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An Annotated Bibliography of
Gilpinia hercyniae (Hartig),
European Spruce Sawfly.

by

P.H.W. Adams* and

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1981

DEPARTMENT OF FORESTRY
COMMONWEALTH FORESTRY INSTITUTE
UNIVERSITY OF OXFORD



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AN ANNOTATED BIBLIOGRAPHY OF GILPINIA HERCYNIAE

(HARTIG), EUROPEAN SPRUCE SAWFLY

SUMMARY

In the manner of classical biological control severe outbreaks of European spruce sawfly, Gilpinia hercyniae (Hymenoptera; Diprionidae), have been regulated mainly by the action of a nuclear polyhedrosis virus disease but also by the intervention of parasitic insects. Over 260 papers covering all aspects of G.hercyniae between 1834 - December, 1979 are listed, the majority with abstracts. A subject index is provided.

1 INTRODUCTION

Gilpinia hercyniae (Hymenoptera, Diprionidae), European Spruce Sawfly, is only one of many insect defoliators of spruces (Picea spp.). However, in the decline and subsequent stabilisation of populations in two major outbreaks, one in Canada in the 1930's and the other in Wales during 1968-72, a nuclear polyhedrosis virus disease has played a dominant note. Very extensive introductions of parasitic insects also played a significant, though secondary part. The natural ecology and dynamics of this very epizootic virus have been more intensively documented than that of any other pest of forestry or of agriculture. The study has revealed an interesting picture of a microbiological agent acting successfully in the manner of classical biological control. In addition, by work on both sides of the Atlantic ocean, some of which is still in progress, the fundamentals of the epizootic process are illustrated. From such emerging principals much can be derived that has general value in interpreting the dynamics of epizootics and the relationships of pathogens with their insect hosts and environment. In addition to their intrinsic interest such findings have value in the management of pest populations and here knowledge of the rate of growth of infection and the inseparable consideration of its dispersal capacity are particularly important.

Documentation of epizootics of virus diseases in insect populations has been unsatisfactory. Though 'wilt' and 'polyhedroses' have been recognised as diseases of insects since the late 19th Century, their viral aetiology was not appreciated until the 1940's. For instance, Balch (1939) referred to what was probably nuclear polyhedrosis virus in G.hercyniae larvae in Canada as 'a type of 'wilt''. Furthermore, the onerous process of diagnosis of disease in large samples of insects, essential in recording epizootic progress, may have had a discouraging effect.

Growing dissatisfaction with the performance, and even the continued availability, of chemical pesticides has a beneficial influence on the development of other forms of insect control. Among alternative methods the use of microbial pathogens must take high priority for not only can many of these be formulated and stored with comparative ease but they can mostly be applied to crops using existing machinery. In many parts of the world very considerable

research and development effort is being put into microbial pesticides with especial emphasis on the use of nuclear polyhedrosis viruses. Such work cannot fail to benefit from an understanding of the ecology and epizootiology of insect diseases. Conversely, we must hope that this growing applied interest will generate further basic epizootiological and ecological studies.

Though well supplied by specialist literature, as witness over 260 entries in this bibliography, the dramatic control of European Spruce sawfly by a virus disease has often been neglected by compilers of the more general accounts of biological control of insects and of insect population dynamics. The infrequency of outbreaks of the host insect must have contributed to this, notwithstanding that it is precisely those insects which have demonstrable pest potential, but in which biological control is effective, that provide the most intriguing and significant examples of control.

Some notes on the confused history of the taxonomy of the sawfly itself will be found useful in reconciling the writings of different authors.

The genus Gilpinia is not naturally represented in the New World and confusion arose over which of the two morphologically closely similar species had been accidentally introduced into North America. The main steps in the process of sorting out this puzzle were intertwined with revisions at the generic level within the sawfly family Diprionidae. These steps are listed below.

- 1834 - Lophyrus polytomus described by Hartig.
- 1837 - Lophyrus hercyniae described by Hartig.
- 1910 - Rohwer points out Lophyrus is preoccupied and that the proper genus is Diprion.
- 1912 - Enslin perpetuates the genus Lophyrus and relegates L. hercyniae as a synonym of L. polytomus.
- 1913 - Escherich still recognises polytomus and hercyniae as distinct and continues to place them in Lophyrus.
- 1938 - S.G. Smith discovers cytological and biological differences between 'Diprion polytomum' in Canada and in Europe.
- 1939 - Possibly for the last time the genus Lophyrus is used, by Tragardh.
- 1939 - Benson proposes a new genus Gilpinia in which he places polytoma. He appears not to recognise hercyniae as distinct.
- 1940 - S.G. Smith now recognises two European forms one of which is cytologically identical with the Canadian form of D. polytoma.
- 1941 - The separate identities of Gilpinia polytoma and G. hercyniae are re-established by Reeks and the latter species alone is shown to be present in N. America.
- 1942 - The name Gilpinia hercyniae begins to come into use in the literature (e.g. Morris, 1942; Balch, 1942; Prebble, 1943). However some authors persist in the use of Diprion whilst others begin to revert from Gilpinia to Diprion (c.f. Balch, 1942 and 1958; Reeks, 1952 and 1953).
- 1974 - From Washington D.C., D.R. Smith publishes a check list of world Diprionidae in which he lists hercyniae and polytoma under Gilpinia. This can be taken as official N. American acceptance of Benson (1939).
- 1975 - Nevertheless some authors (e.g. Kaya, 1975; Smith, 1976) continue to perpetuate Diprion hercyniae.

This bibliography covers the period 1834-December, 1979.

2 BIBLIOGRAPHY

AIZAWA, K. (1963).

The nature of infections caused by nuclear polyhedrosis viruses.

Insect Pathology - an advanced treatise, Vol. 1, 381-456, ed. Steinhaus, E.A., Academic Press, New York.

A comprehensive review of nuclear polyhedrosis. The NPV of Diprion hercyniae is mentioned in a section on Hymenoptera, and is also referred to in the sections on susceptibility (concerning prepupal immunity) and infectivity (loss of virulence in storage).

ANDRÉ, E. (1879).

Species des Hyménoptères d'Europe de d'Algerie.

Beaune, France. Vol. 1.

Lophyrus polytomus and L.hercyniae are keyed as separate species.

ANGUS, T.A. (1956).

The reaction of certain lepidopterous and hymenopterous larvae to Bacillus sotto toxin.

Can. Ent. 88; 280-283.

Bacillus sotto is a pathogen of Bombyx mori larvae. The toxin it produces is associated with the crystalline inclusion found in sporulated cells of the micro-organism. The effect of the toxin on several insect species is recorded, including Diprion hercyniae (Htg), which is not susceptible; which is probably because the toxin is not soluble in its gut due to the comparatively low pH of 8.5.

ANON. (1953).

Distribution maps of insect pests, Series A, Nos. 34 and 35.

Commonwealth Institute of Entomology.

Map No. 34 shows world distribution of Gilpinia polytoma, and map No. 35 shows world distribution of Gilpinia hercyniae.

ANON. (1971).

Sawflies strike spruce.

Entopath. news 66; 10-12.

The outbreak of Gilpinia hercyniae in central Wales is reported on. A brief description of its life-cycle is given and damage symptoms are described. Also, two other species are mentioned; Pristiphora abietina on young Norway spruce and Pristiphora subarctica on older Norway spruce.

ANON. (1974).
Spruce sawfly, Gilpinia hercyniae.
Entopath. news 70; 12-14.

A brief description of the situation in Wales in 1974, and of economic damage caused by the sawfly.

ARUGA, H. (1963).
Induction of virus infections.
Insect Pathology - an advanced treatise, Vol. 1; 499-530, ed. Steinhaus, E.A., Academic Press, New York.

This review covers factors controlling the occurrence of virus infection under natural conditions; and induction by stressors, genetic factors and physiological conditions, also, there is a section on the mechanism of induction which refers to egg infection in the NPV of Diprion hercyniae.

ATWOOD, C.E. (1937).
The European spruce sawfly situation in western Quebec and Ontario.
Rep. ent. Soc. Ont. 68; 48-50.

The distribution of Diprion polytomum (Htg) on spruce in eastern Canada is briefly outlined. Two generations were observed in 1937. In rearing tests, the first adults emerged as early as 24th May, their offspring spun cocoons in mid-July and emerged as adults in late July or early August, and the second brood larvae were fully grown in late September.

ATWOOD, C.E. (1943).
A note on the artificial dissemination of disease attacking Gilpinia hercyniae (Htg).
Unpublished Rept, Forest Insect Laboratory, Fredericton N.B.

Not seen.

ATWOOD, C.E. (1960).
Present status of the sawfly family Diprionidae (Hymenoptera) in Ontario.
Proc. ent. Soc. Ont. 91; 205-215.

An annotated list is given of the 16 species of Diprionine sawflies found in Ontario, with an outline of their life histories and a discussion of the systematics of the group. Three of these, Neodiprion sertifer (Geoffr) and Diprion similis (Htg) on pines, and Gilpinia (Diprion) hercyniae (Htg) on spruce, were introduced from Europe. The others are indigenous, and the most important of them is N. swainei (Middleton) on jack pine. Control by DDT sprays and natural enemies is discussed.

BAIRD, A.B. (1937).
Biological control of the spruce sawfly Diprion polytomum Hartig.
Pulp Pap. Mag. Can. 38; (4) 311-315.

The programme of parasite introduction to eastern Canada is described. Egg, larval and cocoon parasites, 20 species in all were identified as suitable and liberated. Details of the laboratory rearing of one species of cocoon parasite, Microplectron fuscipennis, are given. The prospects of success of the programme are discussed.

BAIRD, A.B. (1939a).
Biological control of insect pests in Canada with reference to the control of the European spruce sawfly Gilpinia polytoma (Htg).
Rep. ent. Soc. Ont. 70; 51-56.

A review of biological control by parasites of several insect pests. The extent of the operation to introduce European parasites to control Gilpinia polytoma is described. Nearly 500 million parasites had been released. By 1937, some cocoons collected near a point of introduction of Microplectron fuscipennis showed up to 60% parasitism. This figure increased and the following year up to 75% parasitism was found in New Brunswick.

BAIRD, A.B. (1939b).

Progress report on biological control of the spruce sawfly Diprion polytomum Hartig.

Canad. Pulp Pap. Ass., Woodlands Sect. Index No. 480 (F-3) 1-6.

Not seen.

BAIRD, A.B. (1940).

A review of the spruce sawfly parasite situation.

Unpublished paper, Annual meeting of the Woodlands Section, Canadian Pulp and Paper Association, January 24-26, 1940.

The programme of parasite introduction from 1932 up to 1939 is described. Sawfly cocoons were imported from Europe in large numbers and parasites reared from them for release in Eastern Canada. By 1939, nearly 500 million parasites of several species had been released. Details of rearing and field introduction of the parasites are given. The results of the programme so far are discussed.

BAIRD, A.B. (1940 & 1941).

Spruce sawfly parasite situation 1940.

23rd Annual Meeting Proc. Woods Section Can. Pulp. and Pap. Association No. 616 (H-2) (10) Conf. ppr. and Pulp. Pap. Mag. Can. 42 (2): 159-161.

The programme of parasite introductions in Canada and the USA is reviewed. The biology and degrees of success of several species, mainly Microplectron fuscipennis on cocoons and Exenterus, Lamachus and Sturmia spp. as larval parasites are briefly described.

BALCH, R.E. (1934).

The European Spruce Sawfly (Diprion polytomum Hartig).

Spec. Circ. Div. For. Inst. Dept. Agric. Canada no. 8, 3pp, Ottawa March 1934. Rev. App. Ent. A22; 496.

Spruce infested with the sawfly was first observed in the Gaspé Peninsula in 1930. Spraying or dusting with calcium arsenate when the young larvae appear is completely effective, and may be used for control on valuable trees.

BALCH, R.E. (1936).

The European spruce sawfly outbreak in 1935.

Can. Ent. 68; 23-31.

The distribution and intensity of the infestation is reviewed, and the level of cocoon predation is discussed. The insect's bionomics and the damage to spruce are described.

BALCH, R.E. (1937).

The spruce sawfly outbreak in 1936.

Pulp Pap. Mag. Can. 38; 249-255.

Not seen.

BALCH, R.E. (1938).
Estimation of spruce sawfly hazard and need of salvage.
Canad. Pulp. Pap. Ass. Woodlands Sect. Montreal pp. 6.
Rev. Appl. Ent. 26; 6.

Suggestions are made for the collection of information on infestations of spruce by the sawfly. Both the condition of the trees and the abundance of the insect should be examined.

A method of estimating the degree of damage visually is given, using the amount of frass, the numbers of cocoons in litter samples, and larval samples.

BALCH, R.E. (1939a).
The outbreak of the European spruce sawfly in Canada and some important features of its bionomics.
J. econ. Ent. 32 (3); 412-418.

Notes on the life history of the insect, the number of generations per year, diapause, reproduction, flight, feeding habits, evidence of European origin and current distribution.

BALCH, R.E. (1939b).
The spruce sawfly outbreak in 1938.
Pulp Pap. Mag. Can. 40; (3), 199-204.

Not seen.

BALCH, R.E. (1940).
The spruce sawfly outbreak in 1939.
Woodlands Rev. 11, (3), 5-9.
Pulp. Pap. Mag. Can. 41; (2), 249-253.

A virus disease occurred during the hot dry summer of 1939 in southern New Brunswick (a two-generation area). The success of the parasites Microplectron fuscipennis and Exenterus sp. in biological control is described.

The current status of the pest in relation to natural control, introduced parasites, distribution and damage is reviewed. It is concluded that the 1939 weather conditions, diapause factors, disease and parasites have combined to prevent important increases in sawfly populations, and in many places a reduction has been noted.

BALCH, R.E. (1941).
The spruce sawfly outbreak in 1940.
Pulp. Pap. Mag. Can. 42; (3), 219-222.

Not seen.

BALCH, R.E. (1942).
The spruce sawfly outbreak in 1941.
Pulp. Pap. Mag. Can. 43; 385-388.

A report on the distribution and infestation of Gilpinia hercyniae in eastern Canada during 1941; on the damage caused and the effect of control factors including weather, disease, parasites and mammal predators. It seems unlikely that outbreaks of the severity and extent of those occurring up to 1938 will be repeated.

BALCH, R.E. (1943).
European spruce sawfly in 1942.
Pulp. Pap. Mag. Can. 44; 279, 281-282.

A brief report on research for the year, during which further decreases are reported in the Gilpinia hercyniae population in Canada.

BALCH, R.E. (1946).

The disease of the European spruce sawfly.

Bi-m Prog. Rep. For. Insect Invest. Dept. Agric. Canada 2 (5), 1.

Infection of feeding larvae just prior to cocoon formation leads to cocoon stages and adults carrying disease. The method of vertical transmission is under study. Dried extract of diseased larvae had been used to establish the disease in Newfoundland. Special sterile methods of larval sampling and rearing are necessary to determine the percentage infection.

BALCH, R.E. (1958).

Control of forest insects.

A. Rev. Ent. 3; 449-468.

A review of literature, which mentioned Diprion hercyniae as an example of biological control. The introduction of parasites, and the virus epizootic are briefly discussed.

BALCH, R.E. (1960).

The approach to biological control in forest entomology.

Can. Ent. 92; 297-310.

Biological control of European spruce sawfly and Balsam woolly aphid Adelges piceae in Canada is referred to. The general ecological concepts of biological control using natural enemies and pathogenic micro-organisms are discussed. The use of life-table studies in assessing the results is recommended.

BALCH, R.E. and BIRD, F.T. (1944).

A disease of the European spruce sawfly, Gilpinia hercyniae (Htg) and its place in natural control.

Sci. Agric. 25; (2) 64-80.

An account is given of the history of the disease and of the life cycle of the insect. Mortality caused by the disease is estimated from the results of population studies, and is demonstrated to be connected with dramatic falls in population levels of the insect. The nature of the disease itself is described.

BALCH, R.E. and HAWBOLDT, L.S. (1943).

Report on forest insects in New Brunswick, 1942.

Rep. Dep. Lands and Mines New Brunswick 1942; 116-118.

A further reduction in numbers of Gilpinia hercyniae in New Brunswick is reported, the virus disease being the major control factor. Other forest pests are reported on. A similar review by the same authors is given in: Report of forest insect conditions in Nova Scotia, 1942.

Rep. Dep. Lands for Nova Scotia, 1942; 50-54 (1943).

Both publications from Dominion Entomological Laboratory, Fredericton, N.B.

BALCH, R.E., REEKS, W.A. and SMITH, S.G. (1941).

Separation of the European spruce sawfly in America from Gilpinia polytoma (Htg) (Diprionidae, Hymenoptera) and evidence of its introduction.

Can. Ent. 73; 198-203.

The taxonomical status of the insect is reviewed with reference to morphology, cytology and reproduction. It is concluded that the thelytokous European species was introduced to Canada.

BALCH, R.E. and SIMPSON, L.J. (1932).

A European spruce sawfly, Diprion polytomum (Hartig) attacking spruce in the Gaspé Peninsula, Quebec.

Can. Ent. 64; 162-163.

