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Studies in the Physical Ecology of the Noctuidae

By WILLIAM C. COOK
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UNIVERSITY FARM, ST. PAUL

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CONTENTS

ILLUSTRATIONS

STUDIES IN THE PHYSICAL ECOLOGY OF THE NOCTUIDAE

By W. C. Cook

INTRODUCTION

This paper gives the results of an attempt to determine the effects of the various meteorological factors on the distribution, seasonal abundance, and activity of certain species of the insect family Noctuidae, which are commonly classed as cutworms and army worms. As yet the studies include but few species, but the results so far obtained seem of fundamental importance, and the methods used, altho somewhat novel to entomologists, are applicable to the solution of many similar economic problems.

DEFINITIONS OF TERMS

Physical ecology may be defined as the study of physical factors in their relation to the ecology of a species. Such factors are light, heat, and moisture as opposed to associational factors such as parasites, or chemical factors such as food relations. The study of these physical factors under field conditions comes within the realm of meteorology, and the factors themselves fall into two general classes, weather and climate. Prof. J. Warren Smith ('20, p. 1)[1] makes the following comparison of these groups:

"Weather is the condition of the atmosphere at a definite time. It includes all the phenomena of the air that surrounds us, such as pressure, temperature, moisture, wind, and the like.

"Climate deals with the averages and the extremes of the weather that prevail at any place. Thus it will be seen that weather relates to time and climate to location."

LITERATURE

Most of the previous work on insect forms has been confined to laboratory experiments under controlled conditions or to the drawing of general conclusions from a superficial study of field data, without subjecting the data to any form of mathematical analysis. This is the case in the early development of any branch of science, the qualitative form preceding the quantitative. Our entire knowledge of quantitative physical ecology may be said to consist of a few definite laws of growth deduced from laboratory experiments, and a few broad generalizations on the effects of climate on animal and plant distribu-

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[1] Dates in parentheses refer to titles in the list of literature cited at the end of the paper.

tion and activity. Some of the more important of these deductions are worthy of mention in connection with this specific problem.

Working under controlled laboratory conditions, Sanderson and Peairs ('13) determined that the effect of temperature upon insect growth might be represented by a rectangular hyperbola of the formula $XY=A^2$, A being a constant, called by them the thermal constant, X being the temperature, and Y being the time of development. By plotting X against $\frac{1}{y}$, the plot becomes a straight line which intersects the temperature axis at the point $\frac{1}{y}=0$, or point of no growth, which they called the developmental zero. The quantity $\frac{1}{y}$ they have termed the index of development, and it represents the part of total growth accomplished in one day. In most cases in which this method of plotting was used, it has been found that the relations outlined above hold true for the portion of the temperature range which is approximated under field conditions, and that the developmental zero found mathematically is a very close approximation to the point of dormancy under field conditions.

W. D. Pierce ('16) showed that the effect of temperature combined with humidity was to change the developmental zero of Sanderson to an elliptical curve whose foci were the optimum condition, and that Sanderson's curve of growth was a zone inside of this ellipse. Any cross-section of this zone, parallel to the humidity axis, gave a hyperbolic temperature curve, as before.

Studying the distributional data obtained by the United States Biological Survey, C. H. Merriam ('98) formulated a general law of animal and plant distribution, as follows ('98, p. 54).

"Investigations conducted by the Biological Survey have shown that the northward distribution of terrestrial animals and plants is governed by the sum of the positive or effective temperatures for the entire season of growth and reproduction, and that the southward distribution is governed by the mean temperature of a brief period during the hottest part of the year."

By the term "effective temperatures" is meant all temperatures above 43° F, which was then regarded as a general developmental zero.

Sanderson ('08) showed quite conclusively that the northward distribution of some insect species was limited, not by the sum of effective temperatures, but by the minimum winter temperature, and recommended the inclusion of this factor in Merriam's law.

A. D. Hopkins ('18) has formulated an empirical bioclimatic law, stating that in general, in temperate North America, the time of occurrence of any given periodic event in life activity becomes later in the spring and earlier in the fall as we progress northward, eastward, and upward. The general rate of change is four days for each degree of latitude, each five degrees of longitude, and each four hundred feet of altitude.

The bioclimatic law does not represent conditions on the Pacific Coast, and there is a gradually decreasing error in its application until the region well east of the Rocky Mountains is reached. As the author of the law has stated, it is a purely empirical deduction from field observations, and apparently the basis of the law is the gradual change from marine to continental climate progressing from east to west as we go inland. Possibly a restatement of the law, based upon distance from the ocean rather than upon westward progression, would give smaller errors in the western part of the range.

Aside from the general problem of the effects of climate upon animal distribution, efforts have been made to connect certain climatic conditions with specific insect outbreaks. No attempt will be made here to include all the work done on this problem, but a few abstracts will be given to show the general character of the work.

One of the early attempts in this direction was the hypothesis advanced by Asa Fitch ('60) to account for army worm outbreaks. It is quoted in full ('60, p. 121).

". . . more briefly expressed, my view is this—a dry season and dry swamps multiplies this insect. And when it is thus multiplied, a wet season and overflowed swamps drives it out from its lurking place in flocks, alighting here and there over the country. But on being thus rusticated, it finds our arable lands too dry for it and immediately on maturing and getting its wings again, it flies back to the swamps, whereby it happens that we see no more of it."

This view was also supported by C. V. Riley ('70, '76), and shows that even in this early stage in the development of entomology, it was recognized that climatic factors might explain insect outbreaks.

Charles G. Barrett ('82) gives notes on the distribution of various Noctuid species in an English district following two types of winter conditions, and concludes that the abundance or rarity of native species is largely determined by climatic conditions. Four successive mild winters made certain species, which were ordinarily common, very rare, and other ordinarily rare species quite common. Following these winters came three severe winters, after which the normal balance was restored.

In considering the relation of precipitation to insect distribution, Criddle ('17) cited the Rocky Mountain Locust as an example of an insect which is increased greatly during dry seasons, and also states that in Manitoba the Hessian Fly is checked by a drouth sufficient to ripen the wheat prematurely. He shows that the combination of light snowfall and low winter temperature has been fatal to the Colorado potato beetle in most parts of Manitoba, and considers that it will probably never be a major pest in that region.

In the realm of plant ecology, especially in the study of the economic crop plants, there is a rapidly increasing body of work upon the mathematical study and analysis of climatic relations. J. Warren Smith ('20) brings together the principal work relating to the effects of climate upon crops, using statistical methods for the more or less exact definition of critical growth periods. In many cases it is now possible to predict the amount of a given crop on a certain area if the weather conditions during these critical periods are known. This work is very valuable and suggestive, and the methods used there have been adopted in part in this paper.

LINES OF STUDY PURSUED

This paper is based upon studies along three distinct but related lines, laboratory experiments upon temperature and soil moisture relations, attempts to correlate these results with the conditions surrounding outbreaks of three species in the field, and a statistical interpretation of data relative to the effects of weather conditions on moth flight. The work was begun at University Farm, St. Paul, in 1919, in connection with cutworm investigations undertaken for the Minnesota Agricultural Experiment Station, and carried through two seasons, during which time all the original data relating to Minnesota conditions were secured. During 1921 the work was carried on in Montana in connection with investigations of the life history and control of the Pale Western cutworm (*Porosagrotis orthogonia* Morr.) for the Montana Agricultural Experiment Station, and all the original data relating to Montana conditions were obtained. The writer wishes to acknowledge his indebtedness to the authorities of both stations for the opportunity to study the problems, and for many courtesies extended during the work; and especially to Dr. R. N. Chapman, of the University of Minnesota, under whose direct supervision most of the Minnesota work was done, and whose advice and assistance have been invaluable. He also wishes to thank Mr. U. G. Purssell, Mr. C. M. Ling, and Mr. W. T. Lathrop, Meteorologists of the United States Weather Bureau at Minneapolis, Havre, and Helena, respectively, for their co-operation in supplying meteorological data used in these studies.

METHODS USED

In a previous paper (Cook '21), the author published the Minnesota data relative to the effects of weather upon moth flight, using the method of partial correlation in their interpretation. This paper extends this discussion, using similar methods in this part of the work These methods are well explained in Yule ('19) and Smith ('20). The method of correlation depends upon the basic assumption that the relation between the factors studied lies along a straight line, which is approximately the case with the moth flight data, with the same exception noted in the previous paper ('21, p. 53). Partial correlation assumes a casual relationship between the factors correlated, which is justified in the work on moth flight, but can not be readily assumed in the work on the relation of climatic conditions to larval growth, so that in this latter case, only total correlation is used. It was found, upon plotting the points of the general climatic relations shown in Plate IV, that these did not lie along a straight line, so a curve was fitted to them by the method of least squares (Leland '21). Several other somewhat simpler but less accurate methods may be found in Lipka ('21), which is a valuable aid in this sort of work.

In any study of the relation of organisms to their environment, it is necessary to develop some method of correlating laboratory experiments with field observations. The laboratory experiment shows what the organism will do in a certain controlled environment, while the field observation shows what it does under constantly fluctuating conditions. If we can reduce the field condition to some sort of an expression representing the optimum condition and can determine the optimum under controlled conditions, then we may say that the two conditions are equivalent. Because of the wide fluctuations in field conditions, it is necessary to treat the mean of a large series of observations instead of using a single observation, and the only available method of determining field relations is that of statistics, which has wide social and biometric applications. The accuracy of the result varies as the square root of the number of observations, so that long series of data yield more accurate results than short series.

COMPARATIVE CLIMATOLOGY OF MINNESOTA AND MONTANA

The studies on which this paper is based were carried on under two essentially different climatic conditions, and these differences are best brought out by a comparison. It is difficult to compare two large areas, so the two points where moth flight experiments were conducted were selected as typical, and their climatic features compared.

