THESIS PRESENTED for the DEGREE of

DOCTOR of PHILOSOPHY

in the

UNIVERSITY of EDINBURGH

by

D. STEWART MacLAGAN, D.Sc.(Edin.), F.R.E.S.

'THE QUANTITATIVE ANALYSIS of CLIMATE in RELATION to INSECT ABUNDANCE.'

CONTENTS of PART I.

PART I.

'Nature must be considered as a whole if she is to be understood in detail.'

- Bunge.

I. GENERAL INTRODUCTION.

Within the last ten years a number of related sciences, particularly geography, soil science and plant ecology, have undergone remarkable developments. Although working, for the most part, in ignorance of each other's discoveries, the researchers in these fields have now realised that the soils, the vegetational, and faunal associations of a natural environment are causally related, directly, and indirectly, through climate. The scientists engaged in these researches recognise that some of the outstanding developments in their respective fields of study have resulted from a consideration of climate on a quantitative basis.

It is a fundamental concept of plant ecology that every distinct climate produces a characteristic plant association. "These units are termed climaxes or formations; they are the product of climate, and, hence, are controlled by it. Each formation is the highest type of vegetation possible under its particular climate."[1] The natural classification of soils propounded by the Russians, especially Glinka and his colleagues, has forced pedologists to conclude that "climatic forces are the predominant soil-forming agencies/

agencies of the world."[2] Koppen[3] was the first to attempt a classification of world-climates, based on the quantitative analysis of meteorological data. He realised that the critical factors affecting the distribution of the various climax plant-formations were climatic, and he tried to discover the minimum or maximum values of mean monthly precipitation and temperature which might delimit the various vegetation-types.

Considerable advances on this pioneer work have been made recently by an American, Thornthwaite[4], who utilises two new climatic concepts, namely, temperature efficiency and precipitation effectiveness, in his classification of the climates of the earth. The feature of Thornthwaite's classification which is of particular interest, ecologically, is his adducement of empirical climatic values which delimit the more important types of vegetation and soil; and thus, aptly demonstrating the intimate relationship of natural complexes. In view of these advances in what are, fundamentally, ecological studies, one may well ask what contribution has been made by animal ecologists working on parallel investigations.

II. BIO-CLIMATIC INVESTIGATIONS.

Regarding the physiological effects of temperature and humidity on the various vital processes of animals, a mass of data have been obtained, and would appear to be accumulating/

accumulating at an ever-increasing rate, but there is a lack of coordinating principles and effort to synthesise the results. When one considers the effects of physical factors, in general, on the distribution and abundance of animals in Nature, one realises how limited the knowledge of this subject really is. The earliest attempt to make a systematic study of the distribution of animals is represented by the classical work of Wallace[5] (1876), but the criteria of his faunal areas are phylogenetic rather than ecological. Towards the close of last century, Merriam[6] (1898) published his work on the 'life-zones' of North America—the first comprehensive effort to formulate a general principle governing the rôle of climatic factors in the distribution of animals. This work has found considerable acceptance in America, especially among ornithologists, but the author did not follow up his work in an attempt to analyse the real causes for the delimitation of the life-zones. Moreover, Sanderson[7] showed that the northward distribution of some species was not limited by the sum of effective temperatures (as maintained by Merriam) but by the minimum winter temperature. Hopkins[8] (1918), after many years of observation, formulated an empirical bioclimatic law, which states that, "in general, the variation in the time of occurrence of a given periodic event in life activity, in temperate North America, is at the general rate of 4 days to each degree of latitude/

latitude, 5 degrees of longitude, and 400 feet of altitude; later northward, eastward, and upward in spring and the reverse in autumn." The basis of the law is apparently the gradual change from marine to continental climate as one proceeds from east to west. Hopkins' bioclimatic law has been put to practical use in the computation of 'fly-free dates' for sowing wheat so as to escape the depredations of the Hessian fly. Olbricht[9] (1923) has examined the effects of climate in relation to the general distribution of animals, and describes an 'ophelothermal' region of the northern hemisphere, which, in virtue of its climatic energy, has produced the greatest development of higher organisms.

Apart from the general problem of climatic effects upon the general distribution of animals, numerous attempts have been made to correlate 'plagues' of specific animals with certain climatic conditions, and much work of this kind has been undertaken by economic entomologists. The literature on the subject has been ably reviewed by Uvarov[10] (1931) so that only a brief review of the earliest surmises and the outstanding contributions to the problem, will be mentioned; and in addition, only in so far as climate affects insects - the subject of this study. For centuries the belief was that the sun engendered insect-life; and Hamlet exclaims, "For if the sun breed maggots in a dead dog/

dog, being a god, kissing carrion," etc. Duncan,[11] writing in 1836, says, "The sudden increase and diminution of many of the lower animals, particularly insects, is one of the most perplexing considerations that attach to natural history." Several years later, Westwood[12] (1852) comments on the problem as follows. "The periodical development of vast numbers of individuals of certain species of obnoxious insects is one of those phenomena of the science of entomology which require more attention than has yet been bestowed upon them .... and if we regard the peculiarities of the atmospherical changes as mainly influencing their development, we shall not be far from correct." This shows that even in the developmental stages of their science, entomologists realised the importance of climatic factors in relation to insect-outbreaks. With the great development of systematic and morphological studies during the latter half of the nineteenth century the early natural history view-point lapsed, temporarily, but has returned with renewed vitality, largely on account of the unprecedented advance of economic entomology, and the attempts of workers in that field to seek a scientific explanation of insect-outbreaks, based on the quantitative analysis of the whole environmental complex. The following are only a few of the noteworthy contributions to this subject.

III./

III. CLIMATIC LIMITATIONS to INSECT-OUTBREAKS.

Certain moths, which copulate only during flight, are dependent upon a particular combination of light-intensity and temperature for the accomplishment of this process, which may thus become of supreme significance in the natural control of the species. Partial darkness and a temperature above 16.5°C. are necessary for copulation and oviposition of the Codling moth (Isely and Ackerman,[13] 1923). The chief factor influencing outbreaks of the Angoumois grain moth in the vicinity of Philadelphia is a favourable temperature from June to October (Simmons and Ellington,[14] 1925). High precipitation during the flight-period of the adults checks the activities of bark-beetles, lowers their reproductive rate, and drowns larvae in the excessive sap (Blackmann,[15] 1924). Kirkpatrick[16] (1923), studying the natural control of the Cotton-seed bug in Egypt, found that every stage in the life-history is profoundly affected by climatic factors, and that only 4.5-7.7% of the adults survive the quiescent season. Bodenheimer's[17] (1928) work on the Almond sawfly in Palestine shows that the mortality due to entirely climatic causes attains 96%. An intensive study of the European corn-borer has led Thompson and Parker[18] (1928) to conclude that control is effected by a complex of meteorological, parasitic, and agricultural factors, and that the greatest/

greatest mortality is due to 'intrinsic' causes affecting the larvae, which are so delicate in the early stages that they die off in immense numbers, even in the 'normal' environment; but does not this indicate a disharmony with the environment on account of unfavourable temperature-humidity conditions? Within the writer's knowledge, the best work dealing with the quantitative analysis of environmental factors is that of Cook.[19] The methods, logical procedure, and critical perceptiveness of this worker are altogether outstanding, and some of the methods utilised in the latter part of this paper resulted from the suggestiveness of Cook's work. In his studies on cutworms he found that each of three species has its own definite optimum and limiting soil-moisture requirements, which vary with the temperature; and in addition, there are certain sequences of climatic conditions which must be fulfilled in any season before an outbreak can occur. Thus, he expresses the soil-moisture requirements of the army worm, Cirphis unipuncta, in terms of precipitation and temperature, by means of the logarithmic formula - $\log Y = 9.5818 - 10 + .0099\,X$ — where X represents temperature and Y precipitation. Any place whose climatic conditions approach the curve of this equation is liable to severe infestation by the army worm, provided the following additional requirements are satisfied. The sum of the mean temperatures for September, October/

October, and November must approximate to $3 \times 46.9^{\circ}F$, and there should be a positive correlation between the temperature of October and the mean December-January temperature. MacLagan[20] (1932), from a detailed ecological study of the Collembolan, Smynthurus viridis, found that there are different optima and limiting conditions for each stage of the life-cycle. He constructed a theoretical distribution-map for the species, showing regions of the world which were climatically favourable for increase. Some of the fundamental results of this study have been confirmed recently by Hamilton[21] (1936).

A survey of the literature shows, therefore, that apart from a few broad generalisations on the relations of climate to animal-distribution and the heavy mortality in certain stages of the life-histories of insects, our knowledge of the causal relationships between climate and animal-populations is surprisingly scanty. There is no need to emphasize the difficulty of the problem, but it seems that the chief reasons for this state of affairs are - (i) an exaggerated estimation of the controlling value of natural enemies, (ii) failure to appreciate the differential effects of climate upon the various stages of an insect's life-cycle, and the handicap which this imposes upon environmental adaptation, (iii) the lack of efforts to apply available mathematical techniques to the problem of evaluating/

evaluating the rôle of climatic factors in the production of 'plague'-conditions. Hence, the following aspects of the subject will be considered forthwith -

(A) - The Seasonal Rhythm of Insect-Abundance.

(B) - The Periodicity of Insect-Outbreaks.

(C) - Graphical and Statistical Methods for Evaluating the Rôle of Climate in the Production of Epidemics of Insects.

IV. THE SEASONAL RHYTHM of INSECT-ABUNDANCE.

Our knowledge of the insect-fauna of the soil has greatly increased since the pioneer work of Cameron[22] (1913); and the contributions of Buckle[23] (1921), Morris[24] (1927), and Thompson[25] (1924) are particularly important, but there is still a lack of information concerning the relative abundance of insects throughout the year. With a view to reducing this deficiency, a census of the insect-population of grassland was undertaken. The method used was to make a definite number of strokes with a sweep-net over a particular area, taking care to execute the strokes in the same manner, and at the same time of day. A sample was taken during the first week of each calendar month, usually on the third day, but it was sometimes necessary to postpone operations for a day or two, on account of wet or windy weather. The area chosen consists of pasture which has not been disturbed by cultivation for more than five years and

is/

is only lightly grazed for a few months in late autumn. The sampling area is, therefore, an excellent approximation to a natural environment, and provides almost ideal conditions for conducting this type of investigation. As the soil is of a light, sandy nature, the grass-cover is always rather short, but there is a thick mat of clovers at the base of the coarser grasses. The figures for each month represent the results of twenty-five wide sweeps of the net, the strokes being executed slowly but firmly, with considerable downward pressure on the herbage, and an advance of one yard being made at the end of each stroke. ~~of the net~~.

An examination of the data presented in Table I reveals the extraordinarily large number, and the variety of insects, which are supported by a clover pasture. The average number per stroke per month is 10.89. A superficial examination of this particular pasture gives a poor impression of the actual density of organisms. No attempt will be made to discuss the biotic relationships of this grassland-community (interesting though they be), as it is the general effects of climate upon the seasonal trends of the population that are of primary interest, for the moment. Only the adult stages are represented by the data, with the exception of the Hemiptera and Collembola, for which the data includes the nymphs, as the habits and habitats of nymph and adult stages are fairly similar in these orders.

As/

TABLE I.

	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sep.	Oct.	Nov.	Dec.	Order
Curculionidae	1	1	2		6	78	113	43	37	28	8	3	Coleoptera
Chrysomelidae	0				4		2	7	3	4	1		
Staphylinidae					6		1		1				
Lathridiidae							7		1	2			
Nitidulidae							5	4					
Silphidae		1		3									
Elateridae					1								
Cantharidae						5							
Anthomyidae					2	5	1	2	4				Diptera
Geomyzidae		1		1			3		7	4			
Ephydridae							3	5	398	1			
Oscinidae					1	8	12	5	8	2	1		
Borboridae	1				2	1	12			3	2		
Ortalidae							22	3	2				
Cordyluridae							9						
Sepsidae							4						
Helomyzidae							8						
Phoridae							2			1			
Bibionidae					2								
Longopteridae	4	3		2	10	1	2			6	6		
Dolichopodidae								1					
Empidae							1						
Stratiomyidae							1						
Mycetophilidae						1							
Pipunculidae								1	3				
Cecidomyidae						20			6		3		
Syrphidae						1							
Apidae							7		5				Hymenoptera
Bombidae													
Proctotrypidae							1	5	1	3	1		
Cynipidae						2	4	1		2	1		
Chalcidae					2	3	29	13	65	6	2		
Braconidae					3	3	15	3	27	7	1		
Ichneumonidae					1	7	12			3			
Psyllidae							2						Hemiptera
Aphidae	1			1	3	39	36		10	6	5		
Delphacidae		6	1	9	56	2		4	3	3			
Cercopidae	3	1					5	66	23			7	
Jassidae			1	2	10	27	48	51	176	384	60	5	
Capsidae				1	1	5	84		35	8			
Reduviidae	1								16	2			
Cimicidae	1		1										
Tortricidae						2		4					
Forficulidae							3	2		1			
Collembola	7	0	0	0	127	187	124	0	183	10	149	14	
Remarks	Frost & snow lately	Severe frost lately	Abnormally cold	Warm - ground dry	Warm and sunny	Windy & wet lately	Soil drying-out	Ground very dry	Herbage parched	Nights cold	Herbage still green	Been wet and windy	

As the majority of the species are phytophagous, and many are parasitic, it might be thought that the presence of the insects is dependent upon the presence of the hosts (plant or animal) i.e. upon the food-supply. This is certainly correct, but as the host is normally present in abundance, and for a longer period than the organisms deriving support therefrom, the food-supply seldom acts in a limiting capacity to abundance. Besides, the conditions under which a phytophagous insect can multiply are usually much more restricted than those necessary for the well-being of the food-plant, so that the climatic factors are usually the ultimate determinants of the insect's abundance, provided the latter is not hampered unduly by parasites or predators.

(1) Seasonal Distribution of Families. - Regarding the seasonal appearance of the different families, ~~therefore~~, it is obvious that climatic conditions have a differential effect thereon, warm dry conditions favouring some, e.g. Jassidae, and warm moist conditions favouring others, e.g. Collembola. Again, the members of certain families appear, on the whole, to be tolerant of great cold but succumb to heat, e.g. Longopteridae and Delphacidae. On the other hand, certain multivoltine species (those with several generations in the year) of the Curculionidae and Jassidae, exhibit such a marked tolerance to diverse climatic conditions, encountered over many months, that one may justifiably/

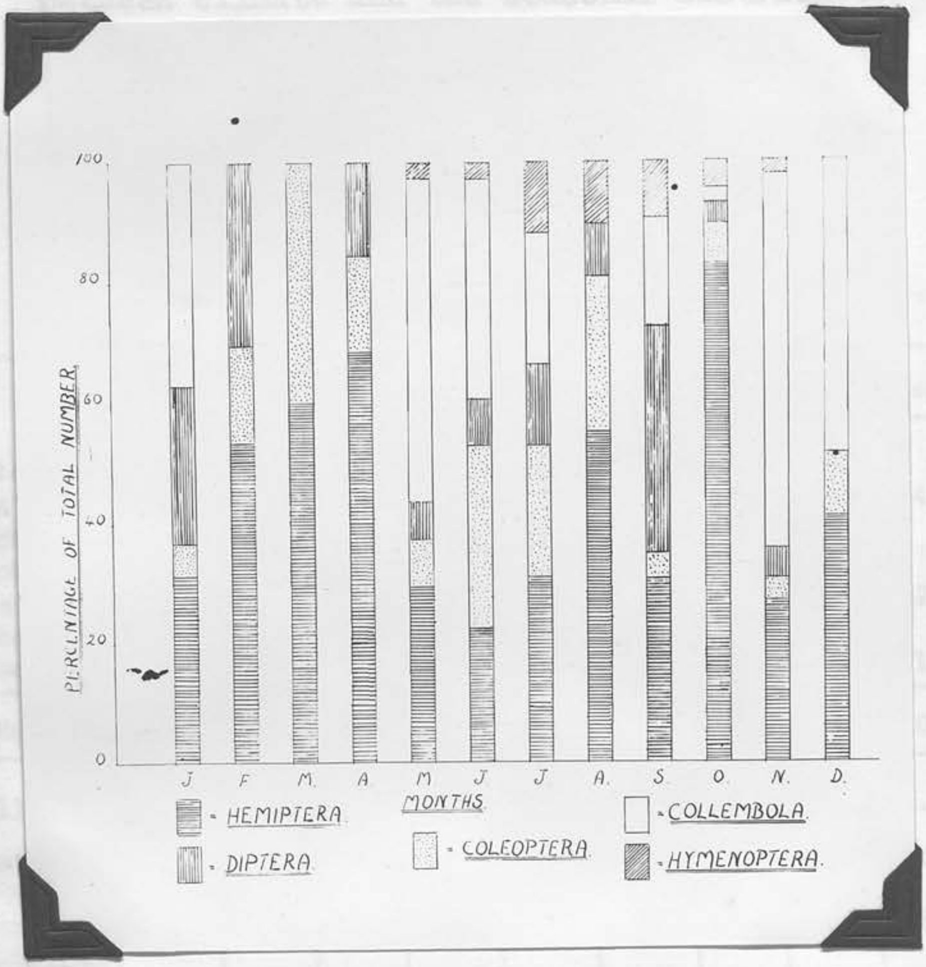


Fig. 1. - Seasonal Variation in Composition of Insect-Fauna.

justifiably postulate some physiological reorganisation or "hardening" process within the organism to bring about adaptation to a changing environment. Further than this one can hardly venture without reference to particular species, but there are some interesting general relationships between climate and the seasonal distribution of insects, as shown by totalling the numbers of individuals in the various orders. The collected totals are presented, together with relative meteorological data, in Table II.

TABLE II.

	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
Coleoptera	1	2	2	3	17	83	128	54	45	34	9	3
Diptera	5	4	0	3	17	38	80	17	428	18	12	0
Hymenoptera	0	0	0	0	6	15	69	22	98	21	5	0
Lepidoptera	0	0	0	0	0	2	0	4	0	0	0	0
Hemiptera	6	7	3	13	70	78	175	121	263	403	65	12
Dermaptera	0	0	0	0	0	0	3	2	0	1	0	0
Collembola	7	0	0	0	127	187	124	0	183	10	149	14
Total Number	19	13	5	19	237	403	579	220	1017	487	240	29
Rainfall (ins.)	.89	.54	.02	.95	2.57	0.92	1.56	1.32	0.19	4.09	6.2	5.7
Temperature (m. min.)	30.1	25.9	32.2	35.6	42.7	48.2	51.9	51.5	52.0	42.3	37.5	36.4
Soil Temp. (at 4 ins.)	33.1	33.1	44.2	48.6	59.8	65.9	70.9	68.5	68.3	52.3	44.3	40.9
Av.Rel.Hum. (at 3 p.m.)	91	88	56	56	57	63	57	55	53	71	83	83

(2)./

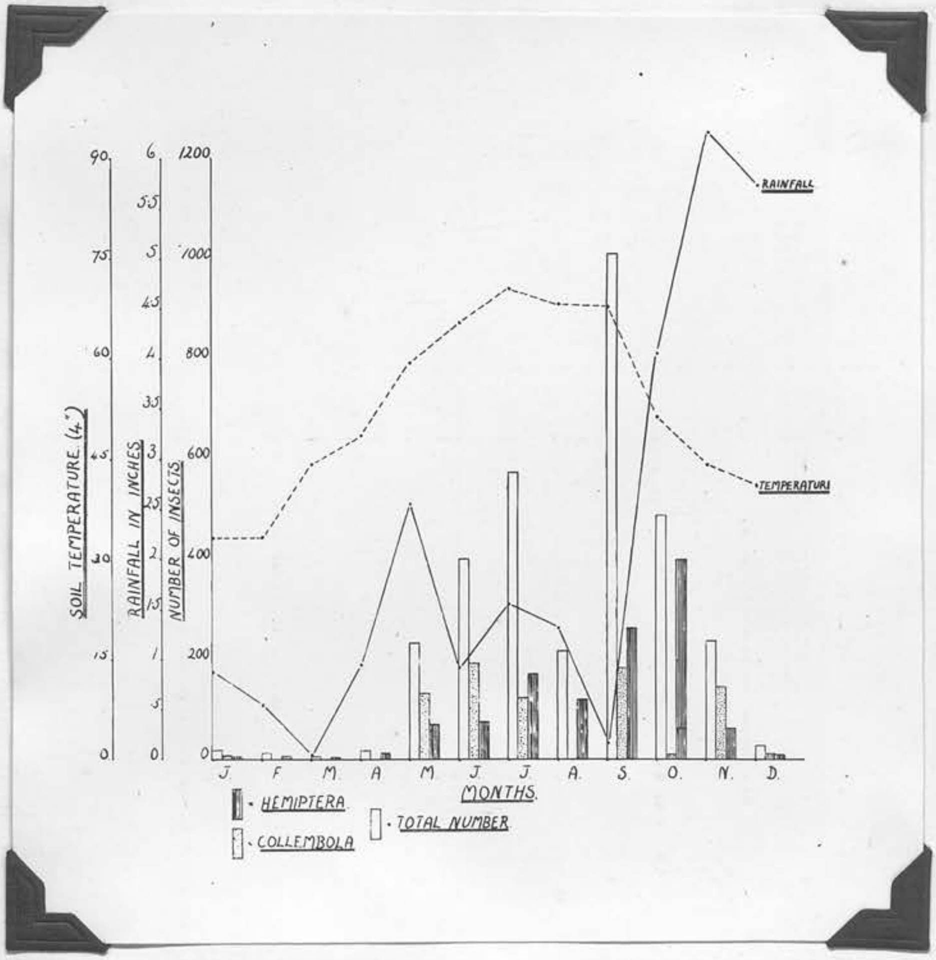


Fig. 2. - Seasonal Distribution of Total Insect-Population and Two Most Numerous Orders.

