with a rotary microtome. Saffranin and light green gave brillant contrasts between the stylet sheaths and the cell wall, between the cell wall, the cytoplasm, and the nucleus, and between the xylem and the phloem. Eosin and methylene blue gave good results but less striking contrasts. Sectioning of the older bark and wood on the stems was more difficult, because of the presence of stone cells and the hardness of the wood. Hydrofluoric acid was tried as a softening agent and celloidin for embedding, but results were unsatisfactory. Sections of the stems were made from fresh material with a sliding microtome, and were of value although they could not be cut thinner than 20 microns.

As already stated the stylets or stylet tracks were found always between the cells, and, after penetrating the epidermis or the periderm, they occurred only in the parenchyma of the cortex or the phelloderm. In young shoots they reached the phloem occasionally but did not enter it (Fig. 22). They were seen also in the meristematic tissue at the bases of young buds (Fig. 21). In older bark the limit of penetration was generally about 1 mm. below the phellogen.

Effects on cortical parenchyma. — The first result of the insertion of the stylets is an enlargement of the cells neighboring the tracks. This is accompanied by an enlargement of the nuclei and a thickening of the cell walls. The thickening is most noticeable in the walls contiguous to the tracks (Fig. 20). Nuclei are often attracted to the side of the cell that is in contact with the stylets (Fig. 21).

As this hypertrophy develops, giant cells of irregular shapes may be produced, having diameters as much as 6 or 7 times as large as those of normal cells. The walls of these cells show many ridges on the inner surface (Fig. 24). Two nuclei are not uncommon. These very large cells were seen only where the insect had developed to the adult stage and considerable feeding had taken place, but distinct enlargement follows the insertion of the stylets of the neosistens even if it dies while in the dormant stage. The cytoplasm of the enlarging cells has a granular appearance and is strongly stained.

The hypertrophy of the cells surrounding the stylet tracks is followed closely by hyperplasia in the neighbouring parenchyma, and both phenomena contribute to the swelling of the cortex or bark. In shoots that were infested in the spring well-defined pockets of the abnormal, enlarged cells were found by the end of the growing season, with evidence of proliferation in the surrounding tissue. This often took the form of a stimulation of the activity of the phellogen (Fig. 23).

The following season these pockets of abnormal tissue were generally surrounded by a secondary phellogen, which produced several layers of purplish cork cells on the inside and contributed to the proliferation of the parenchyma on the outside. The abnormal cells disintegrated, were infiltrated

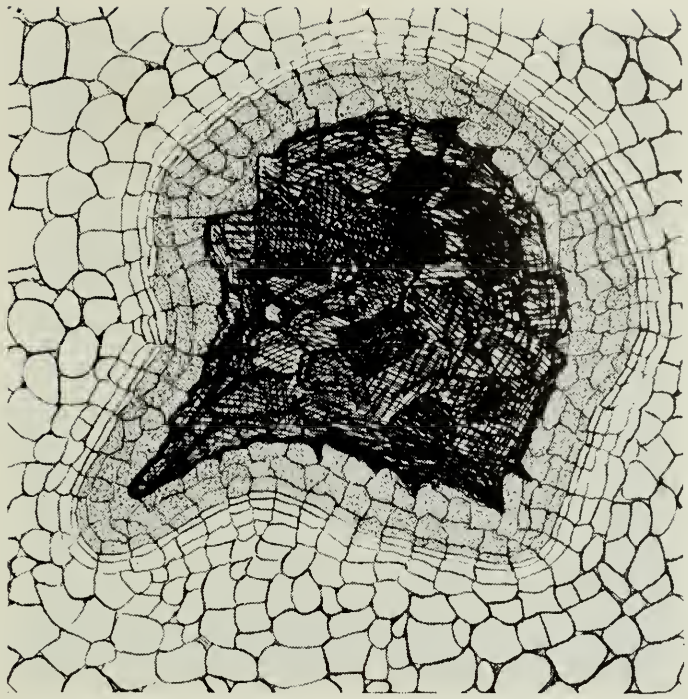

Fig. 39. Section through pocket of dead tissue caused by feeding of *Adelges piceae* and surrounded by purplish cork cells produced by secondary phellogen.

with resin, and became completely enclosed in cork tissue (Fig. 39). They were thus encysted in the bark and formed the purple pockets that are often found in 'gouty' twigs.

In heavily infested stems, a similar secondary cork cambium often appears 2 or more millimeters beneath the surface, leaving a superficial layer of dead cells which protects the living bark beneath from further attack. It is similar to the 'wound cork' that occurs in many plant tissues (8).

The above descriptions apply to *Abies balsamea*. It was found that swellings did not occur on *Abies nordmanniana* or *Abies pectinata*. Sections were made in January of a shoot of *A. pectinata* that had been infested the previous June. Fig. 25 shows that pockets of enlarged cells had been formed but no proliferation, or abnormal division of the cells in the neighbouring parenchyma, had followed. There is evidently a difference in the reaction of the European and American species of *Abies* to the feeding of *Adelges piceae*.

This difference apparently applies equally to *Adelges nüsslini*. Chrystal (10) showed that *A. nüsslini* produces pockets of hypertrophied parenchyma in the young shoots of *Abies pectinata, Abies nordmanniana,* and *Abies grandis* but that swellings resulted only in the last species. He considered that since the production of swellings was dependent on the species of host rather than on the species of insect this might indicate that *Adelges nüsslini* and *A. piceae* were biological races rather than separate species. The established differences in morphology and life-cycle, however, do not support this conclusion.

Chrystal showed very clearly that the feeding of *A. nüsslini* resulted in a partial suppression of the growth of the xylem ring, although once the xylem was formed it was not affected. He concluded that the reduction in the amount of xylem formed was the cause of the withering of the new shoots that is characteristic of trees infested by *A. nüsslini*. The swellings on *Abies grandis* were attributed to an increase in the phloem region.

