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STEPHEN A. FORBES, *Chief*

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An Experimental Investigation of the Relations of the Codling Moth to Weather and Climate

BY

VICTOR E. SHELFORD

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ERRATA

Page 2, line 6, for *loan* read *loam.*

Page 4, line 18 from bottom, beech (after water beech) should be followed by a semicolon.

Page 138, line 10 and line 14 from bottom, for *Dane* read *Dann.*

Page 139, line 5, for *Dane* read *Dann.*

Page 180, line 5 from bottom, delete *D.*

Page 198, line 19 from bottom, for *March* read *March 16, 1918.*

Page 221, line 22, for *data* read *date.*

Page 278, lines 17 and 18 from bottom in right-hand column, for *150* read *158.*

Page 285, line 24 in left-hand column, for *Franeh* read *French.*

Page 321, table III, center column, for *1.02* read *1.00+*; for *1.04* read *1.02;* for *1.06* read *1.04.*

Page 411, line 4, for *pupation* read *breaking dormancy* .

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ARTICLE V.—*An Experimental Investigation of the Relations of the Codling Moth to Weather and Climate.* BY VICTOR E. SHELFORD.

INTRODUCTION.

The varied effects of the variable weather of current and preceding seasons on the rate of development of an insect, and hence on the time of appearance and period of continuance of each of its stages, and even on the number of generations in a year and the number of individuals in each generation, are often causes of uncertainty as to the best time to take steps for the control of an injurious species and as to the necessary intensity of control measures; and heavy losses often occur because the times chosen and the activity and thoroughness of the operation do not fit the pattern of the seasonal life history. It has hence become necessary to learn for each important insect species the facts of its life history under normal or usual conditions and the effects of unusual weather to retard or hasten its transformations and to diminish or increase its numbers.

This problem was brought to a crisis in Illinois in 1914, when an unusually hot and dry summer in combination with other favorable conditions in the southern part of the state so accelerated the development of the codling moth and so increased the number of the third generation and other late larvae, usually economically insignificant, that the most intelligent and careful apple growers suffered heavy losses, due to a lack of harmony between their standard spraying program and the larval periods of the successive generations of the codling moth. (Sprays are effective only if applied so as to have the poisons on the apples early in the larval period.) A serious study of the life history of this insect under field conditions was consequently begun, in the fall of 1914, and was continued with an elaborate equipment through the three following years. The results were published by the State Entomologist's Office* and the State Natural History Survey**, in 1916 and 1922, respectively.

These studies added materially to dependable information on this subject, but as they could deal only with such weather conditions as happened to occur in these years, their range was far too limited to warrant final conclusions concerning the effects of every kind of season likely to occur in Illinois.

The questions involved in so complex a problem called for long continued research by a climatologist provided with an ample equipment by which various kinds of weather could be artificially imitated in laboratories where the insects studied could be maintained under otherwise normal conditions. The present paper is the product of a series of such

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* Life history of the codling moth, by Stephen A. Forbes and Pressley A. Glenn, 29th Report, pp. 1-21. (1916)

** Codling moth investigations of the State Entomologist's Office, 1915-1917, by P. A. Glenn, Vol. XIV, Art. 7. (1922)

studies and experiments begun in 1917 and carried on continuously throughout the whole of each year, to and including 1922, in laboratories of the University of Illinois, equipped for the purpose in part by the Natural History Survey. While this paper is, therefore, necessarily technical and aimed especially at an improvement of apparatus and methods of climatological research, the application of conclusions to practical ends has been kept steadily in view, and a summary rehearsal of their uses to horticulture and of the methods of their application follows.

The weather in its relation to the codling moth is made up of several variable elements, each largely or completely independent of the others in its variation, and all of unequal effect on the life history of the insect and of unequal effect also upon the insect in the different stages of its development. The most powerful of these variable elements are temperature and humidity, but light, rainfall, air-movement, and rate of evaporation (the rate at which moist objects give up their moisture to the air), are too important to be ignored. By their various degrees and combinations these several elements make up a great number of kinds and gradations of weather whose effects upon insect life can be ascertained only by an experimental variation of each element separately and of various combinations of them taken together. Since they are not measurable by any single scale of magnitudes applicable to all of them—differences in heat, light, and humidity, for example, being expressed in different terms—there is no way in which their combined efficacies can be expressed in a single series of numbers except by a study of their joint effects upon the behavior, activities, and rates of development of the insect under examination.

The most convenient and practically the most important method of such a study is to experiment with artificial variations of these weather elements upon the rate of progress of an insect through its successive developmental stages, and upon the percentage of those in each of the earlier stages which survive to pass on into the next stage. The varying significance to the codling moth of different combinations of various degrees of temperature, humidity, illumination, etc., acting conjointly, may be stated in terms of the average time required under each combination for the hatching of the egg, the growth and pupation of the larva, or the transformation of the pupa to the adult insect; and the numbers thus obtained may be so tabulated that one knowing the meteorological data of a season up to a certain date may learn by reference to the table just where the insect is in the course of its development at that date, and then calculate the approximate date at which this stage of development will be completed and the insect will pass into the next stage.

As only two series of meteorological data can be carried on the same table, it has been found most convenient to construct a table of rates of development based on data of the two most potent elements, temperature and humidity, and to apply to the figures of this table any corrections which may be called for by facts concerning the other elements. Such tables and corrective data have been prepared for the codling moth, and they will be found, together with directions for their use, in PART ONE (pp. 318-327). Schemes for any necessary modification of the tabulated values are explained in PARTS TWO and THREE.

It will readily be seen that this indirect method of the application of weather data to the needs of horticulture presupposes the making and compilation of accurate and comprehensive meteorological data at numerous stations, each representing a definite district, and their continuous translation into terms of the rate of development of the insect. This is work for an expert with ample time at his command for such surveys, and inferences to be drawn as to the time and nature of practical control measures must have timely distribution by him to those concerned. Such conclusions and directions are at present formulated and distributed from time to time by the entomologists of the Natural History Survey, mainly through the farm advisers of the various counties of the state, but it is to be hoped that these farm advisers will presently become sufficiently acquainted with the method and sufficiently practiced in its application to be mainly independent in its use, subject only to the general supervision and advice of the entomologists.

It is also to be hoped that other entomologists will find themselves interested and enabled to continue investigation in this fruitful field, thus bringing to positive conclusion many matters left more or less in doubt in the present paper and attacking other problems here left untouched. To all such, it is believed that the third, especially technical, part of Dr. Shelford's discussion will have a high and indeed an indispensable value.

STEPHEN A. FORBES.

FOREWORD.

The present paper is divided into three parts for the convenience of three classes of readers:

PART ONE, for those who would apply the results of this investigation directly to the prediction of the time of appearance of the codling moth in its several stages in Illinois and in other places where weather conditions are similar, in order to set dates for spraying.

PART TWO, for those who would check the constants, climatological methods, and conclusions regarding the codling moth with data obtained in unusual years or in other climates.

PART THREE, for those who would utilize the methods here described in the investigation of the same or other organisms.

PART ONE.

PREDICTION PROCEDURE.

THE PROBLEM OF PREDICTING THE APPEARANCE OF THE CODLING MOTH

The codling moth is the most destructive insect infesting apples. Its larva, commonly called the apple-worm, eats its way into the fruit to the seeds, forming dark masses of frass, or castings, at the end of the hole and in the core. It is found wherever apples are grown throughout the world. It also attacks pears, quinces, wild haws, peaches, English walnuts, and other fruits. Its life history, appearance, and habits, together with control measures used against it, have been described by Metcalf and Flint* as follows:

Life History, Appearance, and Habits: The Codling Moth passes the winter in the full-grown larval stage in a thick silken cocoon. The larvae are pinkish-white caterpillars with brown heads and are about three-fourths of an inch long. These cocoons are generally spun under loose scales of the bark on the trunks of apple trees, or other shelters about the base of the trees, or on the ground nearby. Many of the larvae winter in, or around, packing sheds. They remain dormant, and are able to withstand low temperatures. A drop in temperature to —25° F., or below, will kill many of the larvae. During the winter, birds, especially chickadees and woodpeckers, find and eat large numbers of the larvae. In the late spring the worms change inside their cocoons to a brownish pupal stage and, after a period of from two to four weeks or more, they emerge from the cocoons as grayish moths with somewhat irridescent, chocolate-brown patches on the back part or tip of the front wings. The moths have a wing expanse of from one-half to three-fourths of an inch. During the day the moths remain quiet, usually resting on the branches or trunk of the tree. The coloring of the wings is such that it blends with that of the bark, making the insect very inconspicuous. About dusk of the evening, if the temperature is above 60° F., they become active, mate, and the females lay their eggs. If the temperature is low, they remain quiet, and few eggs will be deposited. Each female usually deposits more than fifty eggs during her life time. The eggs are white, flattened, pancake-shaped, and about one-twenty-fifth of an inch in diameter. The eggs of the first generation are laid one in a place, almost entirely on the upper side of the leaves, usually a short distance from a cluster of apples. They are laid two to four weeks after the apples have bloomed, and hatch in six to twenty days depending on the temperature and, to some extent, on the rainfall. The worms feed slightly on the leaves but in a short time crawl to the young apples and chew their way into the fruit, usually entering by way of the calyx cup at the blossom end. After entering the fruit, they work their way into the core, often feeding on the seeds. Some of the infested fruits drop from the tree and the larvae complete their growth on the ground. Upon becoming full grown, they burrow to the outside of the apple and either crawl to, or down, the trunk of the tree, or drop to the ground and crawl back to the trunk or to some other object on which they spin their cocoons, and change as before to the pupa, and later to the adult stage.

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* The passage quoted is from "Destructive and Useful Insects," a text by C. L. Metcalf and W. P. Flint, which is now (1926) being used in mimeographed form (3 volumes) for instruction of classes in the University of Illinois.

In the latitude of southern Illinois, there is nearly a full first, nearly a full second, and a partial third generation of this insect in one season. In the latitude of northern Illinois, there is nearly a full first generation, a partial second, but no third generation. The emergence of the moths of the second generation extends over the entire summer, and eggs of this generation may be deposited in the north part of the United States as late as mid-August, or even the first of September. In the south, eggs may be laid as late as October.

Control Measures: While the Codling Moth, if left to itself, will infest from 20% to 95% of the apples in an orchard, it is possible to reduce the numbers of this insect so that less than 5% of the apples will be injured.

Spraying with arsenate of lead at the rate of from one to two pounds of powder to fifty* gallons of spray material is the standard remedy for the Codling Moth. It is highly important, however, that the sprays for this insect be applied at the proper time. The first and most important spray is that known as the petal-fall, or calyx, spray, which is applied when about three-fourths of the petals have fallen from the apple blossoms. The spray should not be applied when the trees are in full bloom because of the danger of poisoning honey bees. Special care should be used to hit the open calyx end of the apples and fill the calyx cup with the poison spray. Careful spraying that fills the calyx cup at this time will poison any young Codling Moth caterpillars that try to enter the apples at the blossom end for the remainder of the season. If spraying is delayed for more than a week after the petals fall, the calyx cup will have closed, and it will be impossible to force the spray into the calyx cup. A second application of spray should be made one week to ten days after the fall of the petals, and a third, three weeks after the petals fall. These sprays are all for the first generation of the Codling Moth.

The larvae of the second generation usually begin hatching from the eggs about nine weeks after the fall of the petals. However, this period is subject to considerable variation, sometimes as much as three weeks in different seasons. Owing to this fact, the time of the appearance of second and third generation larvae should be obtained in advance from the entomologist. If the notice of the time of appearance of the second generation larvae cannot be obtained in this way, the spray for the second generation should be applied nine weeks after the fall of the petals, and, in years when the Codling Moth is abundant, another spray should be given two weeks later.

* * *

In the South, a spray for third generation Codling Moths should be applied about August 15, and, during hot dry years, another spray should be given to winter varieties of apples about September 1.

Aside from spraying, there are several other measures which help in keeping down the Codling Moth. These consist of a thorough clean-up of the orchard, scraping the loose bark from old trees when the bark is scaling badly and, in cases of exceptional abundance, banding the trees during the summer. To get the best results from banding, place a strip of dark-colored building paper or tar-paper, four or five inches wide, tightly around the tree at a height of about two feet from the ground. Allow the ends to overlap slightly, fastening them with a large tack. These bands should be examined at least once a week and the Codling Moth larvae under them killed. The bands should be in place not later than June 1 in the latitude of southern Illinois, and June 15 in the latitude of northern Illinois. Experimental work in Illinois has shown that the tar-paper or building-paper bands are more attractive to the Codling Moth larvae than bands of burlap or cloth. Removing cull apples from the orchard, and a thorough clean-up of refuse and rubbish around the packing shed, will also help in keeping down the numbers of this insect.

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* If the *paste* arsenate of lead is used, double the amount.

"Two questions of special practical interest present themselves: one, the number of generations in a year; and the other, the time when the eggs of each generation hatch to give out the young worms. To these we may add a third question, as to variations in the number of generations and the times when the young larvae of each appear in different parts of the state, and in successive years of unlike weather conditions."*

Weather conditions, especially temperature, humidity, rainfall, and sunlight, have a great deal to do with the rate of development of the codling moth, with the time when the different generations make their appearance, reach their largest numbers, and disappear, and with the size and importance of the last or third generation of the year. The course of these events must be carefully and intelligently observed in order that spraying operations may be properly timed—to put the effective poisons on the apples when the larvae of each generation are to appear.

Measurement of development. Each stage in the life-cycle of an organism requires a certain period of time depending on weather conditions. The better the conditions, the shorter the time, and *vice versa,* within certain limits set by the nature of the organism. If development went on always at the same rate, the number of days or hours from the beginning to any point in the stage would be a direct measure of the amount of development which has been accomplished to that point. This is implied in such common expressions as "a year's growth" or "a day's growth," in which time alone is used as a measure of development on the assumption that the rate of growth is constant over a number of days or years. But rates of growth, or velocities of development, vary with conditions, so that it is necessary to refine this method by taking into account all factors affecting the process.

In attempting to predict the time of appearance of insect pests, to estimate the abundance of a pest or its enemies, and to arrange spraying schedules, phenologists have taken account of temperature as well as time by using "degree-days" in estimating development. They commonly get a total number of "degree-days" for a stage of development by taking for each day from the beginning to the end of the stage the number of degrees which the day's mean temperature shows above a certain assumed starting point, or "threshold", and summing the number of degrees thus obtained for all the days to the end of the stage. This "summing of effective temperatures in degree-days" is sometimes fairly useful for estimating development within certain limits of temperature. Glenn ('22) made corrections for high temperatures but not for low temperatures and for variations in humidity and other factors. This method is never very accurate, however, because medial temperatures and humidities (where the rate of development is directly proportional to temperature) are exceeded almost every day in our climate, and because development takes place at temperatures lower than the

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* Quoted from a paper "On the life history of the codling moth", by Stephen A. Forbes and Pressley A. Glenn, 29th Report of the State Entomologist of Illinois (1916).

"threshold" usually assumed. It is perhaps least successful in the spring of the year, when there is greatest need of reliable prediction in fixing spraying schedules for control of the codling moth.

The older "degree-day" method (Simpson '03) fails to give dependable results. Glenn's method is not sufficiently accurate to enable one to evaluate the effects of factors other than temperature, and hence it is most likely to fail in unusual seasons. A new method is needed, therefore, which will take into account the effects of all variations of all these factors in units of time shorter than the day. The method herein described aims to meet this need by using the amount of development accomplished in one hour as the basis of calculation.. This amount is a small fraction of the total development which makes up the stage in the life-cycle of the insect. The new unit is called the **developmental unit** and is to be defined with reference to the total development of which it is a part. It is not a "degree-hour," for it is not a measure of external conditions, but a measure of the response of the organism to those conditions. This response, moreover, is modified by other factors besides temperature; and so the *developmental unit,* taking into account all the phenomena affecting the process, is to be thought of properly as the *effect* of a "phenomena-degree-hour." (See *pheno-hour,* p. 332.)

Definition of the unit of development. The *developmental unit,* to be more specific, is the effect of one degree of mean medial variable temperature, operating for one hour in conjunction with mean medial variable humidity and with the air movement, light intensity, and other conditions normal to the habitat of the organism. In the case of insects and many other organisms whose development cannot be measured directly, this effect is best calculated in terms of the total time required to accomplish the stage of the life-cycle under consideration; for this time is shortened in direct proportion to rise of temperature within medial limits, so that the difference between the time required at a certain degree and the time required at another degree may be taken as a measure of the difference in amounts of development accomplished at those two temperatures. The *developmental unit,* for any stage in the life-cycle of the insect, is, therefore, defined as the difference in amount of development produced in one hour by a difference of one degree of mean medial variable temperature (other conditions being average), as shown by the difference in time required to complete the stage.

Developmental totals. The pupal stage of the codling moth, for example, which was considered by Glenn ('22) as requiring an average of 265 "degree-days" for complete development under normal conditions in Illinois, is here considered as normally consisting of 6,480 *developmental units* (hour units), this new total being the result of calculations based on data covering ten years of observation and experimentation, including Glenn's original data. The "degree-day" total took no adequate account

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TABLE I.

VELOCITY VALUES (NUMBERS OF DEVELOPMENTAL UNITS PER HOUR), FOR VARIOUS MEAN VALUES OF VARIABLE TEMPERATURE AND HUMIDITY, APPLICABLE TO THE CODLING MOTH PUPAE AND EGGS UNDER WEATHER CONDITIONS.

	32	34	36	38	40	42	44	46	48	50	52	54	56	58	60	62	64	66	68	70	72	74	76	78	80	82	84	86	88	90	92	94	96	98	100%	
105°F.	17.9	18.6	19.0	19.3	19.7	20.1	20.3	20.4	20.5	20.5	20.4	20.4	20.3	20.2	20.1	19.8	19.5	19.3	18.9	18.4	18.2	17.5	16.9	16.3	15.8	15.0	14.3	13.0	12.1	11.3	10.5	9.8	9.1	8.2	7.4	105°F.
104	19.4	20.0	20.4	20.9	21.2	21.4	21.6	21.6	21.7	21.8	21.8	21.7	21.6	21.5	21.1	21.2	20.9	20.4	20.3	20.0	19.5	19.0	18.4	18.1	17.4	16.8	16.0	15.1	14.1	13.2	11.8	10.7	10.3	9.5	8.5	104
103	20.9	21.4	21.9	22.5	22.8	23.2	23.4	23.5	23.7	23.7	23.5	23.6	23.4	23.2	22.9	22.6	22.4	22.0	21.7	21.4	21.1	20.7	20.2	19.7	19.3	18.4	18.1	17.1	16.2	15.6	13.9	12.8	11.8	10.5	10.0	103
102	22.4	23.2	23.7	24.3	24.6	24.8	25.2	25.4	25.6	25.6	25.6	25.5	25.3	26.0	24.8	24.6	24.4	23.9	23.5	23.3	22.5	22.0	21.5	21.3	20.7	20.3	19.7	19.1	18.2	17.3	16.1	15.1	13.9	12.7	11.5	102
101	24.0	24.6	25.4	25.7	26.0	26.4	26.7	26.7	26.7	26.7	26.7	26.7	26.7	26.5	26.4	26.2	26.0	25.7	25.5	24.9	24.6	24.1	23.5	22.8	22.3	21.7	21.4	20.5	20.1	19.3	18.2	17.1	16.0	14.9	13.7	101
100	25.5	26.1	26.7	27.1	27.4	27.6	27.7	27.8	27.9	27.9	27.9	27.9	27.8	27.8	27.6	27.5	27.2	26.9	26.7	26.7	26.3	25.9	25.5	24.7	24.4	23.5	23.1	23.4	21.6	21.2	20.3	19.3	18.1	16.9	15.8	100
99	26.7	27.5	28.0	28.5	28.7	28.9	29.0	29.1	29.2	29.2	29.2	29.2	29.1	29.1	29.0	28.9	28.9	28.7	28.4	27.8	27.6	27.2	26.9	26.8	26.4	25.7	25.2	24.4	23.5	22.8	21.8	21.4	20.3	18.9	18.0	99
98	28.1	28.9	29.2	29.5	29.9	30.0	30.1	30.2	30.3	30.4	30.4	30.4	30.3	30.2	30.1	30.0	29.9	29.6	29.4	29.2	29.0	28.8	28.1	27.8	27.6	27.2	26.7	26.2	25.7	21.8	23.5	22.9	21.8	21.3	12.6	98
97	29.7	30.1	30.5	30.8	31.0	31.1	31.4	31.5	31.7	31.8	31.8	31.8	31.7	31.6	31.5	31.4	31.1	31.0	30.8	30.5	30.2	30.0	29.7	29.4	29.1	28.7	28.3	27.8	27.3	26.9	25.8	25.1	23.8	22.9	22.2	97
96	30.8	31.4	31.8	32.0	32.2	32.4	32.7	32.9	33.0	33.2	33.2	33.2	33.2	33.2	33.0	32.9	32.6	32.3	32.1	32.0	31.7	31.2	31.0	30.8	30.4	30.0	29.7	29.1	28.8	28.3	27.8	27.0	26.0	25.1	24.3	96
95	32.1	32.7	33.2	33.4	33.6	33.8	33.9	34.0	34.1	34.2	34.2	34.4	34.4	34.4	34.2	34.2	34.1	33.9	33.8	33.5	32.2	33.1	32.4	32.2	31.9	31.6	31.2	30.8	30.4	30.0	28.9	28.6	27.9	27.2	26.3	95
94	33.6	34.0	34.2	35.4	34.7	35.1	35.3	35.3	35.4	35.5	35.5	35.6	35.6	35.5	35.5	35.4	35.4	35.3	35.2	35.0	34.8	34.5	34.2	34.0	33.7	33.3	33.2	32.3	32.1	31.7	31.0	30.7	29.9	28.9	28.5	94
93	34.9	35.3	35.5	35.8	36.1	36.3	36.4	36.4	36.5	36.6	36.7	36.8	36.8	36.8	36.7	36.6	36.6	36.5	36.4	36.4	36.4	35.9	35.5	35.3	35.1	34.9	34.6	34.2	34.0	33.5	33.0	32.2	31.7	31.0	30.7	93
92	35.9	36.4	36.8	37.2	37.5	37.5	37.6	37.6	37.6	37.6	37.6	37.7	37.7	37.6	37.6	37.6	37.6	37.6	37.6	37.5	37.5	37.3	37.2	37.0	36.8	36.5	36.4	35.8	35.4	35.2	34.7	34.2	33.7	33.2	32.3	92
91	37.3	37.6	37.6	37.7	37.7	37.8	37.8	37.8	37.5	37.5	37.5	37.6	37.5	37.7	37.7	37.5	37.5	37.5	37.6	37.5	37.5	37.5	37.5	37.5	37.5	37.1	36.9	37.6	37.5	37.1	36.5	36.4	35.8	35.3	34.8	91
90	37.5	37.6	37.6	37.6	37.7	37.7	37.8	37.6	37.8	38.0	38.0	38.1	38.1	37.6	37.6	37.6	37.6	37.6	37.6	37.6	37.6	37.6	37.6	37.7	37.7	37.7	37.6	37.6	37.6	37.6	37.5	37.5	32.8	37.3	37.2	90
89	36.3	36.5	36.5	36.6	36.7	36.9	37.1	37.4	37.5	37.5	37.6	37.6	37.7	37.8	37.9	38.0	38.0	38.0	38.1	38.1	38.1	38.2	38.3	38.4	38.5	38.7	38.7	38.7	38.7	38.7	38.7	38.7	38.7	38.7	38.7	89
88	35.2	35.3	35.4	35.5	35.6	35.7	36.0	36.0	36.2	36.3	36.4	36.5	36.7	37.0	37.1	37.4	37.5	37.5	37.5	37.6	37.6	37.6	37.7	37.7	37.8	37.9	38.0	38.5	38.6	38.7	38.7	38.8	38.8	38.8	38.9	88
87	34.0	34.1	34.2	34.5	34.6	34.7	34.8	35.1	35.1	35.2	35.3	36.4	35.6	35.9	36.0	36.2	36.3	36.4	36.4	36.4	36.5	36.6	36.7	36.7	36.8	37.0	37.1	37.4	37.5	37.7	38.3	38.5	38.6	38.7	38.8	87
86	33.0	33.2	33.2	33.3	33.4	33.5	33.7	33.7	33.9	34.0	34.1	34.2	34.6	34.8	34.9	35.0	35.2	35.3	35.3	35.3	35.4	35.5	35.6	35.6	35.8	35.3	36.0	36.2	36.4	36.5	37.0	37.4	38.5	38.6	38.7	86
85	31.9	32.1	32.2	32.3	32.5	32.6	32.7	32.9	33.0	33.2	32.1	33.3	33.5	33.7	33.7	33.9	34.1	34.1	34.2	34.2	34.5	34.5	34.6	34.6	34.7	34.8	35.0	35.1	35.3	35.5	35.9	36.3	36.6	37.0	37.4	85
84	30.9	31.0	31.2	31.2	31.5	31.6	31.8	32.0	32.1	32.1	32.2	32.3	32.5	32.7	32.9	33.0	33.2	33.2	33.3	33.4	33.4	33.5	33.6	33.6	33.7	33.7	33.9	34.0	34.2	34.4	34.7	35.1	35.3	35.5	35.8	84
83	29.9	29.9	30.0	30.2	30.4	30.5	30.7	30.9	31.0	31.0	31.2	31.4	31.6	31.8	31.9	32.0	32.1	32.1	32.2	32.3	32.3	32.4	32.4	32.6	32.6	32.7	32.8	33.0	33.2	33.3	33.6	33.9	34.2	34.3	34.4	83
82	29.0	29.0	29.1	29.3	29.4	29.5	29.6	29.8	29.9	29.9	30.0	30.3	30.5	30.8	31.0	31.0	31.2	31.2	31.3	31.3	31.3	31.4	31.4	31.5	31.6	31.7	31.8	32.0	32.1	32.2	32.4	32.8	33.0	33.2	33.2	82
81	28.0	28.0	28.2	28.4	28.4	28.5	28.7	28.8	28.9	28.9	29.0	29.2	29.4	29.8	29.9	30.0	30.2	30.3	30.3	30.4	30.4	30.4	30.5	30.5	30.6	30.6	30.7	30.8	31.0	31.2	31.4	31.8	32.0	32.1	32.2	81
80	27.0	27.0	27.1	27.3	27.4	27.5	27.6	27.7	27.8	27.8	28.0	28.1	28.4	28.6	28.7	28.9	29.0	29.1	29.3	29.4	29.4	29.5	29.5	29.6	29.6	29.8	29.8	29.9	30.0	30.2	30.4	30.7	30.9	31.0	31.0	80
79	26.0	26.1	26.2	26.3	26.4	26.5	26.7	26.7	26.7	26.9	27.0	27.2	27.3	27.5	27.6	27.8	27.9	28.1	28.4	28.5	28.5	28.6	28.6	28.6	28.6	28.7	28.8	28.8	28.9	29.0	29.3	29.8	29.9	29.9	30.0	79
78	25.0	25.1	25.2	25.3	25.4	25.4	25.6	25.7	26.7	25.8	25.9	26.1	26.3	26.7	26.7	26.7	26.9	27.0	27.2	27.3	27.3	27.4	27.4	27.6	27.5	27.5	27.6	27.8	27.8	28.0	28.3	28.6	28.8	28.9	27.9	78
77	24.0	24.1	24.2	24.3	21.4	24.5	24.5	24.6	24.8	24.9	25.0	25.1	25.3	25.4	25.6	25.7	25.8	25.9	26.0	26.1	26.2	26.2	26.3	26.5	26.5	26.5	26.6	26.7	26.7	26.9	27.2	27.5	27.7	27.8	27.9	77
76	23.0	23.1	23.3	23.4	23.4	23.5	23.6	23.7	23.8	23.8	23.9	24.1	24.3	24.5	24.6	24.8	24.8	24.9	25.0	25.1	25.1	25.2	25.2	25.2	25.2	25.3	25.4	25.4	25.6	25.7	26.0	26.6	26.6	26.7	26.7	76
75	22.1	22.1	22.2	22.3	22.3	22.4	22.5	22.6	22.7	22.8	22.9	23.1	23.4	23.5	23.6	23.7	23.7	23.8	23.8	23.9	24.0	24.1	24.1	24.1	24.2	24.2	24.3	24.4	24.6	24.6	25.0	25.3	25.4	26.4	25.6	75
74	20.7	20.9	21.1	21.2	21.2	21.3	21.4	21.4	21.5	21.6	21.7	22.0	22.2	22.3	22.4	22.5	22.6	22.7	22.8	22.9	22.9	23.0	23.0	23.0	23.1	23.1	23.2	23.2	23.6	23.6	23.8	24.0	24.1	24.3	24.4	74
73	19.7	19.9	20.1	20.2	20.4	20.5	20.6	20.6	20.7	20.8	20.9	21.1	21.2	21.3	21.3	21.4	21.5	21.7	22.0	22.0	22.0	22.0	22.2	22.2	22.2	22.3	22.3	22.4	22.5	22.5	22.7	22.9	23.0	23.1	23.2	73
72	18.9	19.0	19.1	19.2	19.2	19.3	19.4	19.5	19.7	19.8	19.9	20.0	20.1	20.2	20.4	20.5	20.5	20.7	20.8	20.9	21.0	21.1	21.2	21.2	21.3	21.3	21.3	21.4	21.4	21.5	21.6	21.8	22.0	22.1	22.2	72
71	18.0	18.1	18.2	18.3	18.4	18.5	18.6	18.7	18.9	19.0	19.1	19.2	19.3	19.3	19.4	19.4	19.5	19.7	19.8	19.8	19.9	20.0	20.0	20.1	20.1	20.1	20.2	20.2	20.4	20.4	20.6	20.8	20.9	21.0	21.1	71
70	16.8	17.0	17.1	17.2	17.3	17.6	17.7	17.7	17.8	17.9	18.0	18.1	18.2	18.2	18.3	18.3	18.4	18.6	18.7	18.9	18.9	19.0	19.1	19.2	19.2	19.2	19.3	19.3	19.3	19.4	19.6	19.6	19.7	19.8	19.9	70
69	15.6	15.7	15.9	16.0	16.1	16.3	16.5	16.6	16.7	16.8	16.9	17.0	17.0	17.1	17.1	17.2	17.4	17.6	17.7	17.8	17.8	17.8	17.9	17.9	17.9	18.0	18.1	18.2	18.2	18.2	18.4	18.5	18.5	18.7	18.9	69
68	14.6	14.7	14.8	15.0	15.0	15.2	15.3	15.4	15.6	15.7	16.0	16.1	16.1	16.2	16.2	16.3	16.4	16.5	16.7	16.7	16.8	16.8	16.9	17.0	17.0	17.1	17.1	17.1	17.2	17.4	17.4	17.6	17.5	17.5	17.5	68
67	13.5	13.7	13.9	13.9	14.0	14.1	14.4	14.5	14.6	14.7	14.8	14.9	15.0	15.0	15.0	15.1	15.2	15.3	15.4	15.5	15.6	15.7	15.8	16.0	16.0	16.1	16.1	16.1	16.1	16.2	16.3	16.3	16.4	16.4	16.4	67
66	12.1	12.6	12.9	13.0	13.0	13.1	13.3	13.4	13.5	13.6	13.7	13.7	13.8	13.9	13.9	14.0	14.1	14.2	14.2	14.4	14.5	14.6	14.6	14.7	14.7	14.8	14.9	14.9	15.0	15.0	15.1	15.2	15.2	15.3	15.3	66
65	11.5	11.7	11.8	11.9	12.0	12.1	12.3	12.4	12.5	12.6	12.7	12.9	12.9	13.0	13.0	13.1	13.2	13.3	13.4	13.4	13.5	13.6	13.6	13.7	13.7	13.8	13.8	13.8	13.9	13.9	14.0	14.0	14.1	14.1	14.1	65
64	10.5	10.6	10.7	10.8	10.9	11.2	11.2	11.3	11.5	11.6	11.7	11.8	11.8	11.9	12.0	12.1	12.2	12.3	12.4	12.5	12.5	12.5	12.6	12.6	12.6	12.7	12.7	12.8	12.8	12.8	12.8	12.8	12.8	12.9	12.9	64
63	9.6	9.7	9.8	9.9	10.1	10.2	10.3	10.4	10.5	10.6	10.7	10.7	10.8	10.9	11.0	11.2	11.2	11.3	11.5	11.6	11.6	11.7	11.7	11.7	11.8	11.8	11.8	11.8	11.8	11.8	11.8	11.8	11.8	11.8	11.8	63
62	8.8	9.0	9.2	9.3	9.4	9.5	9.5	9.6	9.7	9.8	9.8	9.9	10.1	10.2	10.2	10.3	10.3	10.4	10.4	10.5	10.5	10.5	10.6	10.6	10.6	16.6	10.7	10.7	10.7	10.7	10.7	10.7	10.7	10.7	10.7	62
61	8.2	8.3	8.5	8.6	8.8	8.9	9.0	9.0	9.1	9.2	9.2	9.3	9.3	9.4	9.4	9.5	9.5	9.6	9.6	9.6	9.7	9.7	9.8	9.8	9.8	9.9	9.9	9.9	9.9	9.9	9.9	9.9	9.9	9.9	9.9	61
60	7.6	7.7	7.8	7.9	8.0	8.1	8.2	8.3	8.4	8.5	8.6	8.6	8.8	8.8	8.8	8.9	8.9	9.0	9.0	9.1	9.1	9.2	9.2	9.2	9.3	9.3	9.3	9.3	9.3	9.3	9.3	9.3	9.3	9.2	9.2	60
59	6.6	6.8	7.0	7.3	7.4	7.5	7.5	7.6	7.7	7.7	7.8	7.9	8.0	8.1	8.2	8.2	8.3	8.3	8.4	8.4	8.5	8.5	8.5	8.6	8.6	8.5	8.5	8.6	8.6	8.6	8.5	8.5	8.5	8.4	8.3	59
58	5.9	6.1	6.2	6.4	6.4	6.5	6.7	6.8	7.0	7.1	7.3	7.3	7.4	7.5	7.5	7.5	7.5	7.6	7.6	7.7	7.7	7.7	7.8	7.8	7.8	7.8	7.8	7.8	7.9	7.9	7.9	7.8	7.8	7.7	7.6	58
57	5.2	5.3	5.5	5.8	5.9	6.0	6.1	6.2	6.3	6.4	6.5	6.6	6.6	6.7	6.7	6.8	6.8	6.9	7.0	7.0	7.0	7.1	7.1	7.1	7.3	7.3	7.3	7.3	7.3	7.3	7.3	7.1	7.0	6.9	6.7	57
56	4.5	4.7	4.9	5.1	5.2	5.3	5.4	5.5	5.6	5.8	5.9	6.0	5.9	6.1	6.1	6.2	6.2	6.3	6.3	6.4	6.4	6.5	6.5	6.5	6.6	6.6	6.7	6.7	6.7	6.6	6.6	6.5	6.4	6.3	6.0	56
55	3.8	4.0	4.3	4.4	4.5	4.7	4.8	4.9	5.0	5.1	5.2	5.3	5.3	5.4	5.4	5.5	5.5	5.6	5.8	5.8	5.9	5.9	6.0	6.0	6.0	6.1	6.1	6.1	6.1	6.1	6.0	6.0	5.9	5.7	5.4	55
54	3.3	3.4	3.6	3.9	4.0	4.1	4.2	4.3	4.4	4.5	4.6	4.7	4.8	4.9	5.0	5.0	5.1	5.1	5.2	5.2	5.3	5.3	5.3	5.5	5.5	6.5	5.5	6.5	5.5	5.6	6.3	5.3	5.2	4.9	4.7	54
53	2.7	2.8	3.0	3.2	3.2	3.4	3.5	3.6	3.9	4.0	4.1	4.2	4.3	4.3	4.3	4.4	4.5	4.5	4.6	4.6	4.7	4.8	4.8	4.8	4.9	4.9	4.9	4.9	4.9	4.8	4.7	4.6	4.6	4.3	4.1	53
52	2.0	2.1	2.2	2.5	2.6	2.8	2.9	3.1	3.2	3.2	3.3	3.5	3.6	3.7	3.9	3.9	4.0	4.0	4.1	4.1	4.2	4.2	4.3	4.3	4.3	4.3	4.3	4.3	4.3	4.3	4.2	4.1	4.0	3.6	3.3	52
51	1.3	1.4	1.5	1.7	1.9	2.0	2.1	2.4	2.5	2.6	2.8	2.9	3.0	3.1	3.2	3.2	3.3	3.4	3.5	3.5	3.6	3.6	3.7	3.7	3.7	3.7	3.7	3.7	3.7	3.7	3.6	3.5	3.3	3.0	2.5	51
50	0.8	1.0	1.1	1.2	1.3	1.5	1.6	1.8	1.9	2.0	2.1	2.2	2.3	2.4	2.6	2.7	2.8	2.8	2.9	3.0	3.0	3.1	3.2	3.2	3.2	3.2	3.2	3.2	3.2	3.2	3.1	2.9	2.6	2.2	1.9	50
49	0.2	0.2	0.4	0.5	0.7	1.0	1.1	1.2	1.3	1.4	1.5	1.6	1.7	1.9	2.0	2.0	2.1	2.1	2.2	2.3	2.3	2.4	2.4	2.6	2.6	2.7	2.7	2.7	2.6	2.6	2.4	2.2	2.0	1.6	1.3	49
48	0.0	0.0	0.0	0.0	0.1	0.2	0.4	0.5	0.6	0.8	1.0	1.1	1.1	1.2	1.3	1.4	1.5	1.6	1.7	1.8	1.8	1.9	1.9	2.0	2.0	2.1	2.1	2.1	2.0	2.0	1.9	1.7	1.5	1.1	0.7	48
47	......	......	......	......	0.0	0.0	0.0	0.0	0.1	0.2	0.3	0.4	0.5	0.6	0.7	0.8	1.0	1.1	1.2	1.3	1.4	1.4	1.5	1.5	1.6	1.6	1.6	1.6	1.6	1.5	1.4	1.2	1.0	0.5	0.1	47
46	......	......	......	......	......	......	......	......	0.0	0.0	0.0	0.0	0.0	0.1	0.2	0.3	0.3	0.4	0.5	0.6	0.7	0.8	1.0	1.1	1.1	1.1	1.1	1.1	1.1	1.0	0.8	0.6	0.4	0.0	0.0	46
45	......	......	......	......	......	......	......	......	......	......	......	......	......	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.2	0.3	0.3	0.4	0.4	0.4	0.5	0.5	0.5	0.4	0.3	0.1	0.0	......	......	45
44	......	......	......	......	......	......	......	......	......	......	......	......	......	......	0.0	......	......	......	......	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	6.0	0.0	0.0	0.0	......	......	......	44
																				......	......	......	......	......	......	......	......	......	......	......	......	......	......	......	......	43
																				......	......	......	......	......	......	......	......	......	......	......	......	......	......	......	......	42
																				......	......	......	......	......	......	......	......	......	......	......	......	......	......	......	......	41
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																				......	......	......	......	......	......	......	......	......	......	......	......	......	......	......	......	18
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																				......	......	......	......	......	......	......	......	......	......	......	......	......	......	......	......	16
																				......	......	......	......	......	......	......	......	......	......	......	......	......	......	......	......	15
	32	34	36	38	40	42	44	46	48	50	52	54	56	58	60	62	64	66	68	70	72	74	76	78	80	82	84	86	88	90	92	94	96	98	100%	

DEGREES FAHRENHEIT.

