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ENTOMOLOGICAL SOCIETY OF MANITOBA

Vol. 7 December, 1951.

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The contents of this volume are for private distribution and not for publication.

Issued: October, 1952.

LIST OF MEMBERS

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Field Crop Insect
Laboratory, - Brandon.

Vice-President -- A. J. Thorsteinson,
Department of Entomology,
University of Manitoba.

Secretary -- R. R. Lejeune,
Laboratory of Forest
Biology, - Winnipeg.

Treasurer -- F. L. Watters,
Stored Products Insect
Laboratory, - Winnipeg.

Editor-Librarian -- R. J. Heron,
Laboratory of Forest
Biology, - Winnipeg.

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C. Barrett, Field Crop Insect Laboratory, Brandon,
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B. Berck, Stored Products Insect Laboratory,
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Proceedings of the

ENTOMOLOGICAL SOCIETY OF MANITOBA

Vol. 7 December, 1951.

INTRODUCTION

Recently the objectives of our Society have been restated and we will continue as in the past, "to foster the advancement, exchange and dissemination of entomological knowledge".

Our fall meeting featured the free exchange of information and ideas among the membership and prominent guests. It was our great pleasure to have Dr. A.C. Hodson, from the University of Minnesota, keynote a seminar on experimental ecology with a paper on "The Experimental Approach to Ecology". Dr. J. W. Butcher, forest entomologist for the State of Minnesota, and several of our members presented short papers on specific aspects of insect ecology. This seminar is reported in the text of the Proceedings.

Our insecticide committee, composed of members from the University of Manitoba, the Federal Department of Agriculture, and industry, prepared a descriptive list of the commercial insecticides readily available in the Province. This undertaking has provided a useful tool for all workers in the Province. The committee also has in the course of preparation a "Vegetable Insect Control Circular" that will tend to unify the control procedures recommended, keep them abreast of developments, and provide an effective means of disseminating the information.

The executive is gratified by the wholehearted manner in which our membership, both from the professional and commercial fields of entomology, have received and are supporting the recently formed Entomological Society of Canada. It is a great pleasure to believe that satisfactory progress has attended every endeavour of our Society.

The publication of these Proceedings has been made possible by the stenographic assistance provided by the Department of Entomology, University of Manitoba, the Stored Products Insect Laboratory, Winnipeg, the Forest Biology Laboratory, Winnipeg and the Field Crop Insect Laboratory, Brandon. The co-operation of the individuals and institutions concerned is gratefully acknowledged.

W. R. ALLEN,
President.

THE MARCH GENERAL MEETING

The Business Session

A general meeting was held in the Department of Entomology, University of Manitoba, on March 6th, 1951. The meeting convened at 11:00 a.m. Mr. Lejeune suggested that because the president, C.A.S. Smith, and secretary, B.N. Smallman, had resigned because of transfers or impending transfers, and the vice-president, Mr. Allen, was completing graduate studies at the University of Minnesota, interim officers should be elected to conduct the meeting.

R.J. Heron nominated Prof. A.V. Mitchener as interim chairman. A.J. Thorsteinson nominated R.R. Lejeune as interim secretary. It was moved by A. Hedlin that nominations close.

Seconded by W. Romanow.
CARRIED.

Prof. Mitchener then assumed the chair. The minutes of the last meeting were read and approved.

Business Arising Out of Minutes

(1) Mr. S. Pugh presented a brief report on the work of the insecticide committee. He staged that the task of compiling a list of Manitoba dealers and insecticides handled was proving more difficult than anticipated but that progress was being made. Mr. Pugh suggested that the preparation of the list was not the answer to the problem and some other approach should be considered.

(2) Correspondence to and from Mr. Wigmore, secretary of the Entomological Society of Canada, concerning fees was read.

New Business

(1) Election of officers - Prof. Mitchener explained that because of the unusual situation this year a nominating committee composed of the following members was appointed by the executive on Jan. 3, 1951: A.V. Mitchener, C.A.S. Smith, B.N. Smallman. Prof. Mitchener, reporting for the committee, proposed the following slate of officers:

President - W.R. Allen
Vice-President - A.J. Thorsteinson
Secretary - R.R. Lejeune
Treasurer - F.L. Watters
Editor-Librarian - R.J. Heron

There being no further nominations it was moved by J. B. Wallis that nominations close.

Seconded by B.N. Smallman.
CARRIED.

(2) It was moved by J.B. Wallis that the treasurer be empowered to sign cheques for the Entomological Society of Manitoba.

Seconded by B.N. Smallman.
CARRIED.

(3) It was moved by J.B. Wallis that the Executive be empowered to act with respect to the amount that should be charged for Proceedings of the Society. The Executive is also to decide who should be charged and was instructed to report at the next meeting.

Seconded by F.L. Watters.
CARRIED.

(4) It was moved by R.R. Lejeune that the Insecticide Committee be retained as a standing committee, with the same members.

Seconded by A.J. Thorsteinson
CARRIED.

(5) There was some discussion about the need for other standing committees. It was moved by R.R. Lejeune that the new executive appoint a committee to study and recommend approved common names of insects in Manitoba.

Seconded by R.J. Heron.
CARRIED.

(6) A motion congratulating Col. C.A.S. Smith and Dr. B.N. Smallman on their promotions but expressing regret at their departure and appreciation of their work for the Society was proposed by R.R. Lejeune.

Seconded by P. Pankiw,
CARRIED.

The business session adjourned at 12:10 p.m.

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Scientific Business

During the afternoon members convened for the scientific session at which time those present briefly reviewed their current entomological work. Several members from Brandon were prevented from attending due to weather conditions which made the trip to Winnipeg impossible. For this reason reports from the Field Crop Laboratory at Brandon were limited. Only those reports for which manuscripts were submitted to the Editor are included here.

Field Crop Insects:- The following report is from the Field Crop Insect Laboratory, Brandon.

Biological Studies of the More Important Insects Attacking Potatoes in Manitoba

T. V. Cole

I. Colorado potato beetle, Leptinotarsa decemlineata (Say)

Life-History

1. The majority of adults emerged from hibernation at about the same time as early sown potatoes appeared above the ground.

2. The largest number of eggs were present when the potato plants were about three weeks old. Oviposition decreased rapidly in the latter half of July in 1949 and 1950. The average number of eggs laid by each of 20 caged females during 1949 was 1056.

3. Overwintered females were able to produce fertile eggs throughout the summer season whether or not they were fertilized subsequent to spring emergence.

4. The duration of the developmental period averaged 31 days. The incubation period averaged about five days. The larval period required about two weeks, the time spent in each of the four larval instars being, respectively, four, three, four, and three days. The prepupal and pupal periods averaged four and eight days, respectively.

5. First generation adults began to emerge during the latter half of July in 1949, and in the first part of August in 1950.

6. A partial second generation occurred in 1949 during the second week of August. There was no partial second generation in 1948 or 1950.

7. The main movement to hibernation occurred during the last week of August in both 1949 and 1950.

8. The beetles hibernated between depths of two and twenty inches in the soil.

Mortality

1. Adults placed in hibernation did not survive the second winter. All adults placed at different depths between two and twenty-four inches perished when there was no snow cover.

2. First instar larvae perished in cold wind-driven rains.

3. Predators attacked all stages of the Colorado potato beetle. The most important predators were aphid lion larvae, lady beetle larvae and adults, pentatomid nymphs and adults, carabids, and possible small birds.

4. Cannibalism by larvae and adults reduced egg populations.

5. Parasitism by the tachinid fly *Doryphorophaga doryphorae* (Riley) was an important single factor when Colorado potato beetle population was high.

II. Potato flea beetle,
Epitrix cucumeris (Harr.)

Life-history

1. The cold wet spring of 1950 delayed spring emergence until June 16.

2. The oviposition period extended from late June until early in August in 1950.

3. The larvae fed mainly on the potato rootlets but also attacked the tubers causing shallow scars and "pimples". The adults caused the characteristic shot-hole damage to the foliage.

4. The average duration of the developmental stages was: egg, 5.2 days; larva, 24.7 days; prepupa 7.4 days; pupa, 9.7 days.

III. Potato leafhopper, *Empoasca fabae* (Harr.)

Life-history

1. One adult was taken in sweeps made on brome grass on May 19, 1950.

2. In 1950, adults began to appear on potato plants in the first half of July.

3. The average duration of the developmental stages was: egg 16.4 days, nymph 19 days in the laboratory, and 20.6 days in the insectary.

4. Adults were found on partially-green plants until October 13, 1950.

5. The overwintering habits of the insect were not established though most evidence indicated that it migrates into Manitoba each year.

Department of Entomology,

University of Manitoba

A Summary of Results of Insecticide Trials

A. V. Mitchener and A. J. Thorsteinson

Grasshopper Poison Trials

Studies were conducted by Professor A.V. Mitchener to determine: 1. the relative toxic effects of aldrin and dieldrin on the three grasshopper species, *Camnula pellucida* (Scudd.), *Melanoplus bivittatus* (Say) and *Melanoplus mexicanus mexicanus* (Sauss). 2. the number of days these materials remain toxic to these insects on seedling oats and on cabbage leaves. 3. relative speed on toxic action on the three species.

The experiments were conducted at room temperature in cages with 4"x6"x6" dimensions made of wooden tops and bottoms and screen sides.

Treated plants were placed in the cages. Untreated plants were also provided in each cage. During the experiments the cages were stocked with field collected grasshoppers.

The results obtained support the following conclusions:

4. Conclusions:

(1) All three species were readily killed when they were fed oat plants or cabbage sprayed with either dieldrin or aldrin.

(2) Dieldrin at the rate of 2 oz./40 glas. of water gave better kills than aldrin at 4 oz./40 gals. for each of the three species.

(3) Dieldrin was effective for approx. 11 days on all sprayed plants while aldrin was similarly toxic for approx. 5 days on cabbage plants when compared 48 hours after the grasshoppers had fed. Oat leaves sprayed with aldrin gave only moderate control (82%) immediately after spraying and very poor control thereafter.

(4) The clear-winged grasshopper succumbed more quickly to either dieldrin or aldrin than either of the other two species.

(5) Maximum kills were obtained about 48 hours after the grasshoppers had eaten the poisoned plants.

(6) The household detergent "Surf" was used effectively as a spreader or wetting agent for the spray applied to cabbage leaves.

Another series of tests on grasshopper poisons were conducted by A.J. Thorsteinson to determine the lowest concentrations of chlordane, aldrin, dieldrin and gamma benzene hexachloride that could be relied on to give adequate kills when used in baits. The toxicants tested were commercially prepared emulsion concentrates. The benzene hexachloride was supplied by Plant Protection Ltd. through Chipman Chemicals Ltd. The other materials were supplied by Julius Hyman and Co.

Field-collected grasshoppers were tested in screen cages. The baits were prepared by mixing bran with an equal weight of toxicant emulsion diluted to give the required concentrations. On the basis of the results the following conclusions were reached.

(1) The toxicity of chlordane falls off more rapidly as the concentration isreduced than the other materials.

(2) Dieldrin gave a higher percentage mortality after 24 and 48 hours at the lowest concentration tested (1:6400) than did aldrin.

(3) The most toxic material in terms of mortality after 1 day was gamma benzene hexachloride, but after 2 days the mortalities were lower than aldrin or dieldrin.

The lowest concentrations of the materials tested that gave at least 80% mortality were as follows:

Time of Exposure -		24 hours	48 hours
Toxicant -	Chlordane	1:400	1:400
	Aldrin	1:1600	1:3200
	Dieldrin	1:1600	1:3200
	Acridel	1:800	1:800

Control of Flies in a Swine Barn with Dieldrin

An attempt was made to assess the effectiveness of 0.5% dieldrin emulsion spray for the control of flies in a swine barn.

In 1949, 0.5% dieldrin emulsion spray was applied to a relatively small fraction of the total wall and ceiling area at the south end of the barn. Spectacular control of a heavy infestation of flies was obtained.