St. Paul, Minn., is in latitude 44° 58′ N, longitude 93° 03′ W; and Havre, Mont., in latitude 48° 34′ N, longitude 109° 40′ W. Both of these general regions are in the Transition Zone of Merriam ('98), but are considered as separate faunae by Thompson-Seton ('09), who places Minnesota chiefly in the West Alleghenian fauna and Montana chiefly in the Campestrian fauna. Table I, the data for which were secured from Henry ('06), shows the nature of the climatic differences between the two regions, and Figure 1, Plate I, is a climograph constructed from the data of Table I.

TABLE I

CLIMATOLOGY OF HAVRE, MONT., AND ST. PAUL, MINN.

Month	Temperature				Humidity 7 p. m.		Total monthly Precipitation	
	Mean monthly		Daily range					
	Havre	St. Paul	Havre	St. Paul	Havre	St. Paul	Havre	St. Paul
	Degrees	Degrees	Degrees	Degrees	Percent	Percent	Inches	Inches
January	13	12	19	18	76	76	0.8	1.0
February	14	16	21	17	77	76	0.5	0.6
March	27	29	21	18	70	68	0.6	1.6
April	44	48	24	20	44	54	1.0	2.5
May	53	60	25	20	45	51	2.1	3.3
June	61	66	24	19	43	56	2.9	4.4
July	68	74	27	21	35	54	2.1	3.6
August	66	72	29	20	34	55	1.3	3.4
September	55	62	27	20	44	58	1.1	3.3
October	44	50	24	18	56	62	0.6	2.5
November	28	32	21	16	71	69	0.7	1.2
December	22	20	19	16	75	76	0.5	1.2
Meanannual	41	45	23	18	56	63	....	....
Totalannual	....	....	....	....	....	....	14.2	28.6

GENERAL CLIMATIC DATA

Temperature	Havre	St. Paul		Havre	St. Paul
Mean maximum, degrees..	53	56	Average date		
Mean minimum, degrees..	30	36	last spring frost.....	May 17	May 6
Absolute maximum, degrees	108	104	first fall frost........	Sept. 18	Oct. 5
Absolute minimum, degrees	−55	−41	Average length of		
No. days above 90°......	20	7	growing season, days.	124	152
No. days below 32°......	168	158			

The climograph is a diagram originally introduced by Ball ('10) and modified by several workers, of whom Varney ('20) is one of the latest. The mean monthly figures for temperature and humidity are plotted against each other, and the dots for the successive months are connected by a line with arrowheads showing the direction of change in the annual cycle. A recent contribution by Flanders ('22) gives many variations in the use of the climograph for planting various pairs of weather factors.

The summer humidity conditions are radically different in the two regions, the period from April to September representing in Montana a condition of dryness never reached in Minnesota. This dry summer condition practically eliminates the possibility of two-brooded species, so that few such species occur in the plains region of

Montana. Another factor of considerable importance in the ecology of the moths is the large diurnal temperature range in Montana, which restricts flight to the late afternoon and early evening during a large part of the summer season. Winter conditions are very similar in the two regions, so that this factor should not operate to differentiate the two faunae.

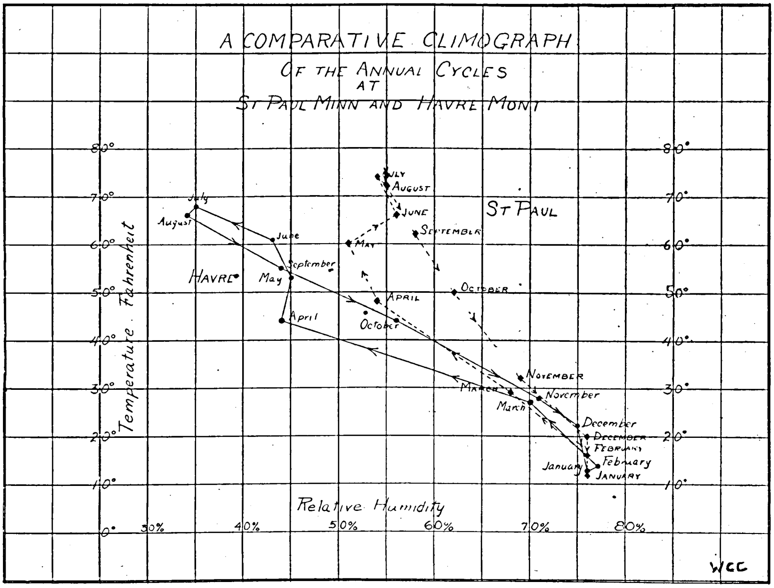

Plate I. Comparative Climatology

Figure 1. A comparative climograph of the annual cycles at St. Paul, Minn., and Havre, Mont.

GENERAL ECOLOGY OF THE NOCTUIDAE OF MINNESOTA AND MONTANA

As would be expected from the radical climatic differences, the Noctuid faunae of the two regions are essentially different, as is brought out in Table II, which is a compilation from Hampson ('03-'09). The species listed as western or eastern are not confined to Montana and Minnesota, but represent roughly semi-arid west and humid east. In order to show the relations of these regions to the generic centers of dispersal, the number of Palearctic species in each genus is included. Roughly, that region showing the greatest number of species is generally the center of dispersal (Folsom '06, p. 383).

The predominating western genera are of western origin, apparently, and none of their species is common to Europe and America, while the typical eastern genera are obviously of European origin. In this connection it is interesting to note the comment of John B.

Smith ('90, p. 11) with regard to the character of our American Agrotid fauna:

"It is suggestive that so large a proportion of our species are from the western part of our country, and that those species are mostly referable to those genera in which the front is modified in some way and the tibial armature heavy. In fact, the distinctive character of our western fauna is shown in the very predominance, and sometimes abnormal development, of tibial and clypeal armature."

TABLE II

NOCTUID DISTRIBUTION IN THE HOLARCTIC REALM

Genus	Number of nearctic species			Number of	
	Eastern No. America	Western No. America	Common to both	Palearctic species	Holarctic species
Euxoa	25	163	10	84	0
Chorizagrotis	0	5	0	4	0
Porosagrotis	1	12	1	0	0
Feltia	7	11	1	3	0
Polia	34	63	2	71	0
Agrotis	22	17	0	79	3
Cirphis	7	7	0	66	3
Parastichtis	12	9	1	16	0
Agroperina	5	3	1	1	0
Sidemia	1	2	1	9	0
Totals					
Western group	67	254	14	161	0
Eastern group	47	38	3	171	6
Grand totals	114	292	17	332	6

The species of Euxoa, Chorizagrotis, and Porosagrotis are regarded by Hampson as representing the highest development of the Noctuid type, and this structural position is borne out by their ecology. They differ from the eastern species in many important respects, in all of which they are more highly specialized than the latter.

LARVAL HABITS

Cutworms may be grouped in three classes according to feeding habits. Climbing cutworms climb plants, eating the foliage without always destroying the main stem. *Lycophotia margaritosa* and *Porosagrotis vetusta* belong to this class. (Slingerland.) The great majority of the eastern species feed at or just above the surface of the ground, and may be called surface cutworms. Examples of this type are *Feltia ducens, Euxoa messoria,* and *E. tessellata.* A third and more recent type in point of development is the group of sub-surface feeders, or subterranean cutworms. Among the comparatively few species known to have this habit, is *Porosagrotis orthogonia* and, possibly, *Sidemia devastator. P. orthogonia* feeds entirely below the surface, cutting off plants from one to two inches below the surface of the soil, and moving from one to another underground, except under abnormal conditions such as heavy rainfall. All the most abundant Montana cutworms are either surface or subterranean feeders, with several species suspected of the latter habit, altho this has not been proved except in the case mentioned.

ADULT HABITS

In the habits of the adults as well as in those of the larvae, the species of the two regions are quite different. In the first place, the cutworm moths of the Montana group are very strong in flight. This was well shown during the early summer of 1921, when thousands of specimens of *Chorizagrotis auxiliaris,* the Western Army cutworm, were captured in Minnesota, Iowa, and Kansas. This species breeds normally in the plains region of Montana (Cooley, '16) and has never been reported in large numbers east of that region. This means that in 1921 the moths must have flown at least three hundred miles from the place where they emerged.

Another peculiarity in the life history of *C. auxiliaris* and *Agrotis unicolor* Walk. (*Noctua clandestina* Harris), as recorded by Strickland ('16), is the habit of aestivation in the adult stage. The moths emerge in June and aestivate for a period of at least three months before maturation of the ovaries and oviposition. None of the common Minnesota species (with the possible exception of *A. unicolor,* which also breeds in Minnesota) are known to have any similar habits. This aestivation is apparently the method chosen by these species to escape the intense heat and drought of July and August in Montana.

Very little is known concerning the oviposition habits of Noctuidae, but all the eastern species whose habits are known lay their eggs directly on green vegetation. This is definitely known for *Agrotis ypsilon, Feltia ducens, Polia lorea, Lycophotia margaritosa,* and *Cirphis unipuncta.* Those Western species whose habits are known, on the other hand, lay their eggs either on trash on the surface of the soil (*C. auxiliaris,* Strickland '16), or in the surface layer of the soil. (*P. orthogonia,* Parker, Strand, and Seamans, '21). Several species of Euxoa are suspected of similar habits, but have not been found ovipositing as yet.

In reproductive capacity the Eastern species in general outrank the Western, with some exceptions. Thus, it was found in Insectary work at University Farm that *L. margaritosa* lays as many as 3000 eggs, an average figure obtained from twenty-eight moths being 1497. *Felita annexa* (Jones, '18), lays as many as 1300 eggs, an average for ten females being 794. *C. unipuncta* has been captured with as many as 800 eggs in the ovaries (Turner '18), and probably lays many more in the field. Among the Western species, *P. orthogonia* averaged 315 eggs each for five females (Parker, Strand, and Seamans, '21), and *C. auxiliaris* laid about 1000 eggs (Strickland '16), which figures are the only ones available for Western species. It is evident that *P. orthogonia,* the most highly developed cutworm ecologically, does not need so high a reproductive capacity, as the eggs, being scattered in small clusters through the soil, have a much larger chance of survival.