(2) Seasonal Distribution of Population. - The total number of insects taken in the collecting net at each sampling period is represented by the height of the columns in Fig. 1, and the number of insects in each order is shown as a percentage of the total for that month by dividing the columns into proportionate lengths. The most obvious features are, (i) the great dearth of insects from the beginning of December until almost the beginning of May, (ii) the comparatively slow rise in numbers throughout the summer, (iii) the rapid fall in the population during late autumn, and (iv) the 'bi-modal' nature of the population-curve. These facts are most readily explained by reference to Fig.2, where the meteorological conditions with which they appear to be closely correlated are presented graphically.

It is obvious that low temperature is the limiting factor to insect-abundance (taking the population as a whole) during the greater part of the year, the seasonal distribution of the fauna being closely correlated with the seasonal trend of temperature. Regarding the available records of the latter it is interesting to note that the best correlation is obtained with the soil-temperature at a depth of 4 ins. The high rainfall of late autumn and early winter undoubtedly contributes to the lowering of the insect-population in these months, whereas a deficiency of rainfall, associated with a high temperature, are the factors responsible/

responsible for the reduction of insects for a few weeks about the end of summer. This explains the 'bi-modal' nature of the population-curve for this particular year, but the curve is probably 'uni-modal' in Britain during all but abnormally warm, dry, summers. As the insect-population was sampled during the first week of each calendar month the numbers obtained are related to the weather conditions of the month previous to that in which the sample was taken.

(3) Factors Affecting the Trend of Population-Growth. - The seasonal trend of the population-curve is largely influenced by the combined total of the Collembola and Hemiptera, of which the Smynthuridae and Jassidae, respectively, are numerically predominant, but although their numbers be omitted from the total population, the general trend of the curve, including its 'bi-modal' character, remains unaltered. If the curves representing the numbers of Hemiptera and Collembola be plotted separately, the trend of the former follows the total population curve extremely closely, whereas the trend of the latter is very erratic, showing that Collembola, on the whole, are more susceptible to the vagaries of the weather encountered from month to month (or probably, day to day) than are Hemiptera. In this connection the different temperature-moisture requirements of the four most important orders, numerically, are shown in Fig. 3.

In/

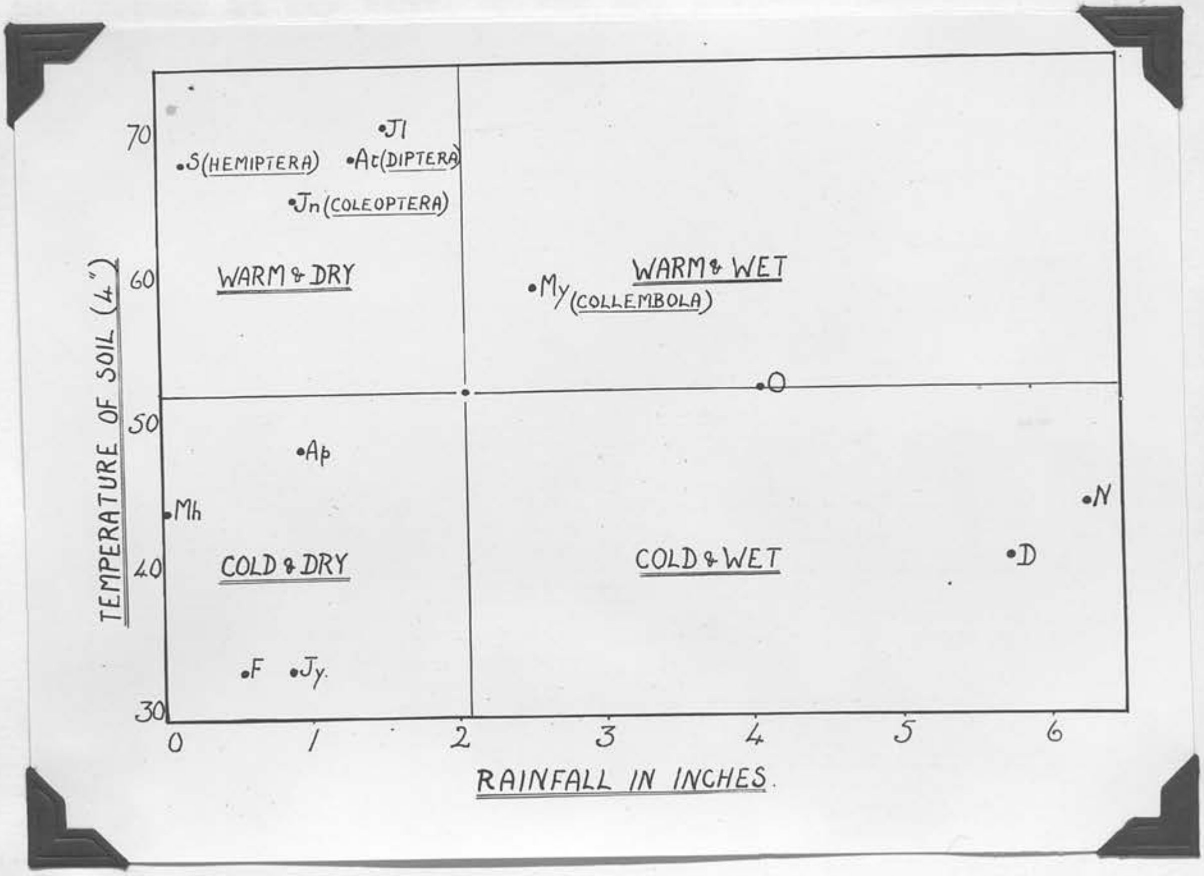


Fig. 3. - Climatic Conditions Favourable to Various Orders of Insects.

In this diagram, the central axes indicate the average monthly rainfall and mean monthly temperature of the soil at a depth of 4 ins. Therefore, the point where the axes cross represents the average temperature-moisture condition for the year, and the four quadrants show, at a glance, the nature of the combined rainfall and moisture-conditions at any time, or for any period, relative to the average condition for the year. A diagram of this kind, combining two factors, has distinct advantages over a diagram which shows only the independent movement of a single factor, since it must be apparent that although one factor may have a major rôle in the limitation of insect-abundance, the optimum conditions are provided by a particular combination of several factors in the environment. The combined movements of only the two major elements of the climatic environment are shown here, but it clearly demonstrates their important effect upon the different orders of insects.

The Collembola differ considerably from all the other orders in respect of their climatic requirements, and attain their maximum numbers in the beginning of June, consequent to the warm, moist conditions, in May. The most favourable conditions for the other orders are found in the 'warm and dry' quadrant. Coleoptera attain their maximum following the weather conditions of June, and Diptera are apparently more/

more favoured by the warmer conditions of August. July was abnormally warm, the high temperature and comparatively low rainfall resulting in a rapid drying-out of the superficial layers of the soil, with adverse effects upon many species, particularly those susceptible to desiccation. The Hemiptera provide a marked contrast to the Collembola, the numbers of the former reaching a maximum following a warm, and very dry, September. From the distribution of Hemiptera throughout the world it seems almost certain that the order, as a whole, is physiologically adapted to withstand great heat and drought in the nymphal and adult stages; and it is, therefore, particularly interesting to find that the members of the order living in the maritime climate of these islands should exhibit the same ecological characteristics, even if only in a modified form.

V. CONCLUSIONS.

Looking back over these results, the most striking conceptions derived therefrom, are the profound impress of the climatic environment upon the seasonal abundance and distribution of the insect-population as a whole, and the differential effects of climate upon the various orders, families, and even species. Hence, while one may legitimately speak, in a general way, of the climatic effects upon different systematic groups of insects, it actually/

actually means that the conditions so described represent the algebraic summation of the climate upon the species living in a particular habitat - in this instance the grass stratum of a permanent pasture. Since it is extremely unlikely that any two species have identical physiological and ecological requirements for their optimum environment, the number of surviving members of a particular taxonomic group is, in reality, an indication of the capacity of the individuals to make the most effective compromise between their conflicting demands of the environment. The fundamental reasons underlying the differential effects of climate upon the various groups, species, and even stages of the life-cycle (MacLagan, 1932) of insects, constitute a serious problem for the physiologist.

REFERENCES to LITERATURE (in Part I.)

(1). Weaver, J. E. and Clements, F. E. (1929): Plant Ecology, New York, p. 421.

(2) Shantz, H. L. and Marbut, C. F. (1923): Vegetation and Soils of Africa, Amer. Geo. Soc. Res. Ser. 13, p. 120.

(3) Koppen, W. (1923): Die Klimate der Erde, Berlin.

(4) Thornthwaite, C. W. (1931): The Climates of North America: Geo. Rev. 21. pp. 633-55.

(5) Wallace, A. R. (1876): The Geographic Distribution of Animals, London.

(6) Merriam, C. K. (1898): Life Zones and Crop Zones of the United States: U.S.Dept. Agr. Bur. Biol. Survey 10.

(7) Sanderson, E. D. (1908): Influence of Minimum Temperature in Limiting Northern Distribution of Insects: J. Econ. Ent. 1. p. 245.

(8) Hopkins, A. D. (1918): Periodic Events and Natural Law as Guides to Agricultural Research: U.S. Mon. Weath. Rev. supp. 9.

(9) Olbricht, K. (1923): Klima und Entwicklung, Jena.

(10) Uvarov, B. P. (1931): Insects and Climate: Trans. Roy. Ent. Soc. 79, pp. 1-247.

(11) Duncan, J. (1836): Account of the Turnip Saw-fly: Quar. Jour. Agric. 7.

(12) Westwood, J. O. (1852): Gardener's Chronicle, Nov. 20th.

(13) Isely, D. and Ackerman, A. (1923): Life-history of the Codling Moth in Arkansas: Bull. Ark. Agr. Exp. Stat. 189.

(14) Simmons, P. and Ellington, G. (1925): Causes of Outbreaks of the Angoumois Grain Moth: J. Econ. Ent. 18, pp. 309-20.

(15) Blackmann, M. W. (1924): Effect of Rainfall upon the Hickory Bark-beetle: Jour. Econ. Ent. 17, pp.460-70.

(16) Kirkpatrick, I. W. (1923): The Egyptian Cotton-seed Bug: Bull. Minis. Agric. Egypt. 35.

(17) Bodenheimer, F. S. (1928): Welche Iaktorm Regulieren die Individuenzahl einer Insektenart in der Naturl. Biol. Zbl. 48 pp. 714-39.

(18) Thompson, W. R. and Parker, H. L. (1928): The European Corn-Borer and its Controlling Factors in Europe: Tech. Bul. U.S. Dept. Agric. 59.

(19) Cook, W. C. (1928): Weather and Probability of Outbreaks of the Pale Western Cutworm: Mon. Weath. Rev. 56. p. 103.

(20) MacLagan, D. S. (1932): An Ecological Study of the Lucerne-Flea (S. viridis): Bull. Entom. Res. pp. 151-90.

(21) Hamilton, A. G. (1936): The Relation of Humidity and Temperature to the Development of Three Species of African Locusts: Trans. Roy. Ent. Soc. 85. pp. 1-60.

(22) Cameron, A. E. (1913): General Survey of the Insect Fauna of the Soil: Jour. Econ. Biol. 8, pp. 159-204.

(23) Buckle, P. (1921): A Preliminary Survey of the Soil Fauna of Agricultural Land: Ann. App. Biol. 8 pp. 135-45.

(24) Morris, H. M. (1927): The Insect and Other Invertebrate Fauna of Arable Land at Rothamsted: Ann. App. Biol. 14, pp. 442-64.

(25) Thompson, M. (1924): The Soil Population: Ann. App. Biol. 11, pp. 349-94.

THE PERIODICITY of INSECT-OUTBREAKS.

CONTENTS of PART II.

PART II.

'Behold, there come seven years of great plenty,
and there shall arise after them seven years
of famine' -

Genesis.

I. INTRODUCTION.

The quantitative study of animal populations - their densities, migrations, and fluctuations - is generally recognised as one of the most important branches of modern animal-ecology. Studies of this kind have shown that one of the outstanding characteristics of animal populations is their instability. For this reason, it seems customary nowadays to criticise Darwin for using the phrase 'balance of Nature', since biological associations are in a continual state of flux, and there is no balance in Nature. The writer cannot accept this interpretation of the phrase, for it seems that what Darwin really implied was not a static balance, but a dynamic equilibrium, such that animals vary in abundance in response to a continually changing environment, but ~~that~~ various factors are always at work to prevent undue oscillations of the pendulum. The object of this paper is to attempt to demonstrate that the fluctuations of insect-populations do not take place entirely at random; or in other words, there would appear to be some degree of regularity in their recurrence, when viewed over a sufficient number of years.

The/

The probable existence of some regularity in the fluctuations of animal-numbers has been a subject of study by several workers. As long ago as 1883, Swinton[1] considered the problem in relation to outbreaks of locusts, and concluded that outbreaks of the Rocky Mountain Locust (Melanoplus spretus W.) coincide with sun-spot minima. Simroth[2] (1908) suggested that the fluctuations in numbers of animals is associated with the variation in numbers of sun-spots, and that different species exhibit a differential response to the variation. Several authors published evidence in support of Simroth's contentions, but contradictory evidence was adduced by others. Recently, Gasow[3] (1925) has studied the outbreaks of Tortrix viridana L., and finds that severe outbreaks occur about every 34 years. Hewitt[4] (1921) pointed out the cyclical nature of the fluctuations in numbers of the fur-bearing animals of Canada, and Elton[5] (1924) has shown that these cycles are synchronous with those of some species in Scandinavia, a fact which naturally suggests that a general climatic pulsation, (probably associated with variation in solar radiation) is the primary cause. This survey of the pioneer work on the subject shows that the idea of a more or less rhythmical fluctuation in the numbers of animals living in a natural environment has been investigated on several occasions, but the evidence has not always been conclusive. This is not surprising in view of the difficulty of obtaining accurate/

accurate, and sufficiently detailed, records. However, evidence in support of this contention is gradually accumulating, especially in regard to wild mammals. The following surveys of severe insect-outbreaks and epidemics of diseases carried by insects, include some of the few available records which extend over a considerable number of years, and are therefore all the more valuable (indeed essential) for the establishment of a periodicity.

II. HISTORY OF SOME NOTABLE EPIDEMICS.

1. Ague. One of the earliest chronological records of an ague-epidemic is the one which raged over England during the two seasons of 1557 and 1558. There are several references to these epidemics in the works of the early chroniclers. The fever of 1558 was particularly acute, and Stow refers to it as a 'quartan ague'. The so-called 'gentle correction' of July and August, 1580, was also an aguish complaint, and not only caused considerable mortality in England, but also among the troops in Ireland.[6] The autumn of 1612 was certainly an ague-season, for when the eldest son of James I died, a letter writer of that time says "it is verily thought that the disease was no other than the ordinary ague that hath reigned and raged almost all over England since the latter end of summer."[7] In 1625 there appears to have been a fairly/

fairly widespread harvest-ague, and in 1638-39 there was "a malignant fever raging so fiercely about harvest that there appeared scarce hands enough to take in the corn."[8] Again, in 1651 there is evidence of an ague which broke out in the seaside villages of Cheshire, Lancashire, and N.Wales. Sydenham's first aguish 'constitution' commenced in 1661 and declined gradually till 1664, after which there was no recurrence until 1678.[9] This 'intermittent constitution' (as Sydenham termed a periodic outbreak of disease) was one of the most noteworthy of the malarial epidemics, lasting until 1680. Following this there is a long interval of freedom from aguish complaints until the years 1727-29. During those three unhealthy years the burials at Norwich were nearly double the registered baptisms, and Patrick Walker[10] refers to "the burning agues, fevers never before heard of in Scotland" as "evidence of God's displeasure appearing more and more against us since the incorporating union." (1707).

Agues were prevalent in Dublin in 1745, and during 1754 spring-agues were recorded as frequent in Carlow and Kilkenny.[11] From this time there appears no evidence of any malarial fever in epidemic form until the years 1780-84. Referring to the spring of 1781, one named Barker[12] says "that very dangerous and obstinate disease, the burning, or as the people in Kent properly enough called it, The Plague-ague, made/

made its appearance, became very epidemical in the eastern part of the kingdom and raged in Leicestershire, the lower part of Northamptonshire, Bedfordshire, and in the fens." Regarding the autumn of 1782 a Liverpool writer says "the quartan ague was very prevalent on the opposite shore of the river in Cheshire; it was universal in the neighbourhood of Hoylake, where many died of it."[13] In 1784 there was an epidemic along both sides of the Severn valley.[14]

At this time agues became epidemic in Scotland, as revealed in the records of cases treated at the Kelso dispensary. The table compiled by Dr. MacKenzie is quoted by Ritchie.[15] It is known, of course, from the 'Statistical Account of Scotland (1791-99)' that certain parishes (e.g. Dron, Arngask and Cramond) were notorious for the prevalence of endemic ague. After the great epidemic of 1780-84 there followed a progressive decline in aguish complaints, indeed almost to extinction, but with slight recrudescences in 1794,[16] 1880,[17] 1826-28,[18] and 1846-47.[19]

2. Infantile Diarrhoea. - The researches of Niven,[20] Graham Smith,[21] and others, have proved without a doubt that flies are an important agency in the carriage of this disease, so that these remarks are confined to the historical aspect. In the first place it should be understood that the enormous weekly mortalities under the heading "griping in the guts", to be recorded by 1728 as 'convulsions', were (as Creighton first/

EPIDEMIC - AGUES.	INTERVAL (Yrs)	SUN-SPOT MAX (FRITZ + WOLFER)
1580	—	
1612	32	1615
1625	13	1626
1638-39	13	1639
1651	13	1649
1661-64	10	1660
1678-80	19	1675
1727-29	47	1727
1745	18	1750
1754	9	1750
1780-84	29	1778
1794	11	1788
1808	14	1805
1826-28	20	1829
1846-47	19	1848
AVERAGE = 11·1 YEARS.		
CYCLE OF YEARS = 11 × n (n = WHOLE NUMBER)		

Fig. 4. - Relation of Epidemic-Agues to Years of Sunspot Maxima.

first showed) mostly deaths of infants from what is now known as infantile diarrhoea. In the autumn of 1669 the deaths from "griping in the guts", as revealed in the London bills of mortality, were enormous, and continued to be high during 1670. Thereafter they fell for a few years and rose sharply in 1675, falling, and rising again in 1680 and '81. The next great season of infantile diarrhoea was in 1684, and this was followed by equally bad seasons in 1688-89, and 1693-94. Coming to the 18th century the first markedly unhealthy summer among infants was 1705. Not till the summer and autumn of 1718 and 1719 was there a similar noteworthy rise in the mortality of infants due to summer diarrhoea. A fairly severe outbreak occurred in September 1723, followed by two particularly bad seasons in 1727 and 1728. Summarising the epidemics, then, in this early period, they occurred at intervals of 5, 5, 4, 4, 5, 11, 13, 5 and 4 years, respectively, which indicates a recurrence every 4th or 5th year. Despite the great decrease of the disease within recent times, and the masking of weather-effects, due to hygienic and therapeutic measures, there is still evidence of a slight increase in the disease every 4th or 5th year. It is interesting, therefore, to be able to demonstrate this recurrence from these old records.

3. <u>Antler Moth</u>. - The first reference to an epidemic of this insect in Britain is in an old agricultural journal - the/

first showed) mostly deaths of infants from what is now known as infantile diarrhoea. In the autumn of 1669 the deaths from "griping in the guts", as revealed in the London bills of mortality, were enormous, and continued to be high during 1670. Thereafter they fell for a few years and rose sharply in 1675, falling, and rising again in 1680 and '81. The next great season of infantile diarrhoea was in 1684, and this was followed by equally bad seasons in 1688-89, and 1693-94. Coming to the 18th century the first markedly unhealthy summer among infants was 1705. Not till the summer and autumn of 1718 and 1719 was there a similar noteworthy rise in the mortality of infants due to summer diarrhoea. A fairly severe outbreak occurred in September 1723, followed by two particularly bad seasons in 1727 and 1728. Summarising the epidemics, then, in this early period, they occurred at intervals of 5, 5, 4, 4, 5, 11, 13, 5 and 4 years, respectively, which indicates a recurrence every 4th or 5th year. Despite the great decrease of the disease within recent times, and the masking of weather-effects, due to hygienic and therapeutic measures, there is still evidence of a slight increase in the disease every 4th or 5th year. It is interesting, therefore, to be able to demonstrate this recurrence from these old records.