In the case of *Adelges piceae* on *Abies balsamea* there may be some interference with the formation of the xylem when larvae settle at the ends of growing shoots, but this does not cause withering of the shoots. The dying

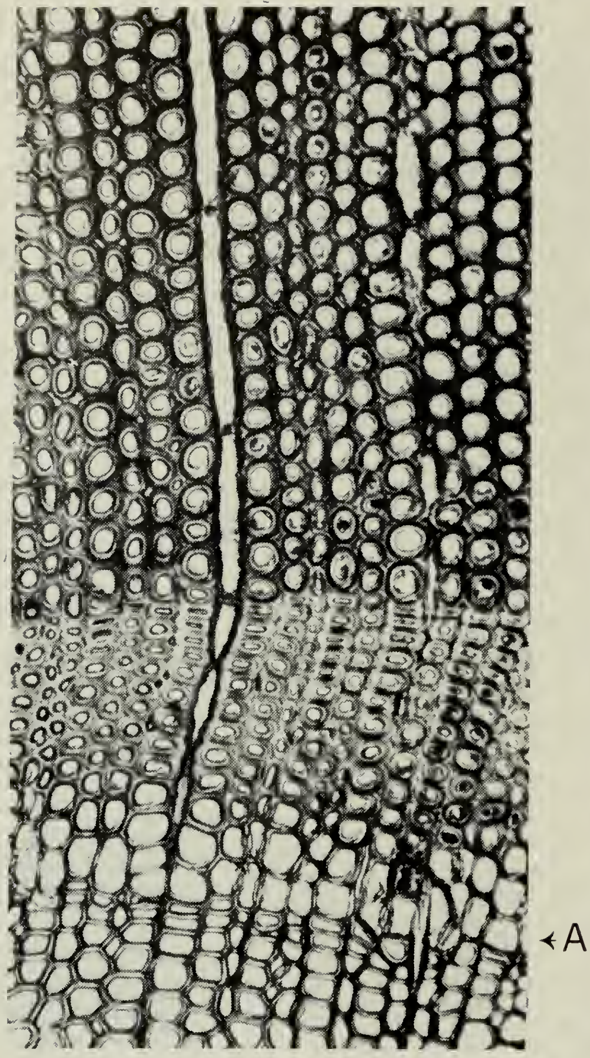

Fig. 40. Transverse section from stem of infested tree. False ring (A), caused by transplanting, followed by abnormal tracheids caused by *Adelges piceae.* Note circular cross section, intercellular spaces, checks in secondary wall. X130.

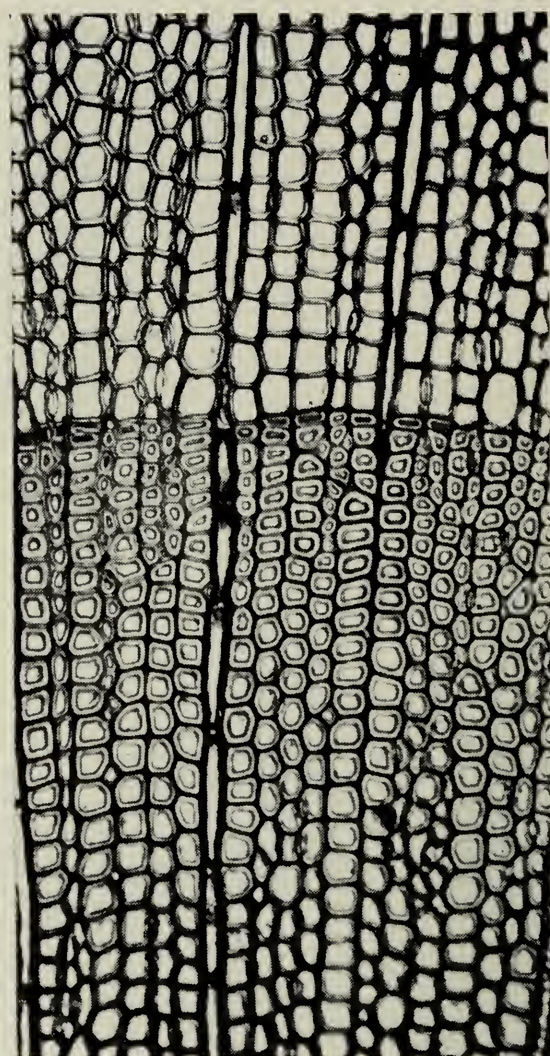

Fig. 41. Transverse section of normal wood from rings of same tree laid down before infestation. X130.

of twigs is generally gradual and results from the accumulated effects of the salivary injections. Abnormal stimulation of growth in the cortex and cambium is accompanied by inhibition of bud growth.

Hypertrophy and hyperplasia are common phenomena in gall formation by insects, as well as in other types of morbid anatomy (8). 'Gout' is a form of insect gall. Although the Adelginae produce galls on spruce, this is the only known case of gall formation by a species of this group on the secondary host.

Effects on xylem. — The nature of the tracheids in the abnormal wood of heavily infested stems was examined by means of fresh sections. In comparison with normal wood they showed the following characteristics.

1. Extreme thickening of the secondary cell wall, resulting in a considerable reduction of the lumen (Fig. 40) and also of the apertures of the pits.
2. Checks in the secondary wall of the tracheids at a greater angle to the longitudinal axis of the cells than in normal wood.
3. A circular rather than rectangular shape in cross section, accompanied by frequent intercellular spaces.

These characteristics, together with the hard, dark, and brittle nature of the wood, are very similar to those of 'compression' wood, or "rotholz", as described by Pillow and Luxford (28). Analysis of samples of wood from infested stems by the Research Department of the Mersey Paper Company, Liverpool, N. S., showed that they contained an abnormally high percentage of lignin.

It was also noted that a row of resin ducts often occurred in the xylem laid down after heavy attack. Such ducts are traumatic in *Abies balsamea* and are not produced in normal wood.

Nature of Injection by Insect

Hypertrophy, hyperplasia, multinucleate cells, and secondary meristematic tissues commonly occur in plant tissue exposed to various stimuli. They may result from the feeding of insects, from infection by fungi, bacteria, or viruses (2, 44), or from mechanical or chemical injury (8).

The abnormalities that follow infestation by *Adelges piceae* are undoubtedly initiated by the salivary injections of the larvae. No evidence has been found of fungi or bacteria in the tissues. Since the stimulus is localized and normal growth is resumed after the insect is removed, there is no evidence that a virus is involved. Attempts by the writer to produce 'gout' in healthy trees by grafting affected twigs of various ages were unsuccessful. It is concluded that the insect injects a chemical substance that is an irritant in small quantities and a toxin in larger quantities. Smith (39) has shown that the salivary glands of 2 species of capsid bugs contained materials that were violently toxic to plant tissue.