Another factor to be considered in connection with reproductive capacity is the ability of the species to produce sudden and severe outbreaks. A species with a high reproductive capacity can multiply very rapidly, and a small number of moths surviving a hard winter can quickly bring up the population to a destructive number. Such species as *C. unipuncta* and *C. auxiliaris* and *L. margaritosa* can produce these sudden severe outbreaks, as is evident from a superficial survey of the general economic literature. On the other hand, *P. orthogonia* does not suddenly appear in large numbers, but produces a gradually increasing population in any given place until checked by climatic conditions, when the cycle is recommenced.

PHYSICAL ECOLOGY OF IMMATURE STAGES

LABORATORY STUDIES

In order to obtain some experimental evidence with regard to the relations of the various stages of Noctuids to temperature and humidity, laboratory experiments were carried on at University Farm, St. Paul, during the winters of 1919-20 and 1920-21. It was the intention of the writer to rear as many species as possible under controlled conditions, but *L. margaritosa* was the only species which was obtained in large enough numbers for this work. As atmospheric humidity has a very small influence on the insect during the larval stages, which are spent in the surface layer of the soil, the moisture of the direct environment, namely, soil moisture, was studied instead.

SOIL MOISTURE RELATIONS

The method used in determining the relations of *L. margaritosa* to soil moisture were in general those of students of plant physiology, being the rearing of the insect in a cage of soil whose known moisture content was held approximately constant by the daily addition of sufficient water to maintain a constant weight. Lantern globes covered over the top with coarse muslin were placed over the soil in a pot holding about five pounds of soil. The original moisture content of the soil was determined, sufficient water added to secure the required moisture content, the weight of pot, soil, and cage taken and held constant throughout the experiment. The freshly-laid eggs were placed on the surface of the soil in the cage, and the insects reared to the adult stage under the same constant moisture condition. A thermograph was kept in close proximity to the cages to give a continuous record of air temperature, and all cages were kept close together in the greenhouse under as uniform conditions as possible. Two sets of experiments were performed, differing slightly in details, and will be considered separately.

First experiment—1919-20.—In this experiment three soils were used; a course sand with a maximum water capacity of about 32 per cent of dry weight; a rich leaf mold with a water capacity of about 52 per cent of dry weight; and a mixture of equal parts of these two, designated as loam, whose water capacity was about 41 per cent of dry weight. Two cages were held at each moisture condition, of which there were sixteen. The cages were examined each morning, and the number and instar of the larvae present noted, so that the figures given represent an average for the larvae of each two cages.

TABLE III

MOISTURE RELATIONS OF LYCOPHOTIA MARGARITOSA
FIRST EXPERIMENT, 1919-20

Water Content per cent of		No. of eggs	Egg period	No. of larvae	Larval period	No. of pupae	Pupal period	No. of adults	Total life	Mortality
Dry weight	Total capacity									
			days		days		days		days	Per cent
				SAND	SERIES					
5.0	15	50	6.0	30	53.0*	0	....	0	59.0*	100.0
7.5	23	17	8.0	14	36.5*	1*	....	0	44.5*	100.0
10.0	32	24	7.0	13	22.3*	0	....	0	29.3*	100.0
12.5	39	18	8.0	12	59.6	2	24.5	2	89.5	96.4
15.0	47	60	7.0	52	58.1	7	22.3	3	92.3	95.0
20.0	63	27	9.0	20	52.5	4	32.0	1	91.0	96.3
Series		196	7.3	141	56.9	14	25.6	6	91.2	96.9
				LOAM SERIES						
5	14	30	7.0	2	8.0*	0	....	0	15.0*	100.0
10	28	30	7.0	14	47.1*	0	....	0	54.1*	100.0
15	42	30	6.0	23	55.6	4	23.2	4	81.2	86.7
20	56	34	7.0	19	51.9	9	23.0	8	85.1	76.2
25	70	28	9.0	14	53.8	4	32.0	2	89.0	92.9
35	98	36	9.0	6	52.7	2	22.0	1	82.0	88.9
Series		191	7.5	78	52.2	19	24.3	15	84.4	92.1
				LEAFMOLD SERIES						
10	19	27	7.0	20	56.5	1*	....	0	63.5	100.0
20	38	28	8.0	22	50.6	1	25.0	1	92.0	88.9
30	57	26	8.0	12	33.0+	0	....	0	39.0+	100.0
40	76	17	8.0	10	48.0	4	23.6	3	80.0	82.4
Series		98	7.7	54	48.3	6	23.9	4	83.0	95.9

*Insects apparently died from lack of moisture before emerging as adults.
+Larvae in this cage killed by a fungous disease.

Considering both duration of stages and mortality, the loam was the most favorable soil for growth. The minimum water requirement of the species seems to be about 35 per cent of the total capacity on each soil, and the optimum is above 50 per cent. There seems to be no upper limit, altho probably a very wet soil is more favorable to the development of fungi in the field, thus reducing the numbers of insects.

Second experiment—1920-21.—The second set of experiments was run as a check on the first, and was conducted in the same greenhouse, under the same general conditions. Only one soil, a loam mixture with a water capacity of 32 per cent, was used, and five cages were run at each of six moisture conditions. In addition to the thermograph as in the first experiment, readings were taken each morning of the temperature of the surface soil in each cage, from which the departure of that temperature from that of the thermograph was computed and the actual temperature condition in the cage determined. Records were kept only of dates of hatching of eggs and emergence of adults, together with the number of adults emerging, from which the mortality percentage is calculated. The results of this experiment are given in Table IV.

TABLE IV

MOISTURE RELATIONS OF LYCOPHOTIA MARGARITOSA
SECOND EXPERIMENT, 1920-21

Water content Per cent of							
Dry weight	Total capacity	No. of eggs	Egg period	Larval and pupal period	No. of adults	Total life	Mortality
			days	days		days	Per cent
5	15	128	7	59.4	15	66.4	88.3
10	31	108	7.5	68.5	13	76.0	87.9
15	47	80	7.5	75.1	11	82.6	86.2
20	62	99	8.5	76.6	25	85.1	74.8
25	78	85	9.0	83.6	12	92.6	85.9
30	94	90	9.0	78.6	21	87.6	76.7

The minimum moisture requirement is not so evident in this experiment as in the first, but there is a definite optimum moisture of about sixty per cent of capacity. In order to show the general trend of both experiments, the data of Table III are combined with those of Table IV to form Table V, in which the various moisture contents are grouped into four general classes.

TABLE V

MOISTURE RELATIONS OF LYCOPHOTIA MARGARITOSA

Water per cent of total capacity	No. of eggs	No. of adults	Total life	Mortality
			Days	Per cent
0 to 35	314	28	71.0	93.2
36 to 50	222	21	84.8	90.5
51 to 65	183	34	85.3	81.4
66 to 100	256	39	88.5	84.8

The general conclusion to be drawn from these experiments is that the Variegated cutworm has a definite moisture requirement, both optimum and limiting, and that the optimum condition is about sixty per cent of the total water capacity of the soil.

TEMPERATURE RELATIONS

Experiments were planned for the rearing of all stages of *L. margaritosa* under controlled conditions of temperature, but it was found that any obtainable constant temperature was too high for the larval and later stages. The mortality was 100 per cent at all temperatures above 23° C., and only a single adult was secured at this temperature. Experiments on the hatching of the eggs were more successful. Table VI shows the results obtained from the exposure of twenty-four masses of 50 to 400 eggs each to three different constant temperatures. Four of the masses exposed to 30° C. failed to hatch, and only a portion of the eggs in the other six masses hatched, showing that this temperature approaches the upper limit of growth. The figures for duration of egg period are weighted according to the number of individual eggs in the experiment. The figures in the columns headed "Index of development" and "Thermal constant" are derived as explained in the introduction in the discussion of the work of Sanderson and Peairs ('13).

TABLE VI

TEMPERATURE RELATIONS OF LYCOPHOTIA MARGARITOSA

EGG STAGE

Temperature (C)		No. of masses	Duration			1/(6) Index of development	(2) x (6) Thermal constant
Observed	Effective		Max.	Min.	Mean		
(1)	(2)	(3)	(4)	(5)	(6)	(7)	(8)
Degrees	Degrees		Days	Days	Days		
23	14.2	10	5.5	5.0	5.2	.192	73.84
27	18.2	4	4.0	4.0	4.0	.250	72.80
30	21.2	10	4.5	4.0	4.1	.244	86.92

In the second series of moisture experiments, daily readings were taken of the temperature of the surface soil of each cage, from which the actual cage temperature was computed. In Table VII are given these temperature figures for the egg stage, together with the data on duration of the egg period and computations of the index of development and thermal constant on the basis of effective temperatures, as in Table VI.

The results of both these experiments are plotted on Plate II, the points for the two series being distinguished by the use of two symbols. The agreement of the two sets is more than accidentally close, and we must conclude that moisture in itself has little influence on the egg stage, except as it acts indirectly, by reducing temperature. Figure 1, Plate II, shows the temperature hyperbola drawn through all the points, and Figure 2 shows the reciprocal line.

TABLE VII

TEMPERATURE RELATIONS OF THE EGG STAGE OF LYCOPHOTIA MARGARITOSA UNDER CONTROLLED MOISTURE CONDITIONS

Water per cent of total capacity	No. of eggs	Egg period	Temperature (C)		Index of development	Thermal constant
			Mean, air	Mean, cage		
			Degrees	Degrees		
15	189	7.0	20	19.88	.143	77.56
31	157	7.5	20	18.99	.133	76.43
47	163	7.5	20	18.26	.133	70.95
62	156	8.5	20	17.15	.118	70.98
78	85	9.0	20	16.44	.111	68.76
94	90	9.0	20	16.52	.111	69.48

FIELD AND STATISTICAL STUDIES

Very early in the course of these studies, in considering the relations of *L. margaritosa* to temperature and soil moisture, it became quite evident that a knowledge of these optimum and limiting conditions should be of great value in a study of the relations of meteorological factors to insect outbreaks. For example, knowing definitely that the optimum soil moisture condition for this species is about 60 per cent of the total moisture capacity of any soil, would it not be a logical step to assume that field conditions during a destructive outbreak must at least approach this condition? If this assumption is correct, and the writer believes it to be, then, working back from this hypothesis, the weather data, in terms of temperature and precipitation, for the infested region during the period of the outbreak, must represent this optimum. This, then, is the first problem. Is there any definite indication of an approximately constant moisture condition in the field, as expressed in the temperature and precipitation records, and, if so, in which parts of the life history of the insect is this relation most pronounced? Further, if possible, it is desirable to analyze the weather data for the period covered by the destructive generation of the insect and by the preceding winter generation, that is, for a period extending at least a year previous to the outbreak, comparing conditions in all months, in order to obtain indications of any relationships which might aid in the climatological interpretation of the outbreak.