A brief report on the initial outbreak in Canada. 2,000 sq miles were infested in 1931 (the outbreak was first noticed at the end of 1930) and white spruce was heavily defoliated. The only biotic control factors present were shrews and mice attacking cocoons. About 75% of the 1930/31 hibernating larvae were still dormant in summer 1932.

BALCH, R.E., SIMPSON, L.J. and PREBBLE, M.L. (1934).

The European spruce sawfly outbreak in the Gaspé Peninsula.

Rep. ent. Soc. Ont. 64, 1933; 57-59.

Rev. App. Ent. A. 23 236.

The first observation of Diprion polytomum on spruce in Gaspé was in 1930. An account is given of the bionomics of the insect, including diapause, effects of climate and sex ratio. The cocoons are spun in the ground, whereas in Europe they are found on the trees.

BALDWIN, H.I. (1939).

The European spruce sawfly in New Hampshire, 1938.

J. For. 37; 876-878.

The pest is thoroughly established in New Hampshire. An estimated 5 million board feet of spruce is expected to die in 3 to 5 years as a result of defoliation. This is a report of the work undertaken on this problem in 1938, which was mainly concerned with the introduction of the cocoon parasite Microplectron fuscipennis.

BALDWIN, W.F. (1954).

Acclimation and lethal high temperatures for a parasitic insect.

Canad. J. Zool. 32 (3); 157-171.

The effect of temperature on survival of females of Dahlbominus fuscipennis (Zett) was investigated in Canada in experiments in which the criterion was the time required for 50% mortality. The insect is a parasite of Gilpinia hercyniae (Htg), but the laboratory host was Neodiprion lecontei (Fitch).

BARCLAY, J.M. (1939).

The oviposition habits of some of the species of the genus Exenterus parasitic on sawfly larvae.

Rep. ent. Soc. Ont. 69, 1938; 29-31.

Observations are recorded on the oviposition habits of 6 species of Exenterus, females of which oviposited on larvae of Gilpinia polytoma (Htg) in the laboratory. The ways in which the eggs are attached to the host larvae are described, and it is shown that the six ichneumonids can be divided into two groups according to the method of attachment.

BEIRNE, B.P. (1975).

Biological control attempts by introductions against pest insects in the field in Canada.

Can. Ent. 107; (3) 225-236.

An analysis of the attempts to colonize at least 208 species of parasites and predators on about 75 species of pests. About 10% of attempts were successful from the economic viewpoint. Numbers of individuals involved in colonization, population dynamics and ecological consequences involved in colonization attempts are discussed in relation to their efficiency in biological control. Diprion hercyniae is mentioned as an example of a pest controlled by introduced parasites and a coincidental virus disease.

BEJER-PETERSEN, B. (1966).

The sawfly fauna on Norway spruce in a Danish plantation with a comparison to some other N.W. European countries.

Ent. Meddr. 34, (3) 221-232.

Sixteen species collected in S.Jutland are listed and records of their periods of appearance for two years are given. The Danish complex resembled the German in number of species (85%) and abundance. Great Britain, another country where spruce is introduced, has only half the German species.

BENES, K. (1975).

Sawflies new to fauna of Czechoslovakia (Hymenoptera, Symphyta).

Acta entomol. Bohemos Lav. 72; 121-126.

Twenty-five species of sawflies are recorded for the first time from Czechoslovakia. A key is provided for the separation of the adult females of the genus Xyela, and notes are given on the world distribution and food-plants of the 25 species, which include Gilpinia hercyniae (Htg).

BENSON, R.B. (1933).

Diprion polytomum (Htg). A sawfly not previously recorded from Britain.

Ent. mon. Mag. 69; 153-154.

A report on the discovery of two specimens, one in the New Forest in 1906 (by Miss E.F. Chawner) and another in Hampshire in 1912.

BENSON, R.B. (1935).

The alien element in the British sawfly fauna.

Ann. appl. Biol. 22; 754-768.

A comprehensive review mentioning Diprion polytomum and its first reported appearance in Britain, and other species on spruce, pine and larch. The other four spruce species mentioned are all of the genus Lygaeonematus, which also has species on larch.

BENSON, R.B. (1939).

On the genera of the Diprionidae (Hymenoptera:Symphyta).

Bull. ent. Res. 30; 339-342.

A key to world genera of Diprionidae. The genus Gilpinia is proposed on grounds of anatomical detail, and divided into two groups; the polytoma group, including G.fennica, pallida, polytoma and virens, and the socia group including G.abieticola, frutetorum, laricis, rufiventris, socia and several lesser known species from parts of Asia.

BENSON, R.B. (1940).

Sawflies of the Berkhamsted district.

Trans. Hertfordshire Nat. Hist. Soc. 21; 177-231.

Sawflies found in the district are listed with notes on their ecology and classification. Specimens of Diprion pini and D.similis are recorded, and a footnote reports that Gilpinia polytoma was bred from a larva found in Whippendale Wood in June 1940.

BENSON, R.B. (1950).

An introduction to the natural history of British sawflies.

Trans. Soc. Brit. Ent. 10, 45-142.

A general account of field collecting notes, biology and natural enemies is followed by a detailed section on the distribution of sawflies. The various geographical origins of sawfly types are discussed, and lists of

species found in Britain are given together with food plants and probable distribution range. Also dealt with are polymorphisms, chromosome numbers parthenogenesis and intraspecific categories. Gilpinia hercyniae is mentioned with regard to its general biology, diapause, mammalian predators, virus, adult flight, dispersal by man, host plant and parthenogenesis.

BENSON, R.B. (1951).

Key to the species of British Gilpinia.

Handbooks for the identification of British Insects VI (2); 46.

Four species are keyed: Gilpinia frutetorum, G. pallida, G. virens and G. hercyniae. A note is given on the confusion that existed between G. hercyniae and G. polytoma, the latter species occurring only in North and Central Europe.

BENSON, R.B. (1954).

Obituary.

Ent. mon. mag. Feb 1954. Vol. XC; 46.

Miss E F Chawner, who died on October 16th 1953, discovered Gilpinia hercyniae (Hartig) and Nematus fagi Zaddah as British species.

BENZ, G. (1960).

Histopathological changes and histochemical studies on the nucleic acid metabolism in the polyhedrosis-infected gut of Diprion hercyniae (Htg).

J. Insect. Path. 2; 259-273.

A study on the time sequence of histochemical reactions following infection of mid-gut cells with NPV. The fate of infected nuclei and the formation of polyhedral inclusion bodies is described.

BENZ, G. (1963).

Physiopathology and histochemistry. Insect Pathology - an advanced treatise Vol. 1; 299-338. ed. Steinhaus, E.A., Academic Press, New York.

A comprehensive review of general insect physiopathology is followed by a section dealing with pathogenic organism, in which both DNA and RNA virus are reviewed. The infection process in Diprion hercyniae is briefly referred to.

BENZ, G. (1967).

Untersuchungen über den Nucleinsäurestoffwechsel gesunder und virusinfizierter Larven der Fichtenblattwespe Diprion hercyniae (Hartig).

Vjschr. naturf. Ges. Zurich. 112, (1); 29-70. (German).

The metabolism of nucleic acids in healthy and diseased larvae was studied, using autoradiographic and biochemical methods. Infection by the virus stimulates the synthesis of DNA, the cell producing enzymes necessary for DNA replication and virus multiplication. It then interferes with chromatin synthesis, and the breakdown of host chromatin is induced. Virogenic stromata are formed and the synthesis of virus DNA begins at very high rate in these structures. When the host DNA has been completely broken down, viral DNA synthesis stops.

BERLAND, L. (1947).

Hyménoptères tenthredinoides.

Faune de France 47; 469pp.

A brief description of Diprion polytoma (Hartig) is given on pp 379-380, with its known distribution in France and a list of its parasites.

BEVAN, D. (1975).
Biological Control: Gilpinia hercyniae.
Rep. Forest. Res., Lond. 1975; 38.

A note on the importing of cocoons of Gilpinia sp. from Austria for the laboratory breeding of parasites prior to release in the field. A few specimens of one ichneumon, Gelinae sp. have been found from cocoons in Wales, and another ichneumon, Lamachus marginatus Brisch from east England.

BEVAN, D. and DAVIES, J.M. (1971).
A spruce sawfly, Gilpinia hercyniae.
Rep. Forest. Res., Lond. 1971; 89.

A brief report on the outbreak of the sawfly in Mid-Wales. A control trial using a natural virus was being planned.

BEVAN, D. and DAVIES, J.M. (1972).
The spruce sawfly, Gilpinia hercyniae.
Rep. Forest. Res., Lond. 1972; 101.

The infestation in Mid-Wales is briefly reported on, as is the outbreak of a virus disease, which may control the insect.

BILLANY, D.J. (1976).
The European spruce sawfly, Gilpinia hercyniae.
Rep. Forest Res., Lond. 1976; 36.

A brief report on the Mid-Wales infestation. Natural parasites found earlier were not found again in 1975, which may be due to the effect on populations of the virus epizootic.

BILLANY, D.J. (1977).
The European spruce sawfly, Gilpinia hercyniae.
Rep. Forest. Res., Lond. 1977; 35.

A brief progress report on the infestations in Wales. The virus epizootic has been successful in controlling population and promoting recovery in some defoliated trees.

BILLANY, D.J. (1978).
Gilpinia hercyniae (Hartig). A pest of spruce.
Forest Rec., Lond. 117, 11pp H.M.S.O.

The status, occurrence and biology of the pest in the U.K. are described. A naturally occurring nuclear polyhedrosis virus was found in populations in Hafren Forest mid-Wales in 1971, where the outbreak was most severe, and spread very rapidly into areas with lower populations. An ichneumonid parasite, Lamachus marginatus is present in populations in Wales and in eastern England, and efforts are being made to introduce parasite species to infestation areas.

BILLANY, D.J., BORDEN, J.H. and BROWN, R.M. (1978).
Distribution of Gilpinia hercyniae (Hymenoptera, Diprionidae) eggs within Sitka spruce trees.
Forestry 51, (1); 67-72.

The distribution of eggs was determined in a total sample of 15,360 needles taken from 16, 16-17 year old Sitka spruce trees in Hafren Forest, mid-Wales. 1.09% of needles were occupied by eggs. The data indicated a preference for eggs to be laid at the top of the crown in one year old needles. Calculations disclosed that 76% of the population would be in one year old needles and 83% would be in the two middle crown layers. Oviposition preference could be accounted for in part, by positive phototaxis, avoidance

of the darker basal and central regions of the tree, rejection of significantly smaller needles in the basal crown level and by fairly immediate acceptance of peripheral foliage by an alighting female. It is concluded that an effective egg survey need only sample one year old needles in the top crown level.

BILLANY, D.J. and BROWN, R.M. (1975).
The European spruce sawfly Gilpinia hercyniae.
Rep. Forest Res., Lond. 1975; 35-36.

A brief progress report on infestation in Wales. A few parasites have been discovered in Hafren Forest, and the virus epizootic is affecting considerable control in Hafren and Ystwyth Forests.

BILLANY, D.J. and BROWN, R.M. (1977).
The geographical distribution of Gilpinia hercyniae (Hymenoptera, Diprionidae) in the United Kingdom.
Forestry, 50; 155-160.

Since 1906 when the insect was first recorded in Britain in the New Forest, the species has spread into 18 counties in England and Wales. In 1970-74, it achieved pest status in mid-Wales, but has remained at endemic levels elsewhere. It has not become well established in northern England and has not yet been found in the extensive spruce plantations in Scotland.

BILLANY, D.J., CARTER, C.I. and FIELDING, N.J. (1977).
The European spruce sawfly, Gilpinia hercyniae.
Rep. Forest Res., Lond. 1977; 36.

A brief report on progress on the introduction of parasites of the sawfly into Britain from mainland Europe, mainly concerning attempts at laboratory rearing of parasites.

BIRD, F.T. (1948).
Control effects of the polyhedral disease of the spruce sawfly.
Bi-m. Progr. Rep. For. Insect Invest. Dep. Agric. Can. 4; (2) (1).

It has been shown that this disease, which terminated the severe outbreak of Diprion polytomum, is caused by a virus which can be stored and established artificially in areas where it is not present. It has been observed in the field for 10 years and no change has been observed in its virulence. The only factor necessary for its ability to destroy the insect is a sufficient number of the host in the forest, and this number has been found to be quite small.

BIRD, F.T. (1949a).
A virus (polyhedral) disease of the European spruce sawfly, Gilpinia hercyniae.
Ph.D. Thesis, McGill University, Montreal, Quebec, 131pp.

The properties of the virus, the infection process and tumour formation are described in detail. Experimental evidence for transmission of virus via the egg is presented. Foliage persistence and the effects of rain, temperature etc. on the virus are described. The effect of the virus on late instar larvae and cocoons is described. The incubation period and effect of temperature on diseased larvae are discussed. The specificity of the virus was tested, and the epizootiology of the virus in Eastern Canada is discussed.

BIRD, F.T. (1949b).
Tumours associated with a virus infection in an insect.
Nature, London 163; 777.

A brief description of the origin and nature of non-malignant tumours formed from mid-gut epithelial cells of Gilpinia hercyniae when it is infected by NPV late in the fifth instar.

BIRD, F.T. (1952).

On the multiplication of an insect virus.

Biochem. et Biophys. Acta 8; 360-368.

The infection processes in the mid-gut nuclei of larvae of European spruce sawfly are described. Infected nuclei increase in size and the chromatin coagulates. Electron microscopy shows that polyhedra arise as bodies 160 μ in diameter containing spherical particles about 20 μ in diameter which increase in number and in size as the polyhedra grow. Multiplication and development of virus particles appears to occur within growing polyhedra as well as in the free state in an infected nucleus.

BIRD, F.T. (1953).

The effect of metamorphosis on the multiplication of an insect virus.

Can. J. Zool. 31; 300-303.

The prepupal stage of the European spruce sawfly is immune to infection by a polyhedral virus disease. The virus multiplies only in the nuclei of the digestive cells of the mid-gut epithelium, and during metamorphosis these are replaced by embryonic cells not susceptible to infection although they eventually develop into digestive cells. The prepupal mid-gut, a temporary gut, is composed entirely of embryonic cells. New digestive cells appear later in the pupal and adult stages and these rapidly become infected with virus.

BIRD, F.T. (1954).

The use of a virus disease in the biological control of the European spruce sawfly, Diprion hercyniae (Htg).

Bi-m Progr. Rep. Div. For. Biol. Dep. Agric. Can. 10; (1) 2-5.

Studies of individual trees have shown that epizootics start each year from infection of a very small % of the larval population. The disease spreads rapidly and causes the greatest mortality in the second generation. Very little virus remains on the trees over winter, owing to the cleansing effect of rains, and initial infection each year is due to transmission of virus via the eggs of infected adults.

BIRD, F.T. (1955).

Virus diseases of sawflies.

Can. Ent. 87; 124-127.

A review of biological control by viruses of Diprion, Neodiprion americanus banksianae and Neodiprion sertifer. Transmission of virus (including by birds), epizootiology and factors affecting pathogenicity (including temperature), are dealt with. Development of both larvae and disease are speeded up at high temperature, but prolonged exposure of Diprion hercyniae to very high temperatures (85⁰F) inhibits virus multiplication.

BIRD, F.T. (1961).

Transmission of some insect viruses with particular reference to ovarian transmission and its importance in the development of epizootics.

J. Insect Path. 3; 352-380.

Viruses transmitted via eggs of infected females of Diprion hercyniae, Neodiprion sertifer and Neodiprion lecontei kill young progeny at an early stage of development. Severe epizootics may develop from the infection of less than 10% of the eggs. Rain appears to be the chief agent for within-tree spread, whereas parasites and other natural enemies, besides infected females, appear to be the chief agents for tree to tree transmission. It is suggested that the most likely explanation of vertical transmission of virus in Diprion hercyniae is ovarian, with the source of infection occurring within the egg.

BIRD, F.I. and BURK, J.M. (1961).

Artificially disseminated virus as a factor controlling the European spruce sawfly, Diprion hercyniae (Htg) in the absence of introduced parasites. Can. Ent. 93; 228-238.

The successful introduction of NPV into a moderately infested, disease-free area without parasites is described. The importance of virus in controlling the sawfly in New Brunswick in the late 1930's is discussed. Weather and parasites are also important. At Sault St. Marie (Ontario), populations remained higher than in New Brunswick after virus had its effect. The reason for this is most likely the presence of introduced parasites in New Brunswick, which are absent in Ontario.

BIRD, F.I. and ELGEE, D.E. (1957).

A virus disease and introduced parasites as factors controlling the European spruce sawfly, Diprion hercyniae (Htg) in central New Brunswick. Can. Ent. 89; 371-378.

Virus is very effective at high host densities and certain parasites are very effective at low host densities. Virus appears to be density dependant. There is a suggestion of an increase in host resistance to the virus.

BIRD, F.T. and WHALEN, M.M. (1954).

Stages in the development of two insect viruses.

Can. J. Microbiol. 1; 170-174.

Various electronmicrographs of thin sections of Diprion hercyniae and Neodiprion americanus banksianae showing NPV polyhedra formation in infected nuclei are accompanied by a description of the biological processes involved.

BOMBOSCH, S. and LUNDERSTADT, J. (1975).

Investigations on the background of the influence of different stands on the increase of forest pests.

