FORESTRY COMMISSION

BULLETIN No. 26

ADELGES INSECTS OF SILVER FIRS

By

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DEPARTMENT OF FORESTRY
ABERDEEN UNIVERSITY

EDINBURGH: HER MAJESTY'S STATIONERY OFFICE
PRICE 8s. 6d. NET

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FOREWORD

Insects of the genus *Adelges* have long been recognised as economically important pests of the valuable timber-producing silver fir trees that comprise the genus *Abies*. In fact the planting of the common European silver fir, *Abies alba*, has had to be greatly restricted in Britain because of the depredations of these insects.

This Bulletin gives the results of Dr. Varty's intensive studies of the *Adelges* insects in relation to forestry, which were carried out in Scotland under the auspices of the Department of Forestry of Aberdeen University. It replaces the former Bulletin No. 7, entitled *The Silver Fir Chermes*, which has long been out of print.

FORESTRY COMMISSION,
25 Savile Row,
London, W.1

March, 1956

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INTRODUCTION AND ACKNOWLEDGMENTS

Adelges nüsslini and *A. piceae*, which together are variously known as the *Adelges* of Silver fir, and as the woolly aphids or *Chermes* of Silver fir, are minute polymorphic insects belonging to the family Phylloxeridae (Aphidoidea, Hemiptera). These two species occur both in Europe and North America where *Adelges* has assumed considerable silvicultural importance because of the susceptibility of certain species of *Abies*. In Britain, where both insects and host trees are introduced species, the persistently severe attack by *Adelges nüsslini* on young trees of *Abies alba* has resulted in the virtual suspension of the planting of this useful species during the last 30 years.

In this investigation over part of the period 1950-1954, the writer's purpose has been to study the biology of the Silver fir *Adelges* as found in Scotland, to consider certain aspects of susceptibility and resistance to attack shown by the various host species, and to assess the current silvicultural significance of these insects.

Throughout this work, the writer has used the *Handbook of Coniferae* by Dallimore and Jackson (55) as the standard reference for tree names, and the *Check List of British Insects* by Kloet and Hinck (93) for insect names.

This investigation has been conducted under the supervision of Professor H. M. Steven, Forestry Department, University of Aberdeen, whose helpfulness and stimulating suggestions have been very much appreciated. The writer is indebted to Dr. E. V. Laing and other members of the staff of the Forestry Department for their co-operation. Thanks are also due to Dr. P. C. de Kock, Macaulay Institute for Soil Research, Aberdeen, without whose help and encouragement the chemical aspects of this research could not have been attempted, and to Dr. R. L. Mitchell, also of the Macaulay Institute, for undertaking certain analyses acknowledged in the text. Finally the kindness of Mr. C. Y. Ross, Head Forester of Dunecht Estate, in providing facilities to use the Forest Garden as a research plot, is gratefully acknowledged.

Chapter 1

TAXONOMY

1. DISCUSSION OF FAMILY RANK

The two species *Adelges piceae* Ratz. and *A. nüsslini* C.B., under discussion in this work are members of the subfamily Adelginae in the family Phylloxeridae of the superfamily Aphidoidea, as recognised in Kloet and Hinck's (93) *Check List of British Insects*. In the course of arrival at this taxonomic status, Adelgids as a whole have suffered the usual vicissitudes of treatment accorded to any group with complex morphological and biological characters. In the early years of scientific investigations following the time of Linnaeus, the group held only generic rank, *Chermes*, in an indefinite position within the family Aphididae; but from 1857 it has been known as a small family, the Chermidae Koch and from 1862 as the Chermesidae Passerini. In time its systematic proximity to the *Phylloxera* group came to be recognised, and in 1889 Dreyfus (58) combined the two under the family Phylloxeridae, yet retained for each group only generic rank. In 1907 Börner(15) renamed this family Chermesidae and elevated each of the two genera to the rank of subfamily, viz. the Phylloxerinae and the Chermesinae. Six years later after further study of the group, he (21) raised each of the subfamilies to separate family status. Within his new family Chermesidae he differentiated two tribes, the Pineini and the Chermesini. Yet in 1915 Cholodkovsky (42) whose authority on the systematics of the group was fully equal to Börner's, considered the Adelgids to be merely a genus within the subfamily Phylloxerinae in the family Aphidae.

Börner's classification came to be tacitly accepted until in 1928 Annand (2) published his important though incomplete *Contribution toward a monograph of the Adelginae, (Phylloxeridae) of North America.* In this work he adopted subfamily rank for the group, which he now named the Adelginae in view of the fact that the old name Chermesinae had been properly allotted to the *Psylla* group, as explained in section 2, p. 2. The writer has accepted this classification on account of its convenience and general acceptance, particularly by Mordvilko (111), one of the great authorities on the classification of aphids and related groups.

The family Phylloxeridae has reached its present taxonomic standing on the basis of a number of common biological and morphological characters, but essentially it is distinguished from the family Aphididae in two ways:

(i) all its generations are totally oviparous whereas those of the true aphids are frequently viviparous;

(ii) the forewing has three oblique veins whereas that of the alate aphid has four.

Within the Phylloxeridae, the subfamily Adelginae is separated from the subfamily Phylloxerinae by the following principal characters:

(i) in apterous forms, by the presence of a well-developed ovipositor in the former and its absence in the latter, and

(ii) in the alate forms, the Adelginae have 5-segmented antennae of which each of the three apical segments is distinguished by a large sensorium, whereas the Phylloxerinae have 3-segmented antennae. They can also be separated on the basis of forewing venation; the Adelginae carry separate anal and cubital veins but in the Phylloxerinae these veins coalesce at the base. The ovipositor of the adult apterous Adelgid, and the antennae of the alate form, are illustrated in Pl. 26 & Pl. 8 respectively.

2. DISCUSSION OF GENERIC TAXONOMY

(1). Chronology of Literature

Generic terminology has undergone a similar metamorphosis with the passage of time. The name *Chermes* was first brought into scientific literature by Linnaeus (101) who used it in the first instance to describe a species of *Lecanium* but later applied it to a loosely defined group of aphids and near relatives including the spruce-gall Adelgids and Psyllids. Burdon (24) stated that the name is derived from the ancient word "kirmis" (Sanscrit "krimi", a worm) which had long been used to denote a dyestuff expressed from insect galls, in parts of the Middle East.

Hartig, 1837 (79) dissolved this aphid group but retained the name *Chermes* for the then little-known spruce-gall Adelgids. From that time until the advent of Börner the generic name *Chermes* was used fairly consistently in references to the Silver fir Adelgids themselves, although at various dates members of the genus were ephemerally allotted to other groups. Annand (2) lists the chronological change in generic nomenclature as follows:—1756 *Chermes* Linnaeus; 1762 *Psylla* Geoffrey; 1773 *Aphis* L., De Geer; 1836 *Adelges* Vallot; 1837 *Chermes* L., Hartig; 1843 *Cnaphalodes* Amyot-Serville; 1844 *Sacchiphantes* Curtis; 1848 *Elatiptus* Amyot; 1848 *Laricethus* Amyot; 1885 *Adelges* Vallot, Girard; 1908 *Chermes* L., Börner.

Meanwhile towards the end of the nineteenth century important biological and taxonomic progress was made by a number of investigators. In the period 1887-9 Blochmann (12, 13), Dreyfus (58, 59), and Cholodkovsky (30, 31, 32) independently discovered sexuality and alternation of host in the genus, which were indispensable contributions to knowledge of systematics and evolution.

Of these early investigators however, Cholodkovsky (34, 35, 36, 38) was responsible for the most searching work on the group, notably in his publications of 1895 and 1896. His work can be said to have promoted the considerable research which followed in the next twenty years and which has continued to stimulate interest in the group to the present day. Among his contemporaries, Nüsslin (119) and Börner (16) made valuable contributions to the literature. In 1908 Börner published his monograph on *Chermes* which is still perhaps the most important taxonomic reference on these species. In this and subsequent publications (20, 21) he set up the genera *Dreyfusia*, *Chermes*, *Gillettea*, *Aphrastasia*, *Cnaphalodes*, *Cholodkovskya* (in the tribe Chermesini) and *Pineus* (in the tribe Pineini) out of the frame-work of the former genus *Chermes*. The Silver fir Adelgids were separately confined within the first of these genera and named in honour of the German biologist L. Dreyfus. In 1915, Cholodkovsky (42) reviewed Börner's work but held his generic characters only valid for subgenera. Annand (2) in 1928 felt strongly that Börner had debased generic rank to practical equality with a species and that his variations of generic character were no larger than those specific differences ordinarily found within a large genus. Accordingly he reduced all the species to membership of two genera *Adelges* and *Pineus*. In this respect at any rate he broadly agreed with Börner's isolation of the Pine Adelgids from all the others. Annand's conclusions have been accepted as the basis of nomenclature in the present study.

Annand had reverted to the name *Adelges* because a number of systematists had correctly suggested that under the international rules of biological nomenclature the name *Chermes* had been preempted by the old Psyllids in accordance with Linnaeus's original designation and description of 1748, later withdrawn. This name *Adelges* dates from an entomological note by Vallot (151) in 1836, and was coined from Greek roots meaning "concealed in the earth" (referring to the mode of life of another closely related group). Nevertheless Annand's classification has not been universally accepted, and some divergence of nomenclature has arisen. North American and British writers have tended to discard Börner's genera in favour of reduction to *Adelges*. On the other hand European authorities have been reluctant to add to the confusion of the literature by casting aside the well-known genera, and in general have continued to refer to the Silver fir Adelgids as *Dreyfusia*. This divergence in nomenclature is well illustrated by comparing the two most recent substantial descriptive publications on these species; Schneider-Orelli (136) (Switzerland 1950) continues to recognise the genus *Dreyfusia*, whereas Balch (7) (Canada 1952) prefers *Adelges* for the same insects.

These designations of generic rank are based entirely on morphological characters, but as the author will show in section 1.6, p. 10, there is some tentative support for the European point of view from preliminary experiments in the application of paper chromatography to taxonomy.

(2). Morphology at the Generic Level

Börner's morphological characters have been widely used by subsequent investigators. In particular, Annand followed the former's utilisation of spiracle numbers, in order to separate his new genera *Pineus* and *Adelges*. Thus within the subfamily Adelginae the genus *Pineus* is characterised by the presence of four abdominal spiracles while the genus *Adelges* is characterised by five. (See Pl. 26). Börner considered this an evolutionary character by which he was able to look upon *Adelges* (his tribe Chermesini) as the more primitive of the two groups. Annand brought to light certain other features which point to the same conclusion. The genus *Adelges* only will now be discussed.

The genus *Adelges* is typically characterised by a pentamorphic life cycle comprising three heterogenous generations on the primary host which is always a species of *Picea*, and two heterogenous generations on the secondary host which may be a species of *Abies*, *Larix*, *Pseudotsuga*, or *Tsuga*. These five generations have received a variety of synonyms particularly between the period 1878 to 1917, but the names adopted by Marchal (106) have proved the most stable and are used in this work. The generations are:

I. Fundatrix;
II. Gallicola;
III. Exsulis sistens, with a daughter generation Exsulis progrediens;
IV. Sexupara;
V. Sexualis.

All these forms are equipped with dorsal glands from which are secreted flakes and filaments of wax; this characteristic has earned them the common name "woolly aphid". Generally speaking, this wax wool is secreted through three lines of wax gland areas, (that is, chitinised plates each with a group of wax pores), running longitudinally on each side of the dorsum. The two innermost rows, one on each side of the mid-dorsal line, are termed the mesial glands; those in the next row on each side are the pleural glands; the outermost row on each side comprises the marginal glands. (See Pl. 26.)

Morphologically the gallicolae and the sexuparae being the winged migratory generations can be grouped together. Each has five instars, the final one being the alate parthenogenetic female. In the adult the head, thorax and abdomen are discrete regions.

The head bears a pair of relatively long 5-segmented antennae with sensoria, compound eyes, three ocelli and a 3-segmented rostrum with short stylets. It is heavily chitinised and equipped with two anterior and one posterior wax gland area on each side. The thorax bears two pairs of wings and three pairs of legs. The venation of the forewings is simple, only the radial sector, and single medial, cubital and anal veins being represented. In the hindwings only the radial sector and the medial vein are present. The legs are relatively long and slender. The thorax is also heavily chitinised. The prothorax exhibits a large marginal gland area, and smaller pleural and mesial gland areas, the latter two frequently fused. The mesothorax and metathorax usually have mesial gland areas. The abdomen is characterised by the variable and specific representation of the wax gland areas and by the distinct ovipositor. The anus opens dorsally on the ninth segment.

The fundatrix and the sistens are the apterous wax-wool-covered parthenogenetic forms, which though dwelling on different hosts, are morphologically very similar. The adult has a broadly ovoid shape, with the head, thorax and abdomen not readily distinguishable except by microscopic examination. The head bears short 3-segmented antennae with sensoria on the apical segment, and a trio of ocelli on each side of the head, and carries ventrally a stout 3-segmented rostrum with long stylets. The head is heavily chitinised and is marked by two transverse rows of wax-gland areas. The thorax is a large area of the body and bears the short, stout, two-clawed legs. A pair of spiracles is present on each of the meso- and metathoraces. The prothorax bears two rows of wax-gland areas set in its chitinous shield but only one row occurs on each of the meso- and metathoraces, which are less heavily chitinised. The abdomen which is broadly based on the thorax, comes apically to a blunt point, at which is set a distinct ovipositor. The anus opens on the ninth abdominal dorsum. Spiracles are present on each of the second to sixth segments. The abdomen however is chiefly characterised by the regular transverse rows of marginal pleural and mesial gland areas on the dorsa of each of the segments 1 to 6. The segments 7 to 9 bear fewer wax gland areas. The degree of chitinisation decreases and finally disappears towards the apex.

The sexuales are the third morphological category. They are very small and increase their body bulk relatively little through their five stadia. The adults are dimorphic, the male being smaller and more slender than the female. Only slight chitinisation is present on any part of the body and wax gland areas are few. The adult body is entirely covered with a coarse wax dust. The head is equipped with a pair of 4-segmented antennae bearing sensoria on the two apical segments. The last segment is distinctly scaly and is terminated by a long bristle. On the thorax and abdomen there do not appear to be any characters of marked taxonomic value, except for the presence of the knobbed bristles on the tarsi.

The immature stages of these various generations bear features of considerable usefulness to the systematist. The generic characters of the larval stages are as follows:

(i) like the adults all the larval instars carry spiracles on the second to sixth abdominal segments, and mesial pleural and marginal plates are arranged in three rows along each side of the dorsum;

(ii) the sistentes and progredientes are quite distinct at all stages;

(iii) the sistens and fundatrix larvae are strongly chitinised and carry distinct setae in the vicinity of the gland areas on the plates; the gland facets or pores are more distinct and more numerous towards the posterior of the body;

(iv) the larvae of the sexuales, progredientes and alate forms are weakly chitinised with variable exposition of the gland facets;

(v) alate forms in the fourth instar have quite separate plates on the head and prothorax;

(vi) the first and nymphal instars are readily identified, but in general there are few absolute features of distinction between the intermediate instars.

3. DISCUSSION OF SPECIFIC TAXONOMY

(1). Chronology of the Literature

It is believed that *Adelges piceae* Ratz. is a truly indigenous species present in Europe on the Common Silver fir *Abies alba* Miller long before the distinguished German zoologist Ratzburg (127) first gave it the binomial title *Chermes piceae* in 1843. The other Silver fir Adelgid *Adelges nüsslini* C.B. is usually considered to have arrived in Western Europe on transplants of *Abies nordmanniana* Spach from the Caucasus, and Schneider-Orelli *et al* (132) indicate that it is unlikely to have been present until the second half of the nineteenth century. The intrusion and dispersion of this species passed by unnoticed until it was widely established in Western Europe. The two species are separable by considerable biological differences but only by minute morphological differences, so that it is not surprising that during the unravelling of their distinct identities considerable confusion and controversy should have arisen.

By the end of the century, *Adelges nüsslini*, still under the guise of *Chermes piceae*, was beginning to attract the attention of continental entomologists through its effects on planting stock of *Abies nordmanniana* and natural regeneration of *Abies alba*. As early as 1889 Dreyfus (59) may have described it when he assigned the name *Chermes funitectus* to a species on the secondary host which he identified, mistakenly it is believed, as *Tsuga canadensis*. A year later Eckstein (62) drew attention to the pest and named it *Chermes nordmannianae*, but failed to adequately demonstrate any specific difference between this and the well-known *Chermes piceae*. The two species continued to be confused under single identity as *Chermes piceae* until the early twentieth century. In 1903 Nüsslin gave an account of the migration of winged individuals of the Silver fir *Adelges* to Norway spruce, *Picea abies* Karst. but did not detect thereby the presence of a second species distinct from *Chermes piceae*. During 1904-8 however, Cholodkovsky (37, 39, 40) produced evidence to show that two separate species were present on the Silver fir and could be distinguished by biological and morphological characters. For the new species now known as *Adelges nüsslini* he used the name *Chermes funitectus* Dreyfus, characterised by its preference for the new shoots of young trees; for the other species living on the bark of older trees he retained the old name *C. piceae*. He also noted that *C. funitectus* promoted a gall on the Oriental spruce *Picea orientalis* Carr. in the forests of the Caucasus, but he did not find *Chermes piceae* anywhere in Russia. Further he claimed to detect slight differences in the individuals of *C. piceae* attacking the imported fir *Abies procera* Rehder in Germany, and termed them *Chermes piceae* var. *bouveri*. Other workers have not confirmed the identity of this variety.

Meanwhile Marchal (105) had detected similar differences between *Adelges nüsslini* and *A. piceae* about the same time; he also claimed that *A. nüsslini* passed through a pentamorphic life cycle when both hosts were present, thus contradicting Nüsslin's assertion that the sexual generation was abortive.

In 1908, Börner (16) published his monograph on *Chermes*, which is certainly the most detailed work on *Adelges* spp. While acknowledging Cholodkovsky's findings, he yet refused to allot the two species separate specific status, and continued to group them together as *Chermes piceae*, on the reasonable grounds that biological variation without adequate morphological distinction did not merit specific separation. Nüsslin (118, 119) countered this decision with even more marked proofs of their biological individuality, as a result of which Börner (19), after working out minute morphological differences, decided to establish the bark-feeding type or "altenrindenläuse" as *Dreyfusia piceae*, and the shoot-feeding type or "jungtriebläuse" under the new name *Dreyfusia nüsslini*. He rejected Cholodkovsky's epithet *funitectus* Drey. (for *Adelges nüsslini*) in view of the uncertainty regarding Dreyfus's original description of the species.

The only British investigator during this period was E. R. Burdon (26) who in 1908 published a paper on the generic characters of *Chermes* and reviewed Cholodkovsky's descriptions of *C. funitectus* Drey. and *C. piceae* Ratz.

The French biologist Paul Marchal confirmed the validity of Börner's findings and accepted the names; in 1913 he (106) produced his masterly "Contribution à l'étude de la biologie des *Chermes*", in which he described the life cycle and morphology of both *Adelges nüsslini* and *A. piceae* in great detail. Steven (146) in 1917 and Chrystal (48) in 1926 both accepted this specific distinction, but the Danish zoologist Boas (14) in 1918 preferred to look upon the two insects as biological races of a single species *C. piceae*. All subsequent writers have elected to distinguish them specifically. In 1928 Annand (2) published incomplete descriptions of the two species *Adelges nüsslini* and *A. piceae*, which had then been recognised as introduced insects in North America.

In 1929, Schneider-Orelli (132) as a result of studies in Switzerland discovered a biological race of *A. nüsslini* dwelling on the main stem of older Silver firs, up to fifty years of age. This race could not be distinguished morphologically from the normal individuals dwelling on the young shoots. He also pointed out considerable variability in the taxonomic characters of the neosistentes of *A. nüsslini*, but clearly showed that these could not be confused with those of *A. piceae*, and that there are no intermediate forms. Börner (22) elevated this biological race on the older stems to the status of a new species, *Dreyfusia schneideri* C.B. in 1932. Hoffman (82) in 1937 described a means of macroscopically distinguishing between *D. piceae* and *D. schneideri*, and in the same year Francke-Grosmann (70) confirmed this distinction and upheld Börner's specific designation of the latter. It is also noteworthy that instead of Börner's specific epithet *nüsslini* she used Eckstein's *nordmannianae;* other European writers have occasionally recognised the precedence of the latter.

In 1935 Francke-Grosmann (69) discovered another closely related species which she named *Dreyfusia prelli*. This species is of rare and local distribution, and since it alternates naturally between *Abies nordmanniana* and *Picea orientalis*, it is probably also of Caucasian origin. Morphologically *Dreyfusia prelli* Grosmann is very similar to *Adelges piceae* Ratz., but it has a pentamorphic life cycle. *A. prelli* has not been found during the author's investigation in Scotland and is not further discussed.

In 1945, after further study of the stem-dwelling form of *A. nüsslini*, Schneider-Orelli (133, 135) concluded that no sharp morphological or biological feature distinguished *Dreyfusia schneideri* from *D. nüsslini* and united them under the latter name. This amalgamation has been accepted by the writer, who has found both forms in Scotland. Since 1945, the taxonomic status of the Silver fir Adelgids has not been modified further, although general references to these forest insects have been fairly frequent. Notable among these was Balch's (7) original description of *Adelges piceae*, "the Balsam Woolly Aphid" as represented in Eastern Canada.

(2). Morphology at the specific level

Adelges nüsslini possesses in full the generic characters outlined in para. 2.(2), p. 4, but *A. piceae* is limited to those represented in the generations on the secondary host. As a group under the old generic name *Dreyfusia* they are distinguished from other *Adelges* spp. by

(i) the presence of a multipartite cephalo-prothoracic dorsal shield in the adult sistens, and

(ii) by the absence of pleural gland facets on the thorax and first six abdominal segments in the neosistens, as illustrated in Pl. 38 and 39.

Adelges nüsslini and *A. piceae* can readily be distinguished by a microscopic examination of the neosistens. This is particularly important because this form is present on the secondary host at almost all times of the year. In each case the neosistens is characterised by the dorsal covering of mesial, pleural and marginal chitinised plates, each roughly rectangular in outline. Gland areas are borne on the inner edge of the mesial plates (bordering the mid-dorsal line) and on the outer edge of the marginal plates. The principal means of distinction of the two species lie in the structure of the gland areas of the mesial plates. In the case of *A. piceae*, each gland area is made up of relatively few, relatively large facets of irregular polygonal shape, defined less distinctly in contour. In the case of *A. nüsslini*, on the other hand, each group is composed of relatively numerous, relatively small, similar facets of round or roughly hexagonal outline always clearly figured. Furthermore in each group a small rounded and domed area enclosing some nine or ten pores on the average, is sharply defined and characteristic. This is completely missing in the gland groups of the mesial plates of *A. piceae*. Specific distinction by this means is illustrated in Pl. 36, 37, 38 and 39.

In other stages and generations a few less conspicuous differences exist. For example the winged individuals of each species can be distinguished on the basis of antennal structure and the size of abdominal gland areas. In *A. nüsslini* the abdominal gland groups of the sexupara adult are large, while those of the progrediens alata of *A. piceae* are small and poorly developed. The antenna of the *A. nüsslini* sexupara bears larger rectangular sensoria, notably on the 4th segment; on the antenna of A. *piceae* progrediens alata, the sensoria are oval and smaller. However these and other differences are not very pronounced.

A means of distinguishing the two species by means of paper chromatography is discussed in section 6, p. 10.

4. DESCRIPTION OF ADELGES NUSSLINI C.B.

(1). Techniques

The writer bases the following brief descriptions on microscopic examination both of living and mounted insects. Most specimens were cleared and mounted for the microscope by means of Speyer's Method, as described by Chrystal (46). Britton's Method, described by Eltringham (65), was used for mounting some of the alate forms because the disposition of the wings can be controlled better by this method.

Linear measurements, which are of some importance in the diagnosis of instar, and descriptions of structural features, relate to the mounted insect only. During the processes of clearing and mounting, the integument of the Adelgid is often stretched slightly beyond the natural dimensions of the living insect, particularly in the less chitinised stages. For each instar the body length is given as the mean and range of a stated number of specimens. It is recognised that where only a small number of insects of each instar were measured, and where integumental stretching has occurred, these means may not always be accurately representative of the true mean dimensions of the living insect.

Descriptions of shape, colour and wax secretions refer to the living insect.

(2). Fundatrix

Egg: (laid by Sexualis) Length 0.35 mm., maximum diameter 0.18 mm. Pale amber, covered with slight powdered wax.

1st instar. Mean length 0.43 mm., range 0.33 to 0.47 mm. (8 specimens). Oval in outline, but dorso-ventrally flattened. Amber when newly hatched, later reddening and finally darkening to shiny black as dorsal chitinisation takes place. Wax secretion: a dorsal fin of white wax flakes arising from the line of mesial glands; similar flakes disposed around the perimeter of the body, arising from marginal glands. Structural characters: dorsal plates heavily chitinised, reticulated and separated by narrow interstices. On each side of the head a single large composite plate. On each side of the prothorax fused mesial and pleural plates, but separate marginal plates. Discrete mesial, pleural and marginal plates on the mesothorax, metathorax and the anterior five abdominal segments. Fusion and reduction of plates on the 6th and 7th segments. Absence of plates on the 8th and 9th segments. Dorsal gland areas borne along the inner edge of the mesial plates and along the outer edge of the marginal plates, as described for the neosistens in Chapter 1, para. 3(2), page 5. Ventrally only a small round gland area on each side of the mesothorax. On the head a pair of antennae of characteristic form common to first instars of all generations of the species; antenna 3-segmented, the apical segment being scaly and much longer than the other two together: it is well equipped for sensory function with two sensoria and a long terminal bristle. On the thorax three pairs of similar legs, and a rostrum. Rostral stylets variable in length, two to four times as long as the body, but typically about 1.20 mm. long. In the newly hatched larva, stylets held in a double loop within the ventral pouch or crumena. (Plate 1.)

2nd instar. Mean length 0.72 mm., range 0.70 to 0.73 mm. (4 specimens). Ovoid but not domed. Red just after moulting, soon darkening to shining black and finally appearing dull grey. Wax secretion: a faint wax bloom is secreted from the thinly chitinised integumental interstices. The glands produce relatively sparse fine wax filaments, especially on the abdomen. Structural characters: dorsal plates moderately chitinised, rounded or subrectangular, with large interstices. Most plates bearing a gland area comprising several circular sharply defined facets. Glands largest on the posterior abdomen, up to 16 facets per group. Each facet faintly and minutely reticulated. Antenna short and 3-segmented; the apical member elongately conical and equal to the joint length of the basal two. The antennae show only slight changes in size and appearance during succeeding stadia. (Plate 2.)

3rd instar. Mean length 1.08 mm., range 0.90 to 1.14 mm. (6 specimens). Shape and colour: As for 2nd instar. Wax secretion: numerous long wax threads both coarse and fine, issuing from gland areas on the ridged abdominal segments; shorter threads issuing from thoracic and cephalic glands. Structural characters: chitinised plates somewhat domed, and bearing the mesial, pleural and marginal gland areas, as in the 2nd instar. Up to 30 facets in the larger gland groups. (Plate 3.)

Adult. Mean length 1.68 mm., range 1.65 to 1.71 mm., (4 specimens). Broadly ovoid, almost globose. Dorsum strongly ridged by segments. Black, but appearing mainly grey due to wax bloom. Wax secretion: the thinly chitinised interstices secrete a wax bloom against which dorsal plates stand out as smooth black areas. Wax wool abundantly produced as long filaments by the glands on these mesial, pleural and marginal plates, especially those on the abdomen. Structural features: a large cephalothoracic shield, fairly heavily chitinised; on the mesothorax, metathorax and abdomen, smaller moderately chitinised, rounded plates. Gland areas especially on posterior abdomen, comprising up to 40 or 50 reticulated facets. Ovipositor present ventrally at the junction of the 8th and 9th segments. (Plate 4.)

(3). Gallicola

Egg: (laid by fundatrix). Length 0.30 mm., maximum diameter 0.15 mm. Amber, darkening slightly as the embryo develops, and lightly covered in wax dust. (Plate 42.)

1st instar. Mean length 0.41 mm., range 0.37 to 0.45 mm. (10 specimens). Shape similar to neofundatrix but narrower. Amber when newly hatched, not darkening thereafter. Wax secretion: slight, fine wax dust covering body, but no wax wool. Structural characters: distribution pattern of dorsal plates approximating to that of the neofundatrix, but plates much smaller, and corresponding interstices much larger. Plates weakly chitinised, each marked by a central seta. Marginal plates present on the 8th abdominal segment; reduction or fusion of mesial and pleural plates on the apical abdomen. Stylets only 0.25 mm. long, thus being shorter than the stylets of the corresponding instar of any other generation. (Plate 5.)

2nd instar. 2nd and 3rd instars were not studied in detail because of the scarcity of galls. Consequently only moult skins taken from mature galls were available for study, and were not wholly satisfactory material. A detailed description of this stage does not appear anywhere in the literature. Structural characters: distribution of dorsal plates similar to first instar, but somewhat reduced on the apex of the abdomen. Plates small and rounded except on the head and prothorax, and very faintly chitinised. Small indistinct gland areas on the marginal abdominal plates, but absent elsewhere. Easily distinguished from the 1st instar by the short, thick 3-segmented antennae; the conical apical segment bears a sensorium and sensorial pores near the tip. (Plate 6.)

3rd instar. Structural characters: no absolute differences from the 2nd instar. Plate distribution similar to 2nd instar, but marginal gland areas containing more facets, up to 12 per area; rarely mesial plates of the abdomen bear small gland areas. Antennae similar to preceding instar but slightly longer.

4th instar. (Nymph). Mean length 1.23 mm., range 1.13 to 1.33 mm., (5 specimens). Elongate oval; easily recognised by the projecting wing pads. Dark brown, the wing pads paler.

Wax secretion: short filaments are secreted but appear to be rubbed off within the gall. A fine wax bloom is secreted from all the non-chitinised areas of the integument. Structural characters: cephalic (and ocular) plates moderately chitinised. Ocular plates showing faint ommatidial structures just anterior to the three ocelli on each side of the head. Prothoracic marginal plates and wingpads moderately chitinised. All the cephalothoracic plates exhibit a minutely verruculose surface. Only marginal plates present on abdomen, up to 8th segment; mesial and pleural plates absent. Fairly large wax gland areas on head and prothoracic marginal plates. Small gland groups present on marginal plates of abdomen, but occasionally as many as 30 facets per group. No mesial or pleural glands on the abdomen. Antennae 3-segmented. In the mature nymph, the 5-segmented antennae of the adult may be seen forming within the nymphal antennae.

Adult. Mean body length 1.35 mm., range 0.95 to 1.73 mm.; mean forewing length 1.88 mm., range 1.33 to 2.53 mm. (16 specimens). Black: wings transparent with greenish veins. Wax secretion: the four large gland areas on the head and the four on the prothorax secrete broad short curly wax strands in a characteristic pattern. The abdominal glands secrete much finer and longer filaments which envelop the eggs. Structural characters: head and thorax heavily chitinised; abdomen only faintly chitinised in small plates. Gland areas of the head and of all the thoracic segments very large with many facets, frequently in excess of 200 per group. Gland areas of abdomen mainly marginal, with 80 or fewer facets per group; elsewhere on the dorsal abdomen only scattered aggregations of wax pores running parallel to the segmental sutures. Antennae 5-segmented, the apical three members being scaly and sensorial. (Plates 7, 8, 9 and 10.)

(4). Sistens

Egg: (laid variously by hiemosistens, aestivosistens, gallicola and progrediens aptera). Mean length 0.30 mm., maximum diameter 0.15 mm. Amber, lightly covered with powdered wax. Structural characters: the ocelli and coiled stylets of the embryo can be seen within maturing eggs. (Plate 53.)

1st instar (Hiemosistens). Mean length 0.39 mm., range 0.35 to 0.45 mm. (20 specimens). There is no significant difference in the sizes of offspring derived variously from hiemosistens, aestivosistens, gallicola or progrediens aptera. Shape, colour, wax secretion, structural characters: identical with neofundatrix. (Plate 11.)

2nd instar (Hiemosistens). Mean length 0.55 mm., range 0.47 to 0.62 mm., (4 specimens). Shape, colour, wax secretion, structural characters: similar to 2nd instar fundatrix.

3rd instar (Hiemosistens). Mean length 0.90 mm., range 0.81 to 1.00 mm., (6 specimens). Shape, colour, wax secretion, structural characters: similar to 3rd instar fundatrix. (Plate 19.)

Adult (Hiemosistens). Mean length 1.13 mm., range 1.08 to 1.17 mm. (4 specimens). Shape, colour, wax secretion, structural characters: similar to adult fundatrix, but the number of facets per gland area is smaller, rarely more than 30. (Plates 12 and 52.)

Note: The above measurements pertain to hiemosistentes living on the young healthy twigs of *Abies alba* Miller. Hiemosistentes developing on less favourable sites, such as the main stems of necrotic trees, and aestivosistentes generally, show considerably reduced dimensions. For example, the smallest aestivosistens adult measured was only 0.72 mm. in length.

(5). Progrediens aptera

Egg: (laid by hiemosistens). Identical with egg stage of sistens, but maturing embryos may be distinguished by the length of the stylet coil.

1st instar. Mean length 0.41 mm., range 0.35 to 0.45 (7 specimens). Oval in outline, dorso-ventrally flattened. Amber, not darkening after settlement. Wax secretion: a slight wax bloom but no wax wool. Structural characters: distribution pattern of dorsal plates almost identical with neosistens, but plates much smaller, more rounded, weakly chitinised and separated by broad interstices. Each plate marked by a central seta. Wax glands absent except for rare cephalic pores, and the pair of ventral mesothoracic glands, each with 4 to 6 facets. One abnormal individual bore dorsally a pair of large cephalic gland areas, each with 30 facets. Antennae, legs and rostrum identical with neosistens. The distinctive feature of the neoprogrediens is the disposition and length of the stylets; in the newly hatched individual they lie in a loop extending half way down the abdomen; the average length of the stylets is 0.43 mm. (Plate 13.)

2nd instar. Mean length 0.47 mm., range 0.42 to 0.48 mm. (4 specimens). Shape, colour, wax secretion: similar to 1st instar progrediens. Structural characters:

very small, rounded, weakly chitinised plates. Small indistinct gland areas, each of 4 to 5 facets, on marginal plates only. Clearly distinguished from the neoprogrediens by the short thick, non-scaly, 3-segmented antennae, of which the apical segment is 0.05 mm. long.

3rd instar. Mean length 0.57 mm., range 0.50 to 0.63 mm. (4 specimens). Flatly ovoid. Slightly darker than preceding instars. Wax secretion: very short strands secreted marginally, and sometimes mesially at the end of the stadium. Structural characters: marginal glands and other characters similar to preceding instar. Marchal (106) says that in general there are no distinct mesial or pleural glands, although sometimes they may be represented by a large isolated gland area on the abdomen. Apical segment of the antenna, about 0.07 mm., (longer than in 2nd instar). (Plate 14.)

4th instar. Length of a single specimen 0.71 mm. More ovoid than preceding instar. Dark brown. Wax secretion: fine, fairly abundant filaments secreted from mesial, pleural and marginal glands. Structural characters: similar to preceding instar, but more heavily chitinised dorsal plates. Marchal (106) distinguishes it by the presence of distinct pleural and mesial gland areas, each comprising a few large facets. Antenna slightly longer (0.08 mm.), more elongately cylindrical, and more scaly.

Adult. Mean length 0.84 mm., range 0.68 to 0.93 mm. (5 specimens). Broadly ovoid. Black. Wax secretion: fine wax filaments secreted in abundance from abdominal glands, and less thickly from thoracic and cephalic glands. Structural characters: similar to sistens adult. Head and thoracic plates heavily chitinised; abdominal plates less heavily chitinised in the posterior region. Marginal, pleural and mesial gland areas clearly represented. Marginal glands containing up to 30 facets, but mesial and pleural glands especially on head and thorax with much smaller numbers, or absent on posterior abdomen. Antennae 3-segmented, cylindrical, scaly and bearing the sensorium at the tip of the apical segment. (Plate 18.)

(6). Sexupara

Egg: (laid by Hiemosistens). Identical with the egg stage of the progrediens aptera.

1st instar. Identical with the neoprogrediens aptera. Nüsslin (121) believed that the sexupara could be distinguished from the progrediens aptera towards the end of the first stadium by the form of the cerebral ganglia.

2nd instar. Identical with the 2nd instar progrediens aptera.

3rd instar. Similar to the 3rd instar progrediens aptera, but no wax wool is produced at any time during the stadium. Marchal (106) points out that there are no gland areas except very small indistinct ones on the weakly chitinised marginal plates of the 5th, 6th and 7th abdominal segments, and rarely elsewhere.

4th instar (Nymph). Mean length 0.77 mm., range 0.68 to 1.17 mm. (5 specimens). Elongate oval, with wing pads clearly visible, body segments strongly ridged. Dark brown, with paler wing pads. Wax secretion: no wool production, but a pale wax bloom is secreted along the mid-dorsal and intersegmental lines. Structural characters: head, prothorax and wing pads strongly chitinised. Cephalic plates separated along the mid-dorsal line. Mesothoracic, metathoracic and abdominal plates weakly chitinised, small, rounded and separated by wide interstices. Mesial and pleural plates absent on posterior abdomen; marginal plates larger and present on all abdominal segments. No gland areas present on any part of the body. Rostrum short. It is interesting to note that the stylet length is similar to that of the 1st instar, and does not alter with instar. Antennae 3-segmented, long and cylindrical. (Plates 15 and 16.)

Adult. Size: mean body length 0.94 mm., range 0.88 to 1.00 mm.; mean forewing length 1.37 mm., range 1.25 to 1.48 mm. (5 specimens). The average adult sexupara is clearly smaller than the average adult gallicola. Shape, colour, wax secretion, structural characters: similar to the adult gallicola but gland areas smaller; glands on abdominal marginal plates containing up to 40 facets. (Plate 17.)

(7). Sexualis

Egg: (laid by Sexupara). Similar to egg stage of sistens.

1st instar. Mean length 0.39 mm., range 0.37 to 0.43 mm. (11 specimens). Oval in outline, similar to neoprogrediens. Amber, not darkening after settlement. Wax secretion: a faint wax bloom. Structural characters: distribution pattern of dorsal plates similar to neoprogrediens. Plates small, subrectangular, weakly chitinised, equipped with a central seta, and separated by wide interstices. No dorsal gland areas, but ventrally one pair present on the mesothorax. Antennae, legs and rostrum similar to neoprogrediens. Stylets very short, carried in a simple loop within the crumena. Schneider-Orelli (132) noted that the male has shorter and the female longer stylets. This sexual dimorphism in the 1st instar is confirmed; two series were found: (i) mean stylet length 0.362 mm., range 0.343 to 0.381 mm. (9 specimens), and (ii) mean stylet length 0.294 mm., range 0.284 to 0.311 mm. (5 specimens.)

2nd instar. Mean length 0.41 mm., range 0.40 to 0.43 mm. (3 specimens). Similar to 1st instar in shape. Amber, not darkening through the stadium. Wax secretion: rare production of very short wax strands. Structural characters: dorsal plates small, rounded and weakly chitinised. Rare wax pores. Antennae 3-segmented; the apical segment short, conical, thick and only faintly scaly; it bears a few short bristles and a sensorium near the tip. (Plate 20.)

3rd instar. Mean length 0.44 mm., range 0.43 to 0.45 mm. (3 specimens). Shape, colour: similar to preceding instar. Wax secretion: short wax strands from marginal and mesial glands more abundant than in preceding instar, Structural characters: very similar to 2nd instar, with no absolute features of distinction. (Plate 22.)

4th instar. Mean length 0.48 mm.; range 0.45 to 0.58 mm. (5 specimens). Shape, colour: similar to preceding instar, but slightly darker. Wax secretion: considerably more wax wool than on preceding instar; wool consisting of very short curly wax strands, arising from mesial and marginal glands, mainly in the thorax and head; each wax strand often consisting of two or three fused filaments. Structural characters: similar to preceding instar, but chitinisation slightly greater and gland facets per group more numerous. It is possible that the female is larger in body size and better equipped with gland facets than the male, but this sexual dimorphism of the 4th instar has not been conclusively established. Antennae 3-segmented; the apical segment is longer, narrower and more scaly than that of the preceding instar; apical segment bearing two sensoria. (Plate 23.)

Adult female. Mean length 0.54 mm., range 0.49 to 0.57 mm. (4 specimens). Elongate oval, and dorso-ventrally flattened. Specimens mounted by the writer are not so broadly oval as those figured by Marchal (106). Dark brown, darker than any of the larval instars. Wax secretion: the motile female is dorsally covered in a coarse fragmented wax powder but secretes no wax filaments until the time of oviposition. Structural characters: small dorsal plates lightly chitinised and carrying mesial, pleural and marginal gland areas on all segments except those at the apex of the abdomen. Mesial and pleural glands very small and indistinct, comprising one or two facets, but marginal glands larger, containing five or six facets. Antennae 4-segmented; the terminal two segments are long, narrow and scaly; a sensorium and short bristles lie at the tip. Legs fairly long. Ovipositor on the sternum of the last segment. (Plate 21.)

Adult male. The writer has not closely studied the male sexualis under the microscope and the following description is condensed from Marchal (106). A little smaller than the female; abdomen narrower and somewhat reduced. Structural characters: no distinct gland areas or pores. Relatively long legs. Antenna 4-segmented, long, with the apical segment narrower at its base and more elongate than in the female.

5. DESCRIPTION OF ADELGES PICEAE RATZ.

Note: The various instars of both sistens and progrediens generations are very similar in size, shape, colour, wax secretions and structural characters to the corresponding stages of *A. nüsslini*. Differences between the two species are recorded.

(1). Sistens (Hiemo- and Aestivosistentes)

Egg: (laid variously by Hiemosistens, Aestivosistens, Progrediens Aptera and Progrediens Alata). Length 0.30 mm., maximum diameter 0.15 mm. Pale amber, covered with wax powder and fragments of wax filaments. (Plate 30.)