PER CENT HUMIDITY.

The rate of development of the codling moth under weather conditions is here expressed in *developmental units per hour* for various mean values of temperature and humidity. (For definitions of developmental units and other terms, see pp 318 and 331.) These values are for the pupal stage but may be used also for the incubation of the egg, because the rate of development in the egg is affected by temperature and humidity to practically the same extent. For rate of development of the larva, see Table VI. For temperatures above 105° F. and humidities below 32 per cent, the rates of development may be read from Fig. 14B, p. 358, from which the values shown in this table were obtained. Note that the values read on Fig. 14B must be multiplied by 1.07 to make them true for weather conditions.

The values in this table represent rates of development for means covering *one-hour* periods for each combination of temperature and humidity. To bring the average individual through the pupal stage requires a normal total of 6480 developmental units. The normal total for incubation of the egg is 3864 developmental units. For modification of these totals, see Tables III-V.

These velocity values must not be used for mean daily temperatures and humidities. They may, however, be multiplied by 2 and thus used for two-hour periods instead of one-hour periods.

of variations in rate of development from hour to hour during the warmer and cooler parts of the day, or for variations in humidity and other factors; neither did it allow for variations in *developmental totals* in different seasons of the year. The developmental total as here used permits the refinement necessary for more accurate prediction.

For convenience in applying the results of this work to prediction of appearance of moths in Illinois, a table of rates of development (Table I) has been prepared, and directions for its use have been outlined. This method, which is less complicated than Glenn's "day-degree" method, can be used by the orchardist without an understanding of all the technical terms employed in the description of the experimental work or the mathematical processes by which the developmental units were derived. Knowing the temperatures and other items of weather conditions for the season, he can read the corresponding values from Table I, select the proper totals from the following tables, and calculate the time for the appearance of the larvae by simple arithmetic. Even in the hands of a novice, who follows the rules of procedure literally, this method should give more accurate results than were possible by the "degree-day" method.

NOTE: In order to apply the values given herein to the development of the insect under climatic conditions differing from those in Illinois, the developmental totals will doubtless have to be modified on the basis of experience (see methods of modification explained in PART TWO). Further experience in Illinois may make some modifications desirable here also.

PROCEDURE FOR PREDICTING THE TIME OF EMERGENCE OF MOTHS.

Spring Pupae.

a. Observe the date of the first pupation of larvae kept out of doors under conditions similar to those in the orchard.

b. On that date, or before, place a Friez hygrothermograph in a standard weather shelter under orchard conditions, taking care to have the pens read the same time for both factors recorded.*

c. From the U. S. Weather Bureau records for the nearest station, determine the total rainfall for the preceding months, Sept., Oct., Nov., Dec., and Jan. From the total of these months, select from Table III (p. 321) the correct *developmental total* for the pupal stage.

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* A thermograph and a sling psychrometer may serve instead of the hygrothermograph.

d. When the record sheet is removed from the hygrothermograph each week, tabulate on suitable sheets the degrees of temperature and percentages of relative humidity which occurred in each hour (or, if more convenient, each two-hour period) of each day of the week, assembling them by days. From Table I, where velocity values are given in numbers of developmental units per hour, take the velocity value for each of these combinations of temperature and humidity. If two-hour periods are used, multiply each velocity value by 2.

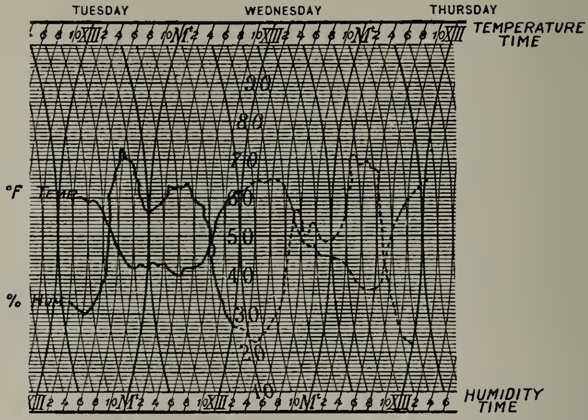

Fig. 1. Tracings of a portion of a hygrothermograph record of weather conditions at Olney, Illinois, April 13-14, 1915. The tracings in solid lines are included in Table II.

For example, refer to Fig. 1, first noting that the time of day is indicated at the top for temperature and at the bottom for humidity. The reading for 2 P. M. Apr. 13 is: temperature 60° F. and humidity 33 per cent. Referring to Table I, we find the velocity value for that combination of temperature and humidity to be 7.7 developmental units per hour, which we may use as the average rate of development for two hours. We thus get 15.4 developmental units for that two-hour period. Again, the reading for 4 P. M. is: temperature 59° and humidity 30 per cent. Another reference to Table I (and Fig. 14B) shows the corresponding velocity value to be 6.4 developmental units per hour, which may be used as the average velocity giving 12.8 developmental units for the period. The time, temperature, humidity, and velocity for all two-hour periods of the 24 hours, of which the above two readings are a part, are shown in Table II.

TABLE II. *Method of Calculating the Amount of Development of the Pupa in One Day from Hygrothermograph Records.*

Applying the values from Table I and Fig. 15 to the record for Apr. 13, 2 P. M., to Apr. 14, 12 M., 1915 at Olney, Ill., as shown in Fig. 1.
(Record supplied by P. A. Glenn.)

Hour.	Temperature (° F.)	Humidity. (%)	Velocity.	Amount of Development in each two-hour period.
2. P. M	60	33	7.7	15.4
4 "	59	30	6.4	12.8
6 "	56	38	5.1	10.2
8 "	47	66	1.1	2.2
10 "	42	70	0.0	0.0
12 "	43	57	0.0	0.0
2 A. M.	42	59	0.0	0.0
4 "	40	63	0.0	0.0
6 "	42	60	0.0	0.0
8 "	47	53	0.4	0.8
10 "	58	34	6.1	12.2
12 M...	62	27	8.3	16.6

Total for the 24 hours = 70.2 developmental units.

Thus, the amount of development of the pupa for that day was 70.2 developmental units. To complete the pupal stage under normal conditions requires a total of 6480 developmental units. (Unusually light or unusually heavy rainfall in the preceding autumn requires a larger or a smaller total for the spring pupa, as shown in Table III.) Thus, if the amount of development is calculated for each day from the beginning of the pupal stage until the sum of developmental units approaches 6480

TABLE III. *Autumn Rainfall Corrections Applicable to the Developmental Total for Spring Pupae, especially first pupations and first maximum.*

(Based on a comparison of Tables VII and VIII with weather data for the periods involved.)

Inches of Rainfall. Sept.—Jan.	Ratio to Normal Total.	Developmental Total.* (hour units)
22	.97	6,300
20	.98	6,360
18	.99	6.420
16	1.00	6,480 (normal)
14	1.02	6,500
12	1.04	6,620
10	1.06	6,740

(more or less, as corrected for autumn rainfall), the end of the stage may be predicted a week or more in advance. Individual variation may permit the first moth to emerge when the sum of developmental units is 8% less than the normal total, so that this correction should be applied in prediction of first appearance.

e. If temperatures above 62° F. occur during cloudy weather or after sunset, the moths will begin laying eggs two days after emerging; if the temperatures are lower, egg-laying is delayed.

Eggs.

From the time the first moth is estimated to have begun laying eggs, proceed with the hygrothermograph records and the velocity values from Table I, as in the case of the pupa, but consider the approach of a total of 3864 developmental units as the time for hatching of the eggs.

Larvae.

From the observed or estimated date of hatching of the eggs of the first generation, in order to compute the time in the apple and in the cocoon, use the rates of development for one-hour (or two-hour) readings of temperature as given on Table V (p. 323). As the sum approaches 18,000 (more or less, depending upon rainfall, as shown on Table VI), forecast the time of pupation of the first generation.

The same procedure may be carried through the season for the later generations, using Tables I–IV for pupae and eggs and Tables V and VI for larvae. Attention must always be given to corrections for individual variation (see footnotes to Tables IV and V) and to corrections for falling temperatures, as shown in Table IV.

TABLE IV. *Falling-Temperature Corrections for Pupa and Egg.*

(Based on Tables IX and X.)

Week of Falling Temperature.	Ratio to Normal Total.	Developmental Total.*	
		Pupa. (hour units)	Egg. (hour units)
1st	.98	6,360	3,792
2d	.96	6,216	3,720
3d	.94	6,096	3,624
4th	.92	5,952	3,552

* NOTE: Individual variation permits first emergence when the accumulated number of developmental units is 8% less than the totals given here. These developmental totals represent averages for all individuals of any lot. The reverse correction of 2% per week of rising temperatures may be applied for the late-pupating individuals of the hibernated generation. See ratio of actual to standard time in Fig. 28.

TABLE V. *Rate of Development of Larva in Apple.*

(Based on recalculation of Glenn's data in comparison with results of constant temperature experiments described in PART THREE.)

Temperatures ° F.	Developmental Units per Hour.	Temperatures ° F.	Developmental Units per Hour.	Temperatures ° F.	Developmental Units per Hour.
44	0.0	64	16.5	84	33.6
45	0.5	65	17.5	85	33.5
46	1.0	66	18.5	86	33.3
47	1.5	67	19.5	87	32.9
48	2.0	68	20.5	88	32.3
49	2.6	69	21.5	89	31.4
50	3.3	70	22.5	90	30.3
51	4.0	71	23.5	91	28.7
52	4.8	72	24.5	92	27.2
53	5.7	73	25.5	93	25.7
54	6.5	74	26.5	94	24.2
55	7.5	75	27.5	95	22.7
56	8.5	76	28.5	96	21.2
57	9.5	77	29.5	97	19.7
58	10.5	78	30.5	98	18.2
59	11.5	79	31.4	99	16.7
60	12.5	80	32.4	100	15.2
61	13.5	81	33.0	101	13.7
62	14.5	82	33.3	102	12.2
63	15.5	83	33.5	103*	10.7

* Velocities for higher temperatures may be secured from Fig. 24 (p. 402). Individual variation permits the first larvae to leave the apple when the sum of developmental units is 16% less than the totals given here, which are for the average of all individuals.

TABLE VI. *Rainfall Corrections Applicable to the Developmental Total for the Larva in the Apple and Cocoon.*

Rainfall while larva is in apple. (Inches)	Developmental Total. (Hour units)
(Picked apples)	15,600
0	16,200
2	16,740
4	17,280
6	17,820
6.66	18,000*
8	18,360
10	18,900
12	19,440

* Normal used in calculation of standard (theoretical) time.

THE USE OF TEMPERATURE DATA ALONE.

a. *Maximum and minimum temperatures.* Daily maximum and minimum temperatures cannot be used to give accurate results, as the rate of development often varies too much from hour to hour..

b. *Thermograph Records.* If it is desired to use temperature alone (i. e., without data on humidity, etc.), thermograph records are necessary. For rough approximations for estimating the progress of the first generation in southern Illinois localities, use Table I as follows: Draw a straight line from T. 45°, H. 80% to T. 63°, H. 77%, continuing this line to T. 90°, H. 42%. Make a list of the velocity values lying nearest to this line and use them for their corresponding temperatures from the thermograph records for one-hour or two-hour periods. This applies to the first generation pupae and eggs. For the second and third generation pupae and eggs, draw the line from 45°, 89% to 70°, 89% and continue to 90°, 60%; and use the velocity values lying nearest to this line for their corresponding temperatures. The results by this method will not be reliable but will probably serve as well as, or better than, summing temperatures in "degree-days".

c. *Sling Psychrometer Readings at 7 A. M. and 7 P. M.* Where hygrograph records are not available, as is often the case in working over old data, it will probably give fair results to use thermograph records for hourly or bihourly temperatures if sling readings are available for humidities at 7 A. M. and 7 P. M. The values on Table I may then be read by using a celluloid triangle as a guide for getting the probable march of temperature and humidity from the 7 A. M. value to the value at the maximum temperature for the day. To make this triangle, draw a line on Table I from the temperature-humidity combination at 30° and 95%, for example (assuming that to be true for 7 A. M.), to the combination at 50° and 73% (which is the probable combination* at the time of maximum temperature on such a day in our climate); measure the angle formed by this line with a vertical line along the side of the Table; then cut the triangle to fit this angle, making it a right triangle for convenience in keeping its base parallel with lines running across the Table. Use the humidities crossed by this line drawn on the table (which line is now the hypothenuse of the triangle), with the corresponding temperatures from the thermograph sheet, up to the maximum temperature. For all clear days, read along the hypothenuse of the triangle made on the basis of the example, for all rising temperatures, beginning with the 7 A. M. combination for the day. For all falling temperatures, follow back across the Table from this maximum along a straight line to the 7 P. M. temperature-humidity combination for that day. (The triangle is not needed here.) If practicable, consider periods when it is raining as having 95 per cent humidity.

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* This probable combination was derived from data on the average daily march of temperature and humidity, obtained by an analysis of many hygrothermograph records.

An Example of Estimation of Seasonal Progress.

The example below, which is designed to show the method of prediction, is based upon Glenn's observations of band collections at Olney for 1916, as shown in his Table 33.*

His observation showed that the first pupa appeared April 13, and that the maximum pupation was April 20. As the preceding autumn and winter had a total rainfall of slightly more than 20 inches, the developmental total should be 6360 (Table III), and the first moths would be expected to emerge May 13—the date on which that total was reached (using velocity values from Table I for the temperatures and humidities as shown in Glenn's hygrothermograph records April and May, 1916). The individual variation would throw it back about two days; the actual time of first emergence was May 11. The day of maximum emergence, reckoned from the date of maximum pupation, should fall on May 19, which was the date observed.

According to Isely and Ackerman, egg-laying is controlled by the temperatures after sunset, taking place in very faint light and above 62° F. In the absence of data on cloudiness and temperature immediately after sunset in May, 1916, we may take the average time as two days for the period from emergence until laying is well begun. On this basis, the first eggs should have been laid on the 14th. The actual date observed was the 14th. The normal incubation total of 3864 developmental units was reached on May 25 early in the morning. The actual time of hatching observed was May 25. (The correction of 8% for individual variation would throw some hatching back to sunset of May 24.)

Pupation should occur when a normal total of 18,000 developmental units (reckoned from the time of hatching of the eggs) is reached, if the rainfall is normal for that period. (An average of 6.66 inches was used as the normal in calculation of standard time.) It may be later or earlier, accordingly as the period in the apple comes at a time with more or less rainfall. With 10.6 inches of rainfall during this period in 1916, we should expect a maximum pupation when a total of approximately 19,060 developmental units was reached, that is, on June 30. Individual variation in larval time (16%) would permit some larvae to pupate six days earlier (June 24).

Counting from June 24, with velocity values from Table I, we get a total of 6480 developmental units on July 5. The correction for individual variation throws the probable date for first emergence of the adult moth one day earlier, or July 4. The first adult actually emerged on July 3.

The first eggs of the second generation should be laid on the 6th. That was also the date observed. A total of 3864 developmental units was reached on the 12th; the actual first larva was observed on the 12th. (The 8% correction for individual variation of the egg amounts to about half a day.)

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* These data were not used in establishing velocity values.

These first larvae of the second generation were in the apples during a period with 1.5 inches of rain, which would fix the total at 16,615 development units. This was reached on August 7. With a deduction of 4 days for individual variation, the earliest probable date for first pupation becomes August 3. The earliest actual date recorded was August 9. Reckoning from August 3, we should expect the moths to emerge on August 12, when 6480 developmental units had accumulated. With the individual-variation correction of one day, the date becomes the 11th. One adult actually appeared August 12, and others followed closely, indicating that some pupae were overlooked. Not knowing the light and temperature after sunset, we would say that some eggs should have been laid August 14, but none were actually found until the 19th; and we should expect hatching on August 20, but no larvae were observed before August 23. This indicates the need of further study of egg-laying and the recording of conditions necessary for egg-laying.

ABUNDANCE OF LATE-PUPATING LARVAE IN SPRING.

It has been supposed by some investigators that the delay in pupation on the part of some larvae in spring is due to external conditions. A large series of larvae were hibernated and the moths brought to emergence under the same condition. (For methods used, see pp. 405 ff.) The results were the same, or essentially so, for the larvae that were soaked in water and those that were merely kept in moist air. The pupations were strung out over a long period, the last emergence being 28 days after the first, at a constant temperature of 72° F. (See Fig. 25, p. 409.) The curve of emergences shown in Fig. 25 B has one main maximum which falls on the 8th day, and also a group of three small maxima centering on the 22d day (72° F.). If such a group is large, as it is likely to be when larvae hibernate in abundance, it may be responsible for damage to apples on trees sprayed to meet the early large group.

The velocity units for larvae in the apple (Table V, p. 323) may probably be used, with fair results, to estimate the time of the late pupation; because the variation in the emergence of moths is determined primarily by the time of pupation, or in other words by delay in larval development.

In the experiments the main maximum emergence came after the accumulation of 4,704 developmental units, the next maximum after an accumulation of 6,480 units, and the center of the last group after an accumulation of 12,936 units. The center of the last group of spring pupations at Olney in 1915 came after an accumulation of 16,152 units; in 1916, of 15,888; and in 1917, of 13,008. These years average 15,024 developmental units for the period. This means that the late group of pupations falls three to five weeks later than the first pupation. This marks the starting point of the pupal stage of the late group, and from this point the date of emergence of the moths may be fairly accurately determined as already indicated. Other maxima occur for pupation, but they are rather irregular. There is a corresponding one between 3,384 and 4,704 units, and one between 6,072 and 8,424 units in the different years at Olney. These units, however, were not determined on the basis of spring larvae, and the totals may need correction; factors other than temperature and humidity no doubt enter into the time of pupation. The moths from the last group of pupations should be closely watched by practical men as a guide for extra sprayings in years when hibernating larvae are abundant.*

ABUNDANCE OF HIBERNATED LARVAE AS AFFECTED BY WEATHER OF PRECEDING AUTUMN AND WINTER.

When the mean monthly temperature and rainfall in autumn and winter are mainly within the limits shown in Fig. 5A (p. 353), that is, when the autumn and early winter are "wet and not too cold," high survival and rapid development proportional to spring conditions may be expected. This statement is based chiefly upon 1914, in which the moths were very abundant. The fall and winter conditions of that year were essentially duplicated in 1925-26, with an almost 95 per cent survival, according to the observations of Mr. Flint and the Illinois field men. The diagrams in Fig. 5, however, were based on the 10 years, 1913-24. Minimum winter temperatures have not been especially considered but should be carefully checked against spring survival by field men.

The great abundance of moths in Illinois during the summer of 1926 is traceable to the large numbers of hibernated larvae and the very favorable weather conditions during May and June. Not since 1914 has there been such heavy damage to orchards over the state as in this year. Recent experience thus proves the need of more accurate methods in order to control the insect in unusual years.

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* The occurrence of darkness and temperatures above 62° F. during egg-laying periods should also be carefully considered, as these conditions have a great deal to do with the abundance of moths (Isely and Ackerman, 1923, Arkansas Agricultural Experiment Station Bulletin No. 189).

PART TWO.

A BASIS FOR THE MEASUREMENT OF DEVELOPMENT.

FORMER METHODS OF ESTIMATING PROGRESS IN LIFE-HISTORY STAGES.

Formerly investigators have relied either upon natural phenomena showing the seasonal progress of plants, *e. g.*, time of leafing, budding, or blossoming, or upon approximate accumulation of temperature as an indication of opportune times for the performance of certain agricultural operations, such as planting, spraying, and harvesting. For the greater part of a century they have assumed that temperatures above the freezing point or above the point at which a plant such as wheat starts growth, can be used directly to ascertain the amount of progress made by plants and animals at a certain date in the spring. Numerous investigators have tried temperatures above various "starting points," some using sun temperatures, others maximum temperatures or mean temperatures; and practically all have considered that the accumulated temperature, or "sum of temperatures" above a starting point, is a measure of plant or animal growth. This sum for a given period is obtained by adding together the degrees by which each day's mean temperature exceeds the assumed starting point. For many years the meteorological office of Great Britain has used 42° F. as the starting point and published the monthly accumulations above this temperature for various parts of the British Isles. A mean temperature one degree above 42° F. continuing for a day has been called a "degree-day" or a "day-degree."

Various Europeans have carried on careful critical studies employing various detailed methods of determining the total accumulated temperature necessary to bring a given plant into bloom or to ripen a crop of grain. This total, however, was found to vary so greatly for the same stage of development of the same variety of plant from season to season and from year to year that there was little or no progress in the field until the Danish physiologist Krogh ('14), while working on the effect of temperature on the development of fish eggs and of frog eggs, made the most important discovery on this subject in the present century, viz.: that development goes on slowly even at temperatures below that commonly considered as the starting point; and that, as the temperature rises, the time required to hatch an egg decreases to a minimum at a certain high point, above which the time again increases.

Glenn ('22), in his work on the codling moth, confirmed the finding of Krogh relative to high temperatures (above 90°F.). He was first to make corrections for the retarding effects of high temperatures. With his correction applied, the accumulated temperature, or "sum of temperatures," for the stages of the codling moth, varied much less from season to season than the totals for the stages of European plants referred to above. Wherever only temperature records are available, his work affords a basis for estimation.

In the present paper, Glenn's data have been worked over in conjunction with new data, and the conception of development here presented is based upon the actual behavior of the codling moth both under controlled experimental conditions and also under actual weather conditions. Only indirect use, however, is made of weather records. The results of laboratory experiments and of outdoor observations have been quite fully correlated, we believe, for the first time. The results have also been compared with the more important investigations of the last century and found to be in accord with the general results hitherto obtained.

A new method for estimating the progress of life-history stages is herein described, which affords a basis for taking humidity into account directly and other factors less directly. The factors secondarily considered are the rainfall during preceding months and the seasonal march of temperature. In the interpretation of the effects of these factors, the value of the climatic diagrams of Taylor ('14) and the observations of Huntington ('19) on man have been confirmed for the codling moth. Furthermore, the findings of Krogh relative to development taking place below the starting point, as ordinarily assumed or ascertained, have been confirmed.

CONDITIONS AFFECTING THE RATE OF DEVELOPMENT.

The most important growing-season factor influencing the development of animals native to moist or rainy climates, is usually temperature, for it is the most variable. It changes almost continuously throughout any twenty-four-hour period, being usually highest about 2 P. M. and lowest about 6 A. M. The duration of minimum temperature varies considerably with the length of day and night, and the duration of maximum temperature also varies; both vary with other weather conditions. The daily march of temperature (from higher to lower and from lower to higher) is irregular on stormy and cloudy or partly cloudy days.

Humidity is probably second in importance to temperature; at least, it is such a continuously accompanying variable of all temperatures and of all temperature changes that it cannot be ignored. The daily march of humidity is fully as striking as that of temperature. Usually, however, when the temperature rises, the humidity falls; and *vice versa*. The humidity accompanying any given temperature varies with the time of year, amount and frequency of precipitation, cloudiness, etc. There is no constant or dependable association between the two which can be expressed in numerical values.

Rainfall influences the rate of development of organisms in a less direct but nevertheless very important way. The amount of rainfall in autumn and winter influences the codling moth's rate of development in spring, probably also its winter survival, undoubtedly its vitality, and hence its rate of increase and success in general.

Air movement affects the organism by controlling the rate of evaporation, or withdrawal of water from the organism. Intensity of light and its color quality have an influence upon the well-being of the codling moth in some of its stages. Light intensity in combination with temperature practically controls egg-laying of the moths (Isely and Ackerman, '23).

Methods of Measurement of Factors.

Combinations of different temperatures and the different humidities which accompany them must be considered because of the important effects of their correlated action upon rate of development. Since they vary from hour to hour, and since there is no certainty as to what humidity will accompany a given temperature, it is necessary either to take readings at close intervals or to use averages over short periods, with the periods or intervals agreeing for the two factors.

Records of average temperature and average humidity for each hour of the day are most desirable for careful experimental or observational work, but under ordinary conditions readings at two-hour intervals are sufficiently accurate for estimating the amount of progress of life-history stages. Either of these methods of reading may be applied to hygrothermograph tracings such as are shown in Fig. 1. The first three columns of Table II (p. 321) show the readings for the solid-line tracings of Fig. 1.

Daily or monthly means of rainfall, cloudiness, and percent or hours of sunshine may be taken from Weather Bureau records. These are required for showing the effects of autumn and winter rainfall and are considered in connection with mean monthly temperatures.

Rate of evaporation has been measured as cubic centimeters of water lost per day from the Livingston porous-cup atmometer.

No accurate measurements of the quality and intensity of light have as yet been made. In the experiments herein described, the diffused light of the experimental cages has been compared with total darkness, and the effect of the light of ordinary electric bulbs passed through red, blue, and green glasses has been determined. While evidence has been obtained showing that these factors have effects, it is not yet possible to apply the results to weather conditions because of the lack of accurate measurement both in the experiments and in nature and because of the impossibility of making tenable comparisons.*

Definitions of Terms.

In order to define terms with which to express the effects of all these phenomena of weather and climate upon the rate of development of an organism, we must regard certain conditions as standard and compare all changes in the rate of its development with its behavior under the standard. Obviously, the conditions normal to the habitat of the species should be taken as standard,* and the most important factor in those conditions should be considered first. We may begin, therefore, with temperature, using the range of temperature within which the codling moth

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* Experiments with photo-electric cells given promise of some aid in the approach to the problem of the effects of varying light.

* The ideal standard is described in PART THREE, p. 359.

develops most rapidly, rather than a degree arbitrarily assumed as a "starting point" for development.

This optimum range of temperature can be determined for any stage in the life-cycle only by a series of preliminary experiments performed at intervals of a few degrees throughout the whole range of temperatures under which the insect is known to thrive. The results of constant-temperature and variable-temperature experiments whose means are comparable, covering this whole range (with variations in humid ty, etc., carefully controlled so as to accompany variations in temperature in a manner closely approximating that characteristic of average weather conditions in the optimum climate for the stage)—the results of such experiments, when properly correlated, should give the necessary basis for defining standard conditions. Under these standard conditions, the time required to complete the stage may be taken as a basis for comparing the rate of development at any temperature.

That range of temperature within which the time to complete the stage is shortened in exact proportion to the rise of temperature is designated as the *medial range;* that is, within the medial range, the increase in the rate of development bears a fixed ratio to the number of degrees which the temperature rises. For the codling-moth larva in an apple, we find that the medial range is approximately from 55° to 75° F., and that for all other stages, including the hibernated larva, the medial range is approximately from 65° to 85° F. *Medial humidities* are those which usually accompany these medial temperatures in normal weather.

Under such standard conditions a given individual may be considered to accomplish a certain amount of development within one hour, this amount being as standard as the conditions which define it. This reaction of the organism to all these environmental phenomena operating for one hour is to be considered as consisting of a certain number of **developmental units**, each of which is a small part of the total development making up the stage of the life-cycle. As the rate of development in any given case is dependent primarily, though not entirely, upon the number of degrees of temperature above the actual threshold of development (whatever that may be),* the *unit* of development may be determined, under standard conditions, from the difference between the rate at one temperature and that at another temperature one degree† higher; and this unit is to be defined with reference to all these conditioning factors, each factor being expressed in the terms in which it is commonly measured.

The **developmental unit** is, therefore, the difference between the amount of development taking place in one hour at a given degree of mean medial variable temperature and the amount of development taking place in one hour at a temperature one degree higher, with

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* The actual threshold is not a fixed temperature but varies with other conditions.

† The Fahrenheit scale is used in this paper. The Centigrade scale, which is preferable for several reasons, is used in a book on Experimental Animal Ecology, now in course of preparation, to be published in 1927 by Williams and Wilkins Company, Baltimore, Md.

the humidity, air movement, light intensity, and other conditions normal to the habitat of the organism in that stage of its life-history. In other words, the **developmental unit** is the effect produced in one hour by one degree of medial temperature in conjunction with all other phenomena characterizing the standard conditions described above. This *phenomena-degree-hour* may be designated as one **pheno-hour.**

While relative velocity of development has heretofore been expressed as the arithmetical reciprocal of the time required to complete a stage in the life-cycle, this new method permits a definition of absolute velocity as the number of developmental units per hour.

The **threshold** of development is the intensity, or quantity, of any factor immediately *above* which development begins to be measurable. For example, the temperature threshold is that degree of temperature just above which development begins to be perceptible in amount. It is not a fixed point but varies, within certain limits, with the humidity and other weather factors and with the generation and the individual. For the larvae in the apple, it varies from 43° to 48° F.; for the pupa and egg, from 44° to 49° F.; and for the hibernated larva, from 43° to 50° F.

The **developmental total** for any stage is the sum of developmental units for that stage. It is calculated by simply adding together all the developmental units for every hour from the observed (or calculated) beginning of the stage to the observed (or calculated) end of it, using velocity values such as those shown in Table I for hourly combinations of recorded temperature and humidity. More briefly, a developmental total is obtained directly by summing the hourly velocity values for the known weather conditions throughout the stage. Similarly, a developmental total for a whole life-cycle may be obtained. *Developmental totals are not constants* but vary with the rainfall of the season and the preceding season, with other weather factors, with the generation, and with the individual. The average, or *normal,* developmental total for any lot of individuals or for any generation under any set of conditions, is, however, useful in the interpretation of data and in the prediction of appearance.

Standard time for a stage is the number of hours (or days) calculated from the normal developmental total for average organisms under standard conditions. Because of the practical difficulties involved, only temperature and humidity are taken into account in the calculation of standard time in this paper. The term **substitution-quotient** is here used to designate one-twenty-fourth of the number of pheno-hours calculated for a stage by the temperature-substitution method as described in PART THREE (pp. 387-393). When correctly calculated, the substitution-quotient is numerically equal to one-twenty-fourth of the normal developmental total for the stage; and it is used only in establishing standards of development and velocity values.

The **velocity values** (numbers of developmental units per hour for different combinations of temperature, humidity, etc., as shown in Table I) are here regarded as **fixed** and **standard** for average organisms in each stage. This is more convenient, mathematically, than to regard the developmental total as fixed. These standard velocity values were derived from data on moths under observation at Olney in 1915 and 1916; at Olney, Urbana, and Plainview in 1917; and at Urbana in 1918, 1919, and 1920. The methods by which these values were derived are too involved for brief description here (see PART THREE), and they need not be completely understood by readers who are interested primarily in the use of velocity values and in the modification of developmental totals for purposes of estimating progress of life-histories.

As has been noted, the direct use of weather data in spray calendars, etc., though of some value, has failed to give results of sufficient accuracy in all years and seasons. In the most successful recent attempt at the direct use of temperature, namely, that of Glenn ('22), the temperatures as occurring were extensively corrected to conform to the behavior of the codling moth. If the last century of phenological observation and "temperature summing" has proved anything, it is that direct application of weather data is largely a failure. This failure is further emphasized by a growing tendency to use plants as indicators. (McLean, '17; Clements, '24—Bibliography.) The researches herein described have shown conclusively that in the case of the codling moth, estimation of progress in development, of abundance, and of fecundity must be based primarily upon the physiological characters and responses of the species. Weather data cannot be used directly. Temperatures summed above the empirical or imaginary "threshold" selected by ordinary methods do not give correct results because they have different accelerative values under different conditions and because temperatures below it are actually effective. Also, high temperatures, above or near 90° F., have a much smaller accelerating effect than they have been expected to show by most investigators excepting Glenn ('22). In this paper all attempts at direct use of weather data are abandoned, the chief reliance is put upon *velocity of development of the codling-moth in its several stages.*

Graphic Representation of Velocity.

The meaning of velocity is well illustrated by reference to rate of movement, or speed of travel, of a machine or animal or man. In all matters of speed of travel, the *reciprocal* of the *time* required to cover a fixed distance is used to represent *relative velocity,* or rate of travel. For example, in the case of a tractor pulling a load 12 miles at various speeds, the relative velocity is obtained from the time as follows:

Time to go 12 mi.	2 hr.	3 hr.	4 hr.	5 hr.	6 hr.	8 hr.	10 hr.	12 hr.
Reciprocals of time	.50	.33⅓	.25	.20	.16⅔	.12½	.10	.08⅓
Miles per hour (12 x reciprocals)..	6.0	4.0	3.0	2.4	2.0	1.5	1.2	1.0

The reciprocal multiplied by the total miles gives velocity in miles per hour. The reciprocals of the time to complete any unit of work are thus a convenient expression of relative velocity.

The activity of cold-blooded animals, such as insects and millipeds, in a general way varies directly with temperature just as development does. Also, rate of progression may be used as an index of physiological activity, and something of the laws governing rate of development may be ascertained from a study of progression.

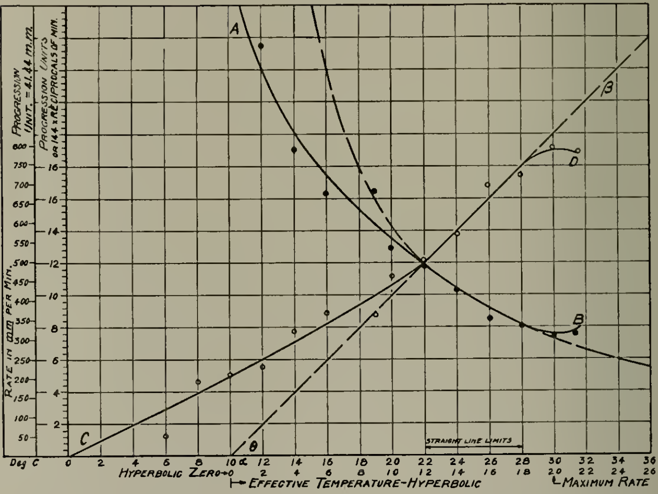

Fig. 2. Rate of creeping of a diplopod at various temperatures, shown in millimeters per minute and in progression units (41.44 mm) per minute. Note how the velocity curve CD departs from a straight line above 28° C. and below 22° C.; and how the time-temperature curve AB differs from an equilateral hyperbola. (Date from Crozier '24.)

