PHYSIOLOGICAL LIFE HISTORIES OF TERRESTRIAL ANIMALS AND MODERN METHODS OF REPRESENTING CLIMATE[1]

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I. INTRODUCTION

Modern ecology had its beginning with the publication of Warming's work on the sand dunes of Denmark. He discovered in these studies that it is possible to classify and arrange the various plant communities which he found there in a natural order. This is the distinctive thing about modern ecology; the ecology of communities of organisms is known as synecology. It enables us in our studies of the peculiarities of various domestic species and pest species to refer them back to the original conditions in which they were found. In other words, it has made it possible for us to locate organisms in their natural environments correctly and in a manner which other trained ecologists can understand. From time to time one hears biologists, particularly zoologists, asking why the term ecology is used and what modern ecology is all about, anyway, but these people have merely neglected to become acquainted with its distinctive features which are synecological or have to do with the ecology of communities.

Perhaps the second distinctive feature of modern ecology lies in the attempt of ecologists to study what are known as physiological life-histories of organisms. By this is meant all physiological changes during the life cycle or during an annual cycle in the case of animals with several generations, and the relations of these physiological changes to external conditions. Ganong (1917) expressed the view that if we could learn the physiological life-history of the plant we would be well on the road to the solution of the ecological problem.

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II. EXAMPLES OF PHYSIOLOGICAL LIFE-HISTORIES

Some of the best known examples of physiological life-histories are suggested by some of the insects. One of the tiger beetles (*Cicindela hirticollis* Say) deposits eggs in June; these hatch in the sandy soil in which they are laid, feed on ants and other insects, molting once or twice during the summer. When the cold weather begins they close their burrows and remain below ground during the winter. They begin feeding again early in the spring, pass to the pupa stage, and emerge as adults in July. After feeding for a few days the adults burrow into the sand and remain until the following June when they come out of hibernation, deposit their eggs and remain in their habitats in some numbers so that in the ordinary summer, one is able to collect these old individuals mixed with the new freshly emerged ones of the next generation. Thus in this species we have two years between generations and some special conditions apparently necessary both in the larva and in the adult, before they will proceed with development at the time of the usual hibernation period.

The codlin moth of the apple passes the winter in the larval stage, pupates after a few warm days in spring. The pupae emerge as adult moths about the time that the apple trees have begun to leaf out. They deposit eggs which on hatching into small larvae provide the so-called worms which are familiar in wormy apples. The small larvae enter the young fruits and after feeding for a time reach the fully grown condition, make their way out, down to the tree trunk where they spin a cocoon, pupate, and produce a moth which again lays eggs for the second generation. Under certain weather conditions a third generation is produced late in the summer, but under certain other weather conditions no larvae of this second generation of moths will proceed with development until after some special conditions of temperature and moisture have been imposed upon them. Thus we see the physiological life-history of the codlin moth varies with weather conditions and presents some special problems, though perhaps problems of a kind which are common to most animals.

III. THE EFFECT OF CONDITIONS ON PHYSIOLOGICAL LIFE-HISTORIES

From the standpoint of insect pests such as the codlin moth it is important to know how external conditions effect the rate of development, fecundity and length of life of the individual. It has long been known that temperature has an important effect. De Candolle, the noted Swiss botanist, stated in 1830 that the time to maturity of wheat, for example, differs with the mean temperature above 6°C. So that the "total degree days" or the number of degrees above 6°C multiplied by the number of days has a constant value. When De Candolle stated this he also stated the time temperature curve for the development of a plant is an equilateral hyperbola, the reciprocal of which is a straight line crossing the axis of temperatures at the temperature at which development does not take place but immediately above which development begins to take place. In the ninety years that have elapsed since this discovery, this principle has been discovered repeatedly and announced as new and original. (See Figure 1). It was not until 1914 that the Danish physiologist, Krogh, working upon the frog's egg discovered that this law holds good only within a limited range of temperature. He published a list of the various species which had been studied and gave the limits within which the law could be expected to hold. It will be seen from Figure 1, particularly from the reciprocal curve, that development is a little too rapid at the lowest temperatures and considerably too slow at the highest temperatures to conform strictly to the equilateral hyperbola and a fixed total temperature for completion of development. Nevertheless this method constitutes a valuable guide in many kinds of study but it has been found in the course of studies carried out on the chinch bug and codlin moth in the University of Illinois Vivarium under the auspices of the Natural History Survey that many factors other than temperature influence