3. Antler Moth. - The first reference to an epidemic of this insect in Britain is in an old agricultural journal - the/

the Farmer's Magazine[22] (1802). Therein is an article entitled 'Account of the Worms which infested the High Sheep Farms in Tweeddale in the months of June and July last'; and from the description of the larva there is no doubt it was ~~that of~~ the Antler Moth. The writer says, "a similar devastation visited the sheep pastures in this country in 1759." The caterpillars were again destructive in 1812 and 1824 on the high lands of Dumfriesshire. Duncan[23] gives an excellent description of the Antler Moth epidemic which occurred over a large portion of Skiddaw in 1824. The account of the ravages concludes by saying that "the quality of the newly grown herbage (6 yrs. after) was materially improved, thus affording another instance of the indirect advantages derived from insects." The hill pastures of the Scottish borders suffered severely from this pest in 1836 and the few preceding years.[24]

Then follows a lapse of over 40 years until 1881, when Miss Ormerod received caterpillars from Clitheroe, Lancashire, where their ravages were of serious moment.[25] Again, in 1884 the upland pastures of southern Scotland were severely damaged by a similar plague, which extended over seven counties, and was particularly severe in Ettrick and Yarrow[26] (Selkirkshire). This plague continued over many of the same areas in the following year. In 1894, hill pastures were injured over a wide area, extending from Roxburghshire/

EPIDEMICS OF CHARAEAS.	INTERVAL (Yrs)
1759	—
1802	43
1812	10
1824	12
1836	12
1881	45
1884-5	3
1894	10
1917	23
AVERAGE - 11·3 YEARS	

Fig. 6. - Recurrence of Epidemics of Antler Moth.

Roxburghshire to Ayrshire,[27] and in 1917 an outbreak of equal severity damaged the mountain pastures of northern England from Derby to Westmoreland.[28] All these epidemics of the Antler Moth were so severe and widespread in their occurrence as to make them impossible of escaping the attention of the most casual observer. Indeed there are repeated references to the myriads of caterpillars leaving the hill-sides bare behind them, to the choking of mountain streams, and to masses of them being held up by the low stone dykes so characteristic of the Border sheep-country.

4. Diamond-Back Moth. - As with the Antler Moth, so with the Diamond-back; while individuals may be taken any year in most localities, there are periodic increases in the population sufficient to constitute a 'plague'. It appears that the first recorded plague-year of the insect is that referred to by Curtis[29] in an article in the Jour. Roy. Agric. Soc. (1842), where he remarks "I have little doubt that this was the caterpillar (Xerostoma xylostella) which Mr. Dalgavings of Forfarshire mentioned as having seriously injured his crop of turnips in 1826. He then alludes at length to a severe attack on turnips in Hampshire in the late summer of 1837. The next recorded epidemic took place in 1851, when Stainton,[30] writing of the species, says "it was excessively abundant throughout the country; the turnip growers/

Roxburghshire to Ayrshire,[27] and in 1917 an outbreak of equal severity damaged the mountain pastures of northern England from Derby to Westmoreland.[28] All these epidemics of the Antler Moth were so severe and widespread in their occurrence as to make them impossible of escaping the attention of the most casual observer. Indeed there are repeated references to the myriads of caterpillars leaving the hill-sides bare behind them, to the choking of mountain streams, and to masses of them being held up by the low stone dykes so characteristic of the Border sheep-country.

4. Diamond-Back Moth. - As with the Antler Moth, so with the Diamond-back; while individuals may be taken any year in most localities, there are periodic increases in the population sufficient to constitute a 'plague'. It appears that the first recorded plague-year of the insect is that referred to by Curtis[29] in an article in the Jour. Roy. Agric. Soc. (1842), where he remarks "I have little doubt that this was the caterpillar (Xerostoma xylostella) which Mr. Dalgavings of Forfarshire mentioned as having seriously injured his crop of turnips in 1826. He then alludes at length to a severe attack on turnips in Hampshire in the late summer of 1837. The next recorded epidemic took place in 1851, when Stainton,[30] writing of the species, says "it was excessively abundant throughout the country; the turnip growers/

growers thought some new blight had fallen upon their crops, but fortunately subsequent years have not shown a continuance of the inordinate numbers." There was an outbreak in Berwickshire in 1863 (Dr. Hardy's notes) and Miss Ormerod mentions in her reports for 1883 and 1884 that the moths were excessively numerous in Yorkshire and the eastern counties of England and Scotland.

In 1891 there occured one of the most alarming epidemics of Diamond-back Moth that have ever been recorded in Britain, and the literature (agricultural and entomological) is full of references to the great damage done to the turnip crop that year - for long remembered by agriculturists as "the year of the caterpillar plague."[31] MacDougall,[32] in his report to the Highland and Agricultural Society for 1901, says he had "many complaints about P. cruciferarum", and in 1914 he records an outbreak of the moth as "extensive and serious." The last outbreak took place in 1926, being most severe in the south-eastern counties of England.[33]

5. <u>Leather-jacket</u>. - Another illustration of these periodic epidemics of insects is provided by a species which is well known to the agriculturist as 'the grub'. Despite the looseness of the term, ~~when speaking of 'the grub'~~, the farmer or gardener, has a particular species in mind, namely, the Crane-fly larva, or Leather-jacket. The two species of economic importance are T. paludosa and T. oleracea, and when/

when an epidemic occurs in Britain usually both species are involved, with a preponderance of T. oleracea in England and T. paludosa in Scotland.

One of the earliest references is contained in a note entitled 'Observations on the Natural History and Recent Ravages of the Grubworm,'[34] in the Farmer's Magazine for August, 1817. The correspondent says "the complaints of its depredations on the present growing corn crop, where it has succeeded an herbage one, are very general and loud .... the last crop that was materially injured by the grub was that of 1800." Curtis,[35] writing of Crane-flies, says "Their numbers depend very much upon the seasons, and for this reason sometimes these troublesome larvae are not seen. I believe they abounded in 1816, '17, and '18, and then were lost sight of till 1829." In June, 1845, they committed great havoc amongst Swedish turnips in the Isle of Anglesea. Again, in the Gardener's Chronicle (May, 1858) a correspondent writes as follows - "What can be done for the parks of London? They are suffering from the inroads of a formidable enemy. All about Stafford House, in the Green Park, and in the Regent's Park, the turf is vanishing .... the surface in the early morning is alive with leather-coated grubs."

In her annual reports, Miss Ormerod treats the outbreaks of 1880 and '84 in great detail, and also refers at length to the devastation wrought in 1892. Incidentally, during/

EPIDEMICS OF TIPULA	INTERVAL (Yrs)
1817	—
1829	12
1835	6
1845	10
1858	13
1880-4	22
1892	12
1904	12
1917	13
1925	8
AVERAGE = 10·8 YEARS.	

Fig. 8. - Recurrence of Epidemics of Leather-jackets.

EPIDEMICS OF PHYLLOTRETA	INTERVAL (Yrs.)
1816	
1820	4
1826	6
1838	12
1848	10
1856	8
1859	3
1881	22
1892	11
1899	7
1914	15
1920	6
1926	6
1930	4
AVERAGE = 11·4 YEARS.	

Fig. 9. - Recurrence of Epidemics of Turnip 'Fly'.

during the epidemic of 1884 serious injury was done to the turf of Lord's cricket ground. Regarding the plague of 1904, MacDougall[36] says, "complaints were frequent as to the destructive work of the Leather-jacket." The crop report of the Department of Agriculture for Scotland characterises the 1917 outbreak as "a serious and widespread attack of grub." The last plague occurred in 1925, and Fryer[37] summarises the situation in England in these words - "Leather-jackets were the most serious pest of cereals." The district reports of the Department of Agriculture for Scotland[38] constitute a tale of woe regarding the oat-crop, with comments such as "grub very prevalent", "lea-oats much affected with grub," "badly smitten with grub," and so on.

6. <u>Turnip Flea-beetle</u>. - Turnip flea-beetles (or 'fly') are another excellent subject for studying the periodic outbreaks of insects, as the damage they do renders them familiar to agriculturists, and makes them subjects of comment in agricultural and entomological literature. On this account, numerous records are available for over a century. One of the earliest outbreaks recorded is that of 1816, in the Farmer's Magazine for August of that year. The following comments ~~being~~ are typical. "Turnips that were early sown have suffered much"; "our turnips have again been seriously injured"; "many crops injured by the fly."

This/

This Journal records similar complaints of injury in the number for August, 1820. Thus, in Dumfriesshire, "that pestilent little creature, the fly, has annoyed our turnips dreadfully"; in Cumberland, "the fly continued its ravages throughout the month of June"; and in Norfolk, "the fly was never more prevalent." Curtis,[39] writing in 1841, recalls a serious attack of turnip flea-beetle during the summer of 1826. In 1838, "the flea-fly was very busy," and "their old enemy, the fly, made great ravages among the turnip."[40] Another attack took place in 1848, but no serious injury was done until 1856, a year which was "remarkable for the myriads of the turnip-beetle that prevailed throughout the country."[41] The summer of 1859 was unusually dry, and "the turnip-fly increased to an extraordinary degree, entire fields being swept away by it in the course of a few days."[42]

There was comparative freedom from the pest during the '60's and '70's, but a devastating attack took place in 1881. Miss Ormerod gives a splendid account of this outbreak, and summarises it in these words; "turnip-fly was little short of a scourge over a large part of England and Scotland." An attack was reported from the east of Scotland in 1892, and there are complaints of serious injury to turnips from almost every county in Scotland in 1899. The severity of these attacks may be gauged from the district reports in the Trans. of the High. and Agric. Soc.[43] of Scotland. MacDougall[44] notices the damage done by flea-beetles to turnips, in/

in 1914, in his annual report on injurious insects. Summarising the economic status of flea-beetles in 1920, Fryer[45] says, they were "rather more harmful than usual, and much resowing was necessary." The numbers of the pest were distinctly above the average in 1927, but there was no recurrence of abnormal damage until 1930, which was "an exceptionally bad year .... and only the south-east counties escaped bad infestations."[46] In these epidemics of 'fly' in turnips usually two species are concerned, and occasionally a third one, but on the whole the chief culprit is Phyllotreta undulata. Although the latter species and P. nemorum differ slightly in their life-histories, the general ecological requirements of the two species are somewhat similar.

These epidemiological surveys include all the major outbreaks of the species concerned - none having been omitted, as far as the writer is aware, after an exhaustive search through a variety of literature. Hence, we are now in a position to view the epidemics in retrospect and survey the evidence in support of a periodicity in their appearance.

III. SURVEY OF THE EVIDENCE FOR PERIODICITY.

Concerning ague, which is generally accepted as having been a malarial disease, transmitted by mosquitoes, the/

the evidence is summarised in Fig. 4. It is apparent that severe outbreaks of ague (not merely endemics in malarial foci) occurred at intervals of about eleven years, or a multiple of that figure. The average length of the period is obtained by totalling the number of years between successive outbreaks and dividing by the number of intervals, the latter being assessed as 'one' when the span of years approximates eleven, 'two' when it approximates twenty-two, and so on. By inspection of Figs. 4, 5, 6, 7, 8 and 9, ~~and 7,~~ it will be observed that the period between severe outbreaks of all these species fluctuates about a mean of eleven years, but occasionally the rhythm is broken and the regular pulsation 'misses a beat'. This lapsing of the rhythm in certain instances, notably the ague-epidemics, may be real, or the result of gaps in the historical records at this early period. Coming to the records of infantile diarrhoea, there appears to be a shorter cycle of 4-5 years superimposed on the longer one of eleven years; and this shorter cycle also appears in the Tipulid-epidemics, when they are subjected to highly detailed analysis (q.v. Part III).

From the available evidence, then, the population-fluctuations seem to have an intriguing suggestion of design, if one could only discover the key to their explanation. In casting about for some solar or meteorological parallel to the period suggested by the above analysis, the well established/

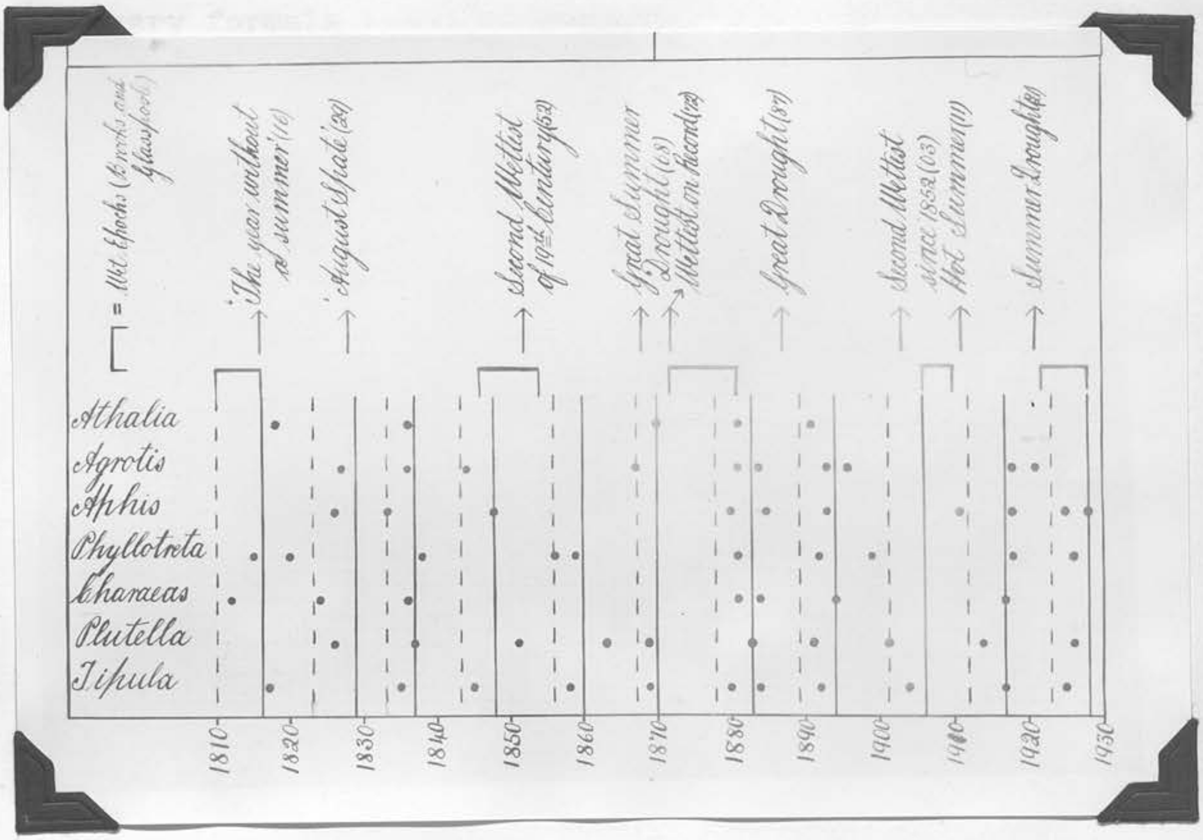


Fig. 10. - Relation of Insect-Epidemics to Sunspots and Weather.

established 11-year sunspot-cycle came to mind. This cycle seems to have been discovered by Schwabe as long ago as 1844, but it was the classical work of Schuster,[47] at the beginning of the present century, that placed the existence of the cycle beyond all doubt. The spottedness is usually expressed as the relative number - a figure obtained by an arbitrary formula - and by following out the variations in this figure from year to year it is possible to identify epochs of maximum and minimum solar activity. Now, in order to show the relation between epidemics of ague and solar-spottedness the epoch of maximum spottedness nearest to each epidemic is indicated in the third column of Fig. 4., and likewise for epidemics of infantile diarrhoea in Fig. 5. The tendency of these epidemics to coincide with sunspot maxima is certainly striking.

The relationship between severe outbreaks of the remaining species and solar spottedness is shown in Fig.~~8~~10 Two other species, namely, Turnip Moth (A. segetum) and Turnip Sawfly (A. spinarum) have been included as additional evidence, although the outbreaks of these have not been detailed. The continuous vertical lines indicate the years of sunspot maxima and the broken lines indicate sun-spot minima, as determined by Fritz and Wolfer. It should be noted that the minima do not necessarily fall mid-way between the maxima or vice versa. In fact, the intervals between/

between maxima and minima tend to be longer than the succeeding intervals between minima and maxima. Also, the intervals between successive maxima or minima are not constant, varying from 9-13 years. The conspicuous feature of the diagram is the tendency of the outbreaks to cluster about, or slightly precede, the years of sunspot maxima, i.e. approximately during the epochs of maximum spottedness. To be more precise, the majority of these insect-epidemics occur during the 5-year interval which commences three years previous to the sunspot maximum and ends one year after it. While one would not expect all species to respond in the same way to variations in the number of sunspots, an explanation of this trend towards mass periodicity, in addition to a distinct periodicity in different species, must be sought in some general climatic pulsation, associated with the periodicity of sunspots.

This involves certain difficulties, since the influence of solar activity on terrestrial weather is not yet completely understood, and the spottedness has different climatic effects in different parts of the world. In Britain, however, the evidence points to lower temperatures and excessive rainfall for a few years following sunspot maxima. Even in the case of tree-growth in America and Europe - in which an indubitable correlation with sunspots has been shown (Antevs)[48] - it has not been possible to obtain

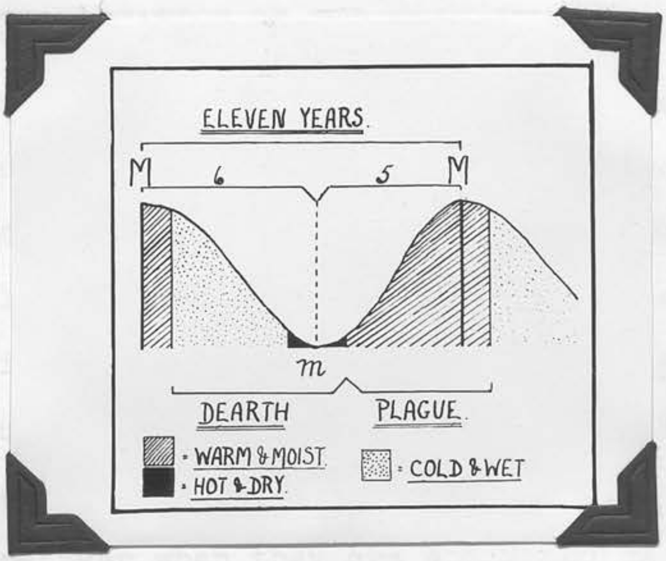


Fig. 11. - Diagrammatic Representation of Relation of 'Plagues' to Sunspots and Climate.

a good correlation with any single climatic factor. This results from the fact that tree-growth is a response to a continually varying complex of environmental factors, of which any one may act in a limiting capacity; and so it is with population-growth of animals in Nature. Speaking in broad terms of climate, the writer is prepared to venture two possible explanations.

IV. INTERPRETATION OF THE PHENOMENA.

The first is that the 5-year interval favourable to insect-increase occurs between the extremes of weather, when conditions are neither too wet nor too dry. This favourable period occurs when the sunspot-curve is rising towards its maximum, but is followed by a period of low temperatures and excessive rainfall, as a result of which insect-populations are decimated. Hardly have they had time to recover when they are subjected to the hot, dry conditions, during the epoch of sunspot minima. However, when the sunspot-curve commences to rise towards its maximum, favourable climatic conditions return, and insect-populations may attain the dimensions of a 'plague'. This interpretation of the mass periodicity is presented diagramatically in Fig.11,9, to which the reader is referred. ~~as a considerable aid to the verbal description.~~ The adverse effects of excessive rainfall and great drought, upon/

upon insect-populations, are well illustrated in Fig.108, and should serve to emphasise the significance of these factors in relation to the above explanation of the periodicities.

The other tentative explanation is that the epidemics may be associated with little known factors in solar radiation, especially in relation to the physiological effects of different wave-lengths. It appears, for example, that different wave-lengths have markedly different effects upon the reproductive and other physiological processes of insects, and recent investigations emphasize the importance of the shorter wave-lengths. Now, it has been definitely shown, by Abbot and others, that the epochs of sunspot maxima are attended by an increase in the energy of the shorter waves, i.e. the blue parts of the solar spectrum are considerably strengthened. The actinic properties of these rays have long been realised although not completely understood, and they may operate either directly upon the organisms or through their food-plants, e.g. by effecting an increased vitamin-content in the latter.

Perhaps neither of these explanations is adequate in itself, but the truth may be found in a modified combination of both, for it must be borne in mind that the insect is a more sensitive climatic integrator than any known meteorological instrument. That is to say, the organic response/

response of the insect is a result of the combined operation of the whole climatic complex, and it is sometimes (not always) difficult to isolate a particular factor as playing the dominant rôle in the adducement of that response. Whatever the ultimate cause, there is little doubt of the reality of this mass periodicity of major insect-outbreaks in Britain; and this means, oddly enough, that the modern science of ecology is able to confirm the findings of one of the oldest sciences, viz. meteorology.

REFERENCES to LITERATURE (in PART II).