Investigators have differed in their conclusions as to the nature of the stylet sheaths produced by sucking insects, but there is considerable evidence that they are composed of substances originating from the insect. Chrystal (10) showed that the sheath formed by *A. nüsslini* consisted chiefly of albuminous substances, and he concluded that the saliva contained ferments that attacked the middle lamella and the proteid contents of the cell. Studies by Smith (39) suggest that stylet sheaths are a product of the saliva acting on the plant proteins.

The fact that infestation by *A. piceae* resulted in the growth of wood similar to 'compression' wood suggested a comparison between the stimuli responsible in each case. Although the study was not completed, several of the experiments are of interest.

Experiments on 'compression' wood.—Two trees, 12 feet high, were bent over and tied together in March, 1933, so that the upper third of each stem was practically horizontal and the tissues on the undersides were severely compressed. The trees were cut and sectioned in March, 1935. It was seen that the 1934 and 1935 rings on the undersides were abnormally wide and consisted entirely of dark wood made up of tracheids with characteristics similar to those found in the wood of stems infested with *A. piceae*. On the upper sides the rings were narrow, pale in colour, and normal in cell structure but with rather small amounts of summer wood. The 'compression' wood in the cross section tapered rapidly on the sides of the stems where the cambial layer began to curve away from the vertical (Fig. 42).

To determine whether the 'compression' wood was caused by compression, a small tree 18 inches high was planted in a box and placed on its side. The stem was forcibly bent and held in such a position that the tip was vertical and compression was maintained on the upper side. The experiment was commenced on June 11. During the summer there was some upward bending of the twigs in the previous year's growth and the new shoots became almost vertical. In September the stem was sectioned and examined under the microscope. The last ring was found to be extremely eccentric. A few rows of normal spring wood had been laid down equally throughout the ring,

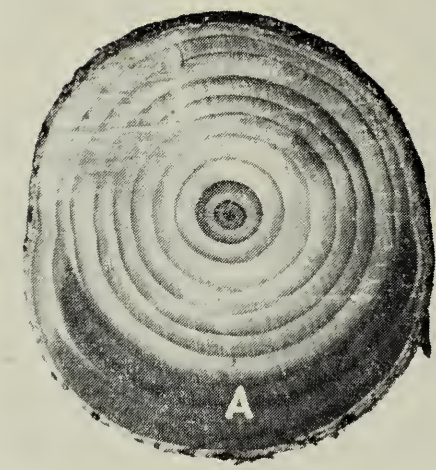

Fig. 42. Section from tree that had been bent over for 2 years. Note 'compression' wood in 2 rings (A).

presumably before June 11. This was followed by pronounced formation of 'compression' wood on the underside and weak development of normal summer wood on the upperside. This showed that the stimulation responsible for 'compression' wood in this instance was a result of gravity, not compression. The conclusion that compression does not cause 'compression' wood in balsam fir was supported by another experiment in which the stems of 2 trees were bound tightly in the spring with 2-inch bands, one with stout string, the other with wire. The wood produced beneath the bands was normal in structure although the ring was small, especially under the wire. In the latter case the ring was strikingly enlarged above the band, and on the underside of the resulting bulge, where the cambial layer had been thrown out of the vertical, some 'compression' wood was formed.

Although it has been concluded by a number of authors that 'compression' wood results from a morphogenic response to gravitational stimuli, many other factors have been held responible (20). In 1942 Wershing and Bailey (46) emphasized the complexity of the problem. They showed that, when the hypocotyledonary stem of young seedlings of *Pinus strobus* L. was treated with indole-acetic acid, growth was stimulated at the point of application and below it. The stimulation was accompanied by an enlargement of cells in the cortex and the formation of "redwood" in the xylem. This suggested to the writer than an auxin played an important part in the abnormal growth produced by *Adelges piceae*.

Experiments with indole-acetic acid. — On June 7, 1943, when the new shoots were about half-grown and the annual ring about one-third formed, 4 vigorous young balsam firs were treated with a mixture of 10 mg. of indole-3-acetic acid to 1 gm. of lanolin. This was applied to parts of new shoots, and small branches, and to areas of 1 square inch on stems about 2 inches in diameter. In one series on each tree the bark was punctured with a fine needle, in another it was scraped with a razor, in another it was shaved to a depth of 1 mm. Checks were treated with pure lanolin. Observations were made during the next 6 weeks, at which time the work was interrupted. In June 1945, however, sections were made of treated branches and stems. The following results were noted.

1. When liberal amounts of the indole-acetic acid and lanolin were applied around most of the shoot it died. Punctured shoots treated with the mixture also died.

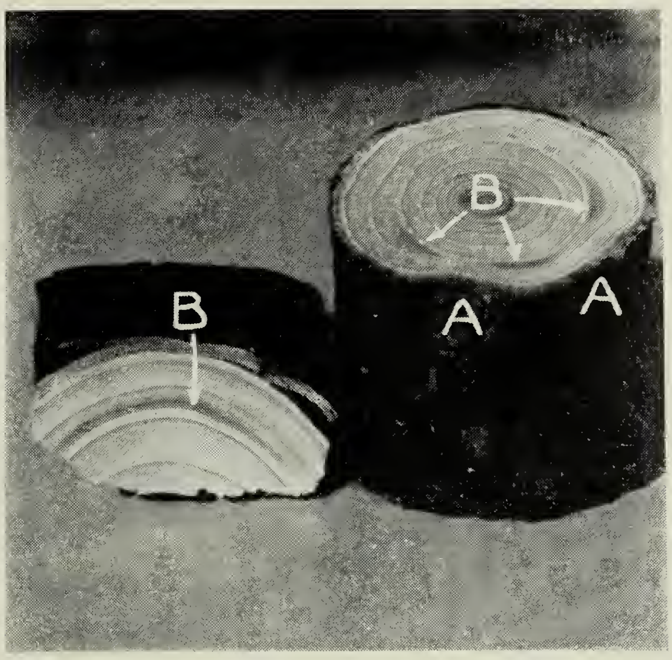

Fig. 43. Sections from 2 trees treated with indole-acetic acid June 7, 1943, and cut June 5, 1945. Left-hand section below treated point. Right-hand section through 2 treated points in A. 'Rotholz' at B.

2. When the mixture was applied to one side of the proximal half of a growing shoot, the shoot bent away from the point of application. This bending reached its maximum after about 10 days. After 6 weeks the shoot was partially straightened. Slight swelling occurred in some cases at the point of application.