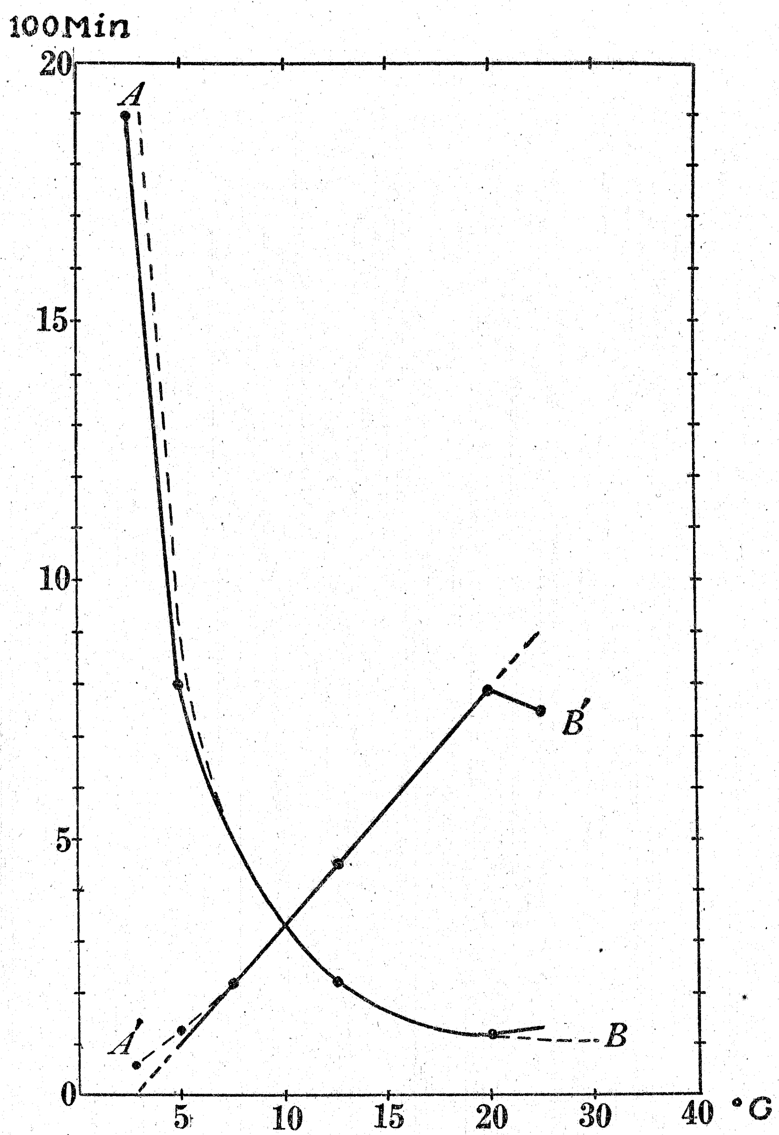

Fig. 1. Curves of the development of the frog's egg at different temperatures. The curve AB is the time temperature curve for development of the first cleavage plane. The curve A'B' is the reciprocal of the time temperature curve, i. e. the $\frac{1}{\text{Time in minutes}}$ plotted on the temperatures in question. The distance above the axis of temperatures represents relative velocity of development.

enter the stream from gas works, tanneries, and manufacturing plants above the lower falls.