(1) Swinton, A. H. (1883) - Data obtained from Solar Physics and Earthquake Commotions applied to Elucidate Locust Multiplication and Migration: Rep. U.S. Ent. Comm. 3. pp. 65-85.

(2) Simroth, H. (1908) - Uber einige Folgen der letzten Sonnenfleckenperiode auf die Tierwelt: Uerh. deuts. Zool. Ges. 18. pp. 140-53.

(3) Gasow, H. (1925) - Der grune Eichenwickler (T. viridana) als Forstschadling: Arb. Biol. Anst. Forst. Landw. 12. pp. 355-508.

(4) Hewitt, C. G. (1921) - The Conservation of the Wild Life of Canada: New York.

(5) Elton, C. (1924) - Periodic Fluctuations in the Numbers of Animals: Brit. Jour. Exp. Biol. 2. p. 119.

(6) Holinshed's 'Chronicles'.

(7) Court and Times of James I.

(8) Graunt's 'Observations upon the Bills of Mortality', 1662.

(9) Sydenham's 'Observationes Medicae.'

(10) Walker, P. (1728) - Life and Death of Alexander Peden.

(11) Rutty's 'Dublin Chronology.'

(12) Barker's 'Epidemicks' (1777-95) - (Birmingham).

(13) Moss, W. (1784) - Familiar Medical Survey of Liverpool.

(14) Coley, W. (1785) - Account of the Late Epidemic Ague - (London).

(15) Ritchie, J. (1920) - The Influence of Man on Animal Life in Scotland.

(16) Willan, R. (1801) - Reports on the Diseases in London, particularly during 1796-1800: (London).

(17) Royston, W. (1809) - On a Medical Topography: Med. and Phys. Jour. 21. p. 62.

(18) Elliotson, J. (1832) - Lecture on Agues: Lond. Med.Gaz.9.

(19) Peacock, I. B. (1848) - On the Influenza or Epidemic Catarrhal Fever of 1847-48: (London).

(20) Niven, J. (1910) - Summer Diarrhoea and Enteric Fever: Proc. Roy. Soc. Med. 3. pp. 131-216.

(21) Graham-Smith, G. (1912) - An Investigation of the Incidence of the Micro-organisms in Surroundings associated with Epidemic Diarrhoea: 41st Ann. Rep. Loc. Gor. Brd., App. B. pp. 304-29.

(22) Anon. (1802) - Farmer's Magazine. 3. pp. 487-88.

(23) Duncan, J. (1843) - Quart. Journ. of Agric. 13. p. 161.

(24) - - New Statistical Account of Roxburghshire, p. 89.

(25) Ormerod, E. A. (1885) - Report of Observations of Injurious Insects, p. 16.

(26) Hardy, J. (1886) - History of Charaeas graminis, on the Borders: Proc. Berwickshire Nat. Club. 11. p.195.

(27) Ormerod, E. A. (1895) - Report of Observations of Injurious Insects, p. 12.

(28) Imms, A. D. & Cole, A. (1917) - The Recent Outbreak of the Antler Moth (C. graminis): Jour. Brd. Agric. 24. p. 514.

(29) Curtis, J. (1842) - Observations on Insects affecting the Turnip-crop: J. Roy. Agr. Soc. 3. p. 71.

(30) Stainton, H. (1854) - Insecta Britannica. 3.

(31) Ormerod, E. A. (1892) - Observations of Injurious Insects in 1891. p. 105.

(32) MacDougall, R. S. (1902) - Insect Attacks in 1901; Trans. High. and Agric. Soc. 14. (5th ser.) p.230.

(33) Fryer, J. C. (1928) - Report on the Occurrence of Insect Pests on Crops in England & Wales, 1925-27, p.19.

(34) Anon. (1817) - Observations on the Natural History and Recent Ravages of the Grubworn: The Farmer's Magazine. 18. p. 315.

(35) Curtis, J. (1857) - Farm Insects, p. 448.

(36) MacDougall, R. S. (1905) - On Some Injurious Insects of 1904: Trans. High. & Agric. Soc. p. 226.

(37) Fryer, J. C. (1928) - Report on the Occurrence of Insect Pests on Crops in England and Wales, 1925-27, p. 15.

(38) - (1925) - Monthly Crop Report (June): Depart. of Agric. Scotland.

(39) Curtis, J. (1841) - Observations on the Natural History of Insects affecting the Turnip crop: Jour. Roy. Agr. Soc. 2. p. 199.

(40) Anon. (1838) - The Farmer's Magazine (District Reports) p. 143, 144.

(41) Anon. (1857) - The Farmer's Magazine, p. 329.

(42) Anon. (1859) - Quart. Journ. of Agric. p. 144.

(43) - (1900) - Trans. High. Agric. Soc. of Scotland (District Reports).

(44) MacDougall, R. S. (1915) - Insect Pests in 1914: Trans. High. Agric. Soc. p. 211.

(45) Fryer, J. C. (1922) - Insect Pests of Crops (1920-21): Minist. of Agric. Miscell. Publ. No. 39. p. 10.

(46) " (1933) - Report on Insect Pests of Crops in England & Wales: Min. Agr. Bull. No. 66. p. 18.

(47) Schuster, L. (1900) - Cambr. Phil. Trans. 18. p. 107.

(48) Antevs, E. (1930) - The Big Tree as a Climatic Measure: Carneg. Instit. Wash. Publ. 352.

(49) Brooks, C.E. and Glasspoole, J. (1928) - British Floods and Droughts.

GRAPHICAL and STATISTICAL METHODS for EVALUATING the RÔLE of CLIMATE in the PRODUCTION of INSECT-OUTBREAKS.

CONTENTS of PART III.

PART III.

'If arithmetic, mensuration and weighing be taken away from any art, that which remains will not be much' -

Plato.

I. INTRODUCTION.

Every scientific problem is, in the last degree, a quest for the relationship between two or more variables. The problem may be stated otherwise, but only when the functional relationship of the variables has been stated precisely i.e. in mathematical terms, has the problem been solved in a truly scientific manner. However, in the initial stages of a science the investigator has usually to be content with descriptive solutions. Ultimately, he or his successors adopt the truly scientific method of inquiry by establishing the quantitative relations between the known variables. The discovery of these interrelations provides the basis for prediction and control, so essential for the applied aspects of a science, and bespeaks the entry of the latter into the highest phase of its development. Although biology is one of the younger sciences, it has made such great advances in the descriptive phase that further development must almost certainly be along quantitative lines.

II. - METHODOLOGY.

In the exact sciences, the methods of studying the quantitative relationship between variables have been used for so long, and have thus attained such a degree of perfection, that they are almost taken for granted. This is not so in the biological and social sciences, but there are perfectly good reasons. The physicist or astronomer has to deal with quantities or variables which can be accurately measured; and further, he is usually able to eliminate irrelevant variables. In the social and biological sciences, on the other hand, the variables are not always susceptible of quantitative measurement, nor is it always easy to eliminate the irrelevant variables. This is particularly obvious in dealing with animal-populations in Nature, where a multiplicity of factors operate simultaneously, and with different intensities on the different phases of the life-cycle. The result is an amazingly tangled skein of interacting and interdependent variables, the unravelling of which demands special methods.

The adaptation of a well-known mathematical technique is preferable to a less familiar one, but the wide 'scatter' of the data imposes such limitations that the only available means of determining the relations between the variables is that of statistics, which have wide applications, but have been utilised only to a very small extent in analysing/

analysing the causes of insect-outbreaks. It seems to the writer that this is a field of scientific endeavour which could be explored with great benefit, and it is proposed to proceed immediately to a consideration of graphical and statistical methods which may be utilised. Stress has been laid on the logical implications of the procedure, for although statistical treatment may be helpful, a blind faith in numbers and formulae would be courting disaster. That is to say, the mathematical treatment must be accompanied by sound reasoning along biological lines.

III. ANALYSIS of 'WARBLE' INFESTATION.

In any virgin field of study it is always advisable to start with the simplest available technique, and much depends upon the judicious choice of material. After due consideration, it was decided to investigate the climatic factors influencing the infestation of cattle-hides by 'warbles.' The chief reasons for this choice are the following. The life-history of the pest is of a nature such that the indefensible stages are sheltered from the "bludgeonings of chance." In the first place, nine months of the life-cycle are passed in the tissues of the host, and if there is any considerable mortality here there is no reason to suppose that it will vary appreciably from year to year, as the body of a mammal is provided with numerous stabilising/

stabilising mechanisms to prevent change of temperature, salinity, hydrogen-ion value, etc. Hence, when entrance to the host's tissues is effected, stability of environment is assured. This elimination of variability from the environment for such a long period in the life-cycle greatly facilitates the task of the investigator. Another important point, which was duly considered, is the freedom of Hypoderma from natural enemies, no parasites or predators having been recorded in Britain, as far as the writer is aware, although it is conceivable that there may be a few pupal parasites. Thirdly, one must consider the period of exposure to the climatic environment; and naturally, the shorter this period is, the easier the task of the investigator becomes, for he can then confine his analysis to a few months, weeks, or perhaps days. Since the eggs hatch in 3-5 days, the young larvae bore into the skin within 6 hours, and the puparia are extremely hard, and usually under cover of vegetation or soil, the only stage which is exposed to the full intensity of the elements, for any length of time, is the adult. This limits the problem to an analysis of the weather during the few weeks of adult-life, and hence Hypoderma is almost an ideal subject for introducing this type of work.

The data were obtained from the 'Aberdeen Hide and Tallow Co.', which keeps a record of the percentage of hides containing/

containing, (a) 1-4 'warble'-holes, and (b) 5 or more 'warble'-holes. Only the latter percentage has been utilised in this analysis, since it provides the better criterion of intensity of infestation. As the company handles a large proportion of the hides of cattle passing through the Aberdeen abbattoirs and the animals are drawn from Banffshire, Aberdeenshire, and Kincardineshire, the figures are an excellent estimate of the actual infestation of cattle by 'warbles' in the north-east of Scotland. Although two species of Hypoderma are concerned, H. bovis has been largely eliminated by taking the figures for April only, as in that month the Hypoderma larvae are mostly H. lineatum. The adult flies attain their maximum abundance during July, and hence from the argument already presented, one would anticipate a correlation between the degree of infestation and the weather during July of the preceding year, although the particular factor influencing the infestation remains to be determined. The data are presented in the table below.

TABLE III.

Year	1931	1932	1933	1934	1935	1936
Warbled Hides (%)	20.1	8.7	19.1	26.6	36.0	40.2
Rainfall (ins.)	1.5	3.06	3.03	3.69	2.45	2.08
M. Max. Temp.	61.8	60.5	62.4	67.7	67.3	66.2
Sunshine (Hrs.)	154.1	74.2	106.3	174.3	205.	217.5

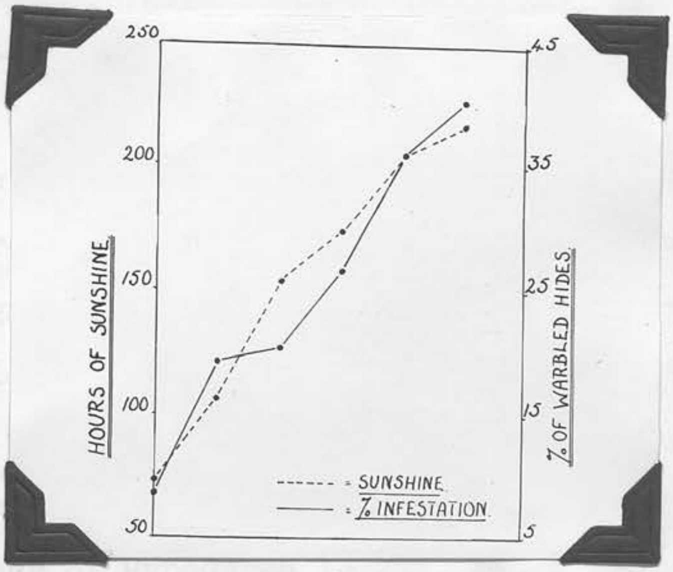


Fig. 12. - Relation between 'Warbled' Hides (%) and Bright Sunshine.

As the result of logical argument, the problem has been reduced to comparatively simple terms, and hence one may reasonably anticipate its solution by correspondingly simple methods. One of these is the 'alignment diagram.' In this case the values of the independent variable are arranged in order of magnitude, and the values of the dependent variable (or variables) plotted in the same order. If the points so obtained tend to fall in a straight line, or a well defined curve, the variables are correlated. Fig.12~~10~~ shows the line obtained for the number of hours of bright sunshine during the preceding July, when the years are arranged in order of percentage warble-infestation. The diagram reveals an excellent correlation between the two variables, the relationship being positive and linear. Despite fluctuations of rainfall and temperature, the amount of sunshine remains the predominant factor affecting the number of Hypoderma larvae, other factors of the environment playing a very subsidiary rôle. The ecological significance of this is ~~simply~~ that the adult flies can tolerate a wide range of temperature and moisture, but the environment (in the N.E. of Scotland) is deficient in the amount of sunshine required to stimulate their reproductive activities, and therefore sunshine is the <u>limiting factor</u> to abundance in this environment. The reader should bear in mind that this is probably one of the simplest examples that one could have chosen for investigation, the degree of infestation/

infestation having been reduced to a single-factor-effect, but, as will be observed later, this condition seldom exists in a natural environment, there being usually several factors operating to check the potential growth of the population.

IV. - ANALYSIS of 'STRIKE' in SHEEP.

This is definitely a more difficult problem than the preceding one, but it can be simplified also by careful scrutiny. In the first place, the number of sheep that are 'struck' varies considerably from day to day, so that daily records of 'strike', and of meteorological conditions, are essential to the establishment of any correlation that may exist. Fortunately, both are available, as a careful record of 'struck' sheep is kept by the shepherds at the experimental farm of the Rowett Institute, and the fields in which the sheep graze are within a mile of the North of Scotland College farm, where official meteorological records are taken daily. The records of 'strike', and the three climatic factors with which the former is most closely associated, are presented in Table IV. It will be observed that only the two months of highest 'strike' incidence, namely, June for the ewes and August for the lambs, are included. In addition, only where the number of cases exceeds 6 in one day, have they been considered. The reasons for this procedure are to eliminate sporadic cases of 'strike' which, in the present state of our knowledge, are rather difficult to account for.

TABLE IV.

Struck Ewes.			Struck Lambs.			Rainfall (ins.)				Sunshine (hrs.)				Max. Temp.			
J.'33		J.'34	Aug.'33		'34	J.'33	'34	A.'33	'34	J.'33	'34	A.'33	'34	J.'33	'34	A.'33	'34.
10th	8	0	2nd	7	5	.03	.01	.02	0.0	6.2	1.7	7.5	10.7	62.0	55	68	68
16	17	5	8.	15	0	.08	.01	0.04	.25	12.9	0.0	14.8	5.2	67.0	68	74	64
18	5	8	13	0	9	.16	0.0	0.0	.04	7.5	8.0	11.6	5.4	60.0	68	62	66
22	0	11	14	13	0	.03	.05	0.06	.2	0.0	9.4	9.6	7.3	60.0	64	67	63
25	7	0	17	7	0	.03	0.0	0.0	.08	6.9	11.9	3.0	1.9	65.0	55	64	65
29	0	9	18	5	7	.01	.02	.07	0.0	2.1	7.0	4.6	9.1	65.0	66	65	64
			21	7	6			.01	0.0			7.9	8.4			67	68
			22	15	12			.07	.04			9.5	8.2			67	68
			23	5	7			.22	.01			3.4	8.4			60	61
			25	5	7			.09	.01			0.0	5.8			61	63
			Average			.03	.02	.03	.16	8.4	7.2	6.4	5.7	63.3	62	66.7	63.1

From mere inspection of the data there is no obvious correlation between the incidence of 'strike' and meteorological conditions, although it is known, especially to practical men, that weather plays an exceedingly important rôle in the production of this scourge of the flock-master. The particular set of weather conditions feared by the shepherd are what he invariably terms, "warm and muggy with blinks of sunshine." In view of this, and the fact that the actual period of activity of the flies seems to be only a few hours in the day, the kind of weather which is conducive to 'strike' may not be adequately reflected in the records of meteorological instruments enclosed in a Stevenson screen, although they might indicate a trend. A valuable method for revealing the existence of the latter is the 'scatter diagram', as it shows the range and associations of the variables, at a glance. The three climatic factors which have the greatest effect upon the incidence of 'strike' in this environment are rainfall, sunshine, and temperature, in order of decreasing significance. This relationship is aptly demonstrated in Figs. 13, 14, and 15. It should be noted that the correlation is between the number of 'struck' sheep and the weather of the second day previous to that on which the sheep were first observed to be attacked.

These diagrams reveal quite plainly the climatic conditions/

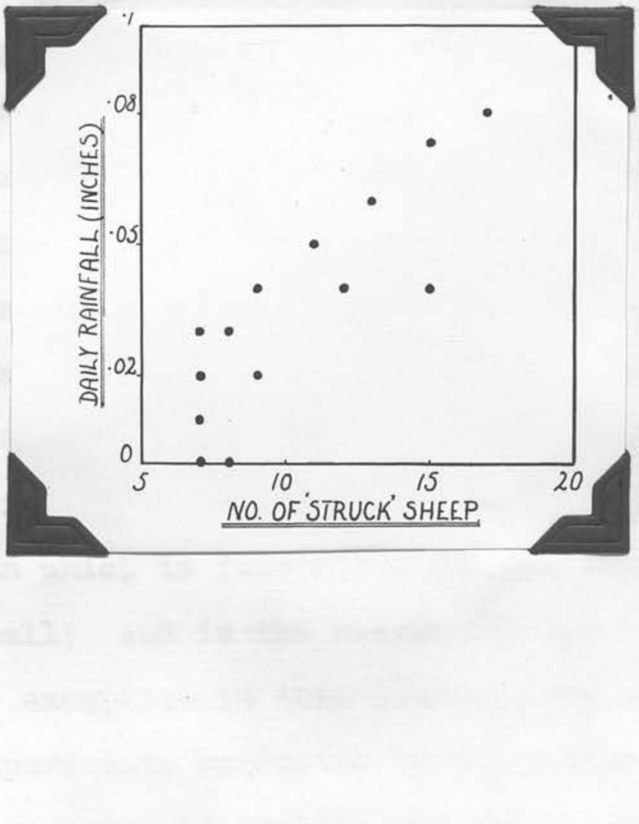


Fig. 13. - Relation between Rainfall and 'Strike' in Sheep.

conditions which are conducive to a high incidence of 'strike'. The number of cases is likely to constitute a serious economic problem when the particular combination of climatic factors is such that the daily rainfall exceeds .03 ins., the number of hours of bright sunshine is not less than 7, and the maximum temperature in the shade attains 65°F. All three factors make an important contribution to the optimum climatic complex for this species of blowfly (L. sericata) in so far as its oviposition activities are concerned, but no single factor is of greater importance than another, since a deficiency of one element cannot be compensated by high favourability of the others. In fact, the general trend of the climatic régime, is of such a nature that temperature and sunshine tend to vary inversely with rainfall, so that the probability of rainfall, temperature and sunshine being in the proportion which is favourable for the blowflies, is rather small; and is the reason for bad 'strike' years being the exception in this country, and not the rule.

Experiments conducted by the writer, in the laboratory, serve to explain why the above combination of climatic factors is conducive to 'strike'. Compared with many other insects, Lucilia sericata has high temperature and moisture requirements for its oviposition-activities, and although the females will 'blow' meat in a diffuse light/

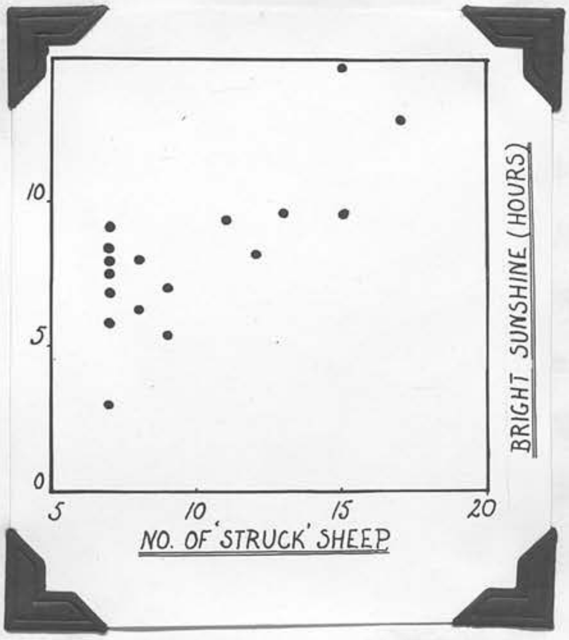


Fig. 14. - Relation between Bright Sunshine and 'Strike'.