3. When parts of branches or stems were scraped to remove most of the cork layer, or shaved to remove about 1 mm. of the outer bark, treatment with the indole-acetic acid produced callous growth and a noticeable thickening of the bark around the circumference of the treated area.

4. In one case where the shaving was rather deep a single row of resin ducts was formed in the wood beneath.

5. In all branches or stems that were treated after scarifying or shaving the bark there was some increase in the width of the ring and noticeable quantities of 'rotholz' were produced. The 'rotholz' and stimulation of growth were most noticeable on each side of the treated spot and below it on the stem, or proximal to it on the branches. On one stem 'rotholz' was formed to a distance of 1½ inches above and 3¼ inches below. Toward the latter part of the growing season the stimulating power was apparently exhausted, as normal wood occurred in the outer part of the ring (Fig. 43).

6. None of the areas treated with pure lanolin showed swelling or 'rotholz'. In these cases the areas of shaved bark were underlain with a secondary periderm without callous growth. No reaction was observed on branches or stems when the indole-acetic acid was applied to lightly punctured or uninjured bark. Apparently it did not penetrate the phellem under these circumstances.

Unfortunately these experiments had to be discontinued and no proper comparison was made between *Abies balsamea* and *Abies pectinata*. A small tree of the latter species was treated, however, by applying the mixture to the sides of growing shoots and to the slightly scarified bark on one side of a 4-year-old twig. It is perhaps significant that no bending or swelling was observed, as this tree does not show swellings when attacked by *Adelges piceae*.

Discussion. — These experiments show that very similar responses are induced in the tree by the action of gravity, by the application of auxin, and by the injections of the insect. Much additional investigation is needed to determine how these different types of stimuli are related. It is possible that the saliva of the insect contains a substance similar to indole-acetic acid. It is perhaps more likely that it causes a concentration of auxin at the point of feeding indirectly, by stimulating its production within the cells or by attracting it from other parts of the tree. This must be what happens when 'rotholz' is produced by a purely gravitational stimulus.

Went and Thimann (45) drew attention to the fact that swellings caused by auxin closely resemble phenomena observed in some of the galls and suggested that it plays an important part in such growths. They instanced the ability of certain gall-forming bacteria to produce indole-acetic acid. De Ropp (11) showed that crown-gall tissue generated a growth-stimulating substance without the immediate agency of bacteria. This produced effects similar to those of indole-acetic acid.

The inhibition of bud growth on 'gouty' trees may be due to the attraction of auxin to the points of feeding. To quote Went (45), "Wherever an auxin production center is located it would cause the bud-growth factor to move toward that place, preventing other non-auxin-producing buds from obtaining this factor."

It seems that a subtance causing similar host response to indole-acetic acid is produced at the point of feeding as a direct or indirect result of the injection of the saliva of the larva, and that this diffuses through the bark to the cambium, with a basipetal tendency in the phloem. The amount produced is dependent on the vigour of the part attacked and the concentration of the attack. If the attack is very heavy the toxic effect of the relatively large amount of saliva injected inhibits rather than stimulates growth. This can be seen when large numbers of larvae settle on a shoot and cause it to stop growing, although they remain dormant and die without feeding. Somewhat similar relationships between the concentration of auxin applied and the reaction in the plant have been noted by workers with growth substances, as well as in the above experiments.

The salivary injections by the neosistentes evidently disturb the normal quantitative relationships between the nutrients and the growth factors in the tree. Whether or not the result is stimulation, or inhibition of growth depends on the size and vigour of the part attacked in relation to the amount of saliva injected.

Several authors have concluded that the saliva of hemipterous insects contains enzymes (26, 47). This may be the case with *Adelges piceae*. The functions of the saliva appear to be to stimulate growth and predigest the food materials in the stimulated cells, the insect obtaining nutritive materials by dialysis through the cell wall. The nature of the resulting abnormalities and their resemblance to those produced by other types of stimuli support Butler's (8) conclusion that "all living cells have the potentiality to react to various stimuli by hypertrophy, hyperplasia, or the development of meristematic tissues, and that pre-existing meristems are not, of necessity, primarily implicated in gall formation".

The content of the saliva and the part that it plays in the growth processes of the cells can only be determined by biochemical studies. Such studies might contribute to an understanding of 'compression' wood and other problems in the regulation of plant growth.*

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* For a review of present knowledge see "Plant Growth Substances", edited by Folke Skoog, published by University of Wisconsin Press, 1951.

Causes of Death

In Eastern Canada *A. piceae* causes more damage to its host than any other adelgid. The closely related species *Pineus strobi* (Htg.), for instance, is often very numerous on *Pinus strobus* L., but causes little obvious injury except occasionally in nurseries and does not kill trees. The explanation seems to lie in the sensitivity of *Abies balsamea* to the salivary injections of *Adelges piceae* and the resulting effects on wood, bark, and shoot growth.

Effect of abnormal wood on conduction. — To determine the relative importance in conclusion of the outer and inner rings of the sapwood of healthy balsam fir, small trees 1 inch in diameter and sections of stems of trees 3 to 4 inches in diameter were placed in water containing eosin. Similar tests were made with trees and sections which had been attacked for several years.

In the normal trees and sections only a few outer rings were stained, the number ranging from 2 to 4 in the top and 3 to 7 in the bottom after 24 hours. There was no evidence of radial penetration of the stain into the wood or phloem. The number of rings stained was greater in the slower growing trees. The rate of staining decreased with the age of the ring. In standing trees, conduction probably takes place in older wood but these results suggested that balsam fir depends largely on a small number of outer rings. The number of normally active rings appears not to exceed the number of year's growth of foliage persisting on the tree, and this is seldom more than 7. In young, vigorous trees most of the conduction appears to take place in the outer 3 rings.

In the stems and branches which had been attacked the eosin failed to penetrate the parts where distinct 'rotholz' occurred and it was not carried above those points where the rings were composed entirely of the abnormal wood. Since trees killed by the insect generally have considerable quantities of this wood in the outer rings the interference with conduction is probably an important factor contributing to the physiological disturbances which result in death. The thickening of the cell wall and the reduction, or occulsion, of the apertures of the pits in the tracheids appear to be sufficient explanation of the poor conduction.