1st instar. Mean length 0.42 mm., range 0.35 to 0.47 mm. (23 specimens). There is no significant difference in size between the neohiemosistens and the various summer generations of neosistentes. Oval in outline, dorsoventrally flattened. Amber, soon reddening then darkening to black after settlement. Wax secretion: A dorsal fin and a peripheral fringe of short wax flakes. Structural characters: differs from the corresponding stage of *A. nüsslini* in the structure of the mesial glands, as explained in Chapter 1, para. 3(2), page 5. Dorsal plates heavily chitinised, and distributed as follows; a composite plate on each side of the head; a fused mesial and pleural plate and a separate marginal plate on each side of the prothorax; discrete mesial, pleural and marginal plates on each side of the mesothorax, metathorax and abdominal segments 1 to 7, but mesial and pleural plates may be fused or reduced on the 6th and 7th segments; no plates on the 8th or 9th segments. These dorsal plates are rectangular and separated by narrow interstices of soft integument. Gland areas located along the inner edge of the mesial plates and the outer edge of the marginal plates. On the ventral surface a pair of small glands on the mesothorax. Stylets long, lying in a double loop within the crumena; total length averaging 1.13 mm. (12 specimens) but ranging from two to four times body length. Antennae of the characteristic first instar type. (Plate 27.)

2nd instar. Mean length 0.57 mm., range 0.48 to 0.67 mm. (10 specimens). Flatly ovoid. Dark brown or black. Wax secretion: fine sparse wool secreted all over dorsal surface, mainly from abdominal marginal glands. Structural characters: dorsal plates moderately chitinised and distributed on the same basic pattern as in the 1st instar, but mesial and pleural plates absent on the posterior abdomen. Plates relatively small, rounded and separated by large interstices. Marginal glands present on all segments except 8th and 9th abdominal segments; mesial and pleural glands not extending beyond 4th or 5th abdominal segment. Gland facets slightly larger than those of the corresponding stage of *A. nüsslini*, and fewer in number, the largest (abdominal marginal gland areas) not containing more than 10 facets per group. Antennae 3-segmented; the apical segment fairly long, cylindrical and non-scaly. (Plate 24.)

3rd instar. Mean length 0.64 mm., range 0.55 to 0.82 mm., (5 specimens). Shape, colour: similar to preceding instar. Wax secretions: more abundant wax wool, including both fine and thick filaments, especially on the abdomen. Structural characters: dorsal plate distribution and gland pattern similar to preceding instar, but gland areas larger. Distinguished from the preceding instar by the short, conical, apical segment of the antenna, and from the corresponding 3rd instar of *A. nüsslini* by the larger but less numerous facets within each gland area. (Plates 25 and 28.)

Adult. Mean length 0.81 mm., range 0.67 to 1.25 mm. (4 specimens). Ovoid, almost globose, with a strongly ridged dorsum. Shining black, but often toned to grey by interstitial wax bloom. Wax secretion: abundant wax wool, especially over the posterior abdomen. Structural features: characterised by the multipartite cephalothoracic shield which is heavily chitinised but poorly glandular. Marginal gland areas represented up to the 8th abdominal segment but mesial and pleural glands absent on the posterior segments of the abdomen. Distinguished from the corresponding stage of *A. nüsslini* by the fact that the number of facets in *A. piceae* is small, rarely surpassing 10 per gland area. (Plates 26 and 29.)

(2). Progrediens aptera

Egg: (laid by hiemosistens). Indistinguishable in size and colour from the sistens egg, but embryos may be differentiated by the length of the stylet coil.

1st instar. Mean length 0.42 mm., range 0.40 to 0.46 mm. (6 specimens). Shape as for neosistens, but slightly narrower. Amber, not darkening after settlement. Wax secretion: a wax bloom over the body. Structural characters: dorsal plates small, oval, weakly chitinised, marked by a central seta and separated by wide interstices. Plate distribution, similar to neosistens but marginal plates present also on the 8th abdominal segment. No dorsal wax glands, but ventrally a small pair located on the mesothorax. Antennae similar to those of the neosistens. Stylets lying in a short simple loop extending half way down the abdomen. Stylets short, mean length 0.60 mm. (6 specimens). Stylet length remains more or less constant during succeeding instars. (Plate 31.)

2nd instar. Mean length 0.47 mm., range 0.45 to 0.49 mm. (4 specimens). Shape, colour, wax secretion: similar to preceding instar. Structural characters: dorsal plates weakly chitinised and very small. Small indistinct gland areas borne on marginal plates only. Antennae 3-segmented, non-scaly and short; apical segment cylindrical.

3rd instar. Mean length 0.55 mm., range 0.51 to 0.60 mm. (4 specimens). Shape, colour: similar to preceding instar, but slightly more ovoid. Wax secretion: short wax strands appearing marginally and mesially towards the end of the stadium. Structural characters: dorsal plates weakly chitinised and small. Small marginal glands and very small, rare pleural and mesial glands.

Antennae 3-segmented; the apical segment short and conical.

4th instar. Mean length 0.63 mm., range 0.61 to 0.65 mm. (3 specimens). Ovoid. Dark brown. Wax secretion: a moderate production of wax wool, mainly of fine threads up to four times as long as the body. Structural characters: dorsal plates small and lightly chitinised. Distinguishable from preceding instars by the presence of distinct mesial and pleural glands as well as marginal glands on all segments except those forming the posterior abdomen. Gland areas well defined with a small number of facets, usually 4 to 8 but occasionally up to 15. Antennae similar to 3rd instar.

Adult. Mean length 0.67 mm., range 0.63 to 0.70 mm. (3 specimens). Broadly ovoid. Dark brown or black. Wax secretion: abundant wax wool, secreted mainly from abdominal glands. Structural characters: dorsal plates moderately large, well defined and well chitinised, especially the multipartite cephalothoracic shield. Gland system well developed with groups of variable size; marginal glands comprising up to 20 facets, notably more than in the adult sistens of *A. piceae*, but not so numerous as in the progrediens aptera adult of *A. nüsslini.*

(3). Progrediens alata

Egg and 1st instar. Identical with the corresponding stages of the apterous progrediens.

2nd instar. Similar to the corresponding progrediens aptera. Marchal (106) states that already the glandular system is less distinct and less well developed than in the corresponding progrediens aptera.

3rd instar. Similar to the corresponding progrediens aptera, but without gland areas, or with only a few indistinct pores on the posterior marginal plates.

4th instar (Nymph). Mean length 0.69 mm., range 0.63 to 0.76 mm. (4 specimens). Elongate oval, and characterised by the projecting wing pads. Dark brown, wing pads paler. Wax secretion: wax bloom only, especially along the mid-dorsal and intersegmental lines. Structural characters: cephalic and prothoracic plates and wing pads moderately chitinised, and in places verruculose. Elsewhere dorsal plates weakly chitinised and small, or represented only by setae in the case of mesial and pleural plates of the abdomen. The absence of these plates distinguishes the stage from the nymphal sexupara of *A. nüsslini.* No gland areas on any part of the body. Antennae 3-segmented, fairly large; the apical segment long and scaly. (Plates 32 and 33.)

Adult. Mean body length 0.95 mm., range 0.90 to 1.05 mm.; mean forewing length 1.35 mm., range 1.25 to 1.45 mm. (4 specimens). Elongate oval. Black; wings transparent with greenish veins. Wax secretion: less abundant wool is produced from abdominal glands than in the case of the alate forms of *A. nüsslini.* The head and thorax usually secrete short thick curly strands after settlement. Structural characters: head and thorax heavily chitinised; on the abdomen, marginal plates small and very weakly chitinised, and pleural and mesial plates frequently absent but represented by a seta or 1 or 2 wax pores. Gland areas on the marginal plates of the abdomen small. Gland areas on the head and thorax absent or small and indistinctly represented, Antennae 5-segmented with small oval sensoria on the three apical segments. The characters of the gland areas and the antennae distinguish it from the adult sexupara of *A. nüsslini.* (Plate 34.)

6. THE APPLICATION OF PAPER CHROMATOGRAPHY TO TAXONOMY

The rapid development of techniques of paper partition chromatography has recently led to its application in taxonomic studies of plants and animals. The paper by Buzzati-Traverso and Rechnitzer (28) has shown that the method can be applied as a means of clear distinction between different species of fish irrespective of their age and size. These authors have also claimed similar uses in taxonomic studies of other animal phyla.

The object of using the method in the present investigation was to see whether paper chromatography could be applied to the taxonomy of a complex group such as the genus *Adelges.* The technique is a simple process of separating out certain organic constituents of fresh materials and fixing them in distinct zones on filter paper. For any one sample, these zones show up as an easily recognisable pattern of bright fluorescent colours under the influence of ultra-violet light. The different samples and specimens of the same species give a constant pattern. Patterns of other species are different, but the closer the taxonomic position of any two species, the more similar are their chromatographic patterns. Only preliminary studies in the method have been made but the results are encouraging for the wider application of the technique.

Technique: A small quantity (about 1 litre) of butanol-acetic solvent was prepared as follows. 4 vols. of N. Butanol, 1 vol. of glacial acetic acid and 5 vols. of distilled water were mixed together in a bottle, then allowed to settle and slightly chilled in a refrigerator. The butanol-acetic solvent forms as the upper layer of the liquid in the bottle, and only this is pipetted off for use.

Filter paper may be cut to any size, but the writer has found it convenient to use rectangular pieces eleven by nine inches. A base line is drawn in pencil along the longer side of the paper, one inch from the edge. Living specimens of different *Adelges* species were crushed on small spots at one-inch intervals along the baseline. In this way a number of different species under comparison may be ranged alongside one another on a single sheet. In tests where adults were being used, 4 or 5 insects of one species pressed into the same spot usually gave sufficient material. Where eggs were being used, some 30 to 40 per spot were required. It is important that the crushed material should not be spread over too large an area; each spot should be kept as small as possible, if necessary by waiting until the body contents of one insect have dried before crushing the next above it.

Next the sheet of filter paper is rolled into a cylinder and clipped in position with a paper clip.

It is then stood in a Petri dish so that the pencilled baseline runs parallel to the rim of the dish. A small amount of chilled solvent, about 40 ml., is then pipetted into the Petri dish. Immediately after the solvent has been placed in the dish it is necessary to cover the whole apparatus with a bell jar, sealed at the base with vaseline so that the butanol is not evaporated and dissipated into the open atmosphere. The solvent is slowly drawn up through the filter paper by normal capillary action. As it passes upward, certain constituents in the insect tissues are dissolved and are also carried upward, but at different speeds. After a few hours the sheet is fully saturated and vertical movement of solvent ceases. By this time the soluble constituents of the insect tissues have been deposited along a narrow belt vertically above each spot. The paper is then removed and quickly dried in front of a fire. The chemical constituents remain fairly stable over many days or weeks. The paper may be viewed under ultra-violet light at any time, but should be treated to fumes from a bottle of concentrated ammonia at the time of viewing.

Results:

(i) For any one species (in the case of *Adelges piceae*, *A. nüsslini* or *A. viridis*) the eggs give a quite different pattern from that given by the larval and adult instars of the insect.

(ii) For any one species the samples of adult insects give a constant colour pattern, regardless of the host tree on which the insect was feeding. Similarly the eggs give a constant pattern regardless of host. For example, there was no difference in the patterns for adult sistentes of *Adelges piceae* feeding variously on *Abies veitchii*, *A. procera* and *A. magnifica*. Also the adult fundatrix of *Adelges nüsslini* on *Picea orientalis* gives an identical pattern to that of the adult sistens of this species on *Abies alba*. Also the eggs laid by the fundatrix of *Adelges viridis* on *Picea excelsa* give a pattern identical with that of the eggs laid by the sistens of this species on *Larix decidua*.

(iii) By means of these patterns *Adelges nüsslini* can be easily distinguished from *A. piceae* by use of either eggs or adults. Nevertheless the patterns for each species are quite similar, as shown in Plate 35.

(iv) It is also easy to distinguish the chromatographic patterns of *Adelges strobilobius* and *Pineus pini* from each other and from the Silver fir *Adelges*. However all bear certain similarities (Plate 35).

These preliminary results show that there are certain chemical affinities in species of *Adelges* which correspond to their taxonomic relationships. In the cases of *A. nüsslini* and *A. piceae* the closely similar patterns confirm the obvious morphological similarities which caused Börner to place both in his genus *Dreyfusia*. In this respect it would be very interesting to compare them chromatographically with other species which have been allotted at one time or another to the genus *Dreyfusia*, such as *Adelges prelli* Grosmann, *A. pectinatae* Cholodk., and the new Japanese species, *A. todomatsui* nov.sp. which Inouye (88) discovered in 1941 on *Abies sachalinensis* Mast. Indeed, a chromatographic study over the complete range of the subfamily Adelginae might prove a novel supplementary means of revising its taxonomic divisions, possibly in favour of Börner's (16) scheme of 1908.

The analysis of the chemical nature of the constituents distinguished by colour in each pattern might also lead to interesting results, especially in the field of insect nutrition. In Plate 35, the blue areas represent anthocyanin compounds, the red areas tannin compounds, and the yellow areas hydroxyphenols, but much more detailed analyses of the soluble substances in insect tissues are feasible.

Chapter 2

LIFE HISTORIES OF ADELGES NUSSLINI C.B. AND ADELGES PICEAE RATZ.

(1). SALIENT FEATURES OF THE LIFE CYCLE WITHIN THE SUBFAMILY ADELGINAE, WITH SPECIAL REFERENCE TO ADELGES NUSSLINI AND A. PICEAE

The detailed researches of a number of European and North American biologists have revealed considerable variations and complexities in the life histories of the species belonging to the subfamily Adelginae. Its species nevertheless exhibit the following common or typical features:

(i) These minute insects occur on conifers only (the tribe Abietineae, family Pinaceae). In this respect they differ from the sister subfamily Phylloxerinae, where the hosts are a number of unrelated phanerogamic plants.

(ii) They exhibit alternation of hosts, and accordingly there are generations specialised for migratory flight. The primary host is always a species of spruce, on which a gall is formed. The intermediate or secondary host may be a larch, Silver fir, hemlock (*Tsuga*), Douglas fir or pine, according to insect species; no gall is formed on the intermediate host.

(iii) The life cycle is typically pentamorphic. On the primary host there are three heterogenous generations, sexualis, fundatrix and gallicola. On the intermediate host there are two heterogenous generations, the sistens and the sexupara.

(iv) This fundamental series of five generations exhibits cyclic parthenogenesis. The sexualis generation in which both males and females are concerned in reproduction, alternates regularly with the other four successive generations in which females only are represented.

(v) The full life cycle occupies two years.

The life cycle is briefly summarised as follows:

(a). The fundatrix (stem-mother) derived from a fertilised egg in summer, settles in the vicinity of a bud of the spruce host and overwinters as the first instar. It remains fixed at this location for the rest of its life. In the spring, feeding is resumed, and the insect passes through three moults to become an apterous adult. It lays parthenogenetically a very large number of eggs within a short period and dies.

(b) The gallicolae arise from the eggs laid by the fundatrix. They hatch at the time of the spring flushing, and as motile first instars settle among the leaf bases of the opening bud on which the parent fundatrix fed. This flushing bud develops in an abnormal manner and produces a gall which encloses the young gallicolae in internal cavities. Within the gall the insects undergo three moults. Eventually during the summer the gall dehisces, and the fourth instar nymphs emerge from the gall; they immediately settle on a convenient leaf, moult again, and become alate adults. They fly to the intermediate host, (larch, Silver fir, hemlock, Douglas fir, or pine) where each lays a small number of eggs beneath its folded wings, and dies.

(c) The exsules sistentes, hereafter referred to simply as sistentes, are the progeny of the gallicolae on the intermediate hosts. Like the first instars of all generations, the neosistentes are motile and actively seek out a suitable feeding site on the tree. After settling in specifically characteristic positions, they remain in diapause until the following spring. Then each resumes feeding, and develops through three moults to become an apterous adult. Each sistens lays a large number of eggs, and dies *in situ*.

(d) The sexupara is only one of the forms of offspring which the sistens procreates. Typically the first-laid egg of the clutch gives rise to a form known as the neoprogrediens which includes the first instar sexuparae; the later-laid eggs become successor neosistentes, which are characterised by entering diapause for a distinct period in the first stadium. The neoprogredientes however experience no period of diapause, always settle on the leaves of flushing shoots, and proceed to develop at once through four moults to the adult stadium. During development they may differentiate into one or both of two forms, the sexupara and the exsulis progrediens (hereafter referred to simply as progrediens). The latter indeed may be winged or wingless, and is known as the progrediens alata or the progrediens aptera respectively. The progrediens oviposits parthenogenetically on the same intermediate host, producing a small number of eggs. Its descendants ultimately serve to increase the population of neosistentes hibernating on the intermediate host during the following winter, although there may be one or more intervening generations of progrediens. The sexupara however is the winged form which migrates to the primary host, where it lays a small clutch of eggs under the folded wings.

(e) The sexualis is the enigmatic generation which succeeds the parent sexupara on the primary host The sexuales are minute dimorphic insects which settle on the needles and develop through four moults to become apterous male and female adults. Each female lays a single fertilised egg. This egg shortly gives rise to a motile neofundatrix which soon settles in diapause for the rest of the season. In this way the two years life cycle is completed and renewed. The typical life cycle is diagrammatically represented in Fig. 1.

This typical dioecious pattern may be:

(i) complicated by the elaboration of subcycles within the holocycle, or,

(ii) simplified in some species by the breakdown of host alternation.

In the first case such a subcycle is confined either to fundatrices and gallicolae on the primary host or sistentes and progredientes on the intermediate host, but never involves the sexuales. Researches by a number of investigators have shown that such parthenogenetic subcycles on a single host occur within the life cycles of most of the holocyclic species in the Adelginae.

In the second case, certain species are confined to a monoecious life cycle on either the primary host or on the intermediate host, and have no capacity either to exhibit alternation of host or to incorporate a sexual generation. Both these cases are well exemplified by species of the Silver fir *Adelges*.

Adelges nüsslini shows holocyclic development requiring Oriental spruce, *Picea orientalis*, as the primary host and the Nordmann fir, *Abies nordmanniana*, or any of a number of other *Abies* species as intermediate host. On the primary host the life cycle is a simple succession of the generations sexualis, fundatrix and gallicola. On the intermediate host it is completed by the generations sistens and sexupara. However, a supplementary parthenogenetic subcycle enables reproduction to take place indefinitely on the intermediate host. This subcycle arises from the offspring of the overwintering sistens, or *hiemosistens* as Marchal termed it. Its eggs hatch out on the one hand as first instar sexuparae and progredientes apterae and as neosistentes on the other. The latter may remain in diapause either:

(a) for a shorter period, developing in the summer as aestivosistentes, which in turn give rise to overwintering neohiemosistentes or

(b) for a longer period, not developing beyond the first instar until the spring of the following year.

The neoprogredientes apterae always develop at once, and their eggs in turn hatch as larvae which may develop after a brief diapause as aestivosistentes or remain in a longer diapause as neohiemosistentes. This series is diagrammatically represented in Fig 1.

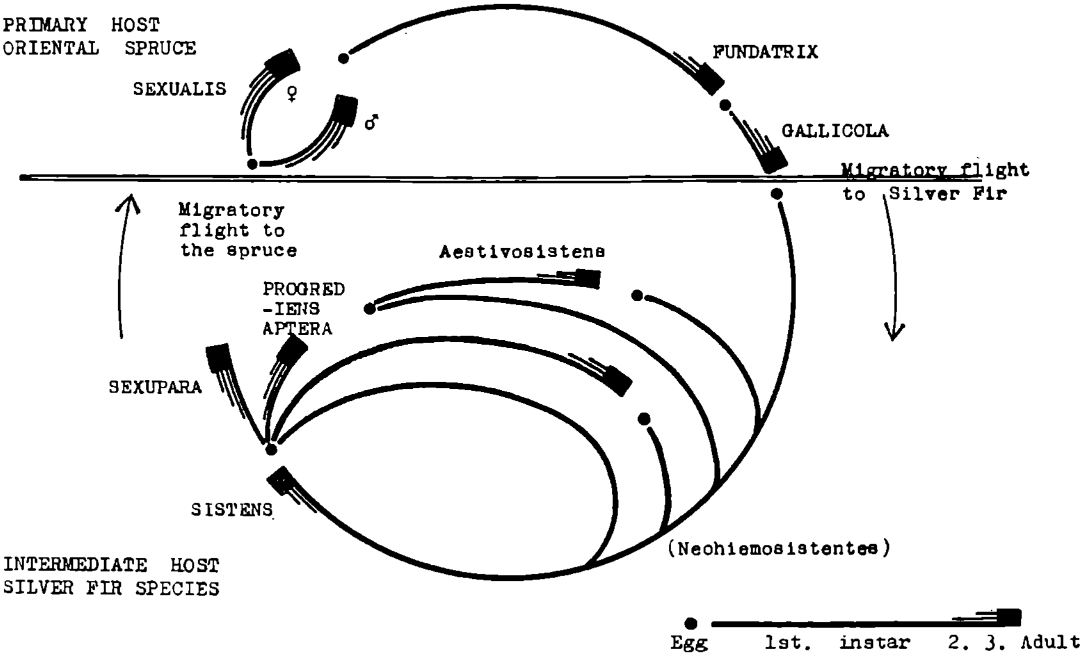

Figure 1. Diagrammatic life-cycle of *Adelges nüsslini* C.B.

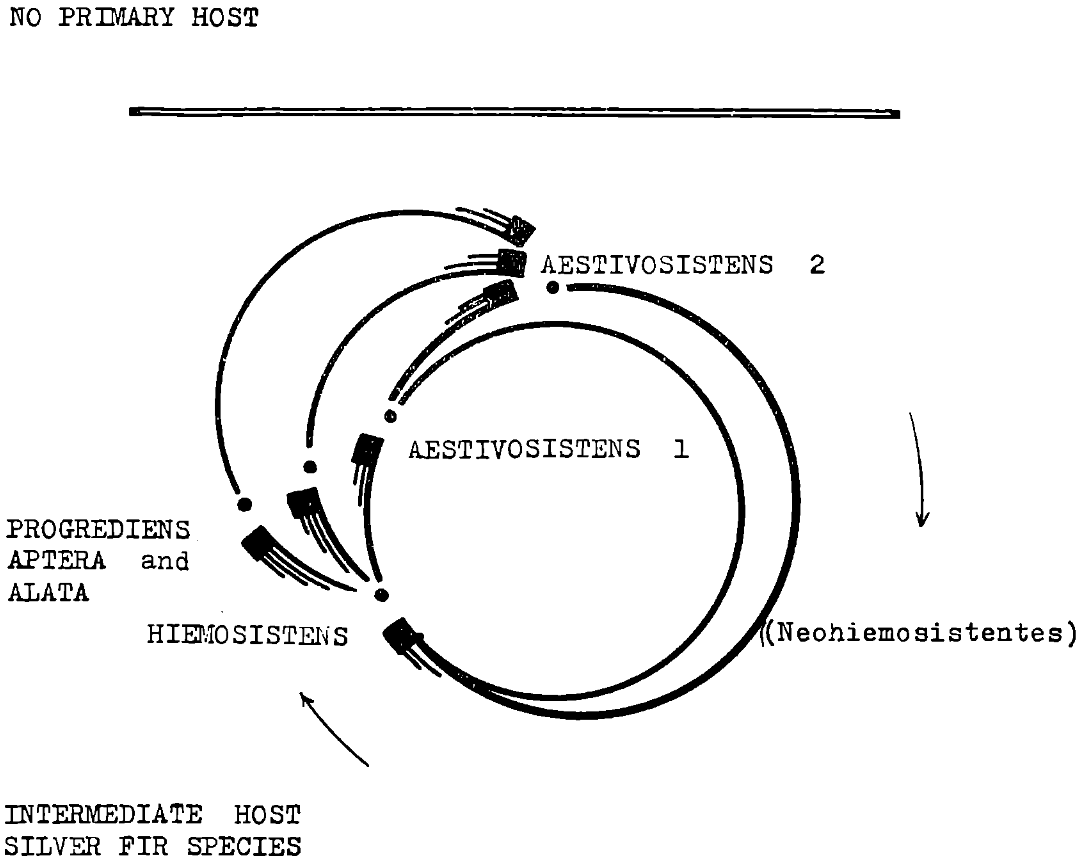

Figure 2. Diagrammatic life-cycle of *Adelges piceae* Ratz. The horizontal bar across the top of the diagram indicates the "lost" migratory flights to and from the original primary host. Compare with Figure 1.

Adelges piceae is a monoecious species confined to the *Abies* intermediate host. Since no sexuparae are produced there is no possibility of holocyclic development. On the intermediate host the cycle is essentially an oscillation between hiemosistentes and aestivosistentes, but under favourable circumstances it may be elaborated to include a generation of progredientes apterae and alatae each spring. This life cycle is diagrammatically depicted in Fig. 2.

2. REVIEW OF PREVIOUS RESEARCH

(1). Literature on the Biology of subfamily Adelginae

Our present knowledge of the biology of the Silver fir *Adelges* arose in the first instance from studies of the subfamily Adelginae as a whole. The members of the subfamily have a common ancestral background resulting in common biological characters, and consequently the discovery of any feature in one species has led to the discovery of a corresponding or parallel feature in the others.

The earliest references to *Adelges* spp. were mainly descriptive works such as Mattioli's sketch of the gall of *A. abietis* in 1565, Clusius' woodcut illustration of the same in 1576, and the general references to the gallicolae by Linnaeus (100) and by Geoffroy (76) in the eighteenth century. De Geer (75) in 1773 published an accurate study of the life history of *A. abietis*, and in the mid-nineteenth century Hartig (79), Kaltenbach (91), Ratzeburg (128) and Leuckart (99) made biological observations on this and other members of the subfamily.

The discoveries of the existence of the sexualis generation by Blochmann (12) in 1887, and of alternation of host by Blochmann (13), Dreyfus (57, 58, 59) and Cholodkovsky (30, 31, 32) in 1889, in species of the Larch Adelgids were the keys to fuller knowledge of the subfamily. From then onwards the intensive researches of a number of investigators completed the life histories of all the known species by application of these features. Cholodkovsky himself in a long series of papers extending over a quarter of a century elaborated the life histories of many of the species, notably in his monograph (35) of 1896 and his comprehensive paper (42) of 1915. Knowledge of the biology of the group was broadened by the experimental work of Nüsslin (119, 120) and Börner (15, 16, 17, 18, 20); the latter's consideration of the phylogenetic status of the subfamily is of particular interest. Another important contributor of the same period was Marchal (106) notable for his detailed experimental work on the life history of the Adelgids on Silver fir and on Pine.

Interest in the group was not confined to Continental Europe. As early as 1903-4 Stebbing (142, 143) had discovered a Himalayan species and elucidated its life history and the process of acquisition of wings. Contributions to knowledge of the North American species came from Gillette (77), Patch (123), Chrystal (43, 44, 45, 46) and Balch (5). In Britain, Burdon (25, 26) had stimulated interest in the early years of the twentieth century. In 1917 Steven (145, 146) published results of a detailed study of the Larch Adelgids in Scotland, and a general survey of the British species of *Adelges* with particular reference to their forest importance. Speyer's (140, 141) studies of *A. strobilobius* in England confirmed earlier expositions of its biology and led to an interesting hypothesis on evolution in the subfamily.

These investigations in the first quarter of the twentieth century elucidated the life histories of the great majority of the species, and later workers have turned their attention mainly to broader aspects of Adelgid biology, such as the mechanism of feeding, the reaction of the tree, and forest importance; detailed references to the literature on these features will be made in subsequent chapters. But even in recent years there has been room for original work on the life histories of little-known species. Francke-Grosmann's (72) study of the ecology and life cycle of *A. prelli* falls into this category, as does Balch and Underwood's (6) paper on *Pineus pinifoliae* Fitch in 1950.

(2). Literature on the biology of Adelges nüsslini and A. piceae

The study of the indigenous species *Adelges piceae* was initiated in 1843 by Ratzeburg (127) who described it as a new species and noted its life cycle as a succession of parthenogenetic generations (the sistentes). Thereafter, further progress in knowledge of the species lay in abeyance until the later years of the century. At that time its near relative *A. nüsslini* was spreading through western Europe both by natural means and by the distribution of transplants of its native host *Abies nordmanniana* on which it had been unwittingly introduced. The presence of *Adelges nüsslini*, however, was not perceived at first, and the serious injuries inflicted upon young transplants of Nordmann fir and natural regeneration of Common Silver fir were generally attributed to *A. piceae*. Dreyfus (59) in 1889 and Eckstein (62) in the following year suspected the existence of two species under the single name, and chose to distinguish *A. nüsslini* as a separate species (syn *A. funitectus* Drey., 1889, *A. nordmannianae* Eck. 1890) on quite inadequate biological grounds, but its authenticity was not generally recognised for a number of years, and on this account the early literature on the life cycle of each species is rather confused.

In 1903, Nüsslin (117) who at that time believed that only one Silver fir species of *Adelges* existed in Western Europe observed the migration of the sexupara generation from Silver fir to Norway spruce; he also discovered and described the sexualis generation, which he observed to reach adulthood, but not to produce offspring. He concluded that sexual development in the "twig-dwelling form of *Adelges piceae*" (really *A. nüsslini*) was rudimentary, and that completion of the life cycle was impossible because of the non-existence of fundatrix and gallicola generations on the spruce. This careful piece of work nevertheless lacked an experimental basis, and Nüsslin failed to detect that two distinct biological species were present on the Silver fir.

Cholodkovsky (37) in 1904 asserted that two species were involved, one the true *Adelges piceae* Ratz. living a monoecious cycle on *Abies alba*, and the other *Adelges funitectus* Drey., a dioecious species originating in the Caucasus and alternating between species of silver fir and spruce of that provenance. In 1906-7, Marchal (104, 105) experimentally confirmed Cholodkovsky's findings. Nüsslin (118) accepted these observations, although in the absence of more definite morphological distinction he still preferred to look upon the two forms as races of a single species. Börner (19) then amassed convincing biological and morphological proof of their separate identity, and in 1908 established *A. nüsslini* nov. sp. and *A. piceae* as separate species.

In 1913 Marchal (106) described the life cycles of *A. piceae* and *A. nüsslini* in the light of his own experimental work in France. This detailed and accurate work has been fully confirmed and widened by a number of investigators in several other countries, such as Steven (146) and Chrystal (47, 48) in Britain, Boas (14) in Denmark, Schneider-Orelli (132, 136) in Switzerland, Francke-Grosmann (70) and Hofmann (84, 85) in Germany, and Balch (7) in Canada.

(3). Theories of Evolution

The consideration of the ancestral nature of Adelgids must necessarily be speculative in view of the paucity of fossil evidence. The theories advanced by a number of investigators have been based only on the evidence of certain biological and morphological features common to members of the subfamily, and influenced by analogies with what is known about the evolution of aphids in general.

Of these common features, the most striking is that the holocyclic species of the subfamily Adelginae always utilise a spruce of the genus *Picea* as the primary host, and alternate with an intermediate host limited to one of the other genera of the tribe Abietineae. This fact has led to a number of early theories of migration, of which only one, that by Blochmann (13) will be considered here. Blochmann, subsequently supported by Dreyfus, Nüsslin, Cholodkovsky and Steven, considered spruce to be the primary and original host of the ancestral Adelgid; it was believed that it had an annual cycle rather similar to that of certain present-day aphids in which one or more parthenogenetic winged and wingless generations is succeeded by a winged sexual form at the end of the summer. Migration and alternation of host were developed by adaptation to life on other tree genera following wind dispersal of the alate forms to these hosts.

Blochmann's hypothesis led to an explanation of the polymorphic life cycle, which Dreyfus (57) enunciated as the "parallel row" or "parallel series" theory, as it has been variously translated. This concept arose from the biological resemblances between the subcycle on the primary host and that on the intermediate host. It was assumed that the series of generations originally present on the spruce had been duplicated on the intermediate host in the course of adaptation. Thus, on the primary host the apterous highly fecund fundatrix and the alate weakly fecund gallicola correspond to a parallel series, the sistens and the sexupara on the intermediate host. The sexualis generation was held to be anciently derived from the sexual form of the ancestral Adelgid on the spruce; however, in the course of time the propensity for sexual propagation has been lost to the series on the intermediate host. In the further evolution of this process monoecious cycles have been established by the loss of the series on the alternate host.

Börner (16) in the phylogenetic studies of 1907-8, broadly accepted this interpretation, which he called polycycly. However he did not believe that the inherent capacity for sexuality had been totally discarded by any species. This assertion has been disproved by subsequent research on a number of species, such as *Adelges piceae*. Marchal (106) agreed with Börner that monoecious species had been evolved from primitively sexual species through degeneracy causing loss of part of the polycycle; he also believed that new species could be founded only from primitively bisexual species, never by way of parthenogenesis.

In 1924, after a detailed study of *A. strobilobius*, Speyer (140) enunciated a completely novel interpretation of the course of evolution in the Adelginae. He observed that the life cycle is marked by a striking alternation of form (in relation to fecundity, number of stadia, presence or absence of wings, and stylet length) in the succession of the generations sexuales, fundatrix, gallicola, sistens and sexupara. Therefore he postulated that a definite inherent mechanism of alternation of form is the normal course of development of the insect. He supposed the evolutionary movement to have begun with an ancestral Adelgid which was winged, bisexual and confined to spruce. At an early stage, a primitive apterous fundatrix was produced in simple series with the sexual form; from these two early generations was established a powerful inherent mechanism of alternation. Complete parthenogenesis was established when in the course of time the male sexual form dropped out. This set up a primitive cycle comprising an apterous fundatrix in alternation with a winged gallicola, the former female sexual form. Next, over a long period, this simple cycle was transferred by migration and adaptive selection to host trees of a number of other Abietinean genera, there to run a strictly monoecious course. This stage of evolution has been reached only now by *Adelges (Cholodkovskya) viridana*, which runs a monoecious cycle on larch, where the sistens (the adaptive fundatrix) alternates with the progrediens alata (the adaptive gallicola). In the next stage the sexupara developed from the progrediens alata, and by a repetition of the processes of migration and adaptive selection returned to the spruce. The offspring of the sexupara were at first abortive females, later reproductive males and females, and constitute a new form, the sexuales; the sexuales incorporate novel morphological and biological features and tend to break away from the mechanism of alternation by more closely resembling the parent than the grandparent. Nevertheless they inherited the ancient genetic nature of the species, and their descendants have recapitulated the ancestral fundatrix and gallicola, to complete the holocycle.

Within this scheme the presence of the progrediens aptera runs in no way counter to the mechanism of alternation of form, since it is potentially a winged form. However, this mechanism is by no means perfect; when it breaks down, there may be produced offspring similar to the parent, as in the successive generations of progredientes on the larch in the case of *Adelges strobilobius* or in the successive generations of sistentes in the case of *A. piceae*.

Speyer considered the Larch Adelgids to be of younger stock with an actively evolving mode of life, and the Silver fir and Pine Adelgids, especially the latter, to be more ancient species which have now reached stability in evolution. Annand (2) commenting on Speyer's hypothesis, criticised it on the grounds that morphologically the genus *Adelges* must be considered more primitive then the genus *Pineus*, thus reversing Speyer's assertion.

Subsequently, the well-known authority Mordvilko (110, 111, 112) in a long series of papers on the evolution of aphids in general, has discussed the origin of the Adelginae in the light of a thorough survey of contemporary and fossil Aphidoidea. In the first place, he stated that aphids developed in temperate climates from the early Permian Homoptera. The aphids became grouped very early into their present divisions of familes and subfamilies, and already in Oligocene times the modern genera and even some species had been evolved. He considered the Adelginae to be an ancient group which arose on the ancestral *Picea* host, and had already evolved a simple monoecious cycle before the newer members of the Abietineae (*Larix*, *Pinus*, probably *Tsuga* and *Abies*) had appeared. This assumption places the origin of the Adelginae at least in the early Cretaceous Era. Mordvilko thus came to agree with Blochmann that the spruce was the true primary host.

The evolution of the holocycle and the differentiation of genera and species ran parallel with the evolution of the host tribe Abietineae. On the spruce, the ancestral Adelgid originally consisted of winged sexual individuals only. In the course of time, early-season generations of parthenogenetic winged forms appeared, and the occurrence of sexuales became more and more confined to the end of the season. Next the parthenogenetic generations differentiated into:

(i) the apterous fundatrix, highly specialised, highly fecund, and appearing in spring, and

(ii) one or more generations of winged, less fecund forms. Meanwhile the sexuales had degenerated into the feebly fecund, wingless, larviform character which they still exhibit. At this time the other Abietinean hosts became more abundant. Neither the highly specialised fundatrix generation nor the enfeebled sexuales could utilise these new species as hosts, but the summer generations of winged parthenogenetic females eventually succeeded in adapting themselves. Their offspring on the intermediate host ultimately gave rise to sexuparae equipped with an instinct to return to the primary host for oviposition. In this way was established a facultative alternation of host which later became obligatory in many species.

Concurrently with this development of a complex life cycle, the Adelginae underwent a reduction in size; it is possible that this was induced by the fact that members had to develop within the restricted space of the spruce gall. With diminution of body size followed the reduction of:

(a) wing venation;
(b) the antennae;
(c) the number of abdominal spiracles from eight to six in *Adelges*, and to five in *Pineus*.

Adelgids are the smallest of all the modern Aphidoidea.

Mordvilko (112) also held an interesting hypothesis to explain the origin of *Adelges piceae*. He believed that its original primary host was the Omorikoid spruce which was widely distributed over the northern hemisphere in the Tertiary Era, and which even in Quaternary times has been recovered in western Europe as the fossil *Picea omorikoides* Weber. In the course of time this spruce group has evolved into a few species now represented in some mountain regions of the northern hemisphere. The incidence of *Adelges* species on these Omorikoid spruces has never been fully explored, so that it is not known whether or not primary host generations morphologically similar to *A. piceae* have survived in those regions.

Since 1935, when Mordvilko put forward this theory, the only new evidence has been the discovery of *Adelges prelli* Grosmann which is morphologically similar to *A. piceae* but is holocyclic, apparently on *Picea orientalis* and *Abies nordmanniana*. Since it was discovered in an arboretum in Germany, and not in the Caucasian forests, it does not absolutely disprove Mordvilko's Omorikan hypothesis, which yet awaits further proof.

3. RESEARCH METHODS AND METEOROLOGICAL RECORDS

(1). Research methods

The life histories of the two species *Adelges nüsslini* and *A. piceae* were studied first by observations on the insects naturally occurring in the forests, and second by experimental infections of young trees in the laboratory.

In the second case, experimental infections were made on young planted trees in the Botanical Gardens, University of Aberdeen, and on small potted trees within a heated greenhouse. The greenhouse was necessary partly to avoid excessive predation upon tagged insects under study, and partly to force early flushing of the trees so as to achieve synchronisation of host and insect developments; the need for phenological co-ordination is explained in para. 5(2), p. 33. Infections of young trees were usually made by transferring egg clutches of known origin and identity. Pieces of egg-bearing bark or shoot taken from the forest were tied to a branch of the young tree under infection, and the hatching crawlers distributed themselves. Both in the garden and in the greenhouse, it was necessary to isolate these stocks so as to prevent accidental mixture of the two species. This was accomplished by enclosing each young tree within a muslin cloth cage. The most successful type was made by constructing a sturdy wire frame to fit over the entire tree. Then a muslin sack was fitted over the frame and secured by tightening the neck of the sack around the rim of the pot by means of a cord. Because the thin muslin cloth is liable to decay under the action of rain and wind, it was rot-proofed by impregnation with paraffin wax. In some cases only single branches were required for infections. These were isolated from the rest of the tree by means of similar wire frames with fitted muslin hoods. These cages are illustrated in Plates 40 and 41.

Altogether forty-eight young trees, potted and planted, were used in experiments. They included the following species; *Abies alba* Miller, *A. procera* Rehd., *A. grandis* Lindl., *A. veitchii* Lindl., *A. concolor* Lindl. & Gord., *Picea orientalis* Carr, *P. abies* Karst. and *P. omorika* Bolle.

(2). Field study

Field investigations on *Adelges nüsslini* were conducted at Dunecht Estate, Aberdeenshire between 1950 and 1954. There a small stand of naturally regenerated *Abies alba* (Plate 60) has suffered a heavy attack by *Adelges nüsslini* over recent years, and offers excellent opportunities for the study of all phases of the insect. Young trees of *Abies grandis*, *A. procera*, and *Picea orientalis* were planted there in 1950, to facilitate studies. *Adelges nüsslini* occurs in this plot as a pure stock with no admixture of *A. piceae*. A full description of the site and the outbreak is given in para. 1(2) of Chapter 4, p. 57.

Observations on the seasonal development of *Adelges piceae* were made at Craibstone Estate, Aberdeenshire during the same years 1951-1954. In this estate the insect is widely distributed over small pole-stage blocks of various Silver fir species (Plate 70). There also the insect occurs as a pure stock, and *Adelges nüsslini* is absent.

(3). Meteorological records

Records of temperature and precipitation are tabled in Appendix 1, p. 66. These data have been drawn from the Meteorological Office *Book of Normals* (108), from Air Ministry records taken at Dyce, Aberdeenshire, and from hygrothermographs maintained during 1953 in the Botanical Gardens at Aberdeen and at Dunecht. These data can be summarised as follows. The Aberdeen region is characterised by a temperate climate, with usually a relatively mild autumn and winter, a sunny spring and a cool summer. The rainfall is fairly light but is well distributed over the seasons. The year 1952 was a fairly normal year but was rather wet in the summer. The year 1953 was less normal; it began with warm and very dry weather in the first three months, followed by a wet spring and summer, and ended with a very mild and dry autumn.

The phenology of Adelgids is not well understood, but it is clear that weather has a marked effect on their seasonal development and on the level of population. These aspects are discussed in para. 6(2), p. 35.

4. LIFE CYCLE OF ADELGES NUSSLINI C.B.

(1). Fundatrix

The fundatrix of *Adelges nüsslini* is a generation which in Scotland occurs only rarely in the field, even under the most favourable circumstances, but it is not difficult to produce and rear within the protection of the laboratory.

The neofundatrix hatches after an incubation of less than two weeks from the large solitary egg laid by the sexualis female. The newly hatched crawler usually spends a few hours or days in apparently aimless wandering within the crown of the spruce before finally settling at the base of a bud. In 1953, this pre-settlement phase occurred between the limits of 20th July and 10th August, with a peak of abundance at the end of July. In arriving at a site for settlement, the neofundatrix appears to show no preference for any aspect or section of the crown of the tree, and does not appear to discriminate between the buds of vigorous and non-vigorous shoots. In this respect it differs markedly from the gravity—and light-sensitive neosistens on the intermediate host. Almost all neofundatrices choose to settle on the basal quarter of a bud, but rare individuals, especially if the population is high, may settle on the twig a short distance from the bud; such individuals always die in the 1st stadium.