Collections made in 1892, before pollution became notably apparent, included nine species of gastropod mollusks, three being water breathers and six air breathers, These species were identified as:

Musculium transversum
Musculium partumeium
Bythinia tentaculata
Planorbis trivolvis
Physa gyrina
Physa sayii
Physa heterostropha (=oneida)
Galba catascopium
Galba caperata

Individuals were notably abundant, thickly covering the rocks and the shore. In 1897 it was observed that the sewage was increasing in volume and pollution was becoming more noticeable, the water looking like very heavy, greasy dish water. The river was visited and examined at short intervals from 1898 to 1919. Each year it was noted that pollution was rapidly increasing. In 1907, the water-breathing mollusks, *Musculium* and *Bythinia,* had succumbed and none could be found. The air-breathers, *Galba, Planorbis,* and *Physa,* still held out, though reduced in number of individuals. An examination made in 1910 failed to discover a single living mollusk of any species. Apparently the water had reached such a state of concentrated pollution that even the air-breathing mollusks, which normally come to the surface to take free air, could not adapt themselves to this most unfavorable environment and were either killed or compelled to migrate down the river to a point where pollution was less deadly. During the following years, 1910 to 1913, the river was visited but no mollusks were found.

During the summer of 1912, Mr. G. C. Whipple, professor of Sanitary Engineering in Harvard University, made a study of the effect of the sewage pollution on certain animal and vegetal life in the Genesee River (Fisher, is badly polluted (Shelford, 1918, p. 27; Wells, 1918, pp. 562-567). Young fish are relatively more sensitive than adult fish. It is noteworthy that the more resistant species of fish are inhabitants of sluggish bodies of water, as ponds and shallow lakes, while the least resistant species live in running streams. It seems to be a question of the amount of oxygen necessary for the well being of the fish.

The ill effect of sewage pollution is most marked on the bottom of bodies of water, where a sludge is formed, often of great thickness (as much as ten feet in several cases), consisting of a mass of soft, black, sediment, with a high content of organic matter, in which only a few organisms, normally inhabitants of polluted streams, can live (e. g. septic Protozoa and Rotifera, foul-water algae, and slime-worms, Tubificidae). This effect on the bottom is perhaps the most serious phase of stream pollution because the septic condition of this area continues in operation long after the original source of contamination ceases to operate. This sludge formation renders the bottom unfit for clean-water life upon which many fish depend for food. The time necessary for the recovery of the normal biota of such a stream will in most cases be of long duration, and in the case of a stream polluted with wastes from mines and chemical manufacturies, there may never be a return to the original condition.

In New York State, the Genesee River, at Rochester, has afforded a striking example of stream pollution, of the effect of this pollution on certain animal life in the river, and of the return of this life when the amount of pollution had been largely reduced. This stream has been under observation by the writer for a period of twenty-seven years (1892 to 1919) and collections of the molluscan life have been made from time to time, both before the period of maximum pollution and since that time. The portion of the river studied lies below the lower falls north of Rochester, and about a quarter of a mile below the outfall of several large trunk sewers, the sewage being discharged into the stream in a crude condition. Refuse and other waste matter, both liquid and solid, also