Effect of injury to bark. — When heavy attacks develop over a large part of the surface of the stem, the bark dies down to the cambium and the foliage begins to turn yellow. In about a year the whole crown becomes a bright russet red. When attacks develop more slowly and a smaller part of the stem is heavily infested, the bark may die near the surface only, in which case a secondary periderm is produced, further attack is limited, and the tree may survive. In intermediate cases parts of the bark may die back to the cambium, while other parts remain alive (Fig. 36), but such trees generally succumb later.

Experiments were undertaken to determine the amount of injury to the outer bark that a tree can withstand. Four smooth-barked trees, 5 inches in diameter, 35 to 40 feet tall, were selected in a fully stocked, even-aged stand on a good site. The bark was approximately 7 mm. thick. Between September 8 and 20, 1932, areas of the outer bark near the base were shaved off with a sharp scalpel. The results were summarized as follows.

Tree No. 1. A band 10 inches high was shaved 3 mm. deep. During the following summer a new periderm was produced about 2 mm. below the surface, and the cambium was uninjured.

Tree No. 2. A band 17 inches high was shaved 3 mm. deep. By July, 1933, vertical strips of cambium were dead. In August, 1934, about half of the treated area was alive and consisted of strips bordered by callous and growing rapidly. There was a slight reduction in the width of the 1933 and 1934 rings below the band.

Tree No. 3. Five feet of the lower stem was shaved 3 mm. deep. By July, 1933, the bark and cambium were completely dead under the shaved area but apparently normal above and below. By October the whole tree was dead and the foliage almost red. The 1933 shoots were about two-thirds as long as the 1932 shoots. The 1933 ring was about half as wide as the 1932 ring above the band, but absent below.

Tree No. 4. Six feet of the base of the stem was carefully shaved 1 mm. deep. Part of the cambium died during the summer but several strips were successfully covered by a new periderm, and in August, 1934, these appeared as prominent irregular ridges across the treated area. The tree looked healthy and had almost normal shoot growth.

This type of injury is, of course, different from that caused by the insect. No doubt the sudden removal of the external cork layer and the destruction of some of the under-lying tissue after the growing season was over resulted in considerable drying out of the bark before a new cork layer could be laid down in the spring. The experiments show, however, that the ability of the tree to repair damage to the outer bark is dependent on the depth of the injury and the size of the area affected. Parts of the cambium may be killed, but if the tree is vigorous and a bridge of living cambium and phloem is maintained rapid recovery is possible. If the cambium is killed around the stem in the spring there may be some growth above the injury but the whole tree dies by the end of the summer.

It may be assumed that when a tree is heavily infested over a large part of the stem the killing of a superficial layer of bark tissue 1 mm. or more deep has a serious effect. The failure of such trees to repair the damage as vigorously as those in the above experiments is probably due to the other effects of attack.

Fungi. — No evidence of fungi infecting the bark tissues has been found until after they were dead. Orange fruiting bodies of a species of *Dasyscypha*, probably *D. agassizii* (Berk. and Curt.), were recorded on the bark of the majority of the plot trees about a year after death. Red perithecia, identified by Dr. V. J. Nordin, Laboratory of Forest Pathology, Fredericton, N. B., as *Creonectria cucurbitula* (Sacc.) Leav., occurred in large quantities on occasional trees also about a year after death. Both species are considered saprogenic. Mycelium was found only in dead, discoloured tissue after heavy infestations. Dr. Irene Mounce, Division of Botany and Plant Pathology, Canada Department of Agriculture, made a number of cultures and sections of living infested bark, with negative results.

Conclusions. — It is concluded that death is caused by the following effects of attack by the insect.

1. Inhibition of bud growth and resulting gradual starvation through lack of new foliage.

2. Production of 'rotholz' and partial interference with conduction in the xylem.

3. Killing of the outer tissues of the bark by the toxic effect of the saliva of many larvae. In heavy infestations this may be sufficient to kill the cambium. Production of a secondary periderm results in a resinous-impregnated layer which may interfere with respiration of the underlying tissues, especially as the attack is first directed to the lenticels.

A combination of the first two effects is responsible for the gradual death associated with 'gout', a combination of the latter two for the rapid death associated with heavy attacks on the stem.

EFFECTS ON STAND

Damage in Europe

There are many references in European literature to damage caused by *Adelges nüsslini* and *Adelges piceae*. It is not always clear which species is responsible, but there is little doubt that *A. nüsslini* is generally considered the more destructive of the two (33). This species attacks the needles as well as the bark and has caused injury chiefly to young stands, although recently damage to older stands has been reported (19). Widespread dying of *Abies pectinata* has occurred in Germany and has caused much discussion and difference of opinion among German foresters as to the cause (12, 34). It has been attributed to soil conditions, to *A. nüsslini* and *A. piceae*, and to a combination of factors in which the insects played a secondary role. The behaviour of *A. piceae* in Canada and its evident ability to kill balsam fir growing under favourable conditions may throw some light on this question.*

Mortality in Canada

At the commencement of these studies 24 plots, one square chain in size, were established in Richmond and Hants counties, Nova Scotia, and in York County, New Brunswick.

Fourteen of the plots were in Richmond County, in stands ranging from 40 to 70 years of age. The trees were mainly suffering from light to moderate infestations, which had caused 'gout' and considerably reduced growth of new shoots. During 1929 and 1930 they were attacked by the black-headed budworm, *Acleris variana* (Fern.), which destroyed the new shoots and some of the old needles. Mortality was severe and practically all of the trees over 60 years of age died between 1931 and 1935. This was chiefly attributable to the budworm defoliation, but the susceptibility of the trees to the attack of the budworm had been greatly increased by the reduced shoot growth caused by *Adelges piceae*. The small shoots were quickly killed by the young budworm larvae, and there was a close relationship between the amount of 'gout' and the rate of dying.

Plots 1 to 5 were in Hants County and were not affected by the budworm. The stands consisted almost entirely of balsam fir and white spruce. Fir predominated in all except No. 4, which contained a preponderance of spruce. They were representative of the heavier, localized outbreaks that were common over a large part of the County. The mortality is shown in Table 7 for the years 1931 to 1935. Between 1930 and 1933 the insect was especially numerous in this district and most stands suffered damage. The table indicates how severe the mortality was in some of them. The fact that damage was less severe on Plot 4, which had a small amount of balsam, suggested that attacks develop more rapidly in stands with high balsam content. The plots were too few to form an adequate basis for such a conclusion, but it was supported by general observations elsewhere. There was a tendency for the larger trees to be killed first, as shown by a comparison of the average diameter of the trees that were dead in 1933 with the average diameter for the stand. All sizes, however, were killed.