Forstarchiv, 46, (8); 153-155. (German).

A study on the nutritional quality variations of spruce stands for G.hercyniae, with comments on the possible importance of this in forest management.

BOMBOSCH, S. and RAMAKERS, P.M.J. (1976).

Continuous rearing of Gilpinia hercyniae Htg.

Z. PflKrankh. 83; 40-44.

- (1) The diapause of Gilpinia hercyniae is induced by a short day length of young larvae, old larvae and eonymphs being sensitive towards photoperiod. At 25°C, the critical day length is between 16 and 17 hours. A day-length of more than 17 hours inhibits the induction of diapause.
- (2) Soft walled shade needles are best suited for oviposition.
- (3) Spruce branches which are selected for feeding of the larvae and are treated according to the method of Moore and Clark need not be replaced during the whole experiment. Thus, oviposition, embryonal and larval development can be completed on the same branch.
- (4) Freshly emerged females must be kept separated otherwise they damage each other severely.
- (5) The duration of each stage of development as related to temperature is shown in a table.

BORDEN, J.H. (1971).

Changing philosophy in forest insect management.

Bull. entomol. Soc. Am. 17, (4); 268-273.

A review of North American experiences in forest pest control. Control of Diprion hercyniae by a polyhedral virus is described as being an example of 'sheer luck' in a historical context. Management of forest insects has become more sophisticated due to new techniques, the improved assessment of pest status, and greater knowledge and appreciation of ecological considerations and the side-effects of pesticides.

BRIAND, L.J. (1948a).

Spruce sawfly parasite investigations, Park Reserve, Kamouraska, P.Q.

Rep. Quebec Soc. Prot. Pl. (1945-47); 54-59.

Details of parasite releases, 1934-41 are given and the recovery study method is described.

Microplectron fuscipennis and Exenterus spp. were regularly recovered almost immediately after introduction. Sturmia was found to be attacking another species of sawfly.

BRIAND, L.J. (1948b).

Field studies on Sturmia sp. an important parasite of the European Spruce sawfly.

Rep. Quebec Soc. Prot. Pl. 1945-47, 125-127.

From the information secured to date on Sturmia, it can be safely assumed that it is now one of the most important factors in keeping down the sawfly population in those areas of Quebec under observation.

BROWN, A.W.A. and FLEMING, H.S. (1938).

Recent extensions of the known distribution of the European spruce sawfly.

Rep. ent. Soc. Ont. 69; 22-24.

The known distribution of Diprion polytomum (Htg) in eastern Canada between 1935 and 1938 is recorded. Its range was apparently extending into Ontario from Quebec.

BROWN, R.M. (1973).

The spruce sawfly; Gilpinia hercyniae.

Rep. For. Res., Lond. 1973; 104.

A report on the sawfly infestation in Wales. Severe damage to some plantations has been observed. A nuclear polyhedrosis virus epizootic of the sawfly is under investigation. Vertebrate predation is high, but no naturally occurring parasites have been found.

BROWN, R.M. and BILLANY, D.J. (1974).

The European spruce sawfly, Gilpinia hercyniae.

Rep. For. Res., Lond. 1974; 39.

A brief report on the Mid-Wales infestation. The virus epizootic is under investigation. Parasite material, collected in Europe is being bred prior to release in the infestation areas.

BROWN, W.E. and PAQUETTE, R.G. (1939).

Spruce sawfly infestation as indicated by cocoon populations.

Fox Forest Notes. No. 19;1.

Population studies in New Hampshire from the first heavy infestations in 1937, through to 1939 are covered. The work was disrupted by a hurricane which destroyed most of the study plots. A crude breakdown of cocoon populations expressed as percentage emerged or damaged is given, associated with degree of defoliation. Some degree of establishment of the parasite Microplectron was discovered after one year near its points of introduction.

BUCKNER, C.H. (1955).
Small mammals as predators of sawflies.
Can. Ent. 87; 121-123.

Sampling work carried out in S.E. Manitoba to determine the extent of predation by mice and shrews on cocoons of the larch sawfly, Pristiphora erichsonii (Htg) is described and discussed, with particular references to the difficulties involved in obtaining an accurate estimate of the time level of predation. Earlier work on mammalian predation of Diprion hercyniae cocoons is briefly referred to.

CAMERON, J.W.M. (1962).
The use of viruses in the control of some forest insects in Canada.
Proc. 11th Int. Congr. Ent., Vienna 1960, 2; 769-776.

A review of work, experimental and applied, chiefly with Diprion hercyniae Neodiprion sertifer, N.lecontei, Choristoneura fumiferana and Malacosoma disstria.

CAMERON, J.W.M. (1972).
Implementation of biological control programmes against forest pests.
Proc. North Central Branch, Ent. Soc. Amer. 27; 43-47.
Rev. Appl. Ent. 163; 3639.

Work on biological control of several forest pests including Gilpinia hercyniae is discussed and it is concluded that no particular strategy is completely applicable in all cases.

Interactions between hosts and control agents, the merits of continuing studies through periods of low population and the use of chemicals are discussed.

CAMERON, P. (1882).
A monograph of the British phytophagous Hymenoptera. Vol I.
Ray Society, London, 340pp, 21 plates.

This volume deals with the Tenthredinidae which covers the genus Lophyrus. L.hercyniae is mentioned in a list of species associated with particular groups of food plants.

CARTER, C.I., FIELDING, N. and BILLANY, D.J. (1976).
The European spruce sawfly, Gilpinia hercyniae.
Rep. For. Res., Lond. 1976; 38.

A brief progress report on the programme of parasite introduction into forests in Wales, covering the laboratory rearing of material imported from Central Europe.

CHAWNER, E.F. 1933).
Diprion polytomum Htg. (Hym., Tenth.) in Hants.
J. ent. Soc. S. Engl. 1 (4); 81. Southampton, 16th December 1933.
Rev. Appl Ent. 22; 75

A report on the third finding of the insect in the British Isles. One larva was found at the foot of a spruce tree, from which it had probably been washed by heavy rain. The larvae feed singly near the tops of trees, and their colouring make them difficult to observe.

CLARK, R.C., CLARKE, L.J. and PARDY, K.E. (1973).
Biological control of the European spruce sawfly in Newfoundland.
Bi-mon. Res. Notes 29, (1); 2-3, Newfoundland Forest Research Centre, Canada.
Rev. Appl. Ent. 63; 3274.

The occurrence of the pest in Newfoundland since its discovery in 1940 is described. Severe defoliation in some stands occurred from 1943-51 and 1958-70. NPV was applied as a spray in 1943-4 and 1948 and spread rapidly. Four insect parasites were released in 1943-49, but virus has apparently kept populations too low for them to establish. The cinereous shrew also helps to control the pest.

CLAUSEN, C.P. et al., 1978

Introduced parasites and predators of Arthropod pests and weeds: a world review. Agricultural Handbook No. 480, Agricultural Research Service, United States Department of Agriculture, Washington D.C., 545pp.

A review of the parasite introduction programme to control Diprion hercyniae in Canada is given on pages 298-302. Notes are given on the biology of Dahlbominus fuscipennis, Exenterus abruptorius, E.amictorius, Pleolophus basizonus and Drino bohemica.

CONKLIN, J.G. (1942).

An analysis of the biological control of the European spruce sawfly in New Hampshire, with particular reference to predators.
Abstr. of Doctoral Diss., Ohio State Univ. Press 37; 63-73.

The marked reduction in the sawfly population during the years of investigation here reported could not be attributed to the activities of predators, as it was brought about chiefly by an unidentified larval disease.

COPPEL, H.C. (1954).

Notes on the Parasites of Neodiprion nanulus Schedl (Hymenoptera: Tenthredinidae).
Can. Ent. 86; 167-168.

An individual of Dahlbominus fuscipennis (Eulophidae), which was introduced against Diprion hercyniae, emerged among 11 other species of parasites from a cocoon collection during an outbreak of Neodiprion nanulus, a pine sawfly.

COPPEL, H. and HOUSE, H. (1947).

A description of cages used for the large-scale breeding of Sturmia sp., a tachinid parasite of sawflies.
Can. Ent. 79; 74-80.

This parasite was imported from Europe to control European spruce sawfly and laboratory reared to increase numbers. (c.f. House, H.L., 1943).

CRAIGHEAD, F.C. (1950).

Insect enemies of eastern forests.
U.S. Dept. of Agriculture, Misc. publication No. 657; 679pp.

A brief account of the outbreak of Diprion hercyniae, (Htg) in Canada and U.S.A. is given on pages 559-562.

CROOKE, M. (1953).

Forest Entomology: spruce sawflies.
Rep. For. Res., Lond., 1953; 71.

Seven species of sawflies have been identified on spruce in British forests. Gilpinia hercyniae was taken sporadically throughout the surveyed areas.

CROOKE, M. (1956).

Some aspects of forest entomology in Britain.

Proc. 10th International Congress of Entomology. (4); 233-239.

With the preponderance of younger conifers in British forests, many being exotic species, the presence of defoliating pests is of interest even if they are not currently causing economic damage. Sawflies associated with conifers including Gilpinia hercyniae are referred to. Caution as to their future behaviour is suggested, and long term intensive studies on population dynamics, even on very low density populations, are suggested.

CROOKE, M. (1957).

A brief review of the British conifer feeding sawflies.

Z. angew. Ent. 41; 179-183.

The sawflies occurring on pine, larch, and spruce in Britain are listed and their importance as forest pests reviewed. Certain ecological points are also discussed. Eleven species occur on pine, and seven (all introduced) occur on larch. There are nine spruce sawfly species, and all of these, together with the host, are exotic to Britain. None are economically important, but the most common are Pristiphora abietina Christ., P. ambigua Fall., and P. amphibola Forst. Although not important at present, Gilpinia hercyniae is viewed with caution because of its widespread ravages on fir in Canada.

DAVIAULT, L. (1941).

The European spruce sawfly in the forests north of the St. Lawrence.

La Forêt Québécoise 3, (7); 12-16. (French).

So far little damage has been caused in these forests.

DAVIAULT, L. (1944).

New observations on the European spruce sawfly in the forests north of the St. Lawrence.

28th Report Quebec Society for the Protection of Plants 1936-1943; 39-43. (French).

The appearance of Diprion polytomum in Quebec was regarded with some alarm, and close watch was kept on it. Numbers declined since 1941, principally as a result of larval disease. Should this insect again prove a serious menace, there is now a good deal of knowledge of its parasites and predators.

DE BACH, P., HUFFAKER, C.B. and MACPHEE, A.W. (1976).

Evaluation of the impact of natural enemies.

Theory and Practice of Biological Control, ed. Huffaker, C.B. and Messenger, P.S., Academic Press, New York, 788pp. (255-285).

The history of Diprion hercyniae populations in eastern Canada is discussed in relation to parasites and NPV diseases. It is argued that it is only because population levels were known both before and after the impact of the natural enemies that their combined actual "control power" is known. Life-table type studies do not give this information completely.

DINISH, K.M. (1974)

Nutritional quality of spruce needles for forest insect pests (5).
Investigations on the starch-hydrolysing enzyme (amylase) in larvae
of Gilpinia hercyniae.

Z. angew. Ent. 77; 113-121 (German)

The presence of amylase in the larvae of G.hercyniae and its biochemical properties are described. The enzyme activity (per. mg. protein in the larvae) of the amylase showed a marked increase between larval ages of 12 and 18 days.

DIRKS, C.O. (1944).

Population studies of the European spruce sawfly in Maine as affected by natural enemies.

J. econ. Ent. 37; 238-242.

The insects reached a high population in Maine in 1939. Population study plots were set up, and cocoon samples, larval samples beaten from trees and larvae falling off trees were taken and analysed. A number of important native rodent and insect predators attacked 20% - 50% of cocoons, but seldom appeared to constitute a permanent check when an epidemic was imminent. The European cocoon parasite, Microplectron fuscipennis parasitised a high proportion of cocoons, especially those near the surface, when it became established in Maine. From 1940 to 1942, a "wilt" disease caused a higher proportion of mortality, being prevalent in areas of both high and low population. The disease appears to be an important factor in the decline of the sawfly, and appeared to become less prevalent as populations declined.

DONISTHORPE, H. St.J.K. (1936).

A preliminary list of the Coleoptera of Windsor Forest.

Ent. mon. Mag. 72; 210-219.

Sawfly specimens taken, including the third British specimen of Diprion polytomum, are mentioned.

DOWDEN, P.B. (1939).

Present status of the European spruce sawfly, Diprion polytomum (Htg).
in the United States.

J. econ. Ent. 32; 619-624.

An account of the organisation and results of an intensive survey carried out in 1937 and 1938 to determine the insect's range in the U.S.A., and the severity of spruce infestation. The parasite Microplectron fuscipennis has been bred and liberated on a large scale and is established at several points, and small lots of other parasites have been imported from Canada and liberated.

DOWDEN, P.B. (1940).

Larval disease prevalent in heavy infestations of the European spruce sawfly in southern Newfoundland and Vermont.

J. For. 38; 970-972.

A disease (cause unknown) is reported to have killed large numbers of larvae of Gilpinia polytoma (Diprion polytomum) in southern New Hampshire and Vermont during 1939. The progressive effect of the disease is recorded from daily observations on a 1/5-acre study plot in a heavily infested stand.

ELTON, C.S. (1958).
The Ecology of Invasions by Plants and Animals.
Methuen, 181pp.

The outbreak of European spruce sawfly in Canada in the 1930s is covered in the chapter on the invasion of continents. Significant points noted are the fact that the insect is not a pest in its native territory, and the absence of natural enemies in Canada. The biological control programme involving introduced parasites is mentioned and distribution maps are given.

ENSLIN, E. (1912).
Die Tenthredinoidea Mitteleuropas.
Deutsch. Ent. Zeit., 790pp. (German)

Lophyrus hercyniae is relegated as a synonym of L. polytomus.

ENTWISTLE, P.F. (1971).
Possibilities of control of a British outbreak of spruce sawfly by a Virus Disease.
Proc. 6th Br. Insectic. fungic. Conf.

An account of the spruce sawfly situation in Wales in 1971, discussing possible biological control methods, i.e. introducing NPV, introducing parasites or spraying polyhedral suspensions.

ENTWISTLE, P.F. (1972).
Gradients of dispersal of an insect virus disease.
Abs. 14th Int. Congress Ent. 1972; 221.

The spread of the virus disease of spruce sawfly in a population in Wales in 1971 is compared with data obtained following experimental initiation of a virus epizootic in this host in Canada.

ENTWISTLE, P.F. (1973).
The primary epizootiology of a NPV disease in populations of spruce sawfly, Gilpinia hercyniae.
Vth International Colloq. Insect Pathol. and Microb. Control and Vth Ann. meeting Soc. Invert. Pathol. 1973; 64

The situation in Wales up to 1973 is described, including preliminary work on dispersal gradients of the epizootic, discontinuous horizontal transmission, foliage persistence and population dynamics studies.

ENTWISTLE, P.F. (1974).
New perspectives in pest control with pathogenic viruses.
Land, Oxford U.K. 1 (1); 84-88.

A general discussion based on research in the UK illustrated with an account of a current study begun in 1971, concerning the possibility of controlling Gilpinia hercyniae by a nuclear polyhedrosis virus.

ENTWISTLE, P.F. (1976).
The development of an epizootic of a nuclear polyhedrosis virus disease in European spruce sawfly, Gilpinia hercyniae.
Proc. 1st Internatn. Colloqu. Invertebr. Pathol. and 9th Annual Meeting Soc. Invertebr. Pathol.; 184-188, Kingston, Canada.

Dispersal of the disease from a main epicentre in central Wales appears to involve birds feeding on diseased and dead larvae. Infected adult sawflies may also have a considerable role. Persistence of the virus on foliage between larval generations is important in the initiation of

infection in new generations, and is probably the main reason for the intensely epizootic nature of NPV in the sawfly populations.

ENTWISTLE, P.F. and ADAMS, P.H.W. (1977).

Prolonged retention of infectivity in the nuclear polyhedrosis virus of Gilpinia hercyniae (Hymenoptera, Diprionidae) on foliage of spruce species. J. Invertebr. Pathol. 29; 392-394.

Studies in mid-Wales show that foliage remains infective throughout the winter until immediately prior to the new larval season. This may be due to virus-killed corpses adhering to the trees and releasing supplies of virus as they disintegrate.

ENTWISTLE, P.F., ADAMS, P.H.W. and EVANS, H.F. (1977a).

Epizootiology of a nuclear-polyhedrosis virus in European spruce sawfly (Gilpinia hercyniae): The status of birds as dispersal agents of the virus during the larval season. J. Invertebr. Pathol. 29; 354-360.

During an epizootic of NPV in larvae of Gilpinia hercyniae in Wales, 16 species of birds belonging to six families were found to disperse infective NPV in their faeces. This represents 80% of the total bird number. 90% of droppings collected directly from trees in September contained infective virus. Information on the species composition of the bird fauna in the spruce forest study area and the comparative frequencies of different bird species are given.

ENTWISTLE, P.F., ADAMS, P.H.W. and EVANS, H.F. (1977b).