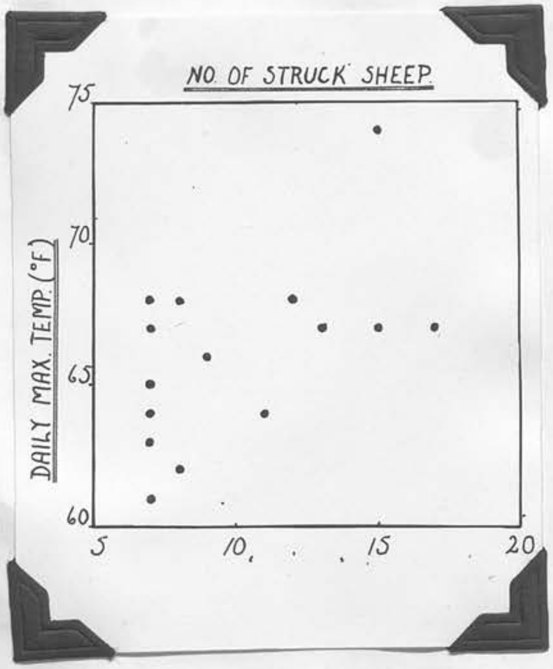


Fig. 15. - Relation between Maximum Temperature and 'Strike'.

light, they are greatly stimulated by sunlight or even the bright light from an electric bulb. The humidity requirement of the flies for oviposition is not so much that of their own bodies (they can live in a dry atmosphere provided there is sufficient moisture in the food) as that of the medium for oviposition. No matter how favourable the thermohyetic conditions of the environment may be, the females will not oviposit on a dessicated medium, and it is an amazing sight to see a gravid female seeking out every crevice and crack in the medium (moister because less evaporation) in order to deposit her eggs. The provisions of Nature are truly remarkable, since the recent work of Evans[30] (1934), shows that the eggs will hatch only in an atmosphere of almost 100% relative humidity, and Davies[31] (1935) finds that the young larvae are highly susceptible to dessication. Hence, in virtue of the laboratory experimentation the meteorological correlations that were obtained become intelligible; high temperature, bright sunshine, and a damp fleece, being the combination par excellence for a high incidence of 'strike.' It will be observed that rainfall has a threshold value above which the number of 'strikes' rises rapidly, but below which they remain fairly constant, indicating that very light showers make no appreciable difference to the normal moisture content of the fleeces, of which a small percentage induce the flies to 'strike', even in the absence of rain.

V. ANALYSIS of TIPULID OUTBREAKS.

1. - Relative Significance of Environmental Factors. - In the previous examples, the relations of the species to weather have been analysed by the use of simple graphical methods in conjunction with quantitative estimates of the destructive stage. Unfortunately, it is not always easy to obtain estimates of this kind, nor can the analysis be always confined to a few weeks or days, since species which are ~~always~~ more or less exposed to the elements, whose life-history extends over a considerable period, may encounter adverse circumstances in every generation, at some stage in the life-cycle. As it is generally recognised by ecologists that animal-populations are controlled by a complex of factors which are continually varying in space and time, any attempt to determine the rôle of the different environmental factors must be extremely difficult, unless they differ considerably in their relative significance. Since controlled experiments in the laboratory are demonstrating, in an increasing number of instances, that each stage of an insect's life-cycle has different thermohyetic requirements, one may logically anticipate that a local environment will be normally deficient in at least one (and probably a few) of the essential factors, which thereby assumes the limiting rôle. Although this diverse physiological ensemble of the insect-species/

insect-species imposes a handicap in the race for increase in numbers, it facilitates the task of the ecologist, by reducing the problem to the discovery and climatological delineation of 'critical' periods in the life-cycle.

2. Critical Periods. - These may result from the high susceptibility of a particular stage to weather conditions, i.e. an intolerance of deviations from a narrow optimal range; or they may be due to the deficiency of an essential factor in a particular environment, at a particular time. As there are wide fluctuations in climate, both seasonably and geographically, even in the restricted confines of an island like Great Britain, it follows that the critical periods may differ in different parts of the country. This means that if averaging effects are to be avoided, the study of the critical periods must be for definite bio-climatic areas; otherwise, good correlations between outbreaks and weather phenomena cannot be expected. These considerations indicate the complexity of the problem, and make it necessary to be content, for a beginning, with good approximations of the effects of the most potent factors. Usually the critical periods are associated with reproduction or the early stages of existence, as these phases are the last to succumb to evolutionary changes, are least adaptable, and hence the most susceptible to adverse environmental agencies.

The/

The determination of the critical periods may be done by two distinct methods, viz. the experimental and statistical. The chief disadvantage of the former is the difficulty of translating the temperature and moisture conditions of an incubator into the standard meteorological records as measured in a Stevenson screen; whereas in the statistical method (analysis of weather data) the results are often difficult to interpret correctly. The ideal procedure consists of a judicious combination of both, but a vast amount of useful information may be obtained from either method. One of the main objects of this paper is to indicate the possibilities of the quantitative analysis of climate in relation to insect-epidemics, as recorded over a number of years.

3. Collection of Data. - This demands fairly detailed accounts of the outbreaks, and involves an exhaustive search through a variety of literature, with a view to obtaining reliable records of the intensity of outbreaks of particular species. In this connection, the epidemiological outlook of the earlier entomologists has been an invaluable aid, being particularly well illustrated in the writings of Duncan, Marsham, Kirby, Curtis, and Ormerod. The collection of data on the abundance of insects is well organised in America and Germany, and has been put on an official basis in England, since 1917, but there/

there is as yet no official organisation for the collection of this class of data in Scotland. Thus, for the compilation of a historical record of outbreaks, over a sufficient number of years to justify statistical treatment of the weather thereof, the investigator must exercise great judgment in the choice of suitable species. This matter has been considered in Part II and need not be repeated here. Another essential precaution is the accumulation of a variety of references from independent sources, so that the opinions of one observer will not unduly influence the final sifting of the evidence regarding the intensity of the outbreak. Bearing the above considerations in mind, one may proceed to the epidemiology of the particular species, and for this purpose it is proposed to take the 'Leather-jacket.'

4. Epidemiology. - In this account of the more important Tipulid outbreaks in Britain, no attempt has been made to record those occurring before 1800, as the unreliability of the meteorological data renders correlation between epidemics and weather conditions a hazardous procedure under these circumstances. Subsequent to the year 1800, the first outbreak occurred in 1813. A reference to the severity of the attack is contained in a letter from the Right Honourable Sir John Sinclair, Bart. to the Farmer's Magazine (1814), wherein he refers to the practice of Mr./

Mr. Ballingal of Sweet Bank, in Fife, of prohibiting the shooting of crows on any part of his farm. He says "during the spring of 1813, the grub was most destructive ... and had it not been for the crow, would have destroyed more grain in the county than all the crows in it would have done in 7 years."[1] In their notable book on insects, Kirby and Spence remark, "In the rich district of Sunk Island, in Holderness, in the spring of 1813, hundreds of acres of pastures have been entirely destroyed by them .... a square foot of the dead turf being dug up, 210 grubs were counted in it."[2]

Another devastating outbreak occurred in 1817, and the agricultural literature contains numerous references, of which the following are typical. "The complaints of its (the grubworm) depredations on the present growing corn crop, where it has succeeded an herbage one, are very general and loud in Scotland."[3] "Considering the great devastation made amongst the young corn this spring, by the grubworm .... it would certainly be satisfactory to hear of a method of preventing such injury to the crops in future."[4] "The ravages of the grub being unpredecented, there were good grounds for serious alarm."[5] These, and similar reports, indicate the severity of the attack, but it seems to have been more serious in Scotland than in England, whereas the 1813 outbreak was of universal occurrence/

occurrence throughout Britain. Curtis,[6] writing of Crane-flies, says "Their numbers depend very much upon the seasons, and for this reason sometimes these troublesome larvae are not seen. I believe they abounded in 1816-18, and then were lost sight of till 1829 and the two following years." From a close inspection of various agricultural reports this appears to summarise the situation correctly, with the exception of an attack which occurred in the east of Scotland and north of England in 1824.[7] From 1829 there was no serious recurrence of the pest until 1845, when severe injury resulted to swedes and oats in the Isle of Anglesea and elsewhere.[6]

The next outbreak occurred in 1857, a correspondent to the 'Quarterly Journal of Agriculture' remarking as follows - "The slug, the wireworm, and the grub, attacked with such virulence as to render it advisable to plough the fields up. We have not seen for many years such destruction committed by these vermin."[8] The above reference applies to Scotland, but some damage was done in England also, although it does not appear to have been so serious. The attack continued in the following year. Another outbreak took place in 1862, and to judge from the numerous complaints, was undoubtedly severe. The 'Quarterly Journal of Agriculture' summarises the situation thus - "May was a very moist month, with a temperature rather/

rather above the average. Oats looked well where not eaten by the grub .... whose ravages have been severe over a wide district of country."[9] The attack was renewed in 1863, as appears from the remark, "That most annoying enemy of the farmer, the grub, has been committing great ravages in the north this year again, and many fields have had to be ploughed over."[10]

From this time there is a lapse of sixteen years until another epidemic occurred, namely, in 1879; and Miss Ormerod[11] summarises the situation thus. "The larvae of these flies appear to have been numerous and injurious generally this year, excepting at the most northerly point of observation." However, in the following year the attack was even more widespread and of greater severity. Damage commenced to be done very early in the season and continued well into the summer. Thus, as early as February in Yorkshire "the grubs were destroying hundreds of acres of autumn-sown wheat"; and early in the year at Ormskirk (Lancashire) "the grubs swarm in almost countless numbers where last year's crop was grass."[12] From Maldon (Essex) it was reported that "Tipulae larvae were exceedingly destructive everywhere." All the above records of damage refer to England, but serious injury was done in Scotland also, although perhaps on a somewhat smaller scale. Thus, "the grubs were found to be very destructive/

destructive amongst strawberries at Oxenford Castle, Dalkeith, as many as from seven to twelve being found at the root of one plant;" and, "at Coltness, Lanarkshire, there was a strong attack of Tipula oleracea."[12]

Another serious epidemic occurred in 1883, Miss Ormerod[13] summing up the situation as follows. "Amongst the many bad crop-attacks of the past season, perhaps that of the Daddy Longlegs grubs was the most widely spread and the most lasting. The attack was reported from many places and from as far north as Caithness in Scotland down to Brighton. It was injurious to grass pastures, oats, and wheat; to beans, peas, and turnips .... more than one kind of Tipula was at work."

Following the severe outbreak of 1883, was that of 1884 - one of the most serious and widespread Tipulid epidemics ever recorded in Britain. The damage commenced in early spring and continued during the summer. The following references will help to convey some idea of the enormous losses suffered by the farming community in that season, as a result of the activities of leather-jackets. One of the earliest complaints came from Bideford (Devon) on the 8th of February, a note sent along with specimens of the grubs remarking as follows. "I am sending you a few grubs collected from a seven-acre field, which they have attacked and destroyed twice .... my foreman had no trouble/

trouble to find hundreds of the grubs."[14] Concerning damage done in the neighbourhood of Spalding (Lincoln) Miss Ormerod says "a farmer at Kirton had a 14-acre field of oats, and likewise his beans, quite destroyed by this pest, and many farmers suffered more or less in that part of Lincolnshire, where the land is heavy."[14] Incidentally, during this serious Tipulid epidemic, severe injury was done to the turf of Lord's cricket-ground. In Scotland, the crop-reporters to the Highland and Agricultural Society complain of injury to the oat-crop. In Lanarkshire, fields of oats were "badly hurt with grub"; in Renfrewshire, "grub destroyed oats after lea to a great extent"; in some districts of Dumbartonshire the oat-crop was "very much damaged by grub," and in Stirlingshire, damage occurred "to an unusual extent."[15] The attack was not confined to the south-western counties, as these reports might indicate, similar complaints of injury being recorded from the north-east, although perhaps not quite so serious. In Aberdeenshire, "oats after lea suffered much by the ravages of the grub in the month of May."[15]

The next outbreak of importance occurred in 1892. From Northallerton (Yorks), the Daddy Longlegs flies were reported as being "in myriads", and the larvae "causing great havoc in two fields of the writer, and in the surrounding country"; while in the neighbourhood of Craven/

Craven Arms (Shropshire) the grubs were noted as "doing considerable damage."[16] This outbreak does not appear to have been universal throughout Britain, the damage being most serious in the Midlands, and decreasing in severity, northward and southward. Another severe outbreak occurred in 1903, but more damage appears to have been done in Scotland than in England. The crop-reporters to the Highland and Agricultural Society are unanimous in their complaints of injury by leather-jackets, the following comments being typical - "lea braird very much cut by grub" (Wigtownshire); "in some districts, oats very much damaged by grub" (Dumbartonshire); "crop greatly injured by grub" (Aberdeenshire); and "oats were extensively injured by grub" (Caithness).[17] As Miss Ormerod ceased publishing her annual reports after 1900, this valuable source of information concerning the economic status of the various insect pests was no longer available, but the efforts of Miss Ormerod had helped to arouse public and official interest in economic entomology to such an extent that her work was, in large measure, continued by the consulting entomologists to the Board of Agriculture, the Royal Agricultural Society of England, and the Highland and Agricultural Society of Scotland. Concerning the grub-epidemic of 1903 in England, Theobald (replying to a correspondent) says, "The larvae you send, and which have bared/

bared six acres of grass, are those of one of the Daddy-Long-Legs, one of our worst grass land pests."

In the following year, the damage caused by 'leather-jackets' was ~~even~~ more serious than in 1903. MacDougall,[18] says, "during the past year complaints were frequent as to the destructive work of the 'leather-jacket', the complaints reaching me being chiefly from Forfarshire and Aberdeenshire." Other counties were affected, however, as the crop-reports to the Highland and Agricultural Society amply testify. For instance, in Dumfriesshire, "lea-oats suffered from grub"; in Ayrshire, the damage to the oat-crop from grub was "much greater than usual"; and in Perthshire, "grain crops suffered considerably from wire-worm and grub."[19] In England, the Board of Agriculture "had many enquiries addressed to them on the subject of injury to the oat-crop by the attack of grubs, and in every case the insect proved to be the leather-jacket."[20] Another epidemic occurred in 1908, and larvae of Daddy-longlegs were sent to the Board of Agriculture with the remark that "acres of oats in South Cumberland and North Lancashire had been destroyed."[21] Considerable losses were also reported from Scotland, where oats were "badly cut with grub in spring" (Wigtownshire); "much damage was done by grub" (Argyllshire); and "leather-jacket thinned the oat-crop to a much greater extent than last/

last year" (Caithness).[22]

From 1917 onwards, more detailed information concerning the economic status of the various insect pests, becomes available, as the Board of Agriculture and Fisheries published a 'Report on the Occurrence of Insect and Fungus Pests on Plants in England and Wales,' and the Ministry of Agriculture now publishes similar reports from time to time. No indication of a universally serious outbreak of grub in England is given in the report on the insect pests of 1917, but in the east of Scotland there occurred an epidemic which is characterised by the Department of Agriculture for Scotland as "serious and widespread."[23] The devastation continued during the spring and early summer of the following year, and in Scotland, at least, was more widespread if somewhat less severe than it was in 1917, but in England serious damage was done. Thus, "crops grown on recently broken grass-lands, or after leys, suffered severely (Northumberland, Durham, E. counties, Bedfordshire, Middlesex, Worcestershire, Kent, Sussex, Monmouthshire, and Carnaervon) .... according to specimens bred out from larvae collected in various parts of the country, T. paludosa Meig. was the chief culprit."[24] In Scotland, the report on the oat-crop, issued by the Department of Agriculture, was as follows - "the crop is generally strong and healthy, but almost/

almost everywhere it is to a greater or less extent affected by grub .... resowing has been carried out on a considerable scale in south-west Perth, Kintyre, and to some extent in south-west Forfar, North Ayr, and Kirkcudbright."[25]

In 1924, an outbreak of considerable severity, in the south and west of Scotland, presaged one of the most serious and extensive Tipulid-epidemics of recent years, namely, that of 1925. The district reports to the Department of Agriculture for Scotland, and to the Highland and Agricultural Society, constitute a tale of woe concerning the oat-crop. Thus, "the grub caused much damage" (Fifeshire); "many fields of lea oats suffered badly from grub" (Perthshire); "oats badly grubbed in many places" (Kincardineshire); and "grub caused a lot of damage to corn" (Rossshire).[26] These remarks are typical of the complaints concerning the ravages of the grub amongst cereals in Scotland during the early summer of 1925. Fryer[27] summarises the economic status of the pest in England in these words - "Leather-jackets (Tipula paludosa Mg. and other species) were the most serious pest of cereals in 1925", and "the 1925 epidemic also resulted in serious losses among strawberries, large numbers of plants being injured or destroyed in practically every strawberry-growing district, including the/

the eastern counties, Kent, Hampshire, and Devon."

The epidemic of 1925 was the most recent one of universal occurrence throughout Britain, but another epidemic occurred in Scotland, particularly the eastern counties, in 1929. The Department of Agriculture comments as follows. "The outstanding feature of the reports on the oat-crop is the prevalence of grub, and to a lesser extent wire-worm, in most districts. The damage done by grub appears to be most extensive in the north-eastern districts, where many fields have been badly thinned, but the south-western districts have also been affected to a greater or less extent."[28] Contrasted with the above conditions in Scotland, the losses in England were comparatively slight. Fryer,[29] summarising the damage done by leather-jackets to cereals during the years 1928-31, says, "On the whole, the damage caused was but little .... in 1928 the pest was locally severe in the northern and midland counties, and in 1929 in the west Midlands, Cambridgeshire and Oxfordshire."

In order to have a variety of independent references to the outbreaks, and, at the same time, avoid cumbersome repetition in the historical account, additional references have been included in an appendix at the end of the paper.

5. <u>Grading of Outbreaks and Delineation of Bio-climatic Areas</u>. - When all available records have been collated the next step is the sorting of the data into five categories, corresponding to five grades of damage, namely, nil or practically nil, very slight, slight, severe, and very severe. Experience shows that it is very difficult to construct a finer grading from subjective estimates of the damage. Fig.16 shows a continuous record of the fluctuations in damage done by leather-jackets in the east of Scotland and north-east of England, since 1879. Only the outbreaks which resulted in severe, and very severe, damage, will be included in the climatological analysis, as it is easier to identify the factors associated with the extremes of population (abnormal abundance or scarcity) than intermediate densities. Despite the comparatively small area of Britain, and its maritime climate, outbreaks of insects do not occur with equal frequency or intensity throughout the country. For this reason, and in view of what was already stated in regard to critical periods, it is essential to study the outbreaks of a particular bio-climatic area, i.e. an area throughout which the numbers of the insect are fairly uniformly distributed in space and time. The choice of the above area for study was based on these considerations, together with the fact that the climate of the area is typified by that of Edinburgh, for which meteorological data extending over 160 years are available.

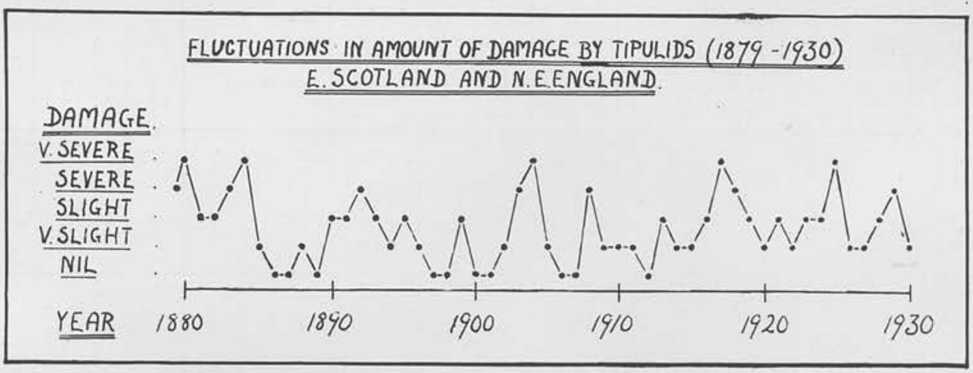


Fig. 16. - Fluctuations in Amount of Damage by Tipulids (1879-1930).

6. Life History. - As a sound knowledge of the life-history is essential for a proper understanding of what follows, it will be necessary to give a brief account thereof. Usually several species of Tipula are involved in severe outbreaks, but by far the commonest in Scotland and the north of England is T. paludosa - the Marsh Crane Fly. This species is one of the latest to appear on the wing. It may be found from the middle of June until the middle of September, or later, but July and August are the times of maximum abundance. The female deposits her eggs just below the soil-surface - a covering of damp, rough herbage making conditions specially attractive. The larvae emerge from the eggs in 2-3 weeks (depending on the weather) and feed throughout autumn, also during mild spells in winter, and again in spring. It is in May, however, when the larvae are almost full grown, that the greatest damage to young cereals, and other grasses, is done. Pupation occurs in the soil from the middle of May until the second week in July, but June is the month in which the pupae are found in greatest abundance. The pupal stage lasts about a month. T. paludosa Mg. was at one time considered to be a synonym of T. oleracea L. It is now accepted that they are two distinct species, with different habits, T. oleracea L. being an early summer species, and T. paludosa a late summer and autumn species.

TABLE V.