The settled neofundatrix inserts its stylets, darkens in colour to black and secretes the characteristic fringe of wax flakes. In this condition it remains in diapause until the spring of the following year. The actual dates of resumption of feeding and development are dependent upon the warmth of the spring and the favourability of the micro-climate. In 1953 the diapause of favourably situated individuals was terminated in early February following an unusually warm January, but in the typical year it does not take place until early March. The resumption of feeding is indicated by the appearance of a minute droplet of viscid excreta or honeydew at the end of the insect abdomen.

Thereafter follow three moults in rather slow succession through the early spring. The rate of development of one typical individual in 1953 was as follows:

	Date	*Duration of stadium following the moult*
Resumption of feeding	18th Feb.	
Ecdysis to 2nd stadium	23rd Feb.	22 days
Ecdysis to 3rd stadium	18th March	28 days
Ecdysis to adult stadium	15th April	46 days

The corresponding developmental course of two other fundatrices under observation followed approximately the same course.

The process of moulting is the same at the beginning of each stadium and is common to all generations. It begins with a partial or complete withdrawal of the stylets from the host tissues. Then the skin splits along the median line of head and thorax, and is gradually pushed backwards as the insect frees its rostrum and legs from the exuvia. The cast skin may lie over the abdominal dorsa for a few hours or days before body movements and expansion cause it to slip to the rear. Since all the instars which succeed the first are fixed and stationary, these exuviae collect in a series near the end of the abdomen, frequently adhering to the honey dew; accordingly the number of skins indicate the current instar of the insect without recourse to microscopic examination. The newly moulted insect inserts its stylets to full length in the basal tissues of the bud, at approximately the same place as the earlier instar, and resumes feeding. Just after ecdysis the insect has a soft and shining skin, but after the first day it grows dull as, first, a wax bloom appears and, later, wax wool.

The renewal of stylets in Adelgids and other Hemiptera-Homoptera has been described by Balch (7), Baranyovits (10), Heriot (80) and Weber (153). The first-named in his work on the sistens of *Adelges piceae* says that the newly moulted insect carries its stylets coiled internally on each side of the cephalothorax, with only the tips joined at the rostrum. Then they are united to form a single tube as they are extruded along the labial groove, and carried in a loop outside the body.

The three adults under observation became adults on the 2nd, 15th, and 16th April respectively and began oviposition about nine days later on the average. In all three cases the adults were killed by predators before completion of their natural lives. However it seems certain that the fundatrix is capable of laying a total of at least 300 eggs at a mean rate of nine eggs per day, and a peak output of thirteen eggs per day in the warmest periods. The following are the observed rates of oviposition by the three individuals A, B, and C.

No. of days after initiation of oviposition	*Total number of eggs laid to date by Insect*		
	A	*B*	*C*
10 days	32	25	27
20 days	116	117	85
30 days	170	236	142
33 days	185	262	165
36 days	200	295	
38 days	210		

The eggs were laid in a compact mass immediately behind one another and held in position by the waxen thread attached to each egg, and by the abundant wax wool secreted throughout oviposition (Plate 43).

Marchal (106) has observed in France that the fundatrix may lay more than 500 eggs. Such powers of oviposition are the more remarkable in view of the fact that each egg is a fifth as long as the adult itself. The eggs are laid concurrently with an abundant secretion of wax wool, under which they are partly concealed. The fundatrix phase is virtually over by early June, even in the absence of predation.

The fundatrix induces a slight swelling of the bud on which it feeds, and this is evident even before the adult stage is reached. The effect on internal tissues is evident at the time of the flushing of Oriental spruce, in mid-May. Usually a few days in advance of normal flushing, the attacked bud opens to reveal a roseate miniature gall, ovoid in shape and about 5 mm. long and 4 mm. in diameter. Each immature gall-leaf is bright red over the swollen basal two-thirds and yellow-pink over the apex, where it bears a few short scattered lines of stomata. Gall development up to this point is entirely due to the fundatrix; in Mid-May, few of the gallicolae have hatched and none can have had any influence on the formation of the gall. In one simple experiment, the fundatrix was removed from the bud in the 3rd instar. In due course the bud opened to reveal the normal immature gall. The gall developed abnormally and remained small (Plate 45).

A solitary instance of attendance by ants on Adelgids was recorded on 9th May, 1953. An unidentified small black ant 2½ mm. long was observed feeding on honey dew excreted by a fundatrix adult. The ant was observed to stroke the fundatrix with its brown antennae as it fed; this is behaviour characteristic of aphid-tending ants.

(2). Gallicola

Partly on account of the rarity of Oriental spruce host trees and partly because of the failure of the sexuales, the gallicola generation of *Adelges nüsslini* is of infrequent occurrence in Europe. Correspondingly the production of galls is at a very low level and few European researchers have investigated their biology. Steven (146) is the only investigator to have recorded their occurrence in Britain. In Scotland their appearance is certainly very rare. Even under the highly favourable conditions in the Dunecht research plot, only infrequent galls were produced during the years of study 1951-1954; on the three young nine-years-old Oriental spruce trees, the writer found no galls in 1951, thirteen in 1952, three in 1953, and 119 galls in 1954.

Larval development. The incubation of the eggs laid by the fundatrix varies considerably according to temperature. In the cold mid-spring of 1953 they hatched in three to five weeks, the first neogallicola appearing on the 13th May and the last a month later. Lack of synchronisation with the host occasions some mortality among these active crawlers. The earliest and latest hatching individuals frequently perish from inability to settle, the former because the gall-bud has not yet flushed and the latter because the gall pockets have already formed and closed. However, the great majority hatch concurrently with the opening of the buds; they immediately enter the spaces between the leaf-stalklets of the immature gall, and insert their stylets to feed.

Within the gall the gallicolae develop through four larval stadia over a period of forty to fifty days. The duration of the separate stadia is not known, but by analogy with the progrediens generation, one can suppose that these four stadia are of approximately equal duration. Within each pocket of the gall the larvae may be free to move about, feeding here and there, as Plumb (126) has reported in the case of the gallicolae of *Adelges abietis* L. Such mobility seems feasible in view of the very short stylets of the gallicola of *Adelges nüsslini* and of the soft undifferentiated tissues comprising the walls of the inner gall. The development of all the occupants of a single gall is probably fairly synchronous, since they all emerge as motile 4th instars during the short period (two to four days, occasionally longer, in early July) during which the gall dehisces. Each nymph settles on a needle not more than two inches away from the gall, but never on the gall itself. There it immediately begins the fourth ecdysis, and casts off its skin in about fifteen minutes. During the moult the nymph is stationary on the needle but immediately afterwards the young adult wanders up and down the shoot, actively flexing and inflating its yellow-green wing sacs. These become fully stretched about an hour later, but retain their bright yellow hue for a few hours until fully hardened. Only then is the adult ready to fly. (Plate 49.)

Gall development. The stimulus to gall formation is supplied by the fundatrix but its full development takes place only in the presence of the gallicola larvae and is accomplished in the seven weeks which follow flushing. Thus in 1952 and 1953, the galls matured in the first fortnight of July. The development of the gall runs concurrently with the elongation of normal shoots on the rest of the tree, but in the galled bud itself linear growth is almost completely supressed. Unlike the galls of *A. cooleyi* Gillette and *Adelges viridis* Ratz., no shoot growth ever takes place beyond the gall.

Even when the attacked bud first opens, its young leaves are already abnormally short and broad, and fairly loosely appressed (Plate 46). The gall, which is invariably symmetrical and ovoid in shape, is formed of a central cone or shoot axis bearing a tight spiral of 30 or 40 leaves. Each leaf is borne on a short swollen needle-stalklet, which ultimately makes up the bulk of the gall. (This needle-stalklet, as explained in para. 2(3) of Chap. 3, p. 40, is represented on the normal spruce twig by the woody cushion on which the needle sits). Leaf development remains rudimentary and it does not grow any longer, although the tip becomes horny. Growth of the gall takes place by the expansion of these abnormal needle-stalklets. The upper part of each stalklet swells and develops as a thick apophysis with a rhomboidal external face bearing the leaf rudiment (Plate 48). The rhomboidal outline of each apophysis is no doubt due to the concurrent swelling and pressure of neighbour stalklets. These apophyses press tightly against one another at the surface of the gall but remain structurally discrete, never fusing. This mode of formation causes the gall to superficially resemble an immature pine cone. (Plates 47 and 48.) The lower part of each needle-stalklet, now concealed within the gall, becomes slightly hollow on each side, so that between any four adjacent stalklets a small cavity is formed. Each gall contains 30 or more cavities, frequently interconnected by narrow slits. Within each cavity up to five nymphs may eventually mature, feeding on the wall tissues. The total population of a single gall varied between 34 and 102 at the time of dehiscence. (Plate 44.)

From its original dimensions of 5 mm. long by 4 mm. diameter, the gall increases to a size of 11 mm. by 9 mm. at the time of maturity (Plate 49). Its colour varies with its age and location. Initially the whole gall is bright red, but as it grows the apophyses turn pink and later green, while the red pigment is confined to their rhomboidal lines of junction and to the leaf rudiments. The horny tip of the leaf is pale yellow. The lower shaded side of the gall, or even the whole of shaded specimens, may become almost completely green. After dehiscence the gall becomes uniformly brown and woody (Plate 49).

The process of gall dehiscence is not understood, although a few investigators have tried to explain it. Börner (16) thought that when the maturing nymphs stopped feeding, the stimulus to sap flow into the gall was withdrawn, and the gall dessicated in consequence. Plumb (126) pointed out that the vascular tissues of the gall remain intact, and that accordingly it is unlikely to be an interruption of water supply which initiates the drying of the gall. Rather he believed that it may be due to stresses set up by the inherent tendency of the needle stalklets to straighten out at right angles to the stem, in consequence pulling apart the gall apophyses.

Occasionally galls were observed to dessicate and open two or three weeks before their normal maturity, so that the larvae in their middle instars died. The reason for this phenomenon is not understood but it is more likely to be due to some physiological impulse than to weakness of the shoot or to external damage. In one case where the base of the gall was half eaten away by an unidentified Tortricid caterpillar, the affected half died, but the rest developed normally in due course.

The adults and their migration. The adult flies from the Oriental spruce and migrates to a Silver fir. This fact, long established by Marchal (106) was confirmed by the following experiments in 1952 and 1953.

Experiment 1. On the 14th July, 1952, an opening gall from which there was a subsequent emergence of 75 nymphs was placed in a cage enclosing a branch of a young tree of *Abies alba.* When the cage was opened a fortnight later, 51 gallicolae adults had settled on the Silver fir foliage, and the rest were dead on the sides of the netting. Of these settled ovipositing adults, 47 had chosen needles of the current year's foliage, and four had stayed on those of the penultimate year's foliage. Each of these laid a small clutch of eggs, which gave rise to neosistentes. These neosistentes developed in the normal way in the following spring.

Experiment 2. On the 9th July, 1952, the branch of a young tree of *Abies grandis* was infected in a similar way with a gall which subsequently produced 80 adults. None settled on the foliage; all were dead on the netting of the cage.

Experiment 3. On the 9th July, 1952, 36 gallicola adults were released over cut branches of *Picea orientalis, Abies grandis, A. alba, A. procera, A. veitchii* and *Pseudotsuga taxifolia* Britt. with their cut ends in a small vessel of water, all enclosed within a large bell jar. One gallicola settled and oviposited on a leaf of *A. alba* but all the others stuck to the moist sides of the jar, or died on the floor. This experiment was inconclusive, probably because of the excessively moist atmosphere of the bell jar.

Experiment 4. On 16th July, 1953, a gall giving rise to 86 adults was placed in the cage enclosing a branch of a young tree of *Abies grandis.* 22 gallicolae settled on the foliage. All chose the shaded side of the leaf. That it was a preference for shade and not for the stomatal surface was shown by the fact that where the leaves had been turned so that the stomatal surface faced the light, the gallicolae nevertheless elected to stay on the shaded, inverted adaxial surface. Each gallicola laid a small clutch of eggs, which hatched as neosistentes, and settled on the twigs. On this host, *A. grandis*, all the neosistentes perished during diapause.

Experiment 5. On the 9th July, 1953, 102 adults emerged from a gall into the cage enclosing a branch of a young tree of *Abies grandis.* A week later only four had settled on the foliage and oviposited. 60 others were still alive on the netting but had apparently refused to settle. The crawlers which emerged from the eggs were neosistentes, but none was alive in the following spring.

Experiment 6. These 60 gallicolae were then placed in a muslin cage with cut branches of *Abies alba, A. concolor, A. grandis* and *P. orientalis.* Four settled on *A. alba*, one on *A. grandis* and one on *A. concolor.* All the rest died on the floor or sides of the cage.

These experiments show:

(i) that a species of *Abies* is the alternative host to which the gallicola migrates;
(ii) that the gallicola may have low powers of searching for its host;
(iii) that having once arrived on the host it discriminates between the shaded and the sun-lit sides of the leaf and between young and old leaves;
(iv) that there is some indication of a preference for *A. alba* over some other Silver fir species;
(v) that the gallicola appears to have no tendency to remain on the spruce. Marchal (106) however, found a rare tendency for the gallicola to settle and oviposit on the primary host, where the hatching larvae always died.

After the typical gallicola has settled on a leaf, its colour slowly darkens to black and the wax glands become active (Plate 9). Short thick curling strands are secreted from the dorsal thorax and head, resulting in the appearance of a small irregular white cross on a black background (Plates 9 and 10). Concurrently a small number of eggs are laid under the folded wings. The process of oviposition is relatively slow and the clutch is always small. One individual laid 30 eggs in thirteen days, another eleven eggs in nine days. The average size of the clutch was 15 eggs. Almost all the gallicolae died about a fortnight after settling. Their offspring, hatching in two weeks under natural conditions, are neosistentes supplementing the normal population of sistentes in summer diapause.

(3). Sistens

Development of Hiemosistens. There are two generations of sistentes in the life cycle of *Adelges nüsslini:*

(i) the hiemosistens, which is the abundant overwintering form; and

(ii) the aestivosistens, a rare form with midsummer development after a relatively short diapause.

The development of the former will now be considered.

The hiemosistentes arise from the eggs variously laid by gallicolae, parent hiemosistentes, aestivosistentes and progredientes apterae. Whatever their derivation, the neohiemosistentes are all similar. These first instars, rarely later instars, can be found in mid-winter hibernating on the twigs, branches and main stems of the intermediate host, usually on young trees. In their natural occurrence in North-east Scotland, they were almost invariably found on *Abies alba*, but experimentally they were induced to adopt a number of other *Abies* spp. In the late winter or early spring, hibernation ends in the first prolonged spell of warmer weather, and the resumption of feeding is signalled by the excretion of honeydew from the anus. In the normal year most neosistentes resume feeding in the last fortnight of February or the first fortnight of March; in 1953, following an unusually warm January, they were three or four weeks in advance. This early period of feeding lasts about a week before the first moult.

The sistens undergoes three moults to reach the adult stage. The duration of the 2nd and 3rd larval stadia is very variable according to seasonal temperature and microclimate, but in general the three moults follow one another at intervals of two to three weeks. The progress of development of the sistentes is summarised in Fig. 3, which shows the seasonal limits and peaks of abundance of the four instars, and the average duration of the stadia, on the basis of observations on a large number of individuals.

As with the fundatrix, the sistens remains fixed in spring, and by a similar process of moulting it accumulates the exuvia to the rear of the abdomen. (Plate 52.) Feeding however is never on the bud of the Silver fir, but always on the bark, preferably on the thin young bark of the shoots.

The final moult to the adult stage takes place in early April on the average, and is followed by a mean feeding period of seven days before the first oviposition. The hiemosistens is highly fecund and under favourable conditions lays 200 to 300 eggs over a period of two months or longer. (Plate 53.)

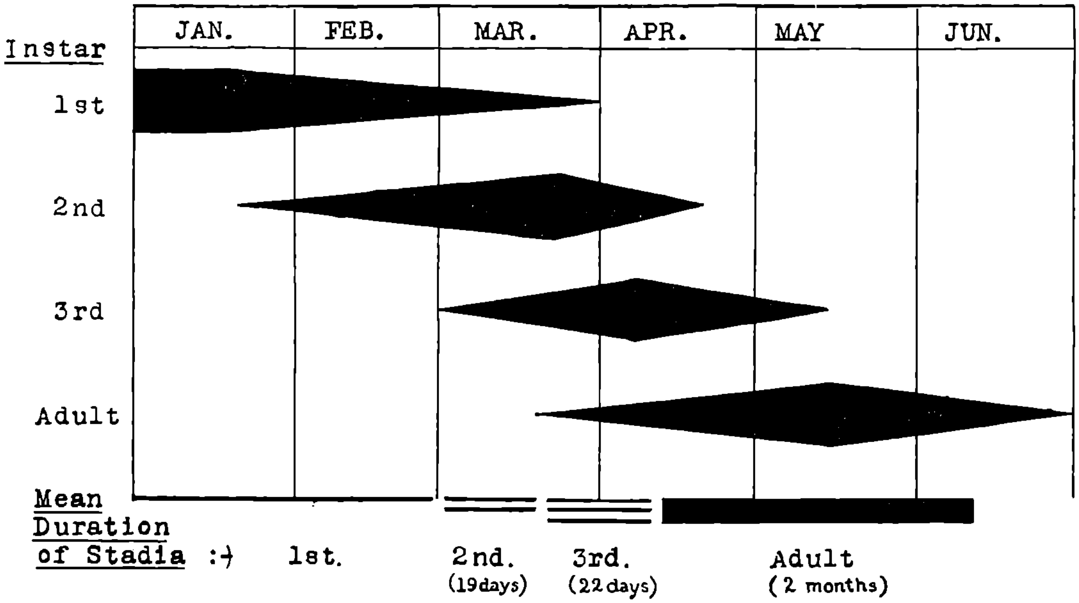

Figure 3. Seasonal development and proportions of the larval and adult instars of the hiemosistens generation of *Adelges nüsslini* on *Abies alba* under forest conditions in Aberdeenshire. The first stadium of the hiemosistens may be 4-9 months.

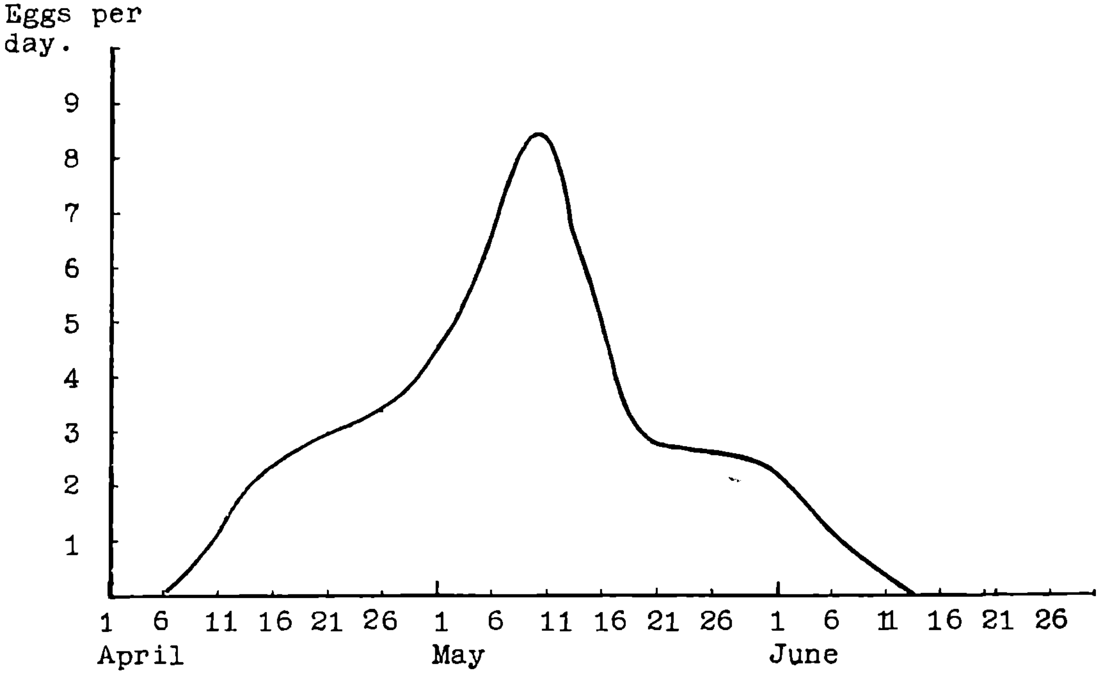

Figure 4. Daily rate of oviposition by a single hiemosistens of *Adelges nüsslini* on a shoot of *Abies alba.*

One individual laid 287 eggs in seventy-six days, another, 231 eggs in sixty-seven days. These totals have been calculated from records of periodic counts of the current size of the clutch in conjunction with estimates of the rate of hatching. The largest number of unhatched eggs ever seen in a clutch was 110. The rate of egg production varies considerably with temperature, but tends to normality, with a peak production, up to ten eggs per day, in middle adult life. The rate of oviposition of a single individual is shown in Fig. 4. The most fecund individuals were always found on the youngest shoots still in relatively healthy condition. On the main stems and necrotic twigs attacked in earlier years, oviposition reached much smaller numbers. Similarly sunlit twigs gave rise to much higher rates of oviposition than shaded twigs.

Settlement of the Neosistens Offspring of the Hiemosistentes. The incubation of the eggs laid by the hiemosistentes varied directly with temperature; in the warmth of the greenhouse the average duration was ten days but at early April shade temperatures in the open it was twenty-two days.

The eggs laid by the hiemosistens adult are predestined to develop into two forms; early-hatching eggs give rise to progredientes, late-hatching eggs to neosistentes. It has been found by limited numerical surveys that a little more than half of the average egg clutch is predestined to develop into neosistentes. This was confirmed by the tally of the total populations on ten young shoots from the crown of a young tree at the end of June; 8,276 or 56 per cent. were neosistentes while 6,431 or 44 per cent. had become neoprogredientes.

Rare neosistens crawlers were present on the trees as early as 28th April, even before the flushing of the new shoots, but these were quite exceptional. Settled neosistentes appeared in abundance at the end of May and the population rose rapidly in the first three weeks in June. Towards the end of June, settlement by neosistentes derived from hiemosistens parents declined, and in early July ceased altogether. This population movement can be illustrated by the periodic tally maintained on eleven growing shoots of a young tree of *Abies alba* in the months of May-June, 1953.

First fortnight of May: Flushing of the buds. Only neoprogredientes settling.
22nd May: Very rare neosistentes settling.
30th May: 518 settled neosistentes (21 % of final total population).

5th June: 926 settled neosistentes (37% of final total population).
8th June: 1,131 settled neosistentes (45% of final total population).
23rd June: 2,251 settled neosistentes (90% of final total population).
3rd July: 2,510 settled neosistentes (100% of final total population).

Behaviour of the Neosistens. The neosistens, being a highly mobile insect, can exhibit reactions and preferences which are denied to subsequent instars. There is no doubt that the neosistens is capable of crawling a considerable distance away from its parent, before finally settling. For example, one individual, already two days old, was placed on a piece of white filter paper in the strong diffuse light of the laboratory (temperature 63° F.). In one hour it had moved 14 inches. At this rate of travel it is able to give full expression to its sensitivities in relation to light, gravity and feeding. Balch (7) writing on the reactions of the neosistens of *Adelges piceae*, says "It was evident that there was a negative geotaxis but a stronger phototaxis in diffuse light. The reaction to strong direct sunlight, however, was negative." These remarks apply equally well to the neosistens of *A. nüsslini.* The highest concentration of settled neosistens is invariably in the upper crown of the young tree, in response to negative geotaxis and positive phototaxis. In an experimental infection of a young *Abies grandis* on 21st May, 1952, 1,000 eggs were placed at the base of the stem. From the hatching larvae, about 600 neosistentes eventually settled; 482 were found on the topmost whorl, including the leader, 100 were on the shoots of the whorl just below, and the remainder were scattered over the lower crown. Almost all settled on the twigs of newly flushed shoots; only six settled on older twigs. There is clearly a very strong preference for the current year's shoots; older twigs and the mainstem are utilised only when space for settlement on younger twigs is very restricted. As many as 200 to 300 neosistentes per linear inch may settle on these young shoots.

Even on a single branch the neosistens exhibits preferences for certain locations. It usually chooses any slight depression or irregularity of the bark such as cracks, slight wounds, leaf scars, leaf bases, the junctions with old bud scales, and the vicinities of other neosistentes. Probably stereotaxis is involved in the selection of such sites. On the vertical leader of a tree all aspects are equally infested. On the lateral shoot, however, the insects congregate mainly on the lower shaded sides; this is interpreted as a preference for diffuse light. On any young shoot of the current year the highest concentration of settled neosistentes is on the proximal end. This is caused solely by the fact that at the time of peak settlement the shoots, although elongating rapidly, are still young and short. The lightly-infested distal portion of each shoot is grown in the later growth period when the number of active neosistentes has declined.

The Aestivosistens. The neosistentes enter diapause after settling in the late spring. For the great majority this diapause extends through both summer and winter until the following spring. In the case of a small minority, however, the resting period may be quite short and the insect develops as a summer generation, the aestivosistens. Both Marchal (106) and Chrystal (47) briefly mention this generation, but give no details of its proportional abundance or its frequency of occurrence. Schneider-Orelli (132) recorded that it occurs as a small part of the total sistens population, at the most 25 per cent.

In 1952, no aestivosistentes were observed at either Dunecht or the Botanical Gardens, but in the following year they were present in various stages of development between the end of June and mid-October. The peak population of aestivosistens adults was reached in the first half of September. Probably the minimum period of diapause is five weeks, but for the typical neoaestivosistens it extends to two to three months. The development and appearance of the aestivosistens through three moults is similar to that of the hiemosistens, but the duration of all four stadia is much shorter, possibly on account of the higher temperatures of the summer months. The adult is of relatively small size and low fecundity; for a single individual the largest total oviposition recorded was only 42 eggs.

A curious and quite unexplained feature of the generation was that it occurred only on *Abies alba.* It was totally absent from young trees of *A. grandis*, *A. concolor*, *A. procera* and *A. veitchii*, although all bore considerable populations of living neosistentes which had been experimentally transferred to them in the spring. However, even on *A. alba* only two to three per cent. of the total neosistens population developed as aestivosistentes in 1953.

Stem Infestations of Older Trees. The first discovery that sistens populations of *Adelges nüsslini* may develop naturally on the main stems of older trees, was made by Schneider-Orelli (132) in 1929. He found that stem infestations of twenty-five to fifty years-old *Abies alba* and even older trees, in the Swiss forests, were frequently caused by *Adelges nüsslini* as well as by *A. piceae*. Further he observed that only sistentes were produced in these infestations and concluded that there existed a separate race which had lost the power of reproduction of the progrediens generation. On the basis of this evidence Börner (22) elevated this race to the status of a new species *Dreyfusia schneideri* C.B. Later, however, Schneider-Orelli (133, 135) after some experimental work concluded that at most only races were involved and that specific distinction was not justified. He also found that in fact a small proportion of progredientes was produced each spring, but that they failed to settle in the first stadium. Hofmann (85) also questioned the specific status of the stem form, and suggested that differences between the nutritional values of shoot and stem accounted for the different proportions of progredientes.

This stem-dwelling form of *Adelges nüsslini* has been found by the writer in moderately heavy infestations on the main stems of 30 years-old *Abies veitchii* at Dunecht Estate, Aberdeenshire, on 38 years-old *A. alba* at Inverliever Forest, Argyllshire, and on 32 years-old *A. alba* at Monaughty Forest, Morayshire. At Dunecht it was found that in 1953 the hiemosistentes began to lay eggs relatively late in the spring and produced small clutches of eggs, probably rarely more than 40. No adult sexuparae or progredientes apterae were produced but in the summer a small population of aestivosistens adults arose. Experimentally, transferences of hiemosistens egg clutches from the stem of *A. veitchii* to young shoots of *A. alba* at the end of May produced a heavy population of neosistentes but no neoprogredientes. Subsequent experimental work to test Hofmann's assumption of a nutritional control of the proportion of progredientes to sistentes, was inconclusive.

(4). Progrediens aptera and Sexupara

Behaviour of the Neoprogrediens. The early-laid eggs from the clutch laid by the typical hiemosistens give rise almost entirely to neoprogredientes. In general appearance and characteristics the motile neoprogrediens closely resembles the motile neosistens. In a similar way it appears to be motivated by negative geotropism and positive phototropism to assemble on the newly-flushing shoots in the upper crown. One small but heavily infested tree of *Abies alba* was sampled on the 18th May, 1953, to give a measure of neoprogrediens population densities on various parts of the crown. These tallies showed an overwhelming preference for the upper crown. Reduced to mean populations per linear inch of new shoot, these counts showed the following ratio: upper crown 133, middle crown 27, lower crown 7 neoprogredientes. On any one shoot, all leaves are settled with equal facility; there is no stratification of density along its length.

Unlike the neosistens, the neoprogrediens almost always settles on the undersurface of the young leaf, or very rarely on the very young elongating shoot axis (Plates 54 and 55). If denied these sites, it always perishes. This frequently happens in nature because the earliest-laid eggs may hatch out before the opening of the buds. Even after flushing it may happen that the young leaves become so heavily populated that late-hatching individuals must settle perforce on one-year-old needles, where they always die without further development.

To explain this inherent choice of the young needles the writer suggests three hypotheses:

(i) The neoprogrediens may be motivated by a sensitivity to moisture, whereby it selects the young needle because its abaxial or under-surface area, equipped with lines of actively transpiring stomata, is damper than any other portion of the tree crown. In support of this supposition may be cited an observation made in early April 1952, before flushing had begun. Freshly-cut branches of *Abies alba*, bearing masses of hatching eggs, were placed inside a deep glass vessel; the cut ends were immersed in an inch of water. The hatching neoprogredientes, finding no new shoots to settle upon, colonised the one-year-old leaves. However, on each branch they distributed themselves not at the upper end in accordance with the instinct of negative geotropism, but at the lower end, especially where the needles lay just above the water line. Only when these leaves were fully populated were those higher up occupied. This distribution indicates that the moisture gradient within the glass vessel played a powerful part in directing their settlement.

(ii) The neoprogrediens may be sensitive to the pH of the tree sap. It is possible that the crawler shows a preference for very acid tissues. Measurements of the pH of newly flushed buds of *Abies alba* have shown that at first both leaf and axis lie between 3.0 and 3.5 on the logarithmic scale; however, in the weeks which immediately follow, pH gradually rises but the levels for leaf and axis diverge; leaf pH remains low (well under 4.0) while twig pH becomes high (soon exceeding 4.0, ultimately 5.0). Such a preference for acid tissues could explain the preference for the young needles, or even the very young shoot axis, or in their absence, the abortive selection of one-year-old needles rather than any other part of the crown. It has been shown by Fife and Frampton (68) that a pH gradient in the petiole of the sugar beet guides the stylets of the leaf hopper *Eutettix tenellus* to feed in the phloem.

(iii) The third possibility is that the shortness of the stylets of the neoprogrediens denies it access to the more nutritive tissues of the twig, but permits the utilisation of the shallow tissues of the leaf. One might further suppose that the stylets can easily penetrate the soft thin-walled, undifferentiated cells of a young leaf, but not the tougher structure of an old leaf.

The development of the Progrediens aptera and of the Sexupara. In a normal year the first neoprogrediens crawlers hatch from the eggs about the end of April, and the last of the brood appears at the beginning of June. The settled larva immediately begins to feed on the underside of the leaf of a young shoot; there is no period of diapause. It remains fixed throughout larval life on its original site of settlement, and undergoes four moults to become adult, accumulating the exuviae at the end of the abdomen. Towards the end of the 3rd stadium, the larva can be distinguished as one of two sister forms, the progrediens aptera and the sexupara; on the dorsum of the former can be seen very short wax strands, but the latter has virtually no wax secretions. In the fourth stadium the distinction is much more clearly marked, since the apterous form has abundant wax wool, while the alate form has distinct wing pads. (Plate 16). Nevertheless, both develop along parallel stadia as the following comparison shows.

PROGREDIENS APTERA AND SEXUPARA: DURATION OF LARVAL STADIA AT DUNECHT FOREST GARDEN, SPRING 1953

TABLE 1.

Stadium	Mean No. of Days			No. of Individuals under observation	Range in days
	Both forms	Sexup.	Pr. apt.		
1st	8			9	6 — 13
2nd	8			10	6 — 12
3rd		8		5	7 — 10
			8	4	7 — 10
4th		10		7	7 — 13
			10	5	7 — 12

Thus the mean rate of development through the four larval stadia in each case was 34 days under field conditions. The distribution of these larval instars through the spring is shown in Fig. 5.

The adult progrediens aptera morphologically resembles the adult sistens but it is less fecund. It remains fixed on the leaf and secretes abundant wax wool which covers both itself and its eggs. (Plate 18).

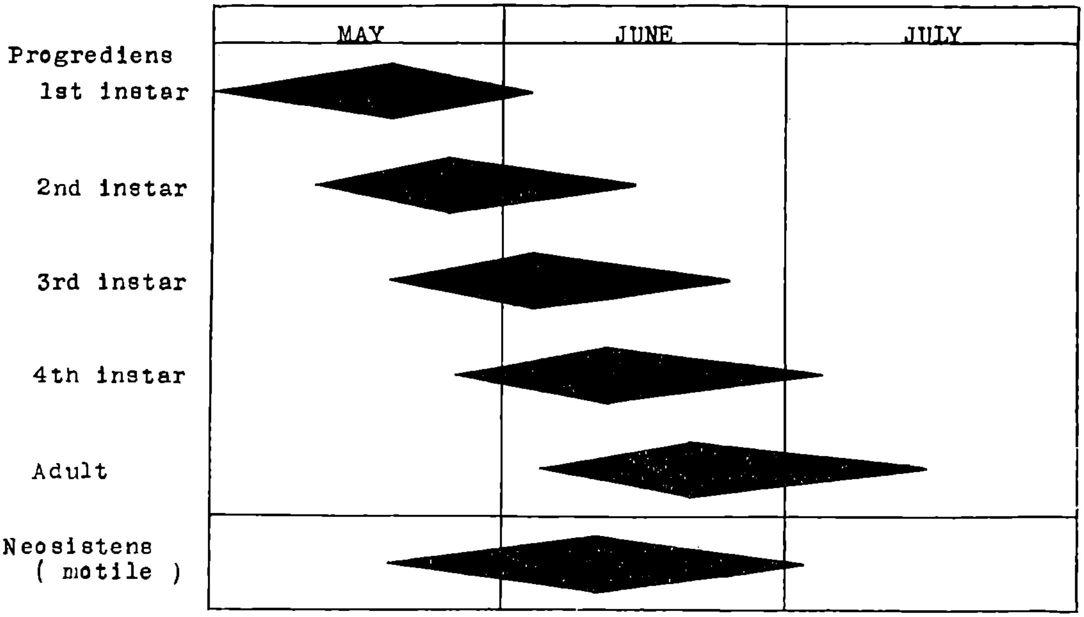

Figure 5. *Adelges nüsslini:* seasonal occurrence of the progrediens generation (alate and apterous) and of the active neosistentes seeking settlement.

The average size of the clutch is only ten to twelve eggs, laid in a week. The eggs invariably give rise to neosistentes similar to those produced by other generations. The offspring of the progrediens aptera thus become only a very small fraction of the mass of neosistentes in diapause. However, they may have some significance in maintaining the annual production of neoprogrediens; this influence is discussed in para. 5(2) of this Chapter, p. 34, dealing with the corresponding generation of *Adelges piceae*.

Relative Proportions of Sexuparae and Progredientes apterae. The progeny of the hiemosistens is clearly differentiated from the embryo stage onwards as sistentes and progredientes. Probably the proportion of each is hereditarily determined. Schneider-Orelli (132) has recorded a first instar individual intermediate in form between the neosistens and neoprogrediens but this is quite exceptional. The progredientes apterae and the sexuparae, on the other hand, are indistinguishable in their early stadia and only later diverge into their separate forms. In the writer's opinion, this divergence is not solely based on inheritance, but is largely controlled by environmental factors. It seems probable that the main factor involved is the nutritional status of the leaves, which is very variable under different densities of population.

The ratio of sexupara to progrediens aptera is not constant in the case of *Adelges nüsslini.* General observations on infested *Abies alba* trees have shown that on those young shoots where the population of neoprogredientes was high, as in the upper crown, the ultimate proportion of sexupara to progrediens aptera was high. Conversely, wherever the neoprogrediens population was low, as in the lower crown, the ultimate proportion of sexupara to progrediens aptera was low. These observations suggested the hypothesis that a denser population per leaf results in an increase in the proportion of winged adults, while a lighter population per leaf results in an increase in the proportion of wingless adults. This hypothesis is supported by the population tallies recorded in Table 2, which follows:

PROPORTIONS OF SEXUPARA TO PROGREDIENS APTERA

Tally of the populations on the leaves of sample shoots taken from the crown of a fourteen-years old *Abies alba* moderately infested by *Adelges nüsslini.*

TABLE 2.

Column	A	B	C	D	E	F	G	H
No. of shoot	Position in crown	No. of leaves per shoot	Original pop. of neoprogs.	Identified sexuparae	Identified progs. apterae.	Identity not determined	Neoprog. pop. per needle	Ultimate ratio of sexup. to progs. apterae
						C—(D E)	C/B	D/E
1	Upper	205	2,086	928	64	1,094	10.16	14.46
2	Upper	192	1,060	410	24	626	5.51	17.08
3	Upper	194	942	327	36	579	4.85	9.07
4	Middle	66	283	106	24	153	4.29	4.42
5	Middle	144	425	81	23	321	2.95	3.52
6	Middle	178	504	72	78	354	2.83	0.92
7	Upper	198	558	103	70	385	2.82	1.47
8	Middle	160	364	76	21	267	2.27	3.62
9	Lower	112	181	23	112	46	1.62	0.21
10	Lower	50	31	1	15	15	0.62	0.07

In Fig. 6, column G is compared with column H; this shows graphically that the density of population per leaf has a direct effect upon the ratio of sexuparae to progredientes apterae. In Plate 51, where shoots A, B, C and D correspond to shoots 2, 3, 9 and 10 in Table 2, the comparative production of progredientes apterae is well illustrated.

These tallies were based on shoots exposed to the normal conditions of the field, where predation takes place at a high rate. Of necessity the enumerations must be done in the restricted period at the end of June, when the sexuparae and progredientes can be differentiated most easily. Even at this optimum period however, it was possible to distinguish the separate identity of only one-third or one-half of the original population of settlers on the needles of each shoot. As a result of heavy predation, unfavourable weather and the flight of sexuparae, only a small proportion of the original population was still living at the end of June. However, presence of nymphal exuviae helped to give almost a complete account of the sexupara population, and the presence of wool on 3rd, 4th and 5th instar progredientes aptera, both dead and living, similarly led to a representative

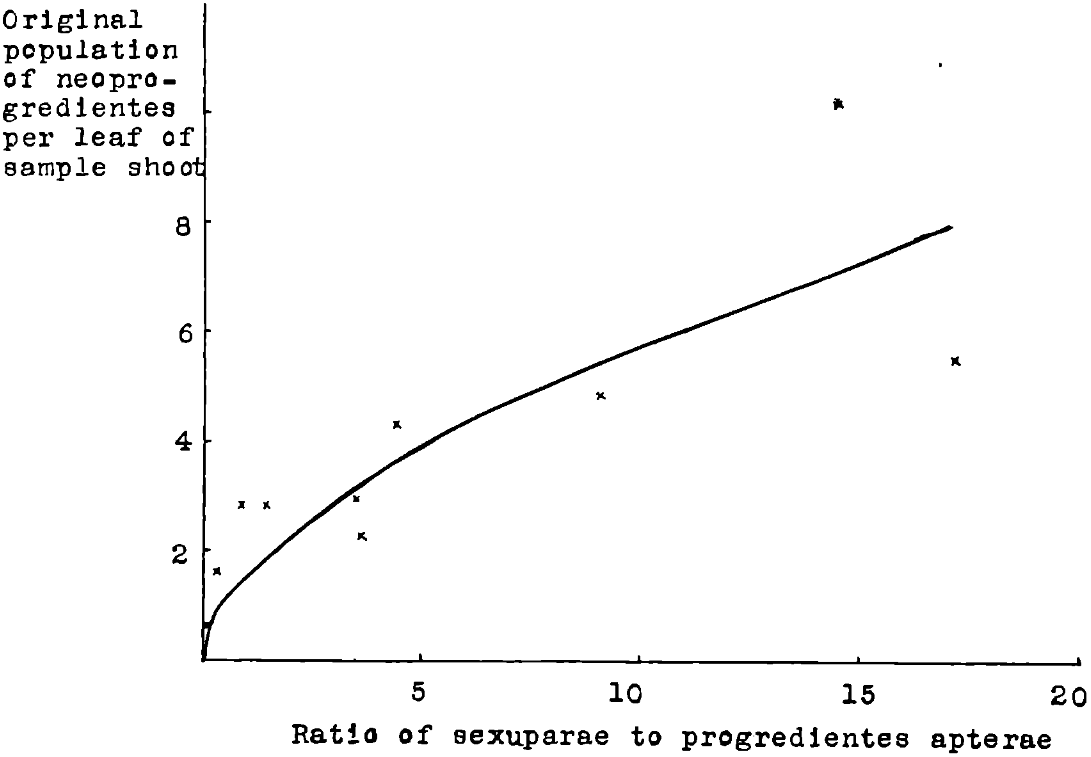

Figure 6. Curve showing the rise in the proportion of winged to non-winged progredientes of *Adelges nüsslini* with increasing density of population on the leaves of *Abies alba* (based on Table 2).

enumeration of the form. Nevertheless it is acknowledged that these counts are not completely accurate.

These data are not considered sufficient to be entirely conclusive. The further proof of the density hypothesis must await experimental infections of young trees in the greenhouse, where controlled densities of population and the minimum interference from predators and weather could be assured.