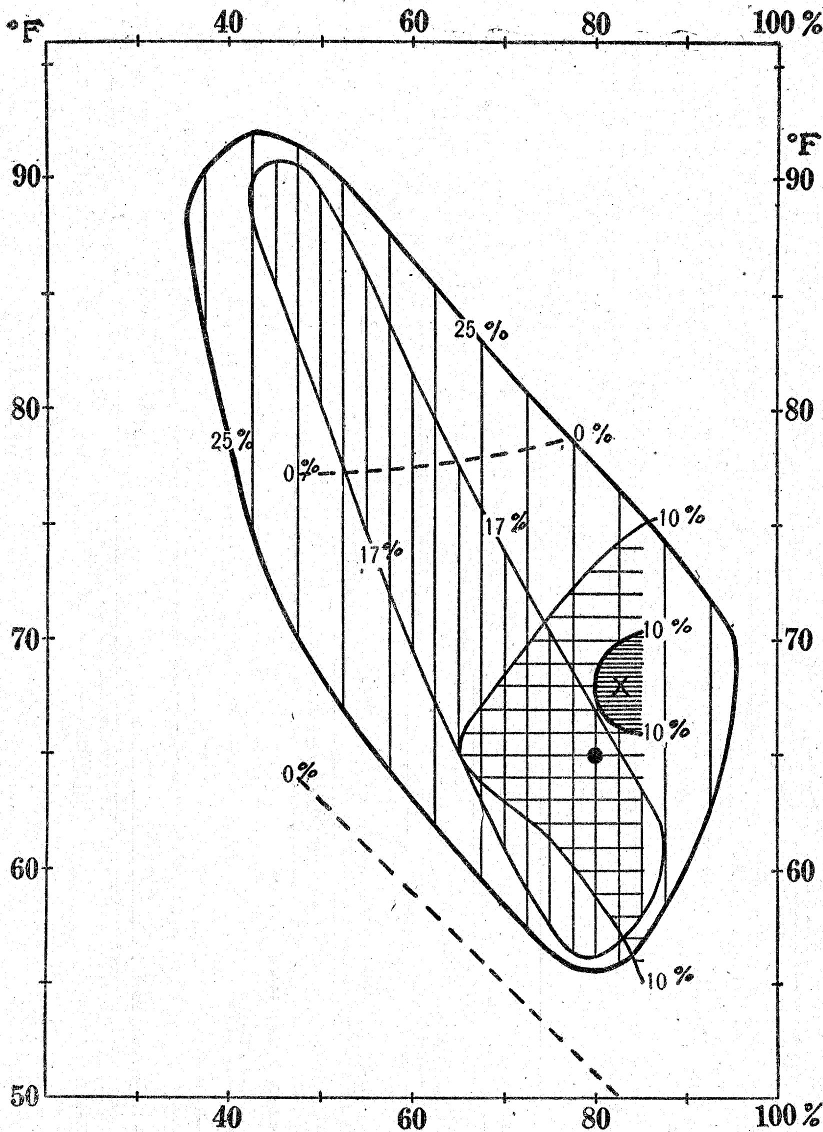

Fig. 3. Climograph for the death-rate of man shown with horizontal rulings. The broken lines (0%) are drawn along the combined temperature and humidty conditions under which the death-rate is normal and hence the deviation from normal 0%; for the white man. The curve bounding the sparsely ruled area and labeled 10% passes through the temperature and humidity conditions in which the death-rate is 10% below normal for the white man; the lowest death-rate 65°F. and 80 per cent humidity is shown by a black dot. The closely ruled area shows a death rate 10% less than normal for the negro and the x is placed near its center on a humidity of 81 per cent and a temperature of 68°F. (after Huntington). The vertically ruled areas indicate the deaths (% individuals) of codlin moth pupae under experimental conditions.

the length of the stages ten or more per cent as compared with the constant temperature of the same numerical value (see Figure 4 B). Another very interesting result of the experimental work is the demonstration of the fact that the so-called threshold of development for temperature which is the temperature just above which development begins, differs under wet and dry conditions