In 1950, this treatment was repeated, but although many flies were killed, the fly population was not affected for at least four days and then it dropped each day till it reached a very low level by the end of 9 days.

On the 8th day a second application of spray was made to the whole interior wall and ceiling surface. The fly population remained at a low level for the remainder of the season.

Unfortunately, it was not practical to obtain counts of fly mortality. However, numberous dead flies were observed on the barn floor.

Dieldrin is known to be slow in its toxic action. Therefore, during the height of the fly breeding season a building could become re-infested as quickly as they can be killed by a slow-acting toxicant.

The use of highly toxic insecticides does not remove the necessity for screens and the elimination of breeding places for effective fly control.

Stored Product Insects:-Contribution from Stored Product Insect Laboratory, Winnipeg -

Grain Fumigation Studies

F. L. Watters

The poor storage quality of the 1950 grain crop in Western Canada prompted an investigation of three new fumigants available for treatment of stored grain infested by mites and insects. These were as follows: 80% methyl bromide - 20% chloropicrin, 80% methyl bromide - 20% ethylene dibromide, and 40% methyl bromide - 60% ethylene dibromide.

The fumigants were applied at dosages of either 2 lbs. or 3 lbs. per thousand bushels. Usually they were applied in one pound quantities on three foot squares over the entire surface through cast iron pipes inserted to a depth of two feet. Effectiveness was based on the number of live mites recovered from grain samples taken at the surface and at depths of eight feet before fumigation and ten days later.

The results showed that all fumigants were apparently equally effective in reducing mite infestations irrespective of the dosage used.

Additional information on distribution and persistence of fumigants in bulk grain was obtained with a halide leak detector. These results showed that moderate concentrations of all fumigants remained in the grain two to six days. Satisfactory vertical and lateral distribution of all fumigants was also obtained.

Fumigants may only be accepted for use in stored grain if they are biologically effective and also have no deleterious affect on grain quality. Treated grain samples were submitted for baking and quality tests to the Grain Research Laboratory. The results indicated that the fumigants had no injurious effect on grain quality; the control and treated samples were practically identical in loaf volume and external and internal characteristics.

Comparative Effectiveness of Spot Fumigants In Flour Mills

F. L. Watters

In cereal and food processing plants insects often occur in elevator boots where dead stock accumulates. Since boot stocks are subject to continuous infestation from other parts of the mill the question arises whether the quick-acting spot fumigants presently in use would be as effective as fumigants which remain active over longer periods. Studies were undertaken to compare under practical mill conditions the initial and residual effectiveness of two proprietary spot fumigants ehtylene dichloride and ethylene dibromide with a new fumigant hexachloropropene, which according to laboratory tests has only a residual action.

The results show that the two proprietary fumigants gave complete mortality of adults of the confused flour beetle immediately after application but failed to give appreciable kills 4 to 6 days later. Hexachloropropene was ineffective for two days after application but thereafter continued to give 100 per cent mortality for 62 days when test insects were exposed for 6-day periods. The longevity was attributed to the low vapour pressure and high toxicity of the compound.

Chemical Determination of Insecticides

B. Berck

During 1950, the writer worked on the following:

1. Work was continued on chemical determination of micro amounts of DDT in river water (cf. report in Proc. Ent. Soc. Man. 6:1, 17. 1950). In an arrangement between the Dominion Entomological Laboratory, Saskatoon, and the Stored Product Insect Laboratory, Winnipeg, the writer worked at Saskatoon during June and July with F. J. H. Fredeen, Dr. A.P. Arnason and Dr. J.G. Rempel. Field experiments were conducted in which DDT was applied to a certain larvae of the black fly, <u>Simulium</u> <u>arcticum</u>, Mall. Two of the objectives were: (a) determination of the effect of distance from point of DDT application on DDT content of the water, and (b) elucidation of the role of suspended solids (sometimes loosely called "silt") in affecting the concentration of DDT.

The sensitivity of measuring DDT was increased so that a DDT concentration of one part in 475,000,000 parts of water could be measured satisfactorily. The latter sensitivity was inadequate to measure DDT concentrations of samples taken between 35 and 75 miles from point of application; but when it was found that the suspended solids of river water significantly absorbs DDT, it was possible to approximate DDT:H_2O ratios below $1:10^9$ in the 50- and 75- mile samples, using certain methods. The finding that DDT is absorbed by suspended solids is the basis of a new hypothesis to explain the long-range toxic effects of DDT on black fly larvae. In one of the experiments the treatment was observed to be larvicidally effective to at least 117 miles from point of application. A paper entitled "Microdetermination of DDT in River Water and Suspended Solids," was presented to the Analytical Division of the Chemical Institute of Canada.

2. In collaboration with the Forest Insect Laboratory, Winnipeg, samples were again taken of bark from elm trees which had been experimentally treated four years previously with DDT-xylene emulsion. Chemical and bioassays both showed very definite presence of DDT, and indicated that the DDT residue in the bark had not as yet passed a sub-lethal level. Sampling methods and analytical technique were similar to those mentioned in this journal, 1950.

3. A major item of research in the Stored Product Insect Laboratory is the distribution in space and time of halogenated fumigants applied locally in mills. Data on actual gas concentrations are essential to extend and explain bioassay findings. Measurement of the distribution of fumigant gases can be applied to test the efficiency of different methods of application. Information is required on the degree to which flour and other substrates present in flour mills may sorb fumigant gases, and on the resultant effect on the gas: air composition when fumigant mixtures are applied.

To meet the analytical needs of the foregoing and related problems, investigation of certain electrochemical methods of analysis was tentatively instituted in 1950. Pilot tests with amperometric titration of halides using the rotating platinum electrode were encouraging, and indicated satisfactory developmental prospects for continued investigation. The foregoing polarographic method, with suitable modification, was also found applicable for measurement of DDT residues. Tests on other halogenated insecticides were not tried.

Forest Insects: - Reports from the Forest Insect Laboratory, Winnipeg.

Studies on the Natural Immunity of the Larch Sawfly.

J. A. Muldrew

This report is on studies carried out during the summer of 1950 on the natural immunity of the larch sawfly to the parasite Mesoleius aulicus. It was found that the encapsulated eggs of Mesoleius removed from host larvae can be hatched in an isotonic physiological solution. The immediate effect of the formation of the capsules appears to be the inhibition of all embryonic growth and differentiation. Apparently the life of the embryo is thereafter supported by a very low metabolism. The normal incubation period of Mesoleius is about 7 to 10 days. The majority of encapsulated parasite embryos died within 3 months after oviposition but a few were still viable after spending 7 months within the host larvae.

Two weeks after oviposition about 80 per cent of the encapsulated eggs hatched when transferred to the physiological solution. Upon dissection of the host larvae from which these eggs were removed it was found that approximately 3 per cent of the parasite eggs had hatched within the host. This phenomenon of a relatively high number of eggs being laid by Mesoleius but only a few of these hatching and developing through to the adult stage was found in all sampled areas in Manitoba and Saskatchewan.

The question might be asked: why are not all the eggs inhibited within the host larvae? The indications are that the vigor of the host enters into the picture. A higher percentage of eggs seem to hatch in the more sickly host larvae. Other factors, however, are probably also involved. We plan to test this aspect of the problem more thoroughly during the coming summer.

It is also proposed to compare the reaction to Mesoleius of both the British Columbia larch sawfly and that of Manitoba. Apparently Mesoleius is still very effective in British Columbia. We also plan to study whether or not there is any relation between rearing temperature of parasitized sawfly larvae and the effective parasitism by Mesoleius. We also hope to determine the changes in the blood count of larch sawfly larvae following parasitization by Mesoleius and during the encapsulation process.

Experimental Starvation of Larch Sawfly Larvae

R. J. Heron

During the past summer one of the studies concerning the biology of the larch sawfly, Pristiphora erichsonii (Htg.), which was conducted at our Whiteshell Field Station dealt with the effects of starvation on larval development and survival under laboratory conditions.

Frass drop measurements indicate that approximately 80 per cent of larval feeding occurs during the last stadium. It was found that these ultimate instar larvae were very susceptible to the effects of complete inanition. When deprived of food for more than ½ the normal feeding period (4 + days) mortality was 100 per cent. On the other hand larvae which were starved for an initial period of 3 days survived to form cocoons although their development was somewhat prolonged.

During the initial stages of starvation the larvae searched actively for food. This activity continued for about four days after which the larvae became completely immobilized. This latter state led to death in about 2 days.

The possible role of inanition as a mortality factor under field conditions has yet to be determined. As the host tree is quite readily defoliated and as the period in which actively feeding larvae are present in the field is very prolonged, it is to be expected that starvation may in some cases become a factor limiting population growth.

FALL MEETING OF THE ENTOMOLOGICAL SOCIETY OF MANITOBA

The Business Session

A business meeting was held in the Dept. of Entomology, University of Manitoba, at 9 a.m. Nov. 20, 1951. The president, Mr. W.R. Allen, presided.

Minutes of the last general meeting held on March 6, 1951, were read and approved on a motion by R.D. Bird, seconded by W.J. Turnock.

Business arising out of the minutes.

1. W.R. Allen announced that it was decided to make no charge for the time being for Proceedings distributed to non-members or outside organizations.

2. In the interval since the last meeting Prof. A. V. Mitchener was appointed chairman of a new standing committee, Approved Common Names of Insects in Manitoba. Prof. Mitchener announced that his committee members are Dr. R.D. Bird, W. Stephen and H. R. Wong.

New Business.

General.

3. W.R. Allen described briefly the 1st Annual Meeting of the Entomological Society of Canada held in Ottawa early in November. Main items reviewed were the Director's meeting, the status of the library of the Entomological Society of Ontario, advertising plans for the Canadian Entomologist, fees, and the new Constitution of the national society.

4. It was moved that the President of the Manitoba Society be our representative on the Board of Directors of the National Society. The President will be at liberty to appoint a substitute for the Annual Meeting in the event that he is not able to attend.

Moved by R.D.Bird.
Seconded by Prof. A. V. Mitchener. Carried.

5. It was decided that we continue printing our own Proceedings but that we investigate the possibility of improving the quality of printing.

It was moved by Prof. Mitchener, seconded by W. Stephen, that the chairman appoint a committee to find ways and means of improving the Proceedings. Carried.

Committee Business.

6. Prof. Mitchener reported on the work of the Committee on Approved Common Names. A list of fifteen insect names was presented for approval. Three names were deleted following discussion. It was then moved by L.O. Peterson, seconded by R.J. Heron, that the remaining names be approved by the Society and submitted to the American Association of Economic Entomologists by a member of the Committee.

Carried.

7. A resolution was introduced by R.D. Bird that the Entomological Society of Manitoba recommend to the Entomological Society of Canada that a standing committee be formed to act as a clearing house for common names of insects suggested by members or local societies and that the standing committee submit these names to the Committee on Approved Common Names of the American Association of Economic Entomologists.

Seconded by H.R. Wong.

Carried.

8. Prof. Mitchener reported for Mr. S. Pugh, Chairman of the Standing Committee on Insecticides. Copies of a list, prepared by the Committee, of insecticides products by companies were distributed to the members.

9. After some discussion it was moved by Prof. Mitchener, seconded by F. Birt, that the executive and members of the Insecticides Committee decide on the future policy of the Committee.

Carried.

Treasurer's Report.

10. F.L. Watters outlined the need for prompt payment of dues to the National Society as they were needed to carry on publication of the Canadian Entomologist. The need for additional advertising for the Canadian Entomologist was also emphasized and some correspondence from the advertising manager of the Canadian Society was read.

Other Business.

11. R.J. Heron announced that the 1950 Proceedings were ready for distribution. He suggested that the secretary write to the Entomological Laboratories at Brandon and Winnipeg to express appreciation of their assistance in printing the Proceedings.

12. The secretary was instructed to write to Mr. Wigmore to find out if the Canadian Society proposed to continue distributing Proceedings of the Entomological Society of Ontario to members of the Canadian Society.