Epizootiology of a nuclear-polyhedrosis virus in European spruce sawfly, (Gilpinia hercyniae): Birds as dispersal agents of the virus during winter. J. Invertebr. Pathol. 30; 15-19

In Welsh spruce forest the relationship of birds to NPV of Gilpinia hercyniae larvae was studied outside the larval period. Throughout the non-larval period, birds passed faeces containing infective NPV. It is thought that birds acquired inoculum by feeding on corpses of infected larvae adhering to spruce trees. The proportion of infected droppings declined in the 2 months (May and June) prior to the new larval period. Infective droppings were collected from all six species of birds netted in January. Experimental evidence suggests that birds may carry NPV for at least 6 km.

ENTWISTLE, P.F., ADAMS, P.H.W. and EVANS, H.F. (1978).

Epizootiology of a nuclear polyhedrosis virus in European spruce sawfly (Gilpinia hercyniae): The rate of passage of infective virus through the gut of birds during cage tests. J. Invertebr. Pathol. 31; 307-312

The passage of a nuclear polyhedrosis virus (NPV) of the sawfly, Gilpinia hercyniae, through avian gut was studied during cage tests on Sturnus vulgaris (three individuals), Parus ater (one), Parus caeruleus (five) and Parus major (one). Following brief infection feeds, polyhedral inclusion bodies of the virus could be detected in bird faeces within 0.5hr. Peak passage of polyhedra occurred in less than 1 hour and none were detected after 2.5hr. The faeces of all birds remained infective (in bioassay tests using first instar G.hercyniae larvae) to the end of the day of infection while those of nine birds remained infective to the next day and of six birds to the third day. One bird, P.major, was also infective on days 4, 6 and 7. The infectivity of NPV in faeces stored for two years at +3°C declined by half. Though the scale of their

epizootiological contribution is unknown, the comparatively long retention and passage of infective virus suggests birds may be effective in short- and long-distance transport of baculoviruses.

ENTWISTLE, P.F., ELLEMAN, C.J., HOYLE, S.R., EVANS, H.F. and ADAMS, P.H.W. (1978).

Aspects of the physical behaviour of baculoviruses on plant surfaces. Proc. Internatn. Colloqu. Invertebr. Pathol. and 11th Annual Meeting Soc. Invertebr. Pathol; 57-58, Prague.

Physical loss of baculovirus polyhedral inclusion bodies, as opposed to loss of biological activity, was measured on spruce (Picea abies and P. sitchensis, using Gilpinia hercyniae NPV), pine (Pinus contorta, using Neodiprion sertifer NPV) and cotton (Gossypium sp, using Spodoptera littoralis NPV).

The impression film technique was used, involving the removal of micro-organisms from plant surfaces using double-sided sticky tape, which is stained and examined on microscope slides. Rates of decay in the field were found to be exponential, and half-lives were measured at different times of year. Impure virus persisted for longer periods than pure virus preparations.

ESCHERICH, K. (1942).

Die Forstinsekten Mitteleuropas, Vol. 5. Hymenoptera and Diptera, Berlin 746pp. (German).

Diprion polytomus is described on pages 125-128. Details of its feeding habits and life cycle are given, and the infestation in Eastern Canada and parasite introduction programme are reported on.

ESCHERICH, K. and BAER, W. (1913).

Tharandter zoologische Miszellen: II; Ein Frass von Lophyrus hercyniae Htg.

Natw. f. Forst-u. Landwirtsch 11; 104-109. (German).

An attack of spruce sawfly in Saxony on a 2 hectare plantation is described, but the species is almost certainly L. polytomus. A description of the adult (male and female) anatomy is given. The outbreak was controlled by intensive physical measures. Cocoons were found in the stomachs of sparrows and tits during the winter.

EVANS, H.F. and ENTWISTLE, P.F. (1976).

The development of infection during a virus epizootic in spruce sawfly populations in mid-Wales.

Proc. 1st Internatn. Colloqu. Invertebr. Pathol. and 9th Annual Meeting Soc. Invertebr. Pathol; 350-351, Kingston, Canada.

Studies on three sites show the development of infection following a sigmoid curve, this pattern being repeated for four years, during which larval densities declined. Initially, the epizootic behaved in a density-dependent manner, but at lower populations virus appeared to act independently of density. This was probably due to virus persisting on foliage between larval seasons and initiating infection in larval populations.

FINLAYSON, T. (1960).

Taxonomy of cocoons and puparia and their contents of Canadian parasites of Diprion hercyniae (Htg). (Hymenoptera:Diprionidae).

Can. Ent. 92; 922-941

Descriptions of 13 parasitic species and a key to 28 species are given based on the characters of parasite remains in the host cocoons from which the parasites have emerged.

FINLAYSON, L.R. and FINLAYSON, T. (1958a).

Notes on parasites of Diprionidae in Europe and Japan and their establishment in Canada on Diprion hercyniae (Htg), (Hymenoptera:Diprionidae).

Can. Ent. 90; 557-563.

A general review of parasite introduction to Canada from 1933 to 1940. Methods of rearing parasites are described. Tables showing percentages of parasite emergence from field collected host material are given, and a table lists the 9 species of parasite (Aptesis spp. Dahlbominus fuscipennis, Drino bohémica and Exenterus spp.) giving their respective hosts and countries of origin.

FINLAYSON, L.R. and FINLAYSON, T. (1958b).

Notes on parasitism of a spruce sawfly, Diprion polytomum, (Htg), (Hymenoptera:Diprionidae), in Czechoslovakia and Scandinavia.

Can. Ent. 90; 584-589.

A review of parasites of D.polytomum from cocoons collected in Europe between 1935 and 1939, covering collection and rearing, sex ratio, mortality and emergence pattern of host, incidence of parasitism and patterns of emergence of the parasites.

FINLAYSON, L.R. and REEKS, W.A. (1936).

Notes on the introduction of Diprion parasites to Canada.

Can. Ent. 68; 160-166.

Cocoons of Diprion frutetorum, D.pini, D.polytomum, D.sertifer and D.virens were collected in Europe. Notes are given on the rearing of parasites, their laboratory propagation and early field investigations into the effect of parasite releases in Canada.

FOGAL, W.H. and KWAIN, M.J. (1972a).

Uric acid excretion by midgut epithelium in Gilpinia hercyniae (Htg).

Can. J. Zool. 50; 143-145.

Experimental and histological evidence suggests that uric acid is excreted by the mid-gut epithelium in the sawfly and that this function resides in specialised accessory structures, the gastric crypts.

FOGAL, W.H. and KWAIN, M.J. (1972b).

The effects of temperature on the occurrence of melanotic inclusions and related physiology in a sawfly, Gilpinia hercyniae.

J. Insect Physiol. 18; 1545-1564

When penultimate instar larvae are exposed to temperatures of 30°C, a high percentage develop melanotic inclusions from the mid-gut and/or Malpighian tubules early in the last instar. It is suggested that this is due to increased nitrogen catabolism, since the inclusions contain uric acid.

FORSIUS, R. (1932).

On some hymenopterous parasites bred from Diprion polytomum.

Notul. ent. 12 (4); 86-87.

Rev. App. Ent. A 21; 124.

Exenterus tricolor, Iamachus spectabilis and Holocremnus ratzeburgi are recorded for the first time in Finland, where they were bred from cocoons of Diprion polytomum.

FORSTER, E.W. (1949).

On the taxonomic status of the European spruce sawfly Gilpinia hercyniae (Htg), (Hymenoptera:Diprionidae).

Can. Ent. 81; 112-113.

Further evidence distinguishing Gilpinia hercyniae from G. polytoma on morphological and reproductive grounds.

FRANZ, J. (1955).

The artificial distribution of virus diseases of some sawflies (Diprionidae) within and outside their endemic areas.

Verh. dt. zool. Ges. 1955; 407-412. (German)

The outbreaks of Gilpinia hercyniae and Neodiprion sertifer and their polyhedrosis virus diseases in North America are compared. The virus disease of G. hercyniae remained endemic at low host population densities while that of N. sertifer did not. Two reasons are suggested; that the imported parasite complex (parasites acting as vectors) was more complete for G. hercyniae than for N. sertifer and the gregarious oviposition habit of N. sertifer. Native European populations of N. sertifer were found to be just as susceptible to the virus as Canadian insects.

The general effectiveness of disease in controlling phytophagous insect populations is discussed.

FRANZ, J.M. (1975).

Towards integrated control of forest pests in Europe.

Perspectives in Forest Entomology, Proceedings of a Lockwood Conference on perspectives of forest pest management. ed. Anderson, J.F. and Kaya, H.K. New Haven, Conn., U.S.A.; 428pp. (295-308).

A review of European trends in integrated control of forest pests. Studies on the epizootiology of NPV of European spruce sawfly in Great Britain are mentioned as an example of the possibility of artificial manipulation of disease as opposed to large scale spraying operations.

GHANI, M.A., et al. (1974).

Investigations on primary mortality-causing agents affecting sawfly population in high altitude forests in Pakistan.

Report of the Commonwealth Int. of Biological Control, Pakistan Station, Rawalpindi (unpublished) 18pp.

Studies on population dynamics of pine sawfly Gilpinia pindrowi and spruce sawflies G. polytoma and G. ghani were carried out at varying altitudes. Relative mortalities due to parasites, predators and pathogens are given.

GOBEIL, A.R. (1938).

Domages causés aux forêts de la Gaspésie par les insectes.

Bull. Serv. Ent. Minist. Terres Quebec, no.2., 21pp. Quebec 1938. (French)
Rev. Appl. A27; 275.

The results are given of investigations into the proportion of spruce attacked or killed by Diprion polytomum Htg and Dendroctonus piceaperda. Control methods include felling and bark-stripping of defective trees and by introduced parasites, particularly Microplectron fuscipennis and Exenterus abruptorius.

GOBEIL, A.R. (1940)

Serait-ce la fin de la mouche à scie européenne de l'épinette?

(May this be the end of the European spruce sawfly?)

La Forêt Québécoise 2, (10); 18-20 (French)

A decrease, during 1940 of Diprion polytomum is reported from Quebec. It is attributed chiefly to the widespread destruction of larvae by a new disease which appears to be caused by a virus. Because the pupal stage of the sawfly in Quebec usually extends over several years, this decrease is regarded as temporary.

GOBEIL, A.R. (1941).

La diapause chez les tenthrèdes; Partie I

Can. J. Res. (D) 19; 363-382 (French)

Partie II

Ibid; 383-416

This work consists of a study of some factors involved in breaking diapause in Diprion polytomum Htg. and Pristiphora erichsoni Htg. The optimum overwintering temperature is around 32°F. Neither species was able to survive more than 10 weeks at 0°F. The mean optimum temperature for pupation in D. polytomum was between 75°-80°F at relative humidities of at least 85%. Temperature fluctuations at the commencement of overwintering instigated a diapause which was difficult to break, while similar fluctuations at the end of overwintering accelerated development.

At temperatures around freezing, eonymphs could survive more than three weeks completely submerged in water. Brief periods of immersion in water during overwintering increased the percentage emergence. Metabolism was increased by immersions in sulphuric acid at pH 3.

GOBEIL, A.R. (1942).

Diapause and egg intoxication in Diprion polytomum Htg.

J. econ. Ent. 25; 677-679.

Roubaud's theory, that the length of diapause depends upon the intoxication of eggs by excretory products before oviposition, is tested. A small number of adults were treated in four different ways prior to oviposition. The limited amount of data obtained suggests that the length of diapause is independent of the retention period of mature eggs in the ovaries.

GRAHAM, K. and STARK, R.W. (1954).

Insect population sampling.

Proc. ent. Soc. British Columbia, Victoria 51; 15-20.

(Contr. Div. for Biol. Agric. Can. No. 143)

After a theoretical introduction the second author exemplifies the methods and techniques for three forest defoliators, the European spruce sawfly, the lodgepole needle-miner and the spruce budworm.

GRYSE, J.J. DE (1941).

A brief note on the so-called "mysterious" disease of the spruce sawfly.

For. Chron. 17; 43-44.

A disease of Gilpinia polytoma, which is thought possibly to be a virus but of which little is yet known, is found over most of the area

infested by the sawfly and sometimes kills large numbers of the larvae. It has been particularly destructive to the 1940 larval population in New Hampshire and Vermont and to a lesser extent in Maine and New Brunswick.

HALL, I.H. (1963).

Microbial Control, Insect Pathology - an advanced treatise.

Vol. 2; 477-517, ed. Steinhaus, E.A., Academic Press, New York.

The artificial dissemination of NPV of Diprion hercyniae is mentioned as being the most outstanding example of the use of viruses in biological control in this review, which covers applied aspects and the use of micro-organisms in general biological control.

HANSON, H.S. (1949).

Sawfly Infestations: Sawflies on spruce.

Rep. For. Res., Lond. 1949; 23.

Pristiphora abietina and Gilpinia hercyniae are briefly reported as having been found in several localities in southern England.

HANSON, H.S. (1950).

Spruce Sawflies.

Rep. For. Res., Lond. 1950; 89-90.

Reports of Pristiphora abietina and Gilpinia hercyniae in southern England in 1949 are mentioned. Pristiphora subarctica, P.ambigua and P.amphibola are also reported on, the last two as causing widespread damage in some areas.

HANSON, H.S. (1951).

Spruce sawflies.

Rep. For. Res., Lond. 1951; 106.

Gilpinia hercyniae (and Pristiphora abietina) are still numerous and widespread, but no severe infestations are reported.

HARKER, J.E. (1963).

Tumors, Insect Pathology - an advanced treatise, Vol.1; 191-213.

ed. Steinhaus, E.A. Academic Press, New York.

A general review of tumours in insects. Tumours in Gilpinia hercyniae are referred to in a section on tumours caused by endoparasites.

HARTIG, T. (1834).

Der Entomologische Teilin dem Forstliches und Forstnaturwissenschaftliches Conversations-Lexikon; 990-991.

Nauch, Berlin. (German).

Embodies the original description of Lophyrus polytomus.

HARTIG, T. (1837).

Die Familien der Blattwespen und Holzwespen.

416pp, Berlin (German).

An original work on the classification of sawflies which places diprionids in the genus Lophyrus and distinguishes between L.polytomus and L.hercyniae.

HAWBOLDT, L.S. (1947).

Bessa selecta (Meigen) (Diptera:Tachinidae) as a parasite of Gilpinia hercyniae (Hartig) (Hymenoptera:Diprionidae).
Can. Ent. 79; 84-104.

The bionomics of the parasite are described and reasons are given why it is not an efficient parasite of Gilpinia hercyniae.

HEIMPEL, A.M. (1961).

Pathogenicity of Bacillus cereus Frankland and Frankland and Bacillus thuringiensis Berliner varieties for several species of sawfly larvae.
J. Insect Path. 3; 271-273.

Diprion hercyniae was tested among others, but virulence of the bacteria in all test spp. was low, and there was no suggestion that the bacteria could be used as control agents.

HEIMPEL, A.M. and ANGUS, T.A. (1963).

Diseases caused by certain spore-forming bacteria.
Insect Pathology - an advanced treatise, Vol. 2; 21-73. ed. Steinhaus, E.A.
Academic Press, New York.

This review covers pathogens of the genus Bacillus and clostridial pathogens. A list of the relative virulence of Bacillus cereus in several species of Coleoptera, Hymenoptera and Lepidoptera is given, which includes Diprion hercyniae.

HINKS, C.F. (1973).

The neuro-endocrine organs of larvae of Neodiprion lecontei, Neodiprion swainei and Diprion hercyniae. Hymenoptera, Diprionidae.
Can. Ent. 105; 725-731.

Larva and eonymphs of the three species of diprionid sawflies were dissected and stained to demonstrate the nervous system and endocrine organs. Morphologically and anatomically, the endocrine organs in both larvae and eonymphs of all three species are very similar. Detailed descriptions with a diagram and photographs of sections and parts of the nervous system and endocrine organs are given.

HOUSE, H.L. (1948).

The Laboratory Propagation of Sturmia sp., a parasite of sawflies.
Rep. Quebec Soc. Prot. Pl. (1945-47); 60-62.

An important parasite of European spruce sawfly, it was introduced from Europe and laboratory bred to increase numbers. Details of laboratory propagation are given, with some notes on its bionomics. (c.f. Coppel and House, 1947).

HUANG, P. (1975).

The relationship between the needle structure of Picea excelsa and the behaviour of some needle-eating insect species.
Z. angew. Ent. 77; 264-269.

The feeding behaviour of Semiothisa liturata (Lep. Geom.) and the oviposition behaviour of Gilpinia hercyniae were investigated. The size of the egg pocket in the needle and the egg mortality was found to be related to the thickness of the epidermal cell wall.

IONAITIS, V.P. (1969).

Biology of the spruce sawfly, Gilpinia hercyniae (Hymenoptera, Diprionidae) in the Lithuanian S.S.R.

Zool. Zh. 18; 1185-1188. (Russian).

Observations in Lithuania during 1966 and 1967. The sawfly has two generations per year. Adults emerge during May and July. Larval development proceeds in May-June and July-September.

JAMES, R.A. (1974)

The effect of nuclear polyhedrosis virus and other factors on the reproductive biology of the European spruce sawfly, Gilpinia hercyniae (Htg). Hymenoptera:Symphyta.