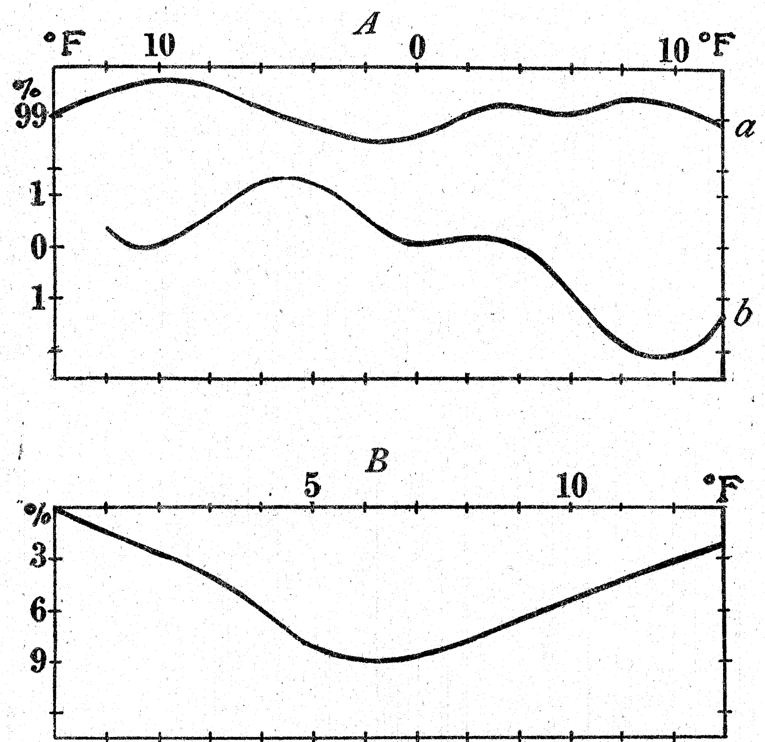

Fig. 4A and 4B. Shown the effects of variability on human efficiency and insect metabolism.

(a) Curve A shows the effect of changes of temperature on the efficiency of 300 men in a Connecticut factory. The center 0 indicates no change in temperature from the preceding day. At the right are shown rises of temperature and to the left fall in temperature in degrees. In general variability favors efficiency. Curve B shows the same for students but decrease in efficiency with rise in temperatures which exceed 5° are evident (after Huntington).

(b) Is a curve showing the effect on the length of the pupal stage of the codlin moth of a daily rise in temperature indicted by the scale. The vertical scale gives the per cent deviation from a constant temperature with the different amounts of increase.

and in different generations in the same year also in different years. The threshold of development for the egg as determined by Mr. Spooner is somewhat lower than that of the pupa, while the threshold of development temperature of the larva is perhaps still lower. These threshold values are calculated by the use of the equilateral hyperbola and its reciprocal as already described and of course the values are only approximate. Calculations of the threshold can usually be made whenever a change in the factor amounting to about 1/3 of the maximum daily range of that factor halves or doubles the length of the stage. Thus the ordinary range of temperature to which the codlin moth may be subjected is at most about 30°C, and lowering the temperature 10° usually nearly doubles the length of the stage. This ratio for temperature is known as the quotient for 10° or the Q_{10}. Likewise the total range of humidity to which the codlin moth may be subjected is almost 90 per cent and lowering the humidity 30 per cent under certain conditions will double the length of the stage and thus a humidity threshold may be calculated under these conditions. The total degree-days for the length of codlin moth stages differs greatly with humidity and other conditions so that the results of experiments do not coincide exactly with the outdoor variable temperature and humidity conditions.

Having noted the effects of various climatic factors on the codlin moth some comparison with man who has been particularly studied will be valuable. Turning to Figure 3 we note that the line representing a death-rate 10 per cent below normal passes through a considerable number of different temperatures and humidities just as does the minimum death-rate of the codlin moth pupae and that both are oblique in the same direction but that man being a warm blooded animal does not show as great a temperature range as does the cold blooded codlin moth. On the same figure we have drawn the 10 per cent below normal death-rate of negroes and the center of this area falls on temperature about 68°F. and humidity about 83, while that of the white man lies at 65° and 80 per cent relative humidity.

These two points are significant first in that our rooms are all too warm and dry being at 70°F. and 30 per cent instead of 65°F and 80 per cent. The negro who came to America from moist tropical Africa differs from the white man who came from somewhat drier and much cooler western Europe.