Fig. 2 shows a curve for the velocity of progression, or rate of creeping, of a milliped, plotted from the experimental data of Crozier ('24). For velocities of progression of 500—750 mm. per minute (temperatures 22°—28° C.), a milliped in an experiment conducted at a temperature one degree higher than 22° adds 41.44 mm. to the distance traveled in one minute. Likewise, an animal in an experiment at two degrees higher than

22° travels 82.88 mm. farther per minute, and so on up to 28°, where a change takes place. The *unit of progression* is 41.44 mm., based upon the effect of one degree Centigrade within the range of medial temperatures, which are marked by the straight-line limits of the velocity curve CD. This same unit is the basis of determining the points at which the effect of one degree higher or lower temperature upon the rate of progression is greater or less than 41.44 mm. in one minute. The *alpha* value (hyperbolic zero) for the data of Crozier is approximately 10° C., a fact of very little actual significance except in the determining of the constant product of the temperature above *alpha* and the time for a definite total distance. This total distance is here assumed to be 5967.3 mm. The portion of the time-temperature curve AB between 22° and 28° C. is a portion of an equilateral hyperbola. The time is that required to travel 5967.3 mm. at the temperatures plotted. An inspection of the curve will show that the mathematical product of time (as plotted) and temperature above 10° C. (as plotted) is 144, and that for each point plotted the reciprocal of the time units multiplied by 144 equals the number of progression units. These relationships are characteristic of the equilateral hyperbola.

The total distance was here arbitrarily taken as 144×41.44 mm. units, or 5967.3 mm. (calculated). If another distance were chosen, the velocity for each temperature would be the same, because the milliped would travel at the same rate, but the number of progression units would differ. The same principle holds good in respect to the different stages of development of an organism. The amount of metabolism required in each stage is comparable to distance to be traveled, while the rate of development remains basically of the same order of magnitude not only for the different stages of the same insect but probably also for all the various insects and, indeed, perhaps for all cold-blooded animals.*

The next step in the way of experiments with the milliped would be the use of *variable* temperatures from 20° to 28° C. Such variability would probably increase the rate of progression slightly for a mean of the varying temperatures as compared with the constant ones, but this difference will be ignored in the absence of data from variable-temperature experiments in this case. For the present purpose, we may assume that the rate of progression as plotted for a certain degree of constant temperature would hold good for the same degree of mean variable temperature; accordingly, we may construct a table of "effective temperature" above 10° C. as the "starting point" (using some of the nomenclature of those writers who have summed temperatures), by assuming a different

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* Evidence of the metabolic basis for the developmental unit is reviewed in PART THREE, p. 361.

mean temperature for each minute of a ten-minute schedule and reading the mean velocity for each minute from the curve in Fig. 2, as follows:

Time.	Actual Temperature. (above 0°C.)	"Effective Temperature". (above 10°C.)	Mean Velocity (Progression units per minute)
1st min.	20	10	10.8
2d min.	30	20	19.0
3d min.	14	4	7.0
4th min.	10.5	0.6	5.2
5th min.	4	(—6) omitted	2.0
6th min.	2	(—8) omitted	0.8
7th min.	12	2	6.0
8th min.	13	3	5.4
9th min.	16	6	8.2
10th min.	25	15	15.0
10 min.	146.5 above 0°C.	60.5 "effective degrees"	79.4 progression units travelled.

Thus, with an accumulation of 60.5° of "effective temperature," a total distance of 79.4 progression units, or 3290.33 mm., was traveled in those 10 minutes of variable temperature; but a comparison of column 3 and column 4 shows clearly that the "effective temperature" is *not* a correct index of the rate of travel or of the distance traveled above 28° C. or below 22° C. (i. e., outside the straight-line limits). Only in the 10th min., with the temperature at 25° C. (i. e., within the straight-line limits) does the "effective temperature" properly indicate the rate of travel.

The development of the codling moth in its several stages, and in fact, the behavior of nearly all other organisms hitherto investigated* with respect to different temperatures, is similar to the activity of the milliped. In a developing organism, however, the processes involved in growth, transformation of parts, etc., do not go on at the same rate at different times within the same stage, and thus only fractions of a whole process are usable as developmental units. Various results of the stimulation of organisms by temperature do bear a definite ratio to the temperature within the straight-line limits of the velocity curve, although not outside those limits.

Further evidence of the nature of development is found in the fact that the total carbon-dioxide given off by an organism such as the pupa of the meal worm is a constant for individuals of the same weight. This total bears a fixed ratio to the sum of the daily amounts of development of the pupa, but not to the "effective degrees" summed above a definite beginning (an imaginary "threshold," which is the hyperbolic zero) ex-

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* Shapley ('20) has a curve for progression of ants which appears to be exceptional in that it turns upward at high temperatures.

cept between approximately 18° and 29° C. The total carbon dioxide is, moreover, the *same* at the high temperatures where the sum of the "effective degrees" is *too great*. The sum of developmental units for constant temperatures is easily derived for the straight-line portion of the velocity curve, as it is simply the product of time units and constant-temperature units. This product has a fixed value under a given set of conditions and has been known as the "thermal constant." The mean of temperatures varying within the straight-line limits of the velocity curve but not going outside these limits (approximately 18° and 29° C. for the meal-worm pupa) also gives a constant product when multiplied by the time. This product is smaller than the time-temperature product obtained within the same range for constant-temperature conditions, because development proceeds faster under variable-temperature conditions. In very carefully controlled experiments on animals, the product is remarkably constant for any one set of conditions. (Krogh '14a and '14b.)

ORDER OF EXPERIMENTATION.

In the determination of velocities for any stage of an organism, the first procedure is to run a series of preliminary experiments with constant-temperatures at five-degree intervals from 45° to 100° F., beginning with 100% humidity at 45° F. and lowering the humidity about 6% with each five degrees rise in temperature. Such experiments would show, for example, in the case of the codling-moth pupa, that the straight-line limits are from a little below 65° to a little above 85°. These should be followed by: (1) a series of experiments under constant temperatures at five-degree intervals from 45° F. to 100° F. with 95%, 85%, 75%, 65%, 55%, 45%, 35% relative humidity; and (2) a series of variable-temperature experiments with daily variations ranging from 65° F. to 85° F. with the following humidities at 65° F.: 100%, 90%, 80%, 70%, and 60%,—and one experiment out of doors. This would make 90 experiments, and for the desired results the material should be uniform, and all experiments should be started on the same day. This would require a minimum of 3,000 individuals; 9,000 would be preferable; and this series of experiments should be repeated with each generation for each of three seasons.

Experimentation on this huge scale could not be done with the facilities available for the work here reported. Moreover, when this work was undertaken, there was no basis in experience showing that such a procedure would be necessary. As a result, the variation in the different stocks caused irregularities in the data, which necessitated much additional calculation. However, our experience indicates that the developmental totals, the thresholds, and the velocity values are different for each humidity, and that the developmental totals differ most.

INTERPRETATION OF EXPERIMENTAL DATA.

It has proved more convenient to establish fixed velocity values for average stocks under average weather conditions than to establish a fixed developmental total. This was done by determining the average developmental total and using it as a standard. For the constant-temperature experiments within the straight-line limits, the average total was 6,936 developmental units for the pupa, and for the variable-temperature experiments it was smaller, approximately 6,480 (average by two methods). This variable-temperature total, 6,480, was used as a normal in adjusting the velocity values *outside the straight-line limits*, because ordinary weather conditions are variable with respect to temperature, etc., and result in more rapid development. This normal total for the pupal stage was verified by elaborate calculations covering all of Glenn's Olney data. Similarly, normal totals were established and verified for the other stages.

The developmental totals used herein are not comparable to the sums of "effective day-degrees" commonly used in direct applications of weather data, for developmental units are not temperature units but are numerical expressions of the response of the organism to temperature and all other conditions, a response which is usually growth or an internal change leading to transformation from one stage to another in the life-cycle. These developmental totals, being based on the **pheno-hour**, are in accord with the concepts of phenology which take into account both weather and the responses of organisms.

CALCULATION OF STANDARD TIME.

In order to compare the results obtained by this method with those obtained by the old method of summing "effective temperatures", it is convenient to express the conditions of development in terms of the **substitution-quotient**, which is approximately equal to the number of "degree-days" summed for medial temperatures. (See PART THREE, p 391 ff. This practice has been followed in Tables VII-XI, in which all of Glenn's Olney data and his Urbana data on pupae are recalculated in terms of standard velocity values. These data were used in the calculation of standard time for each stage, as follows:

Starting with the date of the observed beginning of each stage in each generation in each year, as recorded by Glenn, velocity values (Table I) were set down for the mean temperatures and humidities for all two-hour periods as shown in his hygrothermograph records for the several years covered by his work; the numbers of developmental units (velocity values multiplied by 2, because two-hour periods were being used) were then summed to normal totals, and dates were thus obtained on which the several stages in each generation should have been completed if these velocity values and developmental totals were normally fulfilled. In order to calculate the theoretical time for each individual or group of individuals behaving alike, the sums of developmental units for each day from the beginning of a stage to the actual date of its completion were then averaged, and this daily mean was in each case divided into the normal developmental total, so as to give a number of days approximating the standard time for the stage. This calculated number of days in each case was then compared to the actual number of days recorded for the stage in question. (For more detailed discussion of these methods of calculation, see PART THREE, pp. 381-400.)

a. Pupae.

Standard time for the pupal stage was calculated on a basis of 6,480 as the normal developmental total, this total being divided by the mean daily number of developmental units for the actual period of the stage as recorded by Glenn. For convenience, since most of the data were expressed in days, this calculation was generally done by dividing one-twenty-fourth of the daily mean into 270, which is one-twenty-fourth of 6,480.

The results in detail for a part of the 1915 pupae, with means for groups of 30 individuals, are shown in Table VII; and the results by 30-individual means for all the pupae of 1915–1917 are shown in Table VIII and Fig. 3. The detailed data on the first-generation pupae shown in Table VII are similar, in general, to those on the pupae of all generations; the differences are of a minor character and will be considered later.

The accuracy of this method of measurement of development, as well as the validity of these standard velocity values, is indicated by the fact that the actual time for all the Olney data averaged only 0.1% over the calculated time. The deviation was —0.6% for 1915, —1.4% for 1916, and 2.1% for 1917.* These deviations from calculated time are the averages of the 30-individual groups for the whole of each year. Averaging the means of the three generations for each year gives the following deviations: 1915, —1.5%; 1916, —2.8%; 1917, —1.8%; total average deviation, —2%.

The Urbana data on pupae showed the following ratios of actual to calculated time: 1917, all generations, 99%; 1918, first generation, 119%. The average ratio is 103.6%; with the 1918 set omitted, it is 99.8%. The ratios for individuals vary from 91% to 119.0%. The actual time for the latter part of the first generation shows the largest positive deviation from standard time; it is about standard in the beginning and increases to the end of the generation. The actual time for the second generation is at first shorter than the standard; it then increases and finally falls off again; while that for the third generation is short throughout. This type of deviation is apparently characteristic, though it is due in some measure to factors other than temperature and humidity (see Fig. 28), which are discussed in Part III.

b. Adult Moths.

Isely and Ackerman ('23) ascribed the abundance of codling moths in a given season partly to favorable conditions of light and temperature during the oviposition period. They found that a temperature of 62° F.

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* This 1917 time is high because of a lack of a large part of the data for the second generation. The loss of one hygrothermograph sheet necessitated large omissions at a period when the actual time is usually less than the calculated time.

TABLE VII. *Showing the actual and calculated time from pupation to emergence of moths of the first generation at Olney, Illinois, 1915, based on the original records of P. A. Glenn.*

No. of individuals.	Observed Dates.		Calculated Date for Emergence.	Developmental Total divided by 24.	Mean Daily Velocity divided by 24.	Calculated Time Days.	Actual Time Days.	Ratio of Actual to Calculated Time. %.	Substitution Quotient.	"Degree-days" above 52° F. by Glenn's Method.
	Pupation.	Emergence.								
1	4/13	5/3	5/3 A. M.	273.6	13.7	19.7	20	......	275.8	261
1	4/16	5/2	5/4 A. M.	243.4	15.2	17.8	16	......	*249.1*	232
3	4/16	5/3	5/4 A. M.	258.7	15.2	17.8	17	......	265.7	247
1	4/16	5/6	5/4 A. M.	285.5	14.3	18.8	20	......	*279.2*	268
3	4/17	5/3	5/6 P. M.	247.4	15.5	17.4	16	......	*262.4*	237
2	4/17	5/6	5/6 P. M.	274.1	14.4	18.7	19	......	*269.4*	258
2	4/17	5/7	5/6 P. M.	285.8	14.3	18.8	20	......	*275.0*	269
1	4/19	5/6	5/8 P. M.	255.2	15.0	18.0	17	......	*255.8*	240
2	4/19	5/8	5/8 P. M.	274.2	14.4	18.7	19	......	285.9	257
1	4/19	5/14	5/8 P. M.	350.0	14.0	19.3	25	......	354.2	328
1	4/20	5/10	5/10 M.	270.0	13.5	20.0	20	......	272.4	257
1	4/20	5/12	5/10 M.	293.9	13.4	20.2	22	......	*270.0*	278
1	4/20	5/13	5/10 M.	311.6	13.5	20.0	23	.....	*283.0*	295
3	4/21	5/11	5/11 P. M.	264.7	13.2	20.5	20	......	*270.0*	250
2	4/21	5/12	5/11 P. M.	278.3	13.3	20.3	21	......	283.2	263
3	4/22	5/12	5/12 P. M.	265.6	13.3	20.3	20	......	270.0	251
1	4/22	5/13	5/12 P. M.	288.5	13.7	19.7	21	......	*283.0*	268
1	4/23	5/12	5/13 P. M.	249.4	13.1	20.6	19	......	252.0	235
Mean (30 individuals)				271.8	....	19.3	19.1	101.1	271.4	257
1	4/23	5/13	5/13 P. M.	267.0	13.3	20.3	20	......	270.0	252
6	4/23	5/14	5/13 P. M.	290.0	13.8	19.6	21	......	283.0	275
1	4/24	5/13	5/14 P. M.	246.3	12.9	20.2	19	......	*254.0*	232
1	4/24	5/14	5/14 P. M.	269.2	13.5	20.0	20	......	*268.0*	254
5	4/24	5/15	5/14 P. M.	292.1	13.9	19.4	21	......	293.6	276
1	4/24	5/16	5/14 P. M.	316.3	14.4	18.8	22	......	*312.0*	301
2	4/25	5/15	5/15 A. M.	272.7	13.6	19.9	20	......	*268.0*	257
4	4/25	5/16	5/15 A. M.	296.9	14.1	19.1	21	......	*294*	281
7	4/26	5/16	5/16 A. M.	275.4	13.3	20.3	20	......	280.0	260
2	4/26	5/20	5/16 A. M.	299.8	12.5	21.6	24	......	288.0	276
Mean (30 individuals)				285.3		19.8	20.8	105.0	283.9	269

Column 4 gives the date on which the developmental total reached 6480 (equivalent to 270 substitution-quotient), on a basis of velocity values shown in Table I, assuming that pupation occurred at noon of the day recorded. Column 5 gives the total which was reached on the actual date of emergence, reduced to the same basis. Column 6 gives the mean number of developmental units per day, reckoned from velocity values in Table I, for the actual period of pupal life as recorded. Column 7 gives the theoretical time, in view of the recorded conditions of temperature and humidity, calculated by dividing the mean daily velocity into 6480 as the normal developmental total. This eliminates individual variation. The substitution totals shown in the last column were obtained by the temperature-substitution method explained on p. 393; interpolations are shown in italics.

TABLE VIII. *Showing the actual and calculated time from pupation to emergence for all of Glenn's Olney data, 1915-1917, summing velocity values from Table I to a normal total of 6480 (equivalent to 270 substitution-quotient) and averaging the results by groups of 30 individuals.*

Compare the first two items of this table with the means of 30 individuals shown in Table VII. The mean ratio of actual to calculated time for each generation is given here to aid in determining the effects of factors other than temperature and humidity.

Date of Pupation.	Date of Emergence.	Calculated Time.	Actual Time.	Ratio of Actual to Calculated Time. %	Developmental Total divided by 24.	Substitution-quotient.
Hibernated Generation 1915						
4/13	5/12	19.1	19.3	101.1	271.8	271.4
4/23*	5/20	19.8	20.8	105.0	285.3	283.9
4/26	5/24	22.2	24.2	109.0	295.8	290.0
4/30	5/30	22.1	23.5	106.3	289.9	284.8
5/9	6/9	20.2	21.7	107.4	293.6	288.5
			Mean	105.8		
First Generation 1915						
6/19	7/10	14.3	13.0	91.0	236.7	254.7
6/27	7/10	14.5	13.6	93.8	254.7	270.5
6/28	7/13	14.5	13.1	90.4	244.3	261.6
6/29	7/16	13.8	13.5	97.8	263.5	280.8
7/1	7/15	12.7	13.0	102.3	275.8	275.1
7/4	7/17	11.7	10.9	93.1	252.3	253.7
7/6	7/18	10.9	10.9	100.0	268.4	264.3
7/7	7/20	9.9	9.9	100.0	271.8	264.8
7/10	7/22	9.8	10.1	103.0	276.2	271.3
7/13	7/25	10.6	10.4	98.1	266.4	275.0
7/14	7/27	10.9	10.5	96.3	258.6	258.0
7/16	8/2	11.4	11.1	97.3	262.3	277.0
7/21	8/5	10.3	9.7	94.1	252.5	256.0
7/26	8/7	11.1	11.2	100.9	270.3	257.7
7/28	8/16	11.9	12.0	100.9	272.8	266.3
			Mean	97.3		
Second Generation 1915						
8/7	8/31	14.8	13.7	92.5	250.3	249.3
Hibernated Generation 1916						
4/13	5/15	29.3	28.7	98.0	265.6	263.8
4/16	5/15	27.9	27.7	99.3	269.2	267.5
4/17	5/15	27.3	26.9	98.6	265.7	262 2
4/19*	5/18	27.1	26.7	97.9	267.0	270.0
4/19*	5/19	28.3	27.6	97.6	262.7	265.5
4/20*	5/19	28.9	28.9	100.0	270.4	272.2
4/21	5/20	27.2	27.1	99.6	269.2	269.2
4/24	5/21	24.6	24.9	101.1	273.5	267.1
4/28	5/22	22.2	22.2	100.0	270.3	270.3
4/30	5/23.	20.8	20.9	100.4	272.4	268.2
5/5	5/26	18.1	18.5	102.1	276.9	268.2
5/7	5/27	17.5	18.4	105.0	284.8	269.7
5/9	5/29	17.1	17.7	103.5	281.3	268.7
5/11	6/1	16.4	17.8	108.4	293.9	272.3
5/15	6/7	15.1	16.4	108.8	292.9	278.2
5/24	6/17	16.2	17.2	106.1	287.5	274.0
			Mean	101.7		

* Maximum.

TABLE VIII—Continued.

Date of Pupation.	Date of Emergence.	Calculated Time.	Actual Time.	Ratio of Actual to Calculated Time. %	Developmental Total divided by 24.	Substitution-quotient.
First Generation 1916						
6/20	7/10	10.7	10.3	97.4	260.3	271.1
7/1	7/14	10.8	9.9	91.6	248.0	276.0
7/4	7/15	10.9	9.9	90.7	244.8	260.1
7/5	7/16	10.5	10.2	98.0	261.6	270.8
7/6	7/17	10.0	10.0	100.0	268.6	266.6
7/8	7/18	9.8	9.6	98.0	263.9	267.4
7/9	7/23	9.6	10.0	104.2	279.6	278.5
7/10	7/18	9.5	9.7	102.0	274.6	269.1
7/11	7/21	9.5	9.2	96.9	261.9	262.4
7/11	7/21	9.6	9.2	95.8	257.0	258.0
7/12	7/22	9.6	9.4	98.0	261.0	264.7
7/13	7/21	9.6	9.7	101.1	273.6	271.1
7/14	7/23	9.6	9.1	94.8	255.2	254.8
7/15	7/24	9.7	8.9	91.8	248.3	252.8
7/15	7/24	9.7	10.0	103.0	278.6	276.1
7/16	7/26	9.8	9.4	96.0	259.2	265.0
7/16	7/26	9.9	9.7	98.0	264.8	270.6
7/17	7/26	9.9	9.9	100.0	269.1	278.3
7/18	7/28	9.9	9.4	95.0	256.5	268.2
7/18	7/30	9.9	10.0	101.0	273.6	284.1
7/19	7/30	9.8	9.8	100.0	270.9	277.9
7/21	8/1	9.5	9.4	99.0	267.2	268.6
7/23	8/2	9.4	9.2	98.0	265.8	264.8
7/24	8/3	9.4	9.2	98.0	265.0	271.9
7/25	8/5	9.3	9.4	101.0	274.5	274.2
7/27	8/6	9.2	9.4	102.1	276.6	268.2
7/27	8/7	9.1	9.8	107.5	289.0	295.3
7/29	8/8	9.2	9.4	98.0	277.3	273.2
7/30	8/9	9.2	9.2	100.0	269.3	268.3
7/31	8/10	9.2	9.1	98.9	267.6	273.0
8/2	8/12	9.1	9.1	100.0	273.2	263.1
8/3	8/16	9.5	9.5	100.0	270.8	277.7
8/6	8/18	10.3	10.1	98.2	264.7	264.4
8/7	8/18	10.4	10.2	98.2	263.5	261.0
8/10	8/21	10.3	9.8	96.1	255.4	259.0
8/10	8/22	10.3	10.2	99.1	265.3	262.2
8/12	8/24	10.6	10.1	95.4	255.6	263.0
8/14	8/24	10.5	10.0	95.3	254.9	263.0
8/14	8/24	10.5	10.3	98.2	263.2	258.4
8/15	8/25	10.4	10.0	96.2	258.3	266.1
8/16	8/26	10.6	9.6	90.6	244.8	250.1
8/16	8/28	10.9	10.6	97.4	262.0	264.6
8/16	8/28	11.0	10.1	91.9	245.2	249.0
8/17	8/29	11.5	11.1	96.5	258.6	255.9
8/17	8/30	12.3	11.5	96.7	251.0	250.4
8/18	8/31	13.3	12.1	91.0	243.8	252.6
8/19	9/2	13.5	13.2	97.8	262.5	271.0
8/19	9/4	14.4	13.4	93.2	251.5	259.3
8/21	9/4	14.8	13.9	94.0	254.7	262.0
8/23	9/7	14.1	13.0	92.2	249.4	255.7
8/26	9/11	13.6	12.7	94.4	251.4	260.0
			Mean	97.6		
Second Generation 1916						
8/28	9/12	12.6	11.6	92.2	246.8	245.8

TABLE VIII—Concluded.

Date of Pupation.	Date of Emergence.	Calculated Time.	Actual Time.	Ratio of Actual to Calculated Time. %	Developmental Total divided by 24.	Substitution-quotient.
Hibernated Generation 1917						
4/12	5/19	36.5	37.0	101.4	273.8	269.8
4/12	5/19	34.3	36.2	105.5	285.2	267.1
4/15	5/20	33.1	34.4	103.9	282.9	262.8
4/16	5/21	32.3	34.1	105.6	287.5	281.2
4/17	5/20	32.6	33.0	101.2	275.5	275.2
4/17	5/20	32.5	33.0	101.5	276.6	273.9
4/17	5/19	32.6	32.8	100.6	272.9	272.9
4/18	5/20	33.4	32.0	95.8	257.7	268.8
4/18	5/21	32.6	33.0	101.2	274.9	271.7
4/18	5/21	32.5	33.0	101.5	275.5	271.9
4/18	5/21	32.5	33.0	101.5	275.5	271.9
4/19	5/21	33.8	33.0	97.6	267.7	262.0
4/19	5/21	33.7	32.0	94.9	256.7	259.0
4/19	5/22	33.6	32.1	95.5	258.1	260.0
4/19	5/24	33.2	33.7	101.5	274.2	272.8
4/19	5/24	33.7	35.0	103.8	281.1	283.5
4/19	5/25	33.6	35.2	104.8	282.8	285.4
4/19	5/25	33.4	36.0	107.8	291.3	295.3
4/19*	5/21	33.9	34.4	101.4	274.4	277.0
4/20*	5/24	34.6	34.0	98.3	264.8	272.0
4/20*	5/24	34.6	34.4	99.4	268.9	275.0
4/20	5/25	34.6	35.0	101.1	275.1	280.0
4/20	5/25	34.6	35.0	101.1	275.1	280.0
4/20	5/26	34.4	35.4	102.9	280.6	283.7
4/20	5/29	34.2	36.0	105.5	286.9	288.0
4/22	5/27	34.0	33.9	99.5	270.7	274.3
4/22	5/29	32.9	35.1	106.7	289.5	283.9
4/23	5/27	34.6	33.9	98.0	267.5	263.0
4/23	5/27	34.8	34.0	97.7	273.9	268.6
4/23	5/29	34.1	34.5	101.1	284.3	284.7
4/23	5/27	34.1	34.5	101.1	274.9	273.5
4/24	5/30	34.6	35.0	101.1	277.5	273.4
4/24	5/31	34.2	36.2	105.8	295.1	288.4
4/24	5/30	34.1	34.8	102.0	277.8	278.8
4/25	5/28	33.5	34.9	104.1	284.3	281.5
4/26	5/24	32.6	34.9	107.0	291.7	286.2
4/27	6/1	31.2	31.9	102.2	279.9	276.6
4/30	6/1	28.4	31.1	109.5	287.0	282.9
5/3	6/3	25.6	27.0	105.4	286.1	251.2
5/10	6/5	20.8	22.3	107.2	290.3	283.2
5/16	6/7	18.6	20.4	109.6	296.7	302.9
5/18	6/9	18.5	20.2	109.2	295.2	296.9
5/20	6/20	17.3	18.9	109.2	287.3	303.1
			Mean	102.6		
Partial First Generation 1917						
6/27	7/12	12.1	10.8	89.2	239.1	253.8
7/2	7/15	12.1	11.9	98.3	221.4	242.6
			Mean	93.8		

* Maximum.

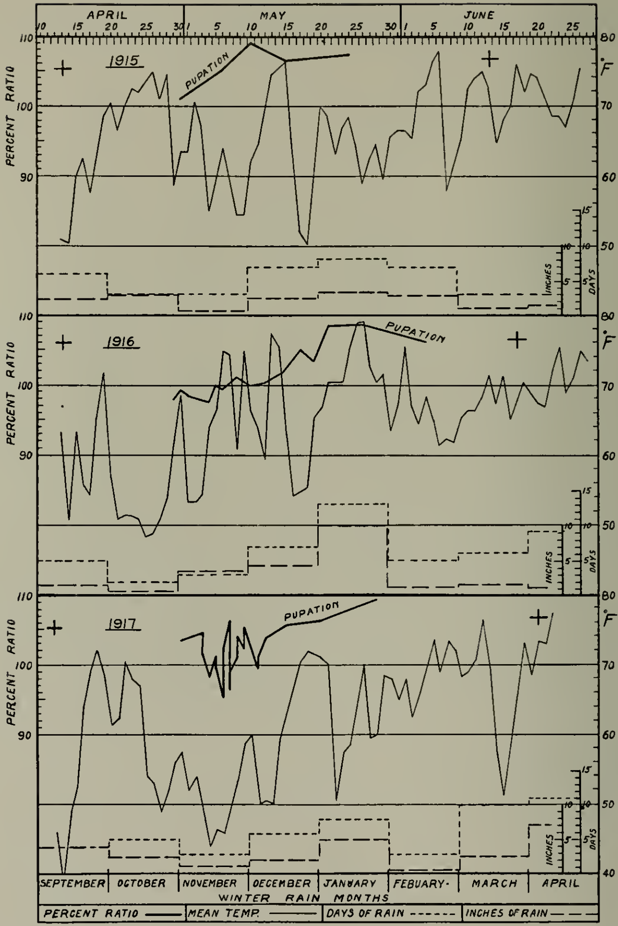

Fig. 3. Graphic summary of data in Table VIII.
(See explanatory note on opposite page.)

TABLE IX. *Showing the calculated and actual time for incubation of eggs from first generation moths at Olney, Ill., (1915).*

For detailed explanations see Table VII.

No. of Eggs.	Dates.	Developmental total divided by 24.	Mean Daily velocity divided by 24.	Calculated time.	Actual Time.	Ratio of Actual to calculated time. (per cent.)
3	5/5 —5/17	159.9	13.3	12.0	12	....
6	5/5 —5/20	175.1	11.7	13.7	15	....
10	5/5 —5/17	159.9	13.3	12.0	12	....
27	5/5 —5/20	175.1	11.7	13.7	15	....
2	5/6 —5/21	185.7	12.4	12.9	15	....
12	5/7 —5/21	173.9	12.4	12.9	14	....
Mean for 60	....	*171.9*	....	*13.1*	*14.1*	107.6
15	5/8 —5/21	166.5	12.8	12.5	13	....
2	5/8 —5/22	182.0	13.0	12.3	14	....
2	5/8 —5/23	193.4	12.9	12.4	15	....
13	5/9 —5/21	160.9	13.4	11.9	12	....
3	5/9 —5/22	176.5	13.6	11.8	13	....
6	5/10—5/21	155.3	14.1	11.3	11	....
1	5/10—5/22	170.8	14.2	11.3	12	....
5	5/11—5/22	160.3	14.6	11.0	11	....
5	5/21—6/2	153.0	12.9	12.6	12	....
Mean for 60	....	*164.8*	....	*12.0*	*12.4*	103.3
87	5/21—6/3	168.6	13.0	12.3	13	....
Mean for 60	....	*168.6*	....	*12.3*	*13.0*	105.7
1	5/21—6/5	189.1	13.5	11.9	14	....
25	5/22—6/3	153.1	12.7	12.6	12	....
19	5/22—6/4	173.6	13.4	12.0	13	....
Mean for 60	....	*163.7*	....	*12.3*	*12.6*	102.4

Fig. 3. Length of the pupal stage of first-generation codling moths in 1915, 1916, and 1917 at Olney, expressed in per cent of standard average time for the stage (scales at the left). The data are plotted for groups of 30 individuals on dates midway between the first pupation and the last emergence of each group. The cross at the left indicates the date of pupation of the first individual of the first group in each year, and the cross at the right indicates the date of emergence of the last individual of the last group. The mean temperature for each day for the whole period covered in each year is plotted according to the Fahrenheit scales at the right, for comparison with pupation graphs. The inches of rainfall and number of rainy days for each month from the preceding September to and including April are plotted below, with names of months at the bottom of the figure.

Table X. *Showing actual and calculated time for incubation of eggs of all generations of moths recorded by Glenn at Olney, 1915-1917, on a basis of 160 as the normal substitution-quotient.*

Dates.	Time for Incubation.		Ratio of Actual to Calculated time. %	Substitution-quotient.
	Calculated.	Actual.		
First Generation 1915				
5/5 —5/21	13.1	14.1	107.6	171.9
5/8 —6/2	12.0	12.4	103.3	164.8
5/21—6/3	12.3	13.0	105.7	168.6
5/21—6/4	12.3	12.6	102.4	163.7
5/23—6/5	11.8	12.3	104.2	167.8
5/23—6/6	10.9	11.9	109.2	212.2
5/27—6/10	9.6	9.0	93.7	152.6
6/1 —6/11	9.2	9.3	101.1	161.1
6/3 —6/11	8.9	8.4	94.4	150.2
6/3 —6/12	8.6	9.0	104.6	167.8
6/3 —6/12	8.5	9.1	107.0	168.6
6/4 —6/13	8.4	8.3	98.8	158.3
6/5 —6/14	8.4	8.2	97.7	157.0
6/5 —6/20	8.0	8.5	106.2	170.7
6/14—6/23	7.7	7.7	100.0	159.2
6/16—6/27	7.9	8.0	101.2	163.3
		Mean	*102.3*	
Second Generation 1915				
7/2 —7/13	9.1	9.0	98.9	157.7
7/7 —7/15	7.0	6.7	95.7	153.0
7/9 —7/24	6.2	6.5	104.9	170.5
7/17—7/29	6.9	7.3	105.8	165.8
7/24—7/30	6.4	6.0	93.8	149.1
7/24—7/31	6.0	6.0	100.0	159.8
7/28—8/3	5.6	5.4	96.5	154.1
7/28—8/6	6.4	6.6	103.1	166.1
7/30—8/8	7.3	7.1	97.3	157.2
7/31—8/21	7.8	7.8	100.0	160.4
8/13—9/2	11.1	10.0	90.1	143.0
8/22—9/4*	11.6	11.2	87.9	152.9
*48 eggs				
		Mean	97.8	
Third Generation 1915				
8/22—9/10	11.5	10.6	92.2	148.7
9/13—9/19*	5.6	6.0	.....	.....
*20 eggs				
		Mean	92.2	

The results are averaged for groups of 60 eggs unless otherwise indicated. The mean ratio of actual to calculated time for each generation is given here to aid in determining the effects of factors other than temperature and humidity.

TABLE X—Concluded.