As it is necessary to deal with a large body of data in order to obtain trustworthy results, it is evident that some method of analysis, preferably some well-known standard method, must be used. For this work the method of correlation, as developed by the writers referred to in the introduction, is well adapted. The meteorological relations of

C. unipuncta in Minnesota have been quite carefully analyzed by this method, and some of the more general relations of *L. margaritosa* and *P. orthogonia,* altho the work done on these last two species is of a preliminary nature, introduced in this paper for purposes of comparison.

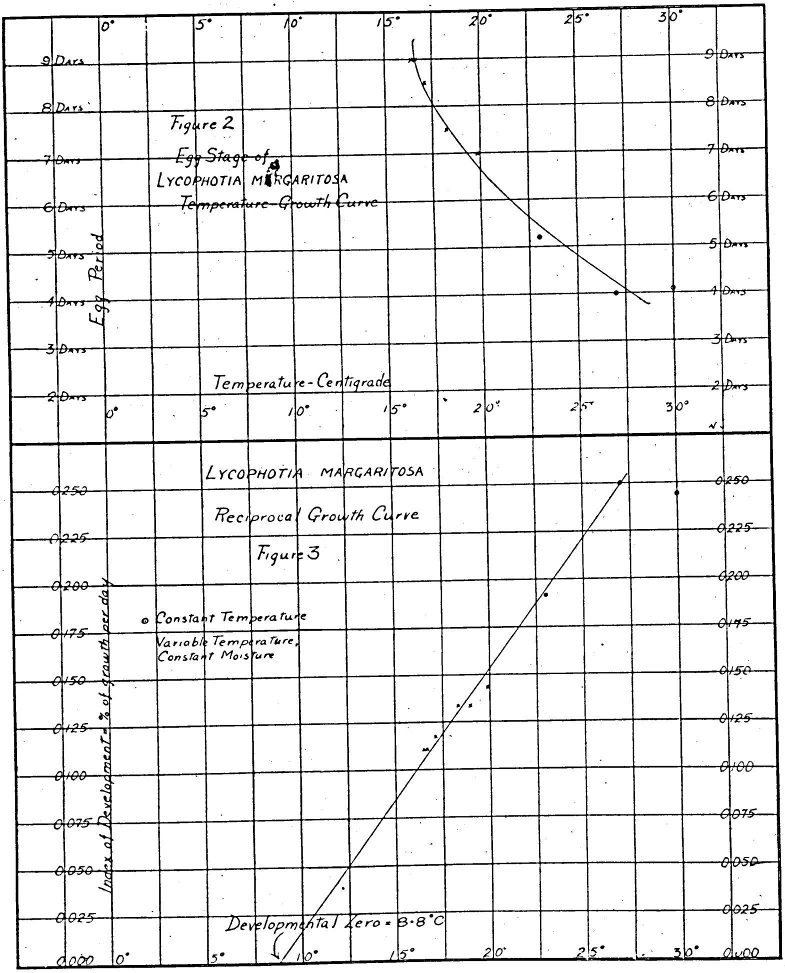

Plate II. Temperature Relations

Figure 2. Hyperbolic temperature-growth curve for the egg stage of *Lycophotia margaritosa.*

Figure 3. Reciprocal growth curve for the egg stage of *Lycophotia margaritosa.*

METEOROLOGICAL RELATIONS OF CIRPHIS UNIPUNCTA

Since 1895 there have been five major outbreaks of the army worm in Minnesota, which form the basis of this study. The general method of attack consisted in determining first the distribution of the insect in each outbreak, plotting the area roughly on a map, selecting all the United States Weather Bureau stations inside this area, and assembling the weather data for each station for the entire year preceding the outbreak. Out of about seventy-five station records so secured, twenty-one points were selected which had been in the area of destructive abundance for at least two of the five outbreaks, and their records were assembled for the entire period, 1895-1920. As some of the records were not complete for the entire year preceding an outbreak, those incomplete records were eliminated, leaving a series of thirty-five records, which were finally used as the basis of the statistical study. This elimination secured a set of records from a single region, each one represented more than once in the series, and all of them in regions more than normally liable to army worm attacks. A description of the area covered by each outbreak, the sources of information concerning each, and a list of the stations used for each in the statistical work follows.

1. 1896. A very widespread and destructive outbreak occurred throughout the southern and southeastern parts of the state. Data in regard to distribution were obtained chiefly from files of the daily newspapers of the region for the period, on file in the Library of the Minnesota Historical Society. The stations used were Farmington, Luverne, Montevideo, and Winona.

2. 1906. A more local outbreak occurred in the southwestern part of the state, extending some distance north of the Minnesota River into the southern portion of the Red River Valley. The distribution of the insect in this and succeeding outbreaks was obtained from records and correspondence filed in the office of the State Entomologist. The stations selected were Alexandria, Bird Island, Fergus Falls, and Morris.

3. 1910. A widespread outbreak occurred over the same territory covered in 1896, but with the most severe damage in the southwestern part of the state. The selected stations were Alexandria, Bird Island, Fairmont, Fergus Falls, Montevideo, Morris, New Ulm, Redwood Falls, and Windom.

4. 1919. A very widespread and severe outbreak of the army worm, accompanied almost universally by *L. margaritosa,* covered the entire southern part of the state and extended up the Red River Valley as far as Crookston. This outbreak and the one in 1920 were per-

sonally investigated by the writer. Selected stations were Albert Lea, Bird Island, Fairmont, Farmington, Grand Meadow, Luverne, Lynd, Montevideo, New Ulm, Redwood Falls, St. Peter, Winona, Worthington, and Zumbrota.

5. 1920. A locally severe outbreak occurred over an area embracing portions of the counties of Rock, Pipestone, Murray, Cottonwood, Lyon, and Redwood. The stations chosen were Bird Island, Luverne, Lynd, and Montevideo.

Complete data for these stations may be found in the files of the "Climatological Data, Minnesota Section," of the United States Weather Bureau.

Having assembled these data, the next step is the search for some methods of interpretation which will bring out the presence of a given moisture condition such as was outlined above. A consideration of the relationship between temperature, precipitation, and soil moisture makes it evident that, considering the variation in the evaporating power of the air at different temperatures, a heavy precipitation at a high temperature would produce the same moisture condition in the soil as a lighter rainfall at a lower temperature. That is, for example, the moisture at 70 degrees F. and four inches precipitation would probably be equivalent to that at 60 degrees F. and three inches rainfall. In other words, if we plot the temperature and precipitation figures for the thirty-five stations on a dot chart, whose ordinate is temperature and whose abcissa is precipitation, placing a dot at the intersection of the axes representing the condition at each station, a positive correlation between temperature and precipitation would represent the presence of an approximately constant moisture condition at all the stations. The closer the relationship, and the nearer the dots approach a straight line, the higher the value of the coefficient of correlation, "r," and the more critical this relationship in the economy of the species.

A series of dot charts, constructed as outlined above, were prepared for the conditions in each month of the year preceding an army worm outbreak, each chart containing the thirty-five points representing the selected stations. The correlation coefficient, "r" was calculated for each chart, together with its "probable error." The significance of "r" is related to its probable error, a value less than three times the probable error being of little significance, and one of more than six times the probable error indicating a very critical relationship. In order to determine whether these correlations were entirely due to the conditions in years preceding army worm outbreaks, a second series of charts was constructed, one for each month, on which the temperature and precipitation for the twenty-one stations for the entire period of twenty-five years were plotted. The difference between the correlations in the latter set and those in the former set indicated the true relationship of these conditions to army worm outbreaks. Both sets of coefficients and probable errors are given in Table VIII. Those months in which the value of "r" was near to six times its probable error, and in which it varies greatly in the months preceding army worm outbreaks from the value for the same month in the whole period, are regarded as critical, and the month and value are repeated in the fourth column.

TABLE VIII

CORRELATIONS OF TEMPERATURE WITH PRECIPITATION

Month	21 Stations entire period 1895-1920	35 Selected stations for period preceding army worm outbreak	Significant correlation or critical period
August	+.129 ±.031	−.007 ±.113	
September	+.038 ±.033	+.421 ±.093	+.421 September
October	−.064 ±.033	+.571 ±.077	+.571 October
November	+.029 ±.033	+.481 ±.088	+.481 November
December	+.017 ±.033	+.135 ±.112	
January	−.251 ±.031	−.227 ±.108	
February	+.319 ±.030	+.242 ±.107	
March	−.390 ±.028	−.416 ±.094	
April	+.012 ±.033	−.318 ±.102	
May	+.096 ±.033	+.548 ±.079	+.548 May
June	−.005 ±.033	+.122 ±.110	
July	−.169 ±.032	+.159 ±.110	

Analyzing the data in this manner shows that without any reasonable doubt, there is present some definite, practically constant moisture condition during the period preceding the outbreak, and that this condition is most marked in the months of September, October, November, and May, or during the larval life of the overwintering generation. The correlations in the winter months are fairly high, but correspond closely to those for the twenty-five year series, and hence are not necessarily related to army worm outbreaks.