Density of progrediens population per leaf is closely related to the nutritional status of the leaf. The chemical effects of feeding on the leaves will be discussed in Ch. 3 (p. 43). All that need be said at this point is that heavy feeding causes debility and chlorosis of the leaf, with a marked reduction in the contents of chlorophyll, of total nitrogen, and of most of the other mineral elements of the leaf. Therefore it seems probable that the production of sexuparae is in some degree the effect of partial starvation.

The phenomenon of higher production of alate forms under conditions of overcrowding is not confined to *Adelges nüsslini*. Davidson (56) has recorded that under the influence of low temperature, poor nutrition or high population densities, the black bean aphid, *Aphis rumicis* L., likewise tends to produce a higher ratio of alate to apterous individuals.

Migration of the Sexupara. The sexupara migrates from the Silver fir to the Oriental spruce. This was clearly demonstrated both naturally in the field and experimentally in the laboratory. In both 1952 and 1953, the flight period extended from the beginning of June to mid-July, with a peak in the second half of June, as shown in Fig. 5. The insect flies completely at random or under the influence of air movements, and finds its host only by accidental contact. In the Dunecht Forest Garden vast numbers of sexuparae were produced, but only a small proportion succeeded in finding the few Oriental spruces within the plot. A few individuals settled on the occasional Norway spruces; this species evidently satisfies the host-selection instincts in some measure. However, no sexuparae settled on a species of *Abies* or any other conifer, and it seems certain that no non-migratory winged individuals (progredientes alatae) are produced.

Having arrived on the host by chance, the selective powers of the sexuparae come into play. The great majority settle on the leaves of the current year's shoots, and only rare individuals settle on penultimate foliage. Each settled insect inserts its stylets in a needle, and within a day or two begins to lay eggs under cover of the wings. The fecundity of the sexupara, like the progrediens aptera, is low and the average size of clutch is only about ten eggs, laid in a week or a little longer. The largest clutch observed held only fifteen eggs. As oviposition proceeds short curly wax strands are secreted from the head and thorax, light wax wool envelops the eggs. (Plate 17). Meanwhile the soft weakly chitinised abdomen grows smaller and smaller until it is reduced to a small exhausted envelope. The sexupara dies less than two weeks after alighting on the spruce.

(5). Sexualis

In the extensive literature on *Adelges nüsslini* there is a paucity of detailed references to the sexualis generation. Only Nüsslin (117), Marchal (106) and Steven (146) have described the general outline of its development from original researches.

In 1952 and 1953 the development of the sexualis generation was observed on young Oriental spruce trees both in the field and in the greenhouse. At field temperatures the period of incubation of the eggs laid by the sexupara is about two weeks. Rare hatching of these eggs was observed in the first fortnight of July. The neosexualis is a small amber crawler which leaves the cover of the folded parent wings to wander apparently at random over the crown for a few hours or days before settling. Its rate of travel is much the same as that of the first instar forms of other generations; one neosexualis travelled thirteen inches over white filter paper in one hour. Unlike the neosistens or the neoprogrediens however, the neosexualis does not show any definite phototaxis or negative geotaxis. Certainly there is no marked movement towards the upper crown and leader. However, the neosexualis has one marked characteristic; it almost always chooses to settle on a leaf at the tip of the new shoot, often lodging among the appressed needles around the young forming bud, where it is particularly difficult to observe. Young shoots of Oriental spruce often retain the bud-scale cap at the distal end for several weeks after flushing, and it is under this hood that the crawlers often aggregate and settle.

Having settled, the neosexualis begins to feed at once and soon excretes a minute globule of honeydew from the anus. It also secretes minute wax flakes from the marginal glands. Thereafter the insect remains fixed on its leaf through the four larval stadia. In the course of development through four moults to the adult stage it changes relatively little in size or appearance, but the instar can be ascertained at any time by counting the number of exuviae to the rear of the abdomen. Finally male and female adults appear, but although dimorphic they can only be distinguished easily under the microscope.

The durations of the four larval stadia are recorded below.

Duration of Larval Stadia of the Sexualis
Table 3.

Stadium	*Mean No. of days*	*No. of individuals under observation*	*Range in days*
1st	5	7	4 — 6
2nd	3	5	3 — 4
3rd	3	14	2 — 4
4th	3	15	3 — 4

These data were drawn from observations on three small potted trees in the greenhouse; the average larval life is fourteen days. Under the lower temperatures of the open air it is probably a little longer. On one spruce at Dunecht ten neosexuales were tagged for observation of rate of development. Only one of these survived to maturity; its larval stadia were: 1st—five days, 2nd—four days, 3rd—four days, 4th—four days. In the field the rate of larval mortality is very great, as is explained in para. 6(2), p. 36.

The main phase of sexualis activity occurs in the month of July. The adults were first seen as early as the 8th July, reached a peak of abundance on the 20th, and were last seen on the 10th August. The duration of the adult stadium is not known precisely, but it is believed to be only a few days.

Adults of both sexes are active crawling insects which can be found on all parts of the tree crown in times of peak abundance. Like the active 1st instar, they do not appear to show preferences for any portion or aspect of the crown.

Marchal (106) found that females greatly exceeded the males in numbers. The writer is not able to absolutely confirm this observation, yet females did greatly outnumber males among the few adults mounted for microscopic examination. Mating was not observed in spite of careful observation, and it is probable that it takes place either at night or under cover of the old bud scales which form a sleeve at the proximal end of the new shoot. The fertilised female lays a large solitary egg under a small pad of fine wax wool and usually dies in situ near the egg. Oviposition takes place only under the bud scale sleeve. There is no evidence that the female ever lays more than one egg; by analogy with the sexualis of other *Adelges* species it can be assumed that a single oviposition takes place. Males were observed to succumb on all parts of the crown.

Thus the sexualis generation reaches fruition on the Oriental spruce, but little is known of its preferences for other species of spruce. It is possible that like the sexuales of *Adelges viridis* and *A. cooleyi* a number of species are suitable as hosts. In the greenhouse it was demonstrated that the sexuales of *A. nüsslini* may develop successfully on the Serbian spruce, *Picea omorika.* Twelve neosexuales were transferred to a two-plus-one transplant (three years old in all) on the 9th July, 1953. Six survived to become adults about two weeks later. No eggs were laid, but in view of the small number of adults and the corresponding possibility of the absence of males, it cannot be inferred that Omorikan-reared sexuales are infertile. At Dunecht, natural infections of Norway spruce by rare sexuparae always resulted in the abortion of the sexualis generation in the early larval stadia. Nüsslin (177) however, has recorded that adults of both sexes have been raised on Norway spruce, although fundatrix offspring did not appear to result.

The sexualis is the last of the successive pentamorphic generations which comprise the two-year life cycle of *Adelges nüsslini.* The larva which hatches from the large fertilised egg is the neofundatrix.

5. LIFE CYCLE OF ADELGES PICEAE RATZ.

(1). Sistens

The generations of sistentes. The sistens generations of *Adelges piceae* greatly resemble the corresponding stages of *A. nüsslini* in morphology, phenological development and such biological characters as the process of moulting and mode of feeding. The sistens of *A. piceae,* however, is typically found on the main stem of pole-stage and middle-aged Silver firs (Plates 56 and 57), although experimentally it can be induced to feed on the young shoots.

The spring generation or hiemosistens gives rise to a summer generation or aestivosistens. Typically only one generation of aestivosistentes is produced, but a few individuals developing early in the summer after a short diapause engender a second generation of aestivosistentes which matures in the autumn. Observations on the phenological occurrence of these successive generations were made on a number of *Abies* species both at Craibstone and in the Botanical Gardens, Aberdeen.

The Hiemosistens. The hiemosistentes arise from eggs laid by the aestivosistentes. They typically overwinter as first instars, rarely as later instars, lodging in close aggregations in favourable crannies and depressions of the bark. The end of hibernation and the initiation of feeding take place in late winter and early spring and are denoted by the excretion of a minute droplet of honeydew from the anus of each individual. The development of the hiemosistens thereafter depends to a large degree upon seasonal temperature and the warmth of the microclimate. In the normal year, it begins in early March, but its initiation varies greatly by individuals. This corresponds to variations in the favourability of the site of settlement. On the south-facing aspects of fairly shaded stems heated by filtered sunshine (but not by continuous insolation, which is lethal), development proceeded earlier and faster than on the north-facing aspects. The seasonal development of the generation as a whole is shown in Fig. 7.

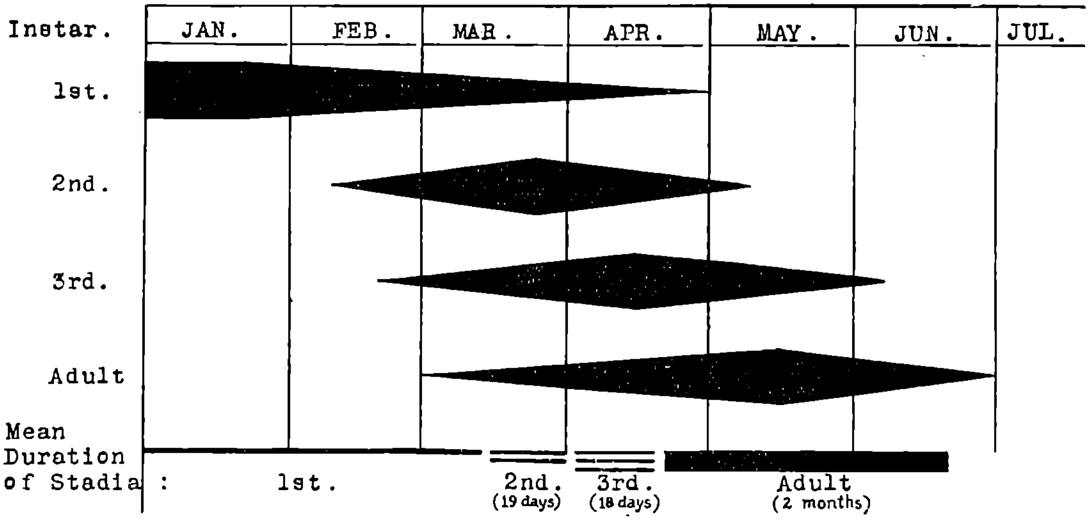

Figure 7. Seasonal development and proportions of the larval and adult instars of the hiemosistens generation of *Adelges piceae* on *Abies procera* under forest conditions in Aberdeenshire. The duration of the first stadium of the hiemosistens may be 3-9 months.

The developing insect remains on the same spot throughout the rest of its life. Three larval stadia precede the adult stage and consequently three moult skins accrue to the rear of the adult. The durations of the larval stadia averaged over a number of tagged individuals distributed on all aspects of the stem are shewn below.

DURATION OF THE STADIA OF THE HIEMOSISTENS

TABLE 4.

Stadium	*Mean duration in days*	*No. of individuals under observation*	*Range in days*
1st (feeding phase)	14	36	7 — 35
2nd	19	32	8 — 28
3rd	18	27	6 — 27
Adult	28	25	1 — 52

In 1952 and 1953 the final moult phase giving rise to adults reached a peak in the second half of April. The adult is capable of living for two months, but on account of heavy predation rarely survives so long. The adult begins to oviposit about a week after its ecdysis. The rate of oviposition tends to follow a normal curve but is greatly influenced by variability in temperature. While the fertility of the hiemosistens may be in the region of 300 to 400 eggs, in practice few adults laid more than 150 eggs, because of predation. The largest counted clutch contained 98 unhatched eggs.

In 1953 the first eggs were seen as early as 6th March. Two weeks later clutches of ten were not infrequent (Plates 29 and 30). Clutches of unhatched eggs reached their peak size in mid-May when batches of 60 were ordinarily present. By the end of June, however, only very small unhatched clutches could be seen and oviposition had virtually ceased. July is in fact a relatively quiescent month when the hiemosistentes are dead and most of the aestivosistentes are in diapause as first instars.

The Incubation of Eggs Laid by the Hiemosistentes. The length of the incubation period for these eggs varies according to temperature. In general it is true to say that an egg laid in April requires a longer period of incubation than one laid in May, but of much more importance is the microclimate of the site in which the egg lies. Thus an egg laid in a clutch laid on the south-facing side of a stem where it experiences filtered sunshine for a considerable period of the day hatches more rapidly than eggs on other sides of the stem, which are subject to sunlight for only a short period of the day. Similarly, eggs on the lower part of the stem hatch more rapidly than those nearer the crown where the shade is complete.

A knowledge of the duration of incubation under given circumstances is essential to the calculation of

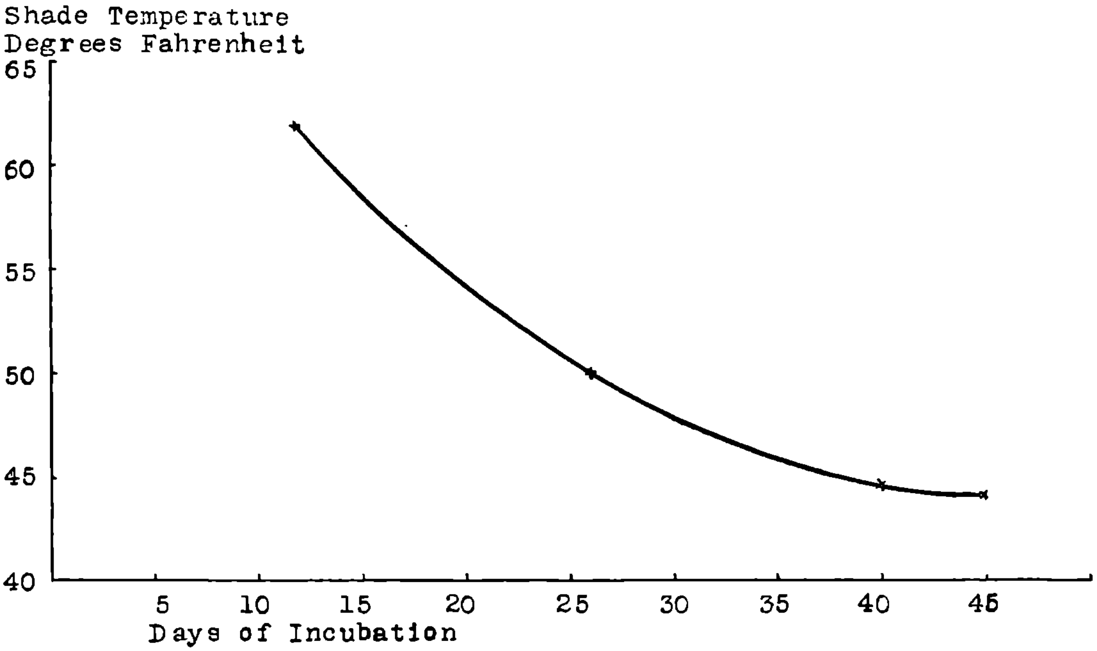

Figure 8. Rate of hatching of eggs laid by hiemosistentes of *Adelges piceae* on the main stem of *Abies procera.*

total oviposition by periodic counts of egg clutches. Accordingly the rate of incubation in relation to heat has been graphed in Fig. 8. It shows that under the most favourable circumstances, incubation may be as short as ten days, but under cold moist conditions several weeks may be required.

Behaviour of the Neosistentes. Neosistentes, derived from hiemo- and aestivosistens parents, can be found crawling on the host at almost all times of the year from April to November inclusive. The neosistens is a minute, active, amber-coloured crawler, well equipped for sensory functions and evidently motivated by a number of complementary instincts in its search for a place to settle.

The behaviour of the neosistens was observed on the main stems of pole-stage *Abies* of various species in the field, and on potted plants in the greenhouse. The preferences of the crawler for diffuse light and moderate warmth are clearly expressed in the disposition of populations on the main stems of trees in the forest. On lightly shaded stems there is a decided preference for the southern face which receives the maximum sporadic and filtered sunlight. On deeply shaded stems populations do not develop at all. On fully insolated stems the northern shaded aspect is overwhelmingly favoured. In this last case the continuous bright sunshine and high bark temperatures to which the southern face of the stem is subjected on hot summer days deter active crawlers and kill any which have already settled thereon in cooler, cloudy weather. This sensitivity to light also prevents the crawler from climbing up the heavily shaded middle stem to infest favourable parts of the outer crown.

The instinct of negative geotropism is probably the weakest reaction, although undoubtedly it may be asserted. In eastern Canada the writer has seen the aggregation of *Adelges piceae* neosistentes on the upper whorls and leaders of young Balsam firs, after a fashion comparable to the infestation of young Common Silver firs by *A. nüsslini* in Britain.

A sensitivity to the accessibility of the young parenchymatous tissues of the host is expressed in the settlement of the neosistentes on any part of the tree. On the main stem favoured sites are the crannies and crevices of the bark, lenticel aggregations, nodal rings, and the callus growth around old wounds (Plates 56 and 57). On young shoots the vicinities of the buds are preferred (Plate 58). In the final choice of any site, stereotropism may be the deciding factor.

The Generations of Aestivosistentes. The crawler progeny of the hiemosistentes is abundant in the field from early May to mid-June, although some individuals can be found a month in advance and in retard of this period. They settle, insert their stylets, and enter diapause without feeding. Unlike the neosistens of *Adelges nüsslini* the period of diapause does not extend until the following spring, but is concluded in the same summer.

The development of the aestivosistentes was closely observed on young potted trees in the greenhouse. Under such warm conditions two generations of aestivosistentes were induced during the summer. Members of the first generation were present from May to September, and members of the second generation from August to November. Their developmental periods were thus overlapping, and the generations were differentiated by appropriate experimental infections of clean trees.

In the case of the first summer generation, the earliest of the neoaestivosistentes broke diapause about three weeks after settling, but typically this resting stage lasted for five to ten weeks. Thereafter the neosistens fed for about a week before undergoing the first moult. The second and third stadia each lasted about five days, and the adult stadium up to five weeks. The fecundity of these adults of the first generation is low, usually 10 to 20 eggs.

The crawlers hatching from these eggs settled in the same manner as those of the preceding generation and entered diapause. The majority hibernated until the following spring. The minority, about 30 per cent. remained in diapause for a relatively short period, five to twelve weeks, after settlement. Their development through three larval stadia corresponded closely to that of the first generation of aestivosistentes, but adults were more fecund and laid 20 to 40 eggs. From these eggs neohiemosistentes arose which hibernated over the remainder of the season and following winter.

Yet another aestivosistens generation was induced in the greenhouse, and contributed to the final build-up of neohiemosistentes at the end of the season. These were the offspring of the progredientes apterae, and rarely of progredientes alatae. The eggs laid by the progredientes hatched in May, and produced neoaestivosistentes which settled and entered diapause. The minimum period of diapause was five weeks, the maximum eighteen weeks, and accordingly developing aestivosistentes could be found at all times from mid-July to early November. Each individual passed through three larval stadia and became an adult capable of laying 30 to 40 eggs.

Thus in the greenhouse, the factors operating in 1953 to produce the neosistens population at the end of the season were:

(i) the neohiemosistens offspring of the first aestivosistens generation.
(ii) the offspring of the second aestivosistens generation.
(iii) the offspring of the aestivosistens generation derived from progrediens parents.

This series of generations is shown diagrammatically in Fig. 2.

In the field the cycle is less complex, since essentially only one generation of aestivosistentes is produced. Hatching from eggs laid by hiemosistentes, the neoaestivosistentes settle in large numbers between mid-May and mid-July. The shortest period of diapause is about a month.

In 1953, two per cent. of all these settlers had become adult aestivosistentes at the beginning of July, and about twelve per cent. by the end of the month. By the end of August 50 per cent. had become adult; the remainder reached maturity at various times up to the end of October. By mid-November the aestivosistens phase was virtually over, but the population of neohiemosistens in hibernation was at a maximum. The typical aestivosistens lays 20 to 40 eggs. It was found that members of the second generation of aestivosistentes are occasionally produced in forest conditions, but the proportion was not established; however, it is believed to be small.

(2). Progrediens

Occurrence of the Generation. The progrediens generation of *Adelges piceae* corresponds in general development to that of *Adelges nüsslini*, giving rise to both alate and apterous adults. However, in function the winged individuals of the two species differ, since the progrediens alata of *Adelges piceae* flies to another Silver fir, while the sexupara of *Adelges nüsslini* migrates to the spruce.

The progrediens generation is abortive in the forests of N.E. Scotland, and probably elsewhere in Britain. Chrystal (47) has noted its absence at Kew Gardens, but Marchal (106) and Balch (7) have reported its rare natural occurrence in Northern France and in New Brunswick, Canada, respectively. The reason for the failure of the generation in Aberdeenshire forests is the imperfect synchronisation between the phenological development of the host and that of the insect. The neoprogrediens can only develop when newly-flushed leaves are available for settlement. In the field the newly-hatched crawlers are present in small numbers from the end of March until the beginning of May. However, in the normal year in Aberdeenshire the new shoots of *Abies* species do not appear until the second half of May. Consequently all the neoprogredientes die of starvation. There is evidently a considerable discrepancy between the temperature thresholds for oviposition by the hiemosistens, and for the flushing of *Abies* spp. Table 21 (Appendix 1) shows that in the average year at Aberdeen the mean shade temperature for mid-April, when the population of neoprogredientes reaches its peak, is 5° F. lower than the mean shade temperature for mid-May, when the flushing of *Abies* species takes place.

Neoprogredientes are produced only from the first few eggs laid by the hiemosistentes in spring. All the other eggs of each clutch become neosistentes. Early-maturing adults give rise to the largest proportion of neoprogredientes, but even so it is probably less than five per cent. of the total clutch laid. Late-maturing adults appear to give rise to a much lower percentage of eggs hatching into neoprogredientes. It is not unlikely that the early nutrition of the parent has some influence in the determination of the progrediens/sistens ratio as Gregory (78) and Wadley (152) have shown in the cases of other insects with a variable alate/apterous form ratio.

Development of the Progrediens. Experimentally, these divorced thresholds of development were drawn together by forcing the flushing of potted *Abies* trees in the warmth of the greenhouse and subsequently infecting the young shoots with early egg clutches taken on infested forest trees. In this way young trees of *Abies alba*, *A. grandis*, *A. concolor*, *A. procera*, and *A. veitchii* were brought into new leaf between early March and early April, at least six weeks ahead of normal flushing. Accordingly they were capable of acting as hosts to the progredientes, which developed on all species with equal facility.

These young trees were infected by tying pieces of bark bearing clutches of unhatched eggs to the foliage. In such infections, 500 to 1,000 eggs in small clutches of one to twenty eggs, were placed on the tree. Infections made between 31st March and 11th April, 1953, produced small populations of progredientes on the trees. Reinforcements added in early May resulted in virtually no increase in the progrediens population, only in neosistentes.

The neoprogredientes settled mainly in the upper portion of the crown. Each crawler fixed itself on the under side of the new leaf, and inserted its stylets, usually but not invariably in the vicinity of a stoma. Each proceeded through four ecdyses to become adult, but could be distinguished towards the end of the third stadium as either the alate or the apterous form. The development of tagged individuals on *Abies alba*, *A. grandis* and *A. concolor* was observed in the greenhouse during April and May; the duration of successive stadia is recorded in Table 5.

Thus in the warmth of the greenhouse the average larval life from hatching is about a month, but individually it may be as short as 24 days or as long as 40 days. In general the duration of the larval period appears to be shorter in the case of the winged form and longer for the wingless form.

In the field one neoprogrediens was taken from the main stem of *Abies veitchii* as early as the 23rd

PROGREDIENS APTERA AND PROGREDIENS ALATA: DURATION OF LARVAL STADIA AT THE BOTANICAL GARDENS, SPRING 1953

TABLE 5.

Stadium	Mean No. of days		No. of individuals under observation	Range in days
	P. alata	*P. aptera*		
1st (not differentiated)	8	8	11	5 — 14
2nd	7	—	3	7 — 8
„	—	9	5	6 — 14
3rd	5	—	3	5 — 5
„	—	7	6	5 — 8
4th	8	—	7	4 — 12
„	—	10	7	7 — 15
Total days	28	34	—	—

March, in 1953. On the potted trees in the greenhouse, neoprogredientes were observed throughout April and early in May decreasing abundance. The first alate adult was seen on the 23rd April and the first apterous adult about a week later. The peak production of adults occurred in the first fortnight of May, and by the end of the month the progrediens phase had almost closed.

The progrediens aptera adult remains fixed on the underside of the leaf. The average duration of its stadium appears to be two to three weeks, during which a small clutch of eggs, rarely exceeding twelve, is laid under a mass of wax wool. On the other hand the progrediens alata, as Marchal (106) discovered, flies away from the host as soon as its wings have hardened, but settles later on a Silver fir host. Experimentally this was difficult to demonstrate, since relatively few winged adults were produced and many of these perished on the sides of cages or were ensnared on spiders' webs in the corners of the greenhouse. The first caging experiment to determine the selectivity of the alatae for species of *Abies alba*, *A. grandis*, *Picea orientalis* and *Picea sitchensis* failed completely since all the insects died without settling. In a second experiment in which young potted trees of *Abies alba*, *A. grandis* and *A. concolor* were offered, only two alatae settled. Both elected to fix themselves on the underside of a young leaf of *A. grandis*, but only one proved fecund. It secreted slight wool and layed two eggs in three days beneath the folded wings.

The crawlers which hatch from the eggs laid by progredientes apterae and progredientes alatae are typical neoaestivosistentes which immediately settle in diapause on the stem or twig and in due course become adults during the summer or autumn. However, they differ in their inheritance from the ordinary neoaestivosistens derived from a hiemosistens parent, as Balch (7) and Marchal (106) have shown. The line of the descendants of a progrediens is marked by the much higher proportion of progredientes produced in subsequent spring seasons. Conversely it might be supposed that in each normal year the tendency to produce progredientes may diminish, since in each spring the generation is aborted through lack of fresh leaves. Yet it may be that every so often there occurs an abnormal or freak season, in which the first oviposition by the hiemosistentes is synchronised with the flushing of the *Abies* buds. In this way successful generations of progredientes, produced at long intervals over the years, might maintain the hereditary tendency to produce neoprogredientes in the subsequent generations of hiemosistentes.

6. POPULATION LEVELS OF ADELGES NUSSLINI AND A. PICEAE, AND NATURAL CONTROL

(1). Population Levels

Fluctuations in population level. Like many other aphids, the Silver fir Adelgids exhibit perennial fluctuations in the level of population in any one district, probably in response to variations in local climate. Little is known about these movements because of the difficulties in making population surveys of these insects over long periods of years. Various writers have referred casually to years of high level and years of low level of population, but none has shown any trend over a considerable period. Schneider-Orelli (136) over many years of study in Switzerland has noted sporadic outbreaks and reductions in the incidence of *A. nüsslini* in certain districts, but can give no evidence of periodicity of their occurrence. Hofmann (84, 85) has made similar observations in the Palatinate of Germany.

In the case of a single stand of *Abies alba* infested by *Adelges nüsslini* the population reaches its peak or recurrent peaks, usually at epidemic level, in the first twenty years of the rotation. Thereafter it recedes gradually until it reaches a very low endemic level in the mature crop. The probability is that it never entirely disappears, so that when the succeeding crop is regenerated under an over-canopy of old trees, a new outbreak on the young growth is likely to take place. *A. piceae* is probably equally persistent at a low endemic level on old Silver firs, but the highest densities are reached when the crop is 25 to 50 years old.

On any single tree there may be one or several peaks of abundance of the Adelgid during this favourable period of growth. Observations on both insect species have shown that typically there is a very rapid rise in population following the first infection of the Silver fir during this vulnerable stage. At the peak of this rise the tree may die; if it survives, the decline in population may be slow or rapid according to the favourability of the nutritional and climatic environment which in succeeding years is accorded to the insect. Schneider-Orelli (136) found that trees which had survived a heavy attack could again experience heavy infestation after years of quiescence.

In the upsurge of a high population, the physiological condition of the tree rather than its absolute age is the controlling factor. For example, at Monaughty Forest, thirty-four-year-old Common Silver firs have maintained a moderate level of population of *A. nüsslini* because they are in the physiological condition of much younger trees; many are still only two to three feet tall and are kept in a state of perennial suppression by the pest and possibly frost. Normal trees of this age are in the pole-stage and have passed the phase of liability to epidemic infestation. The nature of the relationship between the growth stage and population density is not understood. Other aspects of the problem of fluctuation in population, such as climatic and biotic factors, are discussed in succeeding sections.

Biotic Potential. Both *Adelges* species are characterised by an enormous biotic potential. In *A. nüsslini*, the increase of the population on the Silver fir takes place essentially by the annual parthenogenetic reproduction of hiemosistentes. The supplementary effect of aestivosistentes, progredientes apterae and gallicolae can be disregarded. The high fecundity of the hiemosistens would lead theoretically to enormous multiplication of the Silver fir population in a few years. For example if each hiemosistens produced 100 neosistens offspring, then after three years the third generation progeny of a single adult would total 100^3 (i.e. one million) in the absence of restraining forces. In the case of *A. piceae* the biotic potential is even more remarkable, partly because a complete generation of aestivosistentes is incorporated each year and partly because the offspring of the hiemosistentes are all retained on the secondary host, and its powers of reproduction are not wasted on the reproduction of sexuparae. Thus, if each hiemosistens were capable of producing 200 offspring, and each aestivosistens 30 offspring, then after three years the final population of progeny from a single original hiemosistens would total $6{,}000^3$, (i.e. 216,000 millions). These simple calculations have no practical significance, but do illustrate how it is possible for epidemic populations to arise over a few years, provided environmental resistance is somewhat reduced.

In every outbreak the actual densities of these two species are very great. For example, the stratified sampling of the population of *Adelges piceae* on a single stem of *Abies grandis*, 16 inches in diameter at breast height and only moderately infested, gave a tally of almost half a million neosistentes. Similarly, *A. nüsslini* may build up huge populations on the crowns of smaller trees, or on the main stem of pole-stage trees. Only when very large numbers are present does the Silver fir suffer serious injury. On the Oriental spruce, the population level of the various generations always remains very low in north-east Scotland. This is partly accounted for by the relatively low fecundity of the sexuparae and sexuales, but the main reason is the failure of these generations in the face of the biotic and climatic factors of environmental resistance.

(2). The effects of climate on populations

Temperature. Temperature appears to control in large measure such phases of the life history of each species as the incubation of eggs, the settlement of crawlers, the duration of diapause and the onset of development, the rate of larval growth and the rate of oviposition. Variations from normal seasonal temperatures may cause considerable displacement of the seasonal appearance of the various forms. Thus in the exceptionally warm autumn of 1953, the diapause of both neosistentes and neofundatrices of *Adelges nüsslini* ended in October, and when the truly cold weather came the entire population was already in second and third stadia.

Most investigators are agreed that relatively warm years tend to produce an increase of population, while cold years tend to reduction. This is probably the effect of increased reproductivity rather than the effect of reduced environmental resistance, in the warm years.

Frost has no marked effect on the level of *Adelgid* population on Silver firs in north-east Scotland. There is no evidence of unusual mortality among larval or adult hiemosistentes of the two species, following late or early frosts. Low winter temperatures with as much as 12° F. of frost appear to be equally ineffective. Thus the premature development of sistentes of both species in Autumn 1953 did not result in any definite reduction in population during the winter which followed. Balch (7) has concluded from observations in New Brunswick, Canada, that neosistentes of *Adelges piceae* perish at temperatures below —30° F., but that down to this level they are highly resistant to cold.

It is possible however that late frosts may aggravate the injurious effects which neosistentes of *Adelges nüsslini* cause on the Common Silver fir. Professor H. M. Steven has informed the writer that a frost in the late spring of 1946 killed a considerable proportion of the new shoots of young Silver firs in the Dunecht plot; thereafter the incidence of injury to the young crop by *A. nüsslini* appeared to rise sharply. Any of a number of other factors could have been responsible for this rise in population density, but the most probable cause is that frosting of the new shoots caused relative crowding on those which survived. When a small tree is frosted after flushing the leader and uppermost whorl typically escape death. Consequently vast numbers of the crawlers which subsequently hatched, would be compelled to settle in concentration on these surviving shoots, and in this way a relatively small population could cause much heavier damage than would be inflicted in a normal year by the same number of insects per tree.

Summer insolation of infested stems probably has little effect on the absolute population of *Adelges* per tree. However, this summer heat can cause characteristic distributions of the stem-dwelling population according to whether the southern face of the stem is warmed by sunshine filtered through a low crown or heated by direct insolation. The enumeration of the populations of neosistentes of *A. piceae* on two moderately infested trees at Craibstone illustrate the mode of distribution in relation to sunlight. In Table 6, the tree No. 1 had a main stem partly shaded by a deep crown. The main stem of tree No. 2 was almost completely unshaded. Both trees were about 30 years old and of similar size. Populations were counted by stratified sampling of the lower three to seven feet, but tallies have been reduced to density per standard square inch of stem bark.

POPULATIONS OF ADELGES PICEAE NEOSISTENTES PER SQUARE INCH, ACCORDING TO THE ASPECT OF THE STEM FACES

TABLE 6.

Tree No.	1.	2.
Species	*Abies procera*	*Abies grandis*
North	52	184
West	55	168
South	429	22
East	131	115
Date of enumeration	mid-July	mid-July

No doubt these contrasting distributions are caused mainly by the movement of the crawling neosistentes in reaction to heat and light. The intense heat on the southern face of the unshaded stem has a lethal as well as a deterrent action against the neosistentes, as Balch (7) has experimentally shown in the case of *Adelges piceae*.

Wind. The chief effect of wind is the dispersal of the insects within a stand and the spread of infection throughout suitable regions. The insects may become airborne as eggs, first instars or winged adults. Wind, being a random agent of dispersion, is responsible for huge losses of these stages. Experimentally this was proved by placing glass slides, smeared with vaseline, in various places on the perimeters of the Dunecht and Craibstone plots; relatively large numbers of eggs and neosistentes of each species were intercepted in this way. Equally the mortality among the sexuparae of *Adelges nüsslini* must run at a similarly high rate, in view of their random flight and poor searching powers. Johnson (90), in a recent study of aphid migration in relation to weather, states that aphids have no control over their direction of flight at wind speeds exceeding two to three miles per hour and this is certainly the case with winged Adelgids, which are the smallest and weakest of all the Aphidoidea.

Nevertheless, because of their high biotic potential, Adelgids can well afford these losses in the course of winning establishment on other trees by successful migrants. Within any stand, the spread of infection commonly takes place by wind, although the wandering of crawlers across the interlocked crowns of neighbouring trees is no doubt a contributory factor.

The spread of these species over whole states and regions may also have taken place by the agency of wind, but in Britain this means was probably secondary to the distribution of transplants from infested nurseries. In the Maritime Provinces of Canada, as Balch (7) shows, the dispersion of *Adelges piceae* by wind has proceeded at a rate of several miles per year; it is not unlikely that the presence of the species on Balsam fir in Newfoundland, some 70 miles from the mainland, has resulted from its aerial carriage across the sea.

Rain and Humidity. In the literature on the natural control of Adelgids it is generally agreed that increased rainfall causes a marked decrease in the population level. Schimitschek (131) considered that the rate of precipitation in the months March-June was the critical factor for the density of *Adelges nüsslini* in Silver fir stands in the Palatinate, Germany. Wimmer (155) observed that the insect was not present in the highlands of the Black Forest, and claimed that it is unable to persist on north-facing slopes with more than 1,100 mm. of rainfall. Hofmann (85) stated that steady rainfall in the summer months is fatal to the neosistentes of *A. nüsslini* in diapause. Till (147) from observations in Hungarian forests concurs with this opinion. However, Balch (7) the only investigator to attempt experimental work on this problem was unable to show that rainfall had any effect on the stem population of *A. piceae*, other than the washing away of eggs.

The writer is able to offer tentative support to Hofmann's claim that the neosistens is the stage least resistant to steady rain or high humidity. In August, 1952, and September, 1953, following several days of prolonged rain, there were unusually large numbers of dead neosistentes of each species at Dunecht and Craibstone respectively. Rainfall data (Table 22, Appendix 1) show that these were unusually wet months, and the inference is that high humidity or actual drowning caused this mortality. Similarly in the wet spring of 1953, a larger number of larval progredientes perished than in the dry spring of 1952. In all generations the instars which produce a thick covering of wax wool appear to be least affected by rain.

There is a strong possibility that rainfall is a major factor in the remarkable decimation of the sexualis population on the Oriental spruce. It has been observed that the neosexuales have a marked tendency to settle near the tips of new shoots on all parts of the crown. In these new shoots, particularly at the tips, large globules of rain water collect and persist long after the rain has stopped, owing to the sponge-like effect of the close radial arrangement of the leaves. A large proportion of the sexuales in all stages appear to drown in this rainwater, probably because of their minute size and lightness of their wax secretion. Some shoots retain the bud-scale cap over the tip of the shoot for many weeks after flushing. Under the protection of these bud-scale "umbrellas", the sexualis population remains constantly high during the period of development.

To test this hypothesis, a windolite tent was rigged over Oriental spruce No. 1 (Plate 42) in June 1953, to protect it from rain, while Oriental spruces Nos. 2 & 3 were left exposed to the rain. Following the flight of the sexuparae, a roughly similar number of eggs was laid on each tree, and very large populations of neosexuales resulted. In the course of their development the density of population on all three trees was drastically reduced. Nevertheless, in spring 1954, 88 galls developed on the protected Tree No. 1, but only 13 and 18 were produced on Trees No. 2 & No. 3 respectively. This affords confirmation that rainfall is one of the factors involved in the reduction of the numbers of the sexualis generation.

(3). Biotic factors

Birds and Mammals. Predatory animals and the resistance of the tree itself constitute the biotic factors of the environmental resistance to the increase of *Adelges* population. Only the predators will be discussed in this section.

Adelgids are too small to be keenly sought after by birds and mammals. With the exception of Ruedi's (130) observation that breeding tits eat *Adelges nüsslini*, there is no definite reference to birds in a predatory role. In the writer's experience in North-east Scotland, there are no birds seeking Adelgids as food in spite of a very varied avifauna of the mixed farm-forest land. Equally no mammals have been seen to predate upon the Silver fir *Adelges*, although Jensen (89) has established that in Denmark squirrels open the galls of *A. abietis* to devour the gallicolae.

Insects and Arachnids. The insects and arachnids which predate upon members of the Adelginae are general feeders which exhibit no marked preference for the consumption of any one species more than another; indeed they feed with equal facility on most other small aphids such as *Neomyzaphis abietina*, and perhaps on the weaker instars of many other insects. This non-specificity is important in the maintenance of high populations of predators; these density-dependent insects can move to other prey at those times of the year when desirable stages of *Adelges nüsslini* and *A. piceae* are not abundant.

The literature on the European predators is large, and a review of all the references is beyond the scope of this bulletin. In general, authors have listed various ladybirds, hoverflies, lacewings, Capsid-bugs and Anthocorids among the Insecta, and mites, harvest-men, and hunting and web-spinning spiders among the Arachnida. Parasitism of Adelgid species has been quoted but not substantiated. Of the publications by British writers, Laidlaw's (96, 98) studies of *Aphideita* (*Aphidecta*) *obliterata* L. and certain Anthocoridae predaceous on *Adelges cooleyi*, have been found valuable because they relate to Scottish conditions.

The application of biological control by introducing exotic predators is feasible but not promising. In E. Canada, the European Syrphid *Leucopis obscura* Hal. was successfully introduced in 1933, and has given an increased measure of control of *Adelges piceae*, although still inadequate. In 1951 at Fredericton, New Brunswick, the writer witnessed the first liberation of the minute Derodontid beetle, *Laricobius erichsoni* Ros. from France, as a further promotion of biological control, and preliminary reports of its establishment have been favourable.

Franz (74) has recently discussed the considerable value of this beetle in Europe as a means of biological control.

In North-east Scotland the predators play an important role in the reduction of the populations of both *Adelges nüsslini* and *A. piceae*, but their influence is restraining rather than controlling. In general these predators were most abundant on Silver firs in June and July, and accordingly were more effective against the progrediens generation of *A. nüsslini* than against any other. All instars of *Adelges* are eaten but neosistentes in diapause are much less sought after than growing larvae, adults and eggs. Predators are probably a very effective agent of control against the sexuales and other generations on the spruce. The dense populations of *Adelges* on the Silver fir induce correspondingly high densities of predators, especially in early summer. The latter spread to the Oriental spruces; there the low biotic potential of sexuparae and sexuales is inadequate to offset the losses inflicted by the disproportionately high population of predators.

The insects which have been seen to prey on *Adelges nüsslini* and *A. piceae* in North-east Scotland are listed as follows.

Coleoptera. The ladybird *Aphideita obliterata* is outstandingly the most effective predator. On young trees infested by *Adelges nüsslini* this *Aphideita* is abundant from the end of April until the end of June; on stems infested by *Adelges piceae* it is abundant until the end of October. The larval and adult individuals feed on all instars of the *Adelges*, but show some preference for the eggs. Ironically enough, adult ladybirds have been found to take shelter over the winter within the cavities of dried galls of *Adelges viridis.* A number of other Coccinellid species were found in a predatory capacity, but their frequency is always much lower than *Aphideita.* These include *Anatis ocellata* L., *Idalia decempunctata* L., and *Myrrha octodecimguttata* L. To this list might also be added those observed by Laidlaw (98) feeding on *Adelges cooleyi* in Aberdeenshire, namely *Coccinella septempunctata* L., and *Paramyzia oblongoguttata.* No other predatory beetles have been observed, but Crooke (54) has recorded that a number of Staphylinid species feed on *Adelges viridis* on larch in Scotland.

Diptera. The Syrphidae is also a most important aphidivorous family. In Aberdeenshire there is a large number of species which as larvae feed on *Adelges* in all instars. Only one of these has been bred through to the adult stage and identified, namely *Episyrphus cinctellus* Zett., which was commonly found feeding on the progredientes of *Adelges nüsslini.* Hoverfly larvae are most numerous in early summer, but have been found at all times from March to October on infested trees.

The orange-coloured larvae of a Cecidomyid species were found feeding on the progredientes, notably nymphal sexuparae, of *Adelges nüsslini*, but adults were not obtained for determination of identity.

Neuroptera. Probably a considerable number of Hemerobiid species are active predators on *Adelges* species in North-east Scotland, but only *Hemerobius humulinus* L., *H. lutescens* Fabr., and *H. simulans* Walker were identified on the Silver fir, where they fed on the progredientes of *Adelges nüsslini.* To this list can be added *Hemerobius stigma* Stephens and *Kimminsia subnebulosa* Stephens, which Laidlaw (97) found to feed on *Adelges cooleyi* in Aberdeenshire.