	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sep.	Oct.	Nov.	Dec.
Monthly Rainfall (Preceding Outbreaks)	2.07	1.60	1.57	1.55	1.99	2.35	3.22	3.22	2.36	2.64	2.18	2.36
Average of All Years	1.95	1.69	1.53	1.49	1.90	2.16	2.81	2.79	2.39	2.51	2.37	2.21
Difference	+.12	-.09	+.04	+.06	+.09	+.19	+.41	+.43	-.03	+.13	-.19	+.15
Standard Error of Differ.	.26	.24	.24	.23	.25	.29	.34	.22	.29	.36	.26	.30
Coeff. of Variability	50.7	58.	75.8	60.6	59.3	50.6	44.7	29.5	54.2	76.5	52.7	53.4
$\frac{\sigma \text{ (all years)}}{\sigma \text{ (before outbreaks)}}$	1.13	1.2	1.0	1.0	1.05	1.0	1.0	1.58	1.15	1.0	1.0	1.01
Skewness (all years)	+.37	+.16	+.03	+1.1	+.38	-.28	-.14	-.16	+.66	+.77	+.82	+.59
Skewness (before outbreaks)	-.4	+.1	+.46	+.6	-.01	-.12	+.5	-.35	+.3	+.71	+.5	-.1
Differ. in Skewness	.77	.06	.43	.50	.39	.16	.64	.19	.36	.06	.32	.70

TABLE VI.

	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sep.	Oct.	Nov.	Dec.
Mean Monthly Temp. (Preceding Outbreaks)	37.3	39.2	39.8	43.5	48.6	54.1	56.9	56.7	53.6	47.6	41.9	37.9
Mean of All Years ...	36.8	38.3	40.3	44.8	49.9	55.7	58.6	57.8	53.6	47.2	40.9	38.3
Difference	+.5	+.9	-.5	-1.3	-1.3	-1.6	-1.7	-1.1	0.0	+.4	+1.0	- .4
Standard Error of Differ. ..	.65	.76	1.65	.53	.47	.42	.45	.32	.45	.40	.67	.68
Coeff.of Variability	119.	43.9	23.1	17.3	18.0	8.5	10.6	9.9	11.0	11.0	28.5	42.7
$\frac{\sigma \text{ (all years)}}{\sigma \text{ (before outbreaks)}}$	1.25	1.13	1.26	1.18	1.40	1.0	1.26	1.20	1.16	1.36	1.0	1.2
Skewness (all years)	-.73	-.52	-.23	-.5	-.04	-.16	.07	+.45	+.30	-.38	-.52	-.23
Skewness (before outbreaks)	-.3	-.27	+.33	-.25	+.37	+.06	+.53	-.21	+.35	-.26	-.75	-.04
Difference in Skewness	.43	.25	.56	.25	.41	.22	.26	.66	.05	.12	.23	.19
Correlation between Rainfall & Temper.	+.14	+.22	-.20	+.02	+.01	-.35	-.33	+.27	-.06	-.03	-.13	+.28
Stand. Error of Coeff. of Correlation.	.22	.21	.22	.23	.22	.20	.20	.21	.23	.23	.22	.21

7. Analysis of Meteorological Data. - Coming to the climatological analysis of the outbreaks, it is desirable, for a beginning, to obtain a general indication of the difference between 'plague' and 'normal' years. This requires an analysis of the weather during the twelve months previous to the 'plague' condition, as the life-cycle of the species extends over a whole year. In order to obtain an objective interpretation of the deviations from the normal climate the necessary statistics have been calculated, and are presented in Tables V and VI. The significance of the differences is related to their standard errors, a difference of twice the standard error being generally accepted as significant, although Pütter believes that less than this may often be sufficient to establish a significant difference in biological data.

In Fig. 17, the point where the central axes cross represents the average conditions of temperature and rainfall for the respective months of the year, and the deviations during years of severe (and very severe) outbreaks, are measured therefrom in Fahrenheit degrèes of temperature and inches of rainfall. This graphical representation gives a rough estimate of the climatic limitations to optimum conditions, because to bring about a very high population-density the factors which normally inhibit the population-growth of the species (outbreaks being/

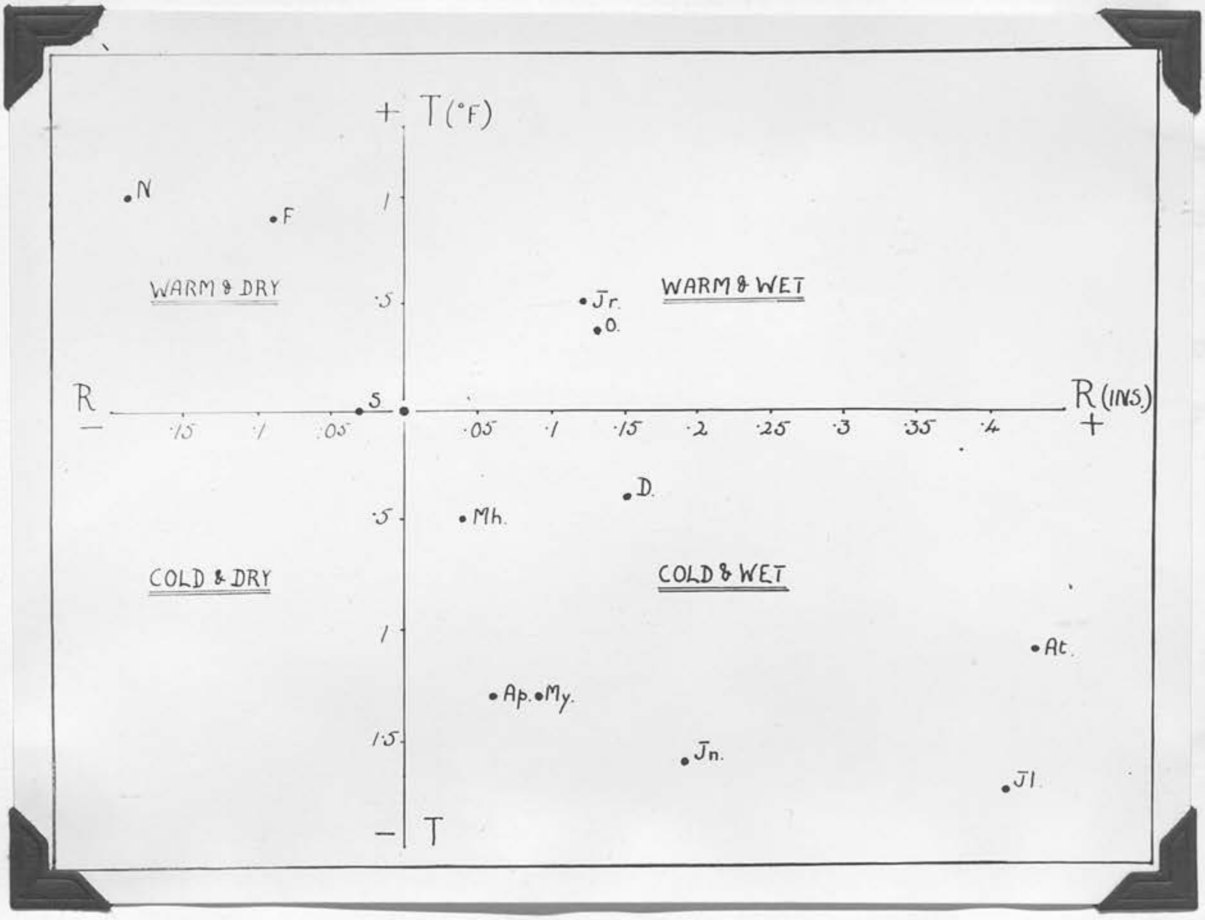


Fig. 17. - Deviations (from the normal climate) of months preceding Outbreaks.

being the exception and not the rule) must be operating with approximately minimum intensity in each phase of the life-cycle. Even without recourse to statistics it seems that the temperatures of June, July, and August preceding a severe outbreak, are considerably lower than the normal temperatures for these months. Examination of the statistics reveals that the differences are actually more than three times their respective standard errors, which undoubtedly proves their significance. Similarly, in regard to rainfall, the difference between that of August preceding a severe outbreak and the normal rainfall for the month is approximately twice its standard error, thereby making the probability of the difference being significant almost 22 to 1.

In order to provide an accurate climatological interpretation of the outbreaks it is not sufficient to prove significant differences between the weather of certain months preceding the outbreak and the average condition for these months, because it is not essential that the averages of the two sets of data should differ significantly before the weather of a particular month may be regarded as an important factor in the production of outbreak-conditions. If there is a marked difference in the variability of the two sets of data, although the means are almost the same, it follows that outbreaks are associated with a restricted range of weather. The next step/

step in the procedure, therefore, is a comparison of the variability of the weather during the months preceding outbreaks with the variability of the weather of these months in all years.

The best method of doing this is by comparing their respective standard deviations. These relations, for temperature and rainfall of each month, are shown in Tables V and VI. Examination of the statistics reveals that the standard deviation of the temperature of May (all years) is 1.4 times the corresponding statistic for May preceding an outbreak. This means that the temperature of May preceding an outbreak falls within a limited range which is a little over one-third of the normal range of temperature for May. Similarly, the rainfall of August preceding an outbreak falls within a limited range which is slightly less than one-third of the range of rainfall experienced in August over a series of years. To a mind which is not mathematically inclined, these relationships of the weather of 'plague' years to the normal climate, are more convincingly demonstrated by graphical methods (q.v. accompanying diagrams).

Shelford (1920) was the first to adopt the climograph method of Ball (1910) for studying the relations of insects to weather and climate. A modification/

modification of this method which increases its possibilities, is the three-dimensional diagram. This makes it possible to correlate the combined variations of two factors with the values of a third; for example, the correlation of thermohyetic conditions with severity of attack. The method is particularly advantageous when the functional value of one factor is affected by the value of some other factor in the environment. Thus, the moisture content of a soil is not directly related to rainfall, as it is influenced by the evaporating power of the air, which is chiefly a function of temperature. Any consideration of soil-moisture must include, therefore, both rainfall and temperature. Since the effects of these two factors upon the Tipulid population seem to be brought about indirectly, through the moisture-content of the superficial layers of the soil, the method is exceptionally valuable in this particular study.

Now, in the three-dimensional diagrams which have been constructed, a dot represents the thermohyetic conditions associated with a severe outbreak, and a dot surrounded by a circle represents the conditions associated with a very severe outbreak. Any relationship indicated by the dots is accentuated by the dots with surrounding circles. The further the dots are removed from the mean condition for the month, the greater their/

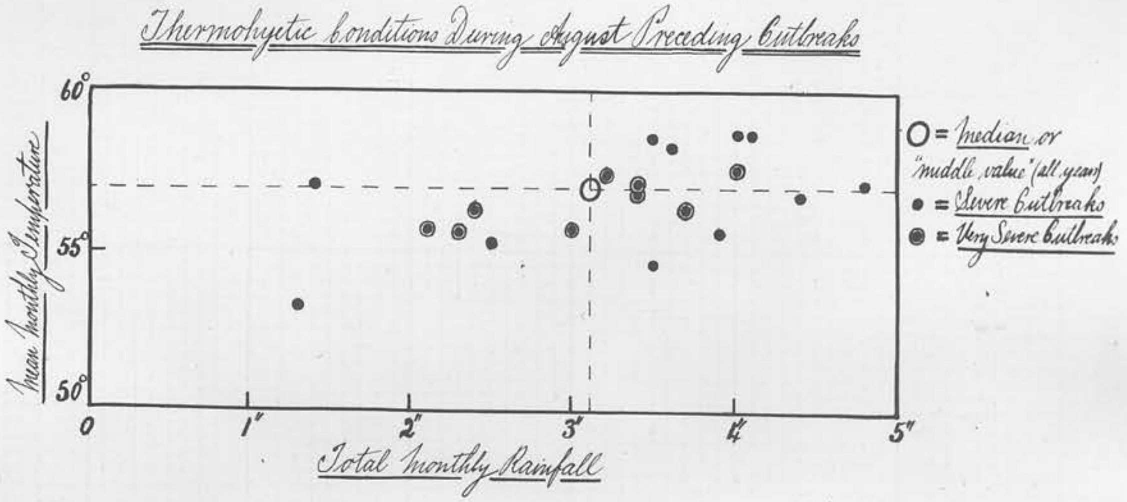


Fig. 18. - Conditions of Temperature and Rainfall during August Preceding Outbreaks.

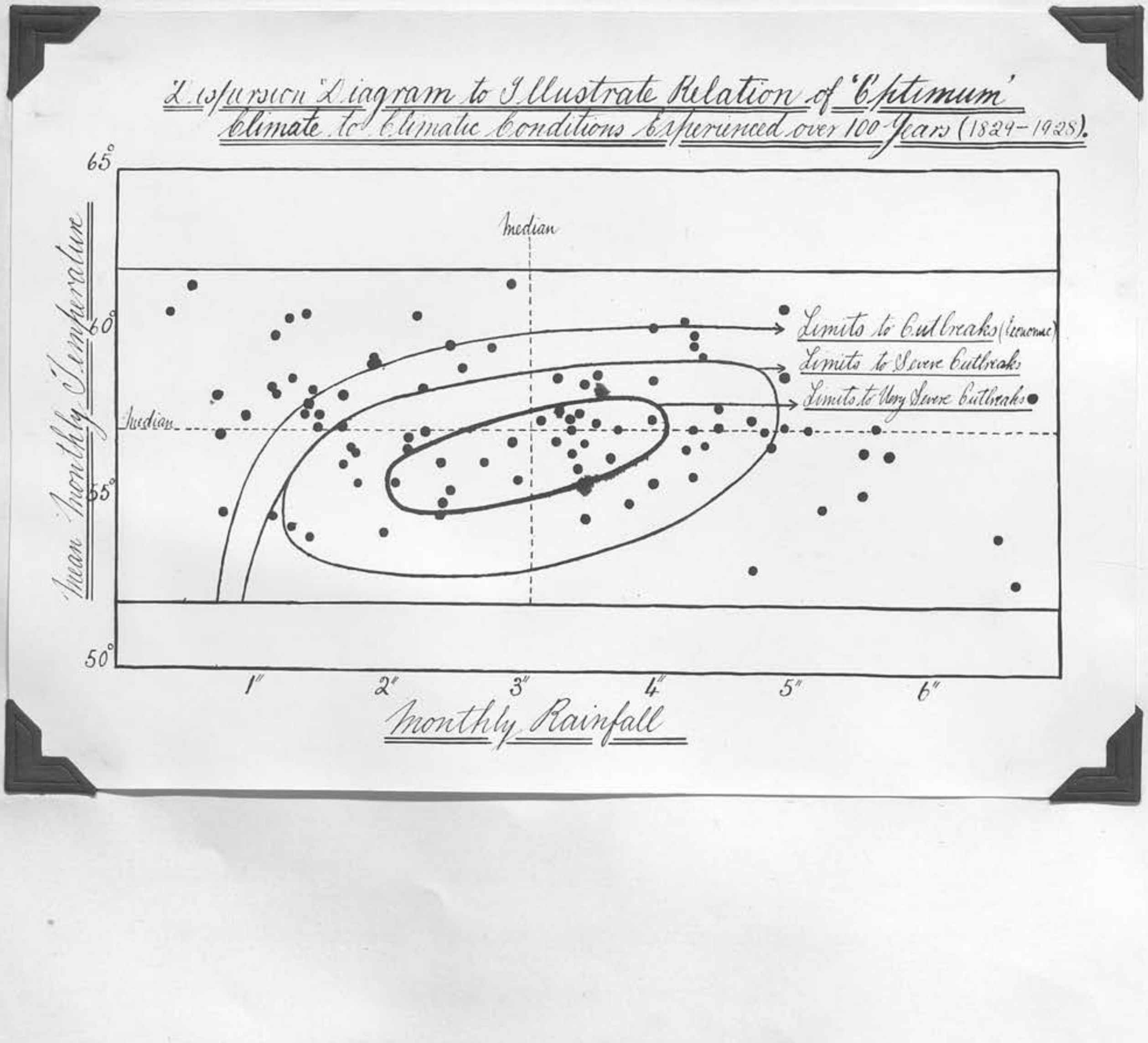


Fig. 19. - Relation of Outbreak-Conditions to the Climate of 100 years (1829-1928) - August.

their concentration,or the more definite their alignment with reference to either axis, the more critical does the climatic relationship become in the economy of the species. Moreover, a positive correlation between the temperature and rainfall of any month suggests the existence of a fairly constant soil-moisture relationship. Since the latter depends upon the evaporating power of the air as well as the rainfall, the curve of temperature versus rainfall should be somewhat similar to that showing the vapour pressure of water at different temperatures, viz., logarithmic. By quantitatively analysing, in this way, the meteorological data associated with severe (and very severe) outbreaks, it has been possible to supply a climatological delineation of these conditions, as the accompanying diagrams show.

In order to confirm that the correlations are the result of the particular climatic conditions during those specified months preceding the outbreak,it is desirable to show, in a dispersion diagram, the relations between rainfall and temperature, over a period of at least fifty years. The difference between the correlations of the two sets of data is the correct criterion of the relationship of climate to outbreak. For example, the correlation between rainfall and temperature for August preceding an outbreak is positive, whereas the correlation between/

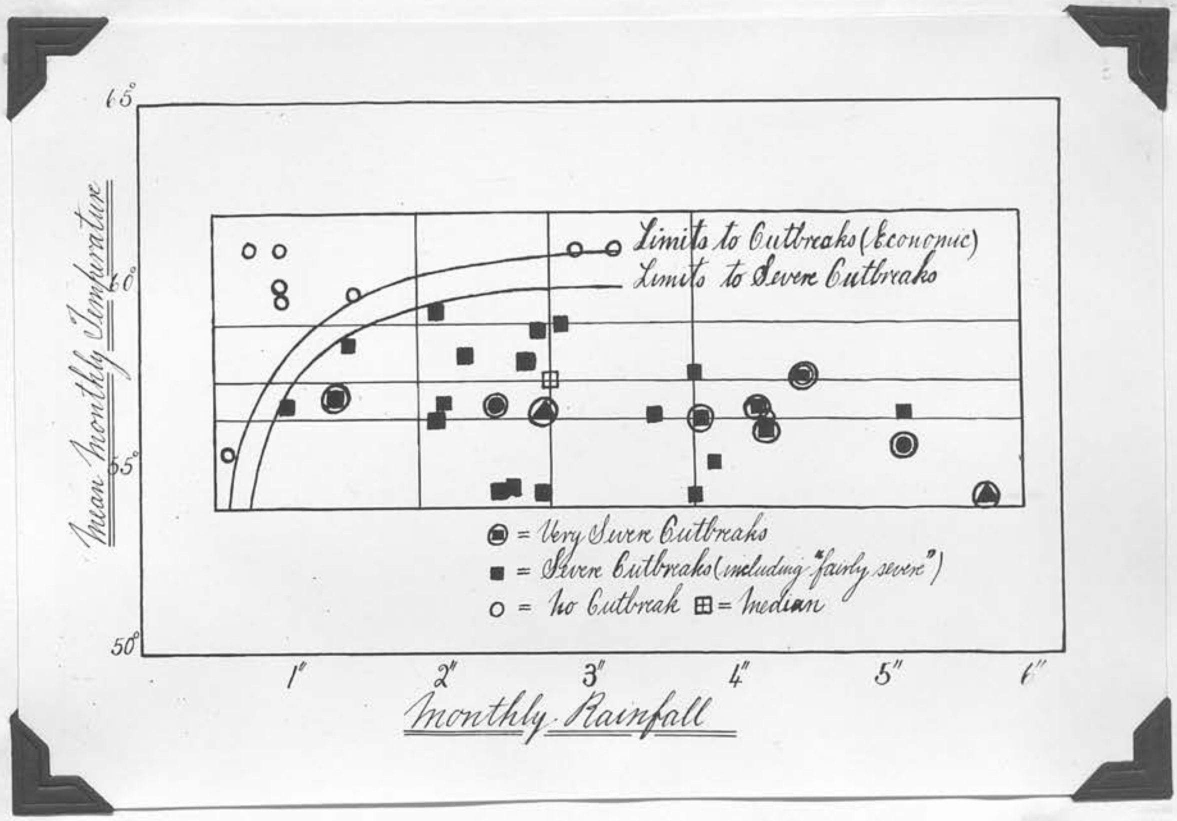


Fig. 20. - Conditions of Temperature and Rainfall during July Preceding Outbreaks.