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* In 1951 G. Wylie, Division of Entomology, Canada Department of Agriculture, reported in correspondence that, in Switzerland and France, infestations of *Adelges piceae* on the trunks of *Abies pectinata* did not appear to cause any mortality or serious damage. Young trees infested by *Adelges nüsslini* were more common and considerable mortality had resulted to trees under 10 feet in height from attack on the twigs. Also, he found no 'gout' or 'rotholz' on *Abies pectinata*.

TABLE 7. — PERCENTAGE MORTALITIES OF BALSAM FIR IN 10 PLOTS IN IMMATURE AND MATURE STANDS OF VARYING COMPOSITION, 1931 TO 1937. NOS. 1 TO 5 IN HANTS COUNTY, N.S., NOS. 21 TO 25 IN YORK COUNTY, N.B.

Plot No.	Type*	Age	Total balsam	Diameter of balsam, inches				Per cent balsam dead						
				All trees		Dead, 1933								
				Range	Aver.	Range	Aver.	1931	1932	1933	1934	1935	1936	1937
1	FS	25-50	59	2-12	5.7	3-12	6.1	58	74	86	Salvaged			
2	FS	25-40	117	1-9	3.1	4-9	5.4	5	11	18	"			
3	FS	25-50	82	2-10	5.0	4-10	5.7	17	34	70	"			
4	SF	20-45	33	1-10	4.5	8	8.0	0	0	3	21	27	Salvaged	
5	FS	25-45	80	1-11	6.1	3-10	6.7	10	23	35	40	47	"	
21	BMF	40-55	30	3-15	7.4	5-15	9.6	7	23	50	66	66	66	73
22	FS	35-50	54	2-8	4.9	4-8	5.5	9	34	56	82	89	—	—
23	SF	30-55	60	3-10	5.5	8-10	9.0	0	3	3	20	27	—	—
24	FS	35-55	56	2-12	6.6	6-9	8.5	0	0	5	59	72	77	80
25	FS	40-60	62	3-10	6.5	—	—	0	0	0	6	16	26	32

*FS — Balsam fir mixed with white and red spruce, fir predominating.
SF — Balsam fir mixed with white and red spruce, spruce predominating.
BMF — Balsam fir mixed with yellow birch and maple.

Fig. 44. Plot 21 in 1932. Two trees in foreground have been killed; trees in background died in 1933. 'Wool' has disappeared from tree at left.

Fig. 45. Balsam fir killed in mixed stand near Plot 21, 1940.

Plots 21 to 25 were in York County, N. B., and represented typical initial infestations which developed between 1931 and 1933, when they were severely checked by winter-killing of the insect above snow. The tree mortality occurring between 1934 and 1936 was due to injury caused before 1934. By 1937 some trees began to die from new infestations built up from the population that had survived beneath the snow. Plot 21 was in a mixture of balsam and tolerant hardwoods ; plots 22 and 23 were in a mixture of approximately equal quantities of balsam and white spruce, plots 24 and 25 were in an almost pure balsam stand. General observations have shown that severe mortality may occur in almost any mixture with other species, as indicated by these plots, but infestations develop most rapidly when the balsam content is high. The tendency for the larger trees to die first was more striking than in the Nova Scotia plots. (Figs. 44, 45).

In 1928 two permanent sample plots were established by the Dominion Forest Service at Albany Cross, N. S., in a 40-year-old stand consisting of 70 per cent balsam fir and the remainder largely red spruce, *Picea rubens* Sarg. One plot was lightly thinned from below by the removal of 10 per cent of the balsam and 5 per cent of the other species, by volume. In 1932 when the plots were remeasured, no abnormal mortality was noted although a number of dead tops were recorded. In 1938, 46 per cent of the volume of the balsam was dead on the thinned plot and 49 per cent on the unthinned plot, compared with 12 per cent and 9 per cent of other species. At the same time 42 per cent of the living balsam showed dead tops on the thinned plot. Careful records were not taken on the check plot, but it was noted that many trees had dead tops. An examination of a number of trees by the writer showed that the mortality and the dead tops had been caused by moderately heavy attacks of *Adelges piceae,* which had commenced about 1927 and were most severe

TABLE 8. — INFESTATION AND MORTALITY BY DIAMETER CLASSES IN 2 IMMATURE BALSAM-SPRUCE STANDS, 1947-1950. PLOT A: 1/5 ACRE, 30-40 YEARS OLD, FREDERICTON, N.B. PLOT B: 1/10 ACRE, 25-35 YEARS OLD, SPRINGFIELD, N.B.

	D.B.H. inches	1947						1950					
		Not infested	Stem attack			Dead with foliage		Not infested	Stem attack			Dead with foliage	
			L.	M.	H.	red	fallen		L.	M.	H.	red	fallen
Plot A	3	15	0	0	0	0	0	11	1	0	0	0	0
	4	52	0	0	1	0	0	46	~~4~~ 3	1	0	0	1
	5	39	0	0	0	0	0	27	8	3	0	1	0
	6	21	2	0	0	0	0	19	3	2	0	1	1
	7	11	0	0	1	0	0	6	5	1	0	0	1
	8	3	0	0	1	0	0	1	2	0	0	1	1
	Total	141	2	0	3	0	0	110	22	7	0	3	4
Plot B	2	6	5	0	0	1	0	0	3	1	0	0	2
	3	15	22	0	0	3	0	0	16	2	0	3	8
	4	3	15	4	1	0	1	0	19	1	2	4	7
	5	4	14	7	3	1	2	0	12	6	0	3	14
	6	0	5	1	2	5	1	0	3	1	1	2	6
	7	0	3	1	2	0	1	0	4	2	0	1	5
	8	0	0	1	1	0	1	0	0	0	0	1	2
	Total	28	64	14	9	10	6	0	57	13	3	14	44

Fig. 46. Young trees killed by heavy attack. Note flat-topped tree on left.

between 1932 and 1935. There was little difference in the attack on the thinned and unthinned areas.

Since 1946 a number of permanent sample plots have been established as part of the Forest Insect Survey of the Fredericton laboratory to follow the progress of infestations. The trees are remeasured each year and classified according to infestation and condition. On some of these plots no infestation has yet developed ; on others a light infestation has shown little change. The results to date on two plots are presented in Table 8 to illustrate the behaviour of active new stem infestations in immature stands.