Hemiptera. Two members of the family Anthocoridae, *Tetraphleps bicuspis* Herrick-Schaeffer, and *Acampocoris alpinus* Reuter, have been frequently found feeding on *Adelges nüsslini* and *A. piceae* in Aberdeenshire. These, the earliest of the predators in each season, have been seen actively feeding as early as 12th March, when only larval sistentes are available. They are most abundant in mid-summer. Laidlaw (96) also recorded the species *Anthocoris nemorum* L. for Aberdeenshire.

Arachnida. It is believed that Arachnids predate extensively on Adelgids but actual observations of their feeding have been infrequent. In June, the apical twigs of young Silver firs become festooned with spiders' webs in which large numbers of winged sexuparae and airborne crawlers are trapped and die. Phalangids in small numbers were observed to visit infested shoots in June but not to feed. Keller (92) has recorded that they feed on the egg masses and winged adults of the larch *Adelges.* Unidentified red mites were active on infested trees during the entire season. They were observed to feed on larval forms of *A. nüsslini*, and even each other. Their numbers were very large and their influence on the population level of *Adelges* is probably considerable. Minute pale brown mites, also unidentified, were found on Oriental spruce shoots wherever the sexualis population was high, but it was not certainly ascertained that they were predaceous.

Chapter 3

THE REACTION OF THE TREE TO ATTACK BY ADELGES NUSSLINI AND ADELGES PICEAE

1. THE GENERAL APPEARANCE OF THE ATTACKED TREES

(1). Attack by Adelges nüsslini

The symptoms of attack by *Adelges nüsslini* have been described and illustrated by almost all investigators of the species, and in Central Europe "tannensterben" or "Silver fir die-back" is a phenomenon well known to foresters. The form of injury on Common Silver firs in Scotland differs in no way from that occurring elsewhere in Europe. Young trees undergoing heavy attack show chlorosis and upcurling of the attacked shoots in the upper crown (Plate 60). The yellowing and kneeing of the leaf is accompanied by abbreviation of growth in all dimensions and a twisting or curling along its length (Plate 61). The attacked shoot develops a swollen twig, particularly at the proximal end where the neosistens population is most dense. In the spring following the first year of heavy attack, various reactions may take place:

(1) Very heavily attacked twigs may dessicate and die, the leaves turning brown and falling off; this frequently happens in warm dry springs, as in 1953, when the disrupted vascular system of the attacked shoot is unable to meet the water requirements of the shoot at a high rate of transpiration.

(2) The shoot may not die, but the buds abort and flushing does not take place.

(3) Late flushing takes place on the attacked portion of the crown, but the new shoots remain small and weak.

(4) In rare years, the neosistentes may die en masse, presumably as a result of climatic factors, and the flushing of the young shoots takes place normally. This rejuvenation has not been observed in Scotland, but it has been described and depicted by Hofmann (85) and Schneider-Orelli (136).

After the more severe effects of injury, the tree dies back slowly, as in successive years the population is maintained in lower portions of the crown. The tree may die entirely in two to four years, or it may persist at a low ebb for much longer. If it persists it may eventually develop a new leader and thereafter a new crown, which may yet produce a perfect tree. The stand at Dunecht contains groups of dead and dying trees, yet among them are trees with enough vitality to have developed secondary leaders. At Inverliever Forest, many trees heavily attacked and dying back 25 to 30 years ago, have now recovered and formed perfect crowns.

Experimentally, attack by *Adelges nüsslini* has been induced on leaves and twigs of other *Abies* species, but the available evidence is that many other species are not so susceptible to epidemic infestation. Further references to experimental infections will be made in this chapter.

On Oriental spruce, the injuries are so slight as to be negligible. The fundatrix may cause the abortion of the bud on a very weak shoot, and in any case the subsequent gall inhibits shoot elongation, but the spruce generations are rare. The formation of the gall, however, is of considerable academic interest.

(2). Attack by Adelges piceae

Adelges piceae is a less serious pest in Europe, and in general causes injury only in a secondary manner. Its presence on the stem is denoted by the appearance of white flocculent wool. Many species show patchy necrosis and increased blistering of the bark; others, such as *Abies procera* and *A. grandis* may exhibit a pathological resin flow from small wounds on the bark and even from areas where no apparent injury, except by the sistentes, is evident. The insect may also dwell on the young twigs, where it causes abnormal swellings on the buds and nodal areas of many species (not including *Abies alba*). The leaves of these shoots are never directly harmed since progredientes are so very rarely produced.

In general *Adelges piceae* is a secondary pest of little forest importance. However, on at least one species, *Abies balsamea* in east Canada, it is a primary pest causing extensive injury and mortality on trees of all sizes; young trees may be killed by bud deformation or 'gout', as Balch (7) terms it, older trees by heavy stem attack. A curious feature of the stem attack is the formation of compression wood or 'rotholz' in the sapwood. *Rotholz* is also formed in *Abies grandis* in Britain, and is further discussed in section 2(4), p. 42.

2. THE ANATOMICAL EFFECTS OF ATTACK

(1). Method of study

The writer's study of the anatomy of attacked tissues has been cursory and was undertaken partly to see whether any gross differences in structure could account for variations in susceptibility to attack, and partly to confirm the more elementary aspects of the detailed studies on the effects of attack by Chrystal (47), Francke-Grosmann (70), Balch (7) and Plumb (126). The work of these authors is reviewed but few new facts or controversial issues are introduced.

Sections were cut by hand, and by a rotary microtome, to a thickness of 0.01 mm. In the latter case the plant tissues were fixed in Carnoy's fluid, dehydrated in alcohol and embedded in paraffin wax. Sections were stained with safranin and light green.

(2). Anatomical Effects of the Feeding by Adelges nüsslini on Silver fir.

The reason for the die-back of the attacked shoots of *Abies alba* and *A. nordmanniana* has been explained by Chrystal (47) as an effect of the feeding by the sistentes. He found that the sistens inserts its stylets into the young twig and seeks out the zone of the cambium and conducting tissues. In this zone the stylets, running an intercellular course, are repeatedly withdrawn and reinserted in a much branched pattern of feeding. The track of the stylets is marked by a proteid sheath which develops in response to salivary secretions by the insect, and which remains in the tissue long after the stylets have been withdrawn. The feeding and complementary injection of saliva result in the inhibition of the normal cambial differentiation into xylem and phloem, which are replaced by abnormal parenchyma. In turn, the dislocation of the vascular strands along the length of the twig results in inadequate conduction of water and dissolved materials, so that the twig may ultimately dessicate. He also studied the effects of attack on the young shoots of *Abies grandis.*

Chrystal's work was confirmed and broadened by Francke-Grosmann (70) who studied the mode of feeding of *Adelges nüsslini*, *A. piceae*, and other aphids which contribute to the die-back of *Abies alba* in Germany. She considered that the Adelgid has two kinds of salivary gland secretions, one which causes the formation of the albuminous stylet sheath, and the other a hypothetical enzymatic material which induces the abnormal parenchyma in place of xylon and phloem. She also distinguished between the patterns of feeding by *Adelges piceae* and *A. nüsslini* (for which she preferred the name *Dreyfusia schneideri*) on the main stem of the older tree. The former feeds in the vicinity of resin canals, while the latter favours the storage parenchyma of the main stem bark. The stylets of neither can penetrate to the cambium, so that wood and phloem differentiate normally. In the case of attack on the leaves by *Adelges nüsslini*, feeding takes place on the conduction tissues within the endodermis, causing great injuries.

Some of the anatomical features described by these authors have also been found by the present writer. In the case of *Abies alba*, transverse sections of the current year's twigs attacked by neosistentes show partial or locally complete suppression of the xylem and phloem rings. They are replaced by giant cells along the track of the stylets, and by the hyperplasia of neighbouring parenchyma. These cells are characterised by their thick walls and dense contents, sometimes with tannin deposition. The proliferation of this abnormal tissue increases with density of population and with the development of the sistens through its stadia. As a result, the base of the shoot where the population is usually highest develops a considerable swelling.

The course of stylet penetration is usually between the walls of neighbouring cells, but in one section the stylets were found to pursue an apparently intracellular path (Plate 64).

Sections of the leaves of *Abies alba* attacked by progredientes show that typically the stylets seek out the phloem and parenchyma within the endodermis, but sometimes other parts of the leaf such as the spongy mesophyll appear to be attacked. Within the epidermis the effect of attack is a slight reduction of the phloem and xylem elements and the growth of a disorganised parenchyma. The vascular tissues do not appear to be ever completely eliminated. Elsewhere in the leaf the effects of attack are the inhibition of normal dimensional growth in cross section, the absence or malformation of the palisade tissue, the reduction in size and number of chloroplasts, and the appearance of necrotic zones of spongy mesophyll.

Sections of leaf and twig of young shoots of *Abies grandis* and *Abies concolor* show similar effects. The twig attacked by neosistentes shows hyperplasia and hypertrophy of abnormal parenchyma in place of vascular tissue. This accounts for the slight swellings observed along the length of the young twigs of both species, on which neosistentes had settled. This condition of the twigs developed in spite of the fact that the neosistentes on both host species perished in the first instar during diapause. The young leaves, which are freely attacked by progredientes of all instars, show modifications similar to those occurring in attacked foliage of *Abies alba.*

(3). Anatomical effects of Adelges nüsslini on Oriental spruce

The processes by which the spruce galls of Adelgid species are initiated and developed have attracted the attention of a very long list of investigators. Plumb (126) gives a very complete chronology of the literature on the research which has taken place. Most of these workers dealt with the formation of the gall of *Adelges abietis* or other larch-spruce species, but their work is relevant to the study of the gall of *Adelges nüsslini* on Oriental spruce. De

Geer (75) in 1773 made the first complete study of a spruce gall, that of *Adelges abietis*, and held that the fundatrix initiated gall development by inserting its stylets into the leaf rudiments within the bud. Leuckart (99) in 1859 found that the fundatrix stylets penetrate into the axis of the bud, not into the leaf rudiments. Winkler (156) published the first histological description in 1878. Dreyfus (60) took note of the difference between the characteristic form of the gall of *Adelges viridis* and that of *Adelges strobilobius*, and came to the conclusion that the specific position of the fundatrix on or near the bud accounted for the specific shape of the resulting gall. Von Tubeuf (150), Börner (16, 20) and Cosens (53) correctly held that the gall is derived from the leaf-stalklets, and not from the leaves as many investigators had supposed. Francke-Grosmann (71, 72) studied the gall of *Adelges prelli* on Oriental spruce and also concluded that it is derived from the cortical tissues of the bud axis and needle-stalklets; she also made interesting observations on the chemical changes taking place in the gall. However, the literature references on the gall of *Adelges nüsslini* have rarely alluded to the mode of formation of the gall. Marchal (106) ventured to say that the fundatrix plays a considerable but not exclusive role in its formation, since the gallicolae also have an important influence.

These researches on the spruce galls have recently culminated in the careful and far-reaching work by Plumb (126) in relation to *Adelges abietis* on *Picea excelsa*. Plumb studied such aspects as the source and nature of the stimulus to gall formation, the site of its action, and the derivation of the abnormal tissues of the gall from the meristematic areas of the bud. He observed that the gall is initiated by the fundatrix (particularly the adult), which feeds on the cortical tissues surrounding the medullary cone of the bud and causes a swelling at the bases of the needle rudiments. The affected cells show hypertrophy and nuclear disintegration. After flushing of the galled bud, the feeding of the gallicolae promotes increased hypertrophy of the cortical cells of the axis and leaf stalklets, resulting in radial increase of these tissues and the corresponding growth of the gall. Plumb does not satisfactorily explain why the pockets in which the gallicolae dwell should be retained and enlarged in spite of the swelling of the leaf stalklets. However, he noted that the epidermal and sub-epidermal layers lining the cavity remain normal, and are apparently unaffected by the feeding and shallow stylet penetration of the gallicolae. The distal end of each needle stalklet expands to close the ceiling of the pocket by the junction of neighbouring rhomboidal facets. He also discussed the structure of the needle stalklet and the leaf tip which it bears, as found in growing and mature galls.

Sections of a two-weeks-old gall of *Adelges nüsslini* on *Picea orientalis* have been cut in the course of the present investigation. They show that its structure and mode of formation are similar to those described by Plumb for *Adelges abietis* on *Picea excelsa*. The gall is undoubtedly initiated by the fundatrix, whose salivary secretions appear to affect the attacked bud around its entire circumference, resulting in the characteristic ovoid shape of the gall. The growth of the gall is brought about by radial increase of the cortex as a result of hyperplasia and hypertrophy of these cells. The axis of the gall is made up of giant parenchymatous cells through which run the unbroken vascular tissues similar to those of a normal shoot of the same age. Vascular strands branch out from the central axis to run through the swollen leaf stalklets into the short gall-leaf. The bulk of the gall is made up of these leaf stalklets, which are composed of large thin-walled cortical cells. These abnormal cells show hypertrophy in all dimensions, but particularly in the direction radial to the gall axis; this accounts for the relatively enormous length of the galled needle stalklet, compared with the normal needle stalklet on the unattacked growing shoot. Another feature of these giant cortical cells is the abundance of starch granules at least in the two-weeks-old gall.

The epidermal cells of the swollen stalklet are relatively little affected. They bear the trichomes which are normal to the young shoot of *Picea orientalis*. Their presence is ample proof that the gall is formed of twig cortex and needle-stalklets, not of malformed leaves. The leaf of *Picea orientalis* never bears trichomes. The trichomes on the swollen stalklet are most abundant on the outer face or apophysis, especially along the lines of junction of neighbouring rhombi. They also occur rarely on the inner walls of the gall cavities where the gallicolae feed.

It is not known exactly in which tissues the gallicolae feed, since the path of the stylets does not appear to be marked by a sheath. However, the gallicolae feed on all walls of the chambers, and their very short stylets must restrict them to the outer layers of cortical cells, not reaching the vascular strands. However, since their feeding is necessary for the further growth of the gall in all parts, it can be presumed that their salivary injections diffuse freely beyond the actual range of the stylets.

The gall leaf itself is a rudimentary leaf tip with a horny point. It contains a central vascular strand surrounded by undifferentiated mesophyllous cells.

(4). Anatomical effects of Adelges piceae on Silver fir

The anatomical effects of the feeding by *Adelges piceae* have been considered by relatively few writers.

Francke-Grosmann (70) has made a histological examination of attacked bark on the main stem of *Abies alba.* She found that the stylets seek out the vicinities of resin canals, where the movement of food materials is active. These cells of the bark cortex are rich in protein but relatively poor in starch. In the course of feeding, storage materials are entirely removed from the cells, some of which hypertrophy or die as a result. In general the stylet sheath extends unbranched into the cortex for its first 0.7 mm., then resolves itself into multiple branches lying between the walls of the cells and covering a feeding zone of 0.7 mm. diameter. Clearly then the stylets are inserted to their full length to feed, but are repeatedly withdrawn for a short distance and reinserted between other cells. The bark itself may be 10 mm. thick, and consequently the vascular tissues of the bast are beyond the feeding range of the sistens. Thus unlike *Adelges nüsslini* on the young shoot, *Adelges piceae* on the stem does not interfere to a marked extent with the production of xylem and phloem and the conduction of sap in *Abies alba.*

More recently, Balch's (7) histological studies of *Abies balsamea* attacked by *Adelges piceae*, have widened knowledge of the effects of feeding. He found that on both stem and twig, attacked cortical cells undergo hypertrophy and hyperplasia both of which contribute to the swellings of the bark. This abnormal swelling is more noticeable in the case of the attacked twig node or bud, where the "gout" may terminate further growth. In the twig these pockets of abnormal cortex may later become surrounded by a secondary phellogen producing layers of cork cells. Ultimately the hypertrophied tissue disintegrates and becomes flooded with resin.

Balch discovered an interesting secondary effect of attack. This is the appearance of a reddish, swollen xylem, called 'compression wood' or 'rotholz' in the sapwood immediately beneath the attacked bark of the main stem of *Abies balsamea.* This is undoubtedly an effect of the insect salivary injections, in spite of the fact that the xylem is outwith the range of the probing stylets. This rotholz is characterised by:

(i) the increased width of the annual ring over the zone of attack

(ii) its compostion of short thick-walled tracheids with a circular cross-section and a reduced lumen

(iii) the presence of traumatic resin canals

(iv) an abnormally high percentage of lignin.

Experimentally Balch was able to reproduce a form of rotholz by the application of indole-acetic acid. Accordingly he considers it possible that the sistens saliva contains a similar auxin.

The limited investigations undertaken by the writer bring a measure of confirmation to the findings of Francke-Grosmann and Balch. Experimentally, young trees of *Abies grandis, A. veitchii, A. procera* and *A. concolor* were infected with *Adelges piceae* neosistentes, and the effect of attack was examined histologically. The neosistentes of *A. piceae* evidently prefer to settle in the vicinities of buds and nodal areas. In the course of time swellings of the buds and nodal areas were produced on all four species (Plates 58 and 59). These swellings were caused by hypertrophy and hyperplasia of the cortical tissues, resulting in large disorganised masses of parenchyma. This parenchyma is composed of giant cells, often with enlarged or disintegrated nuclei and dispersed granular cytoplasm. The anatomical effect on a bud of *Abies veitchii* undergoing early attack is illustrated in Plate 65. Wherever the neosistentes settle on a new shoot, some suppression of cambial differentiation into xylem and phloem takes place. In nodal areas of the branch, attack prevents the normal increment of woody tissue each spring, but xylem tracheids already formed in earlier years are not affected. The stylets never enter lignified tissues. The meristematic zone of the attacked node is stimulated to produce only cortical tissues.

Rotholz formation consequent upon main stem attack by *Adelges piceae* has also been found. This abnormal wood has shown up clearly in disc sections of the stems of pole-stage *Abies grandis* at Craibstone (Plates 66 and 67). Rotholz does not appear to form in *Abies alba*, nor has it been reported to occur in other species, with the exception of *Abies balsamea.* It is interesting to note that the normal timber characters of *Abies balsamea,* (in which Balch originally discovered rotholz* induced by *Adelges piceae*) are almost identical with those of *Abies grandis,* but the timber characters of *Abies alba* are quite distinct.

In the case of *Abies grandis,* it is clear that the rotholz is a pathological condition of the xylem induced by the feeding of the sistentes. It is not merely compression wood which is ordinarily formed on leaning trees. The distribution of this abnormal wood was studied by the stem analysis of a single attacked tree and by observations on the stumps of a number of other *Abies grandis* trees. The following observations leave little doubt as to the association of the rotholz with *Adelges piceae:*

(i) Unattacked trees show only the normal white sapwood, but all attacked trees show the red bands of abnormal wood in places;

(ii) the ring of rotholz is widest where the population of sistentes is highest (Plate 66); thus in general the north-facing aspect of the stem, where the popu-

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* *Rotholz:* A term of German origin signifying "red wood."

lation was very dense, shows pronounced rotholz formation, but the south-facing aspect where the population is sparse, shows only traces;

(iii) the distribution of rotholz corresponds precisely to the distribution of population along the stem; thus even on the most favoured aspect, no rotholz was found above the zone of attack;

(iv) the rotholz is added annually as a result of abnormal stimulation of the cambium in each year of attack. Consequently the depth of rotholz in the stem disc enables the observer to accurately gauge the number of years during which attack has proceeeded at any point on the bark. The examination of one stem of *Abies grandis* showed that rotholz was formed as early as 1944. This corresponds precisely with the recollection of the forester in charge of Craibstone that attack began about ten years ago.

3. CHEMICAL ASPECTS OF LEAF ATTACK BY PROGREDIENTES OF ADELGES NUSSLINI

(1). Aims and methods

The investigation of the chemical aspects of leaf attack was originally undertaken in an attempt to determine the chemical nature of host resistance to infestation by *Adelges nüsslini*. Subsequent experimental infections have shown that host resistance is much more effective against the sistentes than against the progredientes. Thus the use of twigs rather than leaves for chemical analysis might be the more valuable means of approaching the problem of resistance. Experimental infections have also shown that the progredientes are relatively indifferent to host species within the genus *Abies*. Nevertheless the results of these analyses of attacked and unattacked leaves of *Abies alba*, which follow in subsequent sections, are valid to show the general effect of feeding by the progredientes of *Adelges nüsslini.*

The foliage used for analysis was taken only from young trees of *Abies alba*, naturally regenerated in the Forest Garden, Dunecht Estate. The trees from which samples were cut were classed and designated as follows:

Class 1. Unattacked, possibly resistant: A8, A12, A16.
Class 2. Lightly infested: A13, A14.
Class 3. Moderately infested: A9, A17.
Class 4. Heavily infested: A3.
Class 5. Dying back following heavy attack: A15.

These five classes cover the condition of all the living Silver firs in the attacked stand. Accordingly analyses of tissues from successive classes can be considered to give the chemical status of the leaves in progressive stages of attack.

In order to obtain uniform samples, the foliage removed from each tree consisted always of fairly vigorous shoots of the current year's growth in the upper crown of the young tree. All samples were cut during the autumn or winter, that is, after the season of active growth. Thus the analyses do not indicate the condition of the leaves at the time of peak feeding, but after a lapse of several months.

The main features of the work were the qualitative estimation of the degree of chlorosis, and quantitative estimations of sugar, nitrogen and mineral contents of the leaves of *Abies alba.* The results give a measure of the chemical effect of the feeding by progredientes.

(2). Chlorosis of leaves

The reduction in the amount of chlorophyll in attacked leaves was shown by duplicate estimations carried out on the 19th September and 8th October, 1952. Sample shoots were removed from trees A8 (unattacked), A9 (moderately infested) and A3 (heavily infested).

The spectrographic technique of chlorophyll estimation and its results are given in Appendix 2, p. 68. The following is a summary of the relative contents of chlorophyll, using the quantity in A8 (the unattacked tree), as an index of 100 per cent.

RELATIVE AMOUNTS OF CHOROPHYLL IN ATTACKED AND UNATTACKED LEAVES

TABLE 7.

Tree	*Class*	*Percentage of chlorophyll*		
		19–9–52	8–10–52	*Mean*
A8	1	100	100	100
A9	3	32	23	27.5
A3	4	35	19	27

These results show that moderate and heavy infestation result in a drastic reduction of the chlorophyll content of the leaves. This factor in itself is not so important to the healthy functioning of the foliage as might be thought. Pisek and Berger (124) have shown in relation to a large number of plants including conifers that only a small part of the total leaf chlorophyll is necessary for normal photosynthesis.

(3). The sugar content of attacked leaves.

In the Silver fir stand at Dunecht, there has occurred in each spring the browning and death of one-year-old foliage heavily infested by the progredientes of *Adelges nüsslini* in the previous spring. Two hypotheses to explain this phenomenon can be made;

(i) the late frosts may injure the chlorotic foliage;

or

(ii) foliage dries out as a result of inadequate conduction of water through the attacked twigs.

In support of the second hypothesis, anatomical investigation has shown that attack results in reduction of the vascular tissues of the twig, and Chrystal (47) has proved experimentally that the movement of water is impeded by abnormal parenchyma. It might also be expected that in addition the removal of assimilate from the leaves to woody storage tissue would also be hindered by the disrupted vascular system. In that case one might expect the frost hardiness of attacked leaves to be actually increased, since Pisek (125) has proved that increased leaf sugar gives rise to increased resistance to cold.

To test these two hypotheses, the sugar contents of attacked and unattacked leaves were analysed at various times during the autumn and winter of 1952-53. Table 8 shows that, at each date, a series of trees showing progressively serious attack was used. For example, on 19th September, 1952, samples were taken from trees A8, A9 and A3, representing classes 1, 3 and 4 respectively. At that time it was not possible to make a tally of the original progrediens population per shoot, but the numbers of neosistentes were counted to give a comparative guide. Reduced to numbers of neosistentes per standard linear inch of the current year's shoot, the tally gave the following counts: A8 = less than 1, A9 = 100, A3 = 250.

The technique for the estimation of sugar content was Nelson's (115) photometric adaptation of the Somogyi method, of which a summary is given in Appendix 3, p. 68.

The results of the estimations of free reducing sugars (mainly glucose) and of non-reducing disaccharide (mainly sucrose) are given below.

QUANTITIES OF SUGARS IN THE LEAVES OF ATTACKED AND UNATTACKED TREES OF ABIES ALBA

TABLE 8.

Date of sampling	Tree	Class	Free reducing sugar (mgm/100 gm. fresh wt. of leaves)	Non-reducing disaccharide (mgm/100 gm. fresh wt. of leaves)	Ratio: reducing/ non-reducing sugars	Total sugars (mgm/100 gm. fresh wt. of leaves)
19-9-52	A8	1	238	414	0.58	652
	A9	3	803	127	6.32	930
	A3	4	1,467	948	1.54	2,415
8-10-52	A8	1	777	1,345	0.55	2,122
	A9	3	1,234	1,703	0.72	2,937
	A3	4	1,918	1,818	1.05	3,736
29-12-52	A8	1	427	545	0.78	972
	A9	3	1,720	742	2.31	2,462
	A3	4	1,030	514	2.00	1,544
5-2-53	A12	1	715	1,170	0.61	1,855
	A13	2	1,090	1,100	0.99	2,190
	A14	2	756	1,200	0.63	1,956
	A15	5	810	642	1.26	1,452

These quantities show a wide variation in absolute weight of sugar per unit sample of leaves. Even in samples from a single tree cut at different dates there is a considerable variation, but the figures do not in any way show a seasonal trend. Comparisons between different trees, in any one series, show some significant relationships. In almost all cases the total quantity of sugar per unit sample is greater in the attacked leaves than in the unattacked leaves for any one date. The exception is the dying tree A15 (5-2-53) which has a low concentration of leaf sugar, no doubt due to the general debility of the plant. The same relationship holds true for the relative quantities of free reducing sugar; attacked tree leaves hold a greater quantity than unattacked leaves. The quantities of non-reducing disaccharide show a less reliable relationship to attack. It is evident, however, that the ratio of reducing/non-reducing sugars shows some constancy according to degree of attack. In unattacked or lightly attacked leaves there is always considerably more sucrose than reducing sugar; in moderately or heavily attacked leaves the reverse usually holds true.

These observations may be interpreted and summarised as follows:

(i) following infestation of leaves by the progredientes, there is a marked rise in the level of free reducing sugar content, and also possibly of non-

Plate 1. (X 190) *Adelges nüsslini.*

First instar moult skin of the fundatrix. The legs, rostrum and stylets lie under the dorsal plates.

Plate 2. (X 100) *Adelges nüsslini.*

Second instar fundatrix larva. The wax glands on the marginal plates are shown in sharp definition.

Plate 3. (X 80) *Adelges nüsslini.*

Third instar fundatrix larva.

Plate 4. (X 50) *Adelges nüsslini.*

Fundatrix adult.

Plate 5. (X 160) *Adelges nüsslini.*
First instar gallicola. One of the metathoracic legs is concealed.

Plate 6. (X 110) *Adelges nüsslini.*
Second instar gallicola.

Plate 7. (X 20) *Adelges nüsslini.*
Gallicola adult showing the simple Adelgid wing venation.

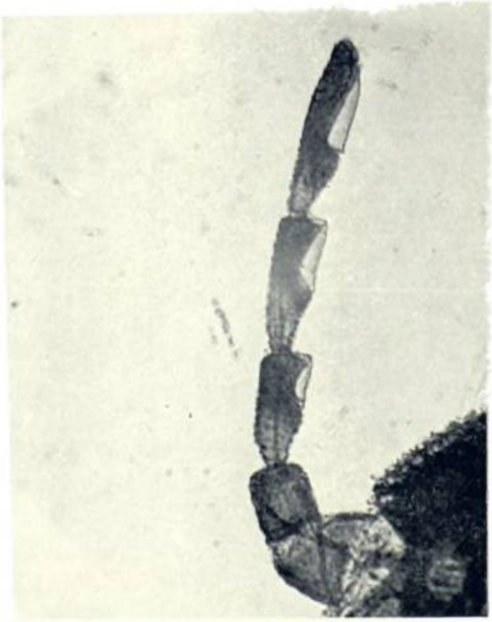

Plate 8. (X 240) *Adelges nüsslini.*
Antenna of the gallicola adult, showing the sensoria of the three apical segments.

Plate 9. (X 18) *Adelges nüsslini.*

This gallicola adult, two days after settling on a leaf of *Abies alba*, is beginning to secrete wax wool from the dorsal glands on head and thorax.

Plate 10. (X 27) *Adelges nüsslini.*

This gallicola adult, ten days after settling on a Silver fir leaf, had laid a clutch of nine eggs, some of which can be seen under the folded wings. The wax wool has become long and abundant. A millimetre scale lies adjacent.

Plate 11. (X 190) *Adelges nüsslini.*

First instar hiemosistens. The stylets have become disunited during mounting.

Plate 12. (X 75) *Adelges nüsslini.*

Aestivosistens adult.

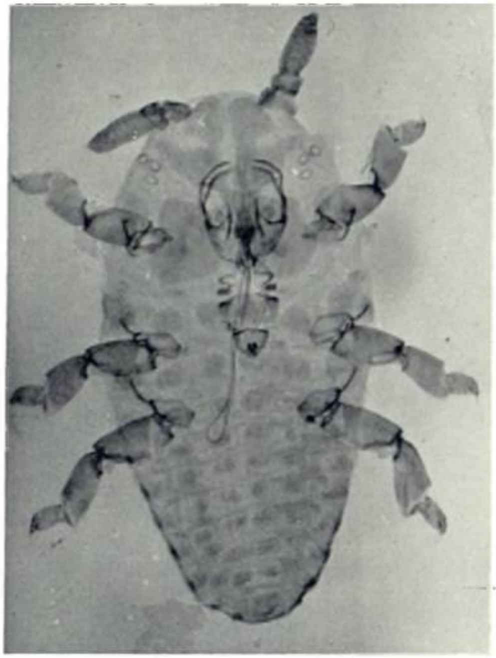

Plate 13. (X 170) *Adelges nüsslini.*

First instar progrediens, showing small weakly chitinised dorsal plates and the short stylets in a single loop.

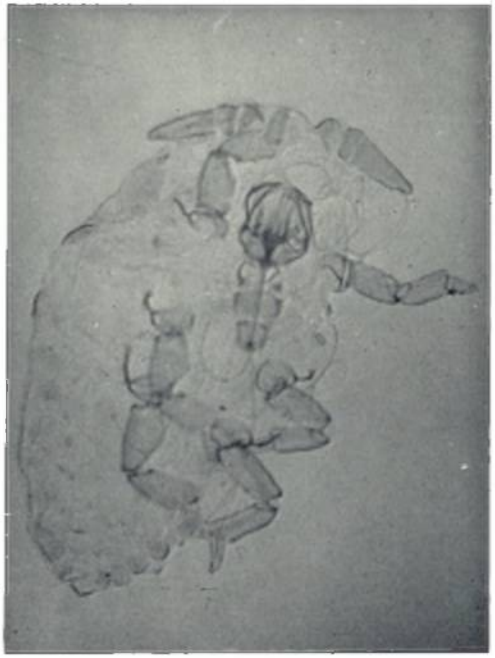

Plate 14. (X 120) *Adelges nüsslini.*

Third instar progrediens aptera. Note the 3-segmented non-scaly antennae.

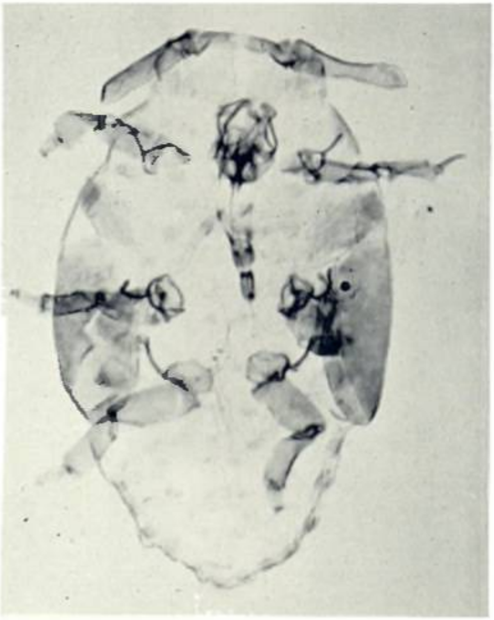

Plate 15. (X 100) *Adelges nüsslini.*

Fourth instar sexupara (nymph).

Plate 16. (X 50) *Adelges nüsslini.*

Fourth instar sexupara feeding on a young leaf of *Abies alba.* The crumpled moult skin of the preceding instar lies adjacent to the abdomen.

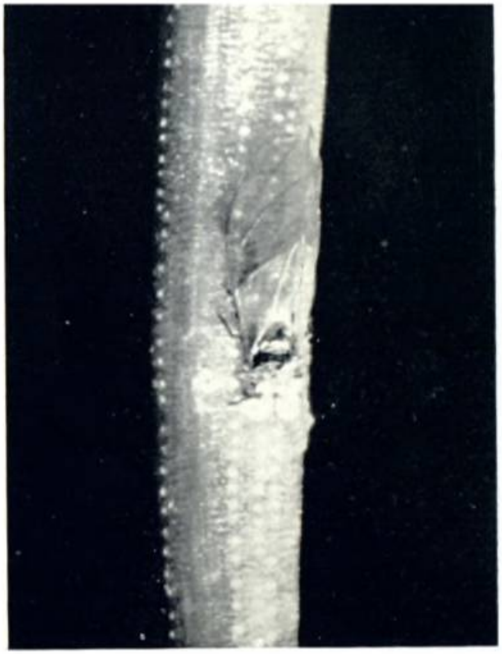

Plate 17. (X 21) *Adelges nüsslini.*

Adult sexupara settled on a leaf of *Picea orientalis* and secreting wax wool.

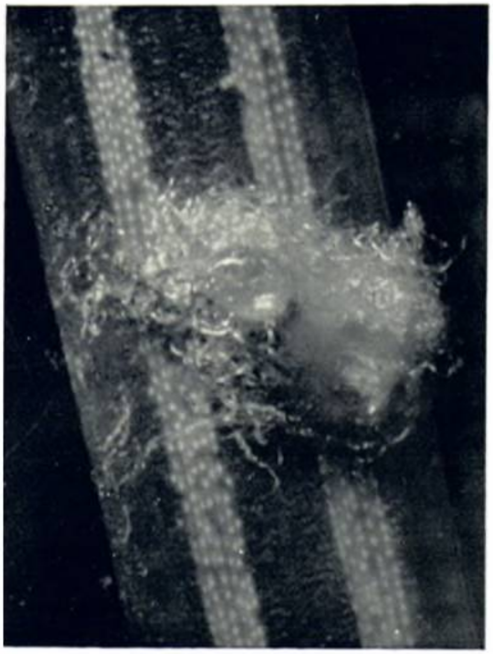

Plate 18. (X 20) *Adelges nüsslini.*

Adult progrediens aptera on leaf of *Abies alba.* The body of the insect and its eggs are covered by a mass of wax wool. A drop of honeydew has been excreted.

Plate 19. (X 25) *Adelges nüsslini.*

Third instar hiemosistens feeding on a twig of *Abies alba.*

Plate 20. (X 160) *Adelges nüsslini.*

Second instar sexualis. One prothoracic leg has become detached from this specimen.

Plate 21. (X 110) *Adelges nüsslini.*

Adult female sexualis.

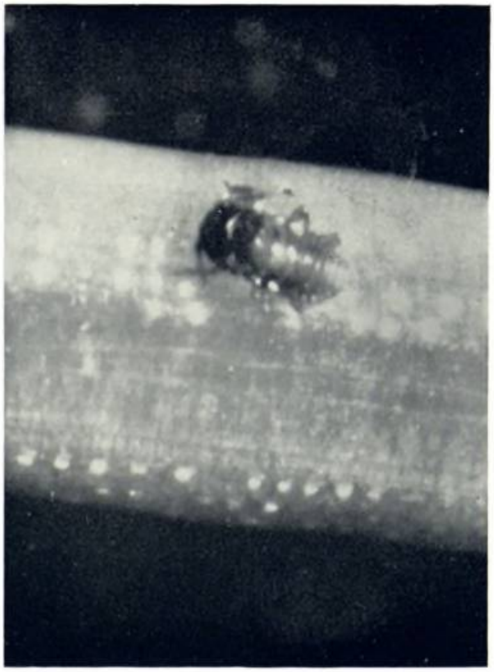

Plate 22. (X 45) *Adelges nüsslini.*

Third instar sexualis feeding on a leaf of *Picea orientalis.*

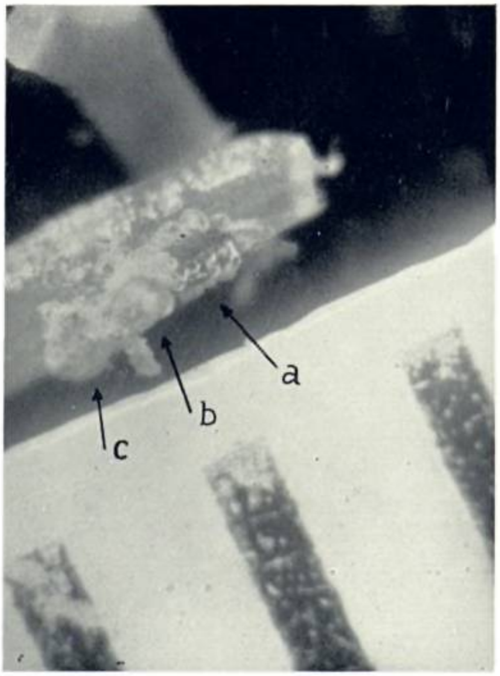

Plate 23. (X 27) *Adelges nüsslini.*

Fourth instar sexualis showing :
a. the marginal wax fringe,
b. honeydew excretion,
c. the moult skin from the preceding instar.
The black bars are part of a millimetre scale.

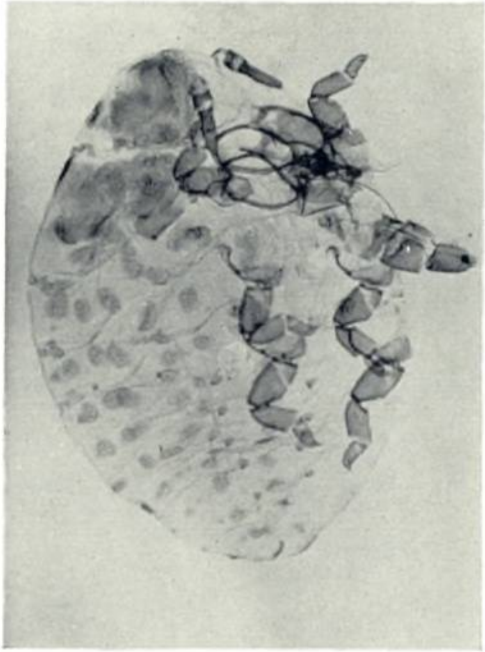

Plate 24. (X 110) *Adelges piceae.*

Second instar hiemosistens. The apical segment of the antenna is cylindrical.

Plate 25. (X 105) *Adelges piceae.*

Third instar hiemosistens. The apical segment of the antenna is conical.

Plate 26. (X 85) *Adelges piceae.*

Adult hiemosistens. The adult is identified at once by the presence of the ovipositor.

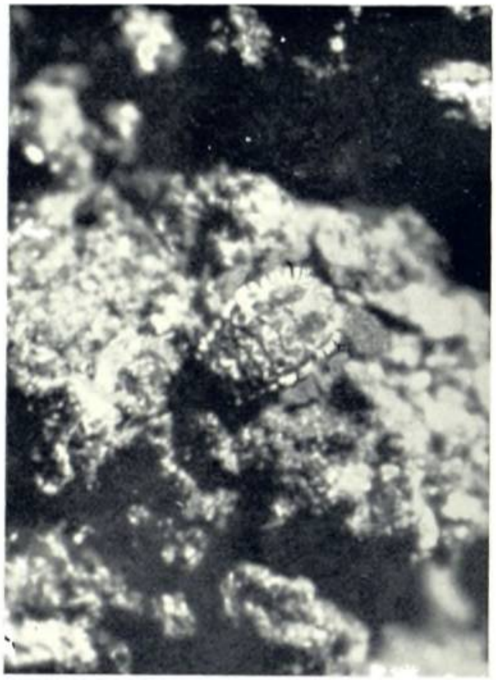

Plate 27. (X 50) *Adelges piceae.*

First instar hiemosistens in diapause. The marginal wax fringe is well shown but the mid-dorsal line of mesial wax flakes has been broken up.

Plate 28. (X 35) *Adelges piceae.*

Third instar hiemosistens. This larva has newly moulted and exhibits very little wax wool, but the deep dorsal furrows between segments are well defined.

Plate 29. (X 55) *Adelges piceae.*

Adult hiemosistens adjacent to her eggs. Most of the body, especially the abdomen, is masked by wax wool, and the eggs are covered by a wax dust.

Plate 30. (X 17) *Adelges piceae.*

Clutches of eggs on the bark of *Abies procera.* The adult hiemosistentes are entirely hidden by wax and eggs.

Plate 31. (X 170) *Adelges piceae.*

First instar progrediens. The small rounded dorsal plates, each bearing a seta, are well defined.

Plate 32. (X 95) *Adelges piceae.*

Fourth instar progrediens alata. (Nymph.)

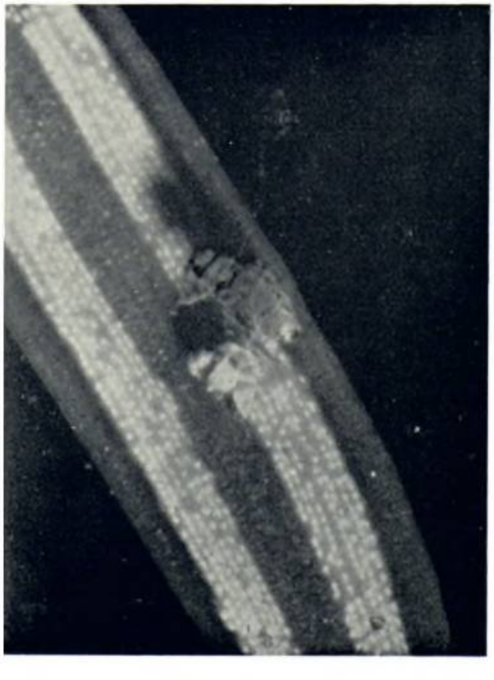

Plate 33. (X 21) *Adelges piceae.*

Fourth instar progrediens alata feeding on a young leaf of *Abies alba.* The moult skin from the preceding instar lies adjacent.