Dates.	Time for Incubation.		Ratio of Actual to Calculated time. %	Substitution quotient.
	Calculated.	Actual.		
First Generation 1916				
5/14—5/26	9.7	9.2	94.9	151.6
5/19—5/27	7.8	8.0	102.6	165.2
5/20—5/27	7.4	7.1	96.0	154.0
5/20—5/28	7.1	6.5	91.5	147.0
5/21—5/28	7.1	6.9	97.2	154.6
5/22—5/29	7.1	7.0	98.6	156.6
5/22—5/30	7.1	7.0	98.6	156.6
5/23—5/30	7.2	7.1	98.6	157.5
5/23—5/31	7.4	7.2	97.3	155.3
5/24—6/2	7.7	7.6	98.7	157.5
5/25—6/7	9.8	9.3	94.9	160.4
5/30—6/12	9.9	10.5	106.1	170.6
6/7 —6/20	9.9	9.5	96.0	153.1
6/12—6/26	9.4	9.7	103.1	166.3
		Mean	98.2	
Second Generation 1916				
7/6 —7/20	5.6	5.5	98.2	155.5
7/15—7/21	5.5	5.5	100.0	158.7
7/15—7/24	5.9	5.9	100.0	160.1
7/18—7/24	6.0	6.0	100.0	158.2
7/18—7/25	6.2	6.0	96.8	156.0
7/19—7/27	6.0	6.3	105.0	166.9
7/20—7/29	5.7	6.2	108.7	172.4
7/24—7/30	5.5	5.7	103.6	165.3
7/25—8/3	5.4	5.3	98.1	155.8
7/28—8/4	5.5	5.7	103.6	164.5
7/29—8/17	6.1	5.9	96.7	151.4
8/10—8/18	6.6	7.0	106.0	168.4
8/11—8/18	6.7	7.0	104.5	167.9
8/11—8/21	6.6	6.7	101.5	163.6
		Mean	101.6	
Third Generation 1916				
8/17—8/24	6.2	6.3	101.6	164.2
8/26—9/4	9.3	9.0	96.8	156.2
8/26—9/12	7.5	7.5	100.0	159.0
9/5 —9/14*	7.6	7.2	94.8	150.2
*39 eggs				
		Mean	98.4	
First Generation 1917				
5/20—6/5	12.6	10.8	93.7	149.5
5/26—6/7	10.8	10.8	100.0	161.2
5/26—6/8	9.5	9.4	98.9	158.5
5/30—6/12	8.8	8.4	95.5	151.3
6/4 —6/16	9.4	8.7	92.6	148.7
6/7 —6/19	10.4	10.1	97.1	154.9
6/8 —6/21	10.7	9.9	92.5	149.2
		Mean	95.7	

Table XI. *Comparison of actual and calculated time for larvae in apples and in cocoons, in groups of ten individuals, for all generations of 1915-1917 as recorded by Glenn.*

Observed Date of Hatching of first individual.	Time in apple.			Time in cocoon.			Observed date of last pupation.	Entire Larval Period.		
	Calculated days.	Actual days.	Ratio A. to C. %.	Calculated days.	Actual days.	Ratio A. to C. %.		Calculated days.	Actual days.	Ratio A. to C. %.
1st Gen. 1915										
6/ 3—	27.9	28.7	102.8	4.1	4.8	117.1	7/12	32.01	33.4	104.3
6/ 4—	27.8	29.1	104.6	5.4	4.6	85.2	7/18	32.1	32.8	102.2
6/11—	28.4	27.6	97.2	4.1	4.1	100.0	7/20	32.0	31.0	96.9
6/11—	28.1	29.2	103.9	3.9	4.5	115.4	7/22	31.6	33.3	105.4
Means	......	......	102.1	......	......	104.4	......	......	......	102.2
2nd Gen. 1915										
7/11—	24.6	25.0	101.6	4.6	4.4	95.7	8/17	28.8	29.4	102.1
1st Gen. 1916										
5/27—	30.4	33.0	108.5	3.7	2.8	75.67	7/4	34.4	35.8	104.1
5/27—	30.2	32.0	105.9	3.3	3.3	100.0	7/8	33.9	35.5	104.7
5/ 3—	29.2	33.7	111.5	3.8	3.6	94.7	7/11	33.3	35.4	106.3
6/ 2—	28.1	34.7	123.5	3.3	3.3	100.0	7/17	32.7	38.5	117.7
6/22— (6 individuals)	25.3	22.9	90.5	3.0	3.7	123.3	7/19	28.8	26.8	93.1
Means	......	......	108.0	......	......	98.7	......	......	......	105.2
2nd Gen. 1916										
7/12—	23.4	22.2	94.9	4.1	3.7	90.2	8/18	27.7	25.9	93.5
7/20—	24.0	21.9	91.3	3.8	3.7	97.4	8/18	28.0	25.7	91.8
7/20—	23.9	23.0	96.2	4.3	4.4	102.3	8/18	28.4	27.4	96.5
7/21—	24.1	20.7	85.9	4.4	4.2	95.5	8/19	28.0	24.4	87.1
7/23—	24.1	21.3	88.4	3.4	3.8	111.8	8/20	27.8	25.1	90.3
7/25—	24.1	21.3	88.4	3.7	4.1	110.8	8/26	27.8	27.2	97.8
7/27—	23.8	21.9	92.0	3.8	4.3	113.2	8/27	28.4	26.2	92.3
7/28— (5 individuals)	23.5	22.0	93.6	4.4	4.7	106.8	9/3	27.3	25.9	94.9
Means	......	......	91.3	......	......	103.5	......	......	......	93.0
1st Gen. 1917										
6/ 4—	28.7	25.8	89.9	4.2	4.7	111.9	7/11	32.9	30.5	92.7
6/ 9—	28.7	25.5	88.9	4.0	4.5	112.5	7/12	32.7	30.0	91.7
6/ 9—	28.5	24.9	87.4	4.8	4.0	83.3	7/12	32.3	28.1	86.9
6/12—	27.9	27.3	97.8	4.4	3.6	81.8	7/20	32.2	30.7	95.3
6/16—	26.7	21.6	80.9	2.6	3.2	123.1	7/16	30.8	24.8	80.5
6/16—	26.4	23.5	89.0	5.2	4.5	86.5	7/19	30.4	27.6	90.8
6/16—	26.4	26.3	99.6	......	4.5	......	7/19	......	31.1	......
Means	......	......	90.5	......	......	99.8	......	......	......	89.7
Means of all	......	......	98.7	......	......	100.4	......	......	......	98.4

On a basis of 750 as the normal substitution-quotient for the whole larval life (650 for the time in the apple and 100 for that in the cocoon). The mean ratio of actual to calculated time for each generation is given here to aid in the determination of the effects of factors other than temperature and humidity. For detailed explanations of the methods of calculation, see Tables V and VII and pp. 401-405.

after sunset was necessary for oviposition and that the maximum number of eggs laid was on the second, third, and fourth days after emergence. In prediction work, therefore, at least two days should be allowed for the time from emergence to egg laying, as very few eggs are laid the first day.

c. Incubation of Eggs.

The hourly velocity values for pupal development (Table I) may be used also for incubation, but the normal developmental total is 3864 instead of 6480. Standard time for incubation, calculated on a basis of 3840 developmental units (from Glenn's 1916 data), is shown in Table X, together with the actual time for groups of 60 eggs for all the Olney data. The method by which the theoretical time for each of these groups was calculated is shown in Table IX. The ratio of actual to theoretical time averaged 98.4 per cent for all eggs recorded; it would be 100 per cent if 3864 developmental units had been used as the normal total. Deviations from standard time for all generations of all years for which data were at hand, are shown in Fig. 28, p. 421.

d. Larvae in Apples.

Hourly velocity values for development of larvae in apples are shown for various temperatures in Table V, p. 323. It is noteworthy that lower temperatures are more effective on larvae in apples than on pupae or eggs. The normal total for the period in the apple is 15,600 developmental units, but an empirical number, 18,000, may be used to cover the entire development of the larvae (except when hibernating) from the time it enters the apple until it pupates, the normal total for the period in the cocoon thus being taken to be 2,400 developmental units. The calculated and actual time for these two parts of the larval period is shown, for means of groups of 10 individuals, covering all of the Olney data (1915-1917), in Table XI and in Fig. 28. The larval period is much more variable than the other stages. The ratio of actual to calculated time for larvae in apples, when averaged by generations for those three years, ranged from 90.5 to 108.0 per cent, with a mean of 98.7 per cent. The second generation of 1916 and the first generation of 1917 fell below the standard time, while all generations of 1915 and the first generation of 1916 were above the standard. On the other hand, the ratio of actual to calculated time in the cocoon, ranging from 95.7 to 104.4 per cent (generation means), was lowest when the ratio for larvae in apples was 101.6 per cent, in the second generation of 1915, and next lowest when the ratio for larvae in apples was 108.0 per cent, in the first generation of 1916. That is, when the time in the apple was comparatively long, the time in the cocoon was comparatively short. This is in accord with the supposition that enzymes are concerned.

In all these calculations, it was assumed that the velocity values derived from the larva in the apple would hold good for the pre-pupal stage in the cocoon at the same temperatures and humidities. The deviation from calculated time may be taken as evidence that these values need to be modified; it is likely, however, that individual variation would still cause considerable deviation even if new velocity values were established for this part of the larval life.

e. Pupation after hibernation.

It is possible to make only a rough, unreliable estimate of the time at which larvae will begin to pupate after hibernation. This has been based upon January 1 as an average date for the beginning of preparation for pupation. The actual time of beginning has varied six weeks on either side of this date in experimental stocks which were under identical conditions except for varying amounts of moisture. This leaves an unsound basis for a beginning, until the subject of hibernation has been thoroughly investigated. It was hoped that the determination of the enzyme content of larvae from time to time might indicate their condition relative to pupation, and the only enzyme, catalase, which has been investigated (see below, p. 443), gave promise of results of value, but a definite correlation has not yet been established. The work of Townsend ('26) has shown that the amount of rainfall and the frequency of rains are of very great importance. The whole subject deserves a thorough investigation. Reliable estimates of progress toward pupation in the spring of an unusual year, when estimates are most needed, are not possible now.

f. Pupae from Hibernated Larvae.

The time of the first pupations will, for the present, have to be ascertained from individual larvae under observation. The pupations are strung out over a long period in spring. There are usually two maxima, as shown in Glenn's charts 1, 2, and 3 and in Fig. 25 of this paper. In Glenn's three cases the first maximum came eight to ten days after the first pupation, and the second maximum came ten to twenty days later. These maxima also occur under uniform temperature and after uniform treatment (Fig. 25), but a correlation with weather is also shown by Glenn's data.

THE EFFECTS OF CONDITIONS OTHER THAN TEMPERATURE AND HUMIDITY.

It is evidently possible to calculate time of appearance of stages and to estimate progress to any date with a fair degree of accuracy from temperature and humidity alone (Tables VII-XI). The calculation of standard time for stages with respect to these two factors has another important value, namely, the estimation of the effects of *other* factors (amount and distribution of rainfall, seasonal march of mean daily temperatures, solar radiation, etc.). Unfortunately, the responses of different stages to these other factors are different, just as in the case with temperature and humidity. This renders it imperative that the different stages be calculated separately.

a. Rainfall.

Autumn and winter rainfall has important effects upon the rate of development of hibernated larvae and of pupae derived from them: when rainfall is heavy, the larvae are more abundant, more of them pupate, and the pupal stages are shorter than when following an autumn and winter with less precipitation. Compare graphs for 1915, 1916, and 1917 in Fig. 3 showing this relation. In all cases, the pupal life is long in all the later formed pupae. A comparison with Glenn's charts 1, 2, and 3 shows that the great mass of pupae had emerged previous to those whose mid-date of pupal life came on May 15. It will be seen that the pupal life of the large groups was longer than normal in 1915, following a dry autumn and winter, and shorter than normal in 1916, following a we. winter; 1917 is intermediate in length of pupal life and in amount of autumn rainfall.

The difference in length of the pupal stage is quite marked, even in the case of Glenn's pupae which were not exposed to rain. The most marked case was that of the 1917-18 larvae which hibernated in very dry conditions in the laboratory and were put out of doors in the spring; the actual time was 119 per cent of the standard time. This is higher than any other recorded.

b. Combinations of Rainfall and Seasonal March of Temperature.

The annual march of temperature and rainfall by months for a year in which the codling moth *flourishes* in southern Illinois are shown in Fig. 4, graph A, beginning with September of the preceding year; the autumn is rainy, and the spring only moderately so. In graph B, which is for a year when the codling moth is scarce in southern Illinois, the autumn is very dry, and the spring very wet. The summer of graph B is cooler than that of graph A; otherwise there is little difference in mean temperature. Graphs A and B in Fig. 5 show, respectively, the general limits of temperature and rainfall for the months of years when codling moths are scarce and abundant; that is, the mean monthly temperature and rainfall for such years fall within the areas marked. Data for the year 1914, when codling moths were more abundant and spraying seemed less effective than in many years, constituted the chief basis for the establishment of the limits shown in graph A of Fig. 5. Answers to a questionnaire sent out by Mr. W. P. Flint to a number of orchardists showed moths abundant near Mount Vernon and Charleston in 1920, and the data for most of the months fit the diagram very well. (See Fig. 30 p. 424.) Data for 1923, a "scarce" year, were taken as a model for most of the months shown in graph B of Fig. 5, but by being extended they have been made to include two-thirds of six years in localities where moths were declared scarce by orchardists. The crosses in Fig. 4 are the centers of the areas outlined in Fig. 5. (See Fig. 25 and explanation.) Graph A of Fig. 6 is a diagram of similar data for 1921-1922 at Olney, a year which A. J. Wharf marked "scarce early" and "abundant late"; it shows a fairly favorable autumn, an unfavorable spring, and a favorable summer. The great influence of rainfall is here illustrated by the fact that the temperature for some months of this year (and for some of the months shown in Fig. 30) was as low as, or lower than, for the corresponding months in the years in which the moths were scarce.

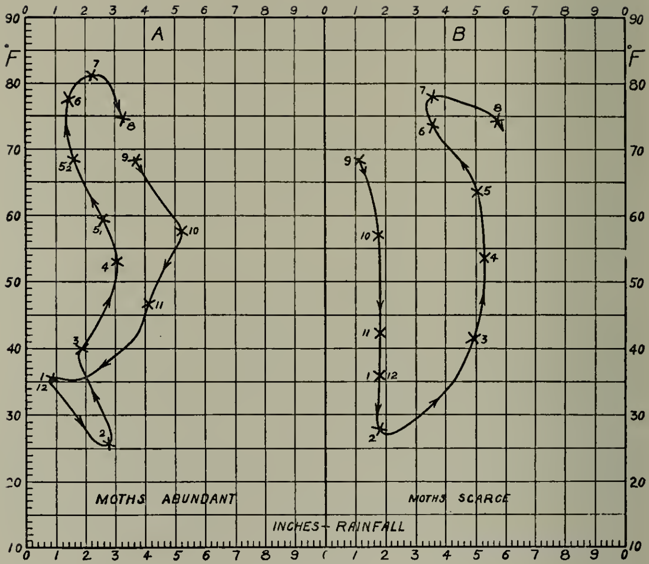

Fig. 4. Ball-Taylor diagrams of temperature and rainfall. A is for a typical year when codling moths are abundant in Southern Illinois; B is for a typical year when they are scarce. The numbers 1—12 on each diagram indicate the months January—December, and the cross beside each number indicates the amount of rainfall and mean temperature for the month. (5_1 = 1st half of May. 5_2 = 2d half of May.) Note that in the abundant year the rainfall is comparatively heavy (4—5 inches) in September, October and November and comparatively light (1—3 inches) in the spring and summer; while in the scarce year it is light (1—2 inches) in the autumn and winter and heavy (4—6 inches) in the spring and summer. Note also the higher temperatures in May (5_2), June (6), and July (7) in the abundant year.

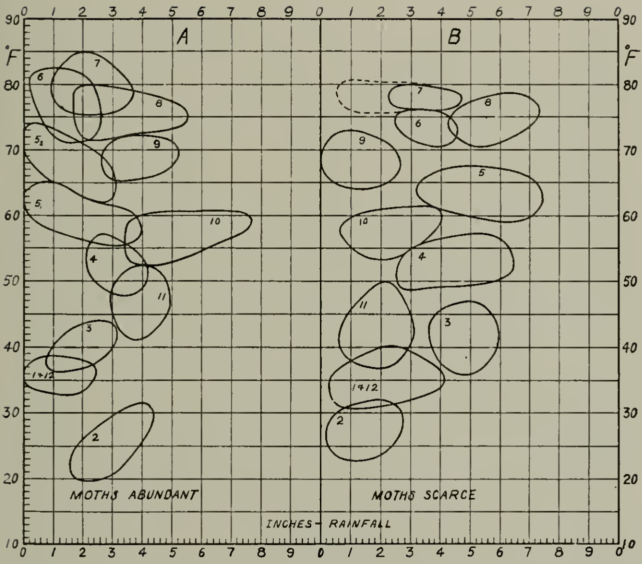

Fig. 5. Limits within which the mean monthly rainfall and temperature fell when plotted for years when the codling moth was scarce and abundant, respectively, in southern Illinois. The areas enclosed by graphs numbered 1—12 include the data for the months January—December over a period of ten years (1914-1924). The centers of these areas are represented by crosses numbered similarly in Fig. 4 (Cf. Figs. 30 and 31).

Figure 7 shows temperature-rainfall graphs (A, B, and C) made up from Weather Bureau records for the years 1914-1917 at Olney. The year 1914-1915, which Mr. Flint rated "moderate" in moths, was most unfavorable in the autumn and, generally, the least favorable of the three years: there was no rain in later winter to compensate for the dry autumn; the spring was too dry except May; and the summer was too wet. In 1915-16, a year for which Mr. Flint rated moths "moderately abundant," the early autumn was still drier, but later rains compensated.

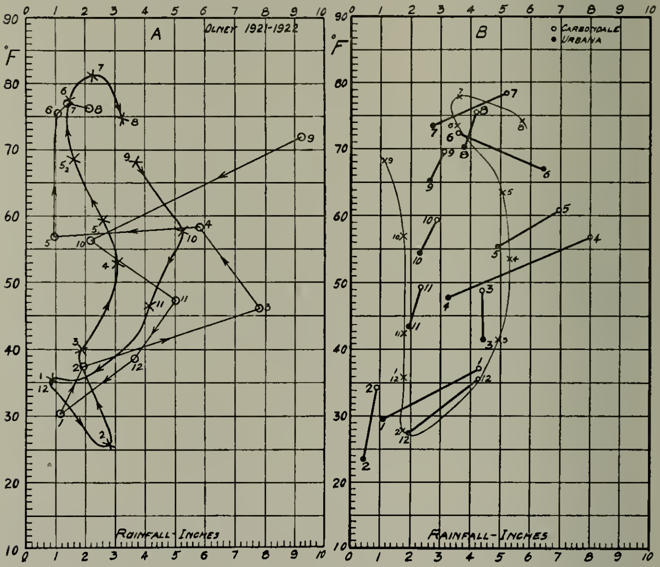

Fig. 6. (A) Rainfall-temperature diagram for a year in which moths were reported "scarce early" and "abundant late," indicating a fairly favorable fall and winter, an unfavorable spring, and a favorable summer. The typical graph for an "abundant" year (Fig. 4) is also shown here for comparison.

(B) Mean monthly temperatures for the year Sept. 1, 1916, to Aug. 30, 1917, at Urbana and Carbondale where the "late" larvae were scarce. (They were more numerous at Springfield and Carlinville where July was warmer and drier. This correlation, however, is not clear enough to justify a definite conclusion.)

May was nearly normal in total precipitation for an abundant year, but the summer distribution of rain was unfavorable to moths. The autumn and winter were too dry in 1916-17, in which Mr. Flint rated the moths "moderate." Of these three years, graph C conforms most nearly to that of a scarce year.

c. Number of late larvae.

The damage to the apple crop of 1914 was, to a considerable extent, due to a large number of late larvae. As nearly as can be judged, such abundance of late larvae is one of the characteristics of the autumn of an "abundant" year. The conditions favoring the development of a third generation are shown in Figs. 4 and 5. The season 1916-17 (September 1-August 31) was especially significant in this respect, as there were few or no late larvae at Urbana and Carbondale, while at Springfield and Carlinville there was a small late or third generation of larvae. The rainfall-temperature diagrams (Fig. 6B) for the two localities without late larvae show dry autumn and wet spring characteristic of "scarce" years. The difference from the "abundant" years is striking. The absence of late larvae in this one year was associated with a rainy July at Carbondale and with low temperatures at Urbana.

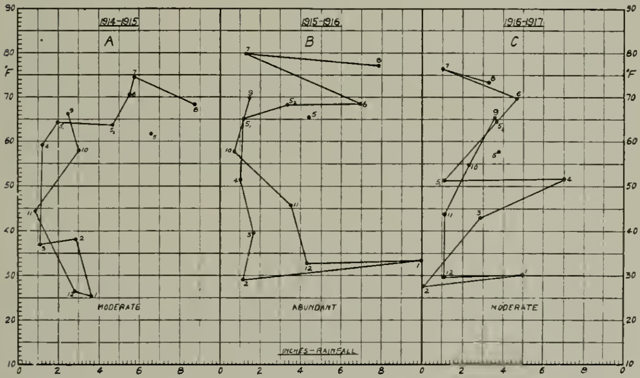

Fig. 7. Ball-Taylor diagrams, or hythergraphs, for three years at Olney.

Modification of Normal Developmental Totals.

Corrections of developmental totals must be made relative to rainfall, variability of temperature, and individual variation. Rainfall corrections are given in Tables III and IV. Rising and falling mean daily temperature and humidity affect the development of pupae and eggs. When the mean daily temperature rises from day to day, the length of the pupal stage is increased to as much as 10 per cent higher than average; that is, the developmental total may be 110 per cent of the normal number of developmental units. When temperature begins to fall from day to day in the middle of August, the developmental total decreases steadily until in the third generation. The decline is about 2 per cent per week, beginning with the first week of falling temperatures in August. The third generation normally requires only 5,952 developmental units for the pupal period and 3,360 developmental units for the incubation period. Pupal and incubation time for the central portion of the second generation in 1915 and 1916 was about standard. For such conditions, Table VI shows corrections to be made.

All estimation is on the basis of average data. Individual variation, however, makes the developmental total for some of the first-generation larvae in the apple 16 per cent less than normal. Corrections of this kind may be made for other stages by subtracting 8 per cent from the normal, when the date of first appearance is desired. When maximum emergence is to be predicted, the correction for individual variation is, of course, unnecessary.

Correction of Low Temperatures Applicable to Glenn's Method.

It would involve considerable calculation to bring Glenn's corrections of high temperatures into accord with the findings by our methods. His corrections, however, proved very valuable and his original data indispensable. His normal pupal total of 265 "degree-days" above 50° F. as the "starting point", or 241 "degree-days" above 52° F., is useful for the medial range of temperatures. The "maximum rate" for pupae and eggs should probably be set at 89° instead of 87° F. At the lower temperatures, between 44° and 60° F., corrections may be applied to his calculations as follows:

To each two-hour reading, add $0.7 \frac{(60 - x)}{2}$.

Thus, if the reading is 46° F., add $0.7 \frac{(60 - 46)}{2}$, or 4.9°, making a corrected temperature of 50.9° F. to be used in getting an effective sum. Such a sum should correspond fairly closely to the *substitution-quotient*, or one-twenty-fourth of the normal developmental total.

PART THREE.

METHODS OF EXPERIMENTATION AND CALCULATION.

1. Theory of Thresholds and Rates of Development.

Calendars of periodic events have been used in connection with agricultural practice for thousands of years. Becquerel (1853) published a Chinese calendar of 700 B. C. which does not differ in its essential features from various published spray calendars. For several centuries attempts have been made to predict development by summing temperatures. According to Becquerel, Reaumur (1735) was one of the early investigators who contended that the mean daily temperature multiplied by the number of days should be used. De Candolle made important contributions and is most often quoted, but one of the outstanding investigations in the last century is that of Von Oettingen (1879) on the Dorpat woody plants, who used the term, "threshold" (perhaps first) for the temperature at which development begins and made his sums from that. De Candolle also recognized the threshold but made his sums above zero Centigrade.

Thresholds. This summing of temperatures has been done on the assumption that the time-temperature relation is accurately represented by an equilateral hyperbola and that the hyperbolic zero marks the actual threshold development.* This assumption is false. The velocity of development does not always bear a fixed ratio to the temperature. Only a portion of the velocity curve, that for medial temperatures, is a straight line. Valuable as this straight-line portion is—it is the only proper basis for beginning any accurate calculation of the effects of temperature and other factors influencing the rate of development of organisms—it alone does not tell the whole story. The complete velocity curve shows a "lag phase" at lower temperatures and falls off at higher temperatures. The hyperbolic zero (*alpha* value) does not mark the actual threshold of development; in fact, the threshold is not a fixed point but varies for different individuals of the same species and for different species. It is, therefore, no simple matter to derive a velocity value for any given temperature. The problem involves the establishment of an absolute unit of development in which to express the effects of all weather phenomena, and the determination of a normal total of developmental units required for the completion of each stage in the life-history of the organism. Ideally, the developmental unit, defined with reference to the straight-line limits of the velocity curve under conditions normal to the habitat of the species

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* The product of the ordinates and abscissas establishing any point on an equilateral hyperbola is a constant; and the reciprocals of the ordinates, when multiplied by the constant and plotted on their abscissas, give a straight line which crosses the temperature axis at a point called the hyperbolic zero (represented by the Greek letter *alpha*) and which exactly bisects the angle between the two axes.

in the region of its greatest abundance, is the difference in the hourly velocity of development (based on the time to complete the stage) at two mean temperatures differing by one degree Centigrade,* these two being averages of temperatures varying at an average rate of approximately one degree per hour in the medial range, e. g., between 20° and 30° C. Practically, the medial range of the conditions in the region where the investigator finds the species thriving is used as standard, and the developmental unit is approximately established by the use of data from experiments which simulate these conditions as nearly as possible. Furthermore, there is a great amount of individual variation, even in the most carefully selected stocks, which necessitates the use of large lots in order to arrive at dependable averages. The variation of the *alpha* value renders the calculations very laborious. The problem is still further complicated by the fact that the developmental total is not a constant, but varies for different individuals of the same generation and for different generations of the same year. (See definitions of terms, pp. 330-333.)

Von Oettingen, in his attempts to find the threshold of development, assumed a series of *alpha* values, calculated time-temperature products for each one, and selected that one which gave the most nearly constant products for different mean temperatures. He also calculated the probable error in his method. Reibisch ('02) calculated the *alpha* value by the formula $(x - \alpha)y = k$, where x is the temperature and y is the time. Krogh ('14), in his work with Johansen on fish eggs, discovered that the threshold so calculated is not the real one, and he undertook in 1914, by studying the time required for embryonic stages of frog development, to determine the relation of the actual threshold to the *alpha* value obtained by Reibisch. He found that the graph representing the velocity of development is flattened out at the lower end and falls off at the upper end, whereas it had always been assumed to be straight. He worked over the published data of Loeb and Wastenys, performed experiments on several additional animals, and thus compiled a table showing the straight-line limits of two species of echinoderms, six species of fishes, one frog, one aquatic insect, and one land insect. This discovery was the culmination of a long series of papers on fish eggs by Apstein ('11), Dannevig ('94), Earll ('78), Reibisch ('02), Williamson ('10), and Johansen and Krogh ('14). Up to the present time all of this work on fishes appears to have been ignored by entomologists, as also the work of phenologists, by investigators of both insects and fishes.

Velocity curves. As was pointed out in PART TWO, pp. 334-338, temperatures above *alpha* may be summed for that part of the velocity curve which is a straight line, but not outside the straight-line limits. Temperatures would probably never have been summed except for the coincidence that, for a part of the temperature range, "effective temperatures" and amounts of development are numerically equivalent. Whenever the results were satisfactory, it was, in fact, amounts of development and not

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* The Fahrenheit scale is used in this paper.

degrees of temperatures that were being summed. A day at 60° F., as shown in curve A of Fig. 8 would give 10 "degree-days" reckoning from 50° (which was assumed as the starting point of development in this hypothetical case). As the curve A is drawn, the same number of developmental units have accumulated. But the century-old assumption that the velocity curve is always a straight line, is erroneous.

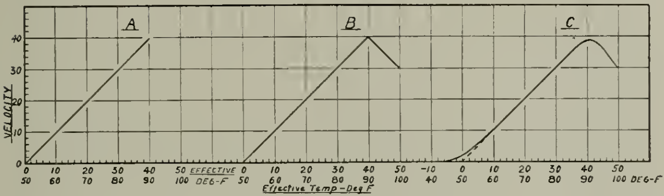

Fig. 8. Curves of velocity of the development. (A) Curve ordinarily assumed by those who sum temperatures. (B) Curve assumed by Glenn ('23) relative to the codling moth. (C) Type of curve found by many experimental investigators.

Glenn ('22) used curve B of Fig. 8 in correcting his sum of temperatures. He first corrected temperatures in the usual way by giving all temperatures below his *alpha* the value of zero. He found it necessary to assume (see pp. 222 and 233 of his article) that the rate of development increased regularly up to an optimum temperature and then decreased at the same rate. For example, if the maximum rate was at 90°, he considered 100° equivalent to 80° as shown in curve B of Fig. 8. He made no comparable corrections, however, for the lag phase at the lower temperatures (see curve C). His work was the first step in the application of correct methods to the summing of temperatures in applied entomology, and his success in the use of temperature data was due to his corrections. He deducted twice the excess above the maximum; and his data were of such a character that such a correction was the best that could then be made. For the pupa he used 87° F. as the maximum. It will be seen, however, that, with the lower temperatures uncorrected for curvature, and the curve turning down sharply at the upper end (compare curves B and C), errors may be large under certain temperature conditions. Where sums of temperatures are used, even if such corrections as Glenn's are applied, the effects of variations of humidity, rainfall, light, and other conditions have ordinarily not been taken into account. The investigation described herein shows that they should be considered.

Evidences of the nature of the velocity curve. Since summing of temperature would be practicable if the velocity curve were a straight line, it is important to bring in more evidence that it is not. Proof that the curve deviates at either the upper or the lower end is to be found in nearly all the data of Peairs ('14) and Sanderson and Peairs ('13) relating to eggs of *Samia cercropia* Linn., *Malacosoma americana* Fabr.. *Carpocapsa (Cydia) pomonella* Linn., and *Margaropas annulatus* Say; and in the full life history of the grain louse and its parasite, as given by Headlee ('14). The development of the Indian corn plant shows a similar curvature, but drops to zero again at high temperatures. (See Lehenbauer, '14, pp. 279-80.) Some work has been done on the germination of fungus spores (Weimer and Harter, '23; Jones, '23), in which similar relations have been found. The authors of the papers did not plot reciprocals or make extended interpretations. These plant curves are similar to the curves for animal activity. Verworn ('99) showed an irritability curve conforming in its main features to curve C in Fig. 8.

The physiologists have studied velocities of development according to a special principle. By chance, the rule published by Van't Hoff to the effect that an increase of 10° C. approximately doubles the rate of chemical reaction, was found by physiologists to apply roughly to the rate of development of organisms (*i. e.*, Q_{10} is about 2). It was assumed to be a constant within the optimum temperature range. They immediately seized upon this as evidence with which to combat vitalism and anti-evolution and show that life is a physico-chemical process, and the Q_{10} has been and still is the chief method of expressing the temperature relations of many physiological processes. Until Krogh's 1914 paper there was no important attempt at analysis by other methods. The only matter in point here is that the lower end of the velocity curve is of such a nature as to fit (for a short distance) a Q_{10} curve with Q_{10} as a constant. Its application by physiologists may be taken as evidence for the curvature of the lower end of the velocity curve. On further analysis, however, it is evident that, as Krogh has pointed out, the Q_{10} is not a constant but, as he shows in the case of the frog's egg, ranges from 53.0 at the lowest temperature to a little more than unity at the highest. This makes it useless for most purposes.

There is, in addition, a large amount of work on toxicity of salts and other drugs to fishes and crustaceans (Warren, '00; Pittenger and Vanderkleed, '15; Powers, '17) in which the concentration-time-to-death curve is very similar to our time-temperature curve. The reciprocal, or the curve for the velocity of the toxicity, is similar to our temperature-velocity curve except in its upper limits. Powers, in particular, has made contributions of much importance to the mathematical relations of such curves. He developed a theory of metabolism suited to his facts.

Altogether, the evidence for the deviation of the developmental velocity from a straight line at low and at high temperatures is strong, and there is no reason why procedure should not be based upon the facts. Glenn ('22) recognized the nature of the upper end of the curve and reduced the high temperatures accordingly. He did not, however, take into account the deviations from a straight line at the lower temperatures. The result is that he figured his sum too small for the pupae; but the corrections which he did make were largely responsible for the superiority of his work over that of many others.

Evidences of a constant total in metabolism. The usual index of the rate of growth and metabolism is the amount of carbon dioxide produced. In the case of insects, the amount produced during definite stages in the life history is probably a *constant* for an insect of a given weight and species. This has been demonstrated for the pupal stage of the meal worm (Krogh '14). Although the amount given off is a constant total, the rate, however, is not the same throughout the pupal life. It is fairly high at the beginning of the pupal period, falls for the middle pupal period, and rises to a very high rate toward its end. It is obvious, then, that the amount of carbon dioxide given off for a given period is not an index of the amount of progress toward completion of the pupal period unless the amount of progress is ascertained by some other method. It is, therefore, necessary to use units based upon the total amount given off during the time necessary for the completion of the stage. The constant holds good under various temperatures. In the case of the meal worm pupa, one degree centigrade within the medial range for one day corresponds to 10/1015 of the total carbon dioxide, or 581.2 cc. (At one temperature above the medial range the "degree-day" produced less than this amount.) There is then an actual basis in the metabolism of growth and activity for the temperature-velocity units.

Further evidence as to a basis in activity is found in a recalculation of Crozier's work on the rates at which a centipede crawls at different temperatures, as shown in Fig. 2, which has already been discussed in PART TWO (pp. 334-337). The form of the curve is the same as that for rate of development.

The constants for different organisms and for different stages of the same organism are different. Though a given velocity value, i.e., a given number of developmental units per hour, may be shifted a little way up or down the temperature scale in different cases, the effect of one degree remains of the same quantitative value for all organisms within the medial temperatures of each. The constants vary according to the amount of work to be done.

Evidence from the standpoint of basal metabolism is found in the fact brought out by Krogh ('14b) that the standard metabolism in relation to temperature is the *same per unit of weight* (respiratory exchange basis) for a dog as for a fish. The curve for the meal-worm pupa was of the same type and the readings of the same order of magnitude; the only difference was that the entire curve was shifted up the temperature scale.* In this comparison of animals from such radically different groups,

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* The readings were taken when the CO_2 output was at a minimum and when respiratory movements and heart beat were also probably at a minimum. This value is more nearly true basal metabolism than the other values. It must be borne in mind that the standard metabolism curve is based upon comparison of metabolism at different temperatures while the pupae were at a particular stage, and that the curves for total growth and development under different temperatures do not agree with the standard metabolism curve at all.

the differences are of the same order of magnitude as the differences in velocity of development of different insects and of different stages of the same insect when the developmental totals are correctly determined. (It must be remembered that these developmental totals are constants only for the same stock and conditions aside from temperature.)

Other methods. Quite independently, botanical workers and climatologists have developed various other methods of estimating stages in life-histories. Koeppen ('86) developed a method of temperature classes. This was modified by Zon ('14) and others. MacDougall ('14) used the area between freezing and the actual temperature tracing as an indicator. Livingston ('13), McLean ('17), Hildebrant ('17), and Clements ('24) grew standard plants as indicators, using the amount of growth as an index in each case. Animals, especially insects, doubtless could be better used as indicative of the favorability of season to economic pests.

2. PURPOSE OF THE PRESENT INVESTIGATION.

It is the purpose of this paper to show:

(a.) That various factors besides temperature have important effects on development.

(b.) That experimental results may be made to have direct bearing on the interpretation of results under actual climatic conditions.

(c.) That the threshold* of development is a variable point and that the approximations used by various workers in summing temperatures are of little or no physiological significance.

(d.) That under actual climatic conditions there is no such thing as a "thermal constant" or "sum of temperatures" in the ordinary biological sense, and that temperature should not be summed without various corrections and adjustments for the effects of other factors.

(e.) That interpretations of conditions may be based on equal-velocity charts for combinations of important factors.

(f.) That conditions of hibernation are of great importance.

(g.) That rainfall and many other factors are of importance at particular periods of the life history.

The difficulties of investigating the relation of organisms to climate are such that, with a few outstanding exceptions, investigators have tried almost everything in the way of short-cuts. Furthermore, the methods necessarily used in climate-simulation experiments on confined animals are complicated. In view of the necessarily long discussion of these methods, the usual order in scientific papers is here violated; the results and conclusion are presented first and are followed by a discussion of methods.

In Illinois, hibernating larvae of the codling moth pupate in April and May, emerge in May and June, and deposit eggs within a few days; these hatch quickly, and the larvae enter the apples in May and June. These first-generation larvae pupate chiefly in July, giving rise to a second generation. There is usually also a small third generation, the larvae of which enter the apples in September.

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* The term "physiological zero" should not be used because metabolism is probably not at a standstill while the animal is alive. The term "threshold" has long been in use and gives better expression to the facts.

The proper beginning point, for a study of life histories in relation to environment, is the adult, since it places the eggs under conditions to which the later stages are subject. In the work in hand, however, studies made of the adult were not sufficient to warrant such a procedure; therefore, to illustrate the methods used, the pupa will be taken up first.

(A) GENERAL RESULTS ON PUPAE.

The series of approximately constant temperature experiments was conducted with a total of 4,000 larvae belonging to the following generations: summer 1917, spring 1918, spring and summer 1919 and 1920. Of these, about 2,000 pupated and 1,100 emerged. About 800 larvae from the 1917, 1918, and 1919 generations were started in variable temperature experiments. Of these, 515 pupated and 370 emerged. About 1,200 larvae, chiefly of the 1921 spring generation, were used in experiments on hibernation and related processes. About 800 of these emerged. The rather high mortality brought the net results of handling 6,000 larvae down to about 50 per cent of our expectation. The 3,000 pupae, however, yielded an ample mass of data from which to draw fundamental conclusions.

Tables XII and XIII show full data on the pupae reared under approximately constant temperatures, and Tables XVIII and XIX show the data from the variable-temperatures. The experimental methods and apparatus are described on pp. 426-435. The containers in which the pupae were held are described on p. 432 and illustrated in Fig. 34. Nearly all containers were ventilated, and records included air velocity, evaporation from the porous cup atmometer, humidity, and temperature, all of which are shown in some detail in appropriate columns. The designations given in the first column of each table refer to stocks, places, and conditions as explained below and in notes at the proper places.*

Each figure for pupal life in days is the average for the number of individuals pupating. An idea of the variation may be had from the data (Table XII) indicating the extreme range in days (the difference between the longest and the shortest time); also from the range for 80 per cent or more of the pupae. This 80 per cent group merely excludes the extreme, though their inclusion often does not modify the average greatly. The winter treatment is given, and the time intervals between

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* In addition to the letters used to designate the various experimental chambers, as explained in the description of methods (p. 434), the following letters were used with meanings as indicated: For Humidity D, dry; M, medium moist; W, moist; WW, very moist.

For air movement and evaporation: H, high air velocity; I, intermediate air velocity; L, low air velocity.

For light: D, dark; L, light; LL, lighter.

For unit R (an ice-box): L, lower shelf; LL, lower left shelf; M, middle shelf; T, top shelf, etc.

O is out of doors; P, in the glass-roofed house; NC, indicates no container covered the sticks in which the larvae and pupae were held.

a, b, c, etc., indicate different experiments under the same or approximate conditions and from the same generation but started on different dates in order indicated by the alphabet.