The next logical step would be to ascertain whether this moisture condition is approximately equivalent in the various critical months, but we will postpone this consideration until some other relationships are studied. Let us next study the relations between successive months, for the purpose of determining the presence of any seasonal succession which is of importance. A consideration of the problem will show that a negative correlation between temperature in two successive months shows the presence of a necessary constant temperature sum for those two months. That is, if a warm September is followed always by a cold October, and a cold September by a warm October, the sum of temperature for the two months will tend to remain constant, and it remains for us to determine the significance of this thermal constant in the economy of the army worm.

In order to test the presence of any such relationships, dot charts and correlations were made by combining the temperature of each month with that following, and with various other months where there seemed to be any indication of a critical relationship. The same procedure was followed with the precipitation data, and the more significant of these correlations are given in Tables IX and X.

TABLE IX

TEMPERATURE RELATIONS BETWEEN SUCCESSIVE MONTHS PRECEDING ARMY WORM OUTBREAKS

September	October	November	December	January	June	July
September	−.924	−.723	−.665	−.745	−.619	−.718
	October	+.796	+.781	+.884	+.785	+.770
		November	+.557	+.760		+.571
			December	+.928		+.378
				January		+.567
					June	+.788
						July

TABLE X

PRECIPITATION RELATIONS BETWEEN SUCCESSIVE MONTHS PRECEDING ARMY WORM OUTBREAKS

September	October	November	December	January	June	July
September	−.364	−.170			−.254	−.361
	October	+.429			+.323	+.556
		November				
			December			
				January		
					June	+.607
						July

Altho no general correlations were made, as in the case of the first set of computations, it seems probable that these correlations given here are all significant, especially those between successive months. The most interesting relationships are found in the temperature conditions in the fall and early winter months. Considering first, September, October, and November, as they are the months in which the young larva prepares for hibernation, it is apparent that there is a very high correlation indicating the existence of a constant sum of temperature for those three months. If September is warm, October and November are cold, and if September is cold, October and November are warm. In order to test for the presence of this thermal constant, the mean temperature for October and November was computed and correlated with the September temperature, which gave a value of —.771 for "r." Then the mean temperature for the three months was computed for each station, and found to be 46.92, ranging from 43.6 to 49.7 F., with a standard deviation of 1.44 degrees. The standard deviations of the monthly temperatures of which this sum was composed were 3.70, 3.47, and 3.56 degrees, respectively.

The significance of this thermal constant in the economy of the insect evidently is in enabling the insect to reach a certain stage in which it is best able to hibernate. Knight ('16) has shown that this species can not hibernate in New York in the pupal stage, and evidently the range in Minnesota is even narrower, probably being restricted to two or three certain larval instars.

Another interesting temperature relationship is that between September and December and January, considered together. The relationship is even higher when October is substituted for September. This shows a very interesting balance between fall and winter conditions. If September is warm, the young larva grows quite rapidly, but its growth is checked by the cold weather in October and November, and this gradual "hardening" process enables it to withstand low temperatures in the early winter. On the other hand, if September is cold, the slow growth is accelerated during the warm October and November which follow, and the larva does not have the gradual hardening period found in the former case, and is evidently unable to withstand such cold weather in the early winter. These relationships are evidently vital to the insect, and a more complete analysis of these and others of lesser importance would probably enable us to predict the occurrence of army worms in any given locality by a study of the weather data for the previous year.

On Plate III are shown a few of these dot charts for the correlations in the fall and early winter months. The relationships are very close for this class of data, and their importance should not be underestimated. Notice particularly the high correlations between temperatures of successive periods, which are almost perfect in one case and of high value in the others.

Now, returning to the consideration of the question raised earlier in the paper as to the equivalence of the moisture conditions in the various months, we will study that point more intensively. First, it will be of value in visualizing the situation to show graphically how the condition in each of these months departs from the average of the region for twenty-five years. This is shown in Figure 4, Plate III. The heavy central axes represent the normal condition, and departures are measured from these in degrees F. and inches of rainfall. A circle represents the position of each month with regard to normal conditions. Six of the months are in the "warm, wet" quadrant, three in the "warm, dry" quadrant, and three in the "cool, dry" quadrant. None of them are in the "cool, wet" quadrant, a condition probably favorable to fungous parasites. The winter months are all warm and none of them very wet, indicating that a warm winter, with light snowfall, and presumably frequent freezing and thawing periods, is favorable to this species. This is also the case with the Pale Western cutworm, to be noted later.

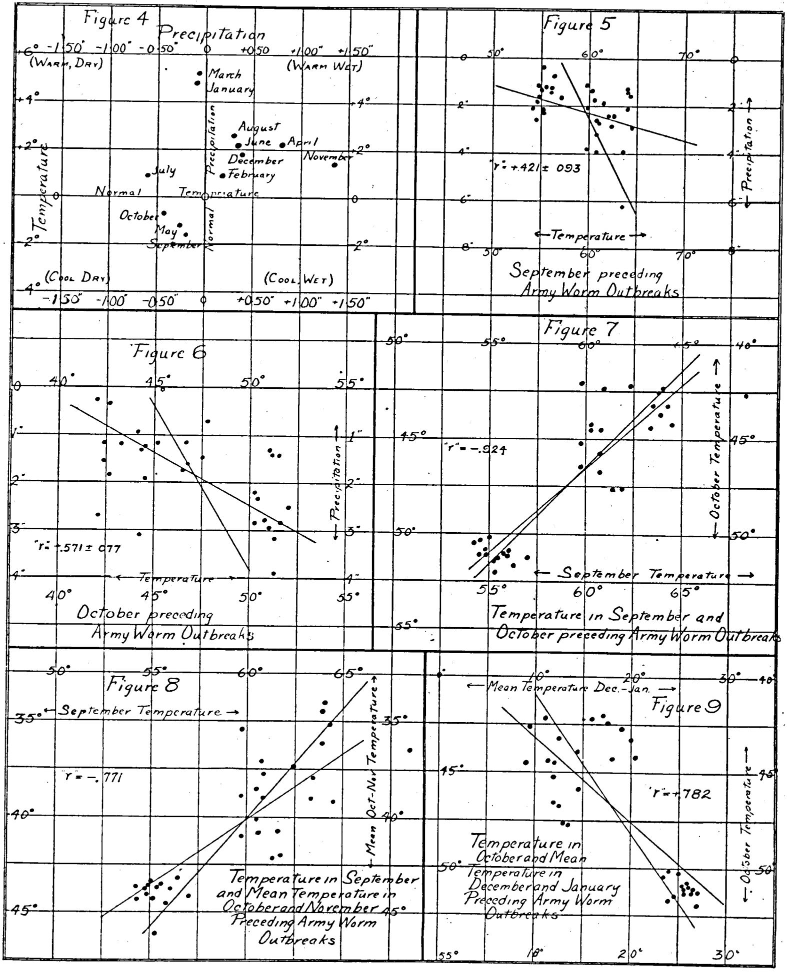

Plate III. Meteorological Relations of *Cirphis unipuncta*

Figure 4. Departures of monthly mean conditions from their respective normals during the period preceding outbreaks of *Cirphis unipuncta*.

Figures 5, 6, 7, 8, 9. Correlations between the weather factors in the period preceding army worm outbreaks.

5. September temperature and precipitation
6. October temperature and precipitation
7. September temperature and October temperature
8. September temperature and mean October-November temperature
9. October temperature and mean December-January temperature

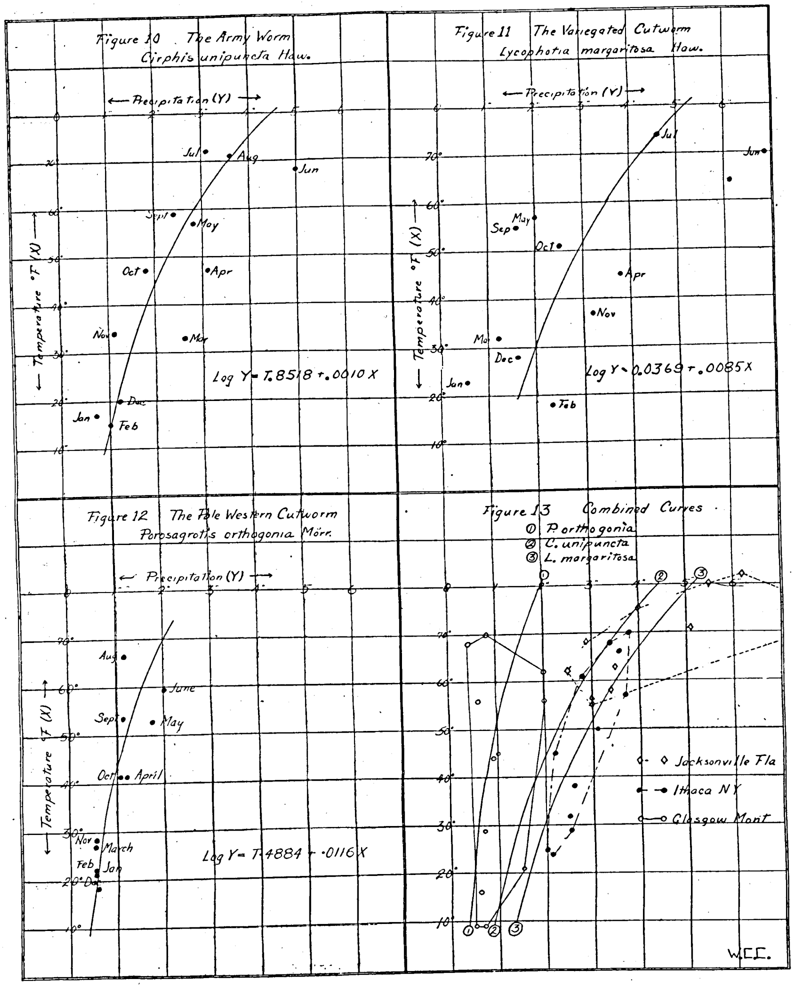

Plate IV. Climatological Relations of Noctuidae

Figure 10. Moisture curve of *Cirphis unipuncta*

Figure 11. Moisture curve of *Lycophotia margaritosa*

Figure 12. Moisture curve of *Porosagrotis orthogonia*

Figure 13. The three curves combined, to show comparative conditions and general distribution.