Thesis in partial fulfilment of M.Sc. degree, Department of Zoology and Applied Entomology, Imperial College of Science, London 49pp.

No effect was found of NPV on the fecundity of adults infected late in the fifth instar stage. Cysts were more common in infected adults, but could not be related to any decrease in fecundity.

JUKES, M.R. (1977).

Extraction of sawfly cocoons from samples of soil and surface litter.

Ann. Appl. Biol. 85, (3); 399-402.

A non-destructive, wet technique to extract sawfly cocoons from a variety of soil and surface litter types is described. The system, involving a pair of tilting, curved sieves was originally developed to extract cocoons of the European spruce sawfly, Gilpinia hercyniae.

KAYA, H.K. (1975).

Insect pathogens in natural and microbial control of forest defoliators.

Perspectives in forest entomology. Proceedings of a Lockwood Conference

on perspectives of forest pest management. ed. Anderson, J.F. and Kaya H.K. New Haven, Conn. U.S.A. 428pp (251-263).

A review mentioning the existence of NPV at enzootic levels in Diprion hercyniae populations, and its introduction to a population in Ontario in 1950 to give long term control.

KNERER, G. and ATWOOD, C.E. (1973).

Diprionid Sawflies: Polymorphism and speciation.

Science 179; 1090-1099.

The historical confusion between Diprion polytoma and D.hercyniae which arose because of their morphological similarity, is mentioned. Otherwise this paper deals chiefly with the many species, sub-species and strains of Neodiprion.

KRISTEK, J. (1973).

The occurrence of spruce sawflies (Nematinae and Diprionidae) in Moravia.

Act. Universitatis agriculturae (Brno) 42, (1); 46-60 (Czech).

The occurrence of Nematinae and Diprionidae were studied from 26 sites in Moravia. The data were obtained partly by beating off foliage and partly by rearing of cocoons. The results revealed the occurrence of 12 species of Nematinae and three species of Diprionidae: Gilpinia abieticola, G.hercyniae and G.polytoma in order of abundance. Species representation in isolated stands was similar to that in groups of stands.

LINDQUIST, O.H. and MILLER, W.J. (1972).

A key to sawfly larvae feeding on the foliage of spruce and Balsam Fir in Ontario.

Proc. Ent. Soc. Ontario. 1971, 102; 118-122.

A key to fourteen species of Tenthredinidae and Pamphiliidae on Abies balsamea and Picea spp., including Diprion hercyniae.

LOVÁSZY, P. (1939).

Some notes on the insect parasites of Diprion polytomum (Htg) (Hymen, Tenthredinidae).

Ann. ent. fenn 5 (3); 225-233.

A sample of 100 sawfly larvae was collected in western Finnish Lapland in August 1939. Of these, 22 and 7 were parasitized by the ichneumonids Lamachus sp. and Holocremnus ratzeburgi respectively, and 5 and 6 by the tachinids Sturmia inconspicua and Ptychomyia selecta. Cases of super-parasitism were observed. Morphological details of the tachinid larvae are given. All but one of the ichneumonids were in the egg stage, indicating that they probably hatch in the host pre-pupal stage.

LUNDERSTÄDT, J. (1973).

Nutritional quality of spruce needles for forest insect pests: (3). Changes in content of chemical compounds of the needles caused by physiological factors.

Z. angew Ent. 73; 340-341. (German).

In spruce needles, such as fed to Gilpinia hercyniae larvae, the content of soluble carbohydrates, of free and of protein-bound amino acids is determined mostly for the duration of one year on material taken directly from the tree. The content of these compounds, as influenced by the age of the needles and by the time during which the cut off branches were kept under semi-sterile conditions, are also described. The amount and the quality of the acids taken up by G. hercyniae based on the analysis of the faeces is shown in the one example of protein-bound amino acids.

LUNDERSTÄDT, J. (1976).

Resorption and food constituents in the digestive tract of larvae of Gilpinia hercyniae (Hym, Diprionidae).

Abstracts: Tenth International Congress of Biochemistry, Hamburg, 1976. (German).

The site and intensity of resorption is dealt with. Contents of the gut were compared with ground freeze-dried spruce needles. The results indicate selective decomposition of proteins and assimilation preferences.

LUNDERSTÄDT, J. (1977).

Nutritional quality of spruce needles for forest insect pests: (8) Studies on the decomposition of proteins from spruce needles within the digestive system of Gilpinia hercyniae larvae.

Z. angew. Ent. 84; 19-31. (German).

The contents of the different sections of the digestive system of Gilpinia hercyniae larvae (late 4th to late 5th instar), were isolated separately and freeze-dried. Their composition as related to proteins, soluble amino acids, soluble carbohydrates and their tryptic digestibility was investigated. The proteins are similar in type to those found both in

larvae and spruce needles. These are indications that the composition of digestive enzymes varies along the alimentary canal. Maximal tryptic digestibility of gut contents is demonstrated in the middle mid-gut.

LUNDERSTÄDT, J. and CLAUS, G. (1972).
Nutritional quality of spruce needles for forest insect pests: (2) Comparative analyses of the compounds in spruce needles and the faeces of larvae of Gilpinia hercyniae.
Z. angew. Ent. 70; 386-403. (German).

As compared with needles, the analyses of faeces show a remarkable decrease in the concentration of glucose, fructose, saccharose and maltose. The diminution of proteins are less than those of sugars and lipids, yet consistent. No utilization of cellulose could be demonstrated. Other changes are described.

LUNDERSTÄDT, J. and HOPPE, I.M. (1975).
Nutritional quality of spruce needles for forest insect pests: (6) The utilisation of nutrients by larvae of Gilpinia hercyniae (Htg) (Hym., Diprionidae) when fed on needles of spruce (Picea abies Karst.) under standard conditions.
Z. angew. Ent. 79 (2); 177-193. (German).

Foliage from two places in West Germany was fed to larvae in the laboratory in 1972, and the content of soluble carbohydrates, carboxylic acids, soluble and protein-bound amino acids, lipids and starches in the leaves and frass of the larvae was determined. The results suggest that it is not the total amount, but the different availability of the plant-borne protein amino-acids that is the critical factor for the metabolic processes determining larval growth, and that the direction and intensity of the metabolic shifts are influenced by the concentrations of the carbohydrates available from needles.

LUNDERSTÄDT, J., POSTEL, U. and REYMERS, A. (1977).
Nutritional quality of spruce needles for forest insect pests: (7) Studies on the body constituents of larvae of Gilpinia hercyniae (Hymenoptera, Diprionidae).
Z. angew. Ent. 82 (4); 380-394. (German).

Fifth instar G. hercyniae larvae were analysed for constituents of the body (without the gut) and of the haemolymph. 92% of the dry weight of larvae without guts are composed of proteins carbohydrates and lipids at a ratio of 2 : 1.5 : 1. Approximately half of the proteins are apparently closely connected to lipids and carbohydrates. The other half have low molecular weight and seem to occur loosely associated to the cell structures. Lymphs and body proteins are differentiated by molar composition and by electrophoresis studies. Larval age affects protein qualities. In terms of dry weight, 5 to 10 times higher amounts of protein were found in larvae than in Norway spruce needles; and a different composition of the two types of protein was found.

LUNDERSTÄDT, J., SCHWARZ, U. and DINISH, K.N. (1975).
On the relationships between carbohydrate metabolism in larvae of Gilpinia hercyniae (Hym. Diprionidae) and the carbohydrate content of their natural food, the needles of spruce (Picea abies Karst).
Z. angew. Ent. 77 (3); 258-263.

The flow of carbohydrates from the spruce needle into catabolic products of the insect was followed indirectly, using the insect, which eats only

plant food in the larval stage. This was done by comparative analyses of the constituents of needles and faeces. The data thus gained are correlated with the in-vitro activities of some important carbohydrate-catabolizing enzymes in relation to larval age. Attempts are made to explain possible control of the population densities of insects on the basis of the food available.

MACALONEY, H.J. (1936a).
The European spruce sawfly in the U.S.A.
J. For. 34 (2); 124-129.

The extent of the infested area is described, and the possibilities of biological control are discussed. The biology of the pest is briefly described.

MACALONEY, H.J. (1936b).
European spruce sawfly.
Proc. 12th Nat. Shade Tree Conf, 145-150.

A description of the current status, recent history and biology of the pest. A brief account of the biological control programme is given.

MACALONEY, H.J. and DOWDEN, P.M. (1951).
European spruce sawfly, (Diprion hercyniae).
Pest Leaflet. Hillaboro N.H. No. 34, pp.4.

A general account of the insect and its control measures.

McGUGAN, B.M. and COPPEL, H.C. (1962).
Biological Control of Forest Insects, 1910-1958, a review of biological control attempts against insects and weeds in Canada.
Tech. Commun. Commonw. Inst. Biol. Cont. 2; 35-127.

A review of 25 insect pests including European spruce sawfly, giving details of number of introduced parasites released and relative success of each parasite species. The artificial dissemination of virus is briefly described.

McINTYRE, H.L. (1939).
Report on forest pest problems in New York.
J. For. 37; 879-883.

Several pest problems are reported on briefly, including the European spruce sawfly, which was not a serious pest in the State at the time.

MAKSYMUK, B. (1975).
Pattern of use and safety aspects in application of insect viruses in agriculture and forestry.
Baculoviruses for insect pest control: Safety considerations.
Selected papers from Environmental Protection Agency - US Department of Agriculture working symposium, ed. Summers, M. et al. Washington, D.C. U.S.A., April 15-18, 1974, 186pp (123-128).

Continuous control of European spruce sawfly, Diprion hercyniae, by polyhedrosis virus is mentioned as an example of the use of insect viruses in forestry. Nuclear Polyhedrosis Viruses and Granulosis Viruses are the most specific, and from a safety point of view, the most promising viral agents for pest control. The chapter describes the techniques

used in field application of viruses, and safety aspects of storage and application.

MARTINEAU, R. (1958).

Recherches sur les facteurs naturels du lutte de la mouche à scie Europeene de l'épinette Diprion hercyniae (Htg) dans le Québec.

Unpublished reports, Forest Biology lab., Quebec.

Abstr. in Ann. ACFAS 1957/58 25, (1959); 90 (French).

Investigations have been carried out since 1955 in Quebec to discover the effects of a virus disease and of parasites on populations of D.hercyniae. Results to date indicate that the virus disease has little effect on populations. Only 2 parasite spp. have been obtained and total parasitization is generally less than 10%.

MARTINEAU, R. (1963).

Facteurs naturels de regulation des populations de la tenthredé Europeene de l'épinette Diprion hercyniae (Htg) dans le sud de Québec. Can. Ent. 95; 317-326.

A report on a study near Quebec city from 1956-60 where climatic conditions were eliminating a substantial part of the population at the outset of the larval development period. Parasites had a small influence, but one species Drino bohémica, seemed to be well adapted in the study area. Predators were taking a heavy toll of the hibernating population. Virus seemed to be the main controlling factor, particularly during the summer.

MAXWELL, D.E. (1955).

The comparative internal larval anatomy of sawflies (Hymenoptera:Symphyta). Can. Ent. 87; supplement 1, 132pp.

Examination of 132 species of sawflies from America, Europe, Africa and Australia has demonstrated the value of internal anatomical larval detail as a taxonomic tool and an indicator of phylogenetic relationship. The salivary glands and Malpighian tubules proved of major importance.

Three sub-family groupings of the Tenthredinidae are suggested on the basis of Malpighian tubule groupings (primitive, intermediate and advanced):

- 1) the Selandrinae, Dolerinae, Athaliinae and Lycarotinae.
- 2) the Nematinae.
- 3) the Blennocampinae, Allantinae, Heterarthrinae and Tenthredininae (the genus Gilpinia comes under sub-family Tenthredininae).

The survey emphasizes the need of a revision of family and sub-family limits. Internal anatomy can be of use in determining the genus and species as well as the family and sub-family.

MILLAR, C.S. and PARRY, W.H. (1974).

Fungi and insects on Sitka spruce - Parts I and II.

Forestry Abstracts 35.(11, 12); 633-639, 709-721, Repr. in

Forestry Abstracts Leading Article Series No. 45.

Part I of this review deals with fungi and includes a table giving the name and location of more than 100 species associated with Sitka spruce. Part II deals similarly with insects and contains the bibliography for both.

MONTEITH, L.G. (1955).

Host preferences of Drino bohemica Mesn. (Diptera:Tachinidae) with particular reference to olfactory responses.

Can. Ent. 87; 509-530.

Four lines of the dipterous parasite, (which attacks Diprion hercyniae) developed by continuous breeding on different host species possessed varying degrees of preference for both hosts and the food plants of hosts. Preference of the parasite for certain plants led to selection of hosts that were not preferred in the absence of the food plants. Exposure of the parasites to the different hosts changed the degrees of preference for them, and the changes were effected through the olfactory and chemotactic sense organs.

MONTEITH, L.G. (1956).

Influence of the Host and its Food Plant on Host-finding by Drino bohemica Mesn. (Diptera:Tachinidae) and Interaction of other factors.

Proc. 10th Inter. Cong. Ent. Vol. 2; 603-606, Montreal August 17-25th 1956. Rev. App. Ent. 47; 265.

Both the host species (such as Gilpinia hercyniae) and their food plants influence the finding of hosts by Sturmia (Drino) bohemica. Their relative importance was investigated in experiments carried out by methods described in an earlier paper.

MONTEITH, L.G. (1960).

Influence of plants other than the food plants of their host on host-finding by Tachinid parasites.

Can. Ent. 92; 641-652.

Rev. App. Ent. 49; 606.

In the laboratory, tests with Sturmia (Drino) bohemica parasitizing Gilpinia hercyniae on Picea glauca showed that odour of the shrub, Ledum groenlandicum, on which the host does not feed, tended to mask the odours of the host larvae and their food plant. The masking effects may be of importance in aiding a larger proportion of the sawfly population to survive.

MONTEITH, L.G. (1962).

Apparent continual changes in the host preferences of Drino bohemica Mesn. (Diptera:Tachinidae), and their relation to the concept of host-conditioning.

Anim. Behav. 10; (3-4); 292-299.

Rev. App. Ent. 52; 381.

This parasite was laboratory reared on larvae of Gilpinia hercyniae, Neodiprion lecontei, N.sertifer, and N.swainei. The degree of preference for each host fluctuated, and these fluctuations are discussed as evidence against the concept of pre-imaginal conditioning of an insect to its host.

MONTEITH, L.G. (1966).

Influence of new growth on the food plant of the host on host-finding by Drino bohemica Mesnil. (Diptera:Tachinidae).

Can. Ent. 98 (11); 1205-1207.

The parasitic tachinid Drino bohémica preferred the odour of old to that of new growth on the food plant of its preferred host (Picea glauca). The new growth directly and indirectly influenced host-finding and host-selection by the parasite.

MONTEITH, L.G. (1967).

Responses by Diprion hercyniae (Hymenoptera:Diprionidae) to its food plant and their influence on its relationship with its parasite Drino bohémica.

Can. Ent. 99; 682-685.

The sawfly prefers the old to new growth of its food Picea glauca. The similarity between the responses by the sawfly and those by one of its parasites, the tachinid D. bohémica, and the significance of the similarity are discussed.

MORRIS, K.R.S. and CAMERON, E. (1935).

The biology of Microplectron fuscipennis (Chalcid), a parasite of pine sawfly, Diprion sertifer.

Bull. ent. Res. 26; 407-418.

This species was collected in large numbers in Hungary in 1934 (in cocoons of Diprion sertifer) for export to Canada as part of the control programme for European spruce sawfly. It was reared on Diprion polytomum cocoons in the laboratory, and its great fecundity and rapid rate of increase are reported on.

MORRIS, K.R.S., CAMERON, E. and JEPSON, W.F. (1937).

The insect parasites of the spruce sawfly Diprion polytomum, Htg. in Europe.

Bull. ent. Res. 28; 341-393.

During the course of collecting parasite material in Europe for shipment to Canada it was found that the insect is host of 31 spp. of hymenopterous and dipterous parasites. These are described in detail, keys are given, and practical notes on rearing the parasites are provided.

MORRIS, O.N. (1968).

Metabolic changes in diseased insects: II. Radioautographic studies on DNA and RNA synthesis in nuclear polyhedrosis and cytoplasmic polyhedrosis virus infections.

J. Invertebr. Pathol. 11; 476-486.

The metabolism of DNA and RNA in the fat-body of two lepidopterans infected with CPV (Malacosoma disstria and Lambdina fiscellaria lugubrosa) and the mid-gut of hymenopteran (Diprion hercyniae) infected with NPV was studied.

In the hymenopteran larval mid-gut, DNA synthesis increases in the early stage of infection, causing the nuclei to swell, while RNA synthesis at first decreases and later increases. Both DNA and RNA synthesis was low in the mid-gut of early pupae (eonymphs) infected as larvae.

MORRIS, R.F. (1942).

The use of frass in the identification of forest insect damage.

Can. Ent. 74; 164-167.

A key, with a photograph, co-presented for the identification of frass of several spruce defoliators in the Diprionidae, Pamphiliidae and Geometridae.

It is suggested that frass drop, in the case of Gilpinia hercyniae (Htg) can also be used for measuring feeding activity and deriving trends of larval population during one or more seasons.