Plot A is in an even-aged stand, 30 to 40 years of age, predominantly balsam. Older nearby stands were almost completely killed between 1933 and 1940, and the plot represents a considerable area of this younger type which was attacked almost 10 years later and showed a few dead trees in 1945. In 1946 only 2 out of 146 trees on that plot were noticeably infested. In 1950 seven of the larger trees were dead and 29 were noticeably infested but the attack was not very severe.

Plot B is in another even-aged stand, slightly younger and denser, and with a higher proportion of balsam. It is surrounded by cleared land. In 1947 many trees died in one part of the stand and formed an almost solid patch of red foliage. The plot was laid out near this patch. The rapid progress of the infestation during the following years is shown in the table. By 1950

Fig. 47. Reproduction killed by larvae dropping from heavily infested tree above.

most of the larger trees and many of the smaller trees were dead. All the remainder were infested.

Both of these stands were on good sites and growing well when attacked. The condition of the surrounding forest suggests that the greater part of both stands will be killed and the residual trees will suffer from 'gout'. It may be noted that in general the larger trees were the first to become heavily infested and killed, although in very active outbreaks, as in plot B, this tendency may be obscured by the number of small trees that become infested from the excess population of overtopping larger trees.

These few examples illustrate the destructive power of the insect in individual stands. Although such attacks are common throughout the area of distribution, the plots are not intended to represent average conditions. No satisfactory data are yet available on which to base an estimate of total loss. The problem is complicated by the extreme irregularity of infestations, but there is no doubt that *Adelges piceae* has caused more damage to the pulpwood stands of the Maritime Provinces than any other insect during the past 25 years.

Other Effects

The effect on growth of individual trees has already been indicated. No data can be given to show what has been the result of reduced growth of surviving trees in terms of annual increment per acre. It can only be stated that high percentages of trees closely examined in a large number of stands taken at random throughout Nova Scotia, Prince Edward Island, and southern New Brunswick showed some degree of 'gout'. The reduced growth of these trees, together with the mortality which has been observed in these areas indicates that the yield of balsam fir has been seriously reduced.

The effect on reproduction varies. Often all the balsam reproduction beneath a heavily infested tree is killed by the falling larvae (Fig. 47). Advance growth which survives may be so severely injured that it fails to grow for 5 to 10 years. Where reproduction is abundant, however, a sufficient number of seedlings generally survive to provide for the replacement of the killed trees. If the stand contains a sufficient number of spruce the effect may be a beneficial thinning favouring the spruce.

Similarly, an attack on a young stand in which spruce predominates may result in a useful thinning which increases the percentage of the more valuable spruce. It is doubtful, however, whether the insect will greatly increase the spruce content of future stands, for balsam reproduction is abundant in the infested stands in this region.

Mention has been made of the effect of 'rotholz' in reducing the value of balsam for lumber. Pillow *et al.* (27) showed that the fibres from this type of wood are shorter than those of normal wood, and much more subject to fragmentation in the pulping process. This, together with high lignin content, affects its value for pulpwood.

Relation to Forest Type

Extensive surveys failed to provide clear evidence of any consistent relationship between forest type, or site quality, and the degree of infestation or damage. Brower (6) stated that, in Maine, trees on thin soils or poorly drained sites have been most severely injured and that they provide the "endemic centers of infestation". The behaviour of the insect in the Maritime Provinces to date cannot be explained in this way. Some of the most severe infestations and highest percentages of mortality have occurred on well-drained sites with relatively deep soils, in mixtures of softwoods and hardwoods as well as in pure softwood types. More intensive study is needed ; but, as suggested by the discussion of natural control, the factors controlling population are complex and seem unlikely to express themselves in a simple relationship to forest type or site, as long as the insect retains its present epidemic status. The danger of severe infestation and important damage increases, however, with the percentage of balsam in the stand.

There appears to be some relationship between density of stand and amount of damage. Thin stands, in which many trees have developed deep crowns, rather frequently have shown more damage than neighbouring fully stocked stands. Infestations are also often noticed first on the edges of a stand. Small forested areas surrounded by cleared land seem to be particularly susceptible. It is possible that exposure may have some effect on the resistance of the trees, but the depth of the crown is also involved.

CONTROL

The first essential for control is that woodland owners should recognize the symptoms of infestation and understand the nature of the damage that may be expected.

Chemical

Tests were made with nicotine sulphate and miscible oils. Various concentrations and dosages were applied to 1-foot sections of uniformly infested logs after covering the rest of the log with paper. Check areas were left between treated sections. Pieces of bark, 3 by 3 inches, were examined under the microscope each day for 3 days after spraying, and the control was estimated by correcting for mortality from other causes as estimated from the checks. The following conclusions were drawn.

1. To be effective with one application an insecticide must be capable of killing the dormant first-stage larva, as it is present on the tree at all times.

2. The dormant larva and the egg are resistant to nicotine sulphate in concentrations up to 1 in 400. Other stages can be killed, but over 50 per cent of the adults may survive because of protection by the wax 'wool'.

3. Miscible oils ('Volck' and 'Kleenup') at a concentration of 1 in 25, applied thoroughtly, will kill all stages, but up to 5 per cent may survive because of protection by lichens or accumulation of 'wool' in crevices. The best time to spray is early April, just before moulting commences.

These results were confirmed by spraying stems and branches of standing trees on April 15, other parts of the same trees being used as checks. Control with oil was estimated at 97 per cent on 2 stems 10 inches in diameter, and 95 per cent on the branches of 2 small trees, where there was some survival under old bud scales. No burning of foliage resulted. Brower (6) reported 100 per cent mortality with lime-sulphur and good results with nicotine sulphate but warned against burning of foliage with oils.

Under forest conditions insecticides will have limited value because of cost and difficulties of obtaining a sufficiently high percentage control. After a winter such as 1933-34, however, it would be practicable to spray the bases of trees and virtually eradicate an infestation in a woodlot under intensive management.

Biological

The discussion of predators and the introduction of *Leucopis obscura* has indicated the possibilities, as well as some of the probable limitations of biological control. The greatest likelihood of success seems to lie in the establishment of predators with high searching ability and capable of attacking the dormant larva and the egg under conditions of light to moderate infestation. The chances of obtaining species suited to the Canadian climate would be greatest in northern Europe and Russia. Further work on this problem is being undertaken by the divisions of Entomology and Forest Biology, Canada Department of Agriculture, in co-operation with the Commonwealth Bureau of Biological Control.