Variability of temperature is stimulating to the codlin moth pupae (see Figure 4 B). The amount of respiratory diseases among children in school rooms with window ventilation and accordingly more variable temperatures is only about half as geat as with fan ventilation. Furthermore Figure 4 A is taken from the work of Mr. Huntington and shows that variable temperatures increase efficiency. The manual laborer's efficiency is increased either by a rise or fall from day to day. Efficiency of brainworkers, especially students, is increased by a fall of temperature from day to day and decreased by a rise in temperature from day to day. And it seems that we have done well to choose the time of year for their most important examinations when the temperature is rising from day to day, it apparently being our purpose to eliminate as many students as possible. It is altogether possible that our schools should begin in the middle of August and close considerably earlier than they do.

Huntington has made a careful study of death-rate in relation to climate and weather and has compared business, school attendance, etc., with health or the death-rate curve inverted. Figure 5, curves A and B, show this relation for the entire eastern United States for 1880-1910. The curves for Great Britian are similar. Curves B and C of Figure 5 show the death-rate in Chicago and damage by chinch bugs in Illinois. During the period from 1885 to 1895 the death-rate in Chicago rose high. These were troublous times with strikes, bloody anarchists, and Haymarket riots at the close of the eighties, due to the presence of a democratic president in Washington and certain wild-eyed agitators in Chicago,