MORRIS, R.F. (1942).

Preliminary notes on the natural control of the European spruce sawfly by small mammals.

Can. Ent. 74; 197-202.

In Eastern Canada, it is common to find as high as 40%-50% control of sawfly effected under epidemic conditions by small mammals. Shrews, voles and mice are involved, the cinereous shrew being most effective. There is seasonal fluctuation in small mammal populations. Dry sites with abundant protective ground cover are preferred. Searching ability is very high, and shrews have the ability of recognising sound cocoons before they open them.

MORRIS, R.F. (1949a)

Differentiation by small mammal predators between sound and empty cocoons of the European Spruce Sawfly.

Can. Ent. 81; 114-120.

The ability to distinguish between sound and empty cocoons is highly developed in the shrews (Sorex and Blarina), moderately developed in the mice (Peromyscus) and practically lacking in voles (Clethrionomys). Shrews (the most insectivorous group) depend largely on their sense of smell for recognizing sound cocoons.

The significance of cocoon collections in population studies is discussed.

MORRIS, R.F. (1949b).

Frass drop measurement in studies of the European spruce sawfly.

Bull. Mich. Sch. For. No. 12, pp. 58.

This paper reports the results of a study concerned with measurements of frass drop for the sawfly larvae carried out between 1939 and 1946. Sufficient evidence was obtained to show that the method is entirely feasible for determining population trends, and is superior to any previously used, both in usefulness of data provided and in respect of time and equipment required. Defects in certain phases of the work are pointed out and improvements suggested.

The method is applicable to many other forest insect defoliators.

MORRIS, R.F. (1951).

The larval Elateridae of eastern spruce forests and their role in the natural control of Gilpinia hercyniae (Htg.) (Hymenoptera:Diprionidae).

Can. Ent. 83; 133-147.

A study was carried out in New Brunswick and Gaspé between 1939 and 1946. Some twenty spp. of larval Elateridae were found in the litter under spruce trees. These are listed and keyed. Populations were comparatively low, and the rate of cocoon consumption was also low. Feeding experiments did not reveal any preference for cocoons.

It is concluded that elaterids play a minor role in control compared to mammal predators.

MORRIS, R.F. (1955).

The development of sampling techniques for forest insect defoliators, with particular reference to the spruce budworm.

Can. J. Zool. 33; 225-294.

The nature of the problems and methods of solution should apply to other insects, but the solutions themselves apply only to spruce budworm.

Problems discussed are: the expression of population data; objectives, timing and mechanics of sampling; selection of the universe and of the sample unit; representativeness in the tree and the stand; correlation between successive samples; transformation of data; optimum sample size; absolute population and incidental data (population intensity, life-table data, and other sampling systems).

Some comparisons with sampling of European spruce sawfly are made.

MORRIS, R.F. (1958).

A review of the important insects affecting the Spruce-Fir forests in the Maritime Provinces.

For. Chron. 34 (2); 159-189.

A review of the literature on Choristoneura fumiferana, Adelges picea, Dendroctonus piceaperda, Diprion hercyniae, Acleris (Peronea) variana and Lambdina (Ellopia) fiscellaria.

MORRIS, R.F. (1959).

Single-factor analysis in population dynamics.

Ecology 40; 580-588.

Black-headed budworm and European spruce sawfly are used as examples. The populations were measured at one point in each generation, and percentage parasitism was determined, so as to learn whether parasitism, the suspected "key-factor" could be used effectively to predict population density in the next generation. Predictive value was higher for budworm than for sawfly. The use of associated factors to improve prediction and the value of single factor analysis are discussed.

MORRIS, R.F. (1963).

Predictive population equations based on key factors.

Mem. ent. Soc. Canada No. 32, 103pp.

Rev. Appl. Ent. 52; 542.

By analysis of long-term population data for some forest insects in the Maritime Provinces of Canada, it was found possible to predict changes in population from one generation to the next with a surprising degree of success. A method of analysis based on the measurements of one or two key mortality factors and employing only simple linear regressions was developed for Acleris variana and Gilpinia hercyniae, and extended to Choristoneura fumiferana.

NEILSON, M.M. and ELGEE, D.E. (1960).

The effect of storage on the virulence of a polyhedrosis virus.

J. Insect. Path. 2; 165-171.

Polyhedra from Diprion hercyniae lose virulence during storage. The loss is gradual and inactivation is reached in 12 years. The polyhedra were stored in dry cadavers at 4.5°C up to 15 years. Virulence, as measured in

days to death in test insects decreases after two years, but % mortality does not change until after eight years.

NEILSON, M.M. and ELGEE, D.E. (1965).
An unusual increase of spruce sawfly numbers in New Brunswick.
Bi-m. Progr. Rep. For. Ent. Path. Br. Dept. For. Can. 21 (2); 1.

The severe outbreak of Gilpinia hercyniae which ended in 1940 was succeeded by a permanent very low population kept in equilibrium by virus and parasites. This equilibrium has been upset, apparently by extensive spraying with DDT, to control spruce budworm. The G.hercyniae population is increasing rapidly and the virus has apparently been eliminated.

NEILSON, M.M. and ELGEE, D.E. (1968a).
Tumor-like bodies in virus-infected and non-infected adults of the spruce sawfly, Diprion hercyniae.
J. Invertebr. Pathol. 10; 70-75.

The tumours are similar to capsules formed in many insects as a defence reaction to internal parasites. Over 10% of healthy adults examined contained tumours. Virus infection increases their incidence. The presence of tumours is associated with reductions in adult size, fecundity and fertility. If present in virus-infected adults, there is a reduction in vertical transmission of virus disease. The factors responsible for tumour formation in healthy adults are unknown.

NEILSON, M.M. and ELGEE, D.E. (1968b).
The method and role of vertical transmission of a nucleopolyhedrosis virus in the European spruce sawfly, Diprion hercyniae.
J. Invertebr. Pathol. 12; 132-139.

Vertical transmission of NPV in D.hercyniae is a result of foliage contamination by diseased and/or externally contaminated adults. This method of transmission provides an explanation for the persistence of this virus in field populations from year to year, especially during periods of prolonged low host densities. Transovarial and trans-ovum transmission occur rarely, if ever. Healthy adults that have been artificially contaminated externally with virus seem to be as effective as diseased adults in transmitting the virus to their offspring.

NEILSON, M.M., MARTINEAU, R. and ROSE, A.H. (1971).
Diprion hercyniae (Hartig), European spruce sawfly (Hymenoptera:Diprionidae);
Biological control Programmes in Canada 1959-1968.
Technical Bulletin No. 4, Commonwealth Institute of Biological Control; 136-143.

The effectiveness of virus and parasites is reviewed for each province affected and it is concluded that the insect no longer poses a serious threat, since its population seems to be in equilibrium with parasites and disease. This is supported by the fact that DDT spraying in one area against budworm caused a temporary upsurge in population because populations were reduced to a level at which natural enemies became rare. After a lag of three generations the parasites reappeared and after seven generations virus reappeared. Pest populations were subsequently reduced to their previous stable level.

NEILSON, M.M. and MORRIS, R.F. (1964).
The Regulation of European Spruce Sawfly Numbers in the Maritime Provinces of Canada from 1937 to 1963.
Can. Ent. 96; 773-784.

A history of the outbreak of the insect, the introduction of parasites and the outbreak of NPV is given with a description of population studies between 1938 and 1963. Morris's key factor approach using parasites, disease and weather is used in the analyses of the data

NIGITZ, H.P. (1974).

Studies on the Nematinine (Hym., Tenthredinidae) on spruce in Steiermark (Austria).

Z. angew. Ent. 75; 264-284. (German.)

Twelve species of Nematinine sawflies were found in middle and southern Steiermark (Styria). Seven of them were discovered for the first time in Steiermark. A morphological description of mature larvae is given, and a key provided. Notes on the bionomics and parasites of the twelve species are given. The distribution of spruce sawflies in Europe is reviewed, including Gilpinia hercyniae, showing that they form a fairly uniform group with only minor differences between the faunas of Finland and Steiermark.

NIKLAS, O.F. (1962a).

A gynandromorph of Gilpinia hercyniae (Hartig) (Hymenoptera:Diprionidae). Dtsch. ent. Ztschr. 9; 311-315.

A gynandromorph male was reared from a batch of larvae collected in Canada. Anatomical details are given of a female from this batch, and of one normal female and male from another brood. Secondary sexual characters of the gynandromorph are described, but a cytological investigation was not carried out because the specimen was detected as a gynandromorph only after its death.

NIKLAS, O.F. (1962b)

Observations on diapause and virosis during the laboratory rearing of the spruce sawflies, Gilpinia polytoma (Hartig) and Gilpinia hercyniae (Hartig). (Hymenoptera:Diprionidae).

Z. angew. Zool. 49; 111-122.

Larvae from various West German spruce stands and cocoons from a Canadian laboratory strain were reared. Cocoons of both species from Central Europe had obligatory diapause needing a cool period for termination, and the percentage of diapausing cocoons was mostly 70-90%. The Canadian material had an average of 28% diapause which could not be influenced by cooling at any season.

Virus disease was absent from G. polytoma, occurred to a low degree in G. hercyniae from Central Europe and a high one in those from Canada. Virosis in original and successive rearings was not generally connected, indicating latent infection, especially in the Canadian material.

The genetic aspects of diapause and the problem of latent virosis are discussed.

OHNESORGE, B. and THALENHORST, W. (1956).

Contributions to the knowledge of Spruce-Sawflies: IV Dispersion.

Z. Pflkrankh 63; 197-211 (German).

The distribution within the biotope (= dispersion) of spruce sawflies (including Gilpinia hercyniae) is determined both by the ecological demands and oviposition habits of adults, and by the ecological differentiation of the biotope. The distribution pattern drawn by oviposition persists through larval development and is still reflected in the cocoon layer. Dispersion is discontinuous when population density is low, otherwise it is more or less continuous according to the climatic differentiation of the biotope. It can be affected in some species by varying stages of bud opening in different trees.

PAQUET, G. (1943).

Bioclimatic study of the European spruce sawfly in Quebec.

Contr. Ent. Serv. Quebec No. 20, pp.20.

Rev. Canad. Biol. 2 (2).

A study was made to determine the dates of cocoon formation of the insect in Quebec in order to provide an index of the relative suitability of the various regions and localities for the development of the sawfly.

PEIRSON, H.B. (1941).

Control work on the European spruce sawfly in 1940.

23rd Biennial Rept. Forest. Comm., Augusta, Maine, 10pp.

Not seen.

PEIRSON, H.B. (1942).

Control Work on European Spruce Sawfly in 1941 (Maine Forest Service).

24th Biennial Rept. Forest Comm., Augusta, Maine, 11pp.

A report covering the distribution and intensity of the infestation in Maine, the work on parasite introduction and natural control factors. The parasites Microplectron fuscipennis and Microcryptus basizonius had been reared on a large scale and were being introduced, with apparent success. The virus disease was probably the most important factor in reducing sawfly populations. Some mortality is also due to larval and cocoon predators. A few specimens of native parasites had also been recorded, but their control value was negligible.

PEIRSON, H.B. and NASH, R.W. (1940).

Control work on European Spruce Sawfly in 1939.

Bull. Maine For. Serv. No. 12, pp19.

The widespread outbreak of Diprion polytomum in Maine seems to warrant an effort to establish parasites throughout the spruce stands of the state. During the last two seasons Microplectron fuscipennis has been thoroughly distributed over most of this area. Although this parasite may become the dominant factor of control in some areas, it appears that it will not effect a state-wide control and that there is need for introducing other species of parasites.

PIMENTEL, R. (1966).

Population ecology of insect invaders of the Maritime Provinces.

Can. Ent. 98; 887-894.

The ecology of several insects that have invaded the Canadian Maritime Provinces, including Gilpinia hercyniae, is studied and the following conclusions are drawn: The area has served as a focal point for many

invasions due to its geography. The relatively simple plant and animal communities makes invasion easier and more successful. The lack of evolved homeostasis between the invader and its adopted community may have been one of the prime reasons for outbreaks in populations of newly introduced species. Both native and introduced parasites and predators have provided effective control of introduced pests.

PREBBLE, M.L. (1941a).

The diapause and related phenomena in Gilpinia polytoma (Hartig): I. Factors influencing the inception of diapause.

Can. J. Res. (D) 19; 295-322.

This first in a series of five papers includes a review of the literature on diapause and an outline of the life cycle of the sawfly in Canada, especially the developmental stages within the cocoon. In studies of factors influencing the inception of diapause, evidence has been secured from offspring of stock from one-generation and two-generation areas that there are genetic differences within the species with respect to the capacity for development without diapause. Environmental factors are capable of bringing on diapause, and such factors are obviously operative during the development of the last seasonal generation of "emergent" field populations. However, analysis of weather conditions and incidence of diapause in such field populations failed to indicate correlation between the degree of diapause and any one environmental factor.

PREBBLE, M.L. (1941b).

The diapause and related phenomena in Gilpinia polytoma (Hartig): II. Factors influencing the breaking of diapause.

Can. J. Res. (D) 19; 323-346.

Field and laboratory experiments have shown the importance of a period of "cold-rest" at a temperature below the threshold of development as a requirement for overcoming diapause in the spruce sawfly, especially in stock from a one-generation area. After cold-rest, maximal development results at a temperature of 74° to 75°F or higher, and after contact with water. Field temperatures are lower and fail to promote and same level of development, but variations between 65° and 45° have little influence on the degree of emergence from the diapause condition, though speed of developments is affected. The benefit of contact with water is reduced or lost if contact occurs only while soil temperature remains below the threshold of development, and if moisture taken up by the cocoon wall is lost by evaporation before it can be absorbed by the larva. The role of the cocoon in water exchanges, and differential effects of abnormal weather conditions upon intracocoon development in one-generation and two-generation area stocks are described.

PREBBLE, M.L. (1941c).

The diapause and related phenomena in Gilpinia polytoma (Hartig): III. Bioclimatic relations.

Can. J. Res. (D) 19; 350-362.

The progress of intracocoon development in relation to temperature and moisture is described for a one-generation and a two-generation area in eastern Canada. In a one-generation area (central Gaspé) the degree of seasonal emergence from overwintered cocoons can be forecast with considerable accuracy by means of sample analyses during the period of pronymphal and prepupal development, since few individuals that have not initiated development by late June do so later in the summer, even though environmental conditions are quite favourable. The technique fails in a two-

generation area (southcentral New Brunswick) because members of the overwintered population may continue to respond to favourable temperature and moisture conditions throughout the entire season.

On the basis of biological and climatic data, the area occupied by the sawfly in Eastern North America is divided into zones representing the probable distribution of one-, two-, and three-generation areas. Intermediate transitional zones are also indicated.

PREBBLE, M.L. (1941d)

The diapause and related phenomena in Gilpinia polytoma (Hartig): IV. Influence of food and diapause upon reproductive capacity. Can. J. Res. (D) 19; 417-436.

Methods of sampling, determination of reproductive capacity, and analysis of data are described. Various physical measurements are positively correlated with reproductive capacity, but regression equations are unsatisfactory for estimation of fecundity outside of the population in which the relationships have been determined, due to variability in the degree of joint variation of size and fecundity under different feeding conditions. Field populations developed on white spruce are more fecund than those developed on black spruce - reductions of 30% or more may result from periodic food shortage.

Reproductive capacity of females emerging over a period of three to five years in each of 20 populations failed to show any consistent trend in relations to the diapause period. From this, and also from the slight reduction in eonymphal dry weight over extended intervals at favourable temperature, it is concluded that the destruction of eonymphal reserves during diapause proceeds very slowly and has no practical effect upon fecundity of females issuing after prolonged diapause.

PREBBLE, M.L. (1941e).

The diapause and related phenomena in Gilpinia polytoma (Hartig): V. Diapause in relation to epidemiology. Can. J. Res. (D) 19; 437-454.

This final paper in the series on diapause in the spruce sawfly describes the direct and indirect influence of diapause on epidemiology (of the sawfly) in different parts of the distribution range in eastern North America. These relate to duration of diapause, degree of diapause in overwintered cocoons, and proportions of the population surviving to participate in the continuation of the infestation. The nature of infestations in different areas is described briefly.

Discussion of features of intraspecific differences and a summary of conclusions derived from all five papers in the series are also included.

PREBBLE, M.L. (1943).

Sampling methods in population studies of the European spruce sawfly, Gilpinia hercyniae (Hartig), in Eastern Canada. Trans. R. Soc. Canada 1943 V; 93-126.

Various methods of cocoon sampling are tested in order to obtain reliable data on population trends, effect of parasites and predators etc. The relative merits of varying sample universes and plot layout are discussed. Intra-tree variability was significantly greater than inter-tree variability.

PSCHORN-WALCHER, H. (1969).

The host specificity of Tachinidae (Diptera) attacking sawflies (Hym-Symph).
Tech. Bull. Commonw. Inst. Biol. Control No. 12; 29-36.

A synopsis is given of the specificity of the European Tachinidae associated with sawflies (Hymenoptera, Symphyta). Five groups with different host-range patterns are distinguished and reviewed in detail. The phylogenetic and ecological aspects of the host-specificity of the sawfly tachinids are briefly discussed. Drino bohémica, which is specific to spruce-feeding Diprionids in Europe, is mentioned (without specific reference to Gilpinia sp.).