The meeting adjourned at 11:15 a.m.

Scientific Business

The scientific session of the fall meeting was held in the Department of Entomology, University of Manitoba, on November 19.

A symposium was conducted on the topic, "Experimental Ecology". Guest speakers on this occasion were Prof. A.C. Hodson, Division of Entomology, University of Minnesota, and Dr. J.W. Butcher, Forest Entomologist, State of Minnesota.

Prof. Hodson set the theme for the symposium with the presentation of a paper entitled, "The Experimental Approach to Ecology". A period of discussion was held following this paper.

The afternoon was devoted to a series of shorter papers concerned with various specific aspects of ecology and related fields. Dr. Butcher discussed population studies; Messrs. Cole and Muldrew dealt with biological control; Mr. Turnock presented a paper on physical factors of the environment and the subject of nutrition was discussed by Prof. Thorsteinson and Mr. Heron.

A period following on the presentation of each topic was devoted to discussion allowing for the free expression of opinion by those present.

The texts of the papers presented at this meeting are published in the following pages of these Proceedings.

THE EXPERIMENTAL APPROACH TO ECOLOGY[1]

A. C. Hodson
Division of Entomology and Economic Zoology,
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Experimental ecology may be defined as trials or special observations made to acquire facts for the development of ecological theories, or made to confirm or disprove such theories; especially when conducted under conditions determined by or under the control of the experimenter. In the strictest sense, ecological experimentation differs from direct observation in that the former implies some manipulation by the investigator, while the latter involves accurate reporting and critical interpretation of what is observed under natural conditions. The ecologist must eventually attempt to interpret correctly what actually is taking place in the field, in spite of the complexities to be expected. Direct observation, with a minimum of interference by the observer, would provide the most complete and desirable type of information for this purpose. However, there are at least three reasons for employing the experimental method.

In the first place, one often is confronted with so many variables or the interdependence of variables that it is very difficult or even impossible to determine their relative importance by direct observation alone. When this is the case it is by experimentation that certain variables can be eliminated or controlled to aid in clarifying the picture. A second reason for turning to experimentation is occasioned by need for the replication of observations. In too many instances the observer may have to wait a year or more before there is an opportunity to make another observation in the field under similar conditions. Finally, it often is necessary to know how an animal will respond over a range of environmental conditions, including extremes likely to occur only rarely if at all under natural conditions. Here the investigator is compelled to employ some form of experimentation unless he is unusually fortunate in the selection of a time and place to carry on his studies. It is important to remember that under all conditions the purpose in making an investigation dictates, to a large degree, whether direct observation, some form of experimentation, or combinations of both methods will provide the most complete and reliable information.

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I propose to discuss briefly some lines of investigation in which the experimental method may be used to advantage, and to comment on the limitations of the experimental method in these instances. Both laboratory and field experimentation will be included in the discussion.

The laboratory studies which have received the most attention have been the determination of biological constants such as temperature coefficients for growth and development, limits of tolerance to several physical factors, and food requirements. Some obvious advantages to be had are the degree of precision of factor control and measurement possible; the opportunity of performing replicated tests; the selection, elimination, and combination of single factors; and the simulation of a variety of natural conditions. However, even if one assumes well designed and conducted experiments and rules out systematic errors, the interpretation of laboratory results in the light of field conditions remains a difficult problem. Much depends on the relevance of the experiment to the field problem under investigation.

Thus, even when there is no questioning of the facts discovered in the laboratory there may be considerable doubt as to their requisite completeness or the correctness of their interpretation.

An example of both the advantages and disadvantages of laboratory studies is afforded by some recent work on insect cold tolerance. Salt (1944) determined the cold-hardiness of the common cattle grub by means of instantaneous measurement of their maximum and minimum undercooling points. From the values so obtained he concluded that killing temperatures fell between 17.7 and 27.7°C. Pfadt (1947) conducted tests with the same species. He subjected his specimens to a range of low temperatures for 1, 4, and 8 hours. His results show considerably higher lethal temperatures than those reported by Salt. The data in both cases show the results of the treatments correctly I am sure, but neither are complete and neither can be interpreted as demonstrating what might be expected under all habitat conditions. Salt (1950) followed up this discrepancy and showed by further experimentation the very important fact that the length of time to which a number of species were exposed to low temperature had much to do with their exhibited tolerance. Even so he cautions one as follows: "Those workers who determined cold-resistance by exposing insects to a series of time-temperature combinations probably obtained valid data within the limits of time and temperature that they used." May I suggest further that to employ these data for predicting winter survival the investigators would need rather exact data on the microclimates to which these insects might be exposed.

The study of insect behavior, particularly their tactic responses to physical and chemical stimuli, is a line of investigation which has been carried on principally in the laboratory.

Experiments attempted under field conditions are never very satisfactory and as a result most of what we know about this phase of biology has been discovered by laboratory testing. It is indeed unfortunate that direct observation of insect behavior is so tedious and unrewarding, because knowledge of behavioristic responses probably would help to explain many obscure events taking place in the field. Laboratory tests of behavior are performed necessarily under quite artificial conditions. Another disadvantage is presented by certain operational difficulties which must be overcome. The possible interaction of variables is a complication which enters the picture frequently. Then there are the responses which may be affected greatly by such things as the age and sex of the experimental animals or the conditions to which they were exposed before being tested. Last but by no means the least of the experimenter's troubles may be occasioned by the way in which the insect exhibits its response. Will it respond in a predictable manner or will it follow the "Harvard Law of Animal Behavior," Park (1939)? Yet behavior studies are made in spite of what might seem to be insurmountable obstacles, and they provide important clues to be followed up in the field.

The studies of Wellington (1948, 1949) on the effects of light, temperature and moisture on the spruce budworm are examples of well conceived and executed laboratory experiments. When combined with his microclimatic studies (1950) they have contributed much toward a more complete understanding of the natural behavior and requirements of this species. One can also find examples of single experiments which considered alone can be somewhat misleading. Kennedy (1937) found that the African desert locust would always aggregate at the driest end of a humidity gradient chamber, even though other experiments showed that moist conditions were most favorable for its survival and development. Doudoroff (1938) tested the temperature preference for a species of marine fish. The average temperature selected was about 26-27°C. This value means little to the fish because the temperature of their habitat seldom exceeds 20°C. These results illustrate the great care that must be taken if experiments of this kind are to be used to explain conditions observed in the field.

Population dynamics, a subject of singular importance to the ecologist, presents an interesting question. On the one hand it is certainly an ecological problem which should be investigated in the field, while on the other hand most of the theories and working hypotheses have been either derived from or tested by laboratory experiments. Take the so-called "principle" of Gause as an example. Numerous recent papers refer to his statement (1934) that two or more species having similar requirements cannot coexist indefinitely in the same habitat as though this conclusion, drawn from laboratory studies with protozoa, were alone sufficient to explain certain natural phenomena. In contrast Elton (1946) has this to say, "The ability of certain groups of species, mostly separated by genetic characters, to exist together on the same area while drawing upon a common pool of resources is one of the central unsolved problems in animal community structure and population dynamics." In fact, there is not one field study, to my knowledge, which supports the "Gause principle" adequately. It is, however, a very fruitful working hypothesis which should be tested in the field both by experimentation and direct observation.

Laboratory studies of population dynamics can be performed with the advantages already cited for laboratory determinations of biological constants. But there may be even more reason to question their relevance as a means of predicting what can be expected under natural conditions. The artificial nature of the rearing conditions, including very restricted space, oversimplification of the population complex, and unnatural food or breeding places leave much to be desired. Yet the opportunities to manipulate and simplify population situations are manifold.

Some recent studies on competition between species of Drosophila illustrate the advantages of the laboratory method and indicate, at the same time, the danger of drawing too sweeping conclusions. Lin (1951) allowed larvae of D. melanogaster and D. funebris to compete for a quantity of yeast insufficient for both. When there was a limited amount of food neither species studied separately could complete its development normally. However, if both species were feeding on the medium D. melanogaster larvae would develop normally at the expense of D. funebris. This result agrees with population cage experiments which have shown that mixed populations of these species reach a state of equilibrium with a large population of D. melanogaster and a small population of D. funebris. The fact that a small proportion of the population is represented by D. funebris might seem to contradict the contention that species with similar requirements do not coexist in the same habitat indefinitely, especially in the light of Lin's study of larval competition. The answer to this question has been given by Merrill (1951) who found that D. funebris showed a marked competitive superiority to the extent of the elimination of D. melanogaster when the medium became dry. Thus the survival of both species in a state of equilibrium can be attributed to fluctuations in the environment which favor first one and then the other of the two species, when the food supply is renewed periodically. What do their results mean in terms of the natural abundance and occurrence of these two species? In the first place, D. melanogaster, although cosmopolitan in its distribution, is generally regarded as a tropical species, while D. funebris is considered an inhabitant of the temperate-zone (Timofeeff-Ressovsky, 1933). Both species are found in the same localities during the summer and both are considered "garbage species" because of their breeding habits. Nevertheless there is no direct evidence to support the view that larval competition between these two species is important as a means of regulating their relative abundance or distribution in nature. However, the experiments of Lin and Merrell are significant contributions to our general knowledge of interspecific competition, a very important element of population dynamics. A frame of reference is established by work such as theirs which may then be set up for comparison with similar situations suspected or known to occur in the field.

When we consider the experimental approach to ecology as it is applied in the field we see at the outset that it has the same advantages and many of the limitations that characterize laboratory experimentation. It may differ in being less artificial and at the same time by being less precise than its laboratory counterpart. In any case some kinds of experimental work must be conducted in the field where some factors can be manipulated while others such as space, the joint action of other factors, natural foods etc. are restricted or altered as little as possible.

Survival studies are among the most common types of experimental work carried on in the field. Usually they involve manipulations such as placement of experimental animals in desired locations, regulation of time and length of exposure, and protection against natural enemies. Modifications of the natural situation such as these are used in attempts to determine the relative importance of the mortality factors which may be operative. In addition, it often is possible to employ known numbers of individuals rather than having to depend on a sampled fraction of a population. An example is afforded by a study which I made on the introduced pine sawfly, <u>Diprion simile</u>.

This species forms its winter cocoons on the needles, twigs, and bark of the host trees, and on the ground, above and below the litter. It was determined that during this stage mortality was caused by rodent predation and parasitism of the cocoons found on the ground, and by parasitism and bird predation on the trees. Bird predation alone caused about 99% mortality in 1943. Laboratory tests indicated that a high mortality of the prepupae resulted after short exposures to temperatures of -13° F. and below. As Minnesota winters usually can do better than that the question arose as to the significance of the 99 percent bird predation which had been recorded for the prepupae exposed on the trunk and in the tree crowns. To answer this question, cocoons were suspended in wire cages in the tree branches, placed on the litter, and buried beneath the litter, and allowed to remain in these positions throughout the winter protected from bird and rodent predation. Even though the minimum temperature that season was an unusually high - 11°F., 100 percent of the cocoons in the trees contained dead prepupae when examined in the spring. Those on the ground showed over 90 percent mortality, probably because there was no snow cover until February that winter. The cocoons protected by the litter were injured very little for 80 percent survived to pupate and emerge. Thus what appeared to be very effective control by birds was of no real importance because low temperature would have killed the tree population in the absence of this predation. Bird predation assumed even less importance in this case because it was found later that over 75 percent of the cocoons were spun in the litter where the birds did not have access to them, a fact discovered by direct observation. It is worth mentioning the fact that this field experiment was performed as the direct result of a question raised by a laboratory study of low temperature tolerance.