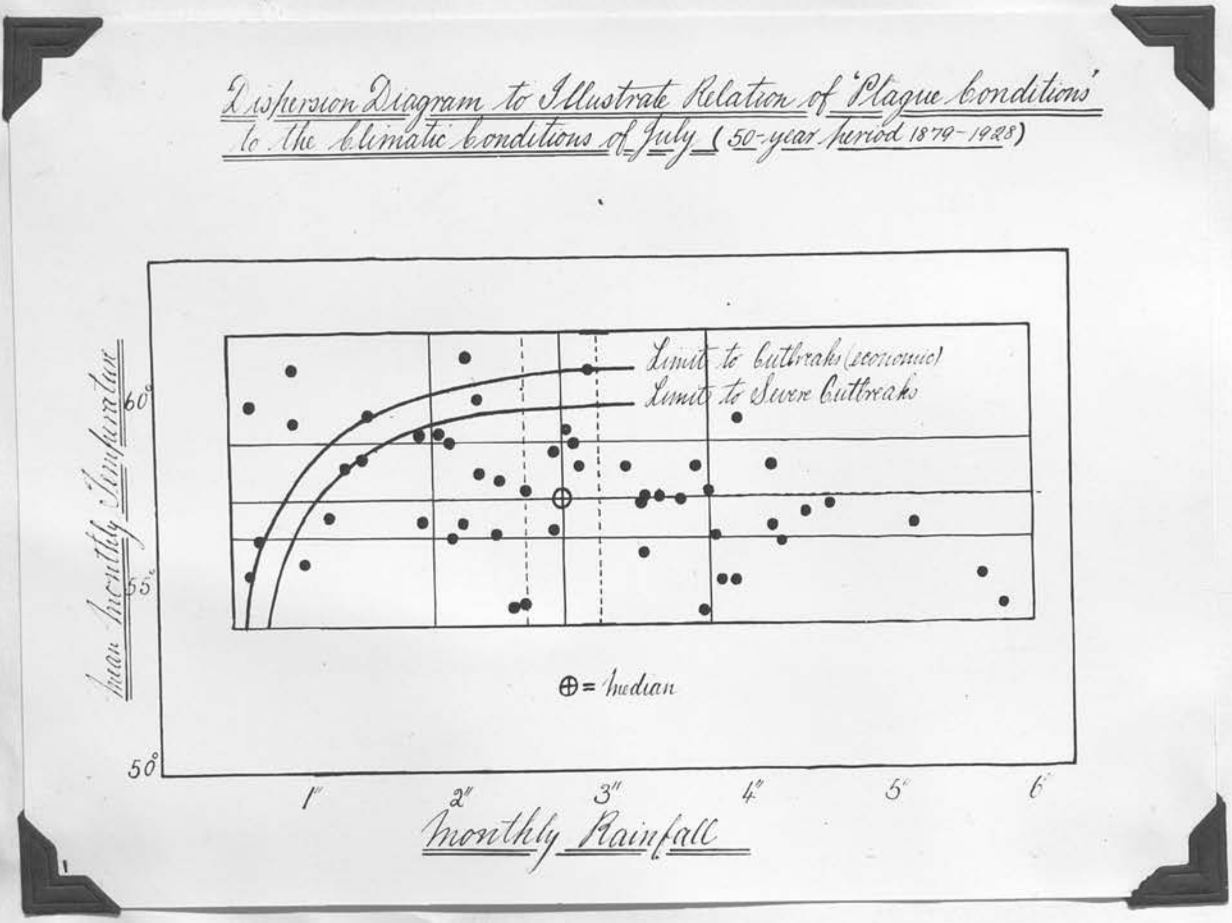


Fig. 21. - Relation of Outbreak-Conditions to the Climate of 50 years (1879-1928) - July.

between these variables for all years is negative, thereby indicating a highly significant relationship between outbreaks and the weather of the preceding August. During the study of these graphs and statistics, it should be borne in mind that the latter provide an objective interpretation of the significance of some of the data, whereas the diagrams present all the facts concerning the relationship between the variables, but leave the interpretation to the judgment of the reader.

In many instances, statistics do not reveal the full significance of the climate, especially correlation coefficients, because their magnitude is lowered by a narrow range of observations, a non-linear relationship between the variables, and the effects of a related, but uncontrolled, third variable. Further, on account of the high sensitivity of certain stages of the life-cycle to changes in climate, differences which would not be deemed significant according to the accepted statistical standards, may have a critical relationship to outbreaks. Certain relationships may be revealed only by certain statistics. In this particular instance, there is no significant difference between the mean temperature of April preceding outbreaks and the mean temperature for the month in all years, nor do the respective standard deviations show any appreciable difference, but calculation/

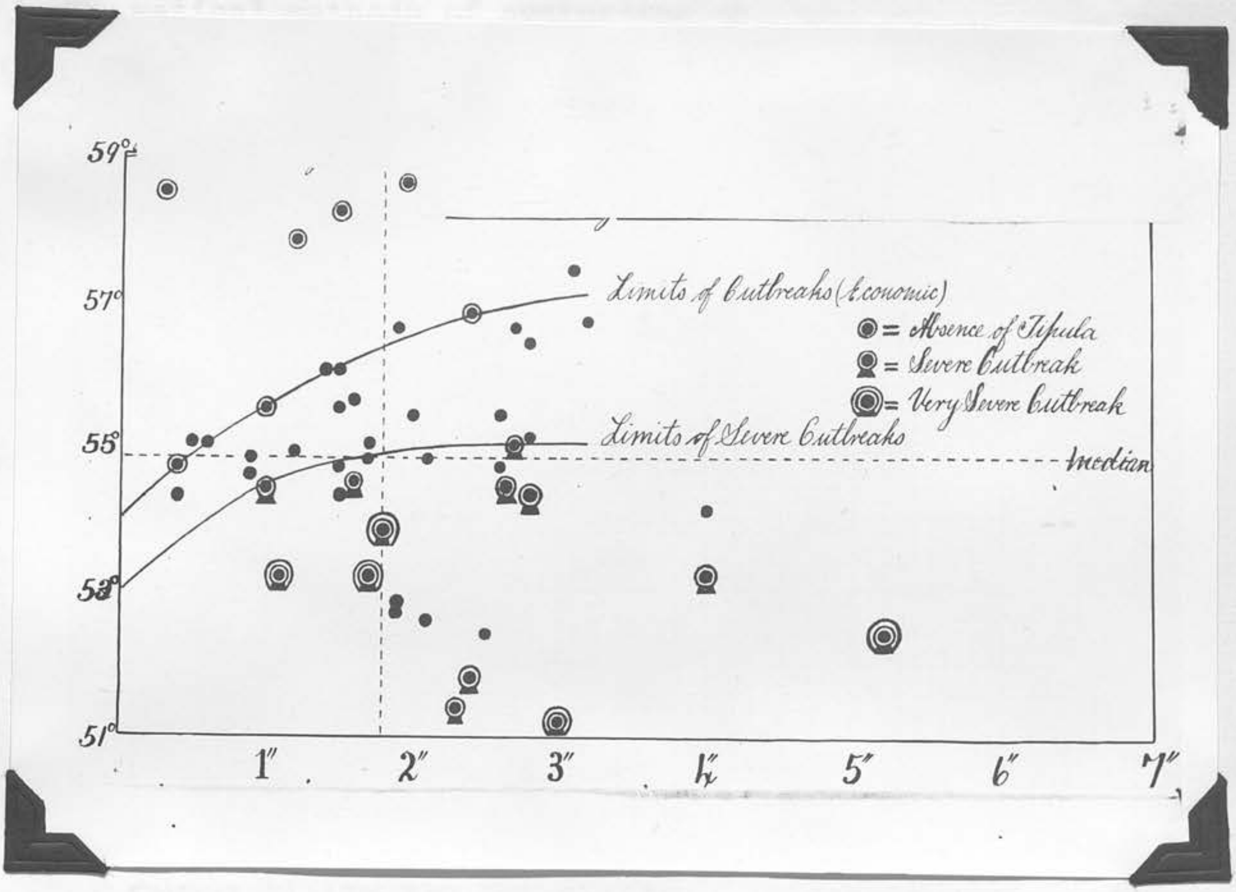


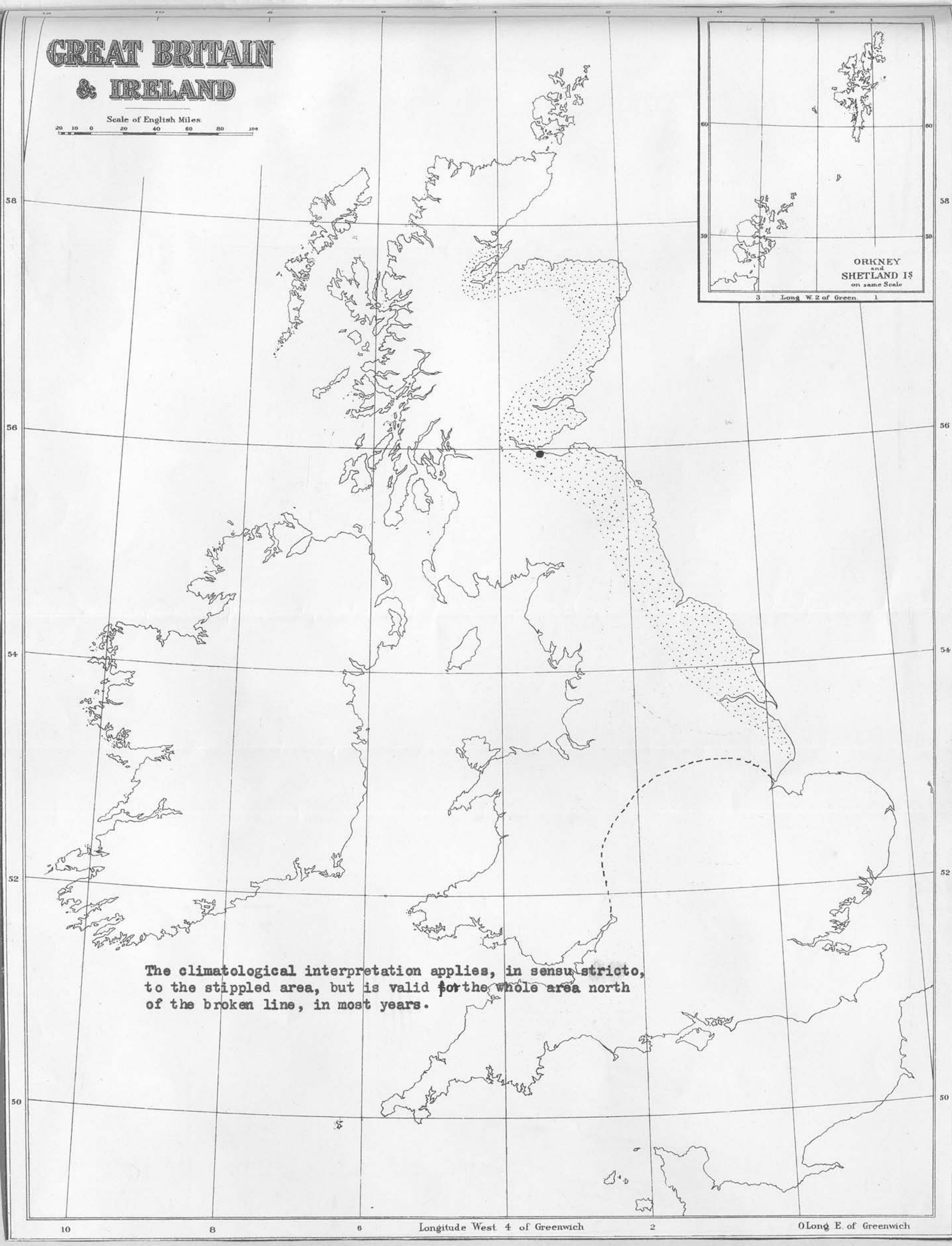
Fig. 22. - Relation of Weather in June before Outbreaks to the June Weather of 50 years (1871 - 1920).

calculation of the skewness reveals that there is a difference in the frequency distribution, sufficient to indicate that a low-temperature in April is not devoid of significance in the causation of an outbreak. Hence, for the present, it is best to regard the mathematical methods of evaluating the rôle of climate as supplementary to the graphical, because in the reverse procedure only a highly refined and highly complicated mathematical technique would prove adequate.

8. Significance of Climatic Variables. - This brings the investigation to a stage when it can be said that the population of leather-jackets in the east of Scotland and north-east of England is controlled by a sequence of factors, of which the major ones are the temperature of May, June, and July (normally too high) and the combined effect of rainfall and temperature in August, which normally results in drying out the soil-surface and grass stratum to a point below the limits of favourability for the species.

9. Criteria of Significant Variables. - The relative significance of the various months can be assessed by the deviation of the climatic limits to outbreaks from the normal climate. Thus, the average deviation of the temperature of June (preceding outbreaks) from the mean temperature/

temperature of the month, is $- 1.6^{\circ}$F., which is nearly four times the standard error of the difference. The nearest approach to this as regards significance is the rainfall of August, due to the highly restricted range which is conducive to outbreak-conditions. Hence, over a period of time, the weather in June will be outside the limits of favourability more often than either of the other months, and August will come next in this respect. While June is the most important individual month in the economy of the species, it is not so important as July and August taken together. To prove this it is only required to calculate the standard deviation for the combined rainfall of July and August preceding the outbreaks. It was found to be .69, whereas the standard deviations of the individual months were 1.33 and .84, respectively, indicating that the sum of the rainfall in July and August tends to be fairly constant in the years preceding outbreaks. This means that as regards biological effectiveness, a low precipitation in July can be offset by a correspondingly higher rainfall in August and vice versa. Enough has been said to demonstrate the method of climatological analysis, but it must be emphasized that a highly accurate determination of significant variables (beyond a few of the major ones) is a will-o'-the-wisp pursuit, since the significance of the/



The climatological interpretation applies, in sensu stricto, to the stippled area, but is valid for the whole area north of the broken line, in most years.

the environmental factors is continually varying in space and time, and the relative significance of the minor ones may be occasionally reversed.

10. <u>Interpretation of Climatological Analysis</u>. - ~~Ecologically~~, The preceding analysis has demonstrated that, in the area studied, the environment during June, July, and August, is more deficient in the supply of the factors that are necessary for the survival and reproduction of the species, than at any other time. This results from the biological peculiarities of the species, in that both eggs and pupae occupy the most primitive of terrestrial habitats (in an ecological sense), namely, the soil surface, which is liable to very great fluctuations of temperature and moisture. Just before emergence of the adults, the pupae wriggle to the soil-surface and remain there with the two cephalic horns projecting above the soil. A high temperature, with consequent dessication of the soil-surface, is fatal at this stage of the life-cycle. The weather of July is of less significance, but this is not unexpected, since the adults are comparatively long-lived, and oviposition can be delayed if conditions are unfavourable. However, high temperatures are definitely harmful. By August, most of the adults are approaching the end of their active existence, and unless there be available, those particular combinations of/

of temperature and moisture required for oviposition and development of the eggs in the soil, there follows a tremendous reduction in the population, and no damage need be expected in the following spring or early summer. As the larval stage is passed in the soil, adverse climatic conditions can be avoided by making vertical migrations, so that the weather in late autumn and winter, is of little significance unless it is cold and wet, when secondary effects ~~may~~ come into operation, presumably bacterial or fungal parasites. On the other hand, ~~the~~ many outbreaks are associated with cool, moist conditions in March and April, a fact which is probably explained by the adverse effects of weather upon the attacked plants, by way of retarding their recovery.

The writer admits that the rôle of natural enemies is an important one, in many instances; but further consideration shows that this factor is also dependent upon weather. While host and parasite are, in a general way, favoured by the same climatic conditions, their optimum climate is very seldom identical, so that certain aberrations of climate may have a differential effect upon host and parasite, resulting in a temporary escape of the host from the controlling effect of natural enemies. Compared with most insects, however, T. paludosa and T. oleracea are not subject to infestation/

infestation by parasites, or to the attacks of predators. Alexander[32] has recorded spiders of the families Lycosidae, Thomisidae, and Epeiridae as natural enemies of Crane-flies in America; and from considerable experience of the family in Scotland, Cuthbertson[33] says "their chief enemies are Scatophagid flies, and spiders of the families Lycosidae and Epeiridae." Few parasites are known, but Rennie[34] has recorded the Tachinid, Bucentes geniculata, infesting the larvae of T. paludosa in Scotland. It must be remembered also, that entomophagous parasites are dependent upon the abundance of the host, and that usually the latter attains outbreak-proportions before the natural enemies overtake it and restore control. Hence there is very little doubt that in this country, outbreaks of leather-jackets are the direct result of favourable climatic conditions, and are not due to a temporary liberation from the control of natural enemies. It is probable, however, that the latter may assume an important rôle in the reduction of the Tipulid population, after severe outbreaks, as they tend to subside very suddenly.

11. Recurrence of Outbreaks. - Before bringing this study to a close there is a matter which deserves consideration. The fluctuations in the amount of damage tend to rise (not always to the same extent) about/

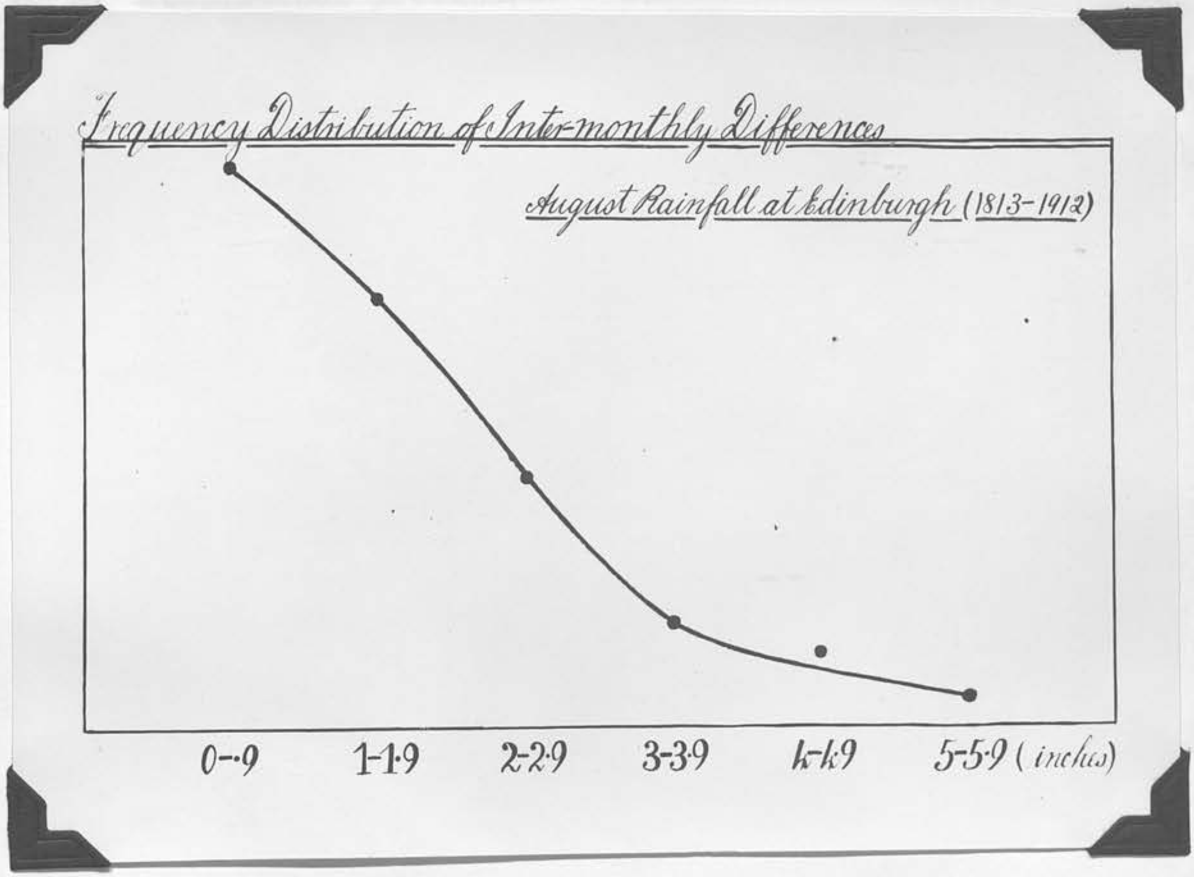


Fig. 23. - Frequency Distribution to Illustrate Tendency of Like Years to Succeed Each Other.

about every fourth year e.g. 1899, 1904, 1908, 1913, 1917, 1921, 1925, and 1929. This naturally suggests a periodicity in the occurrence of outbreaks. Now, without implicating periodicity, a tendency for like years to succeed each other can be demonstrated by the following statistical procedure. Construct a frequency curve of the differences between successive years, taken without regard to sign. If there is a tendency for like years to follow each other, the accumulation of small differences produces a curve of positive skewness, whereas if there is no such tendency, the differences are of a random character and the distribution is normal. This has been done for the August rainfall at Edinburgh over a period of 100 years, with the resultant curve of pronounced positive skewness, as shown in Fig. 23 . To test for the existence of a regular cycle one proceeds as follows, starting with the circle of 4 years which was suggested by the evidence. Make a frequency distribution of the factor being tested, taking the values of every fourth year. There will be four frequency curves, therefore, for the complete period. The amplitude and period of the cycle is directly related to the difference between the modes and the skewness of the distributions. The cyclical nature of the rainfall for August, at Edinburgh, is revealed in Fig. 24, the order being, a very dry August followed by a dry/