PSCHORN-WALCHER, H. (1974).

European spruce sawflies (Gilpinia spp.): Work in central Europe in 1973 and a review of the project to introduce natural enemies into Britain.
Report, Commonwealth Inst. of Biol. Control, Delemont, Switzerland, 11pp.

A report on larval collection, status of Gilpinia spp. in Europe, life-cycle, abundance and habitat preferences. It is suggested that larval parasites are most likely to be successfully reared for Britain, and several ichneumonid and tachinid species are reported on.

REEKS, W.A. (1937a).

Notes on the Biology of Microplectron fuscipennis Zett. as a cocoon parasite of Diprion polytomum Htg.
Can. Ent. 69; 185-187.

An introduced parasite from Europe, its bionomics in Canada shortly after introduction are described. It is a weak flier, and does best in an open stand where the sun's rays can penetrate.

REEKS, W.A. (1937b).

The morphology of the adult of Diprion polytomum Hartig.
Can. Ent. 69; 257-264.

A detailed morphological study of the Diprion polytomum adult is recorded. It is noted that two strains of the insect may exist in Europe, while this paper describes specifically the Canadian adult.

REEKS, W.A. (1938).

Native insect parasites and predators attacking Diprion polytomum (Hartig) in Canada.
Rep. ent. Soc. Ont. 60; 25-28.
(Rev. App. Ent. A28, 416)

Identified indigenous parasites which have been reared from the spruce sawfly in Canada include a phorid, 5 tachinids, 8 ichneumonids and a pteromalid. None is of any importance in control, since out of 301,142 host larvae and cocoons collected in the field during 1931-1937 only 54 produced native parasites (0.018%). Predators, which include pentatomids of the genus Podisus, and an elaterid, are of some importance but do not appear to be a major factor in control.

REEKS, W.A. (1941).

On the taxonomic status of Gilpinia polytoma Htg. and G. hercyniae (Htg.) (Hymenoptera, Diprionidae).
Can. Ent. 73; 177-188.

Hartig's classification of the species is reviewed with detailed description of morphology, cytology and reproduction.

REEKS, W.A. (1952).

Establishment of Exenterus spp. (Hymenoptera:Ichneumonidae), parasites of the European spruce sawfly, near points of introduction.
Can. Ent. 84; 76-86.

Of six spp. of Exenterus introduced into Eastern Canada, four have been recovered from G.hercyniae near points of liberation. E.claripennis was the predominant species recovered until the host population of larvae or cocoons dropped to about one per 4sq. ft. sample. Factors that affected parasite numbers are discussed, especially NPV of host larvae.

REEKS, W.A. (1953).

The establishment of introduced parasites of the European spruce sawfly Diprion hercyniae (Htg) (Hymenoptera:Diprionidae) in the Maritime provinces.
Canad. J. agric. Sci. 33 (5); 405-429.

A report on the status of introduced parasites in the Maritime provinces and in two areas in Quebec after the sawfly outbreak. Notes are given on the establishment, survival, distribution and spread of seven species. Dahlbominus fuscipennis was the only cocoon parasite to be taken in large numbers.

Five species of larval parasite were recovered, including four species of Exenterus and Drino bohémica.

REEKS, W.A. (1954).

An outbreak of larch sawfly Pristiphora erichsonii (Htg) in the Maritime Provinces (Hymenoptera; Tenthredinidae) and the role of parasites in its Control.
Can. Ent. 86; 471-480.

In this account of Pristiphora erichsonii in New Brunswick and Nova Scotia from 1933 to 1953, covering the major outbreak years of 1933-1942, reference is made to the fact that the distinction between eonymph and pronymph is not as clear as in Diprion hercyniae. Also, Dahlbominus fuscipennis (Zett) (which was introduced to control D.hercyniae) was found to be attacking the insect in very small numbers.

REEKS, W.A. (1963).

The European spruce sawfly (Diprion hercyniae) in Ontario 1936 to 1962.
Bi-m. Progr. Rep. For. Ent. Path. Br. Dep. For. Can. 19, (6); 2-3.

A review of the occurrence of the pest, and the introduction of parasites and viruses to control it.

REEKS, W.A. and BARTER, G.W. (1951).

Growth reduction and mortality of spruce caused by the European spruce sawfly Gilpinia hercyniae (Htg).
For. Chron. 27, (2); 140-158, 1-16.

The characteristics and effects of defoliation of spruce by the sawfly are described and compared with those of defoliation by the spruce budworm, and an account given of the outbreaks in the Gaspé, other parts of Quebec and New Brunswick.

RILEY, C.G. and SKOLKO, A.J. (1942).
Rate of deterioration in spruce killed by the European spruce sawfly.
Pulp. Paper Mag. Can. 43 (7); 521-524.

Trees killed by sawfly deteriorate faster than bark-beetle killed trees, because the bark remains intact keeping moisture content high.

ROHWER, S.A. (1910).
Japanese sawflies in the collection of the United States National Museum.
Proc. U.S. Natn. Mus. 39; 99-120.

It is pointed out that the genus Lophyrus is preoccupied and that Diprion should be substituted.

ROSE, A.H. (1974).
Exenterus vellicatus (Cushman) in Ontario.
Bi-monthly Research Notes 30 (4); 23, Gt. Lakes Forest Res. Cent., Sault Ste Marie, Ontario.
(Rev. Appl. Ent. 63; 52-87)

A parasite of G.hercyniae, it emerged from some field-collected cocoons in Ontario, thereby extending its known range.

ROSS, H.H. (1937).
A generic classification of the nearctic sawflies (Hymenoptera:Symphyta)
Illinois boil. Monogr. 15 (2), Bull. 34 (94).

Not seen.

SCHWARZ, U. (1973).
Nutritional quality of spruce needles for forest insect pests: (4)
Studies on 4 enzymes affecting carbohydrate metabolism in larvae of
Gilpinia hercyniae.
Z. angew. Ent. 74; 94-105. (German).

The in-vitro activities of maltase, invertase, gluco- and fructohexokinase are demonstrated as a contribution to model experiments in food quality and development of insects. The enzymes were extracted from the larvae of the sawfly feeding on spruce needles. The activity rates are determined as related to substrate concentrations, activating ions and age of larvae. The results are discussed with reference to the analytical data on compounds occurring in the needles which are usable as a substrate, as well as to biological data of the pests.

SELLERS, W.F. (1942).
The distribution of the European spruce sawfly Diprion polytomum (Htg) in the Scandinavian and Eastern Baltic countries.
Bull ent. Res. 33; 149-152.

The author made a collecting trip over Denmark, Norway, Sweden, Finland, Lithuania, Latvia and Estonia, to discover better or equally good collecting grounds for parasites to those already known in Central Europe.

The most favourable habitats of sawfly were found in one-generation areas under conditions of sun-heat, moisture and shelter near to the upper limits of spruce growth. The least favourable are the drier, less humid places especially in the two-generation areas.

The sawfly was found everywhere on spruce in the whole area covered, from latitude 50° in Denmark to latitude 68° 45' in Finland. Spruce comprises of 25%-40% of the productive forest land of this area.

SEMEVSKII, F.N. (1972).

Evaluation of the regulatory role of population dynamics factors.

Zh. Obshch. Biol. 33 (5); 569-578 (Russian, Eng. summary).

The effect of parasites, predators and diseases on population dynamics is considered. A method of evaluation of the regulatory role of these factors is proposed. In a phase diagram, velocity components of the image point determined by individual factors are plotted. If these vectors are directed inside the integral curves to the singular point, the factor regulates the population density, and vice-versa. Long term data on population dynamics have been applied to this method.

The roles of parasites, predators and diseases are discussed. It is concluded that biotic factors such as parasites and predators rarely perform regulatory functions.

Data on parasitism of Diprion hercyniae by Exenterus spp. and Drino bohémica are used.

SMIRNOFF, W.A. (1974).

Adaptation of Thelohania pristophorae (a microsporidian) on the spp. of Diprionidae and Tenthredinidae.

J. Invertebr. Pathol. 23; 114-116.

Thelohania pristophorae is a pathogen of Pristiphora erichsonii. Its pathogenicity on ten other species of sawfly (on other host plants) was tested. Diprion polytomum (host plant Picea mariana) was included, and was found to be the most resistant species of those tested. Susceptibility varies, and may be affected by the chemical composition of the host plants.

SMIRNOFF, W.A. and BERLINGUET, L. (1966).

A substance in some chemical preparations of Bacillus thuringiensis var. thuringiensis toxic to sawfly larvae.

J. Invertebr. Pathol. 8; 376-381.

Diprion hercyniae was among the most susceptible of 19 species of tenthredinid larvae tested. The substance was a very labile toxin, composed of 17 amino acids and characterized by the presence of one or more peptides of low molecular weight.

SMIRNOFF, W.A. and PHILOGENE, B.J.R. (1968).

The accumulation of Uric Acid in the Fat Body of Sawflies and its Detection.

Can. Ent. 100; 69-74.

Uric acid accumulation in the fat body of eight species of Tenthredinidae and Diprionidae (including Diprion hercyniae) was determined on a qualitative and quantitative basis. Variations were found in the number of crystal agglomerations per cell and in the nature of agglomerations between species. Uric acid dosage revealed considerable variations in concentration. Such variations could be useful for taxonomic purposes.

SMITH, D.R. (1974).

Conifer sawflies, Diprionidae: Key to North American genera, checklist of world species, and new species from Mexico (Hymenoptera).
Proc. Ent. Soc. Wash. 76; (4), 409-418.

A key is given for the identification of the six genera of the family Diprionidae found in North America. Gilpinia and Diprion are keyed as separate genera. The eleven world genera and 91 species and subspecies of the family Diprionidae are listed with the general distribution and host plant genera for each. Three new species from Mexico are described and notes on the occurrence of Neodiprion in Mexico and Central America are given.

SMITH, K.M. (1976).

Virus-insect relationships. Longman, 291 pp.

This book describes all known insect virus diseases and considers applied aspects of insect virology. Three references are made to NPV disease of Diprion hercyniae; concerning the DNA replication process, the immune pre-pupal stage and a general reference to biological control in Canada.

SMITH, S.G. (1938).

Cytology of spruce sawfly and its control in Eastern Canada.
Nature, London, 141, (3559) p. 121.

The Canadian form of Diprion polytomum had a sex ratio of 1:1200, a haploid number of seven, and spun cocoons in the soil. The European form had a much more even sex ratio, the haploid number was six and cocoons spun in foliage. Cytological studies revealed haploid oogonia. To confirm that the Canadian form was introduced from Europe, it was attempted to find this type in Europe. A similar form was found, but the cytological studies had not yet been done.

SMITH, S.G. (1940).

A new form of spruce sawfly identified by means of its cytology and parthenogenesis.
Scient. Agric. 21; 245-305.

The bionomics of the sawfly in Eastern Canada are compared with the European form. They are morphologically similar, but the Canadian form has obligatory parthenogenesis and cocoons in the ground, while the European form has facultative parthenogenesis and usually cocoons above ground.

A cytological study of the two forms revealed that the Canadian females possess 14 chromosomes and the European females possess 12 chromosomes. Some European females with 14 chromosomes were also discovered. It is concluded that two forms of sawfly exist, and that the Canadian obligatory parthenogenesis form is identical to the European obligatory form (14 chromosomes). The facultative form (12 chromosomes) is more common and more widely distributed in Europe than the obligatory form.

SOUTHWOOD, T.R.E. (1977).

The relevance of population dynamic theory to pest status.
The Origins of Pest, Parasite, Disease and Weed Problems, ed. Cherrett, J.M. and Sagar, G.R. pp.35-54, Blackwell, Oxford.

The application of a synoptic model, the r-k continuum (based on natality, natural enemies and intraspecific competition), to pest population dynamics is discussed. Opportunist species, which build up rapidly to take maximum advantage of available food are known as r-strategists. The K-strategists harvest food more efficiently in a crowded environment, and tend to have stabler populations and inhabit stable environments. Diprion hercyniae is quoted as an example of an intermediate type of pest, and the effects of the virus disease and parasites on its population dynamics are discussed in relation to the synoptic model.

STEINHAUS, E.A. (1949).
Principles of Insect Pathology.
McGraw-Hill. 757pp.

All types of insect diseases are covered. Pages 486-493 are specifically on the NPV of Gilpinia hercyniae describing symptoms, epizootiology and its value in biological control.

STEINHAUS, E.A. (1963).
Insect Pathology - an advanced treatise.
Vol. 1, 661pp, Vol. 2 689pp, Academic Press, New York.

Many well-known authors contribute to this comprehensive review. Volume 1 deals with general aspects: chemical, nutritional and genetic diseases; insects as vectors; NPVs; CPVs; granuloses and rickettsioses.

European spruce sawfly and its NPV is quoted in several places: Harker mentions tumours, Benz discusses the biochemical infection processes in the mid-gut nuclei, Vago refers to the immune pupal stage, Aizawa makes several references to the NPV, Bergold refers to the behaviour of free virus particles in the nuclei and presents a list of NPV diseases; and Aruga refers to the NPV in a section on induction of virus infection, and also refers to egg infection.

Volume 2 deals with bacterial, fungal, sporozoan and nematode infections, and with economic aspects. There is a section on epizootiology by Tanada in which reference is made to the survival ability of NPV of European spruce sawfly. Also there is reference to the success of NPV in achieving control of the insect, and to its susceptibility to infection by Bacillus cereus.

TANADA, Y. (1963).
Epizootiology of infectious diseases, Insect Pathology - an advanced treatise, Vol. 2; 423-475, ed. Steinhaus, E.A., Academic Press, New York.

A comprehensive review covering the epizootiology of all types of pathogens. The NPV of Diprion hercyniae is mentioned particularly with regard to its persistence in the population and dispersal.

THALENHORST, W. (1955).
Contributions to the knowledge of spruce sawflies: III The times of appearance of the Diprionini.
Z.PflKrankh 62; 353-361 (German).

In South Lower Saxony, Gilpinia hercyniae, G.abieticola and G.polytoma appear normally in two seasonal generations. First generation larvae (late May - early July) complete their development without diapause and produce, as adults, the second generation (larvae from August to October).

Some mid-summer (July larvae) show a marked tendency to prolonged diapause. This indicates the existence of a univoltine cycle interfering with the normal bivoltine one. The inter-generation limits get confused by variabilities, especially in later larval stages.

THALENHORST, W. (1960).

Contributions to the knowledge of spruce sawflies: VI. Population density of the Diprionidae: levels and fluctuations.

Z.PflKrankh 67; 513-524. (German).

There have been rare outbreaks of spruce sawfly in central Europe. In Southern Lower Saxony a fluctuation occurred in larval populations, with a maximum in 1955 and a minimum in 1958. Population densities were lower at higher altitudes, and the density proportions of Gilpinia abieticola: G.polytoma:G.hercyniae approached 1:2:2. The cocoon density fluctuated inversely to that of the larvae, which was interpreted as a consequence of changes in the amplitude of density "oscillations".

THALENHORST, W. (1962).

Variability in the phenology of Gilpinia species and its effect on population fluctuations.

Proc. 11th Int. Congr. Ent. Vienna 1960, Vol. 2; 159-163.

In observations and experiments with Gilpinia spp., the date after which no larvae were found to develop into imagoes that same year, and before which no larvae were found to go into diapause, remained the 1st August from 1953 to 1958 for G.polytoma, but fluctuated widely and differently for G.hercyniae and G.abieticola. A possible photoperiodic stimulus is suggested for G.polytoma.

THALENHORST, W. (1966).

Contributions to the knowledge of spruce sawflies: VII: Sex ratio

Z.PflKrankh. 73; 57-69 (German).

Figures are given showing the sex ratio for species of different groups (Nematinae and Diprionidae) in 1951-63, and the various factors affecting it are discussed. Gilpinia hercyniae is practically 100% parthenogenetic.

THALENHORST, W. (1968).

Contributions to the knowledge of spruce sawflies. VIII: Numbers of eggs and egg-laying.

Z.PflKrankh. 75; 338-350. (German).

Nematinae and Diprioninae are compared, including observations on the preferences of different species for different stages of bud and shoot development for oviposition, and the position of the egg on the needles. The specific details of the oviposition behaviour of Gilpinia hercyniae are included.

THALENHORST, W. (1973).

German literature on forest protection 1971/72: II: Insects and other arthropods.

Z.PflKrankh 80; 615-625. (German)

A general review mentioning the research on nutritional quality of spruce needles for Gilpinia hercyniae.

THALENHORST, W. (1974).

Contributions to the knowledge of Spruce Sawflies: IX: The temperature/development function of eggs and larvae.

Z.PflKrankh 80; 133-147. (German).

Thirteen species including Gilpinia hercyniae are covered. Certain interspecific differences in the criteria of the temperature - development (T-D) function could be detected, and the relations between temperature optimum, succession of generations and population density at different altitudes are mentioned. In other cases, the T-D function might be responsible for the coincidence in larval development with the growth of spruce needles or with parasites and predators. In these or even in other ways the T-D function might indirectly affect population dynamics.

TINSLEY, T.W. (1973).

Biology and Ecology of Invertebrate Viruses - Nuclear Polyhedrosis Virus of Spruce Sawfly.