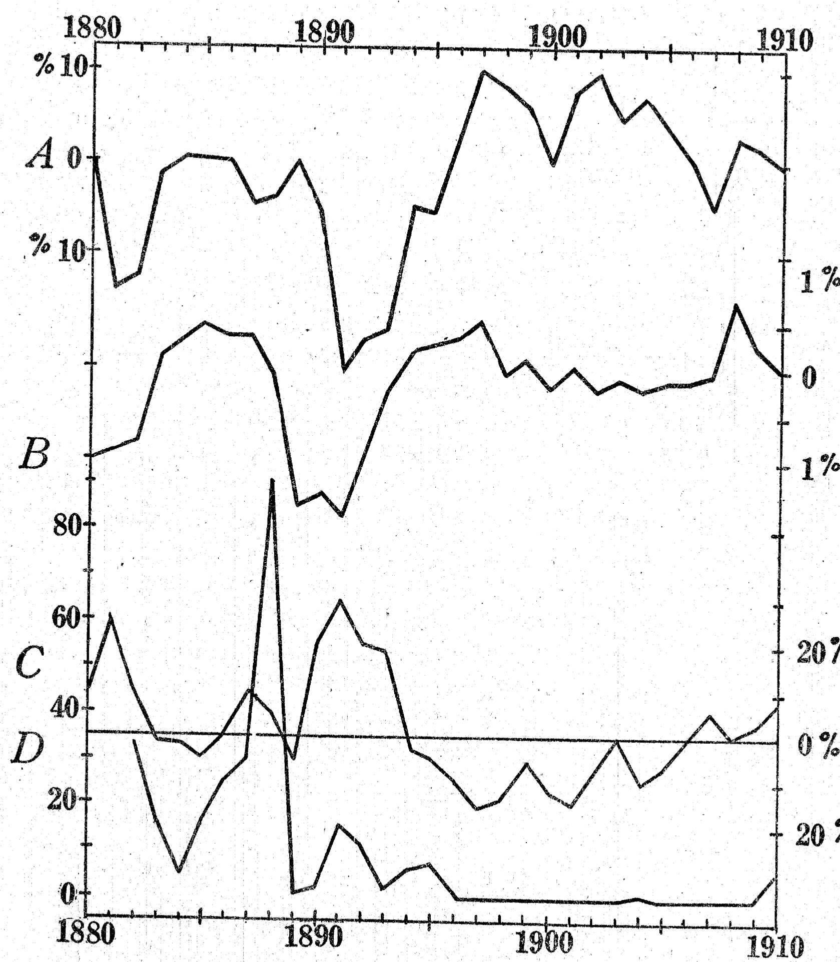

Fig. 5. Showing parallel curves for health, school attendance in eastern United States, death-rate in Chicago and chinch bug infestation in Illinois from 1880 to 1910. Curve A (scale at left) normal health of the general population is shown at 0% while bad health is indicated by per cent below and good health by per cent above. Curve B (scale at right) shows the parallel of school attendance to health. Curve C (scale at right) shows the death-rate in Chicago. Normal death-rate is indicated by zero per cent, high death-rate by per cent above and low death-rate by per cent below. Curve D (original; scale at left) shows relative chinch bug infestation in Illinois from records in the state entomologist's office. The records show three degrees of damage, slight, moderate and severe, by counties. Slight was given a value of 1, moderate 2, and severe 3; these figures were multiplied by the number of counties in each case, and then totaled, and then divided by two for convenience in plotting. There is a good correspondence between chinch bug damage and death-rate in Chicago; the entire state of Illinois would be better.

some of whom were hung and others who should have been! This was followed in the early nineties by a rail strike, panics, etc., due to the same causes as the earlier troubles.

The politicians did not make use of the health and death-rate curves but no doubt would have tried to prove that health was affected by political parties. The probabilities are that these disturbances were due in part, perhaps the larger part to ill-health, brought on by unfavorable weather. A comparison with the chinch bug curve indicates that weather which is detrimental to man is favorable to chinch bugs. Thus we see that with long experience and careful records it may be possible to check and anticipate various pest conditions by comparison with human death-rate, and vice versa.

Another type of work which has been undertaken recently is the plotting of the relation between temperature and rainfall in localities where certain crops are especially grown as compared with localities where it is desired to determine possibilities. One of this type of diagrams shown in Figure 6 which compares a locality in the Illinois corn belt with tropical Australia to show the general method. It is one adopted by Griffith Taylor to represent the climate of tropical Australia and to determine whether or not various crops such as cotton, coffee, etc., could be grown there.

There are further matters of interest in connection with man and his activities with relation to temperature and rainfall which demand some comment. On the basis of his experiments which have already been referred to and the opinion of various scientists whom he consulted, Mr. Huntington has mapped the areas of most stimulating climate and has published maps of these areas. The moist deciduous forest climate of western Europe and eastern North America afford the variability and conditions necessary to high efficiency along with mean temperatures and humidites approaching the optimum for the white race, namely, 65°F. and 80 per cent relative humidity. These areas are also regarded as possessing the highest type of civilization. Mr. Griffith Taylor has shown that the yellow race has successfully settled in tropical regions which have 50 inches of rainfall. He finds that north Australia possesses some area of this sort which is not suited for settlement for the white man and Australia has excluded the yellow race from that which Australia cannot itself make use of. From these brief remarks I hope that I have made clear what is very evident to me, namely, that in dealing with insect pests,