NV indicates that no air was forced through the container, hence not ventilated.

TABLE XII. *Pupae at approximately constant temperature, first generation 1917.*

Designation (see page 363.	No. of adults emerging.	Pupal life in days.	Mean temperature.	Mean humidity.	Maximum temperature.	Minimum temperature	Maximum humidity.	Minimum humidity.	Air velocity mm. per sec.	Evaporation cc. per day.	Variation in time (da.)				% failure to pupate.	Total individuals.	Total pupae.	% Pupal mortality.
											Range of days for pupal life in 80% cases.		Longest and shortest time.					
H*	1	42.	51.8	85	55.4	50	90	80	0	0	......	......	......	......	0	5	5	80
H*	4	47.2	53.5	95	56	50	100	90	0	0	......	......	......	......	0	9	9	55
Z	8	39.4	57.9	45	59	57	55	40	0	0	37	42	37	42.5	10	22	20	60
K	13	23.8	61.7	97	62	61	100	90	0	0	23	25	21	28.5	5	22	21	38
JW	3	21	64.5	70	65.3	63	80	60	10	1.7	21	......	......	......	7	15	14	78
JD	8	22.1	64.5	40	65.3	63	44	36	10	8.9	21	24.5	18	24.5	9	23	21	62
LD	2	?	69	40	70	67	48	35	11	8.3	......	......	......	......	87	16	2	0
LW,	13	13.1	69.5	82	70	67	83	81	11	8.4	12.5	14	12	14	0	19	19	31
MWb	16	10.2	76.7	95	77	76	100	90	8	11.4	9	11	7	12.5	12	24	21	24
MWab	19	9.5	76.5	95	77	76	100	90	8	11.6	9	11	7	12.5	0	42	42	39
MWa	25	10	75.9	95	77	75	.....	mean	.....	11.2	9	11	8	12.5				
MWab	22	10.5	75.8	95	76	75	100	90	8	10.6	8.5	11	8	11	....	....	....	....
MMc	2	8.8	76.6	65	77	76	77	57	38	13.7	8	9.5	8	9.5	84	19	3	33
MMb	12	10.2	76.6	65	77	76	77	57	38	14.6	9.5	10.5	9.5	11	21	19	15	2
MMa	5	11.5	75.7	65	77	73	77	57	30	18.6	11.5	12.5	10	......	0	24	21	75
MDb	8	10.8	76.6	35	78	75	53	28	50	7.7	9.5	13	......	......	19	16	13	38
NWb	13	7.3	89.3	97	93	87	100	95	15	10.6	7.5	8.5	7	9.5	9	22	20	35
NWa	7	7.1	89.6	100	80	89	100	....	10	7.2	6.5	7.5	6.5	7.5	....	....	....	....
NWa	10	7.5	89.3	97	93	87	100	95	10	11.7	6.5	7.5	6.5	7.5	10	20	18	44
NWa	3	8.1	88.7	100	....	......	....	....	.....	11.9	8.0	8.5	......	......	....	....	....	....
NMb	8	7.8	90	58	93	87	65	50	10	15.1	7.5	8.5	6.5	9	13	22	19	58
NMa	10	7.6	89	58	90	89	65	50	10	9.8	7.5	8.5	6.5	......	6	18	17	42
NMab	6	8.1	90.1	58	90	89	65	50	10	....	6.5	8.5	......	9	....	....	....	....
NMab	5	7.4	89.6	58	90	89	65	50	.....	....	7	7.5	......	......	....	....	....	....
NMab	7	7.7	88.6	58	89	88	65	50	.....	....	7	8.5	6	......	....	....	....	....
NWb	5	8	88.7	97	89	88	100	95	.....	5	7 5	8.5	......	......	....	....	....	....
NWb	4	7.6	89.6	97	90	89	100	95	.....	....	7	9.5	......	......	....	....	....	....
NWb	4	7.4	90.1	97	90	89	100	95	.....	....	7	8.5	......	......	....	....	....	....
NDb	5	6.9	90.1	55	93	90	60	50	15	22.3	6.5	8.5	5.5	......	45	22	12	57
NDa	2	9.2	88.8	55	90	89	60	50	15	18.5	8.5	10.0	......	......	0	19	19	88

(*First two items, starred, belong properly to variable temperature.)

TABLE XIII. *Data for approximately constant temperature experiments on hibernated pupae, 1918.*

Designation (see p. 363).	No. of adults emerging.	Pupal life in days.	Mean temperature.	Mean humidity.	Maximum temperature.	Minimum temperature.	Maximum humidity.	Minimum humidity.	Evaporation cc. per day.	Range in days, 80% or more pupae.		Date started.	Interval between beginnings of sets.	% failure to pupate.	Total individuals.	Total pupae.	% pupal mortality.
HDa	13	34.8	58.5	60	65	55	65	55	30	33	37	4/11	...	24	25	19	32
HDb	7	36.7	58.2	60	65	54	65	55	33	34	42	4/25	15	22	19	15	53
HMa	2	39	58	50	65	54	60	45	5	35	43	4/2	...	50	14	7	71
HMb	4	38	57.9	50	65	53	65	45	5.9	36	42	4/25	23	0	5	5	20
HWa	1	33	58.6	90	65	54	100	80	5	.....	33	4/2	...	95	18	1	0
HWb	3	34.6	58.3	90	65	54	100	80	6	30	37	4/25	14	62	8	3	0
HNv	1	35	58.7	97	65	54	99	95	0	35	.....	4/2	...	90	20	2	50
HJDb	1	33	58	50	65	54	65	45	6.8	33	.....	4/25	23	50	6	3	66
LD	14	27.8	63	60	65	59	65	55	2.5	25	30	4/11	0	27	34	25	44
LM	19	26.1	63	75	66	60	80	70	2.3	24	28	4/11	0	40	47	28	32
LW	15	26.1	63	90	65	59.5	98	88	1	24	28	4/11	0	15	21	18	17
KD	6	28.3	62.6	60	67	60	65	55	6.3	27	30	4/6	0	45	20	11	45
KW	14	27.3	62.7	95	67	60	100	90	1.6	26	29	4/6	0	35	31	20	30
AncD	6	17.2	69.5	50	70.5	69	60	35	16	16	18	4/23	0	85	55	8	25
AD	22	20.2	69.5	50	71	68	55	45	6.8	19	21.5	4/11	0	36	45	29	24
AM	17	20.9	69.6	60	71	68	65	55	4.7	19.5	20.5	4/11	0	43	37	21	19
AW	31	20	69.6	70	71	68	75	65	4.4	19	21	4/11	0	30	52	36	14
BADa	4	11.6	80.3	35	83	79	40	30	20.1	10	12.5	4/11	0	76	29	7	43
BDa	24	11.8	80.3	50	83	79	55	45	5.3	10.5	13.0	4/11	0	31	48	33	27
BMa	41	11.2	80.3	60	83	79	65	55	.....	9.5	12.5	4/11	0	27	67	49	17
BWa	27	11	80.3	70	83	79	75	65	.....	10	12	4/11	0	24	50	38	29
BS*DK*	15	11.6	81.5	60	82	80	60	55	0	.....	.....	4/23	...	48	31	16	7
BS*L*	5	10.7	81.5	60	82	80	60	55	0	.....	.....	4/23	...	75	24	6	17
MADc	1	7	90	29	92	90	40	20	16	7	7	4/18	16	50	12	6	83
MADc	14	8.5	90.2	29	92	90	40	20	15	8	9	4/27	25	0	20	20	30
MDc	6	8.1	91	37	92	90	50	35	6.8	8	8.5	4/27	25	50	16	8	25
MMa	1	9	90	44	90	90	60	40	4.6	.....	.....	4/2	...	97	31	1	0
MMc	8	8.2	91.2	44	92	90	60	40	6	8.5	9	4/27	8	65	17	6	33
MWa	1	8	90	51	90	90	70	50	7.4	8	.....	4/4	...	96	27	1	0
MWb	8	8.4	90.3	51	91	90	70	50	6.4	8.5	9	4/19	15	23	13	10	20
MWc	10	7.9	91.2	50	92	90	60	40	6	7.5	8	4/27	23	66	32	11	9
MWWa	8	8.4	91.7	85	92	91	90	80	2.2	8.5	9.0	5/1	...	50	30	15	45
MNv	1	9	90	97	90	90	99	95	0+	9	.....	4/2	...	64	14	5	80
MNv	8	8	91	97	91	91	99	95	0	.....	.....	4/28	...	8	12	11	27
NDa	1	8.5	95	35	95	95	35	35	71	6	.....	2/14	...	90	32	3	66
NWb	1	8.5	95	65	95	95	65	65	27	8.5	.....	3/23	...	87	23	3	66
NWc	3	8.1	95	65	95	95	65	65	13.6	8.5	8	4/17	...	44	25	14	78
NNVc	3	9.5	95	30	95	95	35	25	0+	8.5	10.5	4/17	...	60	33	13	77

The winter treatment of larvae is described on p. 407. The various stocks are indicated by Roman numerals.

The dates of beginning are given to indicate change in stock in storage. See p. 374 for history of stocks mentioned.

Air velocity 8 mm. per sec. except in experiments not ventilated (nv).

HDa, HDb, HMb, HWb, HJDb were from stock III. HMa, HNv, KD, KW, AncD, BS*DK*, BS*L*, MAD, MD, MN, MW, MWW, NWC were from stock IV. LD, LM, LW, AD, AM, AW, BAD, BD, BM, BW, NDa, NWb, were from stock V.

TABLE XIIIa. *(Continuation of Table XIII), 1918.*

Designation (see p. 363).	No. of adults Emerging.	Mean temperature.	Mean humidity.	Maximum temperature.	Minimum temperature.	Maximum humidity.	Minimum humidity.	Evaporation cc. per day.	Date started.	Interval between beginnings of sets.	Total individuals.	% failure to pupate.	Total pupae.	% pupal mortality.
HJda	0	57.4	50	65	54	55	45	6.8	4/2	....	22	96	1	100
H2Wa	0	58	70	65	54	75	65	4.8	4/2	....	11	100	0	0
HJWb	0	58	70	65	54	75	65	4.8	4/25	23	4	0	4	100
JDa	0	58	50	65	54	55	45	5.8	4/2	....	14	100	0	0
JDb	0	58	50	65	54	55	45	5.8	4/25	....	14	71	4	10
HTPnv	0	58	97	65	54	99	95	0	4/26	24	18	0	18	....
KM	0	62.2	75	67	60	80	70	6	4/6	0	16	88	2	....
AncL	0	69.5	50	70.5	69	60	35	16.4	4/23	0	37	100	0	....
BTP	0	80.1	60	.....	....	....	....	0	4/24	....	29	0	29	100
MADa	0	90	29	92	90	40	20	8.1	4/2	....	21	95	1	100
MDa	0	90.3	37	94	88	50	35	6.1	4/2	....	24	5	23	100
MDc	0	90.8	37	91	90	50	35	9.2	4/19	17	22	23	17	100
MMb	0	90	57	90	90	60	40	10.3	4/19	17	5	100	0	0
NDb	0	95	35	95	95	35	35	62	2/25	....	6	100	0	....
NDc	0	95	35	95	95	35	35	37.5	4/17	....	4	25	3	100
NMa	0	95	52	95	95	55	50	19.5	2/14	....	47	96	2	100
NMb	0	95	52	95	95	55	50	19	3/23	34	14	100	0	....
NMc	0	95	52	95	95	55	50	18.9	4/17	59	20	90	2	100
NWa	0	95	65	95	95	....	....	23	2/14	....	32	98	1	100
NNva	0	95	30	95	95	35	25	0+	3/23	....	10	70	3	100
NNVb	0	95	30	95	95	35	25	0+	4/2	....	23	44	13	100

NNva was from stock I. HJWb, JDa, JDb, HTP, BTP, were from stock III. HJda, H2Wa, KM, AncL, MADa, MDa, MDc, MMb, NDc, NMc, were from stock IV. NDb, NMa, NMb, NWa, NNVb, were from stock V.

HJda, H2Wa, KM, AncL, MADa, MDa, MDc, MMb, NDc, NMc, were F (Frozen). HJWb, JDa, JDb, HTP, BTP, NDb, NMa, NMb, Nwa, NNva, NNVb, were NF (Not Frozen).

See p. 374 for history of stocks mentioned.

TABLE XIIIb. *Pupae for hibernated generation at approximately constant temperature, 1919.*

(From stock 45° F., RW, RD, and RM).

Designation (See p. 363).	No. of individuals.	Pupal life in days.	Mean temperature.	Mean humidity.	Maximum temperature.	Minimum temperature.	Maximum humidity.	Minimum humidity.	Air velocity mm. per sec.	Evaporation cc. per day.	% failure to pupate.	Total individuals.	Total pupae.	% Pupal mortality.
(A)RNV	0	....	49.5	100	51	46	100	100	8	0	....	....	....	....
RNVR	0	....	49.5	100	51	46	100	100	8	0	100	6	0	0
RDA	0	....	52.2	36	54	50	40	18	8	0	60	10	4	100
RD	0	....	52.2	36	54	50	40	18	8.9	5.3	100	15	0	0
RM	0	....	52.2	65	54	50	77	43	8	1.9	100	8	0	0
RMA	0	....	52.2	65	54	50	77	43	8	.6	33	3	2	100
RWA	7	86.7	52.2	85	54	50	90	80	8	.6	36	22	14	50
RW	0	....	52.2	85	54	50	90	80	8	.6	100	0	0	0
RMidnv	0	....	52.2	97	54	50	100	93	8	0	100	3	0	100
RtopA	1	50	53.9	97	55	53	100	93	8	0	29	7	5	80
Rtop	0	....	53.9	97	55	53	100	93	8	0	100	6	0	0
HDR	0	....	59.8	68	60	58	75	53	.....	8.5	70	16	5	100
HD	1	42	59.2	68	60	58	72	55	7	7.7	72	11	3	66
HW	4	34.7	59.8	87	62	58	94	75	8	5.5	25	12	9	56
LD	0	....	66.6	55	68	64	67	52	8	3	93	16	1	100
LW	5	19	66.6	71	68	64	90	68	9	10.5	40	10	6	17
ANV(R)	7	15.5	68.7	97	69	67.1	100	93	.....	0	46	21	11	36
BNV	2	7	80.7	97	81.5	80	100	93	.....	0	9	22	20	90
SWS	3	8.3	87.6	96	89	86	100	92	8	0	33	6	4	25
SW	1	9.5	84.3	85	85	83	87	70	9	7.4	80	10	2	50
SAD	0	....	84.3	40	85	83	63	38	8	15.5	100	18	0	0
SADD	0	....	84.3	30	85	83	50	25	7	17	100	13	0	0
MD	0	....	91.8	22	92	90	28	15	9	36	100	14	0	0
MW	2	9.5	91.8	95	92	90	100	92	10	4.2	54	17	8	75
ND	0	....	92.3	14	95	92	16	12	7	23.0	100	29	0	0
NW	1	9	92.3	77	95	92	96	77	11	6.4	83	18	3	66
NWS	1	8	95.3	92	96.0	95	100	90	9	0	66	9	3	66
TH	1	9	81.2	70	81.5	79	72	68	425	15.4	76	13	3	66
TI	2	10.5	81.2	70	81.5	79	72	68	109	12.9	86	15	2	0
TL	9	10.6	81.2	70	81.5	79	72	68	15	8.4	6	18	17	47

Pupal life in 80% cases, for HW, LW. ANV(R), BNV, SWS, MW, TI, TL, was 32-37, 18-20, 14-16, 7, 7.5-9, 9-10, 10.5, 10-11, days respectively.

Longest pupal life for ANV(R) was 16.5 days. Longest and shortest time for TL, was 13.5 and 8.5 days respectively.

TABLE XIIIc. *First generation pupae at approximately constant temperature, 1919.*

Designation (See p. 363).	No. of adults emerging.	Pupal life in days.	Mean temperature.	Mean humidity.	Maximum temperature.	Minimum temperature.	Maximum humidity.	Minimum humidity.	Air flow mm. per sec.	Evaporation cc. per day.	% Failure to pupate.	Total individuals.	Total pupae.	% Pupal mortality.
RLL	0	....	47.5	99	50	45	100	98	8	2.1	100	10	0	0
RLR	0	....	49.3	95	52	48	98	90	8	1.1	73	15	4	100
RMS	1	62	51.9	80	53	50	90	75	8	2.1	62	8	3	66
RD	0	....	51.9	45	53	50	48	28	8	1.6	0	11	11	100
RM	0	....	51.9	72	53	50	82	62	9	2.1	25	12	9	100
RW	1	68	51.9	85	53	50	96	80	9	0.6	21	14	11	91
RRT	0	....	53.6	80	55	52	90	75	7	1.0	72	11	3	100
H1W	1	46	55.4	92	56.3	53.9	100	80	10	4.0	77	9	2	50
HIM	6	44.2	55.4	81	56.3	53.9	88	60	10	9.8	43	23	13	54
H1D	2	49.5	55.4	73	56.3	53.9	82	58	10	10.4	63	13	5	60
TH	3	8.5	82.4	62	84.	81	79	44	620	37.3	96	19	3	0
T1	1	7.5	82.4	62	84	81	79	44	720	21.9	90	10	1	0
TL	0	....	82.4	62	84	81	79	44	3	3.8	70	14	4	100

For HIM, the number of days for pupal life in 80% of cases was 42 to 46. The longest and shortest time was 47 and 42, respectively.

TABLE XIIId. *First lot of hibernated generation pupae, 1920, at approximately constant temperature, including tests of air movement and evaporation.*

Designation (See p. 363).	No. of adults emerging.	Pupal life in days.	Mean temperature.	Mean humidity.	Maximum humidity.	Minimum humidity.	Air flow mm. per sec.	Evaporation in cc. per day.	% failure to pupate.	Total individuals.	Total pupae.	% pupal mortality.
RW*	0	......	48	95	......	......	.....	......	100	9	0	0
AWW$_{I}$	0	......	63.5	92	95	90	14	2.4	94	18	1	100
AWW$_{II}$	2	25.5	62.8	93	95	90	10	4.9	75	8	2	0
AW$_{I}$	0	......	63.5	82	90	70	14	10.0	100	10	0	.....
AW$_{II}$	0	......	62.8	80	89	72	14	3.8	100	5	0	0
AD$_{bac}$	0	......	63.5	68	80	60	14	10.7	100	24	0	0
AD$_{bac}$	3	22.1	62.8	65	70	55	14	11.0	62	16	6	50
AD	0	......	63.5	46	60	40	13	22.2	91	11	1	100
AD	0	......	62.8	50	70	45	14	26.4	100	3	0	.....
ADac$_{I}$	0	......	63.5	27	30	22	14	15.7	100	9	0	.....
ADac$_{II}$	0	......	62.8	30	30	27	14	17.9	.....	.....	.....	.....
BWW$_{I}$	1	7.0	83	91	96	90	14	3.2	66	3	1	0
BWW$_{II}$	......	......	83	96	96	94	14	1.3	100	1	0	.....
BW$_{I}$	0	......	83	85	90	84	14	8.6	100	6	0	0
BW$_{II}$	0	......	83	88	92	84	14	9.7	100	3	0	0
BW$_{III}$	1	9.0	83	95	95	Nv	0	0	0	1	1	0
BM	0	......	83	75	76	50	13	7.0	100	6	0	0
BM	0	......	83	75	80	73	14	10.3	0	0	0	0
BD	1	9.5	83	34	47	31	12	18.9	75	4	1	0
BD	0	......	83	43	55	35	14	26.0	0	0	0	0
BADac	0	......	83	21	30	13	15	19.9	94	18	1	100
BADac	0	......	83	30	31	23	14	26.5	100	7	0	0
BEV$_{I}$	0	......	83	62	80	40	2	1.6	100	6	0	0
BEV$_{II}$	0	......	83	80	85	70	2	5.9	100	1	0	0
BEV$_{2a}$	0	......	83	62	80	40	10	5.5	100	12	0	0
BEv$_{2b}$	0	......	83	80	85	70	10	7.2	66	3	1	100
BEv$_{4a}$	1	?	83	62	80	40	45	13.8	75	8	2	50
BEv$_{4b}$	1	7.0	83	80	85	70	50	14.7	66	3	1	0
BEv$_{6a}$	1	9.5	83	62	80	40	120	15.0	90	10	1	0
BEv$_{6b}$	0	......	83	80	85	70	113	15.0	100	6	0	.....
BEv$_{6c}$	1	?	83	80	85	70	113	15.0	0	1	1	0
BEv$_{10a}$	1	?	83	62	80	40	403	31.0	88	8	1	100
BEv$_{10b}$	0	......	83	80	85	70	403	24.5	100	2	0	0
BEv$_{12a}$	1	9.0	83	62	80	40	520	41.0	83	6	1	0
BEv$_{12b}$	0	......	83	80	85	70	520	55.4	.....	0	.....	.....
BW$_{15}$	12	10.0	83	86	90	80	78	9.5	27	26	19	33
BW$_{25}$	6	10.0	83	86	90	80	78	9.5	40	15	9	33

Max. and Min. temp. any day were respectively, 68° and 61° F. for A; 85° and 81° F. for B.

Pupal life in 80% cases for BW15 and BW25, was 9.5-10.5 days respectively.

Longest and shortest pupal life for AWW$_{II}$, ADBac, BW15, BW 25, was 29 and 22, 24 and 27, 11 and 7, 10.5 and 9.5 days respectively.

(?) indicates that length of pupal life was not ascertained.

(*) Some pupae at beginning.

TABLE XIIIe. *Second and third lots of pupae at approximately constant temperature, 1920, (hibernating generation).*

Designation (See p. 363).	No. of adults emerging.	Pupal life in days.	Mean temperature.	Mean humidity.	Maximum humidity.	Minimum humidity.	Air flow mm. per sec.	Evaporation in cc. per day.	Range of days for pupal life in 80% cases.		% Failure to pupate.	Total individuals.	Total pupae.	% Pupal mortality.
ANv*	3	21.0	63.5	97	100	97	0+	0+	18	24	0	7	7	57
AWW	2	24.0	63.5	93	95	92	50	3.7	23	25	60	5	2	0
AW	2	27.2	63.5	88	92	84	50	5.2	25	29	28	7	4	50
A(BD)	....	....	63.5	65	80	60	50	9.3	......	......	85	7	1	100
AD	....	....	63.5	55	75	45	48	14.0	......	......	83	6	1	100
ADac	....	....	63.5	30	32	24	50	18.6	......	......	100	6	0	....
BWW	2	9.5	83	95	96	90	52	0.8	9.5	9.5	57	7	3	33
B(ADac)	2	10.3	83	29	30	16	50	20.9	10.0	10.5	80	10	2	0
BEv1	4	9.4	83	85	90	80	1	2.7	7.5	10.5	64	14	5	20
BEv2	3	10.3	83	85	90	80	10	7.3	10	11	64	11	5	40
BEv4	1	10	83	85	90	80	50	12.4	10	......	50	4	2	50
BEv6	6	10.7	83	85	90	80	120	13.3	10	10.5	46	13	7	14
BEv10	0	....	83	85	90	80	400	31.9	9.5	10.5	100	5	0	....
BEv12	9	9.8	83	85	90	80	300	24.9	......	......	8	12	11	17
AWW	1	25	63.5	92	95	90	15	4.3	......	......	50	8	4	75
AW	2	27	63.5	88	90	82	14	5.5	......	......	50	6	3	33
ABD	0	....	63.5	65	85	65	14	10.0	......	......	100	7	0	....
AD	2	28	63.5	58	60	45	14	14.0	......	28	55	9	4	50
ADac	0	....	63.5	30	30	24	14	18.4	......	......	100	11	0	....
BW	10	9.3	83	83	92	82	15	11.6	90	9.5	23	13	10	0
BD	1	9	83	42	55	35	13	22.2	......	......	66	6	2	50
EV_4	2	10	83	76	80	70	13	21.3	......	......	60	10	3	33
EV_{10}	2	8.5	83	76	80	70	400	26.0	......	......	75	8	2	0

Second Lot. (All except ANv* larvae collected from bark of trees, March 2.)

The Max. and Min. Temp. any day were, respectively, 66° and 60° F. for A; 85° and 81° F. for B.

Longest pupal life was as follows: For BEvI, BEv6, BEv10,—18, 11, 19, days respectively; the shortest for BEv10 was 5 days.

Third Lot. (Below black line), larvae collected from bark of trees March 22.

The Max. and Min. Temp. any day were respectively, 66° and 63° F. for A; 85° and 82° F. for B.

Longest pupal life for BW and EV_4 was 10 days; the shortest, 8.5 and 9.5 respectively.

TABLE XIIIf. *Three lots of first generation pupae, 1920, at approximately constant temperature.*

First lot above first line; second lot below first line; final lot below second line.

Designation (See p. 363).	No. of adults emerging.	Life in days.	Air flow mm. per sec.	Evaporation in cc. per day.	Variation of time.				% failure to pupate.	Total individuals.	Total pupae.	% pupal mortality.
					Range of days for pupal life in 80% cases.		Longest and shortest time.					
Ev. 1	12	8.9	.002	5.4	8.5	9.0	8.0	10.0	14	14	12	0
Ev. 2	9	8.7	.011	6.2	8.0	9.0	7.5	9.5	12	16	14	36
Ev. 4	4	8.8	.030	16.6	8.5	9.0	......	......	46	13	7	42
Ev. 6	5	9.0	.112	15.1	8.5	9.0	......	10	35	14	9	45
Ev. 10	10	8.4	.400	28.5	8.0	9.0	......	......	18	17	14	28
Ev. 12	......	......	.500	27.2	......	......	......	......	20	5	4	100
Ev. 12a	8	9.0	.450	38.5	8.0	10.0	7.5	......	18	11	9	11
Ev. 1a	4	8.5	.002	......	8.5	9.0	......	......	8	12	11	63
Ev. 2a	3	7.5	.011	7.2	6.5	8.5	......	......	70	20	6	50
Ev. 4a	11	8.8	.030	14.6	8.0	9.0	......	10	40	20	12	8
Ev. 6a	8	9.1	.112	16.4	8.0	9.5	......	10	19	16	13	38
Ev. 10a	8	8.9	.400	32.2	8.5	9.5	7.5	......	36	14	9	11
Ev. 12b	5	8.9	.500	46.0	8.0	9.5	......	......	45	13	7	28
BW	5	19.6	.39	25.5	18	21.5	17.5	......	70	33	10	50
BD	14	18.7	.39	58.6	17.5	21.5	14	23	34	32	21	33
Ev. .0	11	18.1	0	+0	18	20	16	......	11	18	16	31
Ev. 0.0	14	19.4	0	+0	18	19.5	14.5	20	0	25	25	44
Ev. 1.5	16	19.7	.005	7.1	17.5	21.5	16	......	12	25	22	27
Ev. 2.0	5	18.7	.01	9.8	16.5	18.5	......	21.5	16	25	21	75
Ev. 4.0	24	19.1	.02	19.8	17.5	21.5	15.5	25	3	37	36	33
Ev. 5.0	14	20.1	.04	23.4	17.5	21.5	......	27	14	36	31	55
Ev. 6.0	17	21.2	.10	28.7	17.5	24.5	......	26	22	41	32	47
Ev. 8.0	16	22.0	.20	32.7	17.5	24.5	......	27	14	35	30	47
Ev. 10.0	22	19.8	.39	36.2	17.5	21.5	......	26	17	41	34	34
Ev. 12	7	18.1	.47	66.8	18	20.5	15.5	......	28	25	18	61

For the first and second lot the Mean Hum. was 77%, the Mean Temp. 82° F.

For the first lot the Max. and Min. Hum. was 79% and 75% respectively. The Max. and Min. Temp. 83° and 75° F., respectively.

For the sec. lot the Max. and Min. Temp. was 90° and 75°, respectively. The Max. and Min. Hum. 80% and 75% respectively.

For the final lot the Max. and Min. Temp. was 89° and 84° F. respectively. The Max. and Min. Hum. was 65% and 55% respectively for all except BD which was 22% and 18%. The Mean Temp. was 86° F. The Mean Hum. was 20% for BD and 57% for the rest.

TABLE XIIIg. *Pupae, 1918; (above line). light effects; (below line), evaporation and humidity effects.*

Designation (see p. 363).	No. of adults emerging.	No. of days.	Mean temperature.	Mean humidity.	Maximum temperature.	Minimum temperature.	Maximum humidity.	Minimum humidity.	Evaporation in cc. per day.	Date begun.	Total individuals.	% failure to pupate.	% pupal mortality.	Total pupae.
ANC*L*	0	......	69.5	50	70.5	69	60	35	16.4	.....	40	100	0	0
ANC*DK*	6	17.2	69.5	50	70.5	69	60	35	16.4	.....	68	88	25	8
B*L*	5	10.7	81.5	60	82	79	65	50	0+	4/24	23	65	37	8
B*DK*	15	11.6	81.5	60	82	79	65	50	0+	4/24	29	21	6	16
a 203*L*	0	......	77	40	82	72	46	35	.....	4/18	11	64	100	4
a 203*DK*	1	10	77	40	82	72	46	35	.....	4/18	23	91	50	2
b 203*L*	5	8.4	83	60	86	81	66	55	.....	5/23	12	67	0	4
b 203*DK*	12	9.1	83	60	86	81	66	55	.....	5/23	16	25	0	12
a 203*DL*	4	9.6	77	40	82	72	46	35	.....	4/18	26	69	50	8
b 203*DL*	9	9.2	83	60	86	81	66	55	.....	5/23	13	23	10	10
a 203*B*	2	10.7	77.2	40	82	72	46	35	.....	4/18	18	78	50	4
b 203*B*	5	9.2	83	60	86	84	66	55	.....	5/23	10	40	17	6
a 203*G*	0	0	77	40	82	72	46	35	.....	4/18	22	86	100	3
b 203*G*	6	8.7	83	....	86	82	66	55	.....	5/23	13	46	14	7
a 203*R*	1	9.5	78.5	40	82	72	46	35	.....	4/18	16	63	84	6
b 203*R*	2	8.2	83	60	86	82	66	55	.....	5/23	15	80	33	3
TH	3	9.5	79.0	75	83.6	75.1	86	75	14.5	8/14	20	65	57	7
TI	5	9.7	79.0	75	83.6	75.1	86	75	7.9	8/15	21	66	28	7
TL	7	9.5	79.0	75	83.6	75.1	86	75	4.3	8/14	22	45	42	12
TH	3	8.5	82.4	60	.....	.....	79	44	.....	.....	....	....	....	....
TI	1	7.5	82.4	60	.....	.....	79	44	.....	.....	....	....	....	....
TL	0	......	82.4	60	.....	.....	79	44	.....	.....	....	....	....	....
TH	1	9	81.2	70	.....	.....	....	....	15.4	.....	....	....	....	....
TI	2	10.5	81.2	70	.....	.....	....	....	12.9	.....	....	....	....	....
TL	9	10.6	81.2	70	.....	.....	....	....	8.4	.....	....	....	....	....
HHa	13	34.8	58.5	55	65	55	65	55	30.0	.....	....	....	....	....
HMa	2	39.0	58.5	55	65	55	65	55	5.0	.....	....	....	....	....
HHb	7	36.7	58.2	55	65	55	65	55	33.0	.....	....	....	....	....
HMb	4	38.0	58.2	55	65	55	65	55	5.9	.....	....	....	....	....
ANCD	6	17.2	69.5	50	70.5	69	60	35	16.4	.....	....	....	....	....
AD	22	20.2	69.5	50	71	68	55	45	6.8	.....	....	....	....	....

Italic capitals indicate the following: *L*—weak light; *DK*—dark. *DL*—under daylight glass; *B*—blue glass; *G*—green glass; *R*—red glass. Where colored glasses were used the source of light was a 110 v, 60 watt, nitrogen filled incandescent lamp, at a distance of 18 m.

TABLE XIV. *Mortality of hibernating generation of the codling moth at Olney.* (Data supplied by P. A. Glenn, in personal communication.)

Date collected	Number larvae	Number pupae	Number adults	Mortality prior to:	
				pupation, %	emergence, %
A. Cocoons were disturbed to observe pupation.					
1915-1916					
Aug. 30–Sept. 2	86	65	35	24	59
Sept. 2–14	124	74	57	40	54
Sept. 14–17	240	149	116	38	50
Sept. 25–29	159	110	80	31	50
	609	398	288	33	53
1916-1917					
Aug. 22–25	757	545	496	28	34
Aug. 28–31	446	349	299	22	33
Aug. 31–Sept. 2	284	221	186	22	35
Sept. 2– 6	260	184	138	29	47
Sept. 6– 9	204	145	119	29	42
Sept. 9–12	280	211	171	25	39
	2231	1655	1409	26	38
B. Cocoons were not disturbed.					
1915-1916					
Sept. 4– 8	296		251		15
Sept. 8–11	264		196		26
Sept. 11–14	290		234		19
Sept. 17–20	145		114		21
Sept. 20–23	105		77		27
Sept. 23–25	99		83		16
Sept. 29–Oct. 5	147		124		16
Oct. 5–11	63		54		14
Oct. 11–18	100		85		15
Oct. 18–25	75		61		19
	1584		1279		19
1916-1917					
Sept. 12–15	110		87		21
Sept. 15–18	217		180		17
Sept. 18–21	206		172		17
Sept. 21–23	204		179		12
Sept. 23–25	201		179		11
	938		797		16

the placing of lots of the same designation under approximately the same experimental conditions are shown.* The mortality and failure data are also given.

The data were first brought into this form, and much of the material used throughout the paper was drawn from these tables. In the application of experimental results to the interpretation of actual weather effects, *velocity* of development under different conditions is of first importance. Velocity values may be determined in relative terms, without reference to theoretical questions, from the reciprocals of the average *times* (shown in the tables referred to) multiplied by some convenient factor. The velocity values used in this paper were determined largely on that basis.

MORTALITY AND FAILURE TO PUPATE.

Mortality and failure to pupate have important relations to the success of the species. Failure to pupate amounted to about 50 per cent in the constant-temperature experiments taken as a whole. Cases in which dormancy had begun in the autumn and in which it was not broken, due to known lack of proper treatment, were entirely eliminated from consideration. Only failures to pupate on the part of larvae of lots in which other larvae did pupate were considered. However, in all of the hibernated stock, incomplete hibernation changes were no doubt a factor in failure to pupate.

Mr. Glenn, in a personal communication, supplied data on mortality in hibernation (Table XIV) which fall into two groups: In one group the cocoons of the larvae were torn open in the spring for the purpose of observing pupation, and in the other group they were undisturbed. Possibly some of the larvae included in these numbers may have died in the fall before cold weather set in. The notes do not show this fact, but they show the number of larvae which spun up in the cages in the fall of 1915 and 1916. The percentage of mortality of the hibernating generation of 1916-17 was less than that of 1915-16. Possibly this was partly due to greater care in handling the hibernating generation in 1916-17, though reasons are not evident. It could not have been due to the winter cold,

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* Stocks I-V used in 1917-18 were as follows: I and II were collected September 12 at Champaign; III, IV, and V were collected early in October a few miles south of Springfield, shipped to Champaign, and placed with the other stocks. All were held at about 60° F. until Oct. 19 when I, II, and III were transferred to a temperature varying from 28° to 38° F. and later transferred directly to the experimental conditions without "freezing", in all probability, as the 28° temperatures were of short duration. Stock IV was in similar conditions until Jan. 23 when it was put at a constant temperature of 40° F. until experiments were started. Stock V was "frozen" at 25° F. for 24 hours and transferred to the 40° constant temperature.

All other stocks were merely stored at temperatures varying from 35° to 45° F. Subsequent experience has shown that this is as important a period as any in the life history; and in future work, dates of collection, full control, and full record of all conditions must be kept. The work of Townsend shows the importance of this period and indicates that all storage should be at or below 32° F.

because the winter of 1915-16 was, if anything, warmer than that of 1916-17.

Data from Tables XII-XIIIG were used in making Fig. 9, which shows smoothed curves of percentages of larvae failing to pupate in experiments conducted at approximately constant temperatures. The actual failure per cent is shown by circles, and mean data for experiments within two degrees of each other, by crosses. Curves were first drawn through the average points. These were then plotted on cross section paper as in Fig. 10, and the same per cent of mortality connected between the different humidities, and smoothed. (See Huntington '19, p. 252.) The original curves were then corrected to fit the *isofailure* lines of Fig. 10. To make relations of the two figures clear, compare the failure per cent at different temperatures on humidity 95% of Fig. 10, with temperature and failure per cent on that humidity in Fig. 9. (For fuller explanation of these methods of graphic representation of results, see below, pp. 383-393.)