In the early part of this study, it was brought out that a positive correlation between temperature and precipitation in any one month indicated the existence of a nearly constant moisture condition. This line would be approximately straight in considering the range of temperature in any one month, but would probably be a curve when the wide range of annual conditions is considered. As the amount of moisture in the soil is a function of the evaporation of the air as well as of temperature and precipitation, this curve should be of the same general type as the curve which shows the amount of water vapor the air can evaporate at any given temperature, in other words, the vapor pressure curve of water. The formula for this, as given by physical chemists, is approximately

$$2.3025 \frac{\log P_1}{\log P_0} = \frac{18.W}{1.99} \frac{(T_1 - T_0)}{T_0 T_1}$$

We are not primarily interested in the various constants of this curve, P representing vapor pressure; T, temperature, and W the latent heat of vaporization, but we will note that it is logarithmic in nature, and hence, if the temperature and precipitation points for the various months are plotted on a graph, they should be capable of representation by a similar logarithmic curve. Such a graph is shown in Figure 10, Plate IV, and a curve computed to fit the points, whose formula is given in the figure. The writer wishes to emphasize the point that the selection of that particular formula was the result of more or less guesswork, altho the constants are computed by least square methods, and are accurate for that type of curve. It is possible that future work will show that some other form of exponential curve will express the moisture relations of the army worm more accurately. However, the curve is semi-logarithmic, and a plot of the points on semi-log paper shows them to fall in the neighborhood of a straight line, which justifies the assumption of that type of formula.

To summarize the results of the analysis of the meteorological relations of *Cirphis unipuncta,* we may state the following conclusions:

1. The army worm evidently has a definite optimum moisture requirement, as shown by the various correlations, which can be expressed in terms of temperature and precipitation by the logarithmic formula

$$\log Y = 9.85188 - 10 + .00999 X$$

in which X represents temperature and Y precipitation. Substitution of given values of X in the equation give the corresponding log Y, from which Y may be found. This equation represents the general optimum condition, and any place whose annual conditions approach this curve lies within the normal range of the species, and is liable to infestation whenever the particular requirements outlined below are satisfied.

2. In Minnesota, where hibernation takes place in the larval stage, the sum of temperatures during September, October, and November must approach 3 x 46.92° F.

In addition, the temperature for the two months of December and January taken together must bear the relation to that of October expressed by the equation

$$\text{Dec. temp.} + \text{Jan. temp.} = 3.35 \text{ Oct. temp.} - 120.4^\circ$$

which equation is derived from the correlation in Figure 9, Plate III. The above are the most important particular requirements which must be fulfilled in Minnesota before an army worm outbreak occurs. There are probably other minor conditions which combine with these, but which are not so vital. The relation between temperature and precipitation must, at least in September, October, November, and May, approach the general condition outlined above.

METEOROLOGICAL RELATIONS OF LYCOPHOTIA MARGARITOSA

Unfortunately for this study, the only outbreak of this species in Minnesota concerning which we have definite information available was in 1919, in association with *C. unipuncta,* as was mentioned above. With only this single outbreak as a basis, it seemed futile to attempt much statistical work, as the results obtained would be of but slight value. However, a comparative study of the weather data for this outbreak and that for the other four army worm outbreaks should yield some evidence as to the points of difference which made possible the extreme abundance of *L. margaritosa.* Accordingly, the stations listed for 1919 were separated from the rest of the data, and their means computed. These figures, together with those for the Pale Western cutworm, will be found in Table XI.

These means were then plotted in a manner similar to that used with the mean figures for the army worm outbreaks, and a similar exponential curve plotted to fit them, whose equation is

$$\text{Log } Y = 0.03695 + .00845\ X \quad \text{(Plate IV, Fig. 11)}$$

This curve differs chiefly from the army worm curve in the size of the constant term, indicating a larger basic amount of rainfall, and showing that the Variegated cutworm prefers conditions more moist than the army worm.

Knowing from laboratory experiments that the optimum moisture condition for this species is about 60 per cent of total water capacity, we can conclude that this curve represents an approximation to this condition, and hence that the army worm curve, which represents a slightly lesser amount of precipitation for any given temperature, indicates the optimum for that species to be slightly lower, probably in the neighborhood of 45 to 50 per cent of total capacity. The writer has been unable as yet to confirm this fact experimentally, and it would be a matter of considerable interest and value to do so.

Because the data are so meager, it is impossible to draw any conclusions with regard to any necessary succession of seasonal conditions, as was done in the case of the army worm, so this part of the study is incomplete.

METEOROLOGICAL RELATIONS OF POROSAGROTIS ORTHOGONIA

The two species whose climatic relations we have been considering are both normal inhabitants of the humid region of Minnesota, and their moisture requirements are those natural to species of this region. We will now consider these relations of *Porosagrotis orthogonia,* a species whose habitat is a region with a normal rainfall of about fourteen inches per annum, as compared to twenty-eight in Minnesota. It is apparent that the moisture requirement of such a species must be very much lower than those of the former two species, but it is not at once apparent just how much lower it should be.

The Pale Western cutworm is a species which has very recently become of great importance in many parts of Montana. It was first noted in large numbers in 1915, and has since been rapidly increasing. For a sketch of its distributional history, the reader is referred to Parker, Strand, and Seamans ('21). The chief point of interest in connection with its rapid increase is the fact that the last five years (1917-21) have been a period of almost unprecedented drouth over the infested regions, which has evidently been an important factor in the ecology of the species. From distributional data on file at the Entomology Department, Montana State College, maps were constructed as in the case of the army worm, and United States Weather Bureau stations were selected as representative of conditions in the infested regions. As this study is still in the early stages, the distribution and list of stations will not be published.

Two points noted at the beginning of the study are of interest, and will be mentioned. First, a very superficial study of these distributional maps in connection with maps showing the annual distribution of precipitation for the period made it very evident that the greatest amount of damage in any year fell within the area of the state receiving less than twelve inches of rainfall. This shows beyond a doubt the semi-arid character of the optimum condition. Second, a plotting of the monthly means for a period of about a year preceding outbreaks, obtained in each case by the averaging of about forty points, gave the distribution curve shown in Figure 12, Plate IV. Computing the constants for this curve by the method of least squares gave the equation for this species as

$$\text{Log } Y = 9.48837 - 10 + .01158 X$$

Thus this curve, of a similar formula to the other two, varies in the size of the constant term, and also in the greater value of the X term, indicating a greater curvature than in the other cases. An inspection of this curve as plotted shows the much smaller amounts of rainfall necessary to produce the optimum for this species.

Another relation, on which very little work has been done other than a preliminary examination of the data, is the relation to winter conditions. Such an examination showed that winter conditions in years and places preceding outbreaks were warmer than normal, and drier than normal. Thus, this species, like the army worm, can withstand a considerable amount of freezing and thawing better than steady cold weather with a heavy snow blanket.

COMPARATIVE CLIMATOLOGY

Now that the general climatic relations of these three species have been outlined, it is of interest to compare these conditions with each other and with other places, to show the significance of these relations in the consideration of general distribution. Table XI gives the comparative conditions in the months preceding outbreaks of the three species studied.

TABLE XI

COMPARATIVE CLIMATOLOGY

Month preceding Outbreak	*Porosagrotis orthogonia*		*Cirphis unipuncta*		*Lycophotia margaritosa*	
	Temp.	Precip.	Temp.	Precip.	Temp.	Precip.
	Degrees	Inches	Degrees	Inches	Degrees	Inches
August	66.5	1.2	......	......	......	......
September	53.7	1.1	59.4	2.2	55.3	1.6
October	41.4	1.1	47.0	1.8	51.0	2.5
November	28.6	0.6	34.1	2.6	36.9	3.2
December	18.7	0.6	20.1	1.1	27.7	1.6
January	21.1	0.5	17.6	0.7	23.2	0.5
February	22.1	0.5	15.8	1.2	17.5	2.3
March	27.0	0.5	33.0	1.1	31.7	1.2
April	41.4	1.2	46.8	3.1	45.4	3.8
May	52.7	1.7	56.6	2.6	56.9	2.0
June	59.4	2.0	68.3	5.5	69.6	6.9
July	....	....	72.3	3.5	74.3	4.6
Total precipitation	....	10.8	....	25.4	....	30.2

This table shows conclusively the wide variation in the moisture requirements of the three species, a fact which is shown graphically in Figure 13, Plate IV, on which all three of the curves are drawn in their relations to each other.

If these lines really represent the moisture requirements of these species, any location in which one of them is normally found should approach the moisture conditions indicated by the particular line. In order to test this out, three points were chosen, one of which is within range of the Pale Western cutworm, one in the range of the army worm, and presumably, of the Variegated cutworm, and one of which is outside of the range of the army worm, but possibly, under exceptional conditions in the range of the Variegated cutworm. The three points chosen were Glasgow, Mont.; Ithaca, N. Y.; and Jacksonville, Fla. The data for their mean monthly temperatures and precipitations were obtained from Henry ('06), and plotted on Figure 13 in their proper relation to the three curves. The lines drawn connecting the outside points of each station are of no especial significance, but are merely introduced to bring out the general conditions at each point more clearly. In the cases of Glasgow and Ithaca, the points are in very close relation to the respective cutworm curves, showing that they normally approach the necessary moisture condition. The condition at Ithaca is of special interest when considered in connection with the theory of Fitch ('60) which was evolved from a study of New York conditions. Ithaca is normally slightly to the "wet" side of the army worm curve, which accounts for the occurrence of army worms there following dry seasons, as Fitch has indicated.

Jacksonville is not only at a considerable distance from either of the curves for army worm and Variegated cutworm, but the major axis of the polygon lies at a considerable angle to these curves. Thus it would not only take a wide variation in conditions to bring about an army worm outbreak there, but this variation would have to be such as would twist the axis of the distribution through a considerable angle, a condition which practically excludes the possibility of extensive outbreaks in that region.