Lejeune and Filuk (1947) used much the same technique for their investigation of the effect of water levels on larch sawfly survival. They varied the stage of the insect to be submerged, the length of time of submergence, the time when submergence would take place and the depths at which the cocoons would be placed. In addition, they used known numbers of specimens and protected them from predation by caging. They combined laboratory tests, field experimentation and direct observation under natural conditions. By these means they were able to establish certain facts, and in addition they exposed the need for further information on variables that were not controlled or observed completely enough. Bess, et al (1947) performed experiments designed to help explain the spotty distribution and abundance of the gypsy moth in New England. It was commonly observed that large populations developed in poorly stocked stands having a thin litter. By direct observation it was determined that during the day the larvae tend to go down into a deep accumulation of litter. Where there was a poor litter most of them would remain on the trees. This much could be observed directly. Experimentation was employed to learn the significance of the behavior, particularly whether it had anything to do with differential survival under the two conditions of deep and shallow accumulation of litter. By liberating larvae and caging them under both conditions or by preventing them from seeking ground shelter by placing burlap bags around the tree trunks, it was found that larvae liberated in the litter suffered very heavy mortality from predation, while those caged or remaining above the forest floor were attacked only by parasites. Furthermore, the amount of predation in the litter was much greater in rich, deep litter accumulations than otherwise. Again a combination of direct observation and field experimentation was used to good advantage in solving a field problem.

The manipulations of populations in the field to discover obscure facts concerning dynamics has always and probably always will be a difficult line of investigation. However, one new tool, insecticide specificity, has been discovered to be very useful for this purpose. DeBach (1946,1949) devised a means of employing an insecticidal check method for measuring the efficiency of insect parasites and predators. The principle upon which the method stands is that DDT has little effect on the host species and gives a differential kill of its parasites and predators. He has been able to separate the action of parasites and predators so that their comparative effectiveness can be evaluated. This represents a very important contribution because assessment of predator activity always has been difficult to perform. In this case the insecticide is used to control or eliminate some elements of the complex while leaving others relatively undisturbed. Insecticide application can be of value in population studies in other ways. At present I am taking advantage of the fact that a large acreage of woodland was sprayed to control the northern walking stick. The original purpose of the operation was to test the effect of aerial application of several insecticides. Fortunately the control in an 80 acre block was nearly 100 percent so that a large area nearly free of walking sticks was made available. Several thousand eggs were placed in a small plot in the sprayed area this fall. When they hatch in the spring of 1953 I expect to get some quite accurate information on survival, nymphal behavior and adult dispersal. Ordinarily one cannot release large numbers of a pest for a purpose such as this for obvious reasons. In this case the 80 acres are on state owned land and they are surrounded by a large acreage of woodland which already is infested by the walking stick. Of even more importance is the opportunity to follow a population of known initial size instead of just hoping to find such a situation, or holding off people who insist on initiating control measures as soon as an incipient outbreak is discovered.

Population behavior, particularly the dispersion of insects, can seldom be studied effectively by direct observation. The size of the areas involved, the flight habits of the species, and the effect of wind all preclude the possibility of tracing individual or group movements satisfactorily. The closest approximation to direct observation has been achieved by the release and recovery of marked individuals. The results of marking experiments like those of many laboratory experiments are extremely limited in the amount of interpolation and extrapolation of the data which is permitted. The return for the efforts put forth often are very disappointing too. For example, in 1937 several thousand forest tent caterpillar moths were marked, released and trapped with light traps placed at several distances from the point of release. One marked moth was recovered one-fourth mile from the starting point. The small return was not the only disappointment. From other evidence it is quite well established that the moths move several times farther than the distance indicated by this one captured moth. The establishment of a walking stick population in the sprayed area described above was made in an attempt to get direct evidence on their movement instead of depending on the recovery of marked individuals which may become lost among the far great number of unmarked ones in a populated area. Some marking experiments have been more successful than the one reported here but at best they give a very incomplete picture of what is going on.

In conclusion let me state again that experimentation in the laboratory, in the field, or both, especially when combined with direct observations made in the field are needed if we ever are to solve many of the complex ecological problems before us. One of my physiologist friends states that the biotic community seems very "messy" to him and messy it is as compared to what may be studied in a test tube. But there it is!

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THE PROBLEM OF SAMPLING FOR FOREST INSECT POPULATIONS

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Before entering into a discussion of some of the problems involved in determining forest insect population size, it is necessary to consider the purposes which such determinations are to serve. Such a thing as population reduction during a stage intervening between the time of sampling and time of injury compromises the accuracy of predictions which are based upon such samplings. Everyone appreciates that such phenomena occur, yet in many cases, the event itself is not recognized. Even less frequently is it possible to make a quantitative assessment of its influence.

From a practical standpoint, these problems are not of constant concern to the forest entomologist. For example, insect survey requirements can often be met in the detection phase by securing information on frequency of occurrence. This satisfactorily answers the question of presence. Since this is quite often all the knowledge that is required about endemic populations, it is proper to state that a large part of our survey requirements are not concerned with many of the complexities of population analysis which will be discussed here.

When a particular insect is reported with a frequency that gives reason to believe it may be reaching epidemic levels, appraisal and/or control surveys are indicated. The problem of sampling must then be examined in the light of these new requirements.

Appraisal and control surveys differ in the purposes they are to serve. Pre-control survey information may be derived from appraisal survey data but, generally speaking, appraisal data are designed to delimit the outbreak in extent and intensity while pre-control data provides the basis for subsequent evaluation of control measures. In either case however, it is necessary to relate the insect populations present to their injury potential and the usefulness of the information obtained is proportional to the accuracy of these estimates.

It is perhaps unnecessary to acknowledge the many difficulties present in devising satisfactory sampling techniques. For the most part, however, these are purely mechanical and can be resolved in a manner that will permit the entomologist to obtain consistently representative data. Whether the technique of population determination be frass collection, branch sampling, soil sampling or some other method, levels of accuracy are ascertainable and the quality of the estimate is readily apparent. Rarely, however, is it possible to transfer such data from one insect life history stage to another, or from one season to another. It is with some of the problems inherent in such estimates that this paper is primarily concerned. Because it is even more difficult to transfer phenomena observed for one insect species to another species, this discussion will be restricted to the larch sawfly.

Ideally, the appraisal survey objective would be to obtain information on population size in one year that would permit accurate estimates of population and injury for the following year. This is difficult, if not impossible, in the case of the larch sawfly, where samplings are generally made of overwintering pre-pupae in the soil. Rodent predation may reduce the populations by 50-80 per cent (Graham, 1928) and this author further states that 30-100 per cent may not reach the adult stage because of unfavorable temperature, soil, or moisture conditions during hibernation. This would seem in itself, to preclude any year to year predictions of sawfly abundance, but such a conclusion disregards the important and often overlooked distinction that must be made between high and low populations. More important, it ignores the difference between resident populations capable of completely defoliating the host species (assuming 100% overwintering survival) and populations far in excess of those necessary for complete defoliation. This becomes increasingly apparent when the food requirements of larvae, and fecundity of adult female sawflies, are examined.

Food consumption work done by Butcher, 1951, indicates that individual larvae reaching maturity consume on the order of 212.7 mgs. dry weight of tamarack foliage during the course of their development. Foliage volume per tree for representative trees from three stands, diverse with respect to previous defoliation, showed a range of available food volume (needle dry weight) of from 785,032 mgs. to 1,284,712 mgs; or enough foliage to satisfy the requirements of 3,691 and 6,040 larvae respectively. If one can assume that an emerging female represents potentially 60 larvae, the following season (average number of eggs per female), 100 per cent overwintering survival of 3691 and 6040 larvae per tree would provide a population almost 60 times in excess of that necessary for complete defoliation (assuming that females constitute over 99% of the population, as suggested by Lejeune, 1949; and assuming that a complete defoliation one year would not alter the foliage volume the following year). In other words, anything over 62 and 101 surviving adults per tree in these stands must be considered capable of giving rise to 100% defoliation. The excess, or 98.3%, appears to be the degree of natural overwintering mortality that might be sustained by the sawfly and yet still leave it capable of causing complete defoliation the following year. These figures purposely ignore that percentage of foliage volume consumed by sawfly larvae that do not reach maturity. In other words, if mortality happens to be high among the 3rd and 4th instar larvae, these figures are proportionately compromised. First and second instar larvae appear to consume considerably less than 5% of the total of an individual's larval food so that mortality in these two stages, unless larvae were present in tremendous numbers, would not complicate estimates of the number of larvae maturing that were based on figures of foliage consumption per tree. No information is available on larval mortality, but as these figures suggest, it could be considerable on the average.

One obvious conclusion to be drawn from these figures, which are after all preliminary and speculative, is that we have not in the past given too much thought to the nature of epidemic populations. For example, if a fall cocoon survey were made and the figures related to a subsequent 100% defoliation, it might erroneously be assumed that the level observed in the fall was approximately what one might expect would develop into complete defoliation as a general rule, The figures cited earlier, on the other hand, indicate that such a level might be off as much as 98.3%.

The implications of these figures are startling. When one considers the low percentage of survival that is necessary in order for complete defoliation to be repeated, it further highlights the high rate of attrition that must take place due to relatively invariable environmental resistance factors. In the larch sawfly, we are aware of a possible density independent influence, e.g. an extremely critical developmental temperature, and a density dependent influence, e.g. rodent predation, to mention only two. Perhaps, on the other hand, these factors are more variable in their influence than we think. The modulating effect that works to maintain low level populations or that appears to favor gradual as opposed to rapid upward trends may be due to an interplay of many influences which give a cumulative effect that is relatively invariable.

The extreme flexibility of individual influences and their obvious interdependency gives reason to believe that the entire complex must be analyzed before the action of any one factor can be understood. At the present time, few of the important larch sawfly population factors have been studied; undoubtedly many more have not even been identified. A few, at least, can be mentioned which appear to vary with the size of the sawfly population.

One of these is the reduced volume of available food that follows feeding by the larch sawfly. This is manifested in smaller leaves and smaller total dry weight of foliage in defoliated stands as compared with similar foliage characteristics in undefoliated stands (Butcher, 1951). The data on which this comparison is based are inadequate but highly suggestive. A second possible limiting influence, on oviposition, is exerted by retarded underdeveloped terminal shoots which are characteristic of previously defoliated trees. While both of these effects are measurable, and within limits even predictable, there is little evidence that they have entered into the calculations of entomologists who are concerned with predicting larch sawfly abundance.

It is not enough to say that foliage characteristics (e.g. foliage volume and shoot length - shoot number) limit population size in a manner proportionate to previous injury and that proper study would yield information that might permit the entomologist to predict the extent of such influence. If the exact relationship could be established, it would undoubtedly **not** be a straight line beyond a certain point. This is so because the two factors appear to work in harmony to the same end during the initial stages of an epidemic, in the sense that neither interferes with the role of the other in reducing the number of larvae that can survive. In the later stages, it seems quite probable, however, that under some conditions, size of shoots and the number of shoots decrease to a point where there are not sufficient oviposition sites to provide sawfly larvae in quantities able to consume the available foliage. When this point is reached, reduced foliage volume ceases to be a limiting factor. It is of interest to point out here that foliage volume itself could be, and undoubtedly is, a limiting factor during over-population phases of an epidemic, when shoot number and length are adequate to support quantities of eggs in excess of the capacity of the foliage to sustain their development.

There are numerous other observed population influences that could be cited to further elaborate this reasoning. It seems obvious, however, that population studies on the larch sawfly are in much the same elementary state as are those for most other forest insects. That is to say, investigators have been so pre-occupied gathering data on obvious phenomena, such as cocoon predation and parasitism, bird predation of larvae, etc., that their possible usefulness has not been critically examined. It is a little like lifting passages out of context, in hopes that a demand for information can be satisfied, yet at the same time not calling attention to weaknesses in the conclusions which are obvious only when examined in relation to the complete text.

Obviously, it is not going to be possible to properly weigh or determine the many influences that must be understood if prediction and knowledge of population trends is to be improved. With many insects, at present, poorly understood phenomena nevertheless are highly predictable and the usefulness of such predictions has tended to mask our lack of understanding of them. Perhaps it will be possible at some time in the future to relegate population influences to major or minor roles and in the case of the larch sawfly, to achieve a certain degree of predictability. One cannot escape the conclusion, however, that most such influences are dynamic and that their effects will vary as their association with other elements of the complex changes. A relatively high level of accuracy might be achieved with an incomplete understanding of these phenomena, yet there should be no misunderstanding about the shortcomings of the method.