Forest Management

The fact that initial infestations generally obtain their impetus on the larger trees makes it possible to check outbreaks in early stages by cutting the noticeably infested trees. They should be marked by someone carefully trained in the recognition of all stages of infestation, and the best time for such work is in late August or September. Cutting should be done in winter, when no eggs or motile larvae are present and the insect cannot be spread by the operation. It has been found that the overwintering larvae can develop to the adult stage and produce eggs on winter-cut logs. They should therefore be barked or scorched with a blow torch if they are not used before spring. Another method is to burn the slash over them. Little development, however, takes place on tops because of their drying out.

The most practical method will generally be to combine control and salvage by cutting all balsam of merchantable size in stands that have become noticeably infested. This method has been used with success on the forest owned by the University of New Brunswick and also on the City Forest at Fredericton, N. B.

Balsam fir is a relatively short-lived species that is subject to attack by a number of destructive insects. It has, however, great powers of reproduction because of prolific biennial seeding, rapid rooting, and high tolerance of shade. It is the most prevalent softwood species in the Maritime Provinces and tends to increase rather than diminish after cutting and insect outbreaks. Its careful management is therefore of prime importance. As the chief value of this tree is for pulpwood, it should generally be managed on a short rotation, which in many districts may be as short as 50 years. The loss from *A. piceae*, as well as several other species, will be minimized if management is guided by the following principles.

1. Short cutting cycles to reduce the danger of loss between cuts.
2. Favouring of spruce and other silviculturally more stable species in selective cutting. This may mean the cutting of all balsam of merchantable size where spruce predominates.
3. Cutting or girdling of decadent, unmerchantable balsam.
4. Maintenance of full stocking in immature stands.
5. Periodic inspection, and prompt cutting of infested trees or stands.

SUMMARY

Adelges piceae (Ratz.), which spread through Europe during the nineteenth century, was introduced to Nova Scotia about 1900, probably on nursery stock. It is now established throughout the whole of Nova Scotia and Prince Edward Island, the southern half of New Brunswick, and a good part of the northeastern United States. It has also reached two points in Newfoundland.

The species is distinct, morphologically and biologically, from *Adelges nüsslini,* with which it has sometimes been confused. The latter species has not been found in Eastern Canada, although it occurs on the west coast.

In the Maritime Provinces there is no migration to spruce and multiplication depends on two wingles parthenogenetic generations (hiemosistens and aestivosistens), which feed on the stem, branches, and shoots of *Abies balsamea* (L.) Mill. Two other forms (winged and wingless progrediens) arise occasionally from the first few eggs laid by some of the hiemosistentes and feed on the needles. The wingless progrediens produces a few offspring, which become aestivosistentes : the winged progrediens is sterile.

Distribution on the tree is determined by the influences of negative geotaxis and positive phototaxis on the motile larvae, and by the accessibility of young parenchyma at the surface.

Dispersal results chiefly from the surplus population of motile larvae on heavily infested trees. The larvae are carried by surface winds and vertical air currents. The general occurrence of balsam fir in this region makes the chances of successful establishment relatively good and the rate of spread in eastern New Brunswick has exceeded 5 miles per year in recent years.

The sistentes have a high reproductive potential. The chief climatic factor controlling rate of increase is low winter temperature. Only the neosistens can survive the winter and this stage may be completely killed above snow when temperatures drop below —30° F. Other factors associated with low temperature determine the amount of mortality. The protection of a small part of the population by snow is sufficient to prevent extermination and permit establishment throughout most of the range of the host. Sun and rain limit survival on exposed parts of the tree. Direct sun during midsummer kills the insect through high temperatures produced on the surface of the bark.

The ultimate level of population in a stand is determined by biotic factors, the chief of which are the resistance of the tree and insect predators. Trees vary in their suitability as a source of food, and in the amount of shelter they afford. They are also capable of resisting continued attack by laying down a secondary periderm beneath the feeding sites.

A number of native insect predators attack *A. piceae* but their control value is limited by dependence on a dense population of their host. *Leucopis obscura* Hal. has been introduced and has spread rapidly throughout the range of the host, tending to replace native predators. It has, however, a similar limitation and species with greater searching ability are desirable. Ability to attack the neosistens would also be a valuable characteristic, as this stage is present throughout the year.

The long, slender feeding stylets of the insect are inserted intercellularly in the cortex, or phelloderm, where a pocket of parenchyma is probed. Their renewal at moulting, and the mechanism by which they are controlled, are discussed.

The condition known as "gout disease" of balsam fir is a morphogenic response to the salivary injection of the insect. Striking hypertrophy results in the cells immediately affected by the stylets. The enlarged cells have thickened, ridged walls and enlarged, sometimes double, nuclei. Hyperplasia occurs in the surrounding tissue and pockets of hypertrophied cells may be encysted by a purplish secondary phellem.

The cambium is stimulated and produces an abnormal, reddish-brown, brittle type of wood. The tracheids are similar to those of 'compression' wood, which is caused by a gravitational stimulus. Similar results were obtained with applications of indole-acetic acid. Hormonal action is indicated.

The reactions vary with the species of *Abies*. 'Gout' is produced in several North American species, but not in the European species. Abnormal wood growth has been found only in *A. balsamea*.

When a stand first becomes infested the insect multiplies most rapidly on the larger trees, but all sizes may be attacked and killed. Severe attack on the stem may result in death within 3 years without any symptoms of 'gout'. 'Gout' is caused by light to moderate attacks on the new shoots over a longer period. After the first outbreak in a stand the surviving trees begin to show the symptoms of the disease. Some may recover ; others die slowly. Trees suffering from persistent attack have rapid taper and low-quality wood, for both sawlogs and pulpwood.

Death results from inhibition of bud growth, killing of large areas of the outer bark, and interference with conduction caused by the abnormal wood.

Severe mortality and loss of growth have resulted over considerable areas. There is no consistent relation between site, or forest type, and amount of damage. Advance growth is often killed. Where spruce predominates in young stands a desirable thinning favouring the spruce may sometimes result.

The insect may be controlled with oil sprays, but under forest conditions insecticides will be of value only after complete winter-killing above snow. Control may be combined with salvage by special cutting operations. Short cutting cycles, management of balsam fir on a short rotation, favouring spruce in selective cutting, and maintenance of full stocking are recommended.

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