It is hardly conceivable that either of the last two places would ever become dry enough to be infested by the Pale Western cutworm, or that Glasgow would ever be wet enough to be infested by the army worm.

CONCLUSIONS

We may summarize the results of the studies on the relations of meteorological conditions to outbreaks of these three Noctuid species in the following statements.

1. Each of these species has a definite optimum and limiting soil moisture requirement, which has been ascertained directly by laboratory experiments in the case of *Lycophotia margaritosa,* and indirectly, by a study of conditions surrounding outbreaks in the case of the other two species. This moisture requirement is capable of mathematical expression in the form of an equation similar to that expressing the relation of vapor pressure of water to temperature, giving directly the optimum condition in terms of temperature and precipitation during the growth period of the species. These three equations fitted to the data for the three species are:

A. Pale Western cutworm.... $\text{Log } Y = 9.48837 - 10 + .01158\,X$
B. Army worm.............. $\text{Log } Y = 9.85188 - 10 + .00999\,X$
C. Variegated cutworm....... $\text{Log } Y = 0.03695 + .00845\,X$

2. These soil moisture curves may be used to indicate the distribution of each species by plotting the mean data for any station on the same graph and comparing their location with the curve.

3. In addition to these general moisture requirements, there are certain sequences of climatic conditions necessary for the production of the species in large numbers, which must be fulfilled in any season before an outbreak can occur. The temperature relations of *C. unipuncta* during the fall and winter months are an example of such a condition.

4. Of these conditions, those surrounding hibernation seem to be of the greatest importance, and an outbreak seems to be directly related to the percentage of the larvae that survive the winter successfully.

METEOROLOGICAL RELATIONS OF THE ADULT MOTHS

As was already stated, the data relating to the effects of weather conditions on moth flight were secured at St. Paul, Minn., in 1920, and at Havre, Mont., in 1921. The Minnesota data were published in a former paper (Cook '21) together with a part of the present statistical treatment, and these basic data will not be repeated here.

Bait traps were run at Havre between August 1 and September 8, when a cold wave and considerable snowfall practically put an end to moth flight. The traps used were large glazed earthenware receptacles holding about five gallons each. Eleven of these were used during the height of the flight season on two fields, being placed about three hundred feet apart and about three feet above the ground. The bait used was a 10 per cent solution (by volume) of crude beet molasses, obtained from the Great Western Sugar Co., at Billings, Mont. Because of the high evaporation it was found necessary to renew the solution about twice a week.

A record was kept of the numbers caught of each of the more abundant species per night, and a comparative count of the males and females of *Porosagrotis orthogonia,* which was the species on which the most accurate data were desired. As the catches for a few nights at the height of the flight period were too large to be counted by one individual, the entire catch was preserved for each night by drying, and later counted by the following method of sampling. The entire night's catch was placed in a conical pile on a flat surface, and separated by planes through the apex into a series of radiating piles, each of which represented a definite fraction of the catch (one-fourth or one-eighth, depending on the size of the total catch). One of these piles was then carefully examined and sorted, and the rest of the catch merely counted, the total for each species being assigned pro rata from the proportion found in the examination of the fraction. This method was found to give results of relatively high accuracy.

Table XII gives the total figures for the more abundant Noctuids, obtained as described above.

TABLE XII

MOTH FLIGHT AT HAVRE, MONT.
AUGUST 1 TO SEPTEMBER 8, 1921

Species		No. of specimens	Per cent of total catch
Porosagrotis orthogonia	Males	6,450	10.8
	Females	14,614	24.5
Euxoa pallipennis		28,309	47.2
Euxoa quadridentata *		2,826	4.7
Sidemia devastator		2,537	4.3
Caradrina extima		681	1.1
Other species		4,640	7.4
Total		60,057	100.0

*Included in this record are E. quadridentata, E. dargo, E. ridingsiana, and several other closely related species.

Included among the "other species" were *Chorizagrotis auxiliaris, Feltia ducens, Porosagrotis catenula,* and about twenty-five other species, mostly of the genus Euxoa, as well as considerable unidentifiable material. None of these species was present in more than one per cent of the total.

The noteworthy feature of the catch was the great and increasing abundance of *Euxoa pallipennis,* a species formerly very rare, but at present the most common single species. So far as is known, the species is not injurious to crops, but the larva has not been positively identified.

Records of temperature and humidity were available at the experiment station from instruments exposed to field conditions within half a mile of the traps. Pressure observations taken at 6:00 p. m. were obtained from Mr. C. M. Ling, United States Meteorologist at Havre, about seven and one-half miles distant. As pressure varies rather slowly, these readings gave a good index to conditions at the station. The data for catches, temperature, humidity, pressure, and precipitation, together with the five-day sliding average for each, computed as in the former page, are given in Table XIII. The normals, which were not computed for the weather factors in the Minnesota data as published, were also computed for these factors, but the figures are not included. Plate V is a graphical representation of Table XIII. For each factor are shown a straight line representing the seasonal mean, an angular graph showing the daily variations in the factor, and a smoother curve closely approximating the five-day normals.

TABLE XIII
Moth Flight at Havre, Mont., and Meteorological Data

Date	No. of traps	Total	Moth catches			7 p. m. temperature			7 p. m. humidity			6 p. m. pressure			Precip-itation
			Per trap	5-Day normal	Per cent normal	Daily	5-Day normal	Dept. from normal	Daily	5-day normal	Dept. from normal	Daily	5-day normal	Dept. from normal	
(1)	(2)	(3)	(4)	(5)	(6)	(7) Degrees	(8) Degrees	(9) Degrees	(10)	(11)	(12)	(13)	(14)	(15)	(16) Inches
Aug. 1	1	44	44.0	....	....	75	....	....	42	....	....	27.421	....	....	
2	3	38	12.6	....	....	82	....	....	30	....	....	27.271	....	....	
3	3	43	14.3	16.0	89.6	83	74	9	43	39	4	27.211	27.367	−.156	
4	4	19	4.7	8.6	54.6	64	74	−10	41	35	6	27.409	27.372	.037	*
5	4	18	4.5	7.5	60.0	65	73	−8	38	34	4	27.524	27.372	.152	
6	4	29	7.2	7.1	101.3	73	74	−1	25	30	−5	27.443	27.361	.082	
7	4	28	7.0	11.2	62.5	83	76	7	21	29	−8	27.275	27.334	−.059	
8	4	49	12.2	20.7	58.9	84	77	7	24	29	−5	27.153	27.316	−.163	
9	4	101	25.2	22.6	111.4	78	78	0	38	32	6	27.274	27.317	−.043	
10	4	208	52.0	22.1	235.4	71	75	−4	39	40	−1	27.433	27.381	.052	
11	4	68	17.0	20.4	83.4	75	73	2	39	43	−4	27.451	27.462	−.011	
12	4	15	3.7	16.5	22.4	66	74	−8	59	43	16	27.596	27.458	.138	
13	4	17	4.2	6.3	66.7	76	74	2	40	46	−6	27.557	27.382	.175	
14	4	23	5.7	6.9	82.6	81	73	8	37	49	−12	27.251	27.350	−.099	
15	4	5	1.2	7.9	15.2	71	74	−3	54	50	4	27.053	27.257	.204	0.42
16	4	80	20.0	8.5	235.4	70	71	−1	57	59	−2	27.292	27.209	.083	
17	3	26	8.6	13.0	66.1	73	68	5	61	60	1	27.132	27.264	−.132	0.08
18	3	21	7.0	17.5	40.0	59	69	−10	84	57	27	27.316	27.313	.003	0.03
19	3	85	28.3	18.1	156.2	68	70	−2	44	50	−6	27.525	27.298	.227	
20	3	71	23.6	34.0	69.5	75	69	6	39	44	−5	27.299	27.343	−.044	
21	3	69	23.0	49.2	46.8	74	73	1	23	33	−10	27.219	27.319	−.100	
22	2	177	88.5	60.3	146.9	70	75	−5	28	29	−1	27.358	27.259	.099	
23	4	329	82.2	81.6	100.6	77	75	2	31	27	4	27.192	27.271	−.079	
24	7	590	84.3	149.1	56.5	80	75	5	26	28	−2	27.226	27.299	−.073	
25	12	1,558	129.8	246.5	52.6	72	76	−4	27	30	−3	27.360	27.287	.073	
26	12	4,340	361.2	354.9	101.8	76	77	−1	30	27	3	27.358	27.298	.060	
27	12	6,885	574.1	490.8	116.8	77	76	1	37	28	9	27.299	27.312	−.013	
28	12	7,496	624.3	625.0	99.9	81	79	2	14	25	−11	27.248	27.248	.000	
29	12	9,198	766.0	658.3	116.2	76	80	−4	30	23	7	27.296	27.165	.131	
30	11	8,509	794.9	594.0	134.0	83	78	5	16	20	−4	27.040	27.146	−.106	
31	11	5,830	529.8	579.9	91.4	81	76	5	16	23	−7	26.942	27.119	−.277	
Sept. 1	11	2,775	252.1	427.0	59.1	68	73	−5	23	24	−1	27.206	27.112	.094	
2	11	6,136	557.0	269.1	207.1	73	68	5	31	27	4	27.109	27.163	−.054	
3	4	9	2.2	177.5	1.2	58	64	−6	35	32	3	27.265	27.247	.018	0.04
4	11	53	4.8	174.1	2.7	60	63	−3	41	35	6	27.293	27.264	.029	
5	11	778	70.7	94.5	74.9	63	62	1	32	35	−3	27.360	27.282	.078	
6	11	2,606	236.8	93.9	252.1	62	60	2	35	43	−8	27.293	27.279	.014	
7	11	1,731	157.2	92.9	169.4	68	55	13	33	55	−22	27.200	27.285	−.085	
8	11	0	0.0	....	....	48	....	....	74	....	....	27.250	....	....	0.04
9	11	0	0.0	....	....	32	....	....	100	....	....	27.323	....	....	0.86