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THE FACTORS OF HOST DISTRIBUTION AND TIME IN BIOLOGICAL CONTROL - PART I

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Metcalf and Flint (1939) define biological control as being the introduction and encouragement of natural enemies. The natural enemies may be (1) predacious and parasitic insects, (2) predatory vertebrates, (3) nematode parasites, (4) protozoan diseases, (5) parasitic fungi, (6) bacterial diseases, and (7) virus diseases. This discussion will be limited to the consideration of predacious and parasitic insects imported to combat introduced pests.

Sweetman (1936) pointed out that the distribution of host insects could be divided into two broad groups, (a) pests occurring on islands or in insular-like regions, and (b) pests of continental distribution.

The time factor was discussed by Clausen (1951) and he pointed out that, in all successful instances, control was achieved within three host generations or three years after the release of the parasites or predators.

Sweetman has listed twenty-five examples of successful biological control. All but one of these examples occurred on islands or in insular-like regions.

The definition of an insular-like region is debatable. One successful case cited is that of <u>Rodolia cardinalis</u> (Muls.), a coccinellid beetle which gave remarkable control of the cottony-cushion scale, <u>Icerya purchasi</u> Mask. This scale attacks citrus trees in widely scattered parts of the world, i.e., southern France, South Africa, New Zealand, Portugal, Hawaii, Italy, Syria, Egypt, Florida, and California. The cottony-cushion scale has been controlled mainly in citrus orchards and, in turn, citrus growing areas are limited rather narrowly by climatic conditions. There should be some distinction made between the distribution of an insect such as the cottony-cushion scale and one such as the Colorado potato beetle, which is definitely continental in distribution. However, Smith (1936) maintains that California is not an insular-like region or ecological island. If California cannot be considered an ecological island, it would be unfair to consider southern France or South Africa as such. To distinguish between distribution of such pests as the cottony-cushion scale and the Colorado potato beetle, the terms "bounded area" and "unbounded area" may perhaps be more accurately applied. With pests such as the cottony-cushion scale, it may be helpful to consider each infested orchard as being a "bounded" area, rather than treating the entire area in which the orchards occur as one.

The only case of what appeared to be successful biological control listed by Sweetman (1936) against a pest of unbounded distribution is that of the larch sawfly, *Pristiphora erichsonii* (Htg.). According to Baird (1939) the parasite *Mesoleius aulicus* (Grav.) was introduced from England to Canada during the period 1910 to 1913 for the control of the larch sawfly. Liberations were made in central Quebec, southern Manitoba, and northern Michigan. These liberations were so successful that parasites have since been collected from Manitoba and Quebec and distributed in New Brunswick, Nova Scotia, northern Quebec, southern Ontario, and British Columbia. Baird reported that the parasite gave rapid control of the pest in every place in which it was released under suitable conditions. However, in recent years the larch sawfly has built up a resistance to the parasite. The rate of effective parasitism has become very low and the larch sawfly has again reached outbreak numbers. It must be concluded that this case of what appeared to be successful biological control can no longer be considered as such. The same may be true of other cases listed by Sweetman.

A second instance in which biological control appeared to be successful against a pest of widespread distribution was that of the satin moth, *Stilpnotia salicis* (L.). This pest, of European origin, was discovered on both the east and west coasts of this continent in 1920. Baird (1939) states the parasite *Apanteles solitarius* Ratz., a specific satin moth parasite, was released in Canada in 1933. Its increase and spread was phenomenal and the aspen trees were covered with thousands of its white cocoons in the areas previously swarming with caterpillars. However, Craighead (1950) reports that the satin moth remains a serious pest. He mentions several other species of parasites as important as, or more important than, *A. solitarius* in helping to control the satin moth.

In both of these cases where biological control of a pest of widespread or continental distribution occurred it was only temporary. Nevertheless there is in these instances an indication that biological control of such pests is possible.

Smith (1936) disagrees with the suggestion that biological control is more likely to succeed against pests in a geographical or ecological island than against pests of continental distribution. He cites successful introductions of parasites into Hawaii but believes that the main reason for these successes was that there was more financial backing available to permit the experiments to be carried on to a successful conclusion. He admits that "In Hawaii it may be true that the absence of secondary parasites may result in more successful introductions of primary parasites", but he claims successful releases in California equal those of Hawaii and he does not consider California to be an ecological island. Though there have been no cases of continued successful biological control against pests of unbounded or continental distribution, it would seem probable, in Smith's opinion at least, that with more time devoted to this work, success equivalent to that obtained on islands or in bounded areas may be attained.

Clausen (1951) discussed 14 cases of successful biological control in relation to the time required to bring about control after the parasites were released. None of the pests controlled were of continental distribution. Clausen stated, "In the great majority of past instances of full commercial control, where the detailed history of the project is available, definite control was achieved, in the vicinity of the colonization points, within three host generations after release, and in no instance was the time longer than three years, even with hosts having an annual cycle." Of the 14 cases discussed by Clausen, all but one resulted in control of the pest within three host generations. In the one case, control was achieved within three years after the release was made although more than three host generations had elapsed.

In the examples taken by Clausen, the area over which control was obtained was limited to that area over which the adults of the first field generation spread from the colony site. The area of control could be enlarged indefinitely if the initial releases were distributed throughout the area of infestation.

Clausen is of the opinion that introduced parasites or predators do not adapt themselves to unfavourable conditions in a new location over a period of time. Species that are fully effective in the country of origin, yet fail to yield an equal degree of control in another country, are frequently not adapted to the new climate. An example cited by Clausen is that of Centeter cinerea Ald., a larvaevorid parasite of adult Japanese beetles. In Japan it consistently destroys 80 per cent or more of the female beetles before they are able to deposit eggs. The parasite was introduced into New Jersey in 1922, but there the majority of the flies emerged far in advance of the beetles and died before hosts were available for oviposition. It was thought that a process of natural selection, whereby each year only the latest emerging flies reproduced, would eventually produce a strain in full synchronization with the host. After 25 years the seasonal cycle remains the same and the parasite even now is barely able to maintain itself. Clausen states, "There is as yet no instance that can be cited to support the belief that an introduced parasite will adapt itself to a new environment and eventually become more effective than in the years immediately following its importation."

Clausen concluded from his study of successful liberations that control was obtained within three host generations or three years after liberations were made and that parasites and predators were not readily adaptable to unfavourable conditions. From this information he was led to believe that colonization of an imported parasite or predator may well be discontinued after three years if there is still no evidence of establishment, providing the liberations were made under the most favourable conditions possible. He claims, "A fully effective parasite or predator is always easily and quickly established . . . . In many instances there is an excellent chance of establishment from the release of a single pair." This trend of thought is very much in contrast to the policy that has been followed in the past. For example, according to parasite liberations listed in the Canadian Insect Pest Review the parasite *Microplectron fuscipennis* Zett was liberated over the period of years between 1934 and 1948 in an effort to control the European spruce sawfly, *Diprion heroyniae* (Htg.). The total number of parasites liberated was 873,051,694. From Clausen's point of view much time and money have been fruitlessly expended in prolonged efforts to establish many parasites and predators.

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THE FACTORS OF HOST DISTRIBUTION AND TIME IN BIOLOGICAL CONTROL - PART II

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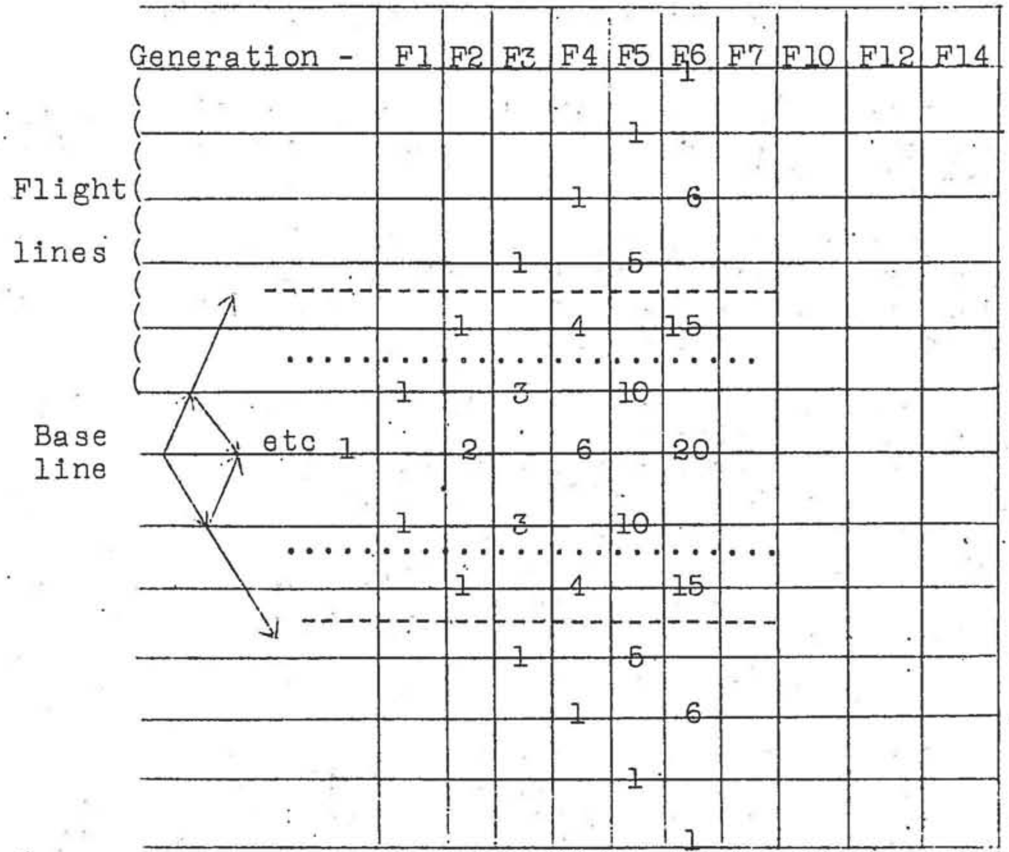
This paper is principally a consideration of W.R. Thompson's paper entitled "The Time Factor in Biological Control" (1951).

In his paper Thompson discusses Clausen's 3-generation 3-year theory of biological control. Thompson is well qualified to do so for he has been publishing papers on biological control since 1922.

He feels that the arguments advanced in favor of Clausen's theses are not completely convincing because the evidence produced does not explain why the observed events happened. Clausen used the inductive method to derive his conclusions, i.e. from the observation and analysis of a series of separate facts he infers a general law. Thompson endeavors to explain Clausen's theses by the use of the hypothetico-deductive method, i.e. he attempts to show, using mathematical computations, and starting with fairly reasonable postulates, that the theses of Clausen can be deduced as a possible consequence.

Clausen's theory applies only to that area over which the adults of the first field generation of parasites will spread. Thompson attempts to show theoretically that routine collections of the host insect, made in the vicinity of parasite liberation points, will show a much higher degree of control than is given by mathematical formulae which relate the total population of the parasite to the total population of the host. He simplifies the treatment by postulating that the host population is uniformly distributed and that the parasite population spreads backward and forward from a point on a base line, migrating in each generation one "flight distance unit". Thompson does not define "flight distance unit" but, seemingly, it is the average distance that the parasites spread in each generation and, apparently, it is assumed to be a constant for each species of parasite. This treatment may be illustrated diagrammatically beginning with an initial population of 1 parasite which has an effective reproductive rate of 2.



% of total population on .87.5 78 71 66 61 57
or within 2nd flight lines (within broken lines).

We see that, on the postulates adopted, the concentration near the base line remains high for a considerable time. The distribution of the parasites within the limits of their dispersion is less uniform than might be anticipated.