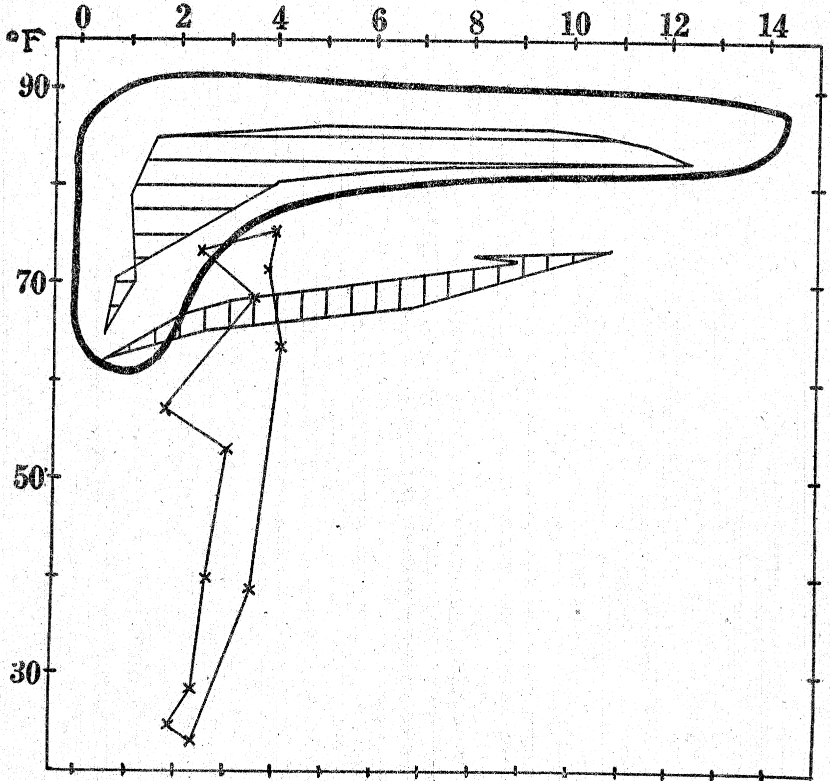

Fig. 6. Hythergraphs or rainfall-temperature charts of several localities. The figures at the top of the chart represent rainfall in inches. The vertical scale is degrees Fahrenheit. The heavy black line represents the rainfall temperature conditions in the Australian tropics. The horizontal rulings fill the space within the plot for Calcutta which is in the center of tropical cotton production; the vertical lines fill the space within the plot for Juiz, Brazil, the center of hill coffee production. One concludes that the Australian tropics are good for cotton but not for hill coffee. The curve with crosses at the angles is for Bloomington, Illinois.

dealing in crop production, in settling questions of such a delicate nature as the exclusion of certain races from certain regions, a knowledge of climatic data and particularly the effect of climatic factors on man and the organisms involved is of prime importance. A few years ago I received a letter from a federal official asking if the Ecological Society of America desired to have any particular kind of weather or climatic records taken, as they were planning a bureau of agricultural meteorology. It is my understanding that similar letters were written to various other biologists and agriculturists but that the weather bureau did not gain very much information as to what kind of records should be taken. This is the fault of biologists who have failed to conduct experiments on the effect of climatic factors on organisms. The character of the records to be made is determined by the

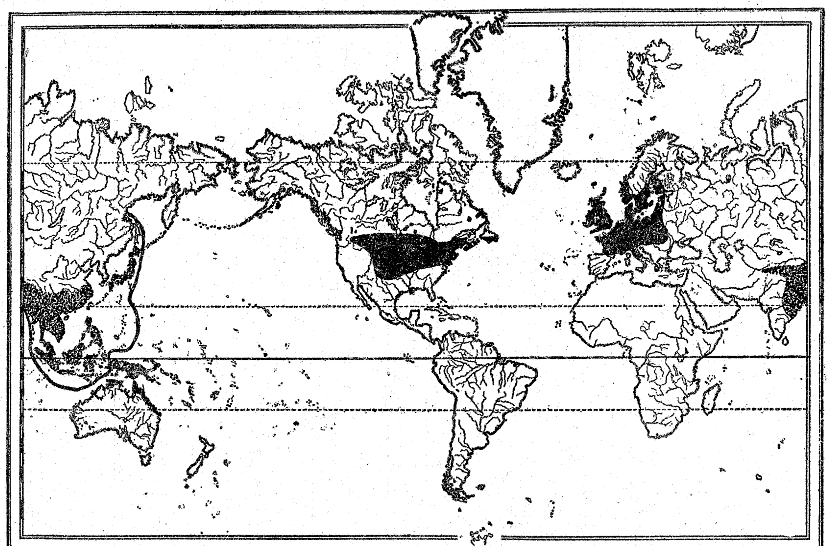

Fig. 7. The solid black shows the areas of most stimulating climate (after Huntington). The stippling shows the area in Asia and the Orient with 50 inches of rain per annum. The yellow race has colonized in the tropics only where there are 50 inches of rain. The heavy line indicates limits of colonization. They are excluded from these parts of Australia which are unfit for white men (after Taylor) but suitable for them.

effects of such climatic factors rather than any schemes that might look well on paper.

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