Plate 34. (X 15) *Adelges piceae.*

Adult progrediens alata settled on a leaf of *Abies alba.* The shrivelled body of a neo-progrediens lies nearby.

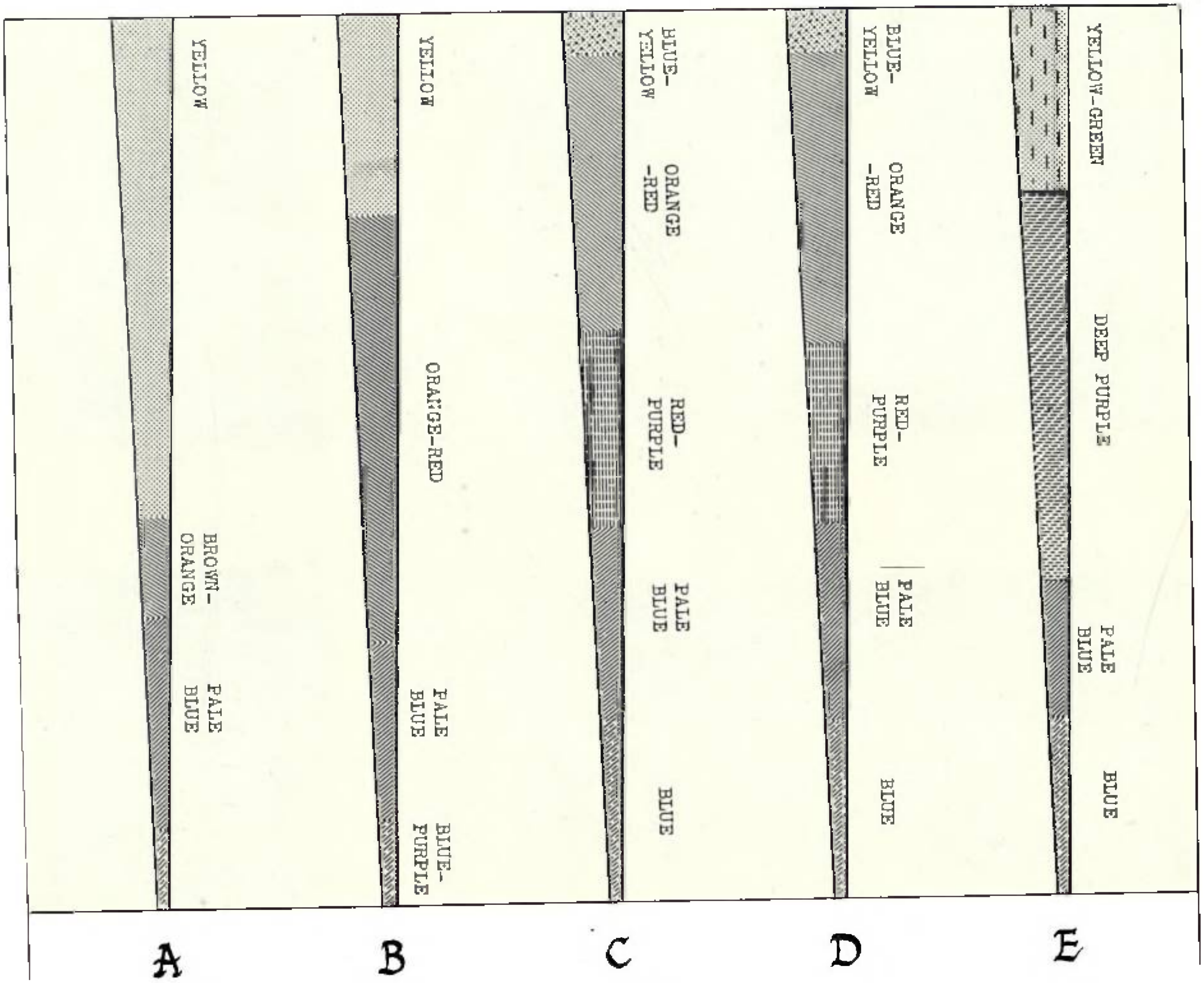

Plate 35. Paper chromatography. Drawings of chromatograms from adults of the following species:

A. *Adelges strobilobius* sistens.
B. *Adelges piceae* sistens.
C. *Adelges nüsslini* sistens.
D. *Adelges nüsslini* fundatrix.
E. *Pineus pini* sistens.

The chromatograms C and D are almost identical, although the insects had been feeding on dissimilar hosts, Silver fir and Oriental spruce respectively. E in the genus *Pineus* conforms least to the general pattern. The blue anthocyanin zone is common to all.

Plate 36. (X 500) *Adelges piceae.*

Mesial wax glands on the dorsum of the neosistens. Portions of the mesothoracic, metathoracic and abdominal segments are shown.

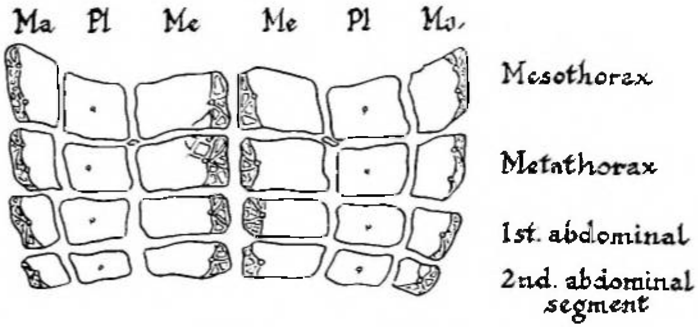

Plate 38. (X 250) *Adelges piceae.*

Line drawing of the dorsal plates of the mesothorax, metathorax and first and second abdominal segments, showing the pattern of the mesial and marginal glands.

Ma. Marginal plates.
Pl. Pleural plates.
Me. Mesial plates.

Plate 37. (X 550) *Adelges nüsslini.*

Mesial wax glands of the neosistens. The stylets are cutting across some of the dorsal abdominal plates.

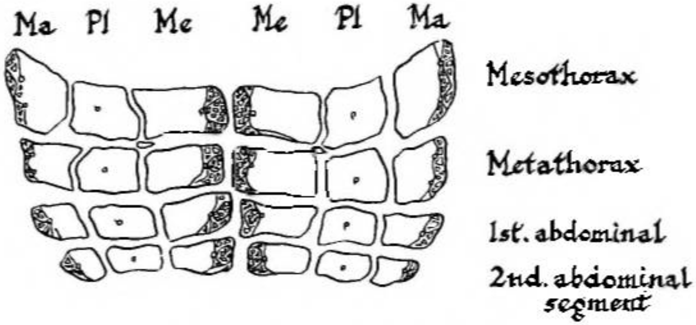

Plate 39. (X 250) *Adelges nüsslini.*

Line drawing of the dorsal plates of the mesothorax, metathorax and first and second abdominal segments, showing the pattern of the mesial and marginal glands.

Ma. Marginal plates.
Pl. Pleural plates.
Me. Mesial plates.

Plate 40. Muslin cages over small trees used for experimental infections.

Plate 41. Muslin sleeve over a branch of a small potted Silver fir.

Plate 42. Oriental spruce tree tented to protect the sexuales from rain.

Plate 43. (X 10) *Adelges nüsslini*.
Fundatrix adult with eggs.

Plate 44. Gall on Oriental spruce dissected to show cavities and gallicola larvae of *Adelges nüsslini*. Up to 5 nymphs may mature in a single cavity.

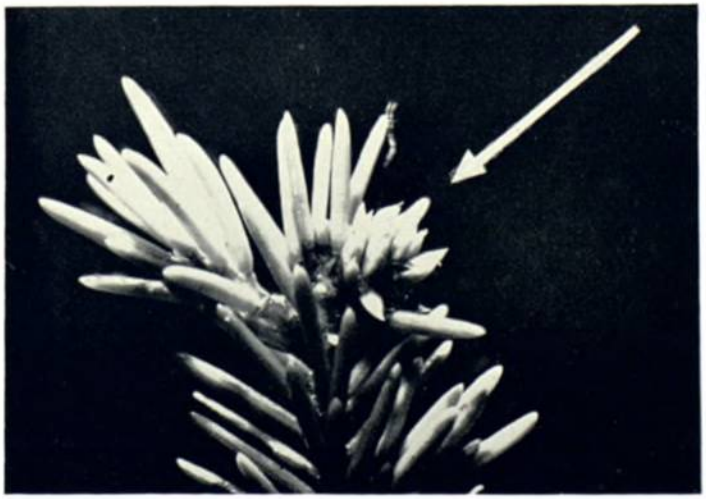

Plate 45. Abnormal gall on Oriental spruce resulting from feeding of larval fundatrix of *Adelges nüsslini* without intervention of gallicolae.

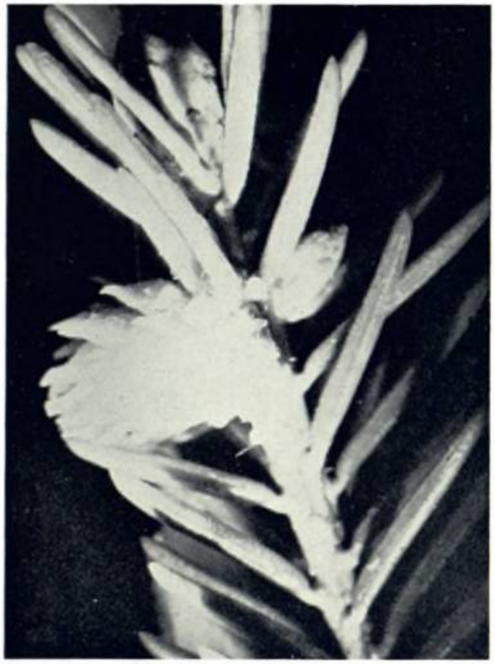

Plate 46. 4-days-old gall on *Picea orientalis* in which the neogallicolae have settled.

Plate 47. 2-weeks-old gall on *Picea orientalis*.

Plate 48. Nearly mature gall, 4 weeks old, on *Picea orientalis*.

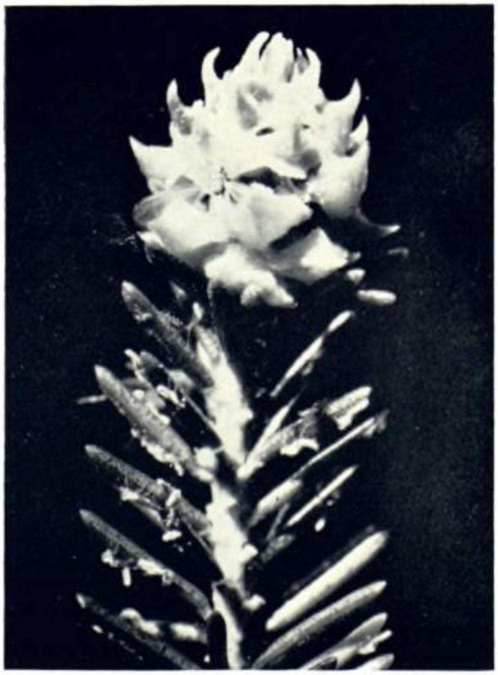

Plate 49. Dehiscing gall on *Picea orientalis*, showing moulting nymphs on the leaves and a young adult gallicola on the gall.

Plate 50. Neosistentes of *Adelges nüsslini* settling on a shoot axis of *Abies alba*.

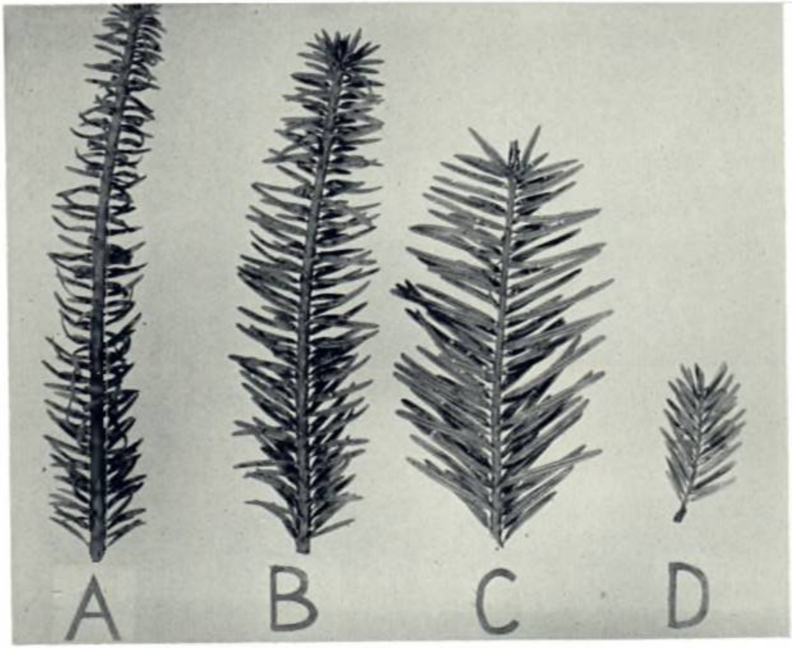

Plate 51. The proportion of winged to wingless forms of the progredientes of *Adelges nüsslini* increases with the density of population. Shoot A, with an initial population of 5.51 neoprogs per leaf, ultimately exhibited a sexuparae/progredientes apterae ratio of 17.08. For Shoot B, the corresponding figures were 4.85 per leaf, and ratio 9.07; for Shoot C, 1.62 per leaf and ratio 0.21; for Shoot D, 0.62 per leaf and ratio 0.07. (See Table 2). This photograph also illustrates effect of attack on leaf size. In the case of Shoot D, the small size of the shoot is due to its shaded position on the tree, not to *Adelges* attack. These shoots are of *Abies alba*.

Plate 52. (X 27). *Adelges nüsslini* hiemosistens adult. A mass of wax wool, honeydew and cast skins has accumulated to the rear of the insect.

Plate 53. (X 25). Egg clutch laid by hiemosistens of *Adelges nüsslini* on a twig of *Abies alba*.

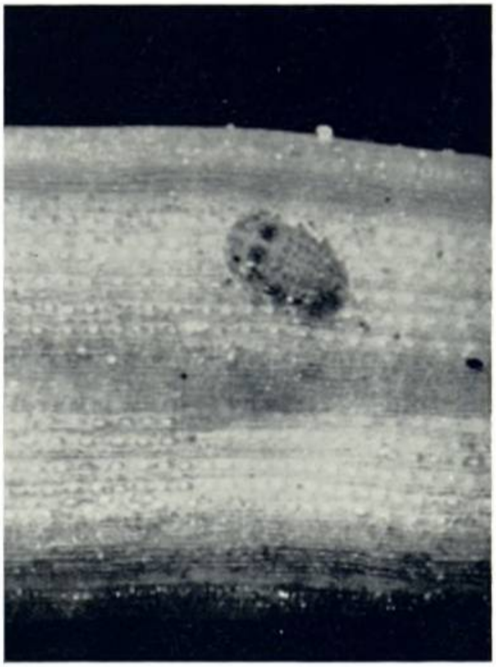

Plate 54. (X 40). Neoprogrediens of *Adelges nüsslini* feeding on the underside of young leaf of *Abies alba*.

Plate 55. (X 10) Neosistentes of *Adelges nüsslini* in diapause on a twig of *Abies alba*. Some larval progredientes can be seen on the leaves.

Plate 56. *Adelges piceae* adult sistentes feeding on bark of main stem of pole-stage *Abies grandis*.

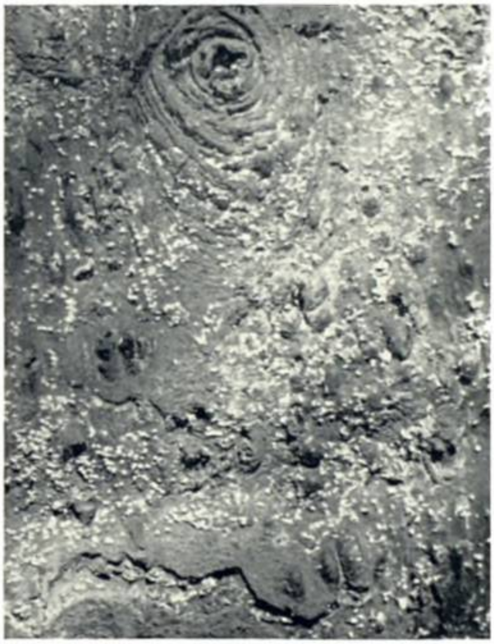

Plate 57. Heavy population of *Adelges piceae* sistentes on stem bark of pole-stage *Abies procera*.

Plate 58. Abnormal swellings of the male flower cups of *Abies procera* due to the feeding of sistentes of *Adelges piceae*.

Plate 59. Abnormal swellings in the nodes of a twig of *Abies concolor*, as a result of feeding by *Adelges piceae* sistentes.

Plate 60. Upcurling of the leader whorl of a young *Abies alba* dying from attack by *Adelges nüsslini.*

Plate 61. Leaf curl of *Abies alba* caused by the feeding of the progredientes of *Adelges nüsslini.*

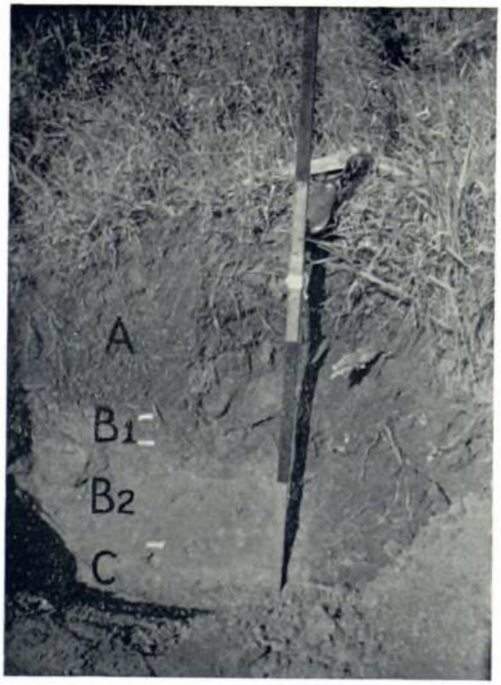

Plate 62. Soil profile in the Forest Garden, Dunecht.

A. 11 in. brown loam, the upper part humified, the lower part slightly leached.

B1. 2 in. horizon showing slight deposition of iron.

B2. 10 in. indurated layer.

C. Parent gravel.

Note that few roots penetrate beyond the B1 horizon.

Plate 63. Dense natural regeneration of Common Silver fir and beech under a mixed overwood in the Forest Garden, Dunecht.

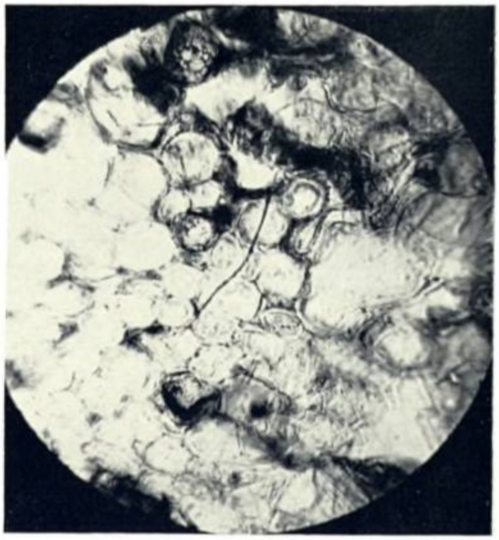

Plate 64. (X 130). Apparently intracellular course of the stylets of a hiemosistens adult (*Adelges nüsslini*) in the cortex of a shoot of *Abies alba*. Some of these cells are abnormally large.

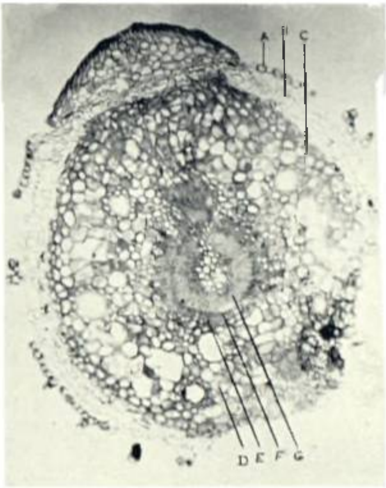

Plate 65. (X 25). Section of a twig of *Abies veitchii* near a bud attacked by *Adelges piceae*. Settlement by the neosistentes began after the new shoot had matured and so the xylem and phloem are intact. The cortical cells shows hyperplasia and hypertrophy at a rather early stage, but already giant cells have been formed, nuclei are enlarged and the cytoplasm is often dispersed and granular.

A. Epidermis: B. Periderm:
C. Collenchyma: D. Cortex:
E. Phloem: F. Cambium:
G. Xylem.

Plate 66. Formation of rotholz on a stem of *Abies grandis* attacked by *Adelges piceae*. The white line defines the inner boundary of the rotholz. Its formation was more pronounced, and older in years, on the north- and east-facing aspects where the population averaged 100 sistentes per square inch, and less evident and more recent on the south- and west-facing aspects where populations averaged 9 sistentes per square inch in the month of February, 1953.

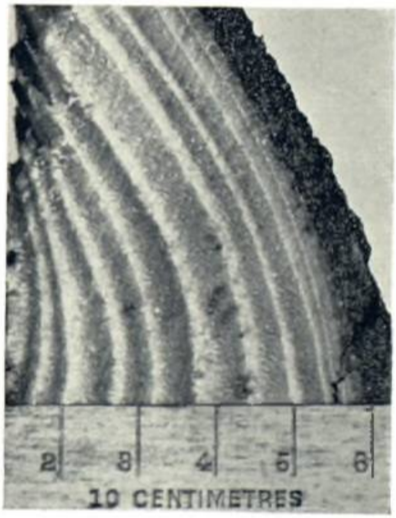

Plate 67. Following the feeding by large numbers of *Adelges piceae* sistentes on the main stem of *Abies grandis*, ring width was abnormally increased by the formation of reddish thickwalled fibres or rotholz.

Plate 68. Dense natural regeneration of *Abies alba* under an overwood in the Forest Garden, Dunecht. The severe outbreak of *Adelges nüsslini* began after the overwood was thinned to promote growth of the young trees.

Plate 69. Natural regeneration of *Abies alba* in a shaded section of the Forest Garden, Dunecht. Although present in adjacent parts of the stand, *Adelges nüsslini* had not become established on these shaded trees.

Plate 70. Site of the outbreak of *Adelges piceae* on pole-stage *Abies grandis* at Craibstone Estate, Aberdeenshire. The thin crowns have resulted from underthinning followed by sudden exposure to wind, and not primarily from the attack by *Adelges*.

reducing sugar. This rise is presumably due to the disruption of the normal conduction tissues of the shoot, preventing the adequate removal of assimilate;

(ii) although the chlorophyll content of the leaves may be reduced to a quarter of the normal level, the tree may be still capable of effective photosynthesis;

(iii) the high quantities of leaf sugar are an insurance against possible frost damage, and frost is not the cause of the spring browning of foliage;

(iv) these analyses contribute little to knowledge of the nutrition of progredientes, because the samples were cut so late in the season. The analysis of newly flushed leaves, both attacked and unattacked, could be expected to make a valuable contribution to this problem. Franke-Grosmann (70) has stated that the analysis of the *Adelges* honey-dew shows only small traces of reducing sugars and no non-reducing sugars, and concludes that the twigs offer the sistentes little excess of sugar. Host tissue analysis would probably make a better approach to the problem;

(v) since it can be assumed that browning of the foliage in spring is due to dessication, any means of limiting transpiration should lower the rate and occurrence of die-back of attacked Silver firs. The maintenance of an overwood should therefore be beneficial to young regeneration in this respect, since the shade would lower the rate of transpiration both by preventing direct insolation of the leaves and by keeping the forest air humid.

(4). The effect of attack on the nitrogen content of leaves

The analysis of leaves of *Abies alba* for nitrogen content was carried out to determine the effects of feeding by the progredientes. Estimations of total nitrogen were made in two series on 27th November, 1952 and 5th February, 1953. Quantities of amino-nitrogen were estimated in a single series on 29th December, 1952. The techniques of analysis are shown in Appendix 4, p. 69.

Results are tabled below.

QUANTITIES OF TOTAL NITROGEN IN ATTACKED AND UNATTACKED LEAVES OF ABIES ALBA

TABLE 9.

Date	Tree	Class	Sample No.	Dry matter	Total N.	Total N.
				Per cent.	mg/gm. dry wt.	mg/100 gm. fresh leaves
27-11-52	A16	1	1	44.6	14.67	654
			2	44.7	15.33	685
	A17	3	1	43.3	5.20	225
			2	42.3	6.12	258
5-2-53	A12	1	—	40.1	9.36	376
	A13	2	—	50.7	3.84	192
	A14	2	—	42.2	4.51	190
	A15	5	—	38.5	5.11	197

QUANTITIES OF AMINO-NITROGEN

TABLE 10.

Date	Tree	Class	Sample	Amino-nitrogen		
				mg/100 ml. solution	mg/100 gm. fresh weight	Mean mg/ 100 gm. fresh wt.
29-12-52	A8	1	1	1.29	8.06	7.31
			2	1.05	6.56	
	A9	3	1	1.56	9.94	9.84
			2	1.56	9.75	
	A3	4	1	1.90	11.87	11.59
			2	1.81	11.31	

These results show that the total nitrogen content of unattacked leaves is much higher than that of attacked leaves. On the other hand there is a slight rise in amino-nitrogen content with intensity of attack. These trends indicate that in the attacked trees the katabolic reactions of metabolism were proceeding faster than the anabolic reactions, resulting in a relative abundance of free amino-nitrogen compared with synthesised nitrogen. The results also suggest the possibility that the progredientes of *Adelges nüsslini* are selective feeders, removing nitrogenous materials from the leaf sap.

Similar analyses in June, during the course of actual attack, might contribute much to the knowledge of Adelgid nutrition.

(5). The effect of attack on the mineral content of the leaves

The purpose of these analyses was to see how far the feeding of the progredientes affected the general and specific mineral status of the leaves. The results of these analyses, which were carried out by the Spectrochemistry Department, Macaulay Institute for Soil Research, are tabled below.

TOTAL PHOSPHATES IN ATTACKED AND UNATTACKED LEAVES OF ABIES ALBA, RECORDED AS GAMMA PHOSPHORUS PER GRAM FRESH WEIGHT

TABLE 11.

Date	Tree	Class	Sample 1	Sample 2	Mean
20-2-53	A12	1	637	616	626
	A13	2	531	—	559
	A14	2	588	—	
	A15	5	501	510	505

MAJOR ELEMENTS IN ATTACKED AND UNATTACKED LEAVES OF ABIES ALBA, IN PARTS PER MILLION FRESH WEIGHT

TABLE 12.

Date	Tree	Class	P	K	Ca	Mg	Na
20-2-53	A12	1	798	173	92.0	18.7	8.4
	A13	2	470	149	74.8	16.8	9.6
	A14	2	634	149	81.6	21.7	4.8
	A15	5	500	112	72.4	14.5	21.6
4-3-53	A16	1		301	> 100	42.8	8.4
	A17	4		165	105	67.0	16.8

TRACE ELEMENTS IN ATTACKED AND UNATTACKED LEAVES OF ABIES ALBA, IN PARTS PER MILLION FRESH WEIGHT

TABLE 13.

Date	Tree	Condition	Co	Ni	Mo	Fe	Pb	Sn	Zn	V
19-3-53	A12	1	0.36	2.0	0.29	355	6.0	<2	73	1.1
	A15	5	0.46	2.4	0.1	162	6.0	<2	42	0.4

Date	Tree	Condition	Ti	Cr	Ag	Cu	Mn	Ba	Sr
19-3-53	A12	1	82	0.7	<0.2	5.0	710	63	16
	A15	5	23	0.7	<0.2	5.5	520	19	5

These results may be interpreted as the effects of general debility in leaves attacked by the progredientes of *Adelges nüsslini.* They throw little light on the feeding habits of the insect. In general the differences between minerals in attacked and unattacked tissues are not sufficiently profound to clearly suggest that any one element may be a controlling factor either in resistance to the insect or in its nutrition. However, sodium might be an exception, since it shows a considerable increase in heavily attacked foliage.

4. SUSCEPTIBILITY AND RESISTANCE IN SILVER FIRS TO ATTACK BY ADELGES NUSSLINI AND ADELGES PICEAE

(1). Definition of Resistance in Host Plants

Both the inherent characters of the tree and the conditions of its environment affect the occurrence or severity of attack by Adelgids. The object of this section is to consider how far and in what ways the inherited nature of the tree results in resistance or susceptibility to attack.

The phenomenon of resistance in crop plants in relation to insect attack is well known and has assumed considerable economic importance in agriculture and forestry. Its many aspects have assembled a very considerable literature, much of which has been digested and incorporated in a recent book by Painter (122). His definitions of the terms used in connection with the problem are precise and relevant to the discussion of resistance in Silver firs, and are summarised as follows.

(i) Resistance of plants to insect attack: the relative amount of heritable qualities possessed by the plant which influence the ultimate degree of damage done by the insect.

(ii) Immunity: an immune plant is one which a specific insect will never consume or injure under any known condition.

(iii) High resistance: a highly resistant plant possesses qualities resulting in very small damage by a specific insect under a given set of conditions.

(iv) Low level of resistance: this indicates the possession of qualities which cause the plant to show less damage or infestation by an insect than the average for the crop under consideration.

(v) Susceptibility: a susceptible plant shows average damage done by the insect.

(vi) High susceptibility: a highly susceptible plant shows much more than average damage done by the insect.

(vii) Pseudo-resistance: apparent resistance resulting from transitory characters in potentially susceptible hosts. Pseudo-resistance may be

(a) host evasion: for example, an early maturing race which passes through the susceptible stage at a time when the pest population is still low,

(b) induced resistance: a temporarily increased resistance due to change in some environmental factor,

(c) escape: lack of injury due to chance non-infestation.

Painter's definitions apply particularly to varieties within a single species of arable crop, but they require only slight modification to be applicable also to tree resistance at the specific level.

(2). Evidence of resistance to Adelgids in the literature

In the literature on the various Adelgids there appear fairly frequent references to resistance shown by various host trees, although the observations are rarely supported by experimental research. Nevertheless these observations do substantiate the belief of the present writer that the host trees, at specific, racial and individual levels, exhibit various degrees of resistance or susceptibility to *Adelges.* Resistance is clearly shown by both primary and intermediate hosts.

In relation to the Larch-Spruce *Adelges*, Tregubov (149) has claimed that *Picea omorika* is immune to attack in its native habitat in Jugoslavia, where it never bears galls although neighbouring *Picea abies* is heavily galled. Nägeli (114) found that in Europe strains of *Picea abies* of mountain origin are less susceptible to Adelgid attack than lowland strains. Wilford (154) reported that individual trees in a plantation of *Picea abies* in Michigan showed high resistance to galling in spite of the interlocking of their crowns with highly susceptible trees. As to the intermediate hosts, Steven (146) and Crooke (54) have stated that *Larix decidua* Mill. is susceptible but *Larix leptolepis* Murr. and *Larix eurolepis* Henry possess a measure of resistance.

In relation to *Adelges cooleyi* Chrystal (49) and Champion (29) have noted the occurrence of apparently resistant individuals of *Pseudotsuga taxifolia* among heavily attacked plantations and natural stands in Britain and North America. Chrystal (46) has also observed specific resistance in *Pseudotsuga glauca* Mayr.

There is also clear evidence of specific and individual host resistance to *Adelges nüsslini.* Since the time of Nüsslin, it has been recognised that Norway spruce shows a high level of resistance to attack by the fundatrix. Marchal (106) discovered that Oriental spruce is susceptible to all three primary host generations, but no one has yet shown that any other species is similarly susceptible. However the intermediate host shows a much more variable range of resistance and susceptibility. The recognised susceptible species are *Abies nordmanniana* and *Abies alba.* In the latter species, territorial strains may be resistant to *Adelges nüsslini,* as Francke-Grosmann (70) has suggested, and certainly individual trees appear markedly less susceptible according to Chrystal (49) and Schneider-Orelli (136). Lofting's (102) provenance studies of *Abies alba* in Denmark show that there are racial variations in inherited resistance to *Adelges nüsslini.* Central European provenances have proved most liable to attack in Denmark, while eastern and southern European strains displayed greater resistance. The probable reason is that these Roumanian and Italian provenances have adapted themselves to resist drought-weakening in their native climates, and thereby accidentally reduced their susceptibility to severe *Adelges* injury. Lofting holds that at many places in Denmark the Common Silver fir grows at the drought limit for the species, and that drought-subject areas suffer the worst *Adelges* attacks because the trees are weakened. Accordingly *Adelges* injury to strains inheriting drought-resistance is greatly reduced. His provenance experiments also showed that pure stock of *Abies nordmanniana* was less susceptible to injury by this insect than were hybrids with *Abies alba.*

Little is known about the susceptibility of many other *Abies* species, but Bavngaard (11) and Tillisch (148), have claimed immunity for *Abies grandis, Abies procera* and *Abies concolor.* Steven (146) has experimentally shown that *Abies grandis* and *Abies firma* Sieb. & Zucc. possess a high level of resistance to infection. Chrystal (47, 48) acknowledged the relative resistance of *Abies grandis* and *Abies procera,* but experimentally proved that they are not immune.

Investigators are agreed that *Adelges piceae* can adapt itself to many hosts within the genus *Abies.* Chrystal (47) has reported the insect to be present on *Abies cilicica* Carr., *A. cephalonica, A. forrestii* Craib., *A. pindrow* Spach, *A. firma, A. procera, A. grandis, A. fraseri* Poir and *A. faxoniana* Rehd. & Wils. Balch (7) has reared the insect on *Abies alba, A. lasiocarpa* Nutt., *A. concolor, A. grandis* and *A. balsamea.* To this list can be added *A. lasiocarpa* var. *arizonica* Lemmon on which the insect was observed by Francke-Grosmann (73), *A. nordmanniana* by Marchal (106), and *A. amabilis* Forbes and *A. magnifica* Murr. by Dallimore and Jackson (55). The relative susceptibility of all these species has not been fully determined, but it is generally agreed that *Abies alba* is a susceptible species which suffers moderately from attack, while *Abies balsamea* is a highly susceptible species with poor power of recovery. Even within these species, individual trees vary considerably in the degree of infestation.

(3). Further Observations on Resistance and Susceptibility

The writer has seen undoubted evidence of resistance to *Adelges* species by host trees in north-east Scotland and elsewhere, broadly corresponding to what has been reported by other investigators. One of the most striking instances occurred in the Botanical Gardens, University of Aberdeen, where an outbreak of *Adelges strobilobius* in 1953 caused severe chlorosis on European larch but left Japanese larch almost completely unattacked. Since both species were approximately the same age and height (5 to 7 feet), and were intimately intermingled with locked crowns, the differential infection could not have occurred by chance, and it may be assumed that Japanese larch possesses a high level of resistance to this insect. The primary hosts may also exhibit varying resistance according to species. In 1951, at Banff (Alberta, Canada) lines of young ornamental trees of the Colorado spruce *Picea pungens* Engel. were heavily galled by *Adelges abietis,* yet the many individual spruce trees of the variety *Kosteriana* Masters, standing in the same nursery lines, showed no sign of galling, and appeared to be highly resistant.

Individuals of Douglas fir also appear to possess a measure of resistance. In the dry summer of 1950, at Millbuie, Black Isle, Inverness-shire, a small plantation of *Pseudotsuga taxifolia* planted in 1945 showed pronounced chlorosis and yellowing of foliage as a result of attack by *Adelges cooleyi,* but two trees in the middle of the stand were completely green and normal and almost uninfested. No subsequent observations on these individuals have been made to confirm the permanence of resistance.

The stand of young Silver firs at Dunecht also shows examples of apparent resistance to *Adelges nüsslini.* Much of the *Abies alba* regeneration has proved susceptible, and no doubt many instances of uninfested individuals are due to pseudoresistance of the escape type. However, there are some examples of *Abies alba* where an inherent resistance appears to be involved. For example, the tree A8 appears never to have been infested, although its crown is interlocked with that of the moderately infested tree A9. Both trees are about eight feet tall and fourteen years of age, and were growing at the same rate until the latter became attacked. Presumably both have almost identical soil sites and microclimate, so that the influence of environmental factors can be discounted. It seems very probable that A8 has a measure of inherent resistance, at least at a low level. This was subjected to experimental test in 1953. On 1st June a single branch was infected with an estimated number of 7,000 eggs from *Adelges nüsslini* hiemosistentes' clutches, and subsequently several thousands of neosistentes settled on the young shoots. By the spring of 1954 this number of developing sistentes had been very substantially reduced, possibly indicating resistance, but the subsequent destruction of the tree in timber operations has prevented further observations.

Some other *Abies* species in the Dunecht stand show a high level of resistance to *Adelges nüsslini.* All the specimens of *Abies grandis, A. lowiana, A. homolepis* Sieb & Zucc. and *A. firma* show no sign of the presence of the insect in spite of being subject to chance infection since at least 1946 and probably earlier. *Abies procera* appears to show resistance at a low level, since on the shoots of young trees and on the main stem and shoots of older trees very small numbers of sistentes have been observed to mature and oviposit. There is no tendency for higher levels of infestation to be reached. *Abies veitchii* is present in the stand in the pole stage (30 feet). The six specimens all show a light to moderate infestation of the main stem, but hardly any infestation of the crown. This species can be classed as susceptible, at least in relation to stem attack by *Adelges nüsslini.*

As to the primary host for *Adelges nüsslini,* the specimens of *Picea abies, P. glauca* Voss and *P. pungens* at Dunecht show no sign of galling by this insect, although some trees at least have regularly intercepted the air-borne sexuparae. However, without experimental proof it is not possible to say that these species are resistant or immune to attack. *Picea orientalis* is definitely susceptible and is successfully used as a primary host by *Adelges nüsslini.*

Adelges piceae appears to be less specific in its preferences for host trees in north-east Scotland, yet degrees of resistance or of susceptibility are exhibited by various *Abies* species. At Craibstone and elsewhere *A. lowiana* Murr. and *A. concolor* have never shown any sign of infection and may be considered highly resistant. Ordinarily *A. grandis* and *A. firma* show no signs of infection and may be similarly classified. However, in recent years a stand of pole-stage *grandis* has been heavily attacked under circumstances unfavourable to the trees, and this outbreak is of unusual interest. *A. procera* and *A. magnifica* usually show resistance at a low level, but at Craibstone have been observed to take on light to moderate infestations. *A. veitchii* and *A. alba* appear to be susceptible in the pole stage. In various places very small populations have been found on mature trees (80 years and older) of *A. alba, A. amabilis, A. cephalonica, A. veitchii* and *A. procera.* North-east Scotland is well equipped with many species of exotic Silver firs of various age classes, but they usually occur as single ornamental trees or as small blocks, so that it is difficult to gauge their reaction to *A. piceae* under true forest conditions.

(4). Experimental infections

(a) On Adelges nüsslini.

A series of infections of small trees was carried out in 1952 and 1953 in order to determine the relative susceptibilities of various species. With two exceptions, small potted trees and slightly larger planted trees were used, so that the tests can only be considered as a measure of the virulence of *A. nüsslini* on juvenile trees.

In greenhouse infections of potted trees, it was found that the progredientes develop quite normally on *Abies alba, A. procera, A. concolor, A. grandis* and *A. veitchii.* All species appeared to be equally and fully susceptible to infection by the progredientes, provided that flushing shoots were available for feeding.

Experimental Infections of Abies Species with Adelges Nusslini Neosistentes

Table 14.

Date	Species of Abies	Tree	Place	No. of Eggs	Survival in following spring
21-5-52	A. grandis	G4(p)	Bot. Gdns.	1,000	nil
30-5-53	,,	G5(p)	,, ,,	3,000	nil
30-5-53	,,	G6(p)	,, ,,	2,000	nil
30-5-53		G7	,, ,,	5,000	nil
30-5-53	,,	G2	Dunecht	2,000	nil
28-4-52	A. concolor	C1(p)	Bot. Gdns.	100	nil
30-5-53	,,	C2(p)	,, ,,	3,000	nil
21-4-52	A. procera	N4(p)	Bot. Gdns.	100	nil. Test partly invalidated by small nos. of eggs and by frost damage to crown.
30-5-53	A. veitchii	V2(p)	Bot. Gdns.	3,000	A small proportion have matured and oviposited in spring 1954. Majority died in 1st stadium.
14-5-52	A. alba	A1	Bot. Gdns.	4,000	A large proportion matured and oviposited in spring 1953. Infestation of tree now complete.
1-6-53	,,	A37	Dunecht	2,000	Old trees: a large proportion matured and oviposited successfully in spring 1954.
1-6-53	,,	A38	,,	2,500	

Tests were also made on these hosts, both in the field and in the Botanical Gardens, to determine their susceptibilities to sistentes. Infections were made by the transference of clutches of eggs laid by hiemosistentes on *Abies alba* at Dunecht. In all cases an adequate settlement resulted, although only one-third to two-thirds of the transferred eggs became neosistentes fixed on the new host. All infested shoots developed slight abnormal swellings, but the persistence of infestation varied considerably according to species. These reactions are listed in Table 14 which follows. The symbol (p) represents a small potted tree.

These experimental infections, as well as those already described in connection with the migration of gallicolae, confirm the field observations that *Abies grandis* and *A. concolor* are highly resistant to *Adelges nüsslini.* It is noteworthy that even though the neosistentes did not survive diapause on these species, their inhibition of normal vascular development in the twigs has resulted in slight but definite chlorosis of the foliage of infected branches. The ready infection of *Abies alba* confirms its susceptibility, but the low survival on *A. veitchii* indicates that shoots may possess a measure of resistance, at least in this individual. The trees A37 and A38 were exceptions to the general use of small trees for infection. These two individuals were large mature trees of *A. alba,* windthrown in the gale of January, 1953, but maintaining root contact with the soil and thus remaining green. In each case the leader and leader whorl was infected, and it was especially interesting that attack has developed successfully in view of the fact that the upper crown of mature trees never becomes infested in nature. It indicates that the nutritional condition of the leader whorl may be quite satisfactory, but that other factors operate in the mechanism of its resistance.