Thompson does not differentiate between bounded and unbounded areas of the host infestation in his discussion, but it would seem that this illustration lends itself to such a differentiation. For example, we may assume that the host infestation occurs in an orchard and that the first generation parasites are able to travel from the release point in the centre to the outer boundary, and that all subsequent generations of parasites remain within the orchard. Using the same rate of parasite build-up as described above we may now compare the build-up in such a bounded area (which will be the total population in each generation) with the build-up in an area of equal size around the liberation point in an unbounded area (i.e. within the dotted lines of the illustration).

Table I

Parasite generation	Parasite population in the bounded area covered by 1st gen. parasites (i.e. total population)	Parasite population in the area covered by the 1st gen. parasites in the unbounded area	
		No. of parasites	% of total parasites within this area
F 4	16	6	37.5%
F 8	256	70	27.3%
F12	4,096	924	22.6%
F14	16,384	3,432	20.9%
F16	65,536	12,870	19.6%
F18	262,144	48,620	18.5%

Table I illustrates that control would be brought about more rapidly in the bounded area than in the unbounded area, but not markedly so. If we postulate a host population of 15,000 within the area of first-generation spread, we see that in the bounded area the parasite would overtake the host at about the 14th generation and in the unbounded area at about the 17th generation.

However, this does not readily help to explain why most cases of control have occurred in bounded areas. It may be that in an unbounded area there is an influx of hosts from adjacent areas into the vicinity of colonization, whereas in a bounded area no such influx of hosts occurs since hosts are not present in the area surrounding the bounded area. Such an influx would extend the time necessary to attain control in an unbounded area. It may also be that in an unbounded area there is a "diffusion" of parasites from the region of high parasite concentration near the liberation point to the region of relatively low parasite concentration a few "flight distance units" away. Such a "diffusion" would not occur in a bounded area since there are no areas of low parasite population adjacent to the area of high parasite concentration (which would be the entire bounded area) to "attract" the parasites. This would make for a more rapid build-up of parasites in a bounded area.

These considerations may help to explain why parasite build-up might be more rapid in bounded than in unbounded areas, but why should a rapid build-up give control and a slow build-up no control? A possible answer is that within a bounded area the primary parasite build-up is so rapid that the hyperparasites and other density-dependent mortality factors are unable to overtake the primary parasite before control is achieved, whereas in the unbounded area the density-dependent mortality factors killing the primary parasite may overtake it before it can control the host.

The following quotation is Thompson's "summing-up":-

"The hypothetico-deductive method of discovering the truth about nature is not a substitute for direct observation. It is precisely the woefully inadequate character of our information on the increase and spread of introduced parasites that makes it so difficult at present to test any of our hypotheses... The energy expended in the introduction, mass breeding and distribution of parasites has been, and still is, quite out of proportion to that expended on efforts to find out and understand what happens in the field. It is only by careful and continuous study of the increase and dispersion of introduced parasites and the exact evaluation of their importance as controlling factors that biological control can rise above the crude empiricism of its present status... Clausen's paper offers a working hypothesis which it is imperative to test, since it may eventually form the basis of a drastic and thorough-going revision of our practical programs and our plans for research."

This quotation raises the following two questions:- (1) How can Clausen's hypothesis be tested? (2) If Clausen's hypothesis is verified, how should the present type of biological control work be changed as a result of this verification?

Possibly the best way to test Clausen's hypothesis would be through careful and continuous study of the increase and dispersion of introduced parasites in the field.

Concerning question (2), (i.e. assuming Clausen's hypothesis is verified, what revisions of the present type of biological control work would be indicated in the light of this verification), one possible program would be the introduction of as many foreign parasites and predators as possible, giving each a 3-year test. Any parasite or predator that did not become established and produce control within 3 years would be dropped and other parasites and predators would then be tried. This brings up the question:- how long would the supply of foreign parasites and predators last? Considering the major forest insect pests, probably most of the easily-discovered foreign parasites have already been introduced and search for other species will probably be a painstaking and difficult task which would become increasingly difficult as the supply became short. If the situation came to the point where the search for more parasites and predators was not economically justifiable, this type of biological control program would then have to cease. We should remember, however, that as far as forest insect pests go, biological control is still a very promising method of control. Cultural control is still largely unproved and hypothetical· chemical control is too costly and is only a palliative.

Another possible method of approach would be to introduce only a few foreign parasites and predators but to make a very thorough study of these, concentrating especially on what happens to them after release. This would involve population estimates of both parasite and host, and, in fact, it would probably be necessary to study most of the factors that influence these populations in various ways. The work would require a large staff and would take many years, but, if the parasites studied did fail to produce full control, the reasons for their failure might be discovered. From a number of studies of this type it might be found that certain characteristics, either of the introduced parasite, or of the host population, or both, must be present in order to ensure the success of any biological control project. These characteristics might then be used by biological control workers in deciding what types of infestations can be controlled and what types of agents should be used to achieve this control.

The general topic heading for these two papers on biological control is "Biological Control as a Specific Aspect of Ecology". So far, the word "ecology" has not been mentioned but I think it is clear that the problems facing biological control workers today are fundamentally population problems and it is the ecologists who will probably play the foremost part in solving these problems. These ecologists will have to have a thorough knowledge of all aspects of animal ecology and probably more than just a smattering of plant ecology.

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DISCUSSION OF THE ROLE OF PHYSICAL FACTORS IN ECOLOGY

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The primary interest in the study of the physical environment in insect ecology concerns the effect of these factors on the relation of the individual, species, or community to the general environment. It is usually desirable to express this effect in terms of survival value, distribution, and/or prediction of population behaviour of the species. There are two types of environmental effects that may be distinguished as examples of (a) developmental and/or toleration physiology and (b) response physiology.

The large and important field of the relation of research on the physical environment to population behaviour has been obstructed by the inability of the worker to provide a controlled environment in which populations can be maintained. A notable exception to this, of course, is the work on insects attacking stored products (Holdaway 1932, Oosthuizen 1935, and Utida 1941) and certain other insects. Because of this difficulty the experimental approach can generally be used only with small numbers of insects and the results are not always readily applicable to the population level.

The study of the physical factors in nature and their effect on natural populations must therefore be largely observational. The factors themselves may be more or less exactly recorded, e.g. meteorological records, the natural population fluctuations can be observed and the relation determined by correlation. The value of this type of study is greatly increased if basic experimental data on the effect of various physical factors on individuals of the species are available.

Historical Development of Physical Research in Insect Ecology:

The importance of the physical environment in the development and survival of the individual and the species has long been recognized. Workers in all phases of biology observed effects of temperature, moisture and pressure on plants and animals in early times. Some of their conclusions, notably the temperature summation theory of Reaumur (1735), are still in use in ecology. Despite these early observations little work that can be classified as conscious research on the physical environment in insect ecology can be recognized before 1900.

Much of the work of the natural historians involved observations of the response physiology of insects. Various aspects of developmental and toleration physiology were also noted. The growing emphasis on the experimental approach touched these fields but during the first two decades of the 20th century little was accomplished in the way of re-orientation or the opening of new fields of study. However, the work of Howard & Fiske (1911), which listed and discussed the natural control factors affecting gipsy moth, was significant in the field of population study.

In the period from 1921 to 1930 ecologists recognized the abiotic environment both as a total unit and in terms of its components. A great deal of the specific research at this time paralleled earlier studies. Several significant papers in the field of bioclimatology, which applied ecological findings to economic predictions, emerged in this decade. Cook (1924), working on the pale western cutworm, correlated temperature and population records with incidence for predictive purposes, and later (1925) used the same technique for the alfalfa weevil. Marcovitch and Stanley (1930) used a drought index as an indicator of the suitability of various parts of the United States for sustaining populations of the Mexican bean beetle. Neither paper attempted to determine experimentally the basic effect of the factors on the insects involved.

Shortly after 1930 the field of research on physical factors was stimulated by several important events. The first was the prominence given to this field by Chapman (1931) in his book "Animal Ecology". In the same year Uvarov published a monograph entitled "Insects and Climate" which reviewed previous literature and classified the climatic factors that affect terrestrial species. In 1932 Uvarov introduced the bioclimatograph as a technique for analyzing the bioclimatic relations of insects.

Since that time workers have been attempting to measure more exactly physical factors and their effect on population size and distribution. The Bonitation Index of Bodenheimer (1938) is a result of this type of work. Beginning with Kirkpatrick (1935), several authors (Gunn 1942, Uvarov 1948, Wellington 1949a, 50a) have been concerned with the measurement of the temperature of the insect in its habitat. These writers have focused attention on the ecoclimate of the insect as it differs from the usual meteorological measurements.

Recent Work on the Physical Environment:

In an attempt to review recent trends in physical ecology current numbers of several periodicals were examined. These journals, Journal of Economic Entomology, Canadian Entomologist, Ecology, Journal of Ecology and Ecological Monographs, contained a total of six papers covering various aspects of this subject.

Tomlinson (1951) reports on the emergence of blueberry maggot adults in relation to observed temperatures and tests the validity of a heat summation figure in predicting emergence. A paper by Henson (1951) is also of the observational type but is based upon previous experimental work on the effect of temperature and atmospheric pressure on spruce budworm adults. His short paper concerns the effects of a thunderstorm on mass flights of this insect. Lejeune (1951) shows how water levels may affect the mortality of cocoons of the larch sawfly in the field. He cites previous experimental work to show the effect of flooding on individual cocoons.

Ghani and Sweetman (1951) subjected book lice to variations of temperature and moisture to determine their effect on the rate of development and survival. Their work is an example of a biological study in which physical factors are discussed only as they affect the development of the various stages.

The remaining two papers, by Shelford (1951a and b), deal with the fluctuations of natural populations. The correlation of populations to physical conditions is referable to sensitive periods in the life histories of the insects studied. These sensitive periods occur most often during the spring months. Rainfall and ultraviolet intensity are correlated with population fluctuations. Chinch bug population fluctuations are critically examined and explained on the basis of optimum conditions of weather (temperature and rainfall) and ultraviolet intensity during the critical spring months. These factors are independent of one another and rapid population increases and outbreaks can occur only when both are favourable. The variations of both factors from year to year make predictions unreliable. This work is based entirely on observations and could be strengthened by experimental exposure of individuals to the factors studied to determine the basic responses.

One other paper deserves mention at this point. This paper by Wellington <u>et al</u>. (1950) is interesting not only for its actual content but because it is the most recent of a series of papers dealing with the physical ecology of the spruce budworm. The previous papers dealt with the effects of physical factors in general (Wellington and Henson 1947), the light reactions of the larvae and adults (Wellington 1948), the effect of temperature and moisture on larvae in regard to response and toleration (Wellington 1949b), and the effects of evaporation on silk-spinning and locomotor activities of the larvae (Wellington 1950b). From this knowledge of the physical requirements of the spruce budworm the critical period was determined to be the spring. Weather records for this period were compared to known fluctuations of budworm populations. From these observations the authors concluded that dry, sunny weather was optimal for this period. Cloudy, damp weather retarded development and increased natural mortality.

From these data the authors concluded that three to four favourable years are required to develop an outbreak population of spruce budworm in a suitable stand of timber. They also postulated that an outbreak of forest tent caterpillar in poplar forming an overstorey above spruce and balsam-fir regeneration created a situation of artificial drought for the spruce budworm and often preceded outbreaks of spruce budworm. This paper is of special interest because of the wide variety of techniques that were used to gather the information. From these sources the overall picture was assembled and a method of predicting future outbreaks developed. This method of prediction has not yet been tested.

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THE ROLE OF HOST SELECTION IN THE ECOLOGY OF PHYTOPHAGOUS INSECTS

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Introduction

It is a commonplace entomological observation that each phytophagous insect is restricted in its feeding to a small fraction only of the plant species that grow in that area. This phenomenon is generally referred to as "host selection".