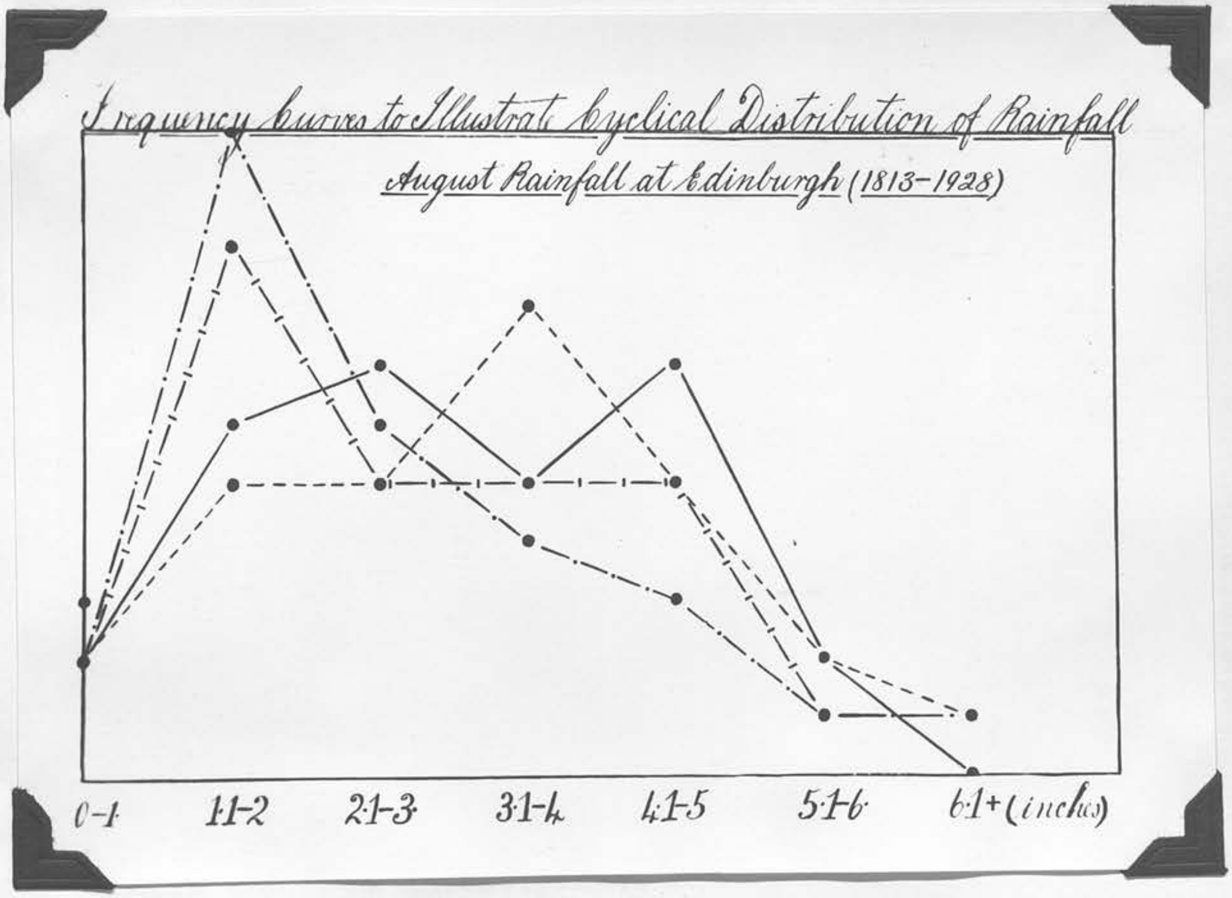


Fig. 24. - Frequency Distributions to Illustrate Cyclical Nature of August-Rainfall.

dry one, followed by two distinctly wet ones. Hence, the tendency for leather-jackets to be more abundant every fourth year has a meteorological basis, being a direct response to the cyclical trend of the weather at a critical period in the life-cycle.

12. Forecasting Outbreaks. - With such a detailed knowledge of the effects of weather and climate, it should be possible, assuming that the climatological analysis is accurate, to construct a climograph of the 'optimum' environment, and to use it as the basis for forecasting outbreaks of the pest. Although a true optimum is probably non-existent in Nature, even the best environment being a compromise, a climograph of the above nature should give an excellent indication of the liability of a locality to infestation by leather-jackets. The nature of the weather in June, July, and August is all that is necessary to forecast the possibility of an outbreak during the following May, in the area investigated, but the climate of the latter resembles the climate of the rest of Britain to a degree which makes it justifiable to say that if all the circumstances in this area are highly favourable for a severe outbreak, then considerable damage may be expected throughout the country. The technique of entomological forecasting undoubtedly requires improvement, but the writer/

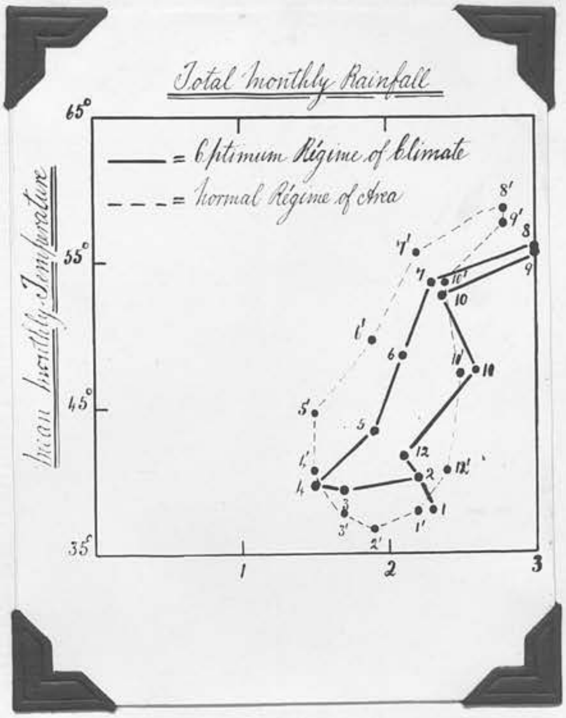


Fig. 25. - Climograph of Optimum Climate for Outbreaks of Leather-jacket.

writer believes that the prediction of abundance and distribution of insect-populations, is full of promise, and will prove to be one of the most efficient weapons in the armoury of the economic entomologist.

SUMMARY of THESIS.

(1). All natural complexes are related, directly or indirectly, through climate. The importance of quantitative methods of evaluating the rôle of various climatic factors is, therefore, apparent.

(2). In addition to a pronounced seasonal rhythm in abundance, plagues and dearths of insects come and go with considerable regularity, when viewed over a series of years. The most important period is one of approximately eleven years, with a tendency to mass periodicity during the years closely following the epoch of sunspot-minima.

(3). Insect-populations are controlled by a complex of continually varying environmental factors, of which the climatic ones assume the dominant rôle in the causation (but not always the termination) of insect-outbreaks.

(4). There are great differences in the relative susceptibility of the different phases of the life-cycle to environmental conditions, so that critical periods can be recognised. As the latter are usually restricted to a few days or weeks associated with reproduction or the early stages of existence, and the damage is caused by a more mature stage, the weather during the critical periods has a high predictive value.

(5). Insect-outbreaks result from an unusual combination of circumstances during a particular period. These 'optimum' conditions are widely separated in space and time, so that the environment normally imposes control, and outbreaks mean escape from control - an abnormal phenomenon.

(6). In addition to the academic interest of the results, particularly in relation to the equilibrium of Nature, it is believed that they may have considerable economic value, by providing a scientific basis for the prediction of outbreaks.

REFERENCES to LITERATURE in PART III.

(1) The Farmer's Magazine (1814): Beneficial Effects of Crows in Destroying Grubs, XV, p. 315.

(2) Kirby and Spence, 7th ed. (1856): Introduction to Entomology, p. 100.

(3) The Farmer's Magazine (1817): Observations on the Natural History & Recent Ravages of the Grubworm, XVIII p. 315.

(4) The Farmer's Magazine (1817): Mixing of Seed-Corn with Salt as a Preservative against Grub, XVIII p. 439.

(5) The Farmer's Magazine (1817): Quarterly Report from Lanarkshire, XVIII p. 367.

(6) Curtis, J. (1857): Farm Insects, p. 448.

(7) The Farmer's Magazine (1824): Report from Cumberland, XXV, p. 384.

(8) Quarterly Journal of Agriculture (1857): Agricultural Summary; p. 73.

(9) Quarterly Journal of Agriculture (1862): Agricultural Summary, p. 494.

(10) Quarterly Journal of Agriculture (1863): Agricultural Summary, p. 83.

(11) E. A. Ormerod (1880): Observations of Injurious Insects; p. 10.

(12) E. A. Ormerod (1881): " " " " p. 9, 10, 13, 14.

(13) E. A. Ormerod (1884): " " " " p. 27.

(14) E. A. Ormerod (1885): " " " " p.

(15) Trans. High. Agric. Soc. (1885): The Cereal and other Crops of Scotland; p. 309, 310, 312, 317.

(16) E. A. Ormerod (1893): Observations of Injurious Insects, p. 47.

(17) Trans. High. Agric. Soc. (1904): The Cereal and other Crops of Scotland; p. 332, 336, 342, 349.

(18) MacDougall, R. S. (1905): On some Injurious Insects of 1904; Trans. High. Agric. Soc. 1905, p. 226.

(19) Trans. High. Agric. Soc. (1905): The Cereal and other Crops of Scotland; p. 354, 357, 363.

(20) Jour. Board of Agric. (1904): XI p. 215.

(21) Jour. Board of Agric. (1908): XV p. 46.

(22) Trans. High. Agric. Soc. (1909): XXI, 5th ser.; p. 315, 319, 329.

(23) Monthly Returns of Crop Reporters in Scotland (Dept. Agric. Scot.): 1st June, 1917.

(24) Report on the Occurrence of Insect and Fungus Pests on Plants in England and Wales, 1918, p. 6.

(25) Monthly Returns of Crop Reporters in Scotland (Dept. Agric. Scot.): 1st June, 1918.

(26) Trans. High. Agric. Soc. (1926): XXXVIII, 5th ser.; p. 263, 266, 271.

(27) Report on the Occurrence of Insect Pests on Crops in England and Wales, 1925-27; p. 15, 27.

(28) Monthly Agricultural Report (Dept. Agric. Scot.): 1st June, 1929.

(29) Insect Pests of Crops, 1928-31: Bull. No. 66, Minist. Agric. & Fish.

(30) Evans, A. C. (1934) - Studies on the Influence of the Environment on the Sheep Blowfly, L. sericata Meig. I. The Influence of Humidity and Temperature on the Egg: Parasit. 26, p. 366.

(31) Davies, M. & Hobson, R. - (1935). The Relationship of Humidity to Blowfly Attack: Ann. App. Biol. 22. p. 279.

(32) Alexander, C. (1920) - The Crane-flies of New York - Part II: Biology & Phylogony, Cornell Univ. Mem. 38, p. 727.

(33) Cuthbertson, A. (1926) - Crane-flies of the Inner Hebrides: Scot. Naturalist. p. 53.

(34) Rennie, J. and Sutherland, C. (1920) - On the Life History of Bucentes geniculata: Parasit. 12. p. 199.

APPENDIX A.

(ADDITIONAL REFERENCES to TIPULID EPIDEMICS).

1813 - 'The lea oats suffered much this season from the grub worm, few fields having escaped its ravages, more or less.' - The Farmer's Magazine: XIV p. 369. (Report from Forfarshire). 'The injury occasioned by that destructive insect (the grubworm) has been very extensive. There are few fields which have entirely escaped its virulence.' - The Farmer's Magazine: p. 369 (Report from Glasgow).

1817 - 'Many fields of oats suffered from the grub, to an extent almost unprecedented in this county.' - The Farmer's Magazine: XVIII p. 358 (Report from Dumfriesshire).

'A good many of those (fields) sown after lea .... were much thinned by that voracious insect the grub.' - The Farmer's Magazine: XVIII p. 365 (Report from Kincardineshire).

'There is scarcely a field that has not suffered more or less from its (the grubworm) depredations.' - The Farmer's Magazine: XVIII p. 371 (Report from Midlothian).

'Those fields so desperately infested with the grub are wonderfully improved' - The Farmer's Magazine: XVIII p. 378 (Letter from Lancaster, England).

1824 - 'The spring sown corns have all come very thick, and are willing to grow; but indications of the grub have appeared among the oats.' - Quart. Jour. Agric.: XII p. 163.

1862 - 'In Foveran and New Machar (Aberdeenshire) the ravages of the grub during the last ten days have called forth loud complaints.' - The British Farmer's Magazine: XLII p. 70.

1863 - 'That most annoying enemy of the farmer, the grub, has been committing great ravages in the north this year again.' - Quart. Jour. Agric.:   p. 83.

1879 - At Maxwelltown, Dumfries, 'grubworms had been counted at the rate of twelve per square foot'; and in Northumberland, 'these grubs were very injurious'.- Ormerod's Report on Injurious Insects of 1879, p.11.

1880 - On the strong alluvial land of North Lincolnshire, 'the T. oleracea grubs were most destructive amongst barley'; and at Spilsby the pest is reported as 'eating the wheat down since February.' Again, at Darnaway Castle, Morayshire, 'a considerable number of grubs were noticed.' - Ormerod's Report on Injurious Insects of 1880, pp. 10-14.

1883 - 'You ask about Tipula larvae in Essex. They are very bad; almost all the early peas are ploughed up, and much of the wheat has suffered.' From Caithness/

Caithness came the report that 'T. oleracea has been very prevalent on clay soils, on corn after rough lea'; and from Cheshire it was reported that 'dozens of the grubs are found under a sod.' - Ormerod's Report on Injurious Insects of 1883, pp. 28-30.

1884 - On the 7th of May, specimens of leather-jackets were forwarded (from near Nottingham) to Miss Ormerod, with the note - 'I send you specimens of the grub that is destroying us acres of beans .... if the soil is slightly scratched they are to be seen by the score on the square foot.' - Ormerod's Report on Injurious Insects of 1884, p. 25.

'There was more damage done by grub in Islay than has been seen for the last 14 years'; 'a good many acres were thinned by grub' (Rossshire); 'the damage from grub was greater than usual, and spread over the whole district' (Shetland). - Trans. High. Agric. Soc. (1885) p. 311, 322, 324.

1892 - 'On land out of condition the crops were very much injured by grub and wireworm (Fifeshire); 'grub was rather destructive in some places (Perthshire). - Trans. High. Agric. Soc. 1893 , p. 230, 232.

1903 - 'Oats were injured by grub' (Dumfriesshire); 'the oat crop was very much damaged by grub-worm in spring' (Argyllshire); 'the oat-crop suffered much/

much from wireworm and grub' (Fifeshire); 'lea-oats were badly thinned by grubworm' (Banffshire). - Trans. High. Agric. Soc. (1904), p. 330, 335, 339, 345.

1904 - 'The oat-crop suffered from grub-worm' (Lanark); 'in some fields grub was very bad' (Argyllshire); 'grub very bad on lea-oats' (Dumbartonshire). - Trans. High. Agric. Soc. 1905, p. 358, 360.

1908 - 'Grub worm more prevalent on the oat crop than usual' (Ayrshire); 'a good deal of damage done in some districts to lea oats by grub' (Dumbartonshire). - Trans. High. Agric. Soc. 1909, p. 316, 319.

1917 - 'Leather-jackets and slugs were specially harmful'. - Report on the Occurrence of Insect & Fungus Pests on Plants in England and Wales in the year 1917 p. 12: (Board of Agriculture - Food Production Dept.)

1918 - 'A large area of oats was affected with grub' (Lanarkshire); 'grub was very bad in lea oats' (Dumbartonshire); 'grub did a certain amount of damage' (Rossshire). - Trans. High. Agric. Soc. 1919, p. 295, 297, 308.

1925 - 'A good deal of damage to lea oats by grub' (Dumbartonshire); 'many acres of Abundance and such varieties were cleaned up' (Forfarshire); 'grub did considerable damage' (Morayshire). - Trans. High. Agric. Soc. 1926, p. 260, 265, 269.

1929 - 'Some fields badly damaged by grub' (Wigtownshire); 'oats were injured by grub in many cases' (Kincardineshire); 'oats suffered in places from leather-jacket' (Dumbartonshire). - Trans. High. Agric. Soc. 1930, p. 223, 231, 227.

APPENDIX B.

(Meteorological Data for the Years Preceding Outbreaks).

Rainfall.

	J	F	M	A	M	J	J	A	S	O	N	D
1813*	.8	2.3	.2	2.0	2.1	2.2	1.3	3.4	1.0	2.8	4.0	.9
1817*	1.8	1.5	.9	.2	2.2	1.9	5.2	2.3	3.0	1.9	.9	2.4
1824	.9	1.7	1.3	.6	2.3	1.0	4.2	3.9	1.8	3.1	1.0	4.4
1829*	2.5	1.6	.3	3.3	1.8	.8	4.6	3.4	2.3	.8	3.9	2.2
1845	1.8	.6	1.7	.40	.15	2.7	2.4	2.1	2.7	.8	3.9	.4
1857	1.5	.4	2.0	1.8	3.1	3.0	2.0	3.5	5.1	.7	1.4	2.7
1862	3.8	.9	4.6	1.3	.7	2.7	3.5	3.6	4.7	2.3	4.0	1.0
1863*	3.4	1.2	.7	2.0	3.7	2.8	2.7	3.7	2.1	3.4	2.0	2.8
1879	1.3	1.8	2.3	2.2	2.7	2.4	.7	4.0	2.8	1.8	2.9	2.2
1880*	.5	1.5	1.5	3.2	1.7	5.1	5.8	2.4	1.6	.9	1.8	1.4
1883	2.2	1.0	1.0	1.4	2.6	2.8	3.7	1.4	1.8	2.6	2.8	4.9
1884*	3.8	1.0	1.6	.8	.7	1.8	4.2	3.2	2.2	2.	1.3	1.0
1892	.9	1.8	1.0	1.0	1.5	.5	2.7	4.4	4.0	1.7	1.4	4.5
1903	3.9	4.0	4.1	1.0	2.1	2.3	2.4	1.3	1.4	1.0	.6	1.6
1904*	2.9	2.4	1.1	1.7	1.2	1.0	3.8	2.5	2.0	5.7	1.5	1.1
1908	2.2	.9	3.1	1.9	2.7	2.4	2.5	3.5	1.3	7.9	1.0	3.8
1917*	1.7	.6	1.1	1.2	1.5	3.0	5.2	4.0	1.5	4.5	3.2	2.9
1918	2.1	2.5	.5	.6	1.4	1.7	1.3	4.1	1.0	2.5	2.0	2.1
1925*	2.6	3.5	2.2	2.9	4.4	1.8	4.2	3.0	2.8	3.4	1.1	3.1
1929	.8	.8	.2	1.6	1.4	5.2	2.1	4.8	2.2	3.0	3.0	1.8

* very severe outbreaks

Temperature.

	J	F	M	A	M	J	J	A	S	O	N	D
1813*	35.6	39.7	43.3	44.8	49.	55.3	57.	57.2	53.3	47.3	39.8	34.9
1817*	38.7	40.3	39.6	44.5	48.2	53.2	55.7	55.6	50.9	46.3	38.5	35.2
1824	39.8	39.	39.6	45.2	51.3	53.3	56.4	55.6	51.9	44.8	44.6	37.3
1829*	32.1	38.8	39.6	41.9	51.2	56.9	57.6	57.	54.6	48.4	44.8	43.4
1845	36.6	35.4	36.6	45.2	48.8	55.	56.9	55.7	53.1	47.1	43.1	33.
1857	37.9	41.1	40.9	44.9	48.1	58.8	59.	58.6	52.7	51.4	42.8	40.4
1862	38.1	40.3	37.4	45.	49.8	54.9	56.6	58.4	53.5	49.5	38.	37.
1863*	38.7	41.2	43.	44.6	50.6	53.4	54.5	56.4	52.6	47.2	36.8	42.4
1879	31.2	34.8	37.4	40.6	51.4	56.8	61.	58.8	54.8	48.9	38.	31.
1880*	37.	43.2	41.6	45.8	46.2	52.4	54.4	56.4	52.	45.6	39.8	34.8
1883	39.1	41.2	36.8	45.8	50.	54.3	57.8	57.1	57.3	48.4	40.	33.6
1884*	41.3	40.7	42.3	44.5	48.8	53.8	56.2	57.5	54.	47.6	41.6	41.1
1892	36.6	37.4	37.4	43.8	48.	55.	58.9	56.8	56.	47.8	41.4	39.7
1903	37.3	42.9	41.9	40.8	45.2	51.4	54.6	54.2	53.3	47.4	44.7	39.4
1904*	39.4	36.3	38.6	45.5	47.5	53.2	56.5	55.4	53.	47.9	42.4	37.2
1908	37.7	40.7	38.5	41.1	46.3	51.8	54.6	54.6	54.1	47.7	42.7	39.3
1917*	35.5	35.9	37.0	40.2	48.6	51.1	56.8	57.6	53.3	47.8	44.4	38.1
1918	36.6	43.	41.2	41.7	49.3	56.4	60.	58.9	56.5	45.1	46.1	38.
1925*	40.7	38.5	40.3	42.5	47.5	54.0	56.8	55.8	52.5	47.8	44.	44.7
1929	36.1	34.1	44.2	41.7	47.5	50.9	56.9	57.1	53.3	48.2	44.7	38.7