Report of the Natural Environment Research Council for the year 1 April 1972-31 March, 1973; 114-155, H.M.S.O.

A brief report of research on Gilpinia hercyniae NPV in mid-Wales.

TINSLEY, T.W. (1974).

Nuclear polyhedrosis viruses, epizootiology of a nuclear polyhedrosis virus in European spruce sawfly.

Report of the Natural Environment Research Council for the year 1 April 1973-31 March 1974; 105-107, H.M.S.O.

A report of research on Gilpinia hercyniae NPV in mid-Wales. The virus has become widely dispersed over several forests, rendering impossible the study of local dispersal of NPV from small epicentres. Several species of birds have been shown to be involved in dispersal of the disease. Bird-droppings collected outside the larval season are also infective.

TINSLEY, T.W. and ENTWISTLE, P.F. (1972).

The use of pathogens in the control of insect pests.

13th Symposium of the British Ecological Society, Biology in Pest and Disease Control; 115-129.

A brief review of the use of Nematodes, Fungi, Protozoa, Bacteria, Rickettsiae and viruses, and some possible hazards in microbiological organisms and their modes of use. The remainder deals in detail with epizootiology, covering survival, dispersal, virulence and inoculum potential, using several examples including Gilpinia hercyniae. Possibilities for future applied studies are also discussed.

TRÄGÅRDH, I. (1939).

Sveriges Skogsinsekter.

Stockholm, 508pp. (Swedish).

Lophyrus polytomum Htg is mentioned on pp341-2, and also L.sertifer and L.pini, in a chapter covering forest pests in Sweden.

TURNBULL, A.L. and CHANT, D.A. (1961).
The Practice and Theory of Biological Control of Insects in Canada.
Can. J. Zool. 39; 697-753.

A general review of biological control in Canada, mentioning Diprion hercyniae.

VAGO, C. (1963).
Predispositions and interrelations in insect diseases.
Insect Pathology - an advanced treatise Vol. 1, 339-379. ed.Steinhaus, E.A.
Academic Press, New York.

A section on natural predispositions refers to the immunity of the pre-pupal stage of Diprion hercyniae and the fact that the disease re-starts when the pupal mid-gut cells mature. The interrelationships between physiological and microbial disorders are reviewed in detail, followed by a section on simultaneous diseases.

VEHRKE, H. (1961).
Distinguishing the larvae of Gilpinia abieticola (D.T.), G.polytoma (Htg) (Hymenoptera:Diprionidae) by the patterns on their head capsules.
Z.angew. Ent. 48; 176-185.

Characteristic dark frontal figures on the head capsules enable separation of the larvae of Gilpinia polytoma from G.hercyniae and identification of the younger instars of G.abieticola. Diagrams are given.

VERZHUTSKI, B.I. (1965).
On some sawfly pests of conifers new to Cisbaikalia.
Izv. sib. Otdel. 1; 105-112, Akad. Nauk. SSR Ser. biol-med Nauk. (Russian)
(Rev. App. Ent. 54; 140).

Notes are given on the habits of four species of sawflies found infesting the foliage of conifers in the Cisbaikala area of the Soviet Union for the first time in 1960-63; Xyela julii (Breb), Diprion similis (Htg), Gilpinia hercyniae (Htg) and G.polytoma (Htg); the first two infested pines and the last two spruce.

WILKES, A. (1942a).
Notes on the laboratory propagation of three European species of Exenterus (Ichneumonidae) parasite on sawflies.
Rept. ent. Soc. Ont. 72; 41-44.

These introduced parasites were laboratory reared to control European spruce sawfly in Canada.

WILKES, A. (1942b).
The influence of selection on the preferendum of a Chalcid (Microplectron fuscipennis Zett) and its significance in the biological control of an insect pest.
Proc. Roy. Soc. (B) 130; 400-415.

The temperature preferences of the parasite are tested and the apparatus and technique described.

WONG, H.R. (1972).

The spread of the European spruce sawfly Diprion hercyniae (Hym-Diprionidae) in Manitoba.

Can. Ent. 104; 755-756.

A report on the distribution and spread from 1969 to 1970 of the insect in Manitoba. No NPV was evident, but one parasite, Palexorista bohémica (Mesn.) was present, and had apparently spread its range into Manitoba along with the sawfly.

WOOLLAT, L.H. (1961).

Gilpinia hercyniae (Hartig) (Hym, Diprionidae) in Devon.

Ent. mon. Mag. 97; 264.

A female was beaten from spruce in May 1960 at Haldon, S. Devon. It was sleeved, one larva resulting, which pupated and emerged in August.

3 INDEX

ADULT STAGE: James, 1974; Neilson and Elgee, 1968(a)(b); Niklas, 1962(a).

ARTIFICIAL CULTURE: Bombosch and Ramakers, 1976; Niklas, 1962(b);

ARTIFICIAL DISSEMINATION/APPLICATION OF VIRUS: Atwood, 1943; Bevan and Davies, 1971; Bird, 1948; Bird and Burk, 1961; Clark, Clarke and Pardy, 1973; Entwistle, 1973; Franz, 1975; Hall, 1963; Kaya, 1975; McGugan and Coppel, 1962; Maksymuik, 1975; Reeks, 1963.

BACTERIAL TOXINS (susceptibility to): Angus, 1956; Heimpel, 1961; Heimpel and Angus, 1963; Smirnoff and Berlinguet, 1966.

BEHAVIOUR: Barclay, 1939; Monteith, 1967.

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CHEMICAL CONTROL: Atwood, 1960; Balch, 1934; Cameron, 1972; Neilson Martineau and Rose, 1971.

COCOON: Brown and Paquette, 1939; Buckner, 1955; Finlayson, 1960; Jukes, 1977; Morris, 1951; Paquet, 1943; Prebble, 1941(a),(b),(c),(d),(e).

CYSTS, TUMOURS: Bird, 1949(a),(b); James, 1974; Harker, 1963; Neilson and Elgee, 1968; Fogal and Kwain, 1972(b).

DAY LENGTH: Bombosch and Ramakers, 1976.

DENSITY DEPENDENCE, DENSITY RELATED FACTORS: Bird, 1948; Bird and Elgee, 1957; Franz, 1955; Neilson and Elgee, 1965; Ohnesorge and Thalenhorst, 1956; Thalenhorst, 1960.

DIAPAUSE: Balch, 1940; Balch and Simpson, 1932; Balch, Simpson and Prebble, 1934; Bombosch and Ramakers, 1976; Gobeil, 1940, 1941, 1942; Niklas, 1962(b); Prebble, 1941(a),(b),(c),(d),(e); Thalenhorst, 1955, 1962.

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DISPERSAL:

(a) OF GILPINIA: Anon, 1953; Atwood, 1937; Balch, 1936, 1937, 1939(a),(b), 1940, 1941, 1942; Benson, 1950; Billany and Brown, 1977; Brown and Fleming, 1938; Crooke, 1953; Hanson, 1951; Ohnesorge and Thalenhorst, 1956; Wong, 1972.

(b) OF PARASITES: Baird, 1940.

(c) OF NPV: Bird and Burk, 1961; Entwistle, 1972, 1973, 1976; Entwistle, Adams and Evans, 1977(a),(b).

EGG, OVIPOSITION, OVIPOSITION SITES: Bird, 1961; Gobeil, 1942; Huang, 1975; Billany, Brown and Borden, 1978, Franz, 1955; Neilson and Elgee, 1968(b); Thalenhorst, 1968, 1974; Ohnesorge and Thalenhorst, 1956.

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EPIZOOTICS, ENZOOTICS: Balch, 1940, 1941, 1960; Balch and Bird, 1944; Bird, 1948, 1949(a), 1954, 1955, 1961; Bird and Burk, 1961; Bird and Elgee, 1957; Brown, R.M., 1973; Clark, Clarke and Pardy, 1973; Dirks, 1944; Dowden, 1940; Entwistle, 1971, 1972, 1973; Entwistle, Adams and Evans, 1977(a),(b), 1978; France, 1955; Gobeil, 1940; Kaya, 1975; Martineau, 1963; Neilson and Elgee, 1965; Neilson, Martineau and Rose, 1971; Neilson and Morris, 1964; Peirson, 1942; Steinhaus, 1949; Tanada, 1963; Tinsley, 1973, 1974; Tinsley and Entwistle, 1972.

FECUNDITY: James, 1974; Prebble, 1941(2); Thalenhorst, 1968.

GENETICS/STRAINS: Balch, Reeks and Smith, 1941; Knerer and Atwood, 1973; Niklas, 1962(a),(b); Prebble, 1941(a),(b),(c),(d),(e); Smith S.G. 1938, 1940.

GROWTH, RATE OF, DEVELOPMENT OF EGGS AND LARVAE: Thalenhorst, 1974.

HABITAT: Sellers, 1942.

HAEMOLYMPH: Lunderstadt, Postel and Reymers, 1977.

HOST PLANT, QUALITY/INFLUENCE OF: Bombosch and Lunderstadt, 1975; Monteith, 1956, 1960, 1967; Thalenhorst, 1968.

IMMUNITY, RESISTANCE (see also LATENCY): Aizawa, 1963; Bird, 1953; Bird and Elgee, 1957; James, 1974; Neilson and Elgee, 1968(a).

INCUBATION (LATENT) PERIOD: Bird, 1949(a).

INFECTION PROCESS: Benz, 1960, 1963, 1967; Bird, 1949(a), 1952, 1953; Bird and Whalen, 1954; Morris, 1968.

INFECTION RATES, DEVELOPMENT OF: Dowden, 1939; Entwistle, 1972, 1973; Evans and Entwistle, 1976.

INOCULUM PERSISTENCE: Entwistle and Adams, 1977; Entwistle, Adams and Evans, 1977(b), 1978; Entwistle et al., 1979; Neilson and Elgee, 1960.

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LATENCY, INDUCTION (see also IMMUNITY): Aruga, 1963; Bird, 1949(a), 1953; James, 1974; Neilson and Elgee, 1968(a); Niklas, 1962(b); Vago, 1963.

LIFE-CYCLE, BIONOMICS (see also DIAPAUSE): Anon, 1971; Atwood, 1937; Balch, 1936, 1939(a); Balch and Simpson, 1932, 1934; Balch, Simpson and Prebble, 1934; Billany, 1978; Escherich, 1942; Nigitz, 1974; Paquet, 1943; Prebble, 1941(e); Pschorn-Walcher, 1974; Reeks, 1937(a); Smith SG, 1940; Thalenhorst, 1955, 1960, 1962, 1968; Verzhutski, 1965.

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PARASITES:

(a) Diptera:

Bessa selecta; Hawboldt, 1947.

Drino bohemia; Clausen et al, 1978; Finlayson and Finlayson, 1958(a); Martineau, 1963; Monteith, 1955, 1956, 1960, 1962, 1966, 1967; Pschorn-Walcher, 1969; Reeks, 1953; Semevskii, 1972.

Palexorista bohémica; Wong, 1972

Ptychomia selecta; Lovaszy, 1939

Sturmia inconspicua; Lovaszy, 1939

Sturmia sp; Baird, 1940; Briand, 1948(a), 1948(b); Coppel and House, 1947.

(b) Hymenoptera:

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Finlayson and Finlayson, 1958(a); Reeks, 1953, 1954.
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Exenterus amictorius; Clausen et al, 1978
Exenterus tricolor; Forsens, 1932
Exenterus vellicatus; Rose, 1974
Exenterus spp.; Baird, 1940; Balch, 1940; Barclay, 1939; Briand, 1948(a);
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Holocremnus ratzeburgi; Forsius, 1932; Lovász, 1939.
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Lamachus spectabilis; Forsius, 1932
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Microplectron fuscipennis; Baird, 1937, 1939, 1940; Balch, 1940; Baldwin, 1939;
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Cameron, 1935; Peirson, 1942; Reeks, 1937(a); Wilkes, 1942(b).
Pleolophus basizonius, Clausen et al 1978

PARASITISM (general - main references): Baird, 1937, 1939(a); Berland, 1947;
Bevan, 1975; Billany, 1978; Bird and Elgee, 1957; Briand, 1948(a); Carter,
Fielding and Billany, 1976; Clausen et al, 1978; DeBach, Huffaker and McPhee,
1976; Finlayson, 1960; Finlayson and Finlayson, 1958(a), 1958(b); Franz, 1955;
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Jepson, 1937; Morris RF 1959; Pschorn-Walcher, 1974; Reeks, 1938.

POPULATION STUDIES (see also LIFE-TABLES): Baird, 1939(a); Balch, 1936, 1938,
1939(a), 1940, 1942; Balch and Bird, 1944; Bird, 1948, 1954; Bird and Burk,
1961; Bird and Elgee, 1957; Brown and Paquette, 1939; Clark, Clarke and Pardy,
1973; Conklin, 1942; Croke, 1956; DeBach, Huffaker and McPhee, 1976; Dirks,
1944; Entwistle, 1973; Evans and Entwistle, 1976; Finlayson and Finlayson,
1958(a); Franz, 1955; Ghani et al, 1974; Martineau, 1958, 1963; Morris RF,
1942; Prebble, 1943; Reeks, 1952; Thalenhorst, 1960.

PREDATION (general - main references): Balch, 1936, 1942; Bird, 1955;
Brown RM 1973; Buckner, 1955; Clark, Clarke and Pardy, 1973; Conklin, 1942;
Dirks, 1944; Entwistle, 1976; Entwistle, Adams and Evans, 1977(a), 1977(b),
1978; Escherich and Baer, 1913; Franz, 1944; Ghani et al, 1974; Martineau,
1963; Morris RF, 1942, 1949(a), 1951; Peirson, 1942; Pimentel, 1966; Reeks, 1938.

PREDATORS (specific):

(a) BIRDS

Entwistle, Adams and Evans, 1977(a), 1977(b), 1978.

(b) INSECTS

Morris RF, 1951; Reeks, 1938

(c) MAMMALS

Morris RF, 1949(a)

PUPA, PREPUPA (see also COCOON): Aizawa, 1963; Gobeil, 1941; Prebble, 1941(a),
1941(b), 1941(c), 1941(d), 1941(e); Reeks, 1954; Thalenhorst, 1962

SALIVARY GLANDS: Maxwell, 1955

SEX RATIO (see also GENETICS/STRAINS): Balch, 1939; Balch, Simpson and Prebble, 1934; Finlayson and Finlayson, 1958(b); Niklas (1962(a)); Smith S.G, 1938; Thalenhorst, 1966.

SOIL: Jukes, 1977.

SPRUCE: see HOST PLANT

STRAINS: see GENETICS

TAXONOMY: see KEYS

TRANSMISSION OF VIRUS:

(a) HORIZONTAL (see also DISPERSAL):

Atwood, 1943; Balch, 1946; Bird, 1949(a), 1955, 1961; Entwistle 1972, 1973; Tinsley, 1974.

(b) VERTICAL (includes INOCULUM PERSISTENCE):

Aruga, 1963; Atwood, 1943; Balch, 1946; Bird, 1949(a), 1953, 1954, 1955, 1961; Entwistle, 1973, 1976; Entwistle and Adams, 1977; Entwistle, Adams and Evans, 1977(b), 1978; Evans and Entwistle, 1976; James, 1974; Neilson and Elgee, 1960, 1968(a); 1968(b).

VECTORS: Bird, 1949(a), 1961; Entwistle, Adams and Evans, 1977(a), 1977(b), 1978; Franz, 1955.

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5 ADDENDUM

ANON. (1975).
Epizootiology.
Rept. Nat. Environ. Res. Council, 1974/75; 112

ANON. (1976).
Epizootiology.
Rept. Nat. Environ. Res. Council, 1975/76; 104

ANON. (1977).
Ecology and epizootiology of insect diseases.
Rept. Nat. Environ. Res. Council, 1976/77; 109

ANON. (1978).
Ecology and epizootiology of insect virus diseases.
Rept. Nat. Environ. Res. Council, 1977/78; 86

ANON. (1980).
Ecology and epizootiology of insect diseases.
Rept. Natur. Environ. Res. Council, 1978/79; 77

The above five give brief reports on the progress of studies of a natural epizootic of nuclear polyhedrosis virus disease in Gilpinia hercyniae in mid-Wales, U.K.

BUSE, A. (1977a).
The importance of birds in the dispersal of nuclear polyhedrosis virus of European spruce sawfly, Gilpinia hercyniae, (Hymenoptera: Diprionidae) in mid-Wales.
Entomologica exp. appl. 22; 191-199.

Droppings of birds from three sites at which larval populations of Gilpinia hercyniae were "free" from nuclear polyhedrosis virus infestation were assayed for infectivity to laboratory reared test larvae. The sites were about 4 km (A), 5 km (B) and 11 km (C) from an area with an NPV-infected G. hercyniae population. The numbers of birds sampled were: site A-4, site B-12 and site C-24. None of the droppings were shown to be infective. On the basis of this trivial level of sampling the author suggests that G. hercyniae adults may be major agents of dispersal.

BUSE, A. (1977b).
Birds and the spread of nuclear polyhedrosis virus disease of European spruce sawfly.
Ann. Rept. Inst. Terrestrial Ecol., 1976; 52-54.

As for Buse (1977a).