Townsend's ('26) results indicate that prolonged exposure to a temperature of 50° F. decreases the percentage of pupation. Baumberger ('17) secured similar results. Townsend showed, further, that soaking in water increases the percentage of pupation and that the number of soakings and the temperatures at which soaking is done are important. Soaking frequently at 50° F., is most effective. The data graphed (Figs. 9 and 10) are representative, however, as they show a great many weather possibilities in combination.

Pupal mortality in constant-temperature experiments is shown for the several mean humidities in Figs. 11 and 12. The method of drawing the curves and smoothing them was the same as in Figs. 9 and 10. In both cases (compare Figs. 10 and 12), the conditions are most favorable, i. e., show low mortality (20% or less) and failure (50% or less), in the neighborhood of 74° F., and 70–75% humidity. There are differences in detail, but a drop in the mortality and failure lines at high temperature for humidities of 75–85% occurs in both, leaving an upward extension of favorable conditions at high temperature, both wet and dry. The diagrams represent the relations in question only roughly, as the data were few and quite irregular. This irregularity was evident in laboratory-hibernated larvae (probably because of differences in contact with water), some lots showing higher mortality and failure to pupate and others showing little or none.

It is evident that variability is very important at the lowest temperatures. One lot of larvae kept at 48°–50° F. showed no signs of pupation until an accident to the thermostat sent the temperature up to 78° for an hour. In about two days several larvae pupated when the temperature was about 48°., but all the pupae died without emerging. In one large series of hibernating individuals, none pupated at 52° F. except within a day or two after being transferred from 70° F. The influence of the higher temperatures apparently persisted a few days. This may result from one or more of the following causes: (a) lag in change of metabolic

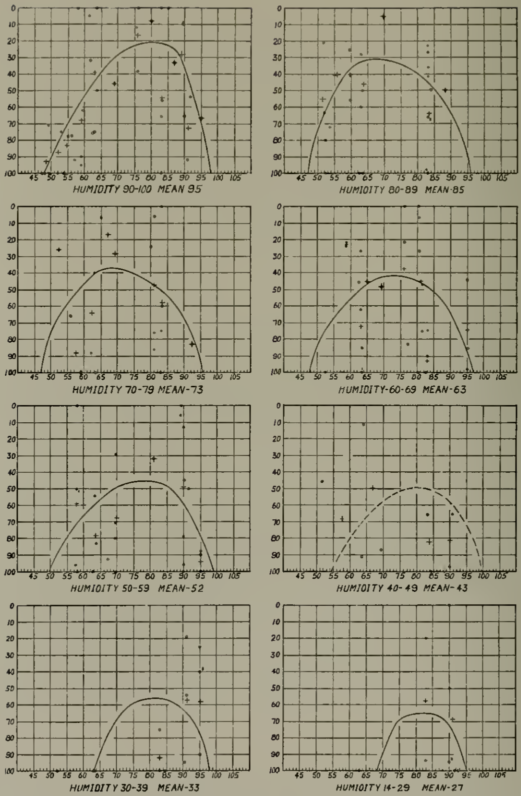

Fig. 9. Curves showing percent failure to pupate under various conditions of temperature and humidity. The circles indicate actual observations and the crosses indicate averages. Circles with crosses inside are single data for the temperature in question. The curves pass through the average of the crosses as well as it was possible to make them. This relation was improved by smoothing the curves shown on Fig. 10.

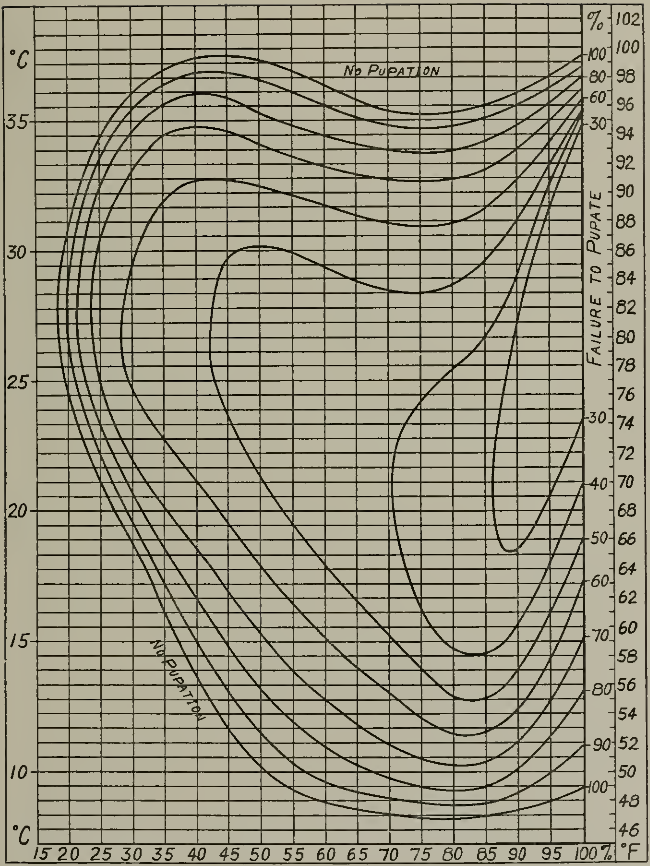

Fig. 10. Chart showing equal failure-to-pupate curves made by connecting the same percent failure on a temperature and humidity chart. Least failure to pupate may be assumed to fall between humidity 90% temperature 70° F. and humidity 100% temperature 88° F.

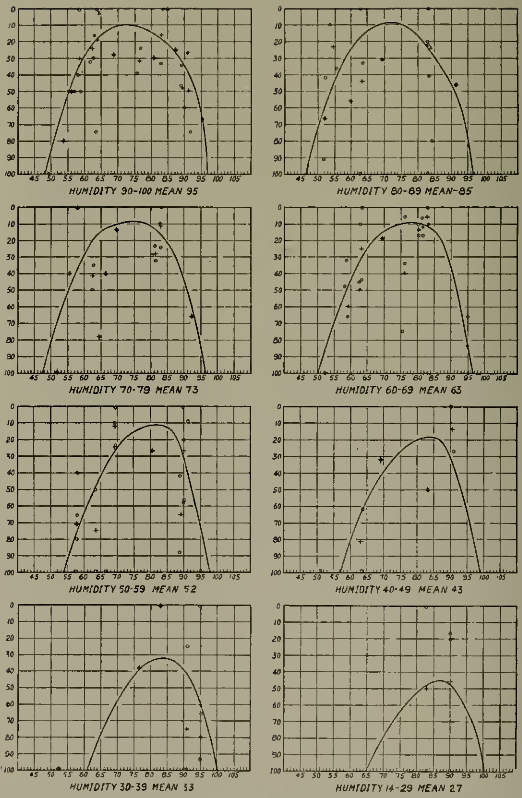

Fig. 11. Curves showing the percent mortality of pupae at different humidities and temperatures. For meaning of symbols see Fig. 9.

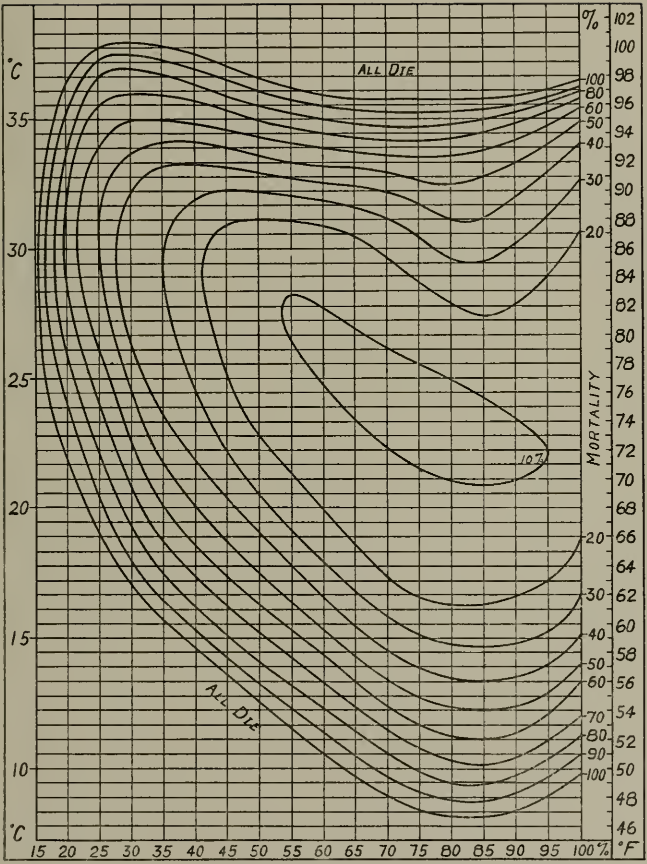

Fig. 12. Chart showing equal mortality curves on a temperature-and-humidity chart. Least failure to pupate may be assumed to lie between humidity 85% temperature 71° F. and humidity 55% and temperature 81° F.

rate or acclimation; (b) stimulation due to change of temperature; (c) development of enzymes at the higher temperature.

The failure to pupate in the variable-temperature experiments was 36%, and the pupal mortality was 28%. This reduced loss is due at least in part to the more favorable effect of variable temperatures as compared with constant ones. In the early approximately constant-temperature experiments, there was more variation and smaller loss than in the later experiments in which the variation was reduced by improving the equipment.

In Townsend's experiments with the 1923-24 generation, the stocks were stored at 50° F. (10° C.); 32° F. (0° C.); and 71.6° F. (22° C.). The percentage of pupation was highest in stocks stored at 50° F., next at 32° F., and lowest at 71.6° F. This indicates that changes go on at 32° F., and that temperatures as low as freezing must be taken into account in considering failure to pupate or the breaking of dormancy.

TABLE XV. *Showing data used in calculation of alpha values by formula* $y\ (x - a) = K$.

	Case.	Designation.	T. °F.	H. %	No. of days.	No. of individuals.	Cases used.	Alpha value calculated.
Spring generation 1918.	a	HNV	58.5	97	34.4	5	c & g	49.0
	b	LW	62.1	95	26.1	15	d & g	53.6
	c	KW	62.8	70	27.3	14	d & f	54.5
	d	AW	69.5	70	20.0	31	f & g	50.9
	e	BW	80.3	70	11.0	27	c & f	48.6
	f	BWW	80.3	95	11.6	7	c & e	49.8
	g	MWW	91.5	85	8.4	8	c & d	44.4
							d & e	56.3
							e & g	44.1
			Mean alpha value for humidities 70-97 per cent.........					50.1
	h	HM	57.9	50	38.2	4	j & n	52.0
	i	LD	61.9	60	27.8	14	k & n	54.6
	j	KD	62.6	60	28.3	6	k & m	54.9
	k	AD	69.5	50	20.2	22	m & n	47.0
	l	BM	80.3	50	11.2	41	j & m	47.7
	m	BM	80.3	60	11.8	25	j & l	50.0
	n	MW	91.8	51	8.1	18	j & k	45.4
							k & l	56.1
							l & n	55.1
			Mean alpha value for humidities 50-60 per cent.........					51.4
Summer 1917.	o	KNV	61.7	97	23.8	13	p & s	50.7
	p	JW	64.5	70	21.0	3	p & r	53.7
	q	LW	69.5	82	13.1	13	r & s	37.8
	r	MW	76.2	96	10.6	41	q & r	47.3
	s	NW	89.3	95	7.5	10	p & q	56.2
							q & s	41.2
			Mean alpha value for humidities 70-97 per cent.........					47.8
	t	Z	57.9	45	39.4	6	u & w	52.7
	u	JD	64.5	40	22.1	8	u & v	52.9
	v	MD	76.6	35	10.8	8	v & w	46.3
	w	ND	89.9	58	7.5	7	t & u	48.3
			Mean alpha value for humidities 35-58 per cent.........					50.0

CALCULATION OF THRESHOLDS AND VELOCITIES.

a. Thresholds. Krogh ('14) showed that the zero of the equilateral hyperbola to which the time-temperature curve partly conforms, is not the actual threshold of development. Values calculated for those parts of the time-temperature curve which conform to the equilateral hyperbola (within the straight-line limits of the velocity curve) do have a significant relation to the actual limits, however, and correct methods of obtaining them are important.

In Table XV are shown the results obtained from a simple formula in calculating *alpha* values for high-humidity and low-humidity experiments of 1917. The humidities above 69% and below 61% have been grouped separately, and the data here serve chiefly to bring out the fact that the calculated *alpha* is lower in the high-humidity experiments than in the low-humidity experiments and also that it is lower in the summer generation than in the spring generation.

TABLE XVI. *Showing the use of Von Oettingen's phenological method of determining the alpha value.**
(See Fig. 13, curves for 95% humidity.)

Assumed alpha values.			56° F.			54.3° chosen first.		52.2° chosen second.	
No. of Pupae.	Days.	Mean temp. °F.	Effective temp. °F.	Product.	Depart.	Product.	Depart.	Product.	Depart.
1	50	53.9	0	0	—191	0	—221	85	—172
1	46	55.4	0	0	—191	51	—170	147	—110
3	34.6	58.4	2.4	83	—108	142	—79	215	—42
1	33.0	58.6	2.6	86	—105	142	—79	211	—16
1	35.0	58.7	2.7	95	—96	154	—67	227	—30
13	23.8	61.7	5.7	136	—55	176	—45	226	—31
14	27.3	62.7	6.7	183	—8	229	+8	287	+30
2	25.5	62.8	6.8	173	—18	217	—4	270	+13
15	26.1	63.0	7.0	183	—8	227	+6	282	+25
1	25.0	63.5	7.5	188	—3	230	+9	282	+25
2	24.0	63.5	7.5	180	—11	221	0	271	+14
3	21.0	63.5	7.5	157	—34	193	—28	237	+20
7	15.5	68.7	12.7	197	+6	223	+2	256	—0
22	10.5	75.8	19.8	203	+12	221	0	241	—16
25	10.0	75.9	19.9						
19	10.2	76.7	20.7	211	+20	228	+7	250	—7
2	7.0	80.7	24.7	173	—18	185	—36	†199.5	—57.5
2	9.5	83.0	27.0	256	+65	273	+52	293	+36
1	7.0	83.0	27.0	189	—2	201	—20	216	—41
3	8.3	87.6	31.6	262	+71	276	+55	294	+37
5	8.0	88.7	32.7	262	+71	275	+54	292	+35
13	7.3	89.3	33.3	246	+55	259	+38	275	+18
10	7.5	89.3	33.3						
4	7.6	89.6	33.6	255	+64	268	+47	284	+27
1	9.0	90.0	34.0	306	+115	321	+100	340	+83
4	7.4	90.1	34.1	252	+61	265	+44	280	+23
8	8.0	91.0	35.0	280	+89	294	+73	310	+53
2	9.5	91.8	35.8	340	+149	356	+135	376	+119
1	8.0	95.3	39.3	314	+123	328	+107	345	+88
			K=191 mean for 62.7°-83.0°			K=221 mean for 62.7°-83.0°		K=257 mean for 68.7°-89.6°	

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* Only results at the same temperature and humidity were averaged together. With a weighted average, the *alpha* value is 54.8° F.

† With 199.5 omitted, the mean is 263.

The calculation of *alpha* values by this simple formula is by no means the best method, for it gives various results depending on how many and which combinations are used. The graphic method commonly used consists of drawing a straight line through the velocities for the different temperatures. Such a line will cross the temperature axis at *approximately* the hyperbolic zero (*alpha* value). If averages for points within one degree of each other are used, the results of the graphic method are fairly satisfactory. Where conditions in the different experiments varied as to humidity, air movement, temperature variation, light, etc., weighted averages should not be used, because the variation in mortality leaves widely different numbers completing their transformations.

The *alpha* value is best determined by Von Oettingen's method, in which the time is multiplied by the temperature above various assumed *alpha* values, that one being chosen as correct which gives the most nearly constant product within the widest range of temperatures. To illustrate this method, Table XVI shows the data used in calculating *alpha* values and in drawing the curve for all experiments having 95 per cent mean humidity (range 90–100%). The *alpha* value to be used in drawing the curve is the one giving nearest a constant for the data which appear to give an approximate constant. Thus, 54.3° F. (in Table XVI) was used because it gave least deviation for the data between 62.7° and 83° F. Higher and lower temperatures were considered as being outside the range within which the data conform to the equilateral hyperbola.

The 95 per cent humidity data are shown here, not because they are best to illustrate the principle, but because they indicate the difficulties. The experimental data were unusually heterogeneous and gave much trouble. Some experiments were ventilated, some were not ventilated, and several generations were included. The date were worked over by all three methods and combined and segregated according to conditions, with unsatisfactory results, suggesting strongly that such experiments for such a purpose should be carried out in the same way and with the corresponding generations. Furthermore, an inspection of the data in Table XVI for the *alpha* value 52.2° F. shows that extending the range of temperatures assumed to conform to the hyperbola would give only a slightly larger deviation from a constant.

b. Velocities of Development of Pupae. Relative velocity is merely the *reciprocal* of the *time* for the completion of a process. Usually, for convenience, and for practical reasons, the reciprocal is multiplied by a rather large number such as 100 or 1000, *ad lib.* Relative velocities based on 300* times the reciprocals of the days from pupation to emergence were computed from the average length of the pupal stage in all the different experiments under approximately constant temperatures. The data (Tables XII, XIII, etc.) were segregated into humidity classes: 14–29%, mean 22%; 30–37%, mean 31%; 40–58%, mean 49%; 60–68%, mean 61%; 70–77%, mean 73%; 80–88%, mean 85%; 90–100%, mean

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* This multiple was chosen at first to place the velocity curve approximately on a 45° angle with the temperature axis.

95%. These classes were then treated as though all the experiments had been run at the mean humidity for the group. It would have been desirable to keep the different generations separate, but this was impracticable because of the small number of emerging moths. The results were segregated according to humidity, regardless of generation or history. A few discordant values shown in the tables were not used in the calculations.

The relative velocities for each humidity were plotted on coordinate paper. Since velocities for temperatures between 62° F. and 87° F. usually fall into an approximately straight line, it was assumed that lines drawn through these points crossed the temperature axis at a point approximating the hyperbolic zero. These several approximate *alpha* values were checked by Von Oettingen's method as in Table XVI, and in some cases by the use of the formula as in Table XV. Each curve was drawn through means of ordinates and abscissas of groups of points, and to the best calculated *alpha* value. (Weighted means, taking into account the number of individuals, were not used, because the stock was different in history, and because the number of individuals put into the experiment was different in practically every case.)

Fig. 13 shows relative velocities $\frac{270}{\text{days}}$ plotted for each average-humidity group of pupae in the constant-temperature experiments. The curves are placed one above the other for convenience and indicate the general form of the first rough curves which had been drawn. The scale at the left indicates the mean humidity for the data included in the curve, the base of each curve being on the mean humidity. The curves were first drawn, as shown by broken lines, for 95, 85, 73, 61, and 49 per cent humidity, and then harmonized as shown by the solid lines. The velocities had been originally plotted as $\frac{300}{\text{days}}$ and were later changed to $\frac{270}{\text{days}}$ on the basis of the crucial experiments AD and AW with variable temperatures (Table XVII, Fig. 15). The final survey of the entire relationship showed that the use of $\frac{289}{\text{days}}$ would have properly compensated for the retarding effect of constant-temperature conditions. The use of these different factors does not change the relations of the relative velocities in any way. It is perhaps impossible to be sure of the correct factor to use in the early stages of a study. This final factor, 289, was the average obtained by a recalculation of the data for all constant-temperature experiments except five out of the fifty-five experiments, which were rejected because they fell too far below the average. Only temperatures between 62° and 89° F. were used in getting the average. A few cases which appeared to have very rapid development, especially with a combination of high humidities and rather high temperatures (which seems to give greater variation than other combinations), were regarded

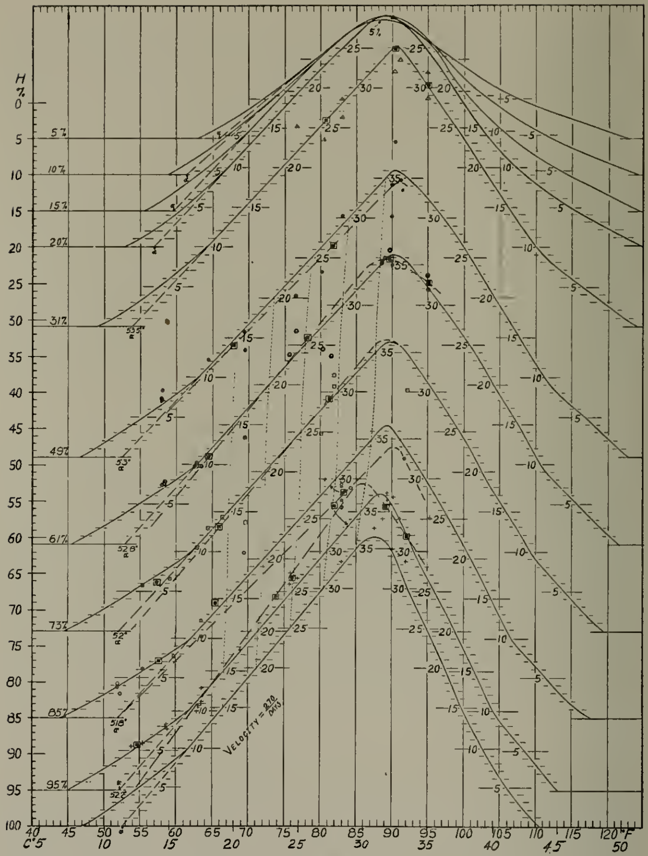

Fig. 13. Curves showing the average velocity of development of pupae under different conditions of approximately constant temperature and humidity. The velocities are derived, from data in Tables XII and XIII, by dividing the mean pupal life in days into 270, and are shown immediately adjacent to the curves. Each curve has its base on the humidity which is mean for the observations; this mean is shown at the left as a scale applicable to the beginnings of all curves. The double squares indicate the mean points through which the curves were originally drawn. The broken lines indicate the curves drawn through these double squares. The solid lines, which are the curves used in subsequent work, resulted from smoothing the various velocity lines of Fig. 14A.

as properly omitted from averages, though the computation of these alone would give a much lower *alpha* value. In these cases, moreover, there was possibly a considerable error in determining the time of pupation.

In the preliminary rough drafts of these curves, the velocity values for the experimental data at medial temperatures fell fairly close to a straight line, but those at lower temperatures did not. It was with some difficulty that a curve was found which would fit these lower points. A hint was taken from the insistence of physiologists upon Q_{10} as a constant, for this suggested some form of concave curve. Accordingly, a curve with the formula $y = \frac{x^{1.5} K}{10}$ was chosen (K being a factor by which the curve should be multiplied to make it fit the experimental data) and was slightly modified for each humidity group until it would pass through the plotted velocity values. Each of these curves thus marked approximately the velocity values from the lower straight-line limit to the approximate threshold of development.* It is noteworthy that the threshold is higher for lower humidities, as is also the lower straight-line limit.

The highest points of the velocity curves for humidities of 95, 61, and 49 per cent give a fair indication of the temperatures at which development is most rapid, namely, 88°, 90°, and 90.5°, respectively, showing that the maximum velocity shifts to a higher temperature as the humidity is lowered. The downward curvatures at the higher temperatures were taken roughly through points plotted from the data available at that stage of the calculations and were later brought into their present position by use of the equal-velocity chart described below.

Another step preliminary to the drawing of the solid-line curves which are shown in Fig. 13 was the harmonizing of the equal-velocity values. For this purpose, velocity values at 5-unit intervals were taken from the straight-line portions of the broken-line curves of Fig. 13 and plotted on co-ordinate paper scaled for humidity and temperature, as shown in Fig. 14A, and the plotted points were connected by broken-line curves.

The waves in these curves are not in accord with our general knowledge of the effects of external conditions on the behavior of organisms. The curves should be more regular. The irregularities probably result, first of all, from the heterogeneity of the material, the extent of which is suggested in Tables XVIII and XIX. For example, the 95 per cent data include various conditions, ventilated and unventilated, and different generations, etc. Secondly, the crookedness of these curves may be partly due to errors in the observation and interpretation of the process of development, particularly as regards the beginning and the ending of the pupal stage. Finally, there is the possibility of errors in the calculation, for the methods used give only approximate results at best.

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*Since a curve with this formula does not pass through O, a formula of the form $y = K (\log x) + c$ is more nearly correct.

The curves in Fig. 14A were, therefore, smoothed as shown, in order to counteract the heterogeneity of the data and to compensate for the probable errors of experimentation and interpretation. This smoothing is not to be construed as a merely mechanical process, but as a kind of averaging of results with a view to the best possible expression of the real effects of temperature and humidity upon the rate of development. The more regular lines in Fig. 14 are thus more truly representative of equal-velocity values than the crooked lines. The best proof that smoothing is justified, lies in the fact that the use of the chart made from these curves gives consistent results.

The harmonized velocity values obtained by the method shown in Fig. 14A were then used in the plotting of the straight-line portions of the solid-line curves in Fig. 13, which are presumably more nearly correct than the corresponding portions of the broken-line curves originally plotted. (The dotted vertical lines through points of equal velocity values in Fig. 13 may be compared with the solid lines in Fig. 14A.) The *alpha* values of these new curves were checked by the Von Oettingen method

Fig. 14A. Method of smoothing velocity curves of Fig. 13. Velocities from Fig. 13 are indicated by dots. The broken lines were drawn connecting these dots, and the solid lines were then drawn by smoothing these lines to bring them into harmony.

and found to be more satisfactory than those of the old curves. The use of 52.2° F. as the *alpha* value for the 95 per cent data gave a nearly constant time-temperature product over a wider range of temperatures than when 54.8° F. was used. This widening of the straight-line limits is in better accord with the data for other humidities; also, the time-temperature product is larger and, accordingly, nearer the presumably correct value for the constant. For the 85 per cent humidity data, 51.8° F. similarly proved to be the best *alpha* value. The data at approximately 83° F. were from air-movement experiments in which the rate of air-flow was not that used as standard in the other experiments; these data were plotted in the absence of other data. The solid line curve, however, is practically an interpolated curve for the plotted points, and it has the same *alpha* value (51.8° F.) as the broken-line curve. In the case of the

73 per cent data, for which 52.0° proved better than 54.0°, the use of the lower *alpha* value is further justified by the fact that some of the hibernated pupae included in these data had not been soaked, winter dryness accounting partly for the low velocity values at 83° F.

PREPARATION OF THE EQUAL-VELOCITY CHART.

After the curves for data covering medial temperatures and experimental humidities (roughly 65°–87° F. and 45–95%) had been smoothed as in Fig. 14A, the points with velocity 35 at the various combinations of temperature and humidity shown in the solid-line curves of Fig. 13 were plotted on a large sheet of co-ordinate paper scaled for temperature and humidity as in Fig. 14B, and a line was drawn through these plotted points, both below and above the maximum velocity, and connected around the low humidity to make the greater part of an ellipse, as shown between 85° and 90° in Fig. 14B. In the same way, other equal-velocity lines were drawn roughly parallel to the 35 line until the scheme was completed for the high temperatures. The velocity values on the lower ends of curves similar to those in Fig. 13, but drawn according to the formula $10\ y = x^{1.5}\ K$, were transferred to the equal-velocity chart, and lines were drawn through them so as to complete that portion for low temperatures. (Fig. 14B is the final form, resulting from much refinement of this rough draft.)

Data from the variable-temperature experiments was then plotted on this rough draft of the chart. The march of temperature and humidity is shown on Fig. 15 for each of these experiments. Only about half of these experiments were sufficiently accurate to use. The velocity values for the experiment DD in Table XVIII (indicated by the line DD on Fig. 15) were then plotted, as is shown in Fig. 16, to determine the *alpha* value. The *alpha* values for experiments AW and AD were determined similarly.

As indicated in Fig. 16, the velocity curves in part of the experiments turn downward at high temperatures. The "summing of temperatures" is done on the assumption that the velocities for the temperature fall on a straight line. In these curves it may be seen that they do not fall in a straight line. Throughout this part of the paper, therefore, wherever the velocity for a temperature does not fall on the straight line, a straight-line *temperature with the same velocity value is substituted* for the actual temperature recorded by the thermograph for the hour in question. The high-temperature slope of the curve shown in Fig. 16 was modified until the sum of temperatures above *alpha* came out approximately 6,480 (or, in other words, until the substitution-quotient came out approximately 270) as it did with AW and AD in Fig. 15, which were concerned with variations within the straight-line limits only. Thus, in Fig. 16, instead of 90°, 95°, 100°, and 105°, which were recorded for two-hour readings, the following temperatures were used respectively: 89.5°, 84.1°, 74.6°, 64.6°. By means of trials with the data of the variable-temperature experiments, the upper part of the equal-velocity chart was tentatively

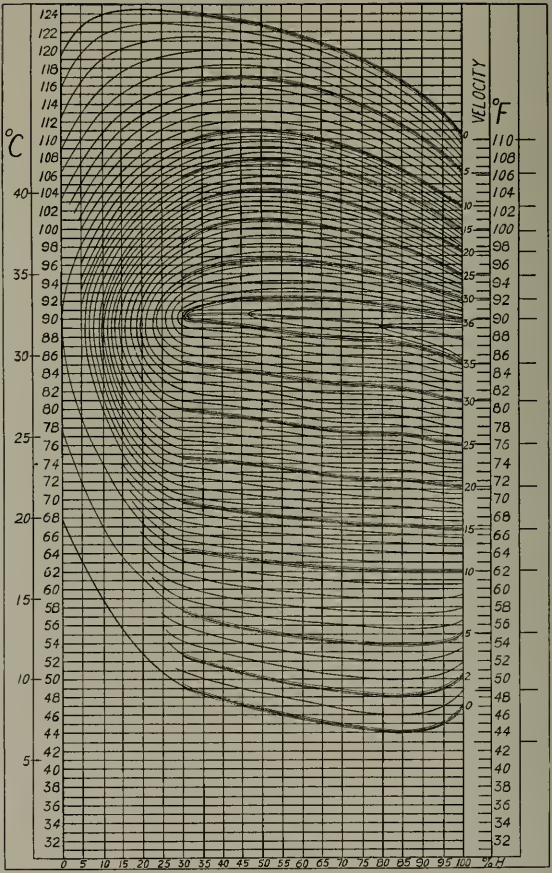

Fig. 14B. Chart of equal-velocity lines for the pupal stage. These velocities were multiplied by 1.07 to correct for variability (see Table I). The curves pass through combinations of temperature and humidity which give the same velocity of development. The curves in Fig. 13 may be likened to cross sections of a hill of which these are contour lines.

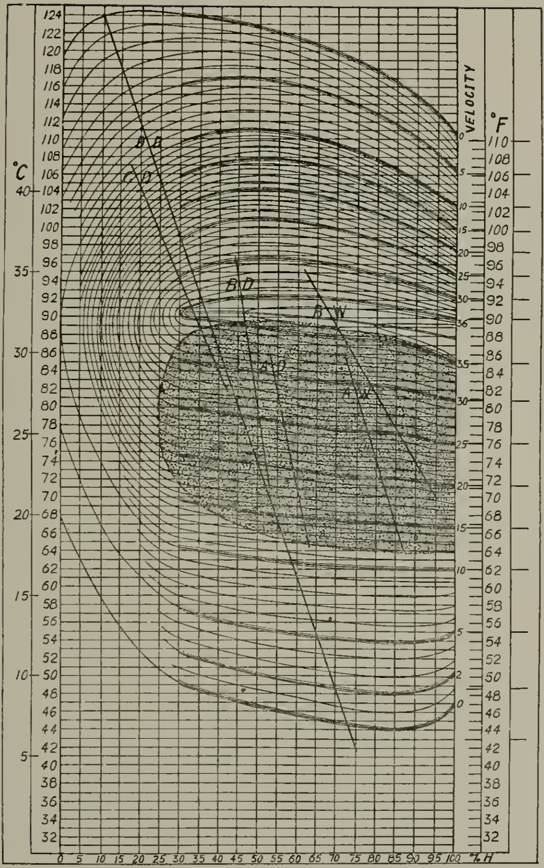

Fig. 15. Equal-velocity chart for the pupal stage, with lines CD, DD, BD, AD, BW, and AW showing the daily march of temperature and humidity in the variable-temperature experiments of the same designation. The shaded area covers medial conditions, that is, conditions within the straight-line limits of the velocity curve. (See Table XVIII, p. 398.)

drawn; while it did not purport to be extremely accurate, it was an approximation serving to check the data available.

With a view to further corrections and adjustments of the chart, the readings of temperature and humidity were taken for representative pupae of spring and summer groups from Glenn's 1915, 1916, and 1917 data, and plotted on the chart in the manner shown in Fig. 17, a dot being placed on the chart for the temperature and humidity of each two hours during the pupal period for each group. The dots between each pair of heavy velocity lines (representing 5 velocity units, except at the low temperatures where the first interval is 2 units and the second is 3 units) were taken together, and mean humidities, H, mean temperatures, P, and mean velocities, V, were computed for numbers of dots, N, as shown at the right of Figs. 17, 19, 21, and 22. The mean velocities were then plotted on the mean temperatures to make a curve similar to Fig. 18. When temperature substitutions were made, it was found that the substitution-quotients were too large for those groups of pupae subjected

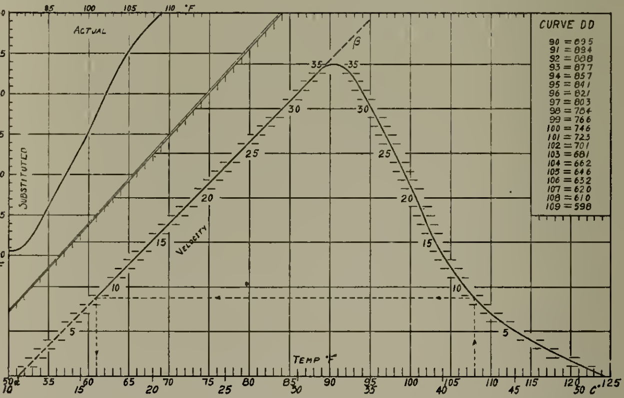

Fig. 16. The long curve is the full-length velocity curve for the experiment DD made by plotting the velocities crossed by the line DD in Fig. 15, on the corresponding temperatures. The curve in the upper left-hand corner is a curve of correction for reducing temperatures outside the staight-line limits to a value with the same velocity on the straight line. Read from the right-hand side of the curve, 109° equals 59.8° on the straight line, etc., as shown in figures at the right. Follow the arrows and broken line beginning on 108° F.

Note: The curves in this article are not drawn with the straight-line portion making an angle of 45° with the base line, as all are trial curves. Figures 16, 18, and 20 were intended to be so drawn, but the draftsman made the vertical scale 1.1 times the horizontal instead of 1.07 (see page 383). The values in Table I, when plotted for average daily variations, make a 45° angle within the shaded area of Fig. 15 when the scale is such that one developmental unit equals one degree of temperature.

to the greater amount of low temperature. The curve for the lower temperature data was then changed to $y = \frac{x^{1.3}}{10} K$, giving a curvature which fitted the data.

FINAL CORRECTION OF THE EQUAL-VELOCITY CHART.

With the equal-velocity chart thus revised, the entire record of variable-temperature experiments on pupae was worked over, in order to check the values on the chart. Table XVII indicates the difference between the substitution-quotients used for this purpose and the uncorrected sums of "effective temperatures." Note that the difference amounts in some cases to thirty or more units. See also Tables XVIII–XIX.

TABLE XVII. *Showing substitution-quotients for variable temperature experiments, in comparison with other methods of calculation.*

Designation.	Range of temperature.	*Alpha* value.	Actual mean daily temperature.	Actual time in days.	Sum of temperature "degree-days" above *alpha* value.	Mean of temperatures corrected by substitution-method.	Substitution-quotient.
First Generation 1917							
AD	65— 84	51.5	69.9	14.9	274	69.9	274
AW	65— 84	51.3	69.5	14.7	267	69.5	267
BD	71— 95	51.6	82.7	9.9	307	79.4	275
BW	71— 95	50.5	82.7	9.1	288	79.4	272
CD	84—103	50.5	88.8	8.0	306	83.9	267
DD	82—103	51.2	87.6	8.3	302	82.8	268
Hibernated Generation 1919						Mean	270.5
RWA*	50— 54	52.8	52.2	89.3	—36	55.8	269
First Generation 1919							
RWB*	50— 53	51.6	51.9	68	+19	55.6	272

* It is not possible to determine a fair *alpha* value in these cases. Various alpha values and curves were tried until a substitution-quotient of 270 was approximated. Note development below alpha in RWA. The day degrees may be derived by subtracting the *alpha* value from mean temperature and multiplying by days because the means are based on actual hours.