(b) On Adelges piceae.

Similar experiments were carried out in 1952 and 1953 in relation to *A. piceae.* Infections were carried out both in the field and in the greenhouse; greenhouse infections are valuable as tests of immunity, but probably do not represent a true gauge of host resistance in the field, due to the abnormal condition of the tree and the greatly reduced effect of climatic and biotic factors unfavourable to the insect.

It was found that the progredientes of *Adelges piceae* developed with equal facility on potted trees of *Abies alba, A. concolor, A. grandis, A. procera* and *A. veitchii* in the greenhouse. This indicates that factors of resistance are less operative or inoperative in the leaf.

In relation to the sistentes, only young trees were used for infections; most were potted trees or transplants, but trees G13 and G14 were thicket stage *Abies grandis* about fifteen feet tall, and were infected on the stem at breast height. Table 15 lists the experiments by species.

EXPERIMENTAL INFECTIONS OF ABIES SPECIES WITH ADELGES PICEAE NEOSISTENTES

TABLE 15.

Date	Species	Tree	Place	No. of eggs	Survival in following spring
7-5-52	A. grandis	G11(p)	Bot. Gdns.	100	nil
10-9-52	„	G15	Craibstone	500	nil
15-9-52	„	G13	„	350	nil
15-9-52	„	G14	„	500	nil
16-10-52	„	G10(p)	Bot. Gdns.	300	nil
6-4-53	„	G12(p)	Greenhouse	500	Very small survival; marked reduction of population in successive generations.
31-3-53	A. concolor	C3(p)	Greenhouse	1,000	Very small survival; marked reduction of population in successive generations.
7-5-52	A. procera	N5(p)	Bot. Gdns.	75	nil
11-4-53 16-5-53	„	N6(p)	Greenhouse	500 700	High rate of survival and multiplication of original population.
7-5-53	A. veitchii	V1(p)	Greenhouse	700	High rate of survival and multiplication of original population.
31-3-53	A. alba	A4(p)	Greenhouse	1,000	High rate of survival and multiplication of original population.
31-3-53 7-5-53	A. alba	A5(p)	„	800 400	High rate of survival and multiplication of original population.

The use of these young trees in a heated greenhouse for experimental infections invalidates to some extent the results as a gauge of susceptibility and resistance for the various species under forest conditions, since *Adelges piceae* appears to flourish best on the main stems of pole stage trees. Nevertheless it is interesting that in the greenhouse *Abies grandis* and *A. concolor* should have cast off the pest, while *A. procera*, *A. veitchii* and *A. alba* have maintained the infestation. The high resistance of the *A. grandis* in the thicket stage to stem infection is also significant.

(5). The nature of the resistance mechanism

Painter (122) has considered the cause of resistance to be generally a complex of factors unfavourable to the insect rather than any single factor. The basis to the host's resistance is three-fold, incorporating:

(i) preferences shown by the insect for oviposition, food or shelter;
(ii) antibiotic factors of the plant operating against the insect;
(iii) tolerance, or the ability of the plant to repair damage or to recover from infestation.

The plant factors of resistance are listed as colour, hairiness or waxiness of the epidermis, lignification or other protective cell structures, growth vigour, growth habit, capacity for recovery and repair, pH concentration, and specialised chemicals such as tannins, proteins and alkaloids.

In the case of the Silver fir *Adelges*, the resistance mechanism appears inoperative against the progredientes, but effective against the sistentes, as experimental infections have shown. A similar phenomenon of differential resistance to the grape *Phylloxera* occurs in certain vines, as Zweigelt (157) has recorded. The vine roots may be heavily galled by the virgo generation but the leaves of the same plant may be quite resistant to the fundatrix generation. Zweigelt explains this phenomenon as an effect of the marked evolutionary specialisation in feeding by the fundatrix, which is unable to adapt itself to the slightly different nutritional environment of the resistant host. The virgo, being a less specialised feeder, is more widely adaptable to different hosts. By analogy with the grape *Phylloxera*, the successful adaptation of the progredientes of the Silver fir *Adelges* to many host species may be the effect of incomplete specialisation of feeding.

The factors of host resistance to the Silver fir *Adelges* will now be considered, mainly in relation to the sistentes. The adverse effect of these factors is particularly directed against the first instars, partly because these are the active crawlers well equipped to express instinctive preferences for food and shelter, and partly because they are the first stage to encounter antibiotic factors of nutrition.

Antibiotic Factors. When the shoots of a resistant species such as *Abies grandis* or *A. lowiana* are attacked by the sistentes of *Adelges*, the great majority perish in first instar diapause. These shoots do not appear to show any gross morphological or anatomical differences from those of a susceptible species such as *Abies alba.* Accordingly there seems a probability that the cause of resistance lies in some chemical factor such as a nutritional deficiency, the pH of the sap, or the presence of some toxic substance. In the foregoing section it has been shown that nutritional deficiencies are not likely to account for attack or non-attack in individuals of *A. alba*, but further investigations, particularly the chemical analysis of recognised resistant species, are necessary to confirm or disprove this hypothesis. In the next section it will be shown that the host pH or some allied factor appears to have some bearing on resistance by species. No investigation to show the presence of toxins has been made, but various references in the literature suggest its possibility. Painter (122) in 1951 commented that little is known about the chemical aspects of antibiosis, and so far no-one has named and isolated a specific chemical causing high mortality of insects on resistant plants. Büsgen et al. (27) have stated that resin is the tree's means of protection against pests and diseases. Francke-Grosmann (73) has recorded that buds of vigorously growing *Abies grandis* often exude enough resin to kill any sistentes of *Adelges piceae* which settle upon them, while weak trees are unable to do so. The present writer has seen copious resin flow from the stem bark of *Abies grandis* heavily attacked by *Adelges piceae*, and while it killed the sistentes along its path, this resin could not be considered a factor of resistance. Furthermore, the leading shoots of young *Abies alba* are abundantly equipped with resin canals, but do not thereby gain any evident protection from the feeding of *Adelges nüsslini.* Tannin is a substance which may repay investigation in relation to Silver fir resistance to *Adelges.* The writer has found that tannin substances, extracted with alcohol, were much more abundant in the bark of attacked *Abies grandis* than that of unattacked individuals. Nienstaedt (116) has recently shown that the high concentration of pyrogallic tannin in the bark of resistant *Castanea* species is responsible for retarding the growth of the chestnut disease *Endothia parasitica.*

Rate of growth. The rate of growth is also a possible factor of resistance, although no simple correlation has been found in relation to attack by Silver fir *Adelges* during the course of this investigation. It is commonly held that vigorous trees are less susceptible to pests and diseases than enfeebled trees. This view is supported by Francke-Grosmann

(74) who found that *Abies grandis* grows less vigorously in the shade, and on such trees weak buds are liable to be killed by *Adelges piceae*. It is disputed by Chrystal (50) who has recorded that *A. cooleyi* rarely attacks unhealthy Douglas fir, such as trees weakened by fungal attack, and by Balch (7) who believed that fast-growing Balsam fir favoured the multiplication of *A. piceae*. Wilford's (154) "careful studies have shown no correlation between immunity and size, rate of growth or morphology," in relation to attack by *A. abietis* on Norway spruce.

Flushing. Francke-Grosmann (70) has considered that the time of bud-flushing is an important factor in the susceptibility of individuals of *Abies alba* to attack by *Adelges nüsslini*. In general she found that early flushing trees are rather more susceptible to twig attack than late flushing trees.

The present writer has also found some relationship between the date of flushing and the resistance of individuals and species to attack by *Adelges nüsslini*, although it cannot be said that resistant trees are invariably late flushing. All trees possess a pseudo-resistance to attack by progredientes of *A. piceae*, because of the delay between the hatching of the insect and the appearance of the new shoot. To a smaller extent this is also true of *A. nüsslini* since early hatching progredientes frequently perish because the buds have not flushed concurrently. Late flushing is partly responsible for the rarity of the progredientes of *Adelges nüsslini* on such species as *Abies grandis*, *A. procera* and *A. lowiana*. At Dunecht in 1953, these three species did not flush until the end of May and the beginning of June, that is, about a fortnight later than the period of peak abundance of neoprogredientes. In the case of *Abies alba* at Dunecht, most young trees produced new shoots in the first fortnight of May, so that young tissues were available for the great majority of crawlers, whether progredientes or sistentes. However, there may be as many as six weeks between the comparable stage of flushing in late and early individuals. Very early flushing trees produced new shoots as early as 23rd April in 1953, and in such shoots some differentiation of the vascular tissues had taken place before the first crawlers arrived. Consequently, the disruption of the conduction system of leaf and twig was not so complete as in trees flushing a fortnight later. Very late flushing individuals, producing new shoots in the beginning of June, escaped leaf infestation almost entirely, but they did not appear to be less susceptible to the sistentes.

Bark Thickness. Bark thickness is effective only as a control over the degree of stem infestation by sistentes of both *Adelges nüsslini* and *A. piceae*. In older bark, where a thick layer of dead cork cells covers the living periderm, the insect stylets are unable to penetrate to the nutritive layers below. In the case of *Abies alba*, bark of a total thickness of 10 mm. has usually a sufficient depth of dead tissue to prevent feeding by the sistentes. This condition is found along the greater length of the stem of mature trees. Certain species such as *A. lowiana* and *A. firma* have a plated or flaky outer layer of dead bark, even on pole stage trees, which may partly account for their high resistance. Balch (7) found that even heavily attacked stems of *A. balsamea* may later develop resistance by virtue of the protection which killed bark subsequently gives to the secondary periderm developing below. In cases where the thinner succulent bark remains unattacked, such as along the upper stem of mature *A. alba*, other causes of resistance must be sought, perhaps in the crawler's avoidance of shade or of smooth surfaces.

Bark Texture. The smoothness or roughness of the bark exercises considerable effect on the degree of infestation. In the case of stem attack, dense populations of both *Adelges piceae* and *A. nüsslini* develop only on coarse-textured bark. Three reasons for this preference are suggested:

(i) rough bark intercepts airborne eggs and neosistentes much more effectively than smoother types;
(ii) rough bark satisfies the crawler's instinct of stereotropism;
(iii) suitable nutritive areas composed of young parenchyma are associated with lentical aggregations and the crannies of the bark.

In the case of *Abies grandis* in the Craibstone stand the largest, fast growing trees were heavily attacked by *Adelges piceae* because they had developed a roughened bark. Unattacked trees showed a lower rate of diameter increment and still had a relatively smooth juvenile bark. Lightly infested trees bore fairly dense populations in the nodal areas, where the bark is roughest. Pole stage trees of *Abies veitchii* in the Craibstone plot have a much roughened bark covered with lentical groups and resin blisters along the lower stem, where dense populations of *Adelges piceae* have developed. In the same plot, pole stage *Abies magnifica* of the same age has a relatively smooth bark, and only nodal infestation has taken place.

The texture of the shoot bark, particularly in relation to the presence or absence of hairs, may also affect the willingness of the crawler to settle, but this possible aspect of resistance has not been explored. Annand (3) found that cotton aphids express a definite preference for glabrous leaves rather than for pubescent ones. Stereotropic responses may be involved in the preference of *Adelges piceae* for buds, and of *A. nüsslini* for the internodal areas of the young shoots.

5. pH STUDIES IN RELATION TO RESISTANCE

(1). Hypothesis of a Relationship between Host pH and Resistance

Since Adelgids are sap-sucking insects, there has been advanced the hypothesis that the degree of acidity of the host tissues is the controlling factor in resistance to infection by the insect. Accordingly it might be expected that Silver fir species known to be resistant to *Adelges nüsslini*, such as *Abies lowiana* and *A. grandis*, would lie within one pH zone, while known susceptible species, such as *A. alba* and *A. veitchii*, would lie within a different pH zone. Further, it could be supposed that the pH of resistant individuals of *A. alba* would lie outwith the zone of susceptible individuals of that species.

Relatively few publications on conifer pH have appeared, and accordingly a good deal of fundamental work on the technique of sampling for pH was necessary. However, the paper by Roberts and Doyle (129) on the pH of conifer leaves in relation to systematy, and the book by Small (138) were valuable guides. The paper by Fife and Frampton (68) on the feeding of the leaf-hopper *Eutettix tenellus* is also relevant. This work shows that in the petiole of the sugar beet leaf there is a rising gradient of pH from the cortical parenchyma inwards to the phloem. This rise guides the stylets to the phloem where the high pH most nearly approaches that of the insect saliva. When this gradient is upset by the treatment of seedlings with carbon dioxide, the insect inserts its stylets in the tissues entirely at random, only rarely reaching the phloem. Treated seedlings thus developed a temporary resistance to curly top virus disease, which the insect can only transmit by way of the phloem.

(2). Sampling

To test the hypothesis of a relationship between host pH and resistance, a series of readings of pH of tagged trees was taken during the period September 1952 to June, 1953. A mechanical fault in the equipment prevented the completion of readings over a whole year. It has become evident that there are considerable local and seasonal variations in the pH of any one tree, and thus sampling for pH should ideally cover a complete year, beginning with the flushing of young shoots in spring. Readings were taken once every month, occasionally more frequently, but it is clear that to obtain truly satisfactory results readings should be weekly, with as many samples per tree as possible.

The instrument used for this work was the Doran Mini pH meter, which is a modern, compact, battery model, in conjunction with a Calomel Electrode and the Doran "Hanging Drop" glass electrode capable of giving precise measurement of pH from as little as 0.15 ml. solution, if need be. The instrument was set up within the Forest Garden, Dunecht, so that the pH of the sample could be measured within a few minutes of its being cut from the branch. The technique for pH work is standard. A volume of 0.5 cc. of leaf or twig tissue is taken from the sample shoot and then crushed in a mortar. To this macerated tissue a volume of 5 ml. distilled water (that is, by 10 dilution) is added and the resultant fluid is strained through a cloth to remove coarse fragments. The pH reading is taken directly on this strained fluid. As a check against error in manipulation of the instrument, two readings from each sample fluid are taken.

It has been found that pH varies both seasonably and locally within a single tree crown. This variation may be summarised as follows:

(i) Variation according to function of the plant tissues. Leaves are always much more acid than the twigs which bear them. The main stem bark lies within the same zone as the twigs. Also sun-leaves are generally more acid than shade leaves but the divergence is relatively small.

(ii) Variation according to age (see Appendix 5, Tables 27 and 28). Older parts of the tree may have a higher pH than younger parts of tree. The pH of leaves rises with the number of years since they were flushed; similarly twig pH tends to rise according to age in years.

(iii) Variation by season (see Tables 16 and 17). In general the pH of any tissue rises through successive seasons following flushing. The sharp rise in pH of the new shoots during active growth following flushing is especially marked (see Appendix 5, Table 29).

(iv) Variation by weather. Activity in photosynthesis appears to result in a lower pH for any portion of the crown. On a cold cloudy day, pH especially of the leaves may be slightly higher than on a warm sunny day.

(v) Local variation within the crown (Appendix 5, Table 30). In similar samples cut from different parts of the crown on the same day, there are yet slight variations in pH which are not wholly explicable, except perhaps in terms of micro-climate.

These observations, although not substantially proven in all respects, made the standardisation of samples a most important feature of the investigation. Two types of plant tissues were used: first, the leaves of the current year's shoot; and second, the twig or axis of the current year's shoot. There is a very considerable divergence between the pH zones of each type. Accordingly it is important that during preparation of the test fluid, no mixture of the two tissues should occur. The leaves must be stripped cleanly from the twig, neither pulling away strips of the twig bark nor breaking off to leave the base of the needle still inserted on the axis. Also, the location of the sampling in the crown was standardised as far as possible. In small trees, the sample shoot was always selected from the middle of the crown where shoots were of moderate length and vigour; the aspect of the crown is not important in small trees. In older trees, the most vigorous shoots from the lower, accessible branches were used, and taken always from the same aspect of the crown. Because of local or diurnal variation of pH within a crown, samples from each tree were taken three times at intervals over the day, when time permitted.

The variability in the pH of samples is very important, and necessitates the use of a large number of samples during the year to give very accurate results. In this investigation, a relatively small number of samples per tree was taken, and the final results are considered to be tentative but very suggestive.

(3). Measurements of pH on Silver fir Species Resistant or Susceptible to Adelges nüsslini

The main series of measurements of pH is presented in Tables 16 and 17, which show values for leaves and twigs respectively, from shoots flushing in spring 1952. The value of pH recorded for any particular date and tree is the mean of the actual readings taken on one or more samples. The number of samples is given in brackets. Trees are grouped arbitrarily as *Susceptible*, or *Resistant*, on the basis of species. However, the actual degree of infestation is somewhat variable according to the individual tree. The tree A8 (*Abies alba*) is an uninfested tree which may be resistant. Tree V3 (*A. veitchii*) although bearing a moderate infestation of the main stem, has not taken any crown infestation and may possess a measure of resistance to twig infection. Among the resistant species tree N3 (*A. procera*) does show in fact a very small stem population so that it cannot be considered wholly resistant. None of the individuals of *Abies grandis* or *A. lowiana* showed any trace of infection by *Adelges nüsslini*. Another factor which should be noted is that the trees are not uniform in age or size. Trees A8, A9 and A3 are young individuals of *Abies alba* averaging fourteen years of age and eight feet in height. G2 is a small *Abies grandis* about six feet tall and nine years old. V3, N3, L1 and L2 are pole stage trees averaging thirty years of age and thirty feet in height. Trees N1 and N2 were 45-foot *Abies procera*, of which the stems were lightly and heavily infected respectively.

In these tables, mean readings for each tree over the period 17th September, 1952, to 25th June, 1953, are shown at the bottom of each column. The resistant group has means between 3.60 and 3.66 for the leaves, and between 4.86 and 5.01 for the twigs. The susceptible group has means between 4.00 and 4.52 for the leaves, and between 5.29 and 5.56 for the twigs. Statistically analysed (Dept. of Statistics, Aberdeen University), it has been found that the differences between the two groups are very significantly greater than the variation between trees within groups (P <0.01). There is also a trend of

COMPARATIVE STUDY OF THE pH OF YOUNG LEAVES OF ABIES SPECIES SUSCEPTIBLE AND RESISTANT TO ADELGES NUSSLINI (SHOOTS FLUSHING IN 1952 AND 1953)

TABLE 16.

	(1) SUSCEPTIBLE				(2) RESISTANT			
Tree	A8	A9	A3	V3	N3	G2	L1	L2
Species	A. alba	A. alba	A. alba	A. veitchii	A. procera	A. grandis	A. lowiana	A. lowiana
Condition	Not infested: possibly resistant	Moderately infested	Heavily infested	Moderate stem infestation	Fairly resistant	Resistant	Resistant	Resistant
17 Sep. 52	4.00(4)	3.68(4)				3.35(3)		
3 Oct. 52	4.21(1)		3.86(3)	4.08(3)	3.40(4)			3.35(3)
15 Nov. 52	4.00(1)		4.06(2)	4.37(2)	3.53(3)		3.24(1)	3.64(2)
29 Dec. 52	4.15(1)	3.82(1)	4.18(2)	4.44(1)	3.78(1)		3.48(1)	3.40(1)
29 Jan. 53	4.15(3)	4.19(3)	4.16(3)	4.36(3)	3.54(3)		3.63(3)	3.63(3)
5 Mar. 53	4.33(2)	4.22(2)	3.99(2)	4.25(2)	3.58(2)	3.60(1)	3.53(2)	3.55(2)
30 Mar. 53	4.20(1)	4.08(1)	4.49(2)	4.62(2)	3.77(2)		3.81(2)	3.77(2)
27 Apr. 53	4.61(1)		4.08(1)	4.82(1)	3.90(1)		3.77(1)	3.65(1)
28 May 53	4.45(1)		3.97(1)	4.65(1)	3.69(1)	3.70(1)	3.70(1)	3.82(1)
11 Jun. 53	4.31(1)			4.85(1)	3.77(1)	3.63(1)	3.86(1)	3.68(1)
25 Jun. 53	4.22(1)		3.92(1)	4.72(1)	3.63(1)	3.70(1)	3.42(1)	3.84(1)
Mean	4.24	4.00	4.08	4.52	3.66	3.60	3.60	3.63

COMPARATIVE STUDY OF THE pH OF YOUNG TWIGS OF ABIES SPECIES SUSCEPTIBLE AND RESISTANT TO ADELGES NUSSLINI (SHOOTS FLUSHING IN 1952 AND 1953)

TABLE 17.

	(1) SUSCEPTIBLE				(2) RESISTANT			
Tree	A8	A9	A3	V3	N3	G2	L1	L2
Species	A. alba	A. alba	A. alba	A. veitchii	A. procera	A. grandis	A. lowiana	A. lowiana
Condition	Not infested: possibly resistant	Moderately infested	Heavily infested	Moderate stem infestation	Fairly resistant	Resistant	Resistant	Resistant
17 Sep. 52	5.35(4)	5.47(5)				4.82(3)		
3 Oct. 52	5.58(1)		5.24(3)	4.98(3)	4.47(4)			4.65(3)
15 Nov.52	5.63(1)		5.23(2)	5.12(2)	4.76(3)		4.64(1)	5.27(2)
29 Dec. 52	5.56(1)	5.20(1)	5.55(2)	5.15(1)	4.90(1)		4.96(1)	4.92(1)
29 Jan. 53	5.45(2)	6.00(3)	5.39(3)	5.22(3)	4.75(3)		5.17(3)	5.20(3)
5 Mar.53	5.32(2)	5.41(2)	5.17(2)	5.28(2)	5.04(2)	5.03(1)	4.71(2)	5.13(2)
30 Mar.53	5.49(1)	5.77(1)	5.49(2)	5.72(2)	5.36(2)		5.51(2)	5.15(2)
27 Apr. 53	5.57(1)		5.52(1)	5.51(1)	5.32(1)		5.08(1)	5.09(1)
28 May 53	5.30(1)		5.19(1)	5.28(1)	5.28(1)	5.01(1)	4.98(1)	5.05(1)
11 Jun. 53	5.06(1)			5.83(1)	5.21(1)	4.68(1)	5.27(1)	
25 Jun. 53	4.70(1)		4.79(1)	5.04(1)	4.63(1)	4.75(1)	4.32(1)	4.61(1)
Mean	5.36	5.56	5.29	5.31	4.97	4.86	4.96	5.01

increase in pH for each tree over the whole period, but this regression on time for an individual tree is quite small, only in the order of an increase of 0.0005 units per day. Thus in support of the original hypothesis of a relationship between acidity and resistance to *Adelges nüsslini* it is possible to say that the resistant species *Abies procera*, *A. grandis* and *A. lowiana* lie within a distinctly lower zone of pH, while susceptible species such as *A. alba* and *A. veitchii* lie in a distinctly higher zone.

Nevertheless, arguments against the hypothesis can be proposed. In the first place, the tree A8, which may be resistant, has pH values for leaf and twig well within the zone of susceptible species. Also the examination of a number of attacked and unattacked trees of *Abies alba* does not show any trend in the pH of newly flushed shoots according to degree of infestation (see Appendix 5, Table 29). Thus the insect's discrimination of host pH does not appear to apply to its preferences for individuals of *A. alba*.

Secondly, the progredientes of all stadia and the settling neosistentes appear indifferent or even attracted to the very acid condition of the new shoots in spring. For example, the pH of leaves of A8, on which progredientes of all instars developed after experimental infection, was as low as 3.38 on 11th June, 1953 (see Appendix 5, Table 29). The neosistens also has to face very acid conditions on first settling although it clearly does not deter or harm the very young insect. The average level of the pH of young sample twigs from five young *Abies alba* trees on 11th June, 1953, about a month after flushing, was 3.39 (see Appendix 5, Table 30). Nevertheless it is possible that the continued low value of twig pH in the resistant species is responsible for the observed fact that introduced sistentes frequently perish in the 1st stadium during diapause.

To the generations on the spruce, also, low pH does not appear to act as a deterrent. For example, the macerated tissues of a gall two weeks flushed gave a reading of 3.23. The neosexuales were found feeding on young shoots on 25th June, 1953, when a pH as low as 3.13 was recorded for the leaves. As to the fundatrix, preliminary observations do not appear to support the hypothesis that a low pH of buds is necessary for resistance. On 30th March 1954, 0.5 gm. samples of buds of spruce species were taken for pH determination and gave the following results.

Tree species	*Normal buds*	*Attacked buds*
Sitka spruce	5.42	—
Norway spruce	5.69	—
Oriental spruce	5.70	5.51

The conclusion to be drawn from all these data is that the degree of acidity of the twigs of *Abies* species or some associated factor may account in part for the varying resistance of Silver firs to infection by *Adelges nüsslini*. Possibly several unrelated factors are involved in the problem of resistance. This investigation scarcely reaches the threshold of knowledge in this interesting field.

(4). Further investigations on host pH and susceptibility to Adelges

Probing investigations of pH in relation to host susceptibility to *A. piceae* and *A. strobilobius* were made on two occasions.

(i) The pH values of the bark of the main stems of trees in the infested stand at Craibstone were measured on 8th January, 1954. Two 60-foot trees of *Abies grandis*, G1 and G2 with light and moderate populations of *Adelges piceae* respectively, were used. Full data are recorded in Appendix 5, Table 31, but a summary of results is given below.

Abies grandis	G1.	G2.
Mean pH of the infested zone (stump to 25 ft.)	4.87	4.76
Mean pH of the uninfested zone (25 ft. to top)	4.67	4.69
Mean pH of the whole stem	4.74	4.72
Total No. of samples at intervals along stem	(13)	(17)
Abies procera	N1.	N2.
Mean pH of the basal six feet of stem	4.97	5.09
Number of samples	(4)	(4)

Thus in the cases of both *Abies grandis* and *A. procera*, there is weak evidence of a higher pH in the infested stem bark.

(ii) The evidence of resistance to *Adelges strobilobius* by Japanese larch and of susceptibility by European larch has been recorded already. On 2nd September, 1953, a preliminary investigation was made into the pH levels of shoots of the two species. Full data are recorded in Appendix 5, Table 32, but a summary of results is given below.

Part of Tree	*European larch (moderately infested)*	*Japanese larch (uninfested)*
Long shoot twigs	4.05(4)	3.82(5)
Long shoot leaves	3.44(4)	3.42(5)
Dwarf shoot leaves	4.29(4)	4.09(5)

The figure in brackets gives the number of samples measured in each case. These results are suggestive of a zonation of pH according to resistance or susceptibility.

It has already been stated that for reliable data, pH measurements should be spread over a whole year, and a large number of samples should be taken. Accordingly the limited data shown above cannot be used as evidence in support of the hypothesis of a relationship between the level of host acidity and susceptibility or resistance to the Adelgid, but it is interesting that they do not dispute it in any way.

Chapter 4

FOREST RELATIONS

1. FOREST STATUS AND DISTRIBUTION OF THE ADELGES OF SILVER FIR

(1). The Spread and Present Distribution of A. nüsslini

Adelges nüsslini is believed to have been introduced into Central Europe on transplants of *Abies nordmanniana* taken from their natural habitat in the Caucasus or possibly Crimea. It seems probable that the insect arrived in Central Europe in the late nineteenth century, since the first probable record of its outbreak is that written by Altum (1) in 1885. He described a stand of mixed ten-year old Nordmann and Common Silver firs suffering a form of injury identical with that caused by *Adelges nüsslini* (Neustrelitz, N.E. Germany).

Since that time it has been reported almost throughout the range of Common Silver fir in Europe, where it has spread quickly both through natural agencies and the carriage of transplants. Its spread in Germany has been described in some detail by Hofmann (84, 85), who has recorded that in general really damaging attacks began about 1920, especially in Southern Germany. In Switzerland the first serious damage was reported in 1913, when Cholodkovsky (41) noted that heavily infested trees were being cut out by foresters. Since that time the pest has extended its active range to the whole country and has caused considerable concern for the future of *Abies alba* to the present day. In 1944, Swiss authorities (67) considered the problem so serious that a questionnaire was sent to all foresters in order to obtain a comprehensive picture of the extent of damage in Switzerland. The presence of the insect has also been reported in Hungary by Till (147) in 1941, in Czechoslovakia by Komarek (94) in 1942, and in Slovenia, Jugoslavia, by Kovacevic (95) in 1952. In France, *Adelges nüsslini* was recorded by Marchal (104) in 1906, and reports by Hubault (87) in 1936, and by the Ecole nationale forestière (64) in 1943 showed that the pest was increasingly important in many districts. The insect is also present in parts of Scandinavia, especially in Denmark, where extensive attacks have taken place since the last decade of the 19th century. Accounts of the severe outbreaks between 1916 and 1926 have been rendered by Boas (14), Bavngaard (11) and Chrystal (48).

In Britain the date of introduction of *Adelges nüsslini* is not known with any certainty. It is probable that it has been present in Scotland at least since 1901, when Bailey (4) described heavy attacks by plant-lice on six to seven years old *Abies alba* planted in Novar, Ross-shire. These early attacks were probably still quite rare, since in 1907 Burdon (26) stated that Silver fir in Britain did not appear to be very subject to attack by *Chermes*. However, in 1917, Steven (146) recorded that *Abies alba* was currently being severely damaged by *Adelges nüsslini*, and already suggested that an alternative, resistant species of *Abies* was needed to replace it. In 1926, Chrystal (48) noted that the Common Silver fir had been virtually abandoned as a planting tree in Britain.

In general it may be said that on the continent of Europe, *Adelges nüsslini* is an alarming but not a catastrophic pest. Its ability to arise suddenly in epidemic populations has led writers to emphasise its destructive capacity, but at present there appears to be normal regeneration and establishment of *Abies alba* in practice in European forests. This freedom from damaging infestation over extensive areas may yet prove a temporary status dependent upon the further dispersion of the insect; on the other hand it may be that the insect has reached a fluctuating equilibrium with its host which in a suitable climate and site may show decreased susceptibility. Certainly in Denmark, where very heavy attacks were experienced some thirty years ago, persistence in planting and tending *Abies alba* appears to have saved the tree as a planting species, although at that time many foresters considered it would have to be abandoned. At the present time *Abies alba* is commonly planted in many parts of Denmark, and the danger from *Adelges nüsslini* is not considered to be over-riding.

In Britain the frequent subjection of *Abies alba* to *Adelges nüsslini* has discouraged the planting of the species, and young plantations are now very rare. Similarly the natural regeneration of the crop appears to be precluded because of its susceptibility to attack. There are in fact very few stands of young *Abies alba* to be seen in Britain today. Nevertheless, mature individuals of the species are widespread, at least in Scotland, and it is accordingly not unlikely that at a very low endemic level, *Adelges nüsslini* persists on these old trees in many parts of the country.

(2). Descriptions of outbreaks of Adelges nüsslini in Scotland

The survey of the distribution of *Adelges nüsslini* in Scotland lies out with the scope of this investigation, but the condition of a few stands has been studied, and notes are given as a forest record. Outbreaks have taken place in young stands of *Abies alba*, and the examples at Dunecht, Monaughty and Inverliever forests show respectively the severity of current attack on natural regeneration, the partial failure of a plantation, and the partial recovery of a plantation following heavy attack.

Dunecht Estate, Aberdeen

Location: The Forest Garden, adjacent to Dunecht House. A full description of the plot was recorded by McNeill (107) in 1945.

Area: 13 acres, enclosed by a steel and netting fence.

Topography: a gentle north-facing slope between 400 and 450 feet above sea level.

Climate: Believed very similar to Aberdeen (see Appendix 1), hence a low, well distributed rainfall and mild temperatures.

Soil: A podsol of the Countesswells Association, lying on a boulder clay derived from granite or granitic gneiss. It has been regraded to a brown forest soil, perhaps as a result of former cultivation since the upper seven inches are a uniform brown loam with good crumb structure in places. Some parts show a light accumulation of raw humus and slight podsolisation. The B horizon shows imperfect drainage and a variably gleyed condition. An indurated layer, the gleyed B2 horizon about eight to ten inches thick, lies a foot below the surface (Plate 62).

Ground vegetation: Varied. Grasses (*Agrostis*, *Holcus* spp.) common, but locally patches of dominant gorse and broom, heath, brambles, mosses (*Polytrichum*, *Sphagnum* spp.), rushes (*Juncus effusus* with *Deschampsia caespitosa*), *Rhododendron* shrubbery, and mixed herbs (*Oxalis*, *Veronica*, *Viola*, *Potentilla* spp.).

Seed-tree cover: Mainly blown in the gale of January, 1953. Previously about 30 mature trees per acre, composed of 60 per cent. mixed conifers (Scots pine, European larch, Common Silver fir, Norway spruce, Douglas fir) and 40 per cent. mixed broad-leaved species (beech, oak, lime and others). There is also an avenue arboretum containing many exotic conifers, including *Abies* spp., about thirty years old.

Natural regeneration: Most of the area is sparsely to thickly covered with young trees of Common Silver fir and beech, mainly germinated 1930-1950. The abundance of these young trees is a striking example of the capacity for natural regeneration of these species given a suitable overwood and protection from grazing animals. (Plates 63, 68 and 69.)

The outbreak of *Adelges nüsslini:* The old seed-trees of *Abies alba* have been found to carry very small numbers of *Adelges nüsslini,* mainly on shaded shoots, and never on the upper crown. It is believed that these trees may have borne for many years an endemic population from which the present infestation of the young trees has arisen. Alternatively the source of the outbreak may have been the Silver firs planted in the avenue arboretum.

The young crop of *Abies alba* is currently undergoing heavy attack by *Adelges nüsslini.* The degree of attack in 1953 has been measured by enumerations from sample plots showing average conditions in the thicker patches of regeneration, but representing only one per cent. of the total area of the Forest Garden. Table 18 shows the results of these enumerations arranged in the following classes of injury. Class 1, all uninfested trees. Class 2 and 3, lightly to moderately infested trees, of which the leaders are attacked but have not yet died. Class 4, heavily attacked trees with dead leaders. Class 5 and 6, trees with marked die-back; dying and dead trees.

Attack on Abies Alba. Dunecht Forest Garden, August/September, 1953.

Table 18.

Injury Class	Height in feet of young trees								Totals	Per cent. of Total
	0—1	1—2	2—3	3—4	4—5	5—6	6—7	7+		
1	83	124	121	78	41	25	12	18	502	70.1
2 — 3	22	22	31	12	4	2	1	0	94	13.1
4	5	25	18	20	13	1	3	0	85	11.9
5 — 6	3	9	10	8	4	0	1	0	35	4.9
	113	180	180	118	62	28	17	18	716	

In these young trees there does not appear to be any correlation between height and severity of attack. Height is roughly correlated to age; for example, trees 1 to 2 feet tall are generally six years old or younger, trees 3 to 4 feet tall are eight years old on the average, and trees 5 to 6 feet tall are ten years old on the average.

The regeneration of *Abies alba* was most satisfactory and abundant before 1947, when the overwood contained some 55 mature crowns per acre and a fairly deep shade was cast. In 1947 about 50 per cent. of the overwood was removed in order to release the young growth. Thereafter the latter has become increasingly infested by *Adelges nüsslini,* and in the course of five or six seasons attack has extended to about 30 per cent. of the young trees. So far, very few trees have been killed outright, and there are signs that many individuals at present dying back will yet recover and develop new leaders. Nevertheless the probability is that the crop will fail to establish itself, partially at least, in spite of the fact that regeneration has taken place under the optimum conditions of lighting. The removal of the overwood in the gale of January, 1953 may lead to intensification of attack by *Adelges nüsslini.*

Monaughty Forest, Moray

Location: Two small plantations (1) 0.9 acre in compartment 80. (2) 0.8 acre in Compartment 69.

Climate: Similar to Aberdeen, but the summer is a little warmer and annual rainfall a little lower.

History: Planted in 1927 with 1,500 two-plus-two-plus-one transplants of *Abies alba.* Early establishment was not satisfactory, and in 1930 Compartment 80 was beaten up with two-plus-one *Abies grandis,* and Compartment 69 with *Abies grandis* and *Picea sitchensis,* numbers unknown.

(1) *Compartment* 80

Topography: A gentle north-facing slope at 450 feet above sea level.

Soil: A moderate podsol with an indurated B2 horizon about a foot down, and impeded drainage.

Ground vegetation: Mixed grasses with local patches of heather, bracken and mosses.

Condition of the crop: The area consisted in 1953 of two large, open, linked glades containing a poor crop of *Abies,* and flanked by neighbouring stands of Douglas fir, European larch and Scots pine. The plot is badly understocked since many of the *Abies alba* appear to have died subsequently to the beating up in 1930, probably as a result of the outbreak of *Adelges nüsslini.* Some of the surviving trees of *Abies alba* are in a suppressed condition as a result of combined frost and *Adelges* injuries. Small trees and the lower crowns of larger trees show varying levels of infestation, but not all are markedly injured thereby. Trees over 15 feet tall appear to be growing very well and have no population of *Adelges nüsslini* in the upper crown, although stem infestaion is common. *Abies grandis* in all height classes is completely free of *Adelges.*

A complete enumeration of all the trees in the plot was made by height classes and is recorded below. The figures in brackets show the numbers of trees moderately and heavily infested and markedly injured by *Adelges nüsslini.*

Table 19. Stocking in the Silver Fir Plot of Compartment 80, Monaughty Forest.

Height in feet									Total
0—5	5—10	10—15	15—20	20—25	25—30	30—35	35—40	40—45	
A. alba 57(32)	32 (6)	25 (2)	33	42	29	8	2	0	228 (40)
A. grandis 0	1	2	7	5	4	8	8	3	38

Thus, out of an original stocking of 1,500 *Abies alba* transplants only 228 have survived twenty-six years later, and only half of the latter have made satisfactory height growth. Yet it can be seen that many trees have recovered completely after being checked, presumably by *Adelges,* for many years after planting. The eventual recovery of others, currently held in check by *A. nüsslini,* may yet bring about a partial closure of the canopy. Yet whatever the outcome, the stocking and increment of this plantation must be considered very unsatisfactory.

(2) *Compartment* 69

Topography: A steep south-facing slope 250 to 350 feet above sea-level.

Soil: A rocky colluvial soil very slightly podsolised, with good crumb structure, free drainage and no indurated layer.

Ground vegetation: Sparse; rare grasses, herbs, mosses.

Condition of the crop: Stocking is adequate and the canopy is fairly close. The *Abies alba* trees show some evidence of suppression in their early years, and the fact that a beating up was required indicates that early establishment was unsatisfactory. This may also have been the result of an early outbreak of *Adelges nüsslini.* However, it seems that the trees recovered fairly well and fairly quickly, possibly because tree growth is very vigorous on this fertile south-facing slope. In 1953, trees of *Abies alba* showed satisfactory height and diameter increments. No trees were suffering heavy attack by *Adelges nüsslini* although small populations were found on some less vigorous shoots and on some main stems. *Abies grandis* has remained entirely uninfested by *Adelges.*

A 50 per cent. enumeration of the trees in this plot was made, and the results were doubled to give a measure of total stocking.

Stocking in the Silver Fir Plot of Compartment 69, Monaughty Forest.
Table 20.

Height (ft.)	Abies alba	Abies grandis	Picea sitchensis	Other species
0— 5	30			
5—10	46			
10—15	42			
15—20	50			
20—25	78		4	
25—30	68		4	
30—35	48	18	20	
35—40	8	8	12	
40—45		8	12	
45+		4	2	
	370	38	54	18

The smaller trees of *Abies alba* are suppressed because of their deeply shaded position, not because of insect attack. The taller trees are in healthy and vigorous condition and should ultimately form a fine stand. Stocking is complete only by virtue of the beating-up with *Abies grandis* and *Picea sitchensis*, without which several gaps in the canopy would be presented. The plot nevertheless illustrates that *Abies alba* is not inevitably doomed to complete failure when *Adelges* infestation does take place.

Inverliever Forest, Argyll

Location: Areas of compartments 124, 136, 176 and 134 on the west side of Loch Awe.

Soils: The district is rich in fine-grained rocks such as epidiorite, quartzite, and basic schists; in the colluvial areas on the lower slopes, where the Silver firs were planted, these parent materials have given rise to deep, fertile brown forest soils.

Ground vegetation: The natural cover of the lower slopes and sheltered pockets consists of an oak-grass community, with bracken and some heath constituents.

Climate: A high mean annual rainfall, about 80 inches, well distributed over the year; a mild winter; a cool summer marred by unseasonable late frosts and relatively few hours of bright sunshine.

History of afforestation: This region of heathland and hill pasture has been the site of afforestation since the early twentieth century. In choosing species for planting, early silviculturists were guided by the growth of the trees in a few planted pockets of old conifers already on the ground. Among these were some fine specimens of *Abies alba*, many of which are still standing. In consequence, during the period 1913-1918, this species was planted in small areas where the deepest and most fertile soils were available. During the early years of the decade beginning 1920 an epidemic of *Adelges nüsslini* occurred in these young plantations. Many of the trees assumed an unhealthy or moribund appearance, and it was finally decided to abandon the Silver fir and to replant with spruce. This was carried out during the period 1925-8; as a cleaning treatment, the Silver fir trees were severed or slashed across at the three or four foot level to eliminate competition with the young spruce transplants. The diameter of some of these stumps suggests that many individuals of Silver fir were already more than 10 feet tall when the cleaning was done.

In 1953, all the former Silver fir plantations were visited by the writer, who found that in general few of the Silver fir trees had survived the double catastrophe of *Adelges* attack and cutting back. Nevertheless, where individuals escaped the cutting out, Silver fir growth has been satisfactory. The best trees have reached 60 feet in top height after thirty-five years. Even some of the severed trees have developed new stems, and are currently growing and competing successfully with the spruce component of the stand. These trees can easily be picked out by the marked kink in the stem at the 3 to 4 feet level.

The replanted areas of former Silver fir are listed below by compartments.

Compartment 124. (25 acres)

Planted in part with *Abies alba* in 1918 on a gentle south-facing slope with a deep but rocky soil. Replanted with Sitka and Norway spruces in 1925-8. Over much of the area there are scattered odd Silver firs, most showing the stem kink indicative of decapitation.