The ecological significance of host plant selection among insects is manifest principally in an effect on the geographical distribution of insect species since phytophagous insects can occur only where suitable host plants are available.

The precise nature of the concept which we call host selection involves certain complexities which require analysis. In so doing, the nature of the role of host selection as an important ecological factor affecting insect distribution will become clearer. The term "host selection" is an inadequate designation of the concept with which we are concerned. In the first place, the word "selection" implies a deliberate choice and there is no basis for a belief that such a complex psychological phenomenon occurs among insects.

Furthermore, while the stimuli which evoke this so called selection are generally correlated botanically with nutritional requirements of the insect, they are nevertheless quite independent of them in the physiological sense. Nutrition, which depends on the presence of adequate nutrients, vitamins and minerals among the host plant constituents and the efficiency of their digestion, adsorption and utilization by the insect, is commonly confounded with the host selection concept but in the strict sense, is quite distinct from it. There appears to be no validity in the notion that insects choose certain host plants <u>because</u> they are nutritionally most suitable for their development. Our knowledge of insect nutrition, although far from complete, leads us to believe that the number of plant species which are nutritionally adequate greatly exceeds the number actually selected by an insect species. While nutritional implications can scarcely be altogether ignored in any comprehensive discussion of host selection in its ecological aspects, it will not be discussed in detail here. A companion paper by Mr. R.J. Heron deals with this ecologically important subject.

However, it is not the anthropocentric nor teleological implications only of the term "host selection" with which we take exception, but the lack of detailed knowledge for most insects concerning the complex of factors which interact in the expression of this phenomenon and the consequent loose usage of this expression. However, enough is known of the host relationships of a few insects to enable us to discuss this problem in the light of concrete examples.

Mechanism of Host Selection

Host selection may be studied from two points of view:

(a) Host selection as expressed by the occurrence of populations of insects on plants in nature.

(b) Host selection as defined by results of insectary experiments which determine

- i. the plants on which insects may be induced to feed under experimental conditions
- ii. the plants on which insects can complete their development.

The discrepancies in the findings obtained in field and insectary studies are primarily due to:

(1) the control which the experimenter can exercise over the phenological and geographical relationships of the insects and the host plants. This discrepancy is of considerable significance in the ecology of injurious or potentially injurious insects since plants of economic value might be introduced into areas where they may be exposed for the first time to insect enemies indigenous in that region. The adoption of the potato as a host plant by the Colorado potato beetle is the classic example of this phenomenon.

(2) the gravid females may not oviposit on all the plant species which are acceptable to and adequate for the development of the immature forms.

Host selection as manifest in nature in the occurrence of insect populations on particular plants is the end result of a complex chain of phenomena which include - in addition to nutrition - olfactory, gustatory, phototactic, hygrotactic, toxicological and phenological relationships as well as geographical distribution of the host plants. Temperature, age and inanition may modify host selection phenomena to a limited extent.

Most of the evidence indicates that responses to stimuli of the senses of taste and smell are the most significant factors which determine what plant species will be attacked by any insect and it is that part of an insect's behaviour which comprises responses to these chemical stimuli that constitutes host selection in the strictest sense. It is only in the laboratory, however, that these effects may be separated from the others, mentioned above, which under natural conditions modify their manifestation in the field.

Host selection in phytophagous insects has two principal aspects:

1. The location of suitable hosts or food finding - By a division of labour, this function is usually performed on behalf of the offspring by the gravid female parent which generally has more highly-developed sense organs including antennae and compound eyes combined with the power of flight. Adult insects which require food for the development of their gonads or the production of energy perform the function of food finding for themselves. In either case, the responses, whether they involve true orientations or otherwise and whether positive or negative, are believed to be governed by patterns of simple stimulus-response reflex mechanisms.

2. The feeding responses of insects to the substrate - The immature developmental stages of phytophagous insects as mentioned earlier typically do not require a highly-developed food-finding faculty. Their contribution to the expression of host selection is manifest in their acceptance or rejection of the food plants available which may be analysed as in the following scheme:

A. Acceptance is manifest by the following steps:

- a. Biting (stimulated by olfactory and probably to a less degree by hygrokinetic stimuli. The threshold of these stimuli is raised by inanition and in the larger instars.)
- b. Mastication (this step and the following one are probably stimulated by appropriate gustatory stimuli).
- c. Deglutition or swallowing.
- d. Sustained repetition of steps a,b,c.
- e. Periods of rest or wandering (the frequency of this phase is inversely proportional to the acceptability of the food plant);

B. Rejection is manifest by:

- a. A failure of the plant to elicit a biting response due to the lack of chemical constituents which provide the appropriate olfactory stimulus, or (if biting occurs):
- b. The failure of the insect to enact steps A (b and c) due to the lack of a plant constituent which provides the appropriate gustatory stimulus, or:

c. The presence of a repellent substance which inhibits or prevents feeding. In general, it appears preferable to think of plants on which the immature forms will feed as acceptable plants and to reserve the term attractive plants for those which are sought by the ovipositing female parent. Attractive plants, however, are generally acceptable.

Classification of Host Plants of Insects

A classification of plants according to plant constituents and other host relationships of significance in relation to attack by a given phytophagous insect species may be devised as in the following:

1. Plants which are either not attractive to the ovipositing females or not acceptable to the larvae, due either to their lack of chemical constituents which positively stimulate the chemoreceptors of the insect or to the presence in their tissues of repellent constituents which stimulate negatively the chemical senses of the adults and/or the larvae.

2. Attractive Plants. Plants that contain chemicals which attract, probably by olfaction, gravid females of the insect species and stimulate them to oviposit on them.

3. Acceptable Plants. Plants that contain chemical constituents which by olfaction and gustation stimulate the feeding stages of the insect to chew and ingest them. This group may be further classified as follows:

   a. Plants that contain constituents which by olfaction or gustation inhibit feeding by repellent action or by masking the stimulus of attractant substances, e.g. *Solanum demissum* with respect to *Leptinotarsa decemlineata* (Say) (Kuhn and Gauhe, 1947).

   b. Plants on which the insects will feed but which contain toxic chemical constituents which hinder vigorous development resulting in low fecundity or actually cause death of the insect, e.g. *Petunia hybrida*, with respect to *L. decemlineata* (Say) (Chin, 1950).

   c. Plants which possess morphological characteristics such as hairiness or toughness of cuticle which deter feeding.

   d. Plants which contain trophic stimulants and are free of chemical constituents and physical characteristics which inhibit feeding but which do not contain a complete complement of nutrients, vitamins and minerals required by the insect.

> A plant cannot be shown under natural condition to be nutritionally adequate unless it is eaten. Therefore, an unacceptable plant can be considered nutritionally adequate only in an academic sense even though we have reason to assume that it contains adequate quantities and the right kinds of nutrients, minerals and vitamins. At all events the experimental proof of such an assumption would entail difficult technical obstacles.

e. Plants which have phenological characteristics out of phase with the requirements of the insect. It appears that the apparent preference of the spruce budworm Choristoneura fumiferana (Clem.) for balsam fir over white and black spruce may be an example of this effect.

f. Plants which do not occur in the geographic range of the insect. The host range of an insect infesting a great botanic garden may be far greater than in the surrounding countryside (Verschaffelt, 1910).

In the light of the above analysis an adequate plant host on which populations of an insect may occur in nature may be defined as an attractive, acceptable and available plant which contains sufficient quantities of the required kinds of nutrients, vitamins and minerals in a form which the insect can digest and assimilate, but does not contain any substance which is poisonous to the insect nor does it possess morphological characters that interfere with feeding.

Probably the best example of the significance of most of these factors in the biology of a single insect species is to be found in the literature on the host relationships of the Colorado potato beetle, Leptinotarsa decemlineata (Say), (McIndoo, 1935; Brues, 1940; Raucourt and Trouvelot, 1936; Kuhn and Gauhe, 1947; Chauvin, 1945, and Chin, 1950).

This insect is confined in its host range to certain plants in the genus Solanum of the family Solanaceae which is well known for the production of complex substances which are of physiological interest, such as toxic alkaloids and glycosides which may serve as attractants. The attractants and feeding stimulants probably occur in all solanaceous plants and possibly others but the host range is restricted by the occurrence of repellent and toxic substances. According to Chauvin (1945) the substances in Solanum species which stimulate feeding in Leptinotarsa are probably flavone glycosides.

Another classic example of the significance of chemical plant constituents in insect selection of hosts is to be found in the biology of insects such as Pieris rapae L., Pieris brassicae L. and Plutella maculipennis (Curt.) which respond to the chemical stimulation of the mustard oil glucosides that occur principally in the Cruciferae but also to some extent in the Resedaceae, Tropaeolaceae and Moringaceae. The host range coincides closely with the botanical distribution of these chemical substances since repellents for these insects apparently seldom occur in this group of plants. The mustard oil glycosides or their fission products which are characteristic of these plants are probably repellent to many other insects but happen to be actually the specific attractants and feeding stimulants of Pieris and Plutella (Verschaffelt, 1910) (Thorsteinson, 1948). On the other hand alkaloidal glycosides in Solanaceae which are of frequent occurrence are not themselves the attractants and while some of the alkaloids are not repellent others are either repellent or poisonous or both.

Classification of Phytophagous Insects

Phytophagous insects are frequently classified according to the number of their host plant species into groups termed monophagous, oligophagous and polyphagous insects. A modification of the meanings of these terms has recently been proposed by Dethier (1947) and his views will be referred to again. The definition of these terms as used in the bulk of the literature may be presented as in the following scheme which incorporates the writer's views on their physiological interpretation:

Polyphagous insects - The necessary attractants and feeding stimulants are widely distributed among plants and range of host plants is restricted principally by the occurrence of repellent or toxic chemical constituents in many plant species, by protective morphological characteristics, by phenological patterns or by failure of congruence in geographic range of insect and plant species.

This interpretation is based on the assumption (which, it must be conceded, is supported as yet by little experimental evidence) that all phytophagous insects require chemical stimulants of some kind to induce and to sustain normal feeding except under the stress of inanition when extreme hunger supersedes normal stimuli.

Oligophagous insects - The necessary feeding stimulants are restricted in distribution to a relatively small number of plants, many or all of which for many insects are related taxonomically.

Monophagous insects - Monophagy is a special case of oligophagy wherein the necessary feeding stimulants for an insect are found in only one plant species that is available to the insect. Two possibilities exist:

a. Only one acceptable plant species exists

b. Only one acceptable plant species is available in the geographic and phenological range of the insect.

Dethiar (1947) as mentioned above has offered an entirely new interpretation to the concept of monophagy and oligophagy. He classifies those insects as monophagous which respond positively to only one chemical or group of related chemical plant constituents, whereas, in his scheme, oligophagous insects are those that respond to several distinct and unrelated chemicals.

Dethier's definition of monophagy which is based on chemical considerations is not without merit. However, since a change in definitions at this stage might introduce greater confusion into the literature it would seem preferable to coin new terms to designate two distinct classes of oligophagous insects which differ in the chemotactic mechanism responsible for their restriction to a limited number of food plants. For example, the insects which respond to only one trophic stimulus substance or a group of related substances might be termed homochemotactic oligophagous insects. Those which respond to several, chemically unrelated trophic stimulus substances might be termed heterochemotactic oligophagous insects.

Minor Factors Affecting Host Plant Selection

The factors, other than those already mentioned, which can affect host acceptance appreciably are temperature, inanition and degree of development of the insect. Other factors such as light and humidity have probably only a minor effect. Moisture in the food seems to be essential, but this factor is relatively constant in nature.

Influence of food and temperature

Temperature may have two effects, as observed by Chin (1950) in the Colorado potato beetle, viz., it increases the rate of feeding and it increases the rate of utilization and hence of growth. While this insect feeds more rapidly at higher temperatures up to an optimum, the total amount of food consumed is not increased. Optimum temperature for rapid feeding and rate of development is 32° C. but optimum temperature for survival is 25° C.