NOTE: When the substitution-total is correct, it is numerically the same as 1/24 the total of developmental (hour) units as defined on p. 332.

In order to check the equal-velocity chart still further, our outdoor and greenhouse observations on pupae at Champaign and Glenn's observations on pupae at Olney were entirely worked over (except where hygrothermograph records were missing for part of 1917). The two-hour temperatures and humidities for the entire periods in which pupae were

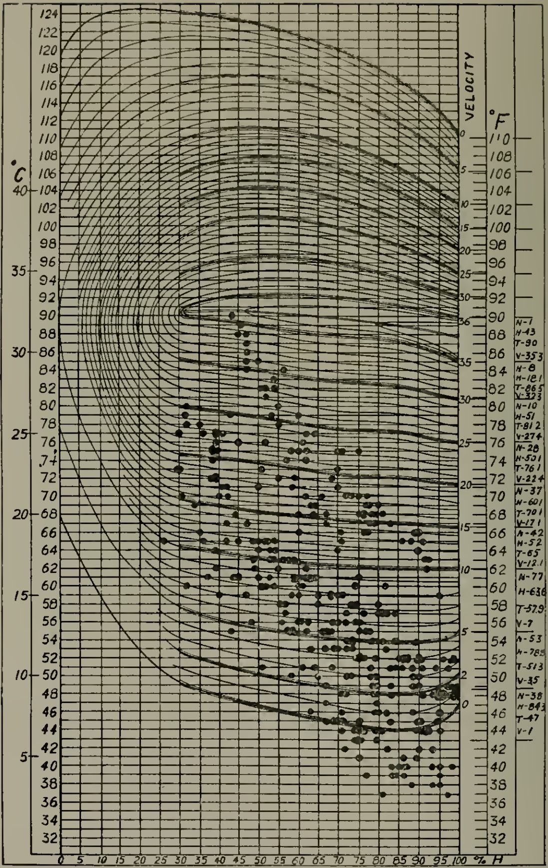

Fig. 17. Pupal velocity chart showing the two-hourly readings of temperature and humidity from April 17 to May 15 at Olney, 1916. Each black dot represents the condition of temperature and humidity at some even hour. The number of items (N), the mean temperature (T), the mean humidity (H), and the mean velocity (V) are for the dots falling between the triple velocity lines (5-unit intervals) are shown in the margin at the right.

under observation had been transcribed in the manner shown in Table II and were now plotted for each group of pupae on the equal-velocity chart as shown in Figs. 17, 19, 21, and 22. The dots lying between the lines which separate the even 5-velocity units were taken together, and the temperatures of the groups averaged together, the velocities averaged together, and humidities averaged together. For example, the averages for the interval between velocity 5 and velocity 10 in Fig. 17 are shown at the right as follows: N, number of readings, is 77; H, mean humidity, is 63.6; T, mean temperature, is 57.9; V, mean velocity, is 7. These mean velocities were then plotted on the mean temperatures as shown in Fig. 18, where velocity 7 will be found plotted on temperature 57.9°, and all other plotted points corresponding to the figures in the margin of Fig. 17.

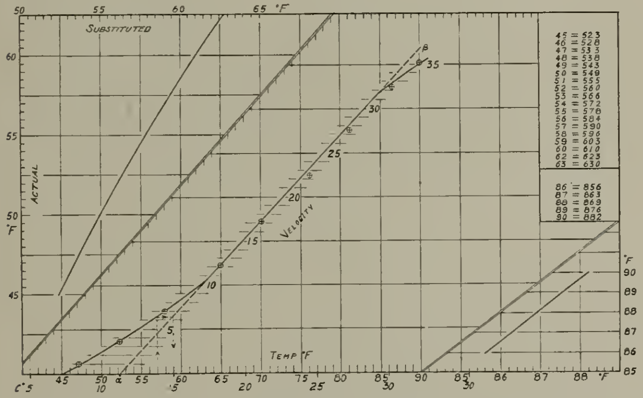

Fig. 18. Curve drawn through the mean velocities (crossed circles) and temperatures shown at the right of Fig. 17. The corrections applied to the actual temperatures are shown in the insets at the corners of the figure. Follow the dotted line and arrows from 57° to 59° F. The actual threshold was estimated to be 45° and the alpha value to be 52.3°. The substitution-quotient was 270.

A curve was next drawn through the points plotted in Fig. 18. The temperatures not on the straight line were dropped out and the temperatures with the same velocity on the straight line were substituted by the method explained on p. 387. To use this method, take for example, temperature 57° F., on Fig. 18, run up to the velocity curve, over to the straight-line extension, then downward as indicated by the arrow, and note that 59° F. is the temperature to be substituted for 57° F. The equal-velocity equivalents of all the temperatures not on the straight line

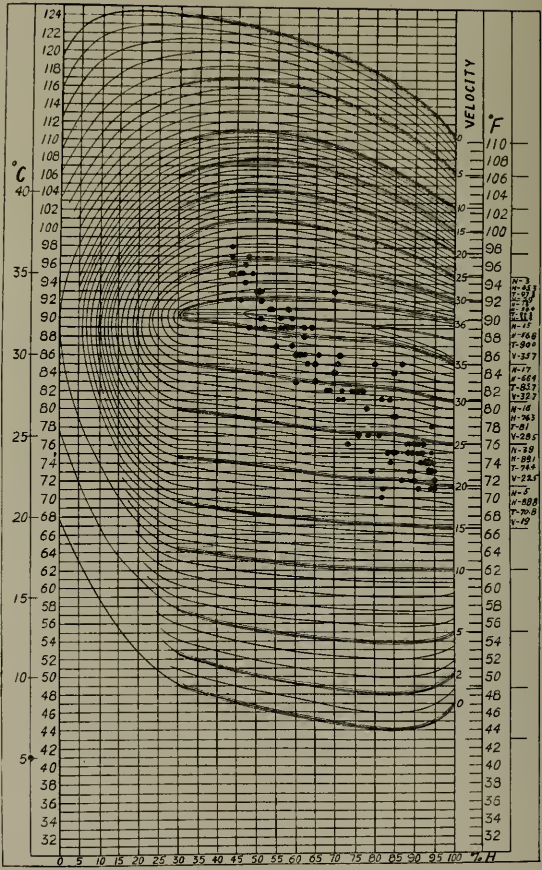

Fig. 19. Pupal velocity chart showing the distribution of temperature and humidity Aug. 1-10, 1916, at Olney. For explanations, see Fig. 17.

are shown in the upper right-hand corner of Fig. 18. For an illustration of the conditions and correction processes for a summer period, see Figs. 19 and 20. Note arrows indicating the equivalent of temperature 96°, which is 83°. The *alpha* values and substitution-quotients for the larger groups of individuals were calculated by the methods indicated above, and those for the smaller groups were interpolated. The substitution-quotient as here derived is practically the same as one-twenty-fourth of the number of developmental units for the stage. The *alpha* value varies with the angle of the average daily march of temperature and humidity (Figs. 15 and 29). The substitution-quotients for the various determined *alpha* values were derived from the temperatures thus corrected by the method explained above.

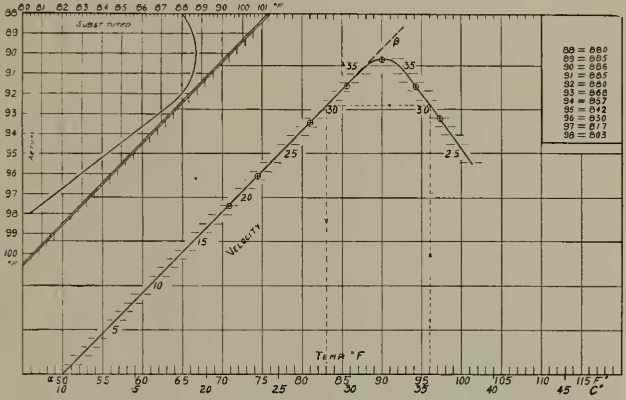

Fig. 20. Showing the velocity curve, alpha value and corrections for temperatures for the weather data recorded on Fig. 19.

For Glenn's 1915 data, this method gave 283 substitution-quotient as the mean of the means of thirty-individual groups of pupae, beginning April 13 and ending May 19 (five aberrant individuals were omitted), and a mean *alpha* value of 51.3° F. for the actually calculated cases. Mortality was low. Of the 1,400 larvae under observation, about 1,054 pupated and emerged. For the first generation, which began pupation June 19, and ended August 7, the mean of the means was 266, and the mean *alpha* value for all calculated cases was 50.6° F. The second generation, which was taken as beginning with the pupation of an individual on August 8 and ending with the last emergence on September 9, consisted of 36 pupae with a mean of 249. This was among the largest deviations from 270. The mean *alpha* value was 50.8° F.

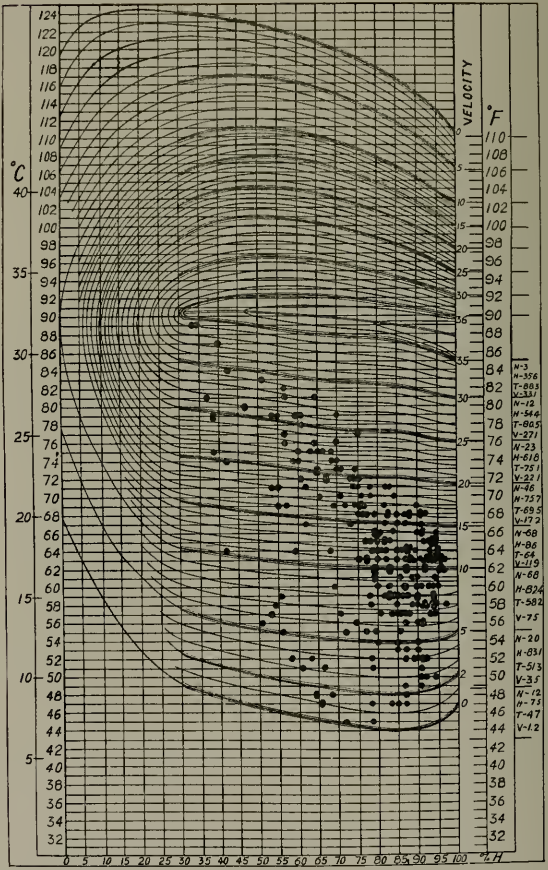

Fig. 21. Pupal velocity chart showing distribution of temperature and humidity May 14-June 4, 1915, at Olney.

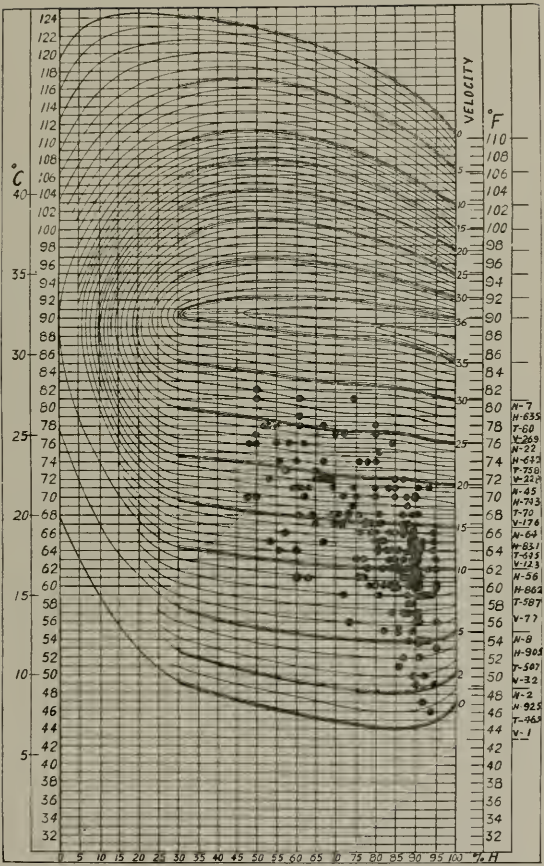

Fig. 22. Pupal velocity chart showing the distribution of temperature and humidity from Aug. 17 to Sept. 3, 1915, at Olney.

TABLE XVIII. *Pupae at variable temperature, first generation, 1917 and 1919.*

Designation.	No. of adults emerging.	Days to pupation.	Mean temperature.	Approximate mean-humidity.	Base temperature.	Elevation in degrees.	Base humidity.	Depression in %.	Maximum temperature.	Minimum temperature.	Maximum humidity.	Minimum humidity.	Evaporation in cc. per day.	% failure to pupate.	Total individuals.	Total pupae.	% pupal mortality.
AD	14	14.9	69.9	55.0	65.6	18.3	50.0	15.0	84.0	65.0	60.0	45.0	8.2	5	20	19	26
AW	9	14.7	69.5	80.0	65.6	18.3	85.0	35.0	84.0	65.0	90.0	50.0	4.1	5	20	19	53
Oa	4	11.4	72.0	73.0	64.3	25.1	86.4	38.7	89.3	60.5	92.6	47.6	16.2	....	....	....	....
Ob	5	11.3	73.0	72.8	64.0	24.8	86.6	39.5	89.2	60.5	92.7	47.6	16.4	....	....	....	....
Oc	4	8.9	73.9	73.9	66.0	23.7	85.8	37.6	89.6	62.0	91.9	48.5	16.9	....	....	....	....
Od	1	8.0	74.8	73.5	67.5	23.2	86.1	36.6	90.7	62.7	91.8	49.0	17.5	....	....	....	....
O (all)	14	9.9	73.4	73.3	65.5	24.2	86.2	38.1	89.7	61.4	92.3	48.2	16.8	9	22	20	30
P	6	11.0	79.1	68.0	71.0	21.7	90.0	36.0	97.5	54.0	95.0	54.0	13.7	15	20	17	65
Oaa	10	9.6	80.6	75.8	73.9	22.7	87.1	35.8	96.4	69.6	93.6	51.7	14.6	....	....	....	....
Obb	4	10.9	81.2	75.3	74.4	23.0	87.0	36.3	97.4	69.9	93.8	49.9	17.3	....	....	....	....
Occ	3	9.3	82.5	70.0	74.0	25.1	83.1	38.1	99.0	69.4	90.7	46.8	19.7	....	....	....	....
O (all)	17	9.9	81.4	73.7	74.1	23.6	85.7	36.7	97.6	69.6	92.7	49.5	17.2	3	35	34	50
BD	14	9.9	82.7	......	74.0	21.0	46.0	20.0	94.5	71.0	57.6	44.2	10.8	0	20	20	30
BW	15	9.1	82.7	......	74.0	21.0	87.6	12.6	94.5	71.0	88.0	75.0	3.9	0	20	20	25
DD	3	8.3	87.6	......	85.0	18.8	98.0	6.0	103.0	82.0	100.0	25	1.5	6	17	16	81
EW	7	8.3	88.5	......	84.5	13.0	99.0	6.0	101.0	84.0	100.0	93.0	1.2	15	20	17	60
CD	9	8.0	88.8	......	86.0	16.0	70.0	35.0	103.0	84.0	70.0	35.0	24.7	5	2	20	54
GW	5	8.6	91.5	......	86.1	23.3	99.0	6.0	109.0	85.0	100.0	93.0	0	48	21	11	54
FD	12	8.3	92.2	......	88.5	12.1	99.0	6.0	103.0	87.0	90	20	1.1	11	19	17	30
D	1	6	82.9	67	76	20	65	20	97.7	70.7	70	45	4.0	63	11	4	75
O	2	11.5	74	69	65	16.2	84.5	44	90.4	60	96	44	17.9	60	5	2	0
P	4	9.4	78.7	60	68.2	23.5	72	38	94.7	68	78	34	13.0	42	7	4	0

Dates of beginning were: AD, AW, BD, BW, CD, CW,—7/25; EW, FD,—7/31; O (all),—8/2. (1917 above, and 1919 below black line.)

For 1916, the hibernated generation showed first pupation on April 13 and last emergence June 17. The mean substitution-quotient was 269 and the mean *alpha* value was 52° F. The first generation began pupating June 20 and ended September 11, with a mean quotient of 266 and a mean *alpha* value of 50.4° F. The second generation consisted of 46 individuals (August 28 to September 27) divided into two groups: 30 with a mean of 246, and 27 with a mean of 277. The mean *alpha* value is 50.9° F.

For 1917, the hibernated generation (first pupation April 3, last emergence June 21), at Olney, gave a mean of 276 and a mean *alpha* value of 51.7° F. The first generation (first pupation June 27, and last recorded emergence August 6) gave a mean of 249. The second generation mean was 254 for 7 individuals. The mean *alpha* value was 50° F.

The mean of all generation means for the Olney data was 266 (substitution-quotient). Omitting third generations and the 1917 second generation, it was 272.

The substitution-quotients for the Champaign data with the number of individuals shown in parenthesis were as follows:

Summer	1917	(15)	267
Summer	1917	(5)	271
Spring	1918	(26)	275
Summer	1919	(2)	263
Summer	1919	(4)	272

The mean substitution-quotient, when the different generations and experiments on different generations are considered separately, is 266; with the third generation omitted, it is 270. The mean *alpha* value is approximately 51.0° F. The lowest value was 49.8° and the highest was 52.5° (at Olney) and 52.9° (in a variable-temperature experiment). These *alpha* values have *no physiological significance*. They are merely important in calculation work. The value is fixed by the ratio between velocities at high temperatures and those at low.* The actual threshold is lower, probably as much as 9° F.; development drops off slowly at the lowest temperatures.

Variation in the substitution-quotient is illustrated by a comparison of the two groups of 1915 pupae. Those appearing on May 14 and emerging June 4 (time 21 days) had a quotient of *287*; while those appearing August 17 and emerging September 3 (time 17 days) had a quotient of *245*. A comparison of Figs. 21 and 22 shows that the distribution of temperature and humidity is about the same for the mass of readings. Very radical changes in the equal-velocity lines would be necessary to make the quotients alike. The velocity curves (see Fig. 20) were identical. The standard time (mean velocity per day divided into

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*Variation in the *alpha* value may be illustrated as follows: Through the two natural groups of dots on Fig. 17, draw two lines (for example, one from H 45% T 88° to H 75% T 67°, and the other from H 35% T 96° to H 70% T 50°); plot any two velocity values crossed by each line against the corresponding temperatures on the scale, and produce the line joining these two plotted points to the temperature axis; note the *alpha* values thus obtained.

270) is 21.7 days for the May lot and 20 days for the August lot, the observed times being 21 and 17 days respectively. No modification of the velocity chart consistent with the experimental or phenological work will correct all these differences. The cause of the differences is to be sought in other conditions and will be taken up later in connection with effects of temperature variability.

TABLE XIX. *Pupae at variable temperatures.*

Designation.	No. of adults emerging.	No. of days.	Mean temperature.	Mean humidity.	Base temperature.	Elevation in degree.	Base humidity.	Depression in %.	Max. temperature.	Min. temperature.	Max. humidity.	Min. humidity.	% Failure to pupate.	Total individuals.	Total pupae.	% Pupa mortality.	Evaporation cc. per day.
HNV8-14	1	42.0	52.7	90	53.6	1	93	3	57	52	95	89	...	...	...	...	0+
HNV16	3	47.0	53.8	90	53.6	1	93	3	55	52	95	89	...	...	...	...	0+
HNVall	4	44.5	53.3	90	53.6	1	93	3	56	52	95	89	30	17	12	66	0+
VNV	1	28.0	57.1	97	55.0	4	99	6	59	51	100	93	...	...	...	...	0+
VNV	3	19.6	60.5	97	63.0	4	99	6	67	54	100	93	...	...	...	...	0+
VNV	4	16.5	62.9	97	64.0	4	99	6	68	57	100	93	...	...	...	...	0+
VNVall	8	21.4	60.2	97	60.7	4	99	6	64	54	100	93	47	24	13	38	0+
RLLNV	7	30.7	56.0	97	55.0	4	99	6	59	51	100	93	0	13	13	46	0+
RLRNV	5	17.7	60.8	97	60.0	4	99	6	63	51	100	93	16	6	5	0	0+
RMRNV	7	17.5	62.4	97	61.4	4	99	6	65	57	100	93	23	13	10	30	0+
RURNV	0	.....	68.0	97	64.0	4	99	10	70	62	100	93	0	17	17	100	0+
SNV	9	8.5	84.5	97	82.5	5	98	6	87	81	100	92	54	39	18	50	0+
ZNV	10	8.9	77	97	76	4	98	6	79	75	100	92	23	22	17	41	0+
VNV	1	103	51.0	90	50.5	4.0	93	3	52.5	50.2	95	89	...	...	...	...	3.0
203*DK*	1	10	77	40	75	8.0	45	10	80	73	46	35	89	18	2	50	....
HID	1	33	58.7	50	57	4.0	55	10	61	56	60	40	...	...	...	...	6.4
B*DK*	15	11.6	81.5	60	80	4.0	65	10	82	79	65	50	50	32	16	6	....
BTP	2	10.0	82.4	60	80	4.0	65	10	84.2	80.6	65	55	0	3	3	33	.0
BADa	8	10.8	83.0	35	81.7	9.5	40	10	91.2	80.4	40	30	56	22	10	20	9.9
BDa	14	10.6	83.0	50	81.7	9.5	55	10	91.2	80.4	55	45	73	30	15	7	8.8
BMa	10	10.4	83.0	60	81.7	9.5	65	10	91.2	80.4	65	55	41	27	16	38	6.9
BWa	7	10.4	83.0	70	81.7	9.5	75	10	91.2	80.4	75	65	45	22	12	42	6.7
BADac	9	10.3	83.0	25	81.7	9.5	30	10	91.2	80.4	30	20	38	21	13	31	10.4
BADb	7	10.6	83.0	35	81.7	9.5	40	10	91.2	80.4	40	30	52	21	10	30	8.1
BDb	8	10.2	83.0	50	81.7	9.5	55	10	91.2	80.4	55	45	40	20	12	33	10.6
BM	5	10.8	83.0	60	81.7	9.5	65	10	91.2	80.4	65	55	70	20	6	16	8.1
BWb	5	10.7	83.0	70	81.7	9.5	75	10	91.2	80.4	75	65	75	24	6	20	13.2
BWWb	0	.....	83.0	90	81.7	9.5	98	18	91.2	80.4	100	72	100	24	0	...	11.3
203*DK*	12	9.1	83.0	60	80	8.0	65	10	88	78	66	55	25	16	12	0	....
BWc	3	9.3	83.0	70	81	9.3	75	10	88.0	80	78	65	80	25	4	0	7.0
BWWd	8	.....	80.8	90	79	8.3	98	18	87.6	78.3	100	72	45	20	8	0	10.1
BWd	3	11.7	80.8	70	79	9.3	75	10	87.6	78.3	75	65	44	9	5	40	70
Oa	6	18.5	64.1	74.7	57.6	21.2	86.1	36.2	77.6	52.8	93.9	49.8	...	...	...	...	18.5
Ob	4	17.4	65.5	74.4	58.5	20.9	86.3	37.5	78.3	54.7	93.4	50.2	...	...	...	...	18.2
Oc	2	12¾	71.7	73.1	64.4	24.0	85.8	38.8	87.3	61.1	92.3	47.4	...	...	...	...	25.9
Od	1	13.0	73.0	71.6	65.5	24.3	85.1	39.1	88.6	61.6	92.1	45.6	...	...	...	...	22.6
Oe	8	12.0	73.4	72.5	66.3	23.8	85.1	38.7	90.1	62.7	92.2	46.6	...	...	...	...	25.0
Of	3	12⅔	74.8	71.4	67.1	23.4	83.7	38.0	91.2	63.9	91.4	46.7	...	...	...	...	21.0
Og	4	12.5	75.8	72.0	68.2	22.9	82.2	38.1	90.6	64.7	89.4	45.2	...	...	...	...	22.2
O (all)	28	.....	....	....	....	....	....	....	....	....	.....	....	20	50	40	30	....

Above first line; first generation 1917.

Above second line; hibernated generation 1918.

Air velocity 8 mm. per sec. except 203DK, BDK which was O+. The italic capitals indicated light condition.

Below second line; hibernated generation 1918, out of doors, segregated into temperature classes. Air movement was not recorded.

(B) ADULT MOTHS.

No experiments were successfully performed on adult moths. The difficulties are great, and little work was attempted. Isely and Ackerman ('23), however, have done some important work. The maximum oviposition at Bentonville, Ark., was on the second, third, and fourth days after emergence, and did not occur except in very weak light.

(C) EGGS AND LARVAE.

Incubation Period. (Data by C. S. Spooner.)

The only complete series of experiments on incubation was that carried on in unventilated phials where the humidity ranged high, as shown by precipitation on the glass walls at the time of many observations, and was arbitrarily taken to have averaged 95 per cent, though there were no readings (Table XX). Data plotted (Fig. 23) for other humidities are based on a limited number of readings. The *alpha* values graphically estimated to be between 50° and 52° F., were approximately the same as those calculated by Spooner. The deviation from the straight line is fairly well indicated at the lower temperatures and also somewhat uncertainly suggested in the neighborhood of 91° F.

These velocities in Fig. 23 are based on an arbitrary total of 161 taken from Glenn's Table I. When placed on the pupal velocity chart, they conform quite closely to the pupal velocities. Bringing them into conformity with the pupal velocities does not shift them more than is to be expected in smoothing. This conformity is also indicated by a comparison of Glenn's velocity (reciprocal) curves for incubation and pupal development. A review of Glenn's data (shown in his Table I), by the Von Oettingen method, gives 155 as the substitution-quotient when 51° F. is used as the *alpha* value. This makes the relative pupal velocities approximately 10/17 of the relative egg velocities. When pupal velocities are reckoned on the basis of 289 as the substitution-quotient, the egg velocities should be reckoned on the basis of 172 for the constant-temperature experiments and 160 for the weather-variable temperatures. This indicates that temperature variability has the same effect on eggs as on pupae. For variable-temperature experiments, 161 proved to be the correct substitution-quotient.

The 95 per cent humidity series calculated on 160 conforms very well with the pupal velocities calculated on 270. The aberrant values at the high temperatures are possibly due to too infrequent observation of progress before the experiment began. Evidently, in these cases there had been progress before the eggs were placed at experimental temperatures. Since these abnormally high velocity values occurred in the 95 per cent set, their presence in the others, where in some cases the humidity was in doubt, was not considered serious. The *alpha* value as determined for the 95 set by the Von O. method is 52.4°, and the substittuion-quotient is 157. Experience with pupae indicates that the actual weather combinations of temperatures and humidities should give about 51.0°. as the

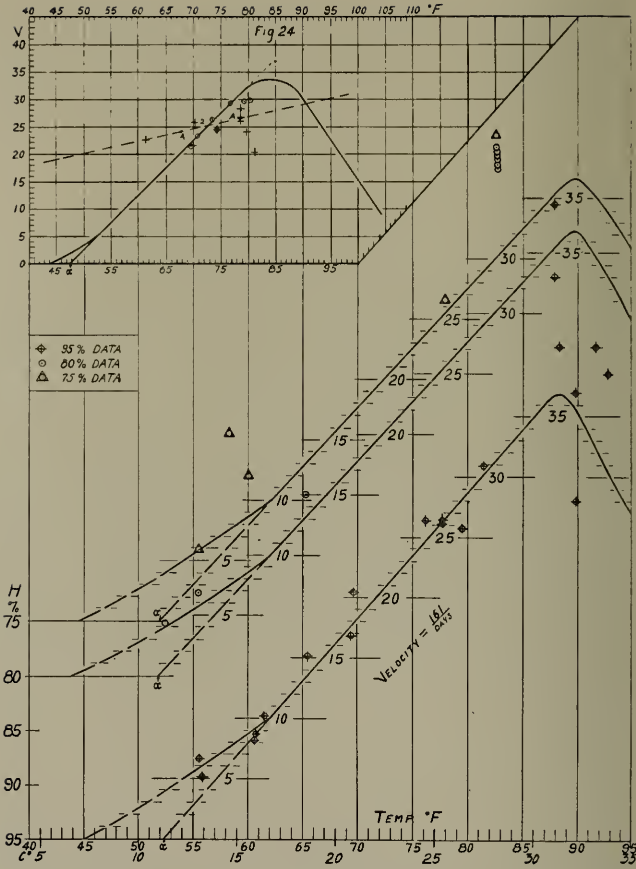

Fig. 23. Velocity curves for the incubation of eggs under approximately constant temperatures, plotted values being obtained by dividing the mean number of days into 161. These are drawn above the humidity shown at the left for the beginning of each curve.

Fig. 24. See explanatory note on opposite page.

alpha value and, therefore, a larger and presumably more nearly correct product of time and temperature above *alpha*. It will be noted that the maximum velocity appears to be at a higher temperature than in the case of the pupae. This introduces a slight error when the pupal velocities are used for incubation at high temperatures. In Fig. 23 this might have been corrected by adding 2 to each velocity value for all temperatures above 89° F. Such a correction is unnecessary in prediction work, as the duration of such high temperatures is usually very short.

Time from Hatching to Leaving the Apple. (Data by C. S. Spooner.) Newly hatched larvae were placed in small cuts in apples. All experiments at 53° and 83° F. were failures. The number successful at each temperature was small (Table XXIII). The small series suggests a relatively smaller effect of temperature increases than is shown by the other stages. One item (temperature 81.0° F and time 32.1 days) was omitted in the calculation of time-temperature products, as its longer time suggested that 81.0° may be above the straight-line limits. The other temperatures and velocities were averaged together in two groups. The lower temperature, with a mean of 67.9°, gave a mean velocity of 24.1. The higher temperatures, with a mean of 78.8° were associated with an average velocity of 26.3. These two points are shown and marked A on Fig. 24. A continuation of the line passing through them would reach 0 velocity at about 40 degrees below the Fahrenheit zero, making it obvious that reasonable thresholds cannot be determined from such a few data with so much variation.

Glenn's data, however, proved much more workable. A comparison of the tangents and *alpha* values of Glenn's reciprocal (*i. e.,* relative velocity) curves for the pupal and larval periods shows that the pupal velocity is 2.8 times that for the larval period. Thus, when the substitution-quotient for the pupa is 270, that of the entire larval period should be about 756. Glenn found an average of 673 "degree-days" for this period. An examination of his Table III, by the Von Oettingen method, gives an *alpha* value of 47.5° F., an uncorrected sum of 763 "degree-days" and a substitution-quotient of 744. A curve was drawn (see circles in Fig. 24) to fit Glenn's data when his reciprocals were multiplied by 763 and plotted on mean temperatures above 47.5° for the larvae from hatching to pupation, and the upper curvature was copied from the curve for the larval development after hibernation (see Fig. 26). Velocities were read from this trial curve and applied to Glenn's original data, in order to correct the upper curvature. (When the upper straight-line limit is too high, the calculated time becomes smaller as the number of high tempera-

Fig. 24. Curve for velocity of development of the larva in the apple. The curve was estimated from experimental data (shown by crosses) and from Glenn's observations shown by circles. The dotted peak is for hibernated larvae under average weather conditions. The velocities are based on dividing the mean number of days into 650 for the period from hatching to leaving the apple, and into 750 for the period from hatching to pupation. The latter figure was obtained from Glenn's corrected temperatures by applying the Von Oettingen method.

ture readings increases, and *vice versa.*) Various curves were thus tried until the velocities shown in Table V were found to give fairly consistent results. The use of the velocities shown in Table V gave calculated time for Glenn's data consistent with the average actual time. There was, however, much greater variation than in other stages. This has been discussed in PART ONE and PART TWO.

TABLE XX. *Showing conditions and incubation period of eggs under approximately constant temperatures.*

The original data are from experiments by C. S. Spooner.

Designation.	No. of individuals.	Year.	Generation.	Mean time to hatching days.	Mean humidity. %	Mean temperature. °F.
R L L	9	1919	......	......	99	46.2
R L R	10	1919	......	......	95	48.0
V N V	10	1918	......	......	95	48.9
V N Vc	12	1918	......	......	95	48.9
R t r	1	1919	......	......	80	51.8
R W	7	1919	......	......	85	52.2
R D	3	1919	......	......	45	52.2
R	1	1919	3rd	37.0	80	52.3
R M	8	1919	......	......	72	52.5
R W	8	1919	......	......	85	53.1
R M	2	1919	......	......	72	53.3
R D	5	1919	......	......	45	53.8
H I D	1	1919	3rd	27.0	75	55.4
H I W	6	1919	3rd	24.1	92	55.4
H I M	9	1919	3rd	23.0	80	55.4
H I N V	1	1918	3rd	30.2	95	55.9
H D	2	1919	1st	13.5	60	57.7
H D R	3	1919	1st	10.5	75	58.1
L N V	4	1918	3rd	19.5	95	60.6
L N V	3	1918	3rd	18.4	95	60.7
L N V	5	1918	3rd	15.7	95	61.5
K W	4	1918	3rd	10.0	90	64.4
A W	18	1920	2nd	10.8	82	65.1
A W	3	1920	2nd	10.8	92	65.5
A N V	10	1918	3rd	9.6	95	69.3
A N V	7	1918	3rd	7.9	95	69.6
B. N. V	2	1918	3rd	6.2	95	76.1
B D	3	1918	3rd	6.3	50	77.0
B. N. V.	4	1918	3rd	6.1	95	77.7
B N V	2	1918	3rd	6.9	95	77.7
B D	6	1918	3rd	6.6	50	78.0
B N V	2	1918	3rd	6.1	70	79.5
B N V	3	1918	3rd	5.3	95	81.4
B N V	3	1919	......	......	95	82.0
B W	9	1920	2nd	3.8	80	82.5
B W	12	1920	2nd	3.7	80	82.5
B W	15	1920	2nd	3.8	80	82.5
B D	15	1920	2nd	4.1	43	82.5
B M	14	1920	2nd	4.1	75	82.5
B W	7	1920	2nd	3.9	80	82.6
B W	11	1920	2nd	3.8	80	82.6
B W	10	1920	2nd	3.9	80	82.6
Q N V	2	1918	3rd	3.5	95	87.8
Q N V	2	1918	3rd	3.1	95	87.8
N N V	1	1918	3rd	4.0	95	88.2
M N V	3	1919	......	......	95	89.1
N N V	3	1918	3rd	4.4	95	89.8
N N V	4	1918	3rd	4.6	95	89.9
M N V	13	1919	3rd	4.0	95	91.6
M N V	1	1919	3rd	4.2	....	92.8

These velocities, when used to calculate standard time for the period in the apple from Glenn's Olney data, were divided into 650, which was regarded as an approximately correct substitution-quotient, though the average time calculated on that basis was 1.3 per cent higher than the actual time. (See Table XI.)

A substitution-quotient of 100 was tried for the time in the cocoon. This gave an average calculated time 0.4 per cent lower than the average actual time. When 750 was tried for the total larval life, it gave a mean calculated time 1.6 per cent higher than the actual average time (Table XI). A substitution-quotient of 738 would make the average calculated time agree with the average actual time for Glenn's data. In view of the small series of observations and the striking variation in time, it was deemed unnecessary to change the quotients used.

It will be noted that 750 and 738 are materially smaller than the 763 used in plotting Glenn's data (circles Fig. 24). This is to be accounted for by the fact that the period of the stage under variable temperature is longer because of the inclusion of temperatures at which development is slower or even at a standstill. Glenn's corrected sum calculated on this basis was 744. His correction, which amounted to 2.5 per cent for mean temperatures between 68° and 78° F., apparently should be 3.4 per cent. For the higher temperatures there are even greater differences between the substitution-quotient and the uncorrected sums.

Turning again to the meagre experimental data, to consider them in the light of the results with the Olney records, we find them in keeping with expectations based on other stages. When plotted on 650 as the substitution-quotient, the curve should fall a little below the curve for variable temperatures, because constant temperatures give slightly slower development. (This difference amounted to 7 per cent in the case of the pupae.) Since the experimental data are so meagre, all are plotted on a 650 basis, and only mean points are shown. With the exception of the 81° point, all data are in the straight-line limits (where means are correct). The 81° point, apparently, is only slightly outside. The mean value of all experimental temperatures and all velocities calcuated on the 650 basis falls on 74.2° F. and velocity 24.65 (see Fig. 24). The variable-temperature velocity line passes through 26.7, and an increase of 8 per cent places the mean of experimental data approximately on the line which is within the range of expectations. The marked variability of the experimental data is, in part, due to differences in kinds of apples (see Table XXI).

Hibernated Larvae.