* Trace

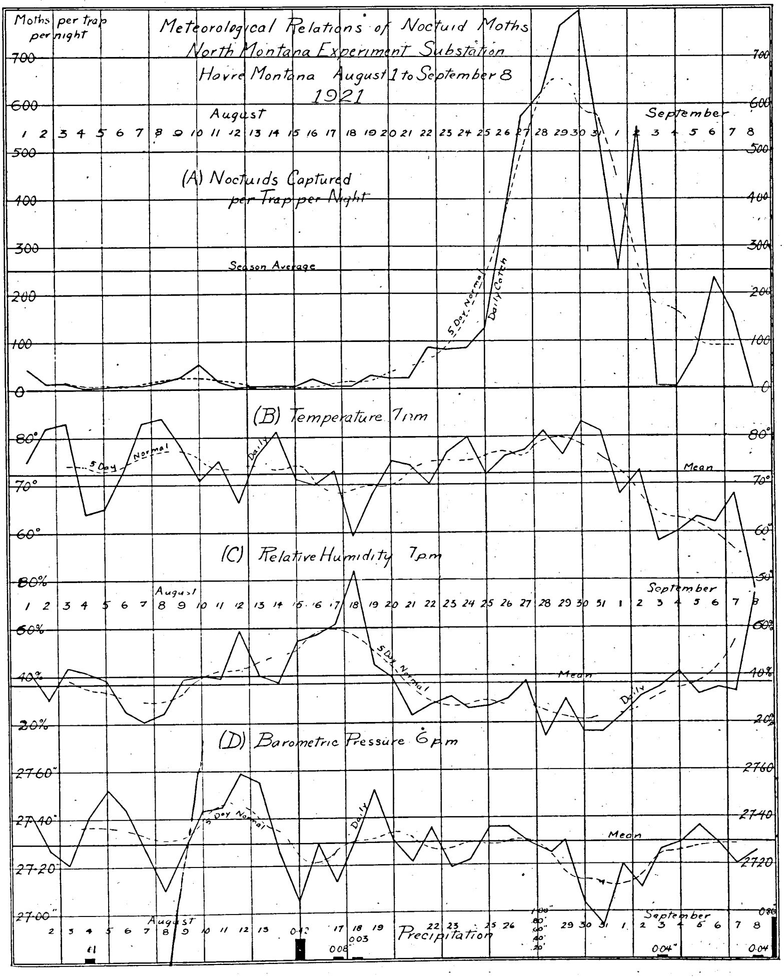

Plate V. Meteorological Relations of Adult Moths

Figure 14.

(a) Number of Noctuids caught per trap per night at Havre, Mont., from August 1 to September 8, 1921.

(b) Temperature at 7 p. m.

(c) Relative humidity at 7 p. m.

(d) Barometric pressure at the United States Weather Bureau Station at Havre, taken at 6 p. m.

METHODS OF STATISTICAL ANALYSIS

In the first place, the object in computing the five-day normal catch was to reduce the figures for the catch from the widely varying daily figures to a common denominator, a percentage, or index number. Then similar normals were computed for the other factors for the sake of uniformity in treatment as well as for the elimination of any long-period trends. (Yule, '19, p. 200). Having these three figures for each factor, we have at our disposal three different methods of statistical treatment, which will bring out the facts from three entirely different angles. For example, a study of the relations between the index catch and the observed values of weather factors will show which particular values of those factors, if any, are most favorable to moth flight. Then, a further study of the relation between the variations in these factors and the variations in the catch will bring out any relationship between a change in any factor and the catch. Finally, a study of the relation between the departure of the normal catch from the season average and the departures of the weather factor normals from their season averages, will show the relationship, if any, which exists between the emergence of the various species and the condition of the weather during the period of emergence. All three of these methods of analysis have been applied to both sets of data, and partial correlations worked out between the catch factor and the various weather factors. These coefficients, obtained in the manner explained in the previous paper, are all given in Table XIV, on the opposite page. The coefficients are divided into three groups, indicated by the designations A, B, and C, corresponding to the three methods of analysis outlined above.

The coefficients of group A, which are the ones published for the Minnesota data in the previous paper, are intended as a measure of the relationship between the index catch and the observed values of the weather factors. It was found necessary to divide the Minnesota data on the basis of humidity, the dividing lines being below 54 per cent and above 50 per cent respectively. The same process was necessary in treating the Montana data, except that the dividing line in this case was drawn below 40 per cent and above 30 per cent. Humidity is the most significant factor in this group, and the largest index catches were secured in times when this factor was near the mean for the season. In other words, the moths flew best in times when humidity was about average for the season. None of the coefficients is large, and the Montana figures would be of little value except that they show the same tendency as the Minnesota figures.

TABLE XIV

Correlations of Moth Flight with Meteorological Factors

Group A—Index Catch and Observed Values
(Columns 6, 7, 10, 13, TABLE XIII)

Humidity below optimum					Humidity above optimum			
Minnesota (54%)		Montana (40%)			Minnesota (50%)		Montana (30%)	
Total	Partial	Total	Partial	Factors correlated	Total	Partial	Total	Partial
+.34	+.28 ±.089	−.11	−.07 ±.130	Catch-Temperature	+.19	+.02 ±.102	+.17	+.10 ±.140
+.37	+.31 ±.087	+.20	+.24 ±.130	Catch-Humidity	−.46	−.35 ±.089	−.27	−.24 ±.130
−.17	−.07 ±.096	−.02	−.18 ±.130	Catch-Pressure	+.18	+.09 ±.101	+.03	−.04 ±.140
+.25		−.45		Temperature-Humidity	−.47		−.25	
−.45		−.46		Temperature-Pressure	−.40		−.22	
−.32		+.57		Humidity-Pressure	−.20		+.03	
Rc. thp	+.45 ±.07	Rc. thp	+.26 ±.12	Multiple correlation	Rc. thp	+.47 ±.08	Rc. thp.	+.30 ±.13

Group B—Index catch with

Group C—Normal catch with

Departures from normals (Columns 6, 9, 12, 15, TABLE XIII)					Normal climatic factors (Columns 5, 8, 11, 14, TABLE XIII)			
Minnesota		Montana			Minnesota		Montana	
Total	Partial	Total	Partial	Factors correlated	Total	Partial	Total	Partial
+.23	+.30 ±.06	+.26	+.31 ±.10	Catch-Temperature	+.20	+.16 ±.07	+.30	+.02 ±.11
−.32	−.14 ±.07	−.32	−.07 ±.11	Catch-Humidity	+.42	+.34 ±.06	−.80	−.77 ±.04
+.18	+.24 ±.07	+.22	+.39 ±.09	Catch-Pressure	−.37	−.16 ±.07	−.68	−.74 ±.05
−.13		−.66		Temperature-Humidity	−.05		−.50	
−.42		−.61		Temperature-Pressure	−.35		−.03	
−.42		+.20		Humidity-Pressure	−.41		+.34	
Rc. thp.	+.44 ±.05	Rc. thp.	+.44 ±.09	Multiple correlation	Rc. thp.	+.48 ±.06	Rc. thp.	+.92 ±.02

Considering the coefficients of Group B, we have a much different condition. In this set of correlations, the effects of variations in the factors were studied, and variations in humidity have the smallest effect of any factor studied. Temperature and pressure both have significant positive correlations, which may be interpreted as follows: When the temperature and pressure are higher, and the humidity lower, on any particular night than the averages of these factors for the five nights of which this one is the center, then the catch is also higher than the average for these five nights. That is, moths fly more freely on warm, dry nights, following cooler, damper nights than when the reverse is true.

It is in group C that the largest values are found for the correlation coefficients. As the figures correlated are averages for five-day periods, the relations must be considered as being relations of the weather factors to emergence. Thus, under Minnesota conditions, more moths emerge in a time of higher temperature and lower pressure and higher humidity than the season average, the humidity being the most important factor, followed by temperature and pressure. In the Montana data temperature was of practically no significance, but there was a very high relationship between emergence and the other two factors, with humidity slightly more important. Evidently, more moths emerge in times of high humidity in humid regions, and more moths emerge in times of low humidity in arid regions. The size of the coefficient of multiple correlation in the latter case, "R"=+.92, indicates that the emergence of moths in the arid regions is almost entirely a function of these climatic conditions.

To summarize these relations; the observed values of humidity have an important bearing on the flight of moths, the largest numbers flying when the humidity is near the seasonal mean. Humidity also affects emergence, more emerging under high humidity conditions in Minnesota and under low humidity conditions in Montana. Variations in temperature and pressure from night to night are of more importance than variations in humidity. Further studies, and the accumulation of more data may affect these relationships, but probably will only intensify them.

CONCLUSIONS

A general consideration of the studies presented in this paper leads to the following conclusions:

1. Each of the species included in this study has a very definite optimum soil moisture requirement, which, broadly speaking, limits the distribution of the species.

2. This requirement may be determined experimentally under controlled conditions, and also indirectly, by a statistical analysis of the weather conditions surrounding outbreaks of that species.

3. In each case, the optimum moisture requirement of the species which occur in any given region is a close approach to the normal climatic condition in that region, so that outbreaks would occur every season were it not that there is also a necessary seasonal sequence of conditions which must be fulfilled in order to enable the insect to reach destructive abundance.

4. This sequence, which may operate either by favoring the destructive insect, by limiting the activities of its enemies, or both, is the controlling factor in the production of outbreaks, and a careful study of such a sequence in the life history of any insect should enable us to predict the possibility of an outbreak of that insect in any given region.

In conclusion, the writer wishes to emphasize the importance of the use of mathematical methods in the study of insect outbreaks, as well as to show its practical application in the examples cited. As the literature of statistics is rather foreign to entomological workers, a few selected titles of especially valuable works, which are of great service in such a study, are listed in the bibliography.

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The Normal and Pathological Histology of the Ventriculus of the Honey Bee, with Special Reference to Infection with Nosema apis

By Marshall Hertig
Division of Entomology and Economic Zoology

UNIVERSITY FARM, ST. PAUL