Increasing temperature toward the optimum does not increase the consumption of less acceptable plants appreciably except in the fourth instar which may eat considerable quantities of foliage of the less acceptable plants. There appears to be a partial breakdown of sensitivity to repellent substances at 32°C.-36°C. in the fourth instar, but the ratio of such foliage eaten to that of S. tuberosum consumed at these temperatures is nevertheless only 23 per cent or less.

The increased consumption of less acceptable food plants at 32 - 36° C, may conceivably be due to changes in the chemical constitution of the leaf tissue by the dissipation by evaporation of volatile repellent olfactory substances or to the decomposition of thermo-labile repellent gustatory substances. At and below the optimum temperature for survival the host preference relations of Leptinotarsa are stable but at higher temperatures the host range is extended. This effect is not decisive enough to abolish differences in degree of acceptability of host plants and this may be but probably is not of significance ecologically. Furthermore Chin (1950) states that mortality is higher at these extreme temperatures.

Fourth instar Leptinotarsa larvae are less fastidious in their feeding habits than younger larvae at normal temperatures, and will feed sometimes on Datura and Petunia which are refused by younger larvae.

At higher temperatures (32°-36° C.) the third instar also becomes less restricted in its acceptance of hosts but these higher temperatures never result in more than a partial relenting of the discrimination against unacceptable plants if the volume consumption of S. tuberosum foliage be taken as a standard.

Starved larvae bite unacceptable substrates more readily than normally fed larvae but do not suffer much loss of discrimination as measured by continued feeding or total quantity consumed.

The fact that the more mature instars are somewhat less fastidious in their choice of hosts may be of considerable ecological consequence in dense insect populations which are subject to starvation through exhaustion of the foliage of their usual plants. If this occurs in the late instars before the normal onset of pupation, they may then be able to complete their development on plant hosts on which they could not have survived in the earlier instars. Since these effects tend to increase survival and possibly fecundity also, host selection behaviour is not without significance under certain conditions with respect to insect population numbers.

Conclusion

In recapitulation, host selection is expressed in nature by the failure in varying degrees of each insect species to establish itself on more than a limited number of the total available plant species in the geographic range of the insect. The factors which predestine this phenomenon include reflex behaviour of the insects to chemical and other stimuli, nutritional relationships, tolerance to plant toxins and the coincidence in time and space of developmental activity of the insect and its host plants.

The ecological significance of host selection is its effect, indirectly on population numbers through the selection of host plants of varying nutritional qualities and directly on insect distribution through its dependence on the geographical spacing of suitable host plants.

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SOME RELATIONS OF THE NUTRITION OF PHYTOPHAGOUS INSECTS TO THEIR ECOLOGY

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In this continuation of the discussion of insect nutrition I will limit myself to a consideration of the nutritional suitability of host plants of phytophagous insects. To what extent do chemical differences in plants affect the growth, development and reproduction of insects feeding on them?

There is a considerable entomological literature dealing with the differential effects of various host plants on the growth and reproductive capacity of specific insects. Reference will be made to only a few examples.

Smith (1949) reared Melanoplus mexicanus (Sauss.) on six different acceptable food plants. Of these, dandelion and wheat had the highest survival value (70 per cent) and alfalfa the lowest survival value (10 per cent). In another experiment 21 varieties of barley were tested and survival ranged from 60 per cent to less than 5 per cent. In both of these experiments the egg-laying capacities of the females exhibited considerable variation depending on the species or variety of the host plant.

Pfadt (1949) working with the same insect tested survival on 32 host plants and his survival values ranged from 0 to 90 per cent. He also found differences in egg production and growth due to different host plants. An important consideration mentioned by Pfadt (and which has rarely been considered by other workers) is that some of the differences in food values of the various plants may have been due to differences in the quantities of food eaten by the grasshoppers. If this is true it concerns the involvement of sensory responses along the lines mentioned by Dr. Thorsteinson in the first part of this discussion.

Different parts of the same plant may evoke different nutritional responses. Lejeune (1950) in a study of the growth of jack-pine budworm larvae (Choristoneura sp.) has shown that larvae feeding in staminate flowers of jack pine had significantly wider head capsules than larvae feeding on foliage.

Within recent years a number of studies have been made of the relationship between the chemical composition of plants and their nutritional value to insects. These studies have met with varied success.

Webster and colleagues (1948) made an intensive investigation of the comparative chemistry of several varieties of sorghum. They hoped to find some correlation between chemical composition and the relative resistance of the varieties to chinch bug attack. Plant tissues and juices were analyzed for sugars, total nitrogen, certain enzymes, hydrocyanic acid (cyanogenetic substances), and tannins. No overall chemical differences were found that could be correlated with chinch bug resistance when a number of varieties were considered. Differences could be found between selected resistant and susceptible varieties, but these always disappeared when a greater number of varieties were compared. A similar lack of success was reported by Turner (1951) in a study of the relation between sugar content of corn and infestation and survival of the European corn borer. Field tests of various varieties of sweet and field corn were made. Sugar content of the plant saps were determined periodically and the extent of infestation and survival of larvae were followed. No correlation was found between sugar content of the host plant and infestation nor survival of the corn borer.

Studies by other workers have yielded more positive results. Maltais (1951) and Auclair and Maltais (1950) have determined the nitrogen content and amino acid composition of varieties of peas showing varying degrees of resistance to aphid attack [Macrosiphum pisi (Kltb.)]. The total nitrogen content of whole plant samples and water extracts of 1 susceptible variety and 2 resistant varieties was determined. The susceptible variety was found to have a higher N content than the resistant varieties. Similarly of two varieties, one susceptible and one resistant, analyzed for amino acids, the former was found to have the higher concentration.

The significance of this latter finding is questionable due to the fact that only two varieties were compared.

A recent paper by Smith and Northcott (1951) reports on the effects of varying N content of plant food on the grasshopper Melanoplus mexicanus. These workers grew Renown wheat in nutrient solutions at three levels of nitrogen. The wheat produced analyzed, respectively, 6.16 per cent, 4.29 per cent, and 3.33 per cent dry weight N (average values). Survival and development were greatest on the high N wheat and least on the low. No individuals developed beyond the last nymphal instar on the low level N. Females fed on wheat with the higher N content laid more eggs but there was no difference between the viability of those produced at the 2 levels. Neither adult weight nor sex ratio were affected.

A different biological response to plant N has been reported by Haseman (1946). The chinch bug was found to mature faster and live longer when nitrogen was withheld from the nutrient solutions on which the corn plants were grown as food. Similarly the greenhouse thrips (Heliothrips haemorrhoidalis) was found to select spinach plants growing on low nitrogen levels rather than those growing on higher levels.

A preliminary note by Arant and Jones (1951) on the influence of nitrogenous fertilizers on the populations of greenbugs [Toxoptera graminum (Rondani)] infesting oats is in agreement with the findings of Haseman. Infestation counts made by these workers showed that the greater the quantities of nitrogen fertilizer applied to plants the smaller was the number of insects per unit of leaf surface. It would seem that this may have been, in part at least, a secondary effect of the better growth of the fertilized plants.

In a study of the fats of the sugar beet webworm (Loxostege sticticalis L.) Pepper and Hastings (1943) have revealed some interesting information concerning fatty acid nutrition and its possible relation to the ecology of this species.

A decrease in the linoleic acid content of prepupae and adults was found to be correlated with a decrease in the relative fertility of the adults. Three host plants were studied for linoleic acid content and lamb's quarters was found to contain more than sugar beets or sage. Lamb's quarters was capable of supporting at least three successive generations of fertile females. It was suggested that the webworm builds up to outbreak proportions on plants other than sugar beets, i.e. plants which are high in linoleic acid.

The importance of chemical differences of various parts of the corn plant in the nutrition of the corn borer (Pyrausta nubilalis Hbn.) has been studied by Bottger (1951). He found the leaves were relatively high in protein (2.80 per cent green wt.) and low in reducing sugars (1.08 per cent green wt.). Larvae fed on leaves showed high survivals but low weights.

Corn internodes were high in sugar content but comparatively low in protein. Feeding larvae exclusively on internode tissue resulted in low survival but surviving larvae were relatively heavy.

When larvae were fed on corn kernels of various varieties differences in weight were more closely related to reducing sugar contents than to protein contents and high weights tended to be associated with high survival.

This study serves to indicate the significance of nutritional differences among the various parts of the host plant. Failure to consider these differences may have accounted, in part, for the inconclusive results of Turner referred to earlier.

In summary, the studies referred to here emphasize the importance of considering the chemistry of the host plants of phytophagous species as one of the complex of factors related to the ecology of the species. The role of chemical factors in determining host selection has been stressed by Dr. Thorsteinson. There is now good evidence that chemical differences between host plants can have significant effects on the growth and reproduction of insects feeding on them. In some cases, possibly in the case of the sugar beet webworm, a nutritional factor may play a principal role in the growth of populations to the outbreak level.

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APPENDIX

A List of Publications in the Library of the Entomological Society of Manitoba.

The following is a complete list of the publications in the library of the Society at the time of publication of these Proceedings. These are deposited in the Department of Entomology, University of Manitoba where they are available to all members of the Society.

Proceedings of the Entomological Society of Manitoba - Vols. 1 - 6. (1945-50 complete)

Proceedings of the Entomological Society of British Columbia - Vols. 43 (1947), 47 (1951), 48 (1952).

Eighty-first Annual Report of the Entomological Society of Ontario. (1950).

Proceedings of the 23rd Annual Meeting of the Central Plant Board, (1947).

Report of the Twenty-first Annual Meeting of the International Great Plains Conference of Entomologists (1948).

Contributions de L'Institut de Biologie de l'Universite de Montreal:-

No. 1. Contribution a l'etude des Insectes du Bouleau.
- L. Daviault (1937).

Nos. 2,3 & 4.
Etudes sur le saumon de l'Atlantique. (Salmo salar L.) I - III.
- D. L. Belding et G. Prefontaine (1938, 1939).

No. 5. The use of calcareous shell to buffer the product of anaerobic glycolysis in Venus mercenaria. - Louis-Paul Dugal (1939).

No. 6. Etude anatomique du systeme nerveux peripherique et des organes des sens de la tete chez l'embryon d'Amia calva.
- W. Bonin (1940).

No. 7. Etudes sur les mammiferes aquatiques.
I La peau du marsoin blanc ou Beluga.
- W. Bonin et V. D. Vladykov (1940).

No. 8. A study of the histological structure of the respiratory portion of the lungs of aquatic mammals.
- Leonard F. Belanger (1940).

No. 9. Recherches biometriques sur les electroencephalogrammes individuels.
- W. Liberson (1941).

No.10. Recherches sur la cicatrisation des plaies. I.
Louis-Paul Dugal et H. Laugier (1942).

No.11. Studies on aquatic mammals. II. A modification of the pectoral fins in the Beluga from the St. Lawrence River.
- V. D. Vladykov (1943).

No.12. Les Tabanides du Quebec.
- G. Chagnon et L'Abbe Ovila Fournier (1943).

No.14. Contribution a l'etude des Orthopteres et des Dermapteres du Quebec. (1944).

No.15. Etudes sur les Mammiferes Aquatiques III.
- V. D. Vladykov (1944).

No.16. Essai de Correlation Sociologique entre les Plantes Superieures et les Poissons de la Beine du Lac Saint-Louis.
- Pierre Dansereau (1945).

Additions au catologue des dipteres du Quebec.
- lr fr. Joseph Ouellet, Universite de Montreal (1941).

Contribution a l'etude des Coleopteres de la Province de Quebec. Gustave Chagnon, Universite de Montreal.

Reference publications on the Various Orders with Personal Notes on Works and Workers. - - R. L. Post (1946).

Preserving Insect Specimens and Preparing Material for Display.
- R. L. Post.

Notes on Taxonomy and Nomenclature. - R. L. Post.

List of Common and Scientific Names of Forest Insects.
- Forest Insect Laboratory, Sault Ste. Marie.