In a corner of the compartment a plot of 0.4 acre was never cut back or replanted, and the original Silver fir crop has grown satisfactorily into a pole stage stand. In 1953, 410 trees remained in this plot, resulting in a closed canopy and a standing volume of 1,745 cubic feet (4,360 cubic feet, underbark per acre) at 35 years. This number of stems represents about half the original planting and indicates that deaths in the rows of trees have occurred at the rate of suppression found in any normal young conifer stand at the same age. It is not known whether or not this block was ever attacked by *Adelges nüsslini*, or if so how intense the attack was. However, it is conjectured that some degree of infestation took place in the early years following planting, partly because neighbouring stands were slashed, and partly because the stem analysis of a single tree showed very slow height growth in the early years. In 1953 the crop was in a healthy and vigorous condition, and almost entirely free of shoot infestation, but about half the trees bore slight to heavy stem infestation by *A. nüsslini*. The latter was apparently stimulated by a brashing carried out in 1950.

Compartment 136. (21 acres)

Planted in part with *Abies alba* in 1918 on a fertile, well-drained, ridged knoll, mainly north-facing. Replanted with Sitka and Norway spruces in 1925. Most of the Silver firs were severed at the 3 to 4 foot level during replanting, but some have recovered and in 1953 were maintaining a place in the upper canopy. On the top of the ridge a number of Silver firs were not decapitated during the cleaning, and in 1953 were growing well, commonly with a d.b.h. of 7 to 8 inches, and a top height of 55 to 60 feet. *Adelges* was not present on crown or stem.

Compartment 176. (17 acres)

Planted in parts with *Abies alba* in 1916, and replanted with other coniferous species in 1925-8. A few Silver firs have survived and are growing well, on the fertile tract of land along the edge of Loch Awe.

Discussion

In summary, the evidence from Inverliever Forest again shows the difficulty of establishing plantations of *Abies alba* in view of the danger of *Adelges nüsslini.* It is not known whether the infestation originated in the nursery from which the transplants were obtained, or whether it was derived from the pockets of old Silver firs already on the ground. It is clear that a very heavy epidemic rapidly developed after planting, and many trees must have died back before the decision to replant was taken. Nevertheless, in view of the high rate of survival in the corner of compartment 124 where cleaning was not carried out, and keeping in mind the rejuvenation of slashed stems elsewhere, it may be wondered whether or not the Silver fir plantations might not have made a good recovery from the outbreak if left to themselves. However, one cannot escape the conclusion that the planting of *Abies alba* at Inverliever is a risky venture, and perhaps an unprofitable one. Even allowing for the possibility of a complete recovery from attack, *A. alba* cannot be expected to give a timber yield approaching that of Sitka and Norway spruces on the same sites at Inverliever.

(3). The distribution and Forest Status of A. piceae

It is generally believed that *Adelges piceae* is a truly indigenous European insect on the Common Silver fir, *Abies alba.* Its natural range on the continent is probably as great as that of the host. However, since its influence on this host is rarely serious, it has not appeared so prominently in the European literature as has *Adelges nüsslini.*

In North America, *Adelges piceae* is an introduced species, no doubt imported on nursery stock from Europe. Balch (7) has traced its spread over the Eastern States and the Maritime Provinces from one or two original centres of infection beginning about the year 1900. Currently the insect is looked upon as a major pest causing severe mortality and loss of growth over considerable areas of Balsam fir, *Abies balsamea*, forest.

In Britain also *Adelges piceae* is an introduced species, but the date of arrival is uncertain. It could not have been earlier than 1603, when its host *Abies alba* was first brought into this country, and it could not be later than the early nineteenth century. The first positive records in the British literature are the brief essays on diseases of the Silver fir written by Miller (109) and Baldon (9) in 1839. Both writers were practicing foresters who described outbreaks of plant-lice which were very probably *Adelges piceae.* It is interesting that both writers referred to the die-back of young trees (young transplants and thicket-stage trees) although *A. piceae* is more often associated with older, pole stage trees. Baldon's note dates attacks by the insect in Scotland at least as far back as 1820; he also ascribed the failure of Balsam fir in Britain to infection by the same insect.

In the British and European literature the presence of *A. piceae* is noted sometimes casually and sometimes deliberately but it is nowhere designated as a major forest pest.

In the course of the present investigation it has been found fairly frequently on ornamental trees of many species, notably *Abies procera*, and in forest stands at Craibstone, Aberdeenshire. Some references have already been made to the sporadic infestations of *A. grandis, A. procera, A. veitchii* and *A. magnifica* at Craibstone. Only in the stand of *A. grandis* was a substantial number of trees affected by the outbreak; it affords a perhaps unique example of heavy stem infestation of this host species, and a brief description follows.

Craibstone Estate, Aberdeen

Location: A half-acre block of *Abies grandis* by Sunnybank cottage on the Craibstone-Kingswells highway, and bordering open fields on the north, south and west perimeters. (Plate 70.)

Soil: A brown forest soil with a large clay constituent.

Condition of the crop: *A. grandis* was planted in 1922. Growth was rapid, but the thinning of the stand was neglected so that stem diameter increment was relatively low, and the crowns remained small, thin and much affected by wind exposure. Height increment was quite good, and by 1952 the mean height of trees was 60 feet. The first thinning was not carried out until the winter of 1948-9. A few months later the central portion of the crop was wind-blown in a storm, and only 60 to 70 trees, mainly the well-rooted trees along the perimeter, stood firm. A few more trees were lost in successive winters, and the crowns of the remainder showed increasing injury from wind-exposure. Finally in the gale of January 1953, the rest of the crop blew down or snapped off.

The spindly and unhealthy condition of this stand of *Abies grandis* may have induced easy infection by *Adelges piceae*, which has probably long been present on the many species of *Abies* growing in the estate. The first sign of attack was noticed in 1932, but even by 1943 infestation was very slight and confined to four or five trees along the northern perimeter. In the latter year a wash of soap and paraffin was applied to these stems, and in the following year they appeared free of *Adelges.* In subsequent years the infestation again became apparent and spread to many of the remaining trees after the first windthrow. In 1950 and later years, many trees bore heavy populations of sistentes, mainly along the basal 10 feet of the stem. This infestation of a resistant host species can be attributed to the unhealthy and non-vigorous condition of stand, which may be supposed to have increased the favourability of the insect's nutritional environment and reduced the host's factors of resistance.

(4). The Effect of Site on the Severity of attack

There is evidently considerable variation in the severity of attack by *Adelges* on Silver firs in different countries, different districts and even different stands. This variation has led to much discussion about the effect of the site on the incidence of injury. No wholly satisfactory relationship has been established, but Chrystal (49) has summed up the situation as quoted: "There are many places where it is quite possible to grow healthy Silver fir even when the *Adelges* is present, but doing no serious harm. The usual explanation given in such a case is to say that the sum total of environmental factors such as climate, soil etc., are so favourable to the tree's growth that the insect never finds conditions favourable for attack on a large scale".

Some investigators have claimed local climate to be the significant factor in the control of intensity of outbreak. Francke-Grosmann (70) stated that when *Abies alba* is grown in warm places outside its natural range, it may grow too luxuriantly and yet suffer from summer drought, so that its ability to recuperate from attack by *Adelges nüsslini* is greatly reduced. Hubault (87) concurring with this view, doubted the advisability of planting Common Silver fir in warm districts and low altitudes in France. Bavngaard (11) studied the distribution of Silver fir and the intensity of *A. nüsslini* over the whole of Denmark, and showed that on the whole attack was less severe in districts with low mean temperatures and heavy rainfall; correspondingly he claimed that the insect thrives best in warm dry climates. Hofmann (85) cautiously asserted that there is no direct relationship between the incidence of attack and the site, but noted that the attacked trees recovered more rapidly on north-facing than on south-facing slopes in the hill forests of Southern Germany. Schimitschek (131) and Wimmer (155) considered rainfall to be the dominating factor; the latter thought that high rainfall accounted for the freedom of *Abies alba* from attack by *Adelges nüsslini* in the Black Forest above 600 metres. Hossli (86) contradicted the rainfall hypothesis, since he showed that in Switzerland heavy outbreaks have occurred in sites with heavy rainfall, and at altitudes up to 1,000 metres.

Soil has also been considered as a factor contributing to severity or reduction of injury by *Adelges*. Hoffmann (85) found that epidemics of *Adelges nüsslini* occurred on *Abies alba* growing above many kinds of geological formation, such as slate, sandstone, and basic rocks. In Denmark, Boas (14) stated that Silver fir crops on compacted clay or raw humus were less likely to recover from injuries by *Adelges* than stands on good soils. Bavngaard (11) found that even in climatic regions unfavourable to the pest, severe outbreaks could occur where trees were sited on poor soils. Chrystal (48) also commented on the striking correlation between poor soil and severity of infestation in Danish plantations. Little has been said in relation to outbreaks of *A. piceae*, but in stands of Balsam fir in the State of Maine, Brower (23) found that poorly drained or thin soils were the sites of heaviest injury to the crop. Balch (7) did not agree that there was any simple relationship between soil type or other site factors and attack on Balsam fir in the Maritime Provinces, but commented that thinly stocked and exposed stands were more frequently attacked than well stocked stands.

In view of the limited number of infested stands in Scotland surveyed in the course of this investigation, it is not possible to draw conclusions as to a relationship between site and severity of injury to Silver fir. The Scottish examples offer little support to the broad trend of views offered by other investigators in Europe and elsewhere. Silver firs at Inverliever with heavy rainfall, cool summers and good deep soils, suffered attacks quite as devastating as those in Monaughty Forest with light rainfall, warm summers and shallow soils. However, there is an interesting comparison between the sites at Dunecht and Compartment 80, Monaughty Forest, in that both have similar dry climates, and a shallow soil underlaid by a thick indurated layer. In each case it may be that the root competition enforced between the trees and other forms of vegetation has resulted in nutritional deficiencies in young trees which have accordingly a lower power of recuperation from attack. It is interesting also that Compartment 69, Monaughty Forest, where the *Abies alba* has made a good recovery from attack, has a deeper, more fertile soil which has not impeded root penetration. At Craibstone, the poor condition of *Abies grandis* following windthrow and wind-exposure in the stand, has led to the unusual infestation by *Adelges piceae*.

The general inference to be drawn from these investigations and from the literature, is that the relationship between site and severity of Adelgid attack is not fully understood, but that good soils and a cool moist climate result in better recovery of the trees than poor soils and a warm dry climate.

2. SILVICULTURAL ASPECTS

(1). The Regeneration of Abies species in Adelges-infested Regions

The silvicultural qualities of the common *Abies* species are well known to many British and European foresters. In Continental Europe, *Abies alba* is the most important member of the genus both within its natural range in the mountains of central Europe and in the many other regions where it has been introduced. In Britain, *A. alba* is said to grow to its largest size in western districts of high rainfall. It is frost tender, windfirm, exposure-resistant and deep-rooting. In mixtures its deep root system does not compete with that of shallow rooted species such as spruce, as Duchaufour (61) has recently shown. It also helps to maintain the fertility of the soil. *A. alba* is a handsome tree which grows to large sizes without extensive butt-rot, and produces good-quality timber. Above all, it is shade tolerant and is well adapted for easy regeneration under an overwood, whether by natural means under a shelterwood system, or by underplanting. This combination of silvicultural qualities is not equalled by any other forest tree in Britain. Of the other *Abies* species, *A. grandis* and *A. procera* have been the most popular during this century. *A. grandis* is characterised by remarkable height and diameter increment, and has useful shade-bearing qualities. *A. procera* is also a fast-growing shade-tolerant species with promise of excellent capacity for natural regeneration. The forest value of other Silver fir species in Britain is not certainly known, although some species, such as *A. concolor* and *A. lowiana*, are growing well in places.

It has already been shown that the importance of *Adelges piceae* to the regeneration of Silver fir crops in Britain is small, and this species will not be further discussed in this section. However, *A. nüsslini* is a very virulent pest of young trees and its silvicultural significance will now be assessed. European foresters have been much perplexed by the problem of safe natural and artificial regeneration of *Abies alba* in view of the incidence of *Adelges nüsslini*. It has been generally agreed by most European investigators, including Bavngaard (11), Sedlaczek (137), Schneider-Orelli (132, 136), Hubault (87), Hofmann (83, 85) and Ruedi (130), that young trees are little damaged when they grow under the shade of an overwood. Also the general belief has followed that natural regeneration under a shelterwood system and underplanting are the solutions to the problem of *Adelges* control. However, Hofmann (83, 85) and Francke-Grosmann (70) have pointed out that when the overwood is opened up to release the new crop, the young trees are in a condition very susceptible to infestation, perhaps because of the physiological upset occasioned by the sudden change of the foliage from shade-leaf to sun-leaf function. Schneider-Orelli (136) has recorded that even when the overwood is opened gradually, as in the selection forests of Switzerland, severe injuries may be inflicted on the young trees by attacks of *A. nüsslini*.

Sedlaczek (137) recommended planting of *Abies alba* with spruce and pine in the belief that the shade of these conifers would help to deter attack. Mixtures and underplanting have not proved a sure remedy. Mackenzie (103) has recorded severe infestation of *Abies alba* underplanted beneath young European larch at Novar, Ross-shire. Elwes and Henry (66) have quoted J. D. Crozier as stating that experiments in underplanting Scottish woods with Common Silver fir have proved a hopeless failure.

The current outbreak on the young crop of Common Silver fir at Dunecht Estate, and minor outbreaks on patchy regeneration at Midmar Castle and at Ballogie Estate, Aberdeenshire, exemplify that the species can be naturally regenerated under a shelterwood in north-east Scotland, but give little support to the hope that they can be successfully established. Equally the partial failure of open plantations of *Abies alba* at Monaughty and Inverliever forests and elsewhere in Britain, is not promising for the success of normal methods of planting. While it is not possible to draw positive conclusions from such limited experience, it can be safely said that the risk of *Adelges nüsslini* infestation continues unabated, and that the large scale use of *Abies alba* cannot be economically justified in Scotland at the present time. There is no reason why the planting of other *Abies* spp., with the exceptions of the susceptible *A. balsamea*, should not continue.

(2). Applied Control Measures Against Adelges

Quite apart from the silvicultural methods of regeneration discussed in the preceding section, there are means of control of *Adelges* by positive intervention in the attacked stand, such as cutting out infested trees, regular thinning and the use of insecticides.

Attempts to control outbreaks of *A. nüsslini* and *A. piceae* by cutting out the infested trees have been made for many years. Baldon (9) had been felling young *Abies alba* infested by *Adelges piceae* for a number of years before his publication of 1839. Cholodkovsky (41) noted that it was also a regular practice in Swiss stands infested by *A. nüsslini* in 1913, and it was evidently still the practice in Switzerland in 1944, according to the report of the Entomological Institute of Zurich of that year. The method has the merit of delaying the spread of *Adelges*, since the cutting out of heavily infested trees must greatly reduce the numbers of airborne eggs and crawlers. However, no amount of cutting short of clear-felling can eliminate the *Adelges*, because where even a few persist, the population is likely to build up to a large size within a short time. Moreover the method has the disadvantage of preventing the possible recovery of attacked trees, and of leaving gaps in the canopy. Perhaps it might be better to cut away only the upper crown, where the bulk of the population is sited on each tree, leaving a four-feet stump with low branches, so that rejuvenation might yet occur, as at Inverliever. However, it is not known whether any form of cleaning treatment is desirable in the infested stand.

Chrystal (48) and Boas (14) have been impressed by the marked improvement brought about by regular thinnings in infested stands of pole-stage *Abies alba* in Denmark. Chrystal observed that first thinnings appeared to result in a temporary increase in infestation of the main stems, but that with successive thinnings the population of insects gradually declines. Miller (109) as early as 1839 suggested green pruning as a method of control of *Adelges piceae*, and Chrystal (51) found it efficacious in reducing populations of *Adelges cooleyi* on Douglas fir, but it has nothing to recommend it in relation to *Adelges nüsslini* on *Abies alba.*

Chemical control against Silver fir *Adelges* has been in practice at least since 1839, when Baldon reported success in washing tress with tobacco liquor. In recent years a considerable number of experimental applications of insecticides have been made, notably by Hofmann (85), Clausen (52) and Schneider-Orelli (136) against *Adelges nüsslini,* and by Muller (113), Smith (139), and Hierholzer and Ludge (81) against *A. cooleyi.* Perhaps the most comprehensive of these was Schneider-Orelli's trials of a large number of chlorinated hydrocarbons and mineral oils on young stands of *Abies alba* infested by *Adelges nüsslini* in Switzerland. He found that even the most successful insecticides could not eliminate the insect, but the population could be drastically reduced. Nevertheless, because of the huge fecundity of *Adelges*, it is necessary to repeat sprayings every two or three years.

It can be said in summary that present methods of combatting *Adelges* are expensive and only temporarily effective. These additional costs of establishment of *Abies alba* confirm the general conclusion that large-scale planting of this species in Britain is not justifiable.

(3). Proposals for Experimental Plots of Abies Species

Although it has been concluded that *Abies alba* is not a satisfactory species for extensive planting in Britain, there is no reason why it should be entirely abandoned. The silvicultural qualities of the species are so useful that some effort to retain the tree should be made. The opinion of Professor Boas may be quoted in this respect: "On the whole, I must express the opinion based on wide experience, that the damage which *Chermes piceae* (i.e. *Adelges nüsslini*) has caused in this country (Denmark), does in no way entitle us to abandon the Silver fir, which we positively cannot afford to lose." (1924). Accordingly it is suggested that the following series of experimental plantings might be carried out to further determine the value of *Abies alba* and to test the susceptibility of other *Abies* spp.

(i) Experiment to determine the feasibility of raising a crop of *Abies alba* free from *Adelges* infection. It has been stated that the spread of *Adelges* takes place through the transport of infested nursery stock and through the wind carriage of the insects in various stages. It ought to be possible to raise uninfested transplants in nurseries remote from other Silver firs of all ages and species. There are many heathland nurseries which would serve admirably in this capacity. These transplants could then be planted on suitable sites equally remote from other Silver fir trees. Several such pure plantations might be formed, at graded ranges from the nearest possible source of infection, say, ½ mile, 1 mile, 3 miles, 5 miles.

(ii) The determination of the effect of site in relation to rainfall, temperature, drainage and soil type is probably beyond the scope of experimental plantings. However, it would be worthwhile to test the effect of the soil factor on the reaction of *Abies alba* to *Adelges*, under conditions otherwise favourable to the tree. For such an experiment, a district of high rainfall and relatively low temperatures should be selected. The district should carry the normal *Adelges* hazard, that is, a sprinkling of mature Silver firs within reasonable range of the proposed plantations. Plantations could be established on (*a*) a deep fertile soil with a northern aspect, (*b*) a shallow, indurated, or peaty soil with a northern aspect.

(iii) To test the susceptibility of the various Silver firs, a plantation of mixed *Abies* species could be formed. These species should include *A. alba*, *A. nordmanniana*, *A. veitchii*, *A. procera*, *A. grandis*, *A. concolor* and *A. lowiana.* In a district exposed to the usual *Adelges* hazard, it would be quite easy to gauge the rate of spread and the severity of infestation in the plantation.

(iv) Other variations might be tried on an experimental scale, such as the underplanting of various species with *Abies alba*, and mixed plantings of the latter with other trees such as beech or spruce.

Since only small plantations integrated in a general scheme of planting, would be required, these experiments should not prove unduly expensive or difficult, and would yield valuable data on the forest significance of the *Adelges* of Silver fir.

SUMMARY

1. The taxonomic rank of the Silver fir *Adelges* has been reviewed, and it has been decided to adopt for these insects the systematic position which Annand proposed in 1928. Accordingly *Adelges nüsslini* and *A. piceae* are considered as two of many species within the comprehensive genus *Adelges*. *Adelges* is one of two genera within the subfamily Adelginae of the family Phylloxeridae. The generic name *Dreyfusia*, which is commonly used in European literature on the Silver fir *Adelges*, is considered obsolete. The specific morphology of *A. nüsslini* and *A. piceae* has been illustrated and described by generation and instar. Some preliminary observations on the value of paper chromatography as a taxonomic technique have been made.

2. The literature on the biology of the subfamily Adelginae has been reviewed with particular reference to *Adelges nüsslini* and *A. piceae*. These species have heterogenous life cycles of great complexity, especially the former, which utilises both primary and intermediate hosts. Field and experimental studies of the biology of these two species have been made, and it has been found that the life cycles in north-east Scotland are similar to those recorded for these insects in other countries.

3. In the case of *Adelges nüsslini* the full cycle of five generations in alternation on Oriental spruce and Silver fir has been observed. It is of interest that the life cycle on the primary host has been observed in full, since the sexualis, fundatrix and gallicola generations have rarely been found in Britain, or indeed elsewhere. Limited studies of population on the intermediate host were also undertaken. The field tallies of progredientes have indicated that the higher the density of population on the leaves, the higher the ratio of alate to apterous forms.

4. In the case of *Adelges piceae*, the progrediens generation does not develop beyond the first instar in the natural conditions of north-east Scotland. It has been successfully reared in the greenhouse and the main features of its development have been recorded.

5. The factors influencing the level of population of these two species such as biotic potential, climatic factors and predators have been appraised and discussed.

6. The Silver fir *Adelges* are acknowledged as important forest pests which cause die-back in the crowns of young Silver firs in various parts of Europe and North America. The anatomical effects of attack on the host have been studied by a number of investigators whose papers are reviewed. A brief study of this aspect was made, which confirmed their findings. The writer's discovery of the formation of a pathological 'compression wood' in the stem of *Abies grandis* attacked by *Adelges piceae* is believed to be the first record of this phenomenon in a host tree in Britain.

7. Some of the chemical effects of attack by the progredientes of *Adelges nüsslini* on the leaves of *Abies alba* have been investigated. It has been found that attacked shoots hold considerably increased quantities of leaf sugar; accordingly it is held that attacked shoots are not more susceptible to frost injury than unattacked shoots, and frost is not the cause of the browning and desiccation of attacked leaves in spring. The chemical analyses of nitrogen and the various mineral constituents of the leaves, attacked and unattacked, served to indicate the general debility of attacked trees; this type of research could be of value in problems of insect nutrition.

8. It has been observed in the field that some individuals and species of the host genera show a degree of resistance to attack by Adelgids. This specific resistance has been experimentally proved. Various hypotheses to account for resistance and susceptibility to attack by *Adelges nüsslini* and *Adelges piceae* have been put forward. One of the most promising of these hypotheses, namely, that the level of host pH has a controlling effect on the level of insect survival, has been investigated in some detail. It has been found that certain resistant species of Silver fir lie within a lower zone of pH than that of certain susceptible species, but further research is required to determine with certainty that resistance is associated with the level of acidity of the host tissues.

9. Finally the forest status and distribution of the Silver fir *Adelges* have been discussed in relation to their international and local occurrence. Some examples of destructive outbreaks in various parts of Scotland have been described but it is not possible to attribute these to factors of the site unfavourable to *Abies alba*. It has been concluded that in Scotland, *Adelges piceae* is only of secondary importance, but that *Adelges nüsslini* is a primary forest pest of wide distribution and persistence on *Abies alba*. Accordingly the formation of stands of this species in Scotland would be a risky proposition, as it has been for many years. Silvicultural methods of control such as natural regeneration under an overwood and underplanting are unreliable, and chemical control is temporary unless repeatedly applied. Therefore the policy of planting *Abies grandis* or other conifers where *Abies alba* might seem silviculturally desirable is correct and should be continued at least in the light of our present knowledge. However, the degree of risk in planting *Abies alba* has not been fully ascertained and it is suggested that some experimental plantings should be undertaken to determine whether or not there might yet be a place for this otherwise desirable tree species.

APPENDIX 1

METEOROLOGICAL DATA

TABLE 21. CLIMATIC STATISTICS FOR ABERDEEN 1881-1915. (108)

	Monthly Mean Temperatures (°F.)			*Mean Duration of Daylight (hours)*	
	Mean	*Max.*	*Min.*	*Length of Day*	*Bright Sunshine*
Jan.	37.9	42.2	33.4	7.4	1.6
Feb.	38.3	43.2	33.4	9.4	2.6
Mar.	40.1	45.7	34.4	11.7	3.8
Apr.	43.7	49.8	37.6	14.2	5.3
May	48.2	54.5	41.8	16.4	6.0
June	53.9	59.9	47.0	17.7	6.1
July	56.6	62.8	50.3	17.1	5.1
Aug.	56.2	62.4	49.9	15.2	4.8
Sep.	53.0	59.2	46.7	12.8	4.1
Oct.	47.3	52.8	41.7	10.3	3.0
Nov.	42.1	46.8	37.4	8.1	1.8
Dec.	38.6	42.9	34.2	6.7	1.1
Ann.	46.3	51.9	40.7	—	3.8

		Rainfall (inches).			
	Days	*Mean*	*Highest*	*Lowest*	*Days with Snow*
Jan.	18	2.2	4.2	0.6	7.1
Feb.	17	2.1	5.0	0.2	6.7
Mar.	20	2.4	4.9	0.4	7.5
Apr.	17	1.9	5.0	0.4	2.8
May	17	2.3	4.9	0.6	0.8
June	15	1.7	4.6	0.5	0
July	17	2.8	5.9	0.6	0
Aug.	18	2.7	6.9	0.7	0
Sept.	17	2.2	6.4	0.6	0.1
Oct.	20	3.0	6.3	0.7	1.3
Nov.	19	3.0	6.4	1.2	2.5
Dec.	19	3.2	8.9	0.8	5.2
Ann.	214	29.5			34.0

TABLE 22. MONTHLY TEMPERATURE AND RAINFALL FOR ABERDEEN, 1952 AND 1953

Taken from Meteorological Records, Dyce Airport

	Mean T°F.	*Rainfall (in.)*	*Mean T°F.*	*Rainfall (in.)*
	1952		1953	
Jan.	33.0	2.5	39.5	1.6
Feb.	37.5	1.3	40.3	1.4
Mar.	40.9	3.6	42.5	0.3
Apr.	45.5	1.5	42.0	2.8
May	50.7	2.4	50.1	2.6
June	52.7	3.1	53.7	2.5
July	57.5	2.2	56.8	4.1
Aug.	56.5	3.9	56.9	3.3
Sept.	48.9	2.1	55.0	4.7
Oct.	45.9	2.7	49.3	1.7
Nov.	37.3	3.6	44.2	2.6
Dec.	35.5	2.9	41.8	2.7
		31.8		30.3

Appendix 1: Meteorological Data—continued

TABLE 23. TEMPERATURE: (BOTANICAL GARDENS, ABERDEEN) 1953

Weekly means, maxima and minima in the year 1953

Week	*Degrees Fahr.* *Mean*	*Max.*	*Min.*
Jan. 6—12	40	50	28
„ 13—19	45	53	33
„ 20—26	42	51	27
Jan. 27—Feb. 2	46	57	28
Feb. 3— 9	39	44	24
„ 10—16	40	47	28
„ 17—23	49	60	34
Feb. 24—Mar. 2	47	61	30
Mar. 3— 9	43	58	28
„ 10—16	44	57	31
„ 17—23	41	65	25
„ 24—30	45	70	32
Mar. 31—Apr. 6	42	54	28
Apr. 7—13	43	68	30
„ 14—20	41	57	31
„ 21—27	44	60	28
Apr. 28—May 4	47	70	36
May 5—11	47	68	42
„ 12—18	49	65	34
„ 19—25	51	70	44
May 26—June 1	51	60	40
June 2— 8	47	60	40
„ 9—15	51	65	45
„ 16—22	54	70	40
„ 23—29	57	76	51
June 30—July 6	54	68	50
July 7—13	53	60	53
„ 14—20	57	64	50
„ 21—27	55	60	48
July 28—Aug. 3	56	65	49
Aug. 4—10	60	72	46
„ 11—17	56	70	48
„ 18—24	53	70	46
„ 25—31	54	68	42
Sep. 1— 7	55	79	41
„ 8—14	54	75	42
„ 15—21	52	—	—
„ 22—28	51	60	40
Sep. 29—Oct. 5	46	70	36
Oct. 5—12	44	62	34
„ 13—19	46	59	33
„ 20—26	50	58	38
Oct. 27—Nov. 2	43	55	32
Nov. 3— 9	44	59	31
„ 10—16	46	58	32
„ 17—23	45	55	30
„ 24—30	47	56	39
Dec. 1— 7	45	55	28
„ 8—14	48	50	36
„ 15—21	39	51	26
„ 22—28	42	50	34

TABLE 24. TEMPERATURES (FOREST GARDEN, DUNECHT ESTATE, ABERDEENSHIRE) 1953

Weekly means, maxima and minima in the year 1953

Week	*Degrees Fahrenheit* *Mean*	*Max.*	*Min.*
Mar. 17—23	43	59	29
„ 24—30	46	70	34
Mar. 31—Apr. 6	41	51	28
Apr. 7—13	45	55	33
„ 14—20	44	58	30
„ 21—27	46	66	33
Apr. 28—May 4	51	72	37
May 5—11	50	68	39
„ 12—18	51	66	38
„ 19—25	53	66	46
May 26—June 1	52	64	43
June 2— 8	48	59	43
„ 9—15	53	66	46
„ 16—22	56	72	45
„ 23—29	61	80	52
June 30—July 6	58	70	51
July 7—13	56	66	50
„ 14—20	56	68	50
„ 21—27	56	67	48
July 28—Aug. 3	—	—	—
Aug. 4—10	61	77	51
„ 11—17	59	70	48
„ 18—24	55	64	46
„ 25—31	55	64	43
Sept. 1— 7	58	80	43
„ 8—14	54	75	43

APPENDIX 2

ESTIMATION OF CHLOROPHYLL CONTENT IN LEAVES OF ABIES ALBA ATTACKED BY PROGREDIENTES OF ADELGES NUSSLINI

Technique: Each sample of leaves of unit weight was crushed in a mortar with acid-purified sand and left standing overnight with approximately 40 ml. of methanol. Thereafter each was filtered through a Whatman's No. 1 filter paper and made up to 50 ml. No anthocyanin was present in the leaves. The coloured extracts were then compared in a Hilger Spekker Photo-electric Absorptiometer using a red filter. At these wavelengths the carotins do not absorb while the chlorophyll absorbs strongly. A standard curve was constructed using the solution from the unattacked tree A8, and serial dilutions of it; the solutions from the other two trees were compared on the standard curve. The solution from A8 adjusted to zero on the Spekker apparatus was used as the index.

Results: Results were obtained as shown in Table 25.

RELATIVE AMOUNTS OF CHLOROPHYLL IN ATTACKED AND UNATTACKED LEAVES

TABLE 25.

Date	Solution of tree (or dilution)	Class	Unit Wt. (gm.)	No. of Leaves	Spekker Reading	Per cent. chlorophyll (AP(D)8 = 100)
19-9-52	A8 soln.	1	1.720	100	0.000	100
	” ($\frac{3}{4}$) ”	—	—	—	0.183	—
	” ($\frac{1}{2}$) ”	—	—	—	0.266	—
	” ($\frac{1}{4}$) ”	—	—	—	0.382	—
	A9 ”	3	1.720	220	0.356	32
	A3 ”	4	1.720	156	0.338	35
8-10-52	A8 soln.	1	1.253	100	0.000	100
	” ($\frac{1}{2}$) ”	—	—	—	0.175	—
	” ($\frac{2}{5}$) ”	—	—	—	0.246	—
	” ($\frac{1}{5}$) ”	—	—	—	0.274	—
	A9 ”	3	1.253	216	0.256	23
	A3 ”	4	1.253	148	0.282	19
Mean	A9	—	—	—	—	27.5
	A3	—	—	—	—	27

APPENDIX 3

TECHNIQUE OF SUGAR ESTIMATION

Nelson's (115) modification of the Somogyi method was used for sugar determinations. The technique gives a measure of the free reducing sugar; it can then be used to give a measure of the total reducing sugar after hydrolysis of the non-reducing disaccharide. The subtraction of the first from the second results in a measure of the non-reducing disaccharide.

A standard range of glucose solutions was prepared in the following quantities per ml.:—(1) distilled water only, (2) 0.025 mg., (3) 0.05 mg., (4) 0.15 mg., (5) 0.30 mg. This range showed increase in sugar content by the increasing depth of blue colour in solutions, which were measured in the Hilger Spekker Photo-electric Absorptiometer. A curve of glucose concentration was prepared from these readings for use in comparing the extracts from leaf tissues.

The extraction of sugars from the leaves was done in the following way (Example 5th Feb. 1953). 3 gm. of fresh weight of each sample was boiled in 50 ml. ethyl alcohol (96%). Each alcohol extract was filtered into a flask, evaporated to dryness under reduced pressure, taken up with water and filtered into 25 ml. standard flasks. Toluene was added as a safeguard against contamination. Further dilution of the solutions was necessary to bring them into the standard range. 1 ml. of each solution was used for the Somogyi-Nelson colorimetric estimation.

Each ml. of soln. was pipetted into a test tube. This was followed by 2 ml. of a mixture composed of 25 ml. Reagent A and 1 ml. Reagent B. Tubes were boiled for twenty minutes in a water-bath, then cooled in running water. 1 ml. of arsenomolybdate was added, then 30 ml. distilled water were buretted into each tube.

These blue solutions were then tested on the Spekker apparatus in 15 ml. cells, using a red filter to give the reading of intensity of colour. These were translated by means of the curve to give values of free reducing sugar.

The values of non-reducing disaccharide were found by first hydrolysing the solutions. 1 ml. solution was heated with 1 ml. 1N H_2SO_4 in a water-bath for fifteen minutes. It was neutralised with 1 ml. 1N Na OH + 1 drop. It was then diluted by 5, and 1 ml. from this dilute solution was taken for colorimetric estimation of total sugar.

Total sugar — free reducing sugar = non-reducing sugar. The latter quantity was multiplied by a correction factor of 0.95.

CALCULATION OF QUANTITIES OF FREE REDUCING SUGAR AND NON-REDUCING DISACCHARIDE

TABLE 26.

Date	Tree	Wt. of fresh leaves in sample	Free Reducing Sugar (F.R.)			Total Reducing Sugar (T.R.)			Non-reducing sugar (N.R.)	
			Spekker	Conversion		Spekker	Conversion		T.R.—F.R. =N.R.	×0.95
		gm.		mgm/ml. soln.	mgm/100 gm. fresh leaves		mgm/ml. soln.	mgm/100 gm. fresh leaves		mgm/100 gm. fresh leaves
19-9-52	A8	2.15	0.967	0.100	238	0.753	0.139	673	435	414
	A9	3.67	0.298	0.236	803	0.769	0.135	937	134	127
	A3	5.24	0.222	0.252	1,467	0.383	0.218	2,465	998	948
8-10-52	A8	1.56	0.949	0.097	777	0.776	0.134	2,190	1,413	1,345
	A9	1.56	0.683	0.154	1,234	0.533	0.185	3,020	1,786	1,703
	A3	1.56	0.283	0.239	1,918	0.305	0.234	3,830	1,912	1,818
5-2-53	A12	3.00	—	0.086	715	—	0.234	1,940	1,225	1,170
	A13	3.00	—	0.131	1,090	—	0.270	2,250	1,160	1,100
	A14	3.00	—	0.091	756	—	0.240	2,020	1,264	1,200
	A15	3.00	—	0.097	810	—	0.186	1,485	675	642

APPENDIX 4

TECHNIQUES OF NITROGEN ESTIMATION FOR LEAVES OF ABIES ALBA

The samples of foliage used for analysis in each series were chosen so as to approximate in physiological function and crown position, and to vary only in degree of attack.

In each series the Kjeldahl method of estimation was used, but only the analyses made on 27-Nov.-1952 will now be recorded. A known weight of leaves (approximately 0.1 gm.) was taken from each sample, dried in an oven and reweighed. This gave the moisture contents listed below.

Tree	*Sample*	*No. of leaves per sample*	*Fresh Weight (gm.)*	*Dry Weight (gm.)*	*% Dry Weight*
A16	1	4	0.1008	0.0450	44.6
	2	5	0.0962	0.0431	44.7
A17	1	8	0.0988	0.0428	43.3
	2	9	0.0939	0.0397	42.3

To each dried sample was added 0.6 gm. Se- HgO- K_2SO_4 catalyst and 2 ml. Anilar H_2SO_4. Each was heated in a Kjeldahl flask for three hours to destroy ring nitrogen compounds. The resultant clear liquid was made up to 25 ml. with distilled water. The NH_3 was estimated in a Markham apparatus by use of a 5 ml. sample with 5 ml. 20 per cent. NaOH. The NH_3 was absorbed in a flask of boric acid and titrated with N/50 H_2SO_4.

The following amounts of H_2SO_4 were required in sample titrations.

Tree	*Sample*	ml. H_2SO_4				*Mean*
A16	(1)	0.510	0.460	0.477	0.439:	0.4715
	(2)	0.475	—	0.459	0.481:	0.4717
A17	(1)	0.177	0.154	—	0.145:	0.1587
	(2)	—	0.166	0.145	0.210:	0.1737

The multiplication of each mean quantity of H_2SO_4 with the factor $\frac{5 \times 14}{\text{Dry weight} \times 50}$ gives the quantity of total nitrogen in mg/gm dry weight.

For example: Sample A16 (1)

$$\text{Total nitrogen} = \frac{0.4715 \times 5 \times 14}{0.0450 \times 50} = 14.67 \text{ mg/gm. dry}$$

weight. The final results have already been shown in Chapter 3, para. 3(4), page 45.

The amino-nitrogen content was analysed in a Van Slyke apparatus on 20th December, 1952. From each sample branch, 4 gm. leaves were taken, dropped into boiling alcohol, extracted overnight, filtered and then evaporated to dryness. The residue was made up to 25 ml. for Van Slyke determination by the Spectrochemistry Department of the Macaulay Institute.

APPENDIX 5

MEASUREMENTS OF pH IN ABIES SPECIES

Table 27. Variation in pH Values of Leaf and Twig at Progressive Ages. (Abies Alba, Dunecht Estate)

Date of Sampling	*Tree*	*Age of Shoot (since flushing)*	*Leaf pH*	*Twig pH*	*No. of samples*
11-6-53	A36	0.1 years	3.37	3.65	5
	(not	1.1 „	4.21	4.76	5
	attacked)	2.1 „	4.33	4.97	3
		3.1 „	4.51	5.12	1

Table 28. Variation in pH Values of Leaves at Progressive Ages. (Abies Alba, Dunecht Estate)

Date of sampling	*Tree*	*Age of Shoot (since flushing)*	*Leaf pH*	*No. of samples*
8-8-53	A8	0.3 years	3.61	3
	(not	1.3 „	3.85	3
	attacked)	2.3 „	3.86	2
		3.3 „	4.09	1

pH Values of Leaves and Twigs of Young Elongating Shoots in Early Summer, 1953. (Abies Alba, Dunecht Estate)

Table 29.

Tree	Approx. date of full flushing	Leaves			Twigs			Lvs.	Twigs	Condition
		28 May	11 Jun.	25 Jun.	28 May	11 Jun.	25 Jun.	Mean 28 May—25 June 1953		
A8	1st week of May	3.55	3.38	3.61	3.83	4.20	4.21	3.51	4.08	Unattacked: supposed resistant.
A3	3rd week of May	—	—	3.68	—	—	3.82	—	—	Heavily attacked.
A27	1st week of May	3.35	3.50	3.31	3.68	3.81	4.00	3.37	3.83	Heavily attacked.
A28	1st week of May	3.43	3.56	3.73	3.53	3.62	4.05	3.57	3.73	Unattacked.
A23	5th week of May	—	—	3.22	—	—	3.63	—	—	Late flushing. Slightly attacked.
A22	1st week of May	3.29	3.33	3.88	3.45	3.62	4.22	3.50	3.76	Slightly attacked.
A36	1st week of May	3.75	3.39	3.25	3.91	3.65	3.88	3.46	3.81	Older tree (25 years). Slightly attacked.
Mean (excluding A3 and A23)	1st week of May	3.47	3.43	3.56	3.68	3.78	4.07			
	No. of samples	(5)	(5)	(5)	(5)	(5)	(5)			

TABLE 30. LOCAL VARIATION OF pH WITHIN A SINGLE CROWN (TREE A36, ABIES ALBA, DUNECHT ESTATE)

Date	Crown position	Newly-flushed shoots		Penultimate shoots	
		Leaves	Twigs	Leaves	Twigs
11-6-52	Upper crown	3.28	3.90	4.30	4.82
	„ „	3.33	3.49	4.32	4.94
	Middle „	3.45	3.63	4.22	4.88
	„ „	3.44	3.55	4.17	4.45
	Lower „	3.45	3.60	4.05	4.72
	Mean	3.39	3.63	4.21	4.76

TABLE 31. pH MEASUREMENTS ALONG THE STEM OF ABIES GRANDIS ATTACKED BY ADELGES PICEAE (CRAIBSTONE ESTATE 8-1-54)

Trees: G1 Lighty infested.
G2 Moderately infested.

Height above Stump	G1	G2	Height above Stump	G1	G2
1 ft.	4.80	4.69	28 ft.	—	4.72
4 ft.	4.80	4.61	31 ft.	4.63	4.63
7 ft	4.80	4.70	34 ft.	—	4.62
10 ft.	4.79	4.84	37 ft.	4.52	4.62
13 ft.	4.89	4.84	40 ft.	—	4.62
16 ft.	4.80	4.83	43 ft.	4.70	4.67
19 ft.	4.90	4.78	46 ft.	—	4.83
22 ft.	4.90	4.78	49 ft.	4.74	4.78
25 ft.	4.78	4.74	—	—	—

Mean Values	1—25 *ft.*	28—49 ft.	*Whole Stem*
G1	4.87	4.65	4.74
G2	4.76	4.69	4.72

pH MEASUREMENTS OF EUROPEAN LARCH HEAVILY ATTACKED BY ADELGES STROBILOBIUS, AND JAPANESE LARCH SHOWING A HIGH LEVEL OF RESISTANCE TO ATTACK. (YOUNG TREES 6FT. TALL IN THE BOTANICAL GARDENS, ABERDEEN. 2-9-53)

TABLE 32.

Tree No.	European Larch			No. Tree	Japanese Larch		
	Long Shoot		Dwarf Shoot		Long Shoot		Dwarf Shoot
	Twigs	Leaves	Leaves		Twigs	Leaves	Leaves
E.L.1	3.91	3.29	4.62	J.L.1	3.60	3.31	4.06
E.L.2	3.75	3.21	3.96	J.L.2	3.68	3.47	4.00
E.L.3	4.07	3.49	4.52	J.L.3	3.86	3.41	3.78
E.L.4	4.55	3.78	4.07	J.L.4	3.67	3.16	4.08
				J.L.5	4.31	3.73	4.52
Mean	4.04	3.44	4.29	Mean	3.82	3.42	4.09

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