It has not been possible to make a careful investigation of the period of dormancy, commonly called hibernation, into which the mature larva of the codling moth lapses in the month of August or even earlier, and in which it remains until it has passed the winter or has received special treatment in the laboratory. Many experiments were tried, but the results were inconsistent.

In a large series of experiments on the length of the pupal stage conducted during the summer of 1917, very few of the larvae collected after July pupated; of those collected on August 18th, only 15 per cent pupated; and none of those collected later. The larvae failing to pupate in the August experiments, together with those collected early in September, after being left until October 19th under the experimental conditions supposedly suitable for pupation, were subjected to various treatment.*

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* Stocks used in the experiments on the length of the larval and pupal periods received better treatment. See pp. 374-380.

TABLE XXI. *Showing conditions and period of growth of larvae in apples under approximately constant temperature. Experiments by C. S. Spooner.*

Designation	Larvae in apple.				Time spent in apple. Days.	Mean temp. ° F.	Kind of apple.
	Into apple 1st observation.		Out of apple.				
L	9/20	10a	10/13	10a	28.8	61.4	Red crab
A	9/10	9a	10/3	11a	29.7	70.0	Maiden blush
A	9/10	9a	9/27	9a	25.0	70.2	Duchess
A	9/10	9a	9/27	9a	25.0	70.2	Red crab
B	9/10	9a	9/25	2p	23.2	78.5	Duchess
B	9/10	9a	9/25	2p	24.1	78.6	Duchess
B	9/2	8a	9/25	9a	24.0	78.6	Yellow crab
B	9/20	10a	9/29	9a	27.0	79.4	Maiden blush
B	9/10	9a	10/3	2p	32.1	81.0	Maiden blush

TABLE XXII. *Pupation and emergence as affected by temperature and humidity. Autumn larvae (1917) soaked in water for 20 hours, Nov. 14th, and placed at 75° F.*

Date started.	Lot used.	Temperature degrees F.	Humidity Per Cent.	Evaporation.	No. of larvae.*	No. of pupae.	No. of adults.	Dead larvae. Per Cent.
9/8	AD	65–85	50	High	16	4	2	75
9/24	AM	65–85	75	Low	13	0	0	100
9/8	BD	75–95	50	Low	12	0	0	100
9/8	BW	75–95	85	High	10	0	0	100
9/11	CD	85–105	40	High	13	0	0	100
9/8	DW	85–105	95	Low	7	0	0	100
9/10	EW	85–105	95	Low	10	0	0	100
8/23	JD	64	44	High	19	9	9	57
8/21	JM	64	80	Low	18	6	4	67
9/9	MD	78	35	High	14	0	0	100
8/23	MW	78	95	High	17	4	4	77
9/5	MM	78	65	Low	12	0	0	100
9/13	RNV	40–75	#	None	9	1	1	89
9/22	RNV	40–75	#	None	19	11	7	42
8/29	SD	69–82	(Dry)	High	19	0	0	100
8/27	SM	69–82	(Moist)	Medium	17	0	0	100
8/29	SW	69–82	(Wet)	Low	12	0	0	100
9/11	TH2	85–95	60	High	22	1	0	96
9/11	TI2	85–95	60	Medium	19	0	0	100
9/11	TL2	85–95	60	Low	14	0	0	100
9/22	TH3	85–95	60	High	14	2	2	86
9/22	T13	85–95	60	Medium	10	0	0	100
9/22	TL3	85–95	60	Low	10	0	0	100

* No. of larvae alive after soaking for 20 hours. The dead were not counted here.

Six sets of about 20 larvae each, which were kept in conditions supposedly suitable for late summer pupation, all died. (a.) Three sets collected August 23d, August 26th, and September 19th, totaling 58 larvae, were held at a temperature of 87° F. and humidities of 80, 60, and 40 per cent, respectively. All larvae in the two sets at the lower humidities died by October 9th, while those in the moistest condition lived to January. There were no pupations. (b) A single set collected August 23d and kept at 90° F. and 55 per cent humidity all died by October 9th. (c) A set collected July 26th and kept at 46°—57° F. all died without pupation by November 14th. (d) A set collected September 10th and subjected to daily variations of temperature between 80° and 100° F. and a mean humidity above 90 per cent, all died by December 19th without pupation.

Five other sets of autumn larvae, which had been kept under conditions the same as the above six sets, were transferred on or before December 19th to an approximately constant temperature of 70°—75° F. and a 90 per cent humidity. (a) Larvae collected September 10th and held at a temperature with daily variation between 80 and 100° F., and a variable humidity with mean about 60 per cent, were transferred to 75° F. on November 20th; and all died by March 20th without pupation. (b) Others kept at 65° F. and 40 per cent humidity and transferred to 75° F. on November 25th, all died by December 19th, without pupation. (c) A set collected September 19th, kept at a temperature varying from 40° to 76° F. to February 15th, and then transferred to a constant temperature of 70° F., showed one pupa. (d) A set collected August 28th was kept at 77° F. and a humidity of 95 per cent until October 25th, and then transferred to 70° F. By March 19th, five had pupated, and the others had died. (e) A set kept at 62° F. and a humidity above 90 per cent was transferred to 70° F. December 19th. By February 15th, five moths had emerged, and the others had died. (Note: Larvae kept at 77° F. would not ordinarily pupate with the treatment described, but those in sets having been subjected to a low temperature might be expected to do so under ordinary conditions.)

Seventy-one larvae, collected between July 25th and August 18th and failing to pupate under the experimental conditions designed tor pupation, were kept 18-20 days below 60° F., being at 22° F. for 6 or 7 days, but failed to pupate when returned to the experimental conditions for pupation.

Four-hundred larvae, placed under conditions shown in Table XXII between August 24th and September 22d, 1917, and kept there until November 14th, were then submerged 20 hours in water and placed at 75° F. Those kept at temperatures below 65° F. and those kept at higher temperatures subjected to greatest amount of evaporation, pupated and emerged in greatest numbers. Representative data are shown in Table XXII.

For the spring experiments of 1918, 1919, and 1920, some of the hibernating larvae were kept at temperatures at or below 32° F. (freezing) for a day or more, but without effect on the number pupating when placed under favorable conditions. In general, no attempt to freeze the larvae was made. They were merely kept at temperatures near 50° F. (This temperature proved to be too high, and pupation results will be discussed later.) The stock usually reached a condition where pupation would take place between December 20th and January 20th, January 1st being an average date.

In the spring experiments, larvae given uniform treatment during the winter showed variation in the length of time to pupation at constant temperatures, regardless of the date of leaving the apple, the date of collection, and the conditions under which they were kept, either before or during the period of low temperatures. In 1920 a large series of larvae was collected, beginning August 16th and running through September 28th. They were kept at a temperature of 70° F. and humidity of approximately 45 per cent until September 23d; between this date and October 23d the temperature was lowered at 50° by steps, first falling to 59° only at night, and then being lowered to a constant 50° on October 8th, and finally to 50° on October 23d. A temperature between 50° and 52° was maintained until December 27th, when it was lowered to 37° and held between 35° and 37° until February 14th, when it was gradually raised to 48°, and on March 15th, to 72°. The larvae were then kept at 72° F. and 85 per cent humidity for observation as to time of pupation and emergence. Owing to apparent discrepancies in the time of pupation recorded by the assistant in charge of daily observations of this experiment, it was deemed best to use only the time of emergence, concerning which there was no doubt. Fig. 25 shows the distribution of emergence in May, 1921. The number of times the groups had spun cocoons, the dates of collection, and the relative humidities are indicated in the margin of Part A of Fig. 25.

There is apparently no consistency in the different numbers of times which the cocoons were spun in the sets of the same humidity and collecting date, nor is there any consistent relation to the moisture treatment during the hibernation period in this experiment. (Fig. 25.) The earliest individuals to appear are by no means consistently from either the "wet" or "dry" lots. The lots labelled "W" had been stored at humidities of 100 per cent and submerged in water once a month long enough to saturate the pasteboards and surround the cocoons with water. Those labelled "D" had been stored at 90 per cent humidity but had not been submerged at all. The lack of results from this submergence has been shown by Townsend to be due to the infrequency of the wetting. (There is an essential difference in the times of emergence if rainfall is heavy.)

The three emergence groups, when added together (Fig. 25B) and compared with Glenn's data on emergence, show main maxima corresponding with his main maxima; and an explanation of the variation in the time required to overcome dormancy (variations in the pupal stage are of a different nature) must be sought in other causes, such as heredity, conditions of the food supply, or weather conditions during autumn.

Field observers have stated that the initiation of dormancy in summer and autumn larvae is due to a temperature of 50° F. or thereabout. Two hundred and five larvae were collected in the summer of 1920 between July 22 and August 14 and subjected to temperatures varying from 39° to 54° F. These larvae were divided into four classes: (a) pupating, (b) failing to pupate, (c) escaping from the corrugated pasteboards, and (d) dying. Those dying and escaping were ignored; only those remaining alive in the pasteboards were considered as having been experimented upon. After those dying and those escaping were deducted, the

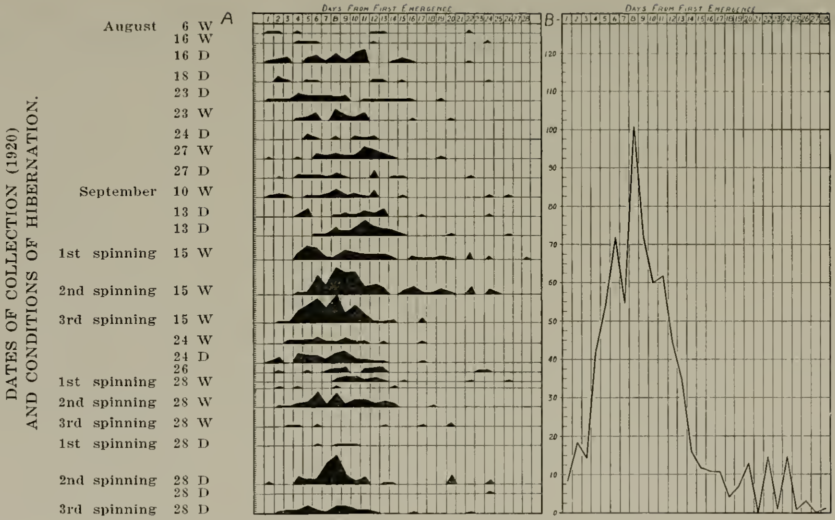

Fig. 25. Part A shows the order of emergence of moths beginning on May 3, which is number 1 of the top scale, and continuing for 28 days; the close scale at the left indicates number of individuals emerging each day in each set. The treatment of the larvae and the date of collection of each set is indicated at the left. W is wet (100% humidity and soaked in water once a month), and D is dry (90% humidity without any soaking in water). All were otherwise kept at the same temperature (72° F.) throughout.

Curve B represents the sum of all emergences shown in Part A. This curve shows three groups commonly recognizable in pupations out of doors, viz., a small group at 2 days, a very large one with its maximum at 8 days, and a somewhat drawnout group beginning at 20. Cf. Glenn's Charts 1, 2, and 3, noting pupation.

remaining 118 larvae (divided into 18 lots) were grouped as follows:

July 22d to 28th,	18 larvae,	17% failure to pupate.
July 31 to August 3d,	37 larvae,	38% failure to pupate.
August 7 to 8th,	28 larvae,	89% failure to pupate.

During the period July 22d to August 8th there had been no minimum outdoor temperatures below 57° F.; all larvae collected in that period, therefore, were experimentally subjected to temperatures below 50°, in order to make them comparable with larvae collected on August 9th and 10th, when outdoor temperature in the early morning fell to 52° F. The lots collected August 9th to August 14th (35°) showed 88 per cent failure to pupate. These experiments showed no indication of cool night effects but rather indicated a seasonal increase in the number of individuals failing to pupate, beginning about August 1st, regardless of minimum temperatures.

The effect of summer and autumn rainfall on the length of time to pupation of hibernating larvae is suggested by the following data: *Case a:* One hundred and eight larvae collected August 20th to September 12th, 1919 (kept at a temperature of 70° and humidity of 40 per cent until August 30th if collected before that date), were subjected to temperature near 32° F. and humidity of approximately 100 per cent until January, when they were placed in conditions favorable to pupation. Between January 26th and February 24th, only 5 larvae, or approximately 3 per cent pupated. The average time to pupation was 19.3 days at 83° F. and 21.5 days at 63.5°. *Case b:* Larvae collected October 20th of the same year (1919) were treated exactly the same as those in *Case a*, and 60 per cent of them pupated, the length of the prepupal stage being as little as 11 days and averaging 17.8 days at 83° F. The pupal life was about 10 per cent shorter than in the case of the sets collected earlier. The differences between those collected on or before September 12th and those collected on October 20th were thus very striking, both in the per cent pupating and in the time to pupation, when the larvae were placed under favorable conditions. The differences lie in the time of emergence from the apple, and in the weather conditions between September 12th and October 20, 1919. There was very little rain during the period of collection in August and the first twelve days of September, but during the latter part of September and the first 20 days of October there were 5 rainy periods and great variations in temperature (26° to 96°). These observations do not show whether it was the condition of food, temperature, moisture, or variability which produced the result. They serve, however, to indicate the necessity for year-round experimentation.

The calculation of velocity values for larvae which had passed the winter under known conditions afforded unusual difficulties because their pupation showed essentially the same seasonal curve as the emergence of moths (Fig. 25). Larvae kept in the laboratory at temperatures of 40°-

50° F. during October (and November and December if desired) and then put under proper conditions, will pupate in the latter part of November, in December, or during January or February. January 1st is about a mean date for pupation outdoors, but the variation is so great as to leave no scientific basis for a starting point in calculations at the present stage of knowledge. January 1st was used by Glenn as a starting point for summing larval temperatures. The time to pupation at 85° (or any other suitable temperature) after dormancy is broken, apparently varies with the length of the dormant period at all temperatures above freezing, if not lower. Townsend demonstrated that changes took place at 32° F. The 1918 experimental series was largely useless for this purpose because they were stored at higher temperatures. The temperatures should be near freezing in the case of larvae designed for determining the time to pupation after dormancy is broken. The 1919 larvae (*Cases a* and *b* described on p. 410) were important in this connection because they were kept at approximately 32° F. for several months and then put into conditions for progress in the latter part of January. These fell into three groups, the first pupating with about 285 accumulated degrees, the second with about 535 accumulated degrees, and the third with about 716 accumulated degrees,—each reckoned above 50° F, as the starting point. (These are uncorrected sums of temperatures obtained by the method which this paper aims to supplant for all purposes except rough estimation.) All hibernated larvae on which data are available fall generally into these three groups, the last being most variable. (Cf. Fig. 25 and Glenn's Charts 1, 2, and 3, showing a small early group, a large middle group, and a final prolonged group of pupations.) All the experiments used in the calculation of relative velocities were constant-temperature ones, and the sum of temperatures above fifty is much more significant for them than for variable conditions. On this basis, a provisional set of velocity curves were constructed (Fig. 26), and a provisional larval-velocity chart was drafted (Fig. 27). Glenn's data beginning January 1, 1916, were worked over, using all temperatures above 43° F., though only those above 44° (the temperature suggested by the experimental data) were considered as affecting development.

The 1918 series included many larvae that pupated. These had been stored at 48° F. or lower, on the assumption that the "threshold" was 50° F. There was, however, some variation in temperature, with the result that when the last experiments were started the larvae were nearly ready to pupate.* Baumberger and Townsend also found that this was a very detrimental temperature. The three groups (early, middle, and delayed) were strikingly shown in nearly all cases, but they seemed unduly crowded together in later cases, suggesting that prolonged mild temperatures tend to reduce the differences between the groups. The earlier and larger groups were used for estimating velocities. This was done by dividing the time into the average sum of temperatures above 50° F. for

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* For this reason the tables of 1918 data are not given here. The other tables, which are given, do not show the three-group pupation.

each group. By this method, the velocity tends to remain constant for any one temperature, but the sum changes. This variation in the sum is evidence that the developmental total is not the same for different individuals; that is, the developmental processes, especially where enzymes are concerned, require varying amounts of metabolism to complete the stage. For example, 280 larvae which pupated at various approximately constant temperatures ranging from 53° to 80° were in three successive groups. When an approximately constant velocity value was obtained by dividing the mean substitution quotient for the group by the time (in days) for each individual at a constant temperature, that velocity value was used for that temperature in making the equal-velocity chart. This calculation was based on the fact that all groups at constant temperatures within the straight-line limits showed a fairly uniform rate of reduction of the time-temperature product, as illustrated in Table XXIII for two collections of larvae wintering out-of-doors.

TABLE XXIII. *Differences in "Pre-pupal" Time-Temperature Products (above 50° F.) for Two Collections of Hibernated Larvae Pupating in Three Successive Groups (Spring of 1920) in Constant-Temperature Experiment.*

Groups of pupations.	1st	2nd	3rd
Assumed Maximum Product for "Pre-pupal" Period, as of January 1st.............	300	525	675
Mean Product for Larvae Collected March 3d............	238	439	602
Mean Product for Larvae Collected March 22d...........	155	245	390
Approximate Per cent Reduction of Product to March 22d	48	53	42
Approximate Per cent Reduction of Product March 3rd—22d	27	37	30

A large series of calculations of *alpha* values, taking the means of the three groups separately, showed no conclusive difference in the "threshold". Some apparent differences were rendered questionable by irregularity of time and small numbers of temperatures within the straight-line limits. There is a suggestion of a slightly lower "threshold" for the later groups, but this is not borne out by calculations based on an assumed *alpha* value of 50° F. For practical purposes the assumption of the same threshold for all three groups is the simpler.

On the basis of 300, 525, and 675 as the respective time-temperature products above 50° F. for the different groups, roughly segregated for

1919 and 1920 larvae (see Tables XXIV to XXVII), the curves shown in Fig. 26 were drawn, and on the basis of these curves the velocity chart (Fig. 27) was constructed. It is a provisional attempt, but it summarizes our experience with hibernated larvae. The method described for the pupae was used with this chart. All two-hourly readings of temperature and humidity above 40° F. from January 1st to the first pupation were entered on the chart. A curve was drawn with *alpha* as 47.5° and the recorded temperatures were corrected; the substitution-quotient proved to be 197 for the first pupation; mean for the first thirty, 227; first maximum, 265; mean of first modal group, 283; second maximum, 441; mean of second modal group, 443; mean of third modal group, 725; mean of last group to first blank day, 758. The figures are quite close to those predicted from the constant-temperature experiments. It was not possible to check over other years, as hygrothermograph records were wanting.

TABLE XXIV. *Hibernated larvae at approximately constant temperature, 1918.*

Designation.	No. of individuals.	Larval life in days.	Mean temperature.	Mean humidity.	Maximum temperature.	Minimum temperature.	Maximum humidity.	Minimum humidity.	Evaporation in cc. per day.	Date		Lot
										Begun.	Last pupae.	
NDa	3	13	95	35	95	95	35	33	22.7	2/14	2/26	V
NMa	2	12.5	95	52	95	95	52	52	12.1	2/14	2/28	V
NWa	2	12.25	95	65	95	95	65	65	10.9	2/14	2/26	V
NNva	14	13.2	95	30	95	95	30	30	+0	3/23	4/15	I
NW	4	11.2	95	65	95	95	65	65	27	3/25	4/5	V
Vnv*	13	26.0	49.1	99	57	44	100	98	0+	4/1	5/9	V
HIDa	1	25	52.7	50	53	50	55	45	5.5	4/2	......	IV
HNV	3	39.7	52.6	97	53	50	99	95	....	4/2	5/12	IV
HMa	7	48.0	52.7	50	53	50	60	45	8.5	4/2	6/1	IV
HWa	1	39.0	52.7	90	53	50	100	80	9.9	4/2	5/11	IV
KM	2	16.5	61.7	75	62	59	80	70	3.0	4/2	4/22	IV
MM	3	8.1	90.0	44	92	88	60	40	0+	4/2	4/13	IV
MAD	2	9.2	90.0	60	92	88	70	50	7.1	4/2	4/15	IV
MN	4	7.0	90.0	95	92	88	99	92	0+	4/2	4/11	
KD	14	19.3	62	60	63	60	65	55	4.0	4/6	5/15	IV
KW	21	17.2	62	95	63	60	100	90	2.9	4/6	5/7	IV
HD	18	50	53	60	53	51	65	55	36.7	4/11	6/12	III
LD	28	21	60.4	60	62	58	65	55	3.3	4/11	5/30	V
AD	31	15.5	69.5	50	72	68	55	45	7.0	4/11	5/23	V
AM	29	14.6	69.5	60	72	68	65	55	4.4	4/11	5/15	V
AW	37	14.6	69.5	70	72	68	75	65	4.4	4/11	5/11	V

Air flow was 8 mm. per sec. for all cages except AW, which was 10.

In working over these data, a new method was devised. The weather data were plotted on the chart only once; and the sum and mean were determined for temperature, humidity, and velocity from January 1st to May 20th, when the last larva pupated. The data were carried forward from day to day in tabular form. This saves time, but the other method with overlapping of plotting on the charts, generally has the advantage of showing the distribution of the two-hour readings associated with the various groups.

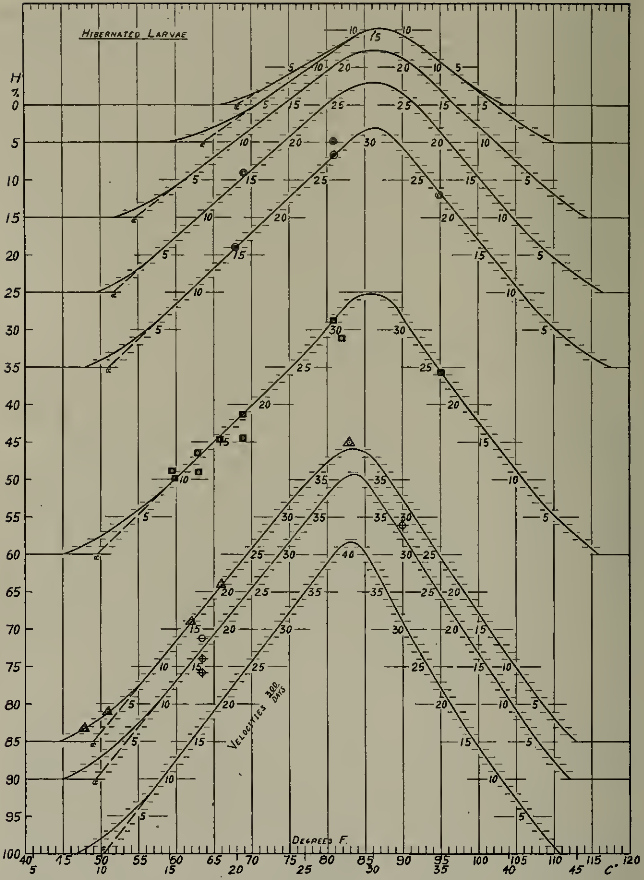

Fig. 26. Showing the data and velocity curves for the "prepupal" period of hibernating larvae. See Figs. 13 and 14 and explanations in text.

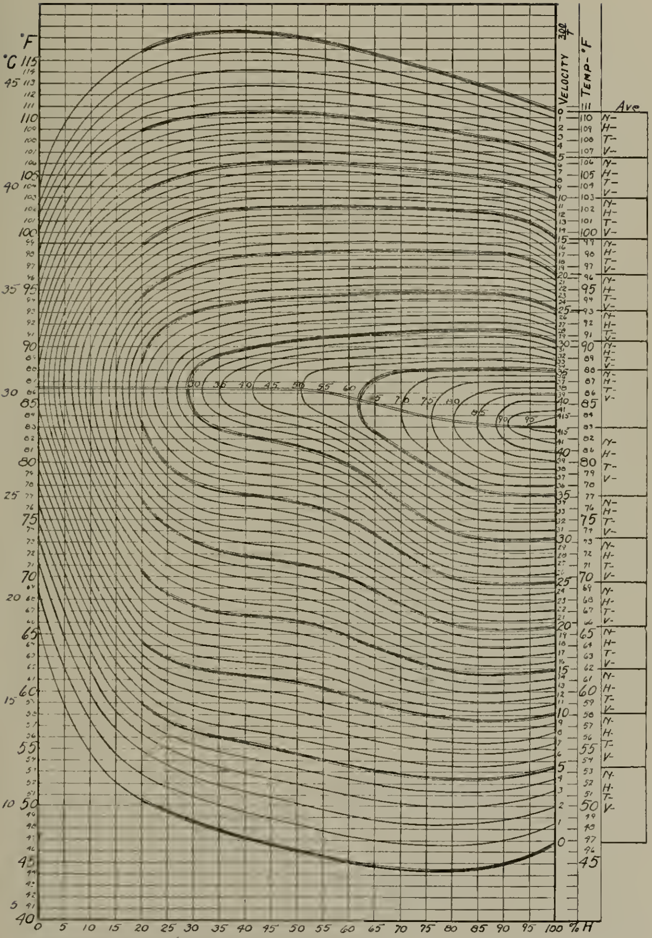

Fig. 27. Trial "prepupal" velocity chart for hibernating larvae (See explanations of Figs. 13 and 14.) The velocities must be multiplied by 1.125. (See p. 416.)

The sum of developmental units for the period January 1 to April 13 in 1916 amounted to 4,992 (after multiplying each velocity value by 1.125 to bring the angle of the velocity curve to 45°). This divided by 24 gives 208 as the substitution-quotient, which is as near as can be expected to the 197 for a first checking of the two methods. This difference is not surprising, for under treatment which did not differ, larvae in one case pupated when put at 85° F. or other temperatures suitable for pupation, as early as December 19, but in other cases did not pupate until March. In general, February 1st seems too early for most larvae.

TABLE XXV. *Hibernated larvae at approximately constant temperature, 1918 (continued).*

Air flow was 8 mm. per sec. for all cages.

Designation.	No. of individuals.	Larval life in days.	Mean temperature.	Mean humidity.	Maximum temperature.	Minimum temperature.	Maximum humidity.	Minimum humidity.	Evaporation in cc. per day.	Date		Lot
										Begun.	Last pupae.	
LM	29	18.3	60.2	75	62	58	80	70	4.2	4/17	6/3	V
LW	18	23.0	60.2	55	62	58	60	50	0.7	4/17	5/8	—
NDc	4	7.25	95	35	95	95	35	35	38	4/17	4/26	IV
NMc	2	6	95	50	95	95	50	50	19	4/17	4/24	II
NWc	14	8.7	95	65	95	95	65	65	13	4/17	4/29	V
NNV	13	8.4	95	95	95	95	95	95	......	4/17	4/30	V
M(A)D	6	13.4	90.5	30	92	88	40	20	8.0	4/18*	5/6	IV
MD	5	8.8	90.5	40	92	88	50	35	11.6	4/19*	5/1	IV
WW	10	10.6	90.5	52	92	88	60	45	4.1	4/19*	5/6	IV
ANcDk	8	15.7	90.8	60	92	88	65	55	16	4/23	5/16	—
HHung	9	9.4	54.3	60	56	52	65	55	33	4/25	5/19	III
HMb	7	7.0	54.3	50	56	52	50	50	6.0	4/25	5/10	III
HW	3	12.3	54.3	90	56	52	100	80	6.0	4/25	5/15	III
HIW	4	5.8	54.3	70	56	52	75	65	5.0	4/25	5/5	III
ID	6	4.5	54.3	50	64	52	50	45	5.8	4/25	5/9	III
HID	3	3.3	54.3	60	64	52	65	55	3.4	4/25	5/2	III
Vv	1	42	48.8	98	53	48	100	95	5.4	4/25	6/6	III
VSh.	19	4	49.0	56	42	60	90	60	......	4/25	5/20	III
VTP	1	1	48	90	54	42	90	90	......	4/26	4/28	V
MAD	19	8.6	91.3	29	92	89	35	20	15.3	....	......	
MD	8	8.4	91.3	37	92	89	40	30	11.7	4/27	5/8	IV
MM	12	10.3	91.3	44	92	89	50	40	9	4/27*	5/12	?
MW	11	9.0	91.3	51	92	89	55	45	7.4	4/27*	5/11	IV
MNv	11	8.0	91.3	95	92	89	100	90	0+	4/28	5/11	?
MWW	17	9.5	91	85	92	90	90	80	......	5/1	5/9	IV

* Submerged.

Townsend got pupation in November in a lot of 1923–24 larvae put in suitable conditions. While they were in-door stocks, there appeared to be no tangible reason for this early pupation. Obviously, winter phenomena are not understood; and, until they are, over-wintering probably can not be put on a scientific basis.

Prediction of the First Pupation of Hibernating Larvae. Our experience with the larvae of the codling moth leads to the conclusion that hibernation is concerned with two physiological conditions: (1) the true dormant period, and (2) the "pre-pupal" period, not as yet distinguishable from the dormant period, but concerned with the changes which lead to pupation. Late autumn larvae which pupate when put at 85° F. have passed the first phase of the process. Larvae may pupate, when put under proper conditions, in November, December, January, or February, or may fail to pupate as late as February. Attention has already been called to the fact that this leaves no scientific basis for a starting date, though January 1 is about average. However, to test the relations of hibernating larvae still farther, a table showing the velocity value for each degree Fahrenheit and each 5 per cent humidity was prepared from Fig. 27. (These velocities were multiplied by 1.125, as before.) The temperature above 43° F. and the corresponding humidity on even hours were transcribed from hygro-thermograph records made by W. P. Flint near Springfield in 1918. The beginning of development was assumed to be January 1. The velocities were then written opposite the combined temperature and humidity, and the developmental units were summed to the date of the first pupation, April 4. The developmental total, from January 1 to the first pupation, was only 3312 instead of 4992 as in 1916. In Flint's Springfield records for 1918 there were no temperatures above 43° F. in January, and temperatures in subsequent months were lower than in 1916. This makes evident that progress at low temperatures takes place, or that January 1st was not the proper date for beginning the calculation for this year. Both are probable inferences, and this trial of the 1918 data confirms the conclusion that we as yet have no means of determining the date at which the larvae pass from the true dormant phase to the "pre-pupal" phase. Accordingly, the table of velocities is omitted. The velocities for average weather conditions as shown on the omitted chart, how-

TABLE XXVI. *Hibernating larvae at approximately constant temperature. 1919.*

Designation.	No. of individuals.	Days to pupation.	Mean temperature.	Mean humidity.	Maximum temperature.	Minimum temperature.	Maximum humidity.	Minimum humidity.	Evaporation in cc. per day.	Date started.	Last pupae.
Anv	3	11.6	69.4	97	71.1	68.2	100	90	0+	5/2	5/17
BNv	2	7.0	80.8	97	81.5	79.7	100	90	0+	3/22	4/4
HW	8	36.2	60.6	85	63	57	90	80	5.5	3/20	5/5
HD	3	47	61.7	63	63	59	65	60	7.7	3/20	5/21
HDR	5	47	61.7	63	63	59	65	60	8.5	3/20	5/4
LD	1	30	66.1	57	67	65	70	50	3.0	3/24	4/24
LW	6	15.6	65.7	86	66.5	65	90	80	10.7	3/24	4/12
MD	0	....	90.1	35	91.0	89	38	20	36.0	3/20	....
MW	10	10.0	90.1	92	91	89	95	90	4.0	3/20	4/2
NS	2	7.0	93.6	97	94	93	100	95	0+	3/22	5/9
NW	3	9.8	95.1	70	96	93	79	60	9.0	3/22	5/4
ND	0	....	95.1	25	96	93	33	16	21.0	3/22	....
RRT	0	....	53.9	97	54	51	100	90	0+	2/15	....
RLRWn	0	....	52.2	97	53	51	100	90	0+	2/15	....
RD	0	....	52.2	40	53	51	44	35	5.3	2/15	....
RM	0	....	52.2	70	53	51	84	54	1.9	2/15	....
RW	0	....	52.2	90	53	51	94	85	0.6	2/15	....
SNV	3	12.5	88.7	96	89.6	86	100	92	0+	5/2	5/19
SW	2	12.0	85.0	85	86	84	100	80	7.0	3/20	9
SAD	0	....	85.0	50	86	84	56	34	15.0	3/20	....
SADD	0	....	85.0	40	86	84	46	25	17.0	3/24	....
TH	.....	....	81.2	70	81.5	79	72	68	15.4	3/20	4/1
TI	.....	....	81.2	70	81.5	79	72	68	12.9	3/20	3/30
TL	.....	....	81.2	70	81.5	79	72	68	8.4	3/20	4/8

Air flow 8 mm. per sec., except TH, TI, TL; these were 425, 109, 1.5, respectively.

TABLE XXVII. *Larvae at slightly varying temperatures; light effects.*

Designation.	No. of individuals.	Days to pupation.	Mean temperature.	Mean humidity.	Base temperature.	Elevation in degrees.	Base humidity.	Depression in %.	Maximum temperature.	Minimum temperature.	Maximum humidity.	Minimum humidity.	Date started.	Last pupae.
BAD	8	10.2	81.5	35	80.2	6.1	38	8	86.2	79.0	40	30	4/11	5/1
BD	36	9.9	81.5	50	80.2	6.1	54	10	86.2	79.0	56	44	4/11	5/1
BM	49	12.1	81.5	60	80.2	6.1	64	10	86.2	79.0	68	54	4/11	4/30
BW	43	11.3	81.5	70	80.2	6.1	72	12	86.2	79.0	76	60	4/11	5/14
203*DK*	2	23.2	81.1	50	80.0	5.7	52	10	85.5	78.6	55	42	4/18	5/17
BSh*DK*	16	11.8	81.5	50	80.0	5.0	47	10	85.3	78.6	55	42	4/23	6/6
Test Pup. B	4	4.1	79.9	50	79.5	3.6	52	8	83.1	77.9	55	44	4/24	4/30
Test Pup. V	1	1	....	......	....	......	.....	......	....	....	......	......	4/26	4/27
203*DK**	12	5.8	81.5	50	80	5.0	52	10	85.3	78.6	55	42	5/23	6/3
BADac	13	6.1	83.5	25	81.5	5.0	30	10	85.3	78.6	30	20	....	....
BAD	21	6.7	83.5	35	81.5	5.0	37	7	90	80.4	40	30	5/23	....
BD	12	8.3	83.5	50	81.5	5.0	52	10	90	80.4	54	42	5/23	6/6
BM	6	5.4	83.5	60	81.5	5.0	62	12	90	80.4	66	50	5/23	6/6
BW	12	7.7	83.5	70	81.5	5.0	72	18	90	80.4	75	54	5/23	6/7
BW	4	10.2	82.9	70	80.4	5.7	76	22	90.9	79.9	82	54	6/5	6/22
BWW	8	12.4	82.9	90	80.4	5.7	76	22	90.9	79.9	100	80	6/5	6/21
B*DK*	16	11.8	81.5	50	80	5.0	52	10	85.3	78.6	56	42	4/23	6/6
B*L*	7	10.7	81.5	50	80	5.0	52	10	85.3	78.6	55	42	4/23	6/8
203*L*	4	14.2	81.5	50	80	5.0	52	10	85.3	78.6	55	42	4/18	5/7
203*DK*	2	23.2	81.5	50	80	5.0	52	10	85.3	78.6	55	42	4/18	5/17
203*L*	4	9	83.5	50	80	5.0	52	10	85.3	78.6	55	42	5/23	6/6
203*DK*	13	6.1	83.5	50	80	5.0	52	10	85.3	78.6	55	42	5/23	6/3
203*DL*	8	25.4	81.5	50	80	5.0	52	10	85.3	78.6	55	42	4/18	5/29
203*B*	......	25.7	81.5	50	80	5.0	52	10	85.3	78.6	55	42	5/18	5/20
203*G*	3	29	81.5	50	80	5.0	52	10	85	78.6	55	42	4/18	5/18
203*R*	6	15.7	81.5	50	80	5.0	52	10	85.3	78.6	55	42	4/18	5/17
203*DL*	10	8.1	83.5	50	80	5.0	52	10	85.3	78.6	55	42	5/23	6/6
203*B*	6	7.1	83.5	50	80	5.0	52	10	85.3	78.6	55	42	5/23	6/1
203*G*	7	7.6	83.5	50	80	5.0	52	10	85.3	78.6	55	42	5/23	6/5
203*R*	3	4.3	83.5	50	80	5.0	52	10	85	78.6	55	42	5/23	5/28

Air velocity was 8 mm. per sec. for BAD, BD, BM, BW,BWW. It was O+ (trace) for 203DK, BShDK, Test pupae B, BDK, BL, 203L, 203DL.

The evaporation for BM, BW, BAD, BD, was 7, 6 and 6.7, 10, 8.8, cc. per day respectively.

The individuals used in BAD, BD, BM, were from lot V; in BshDK, BDK, BL, from lot IV; in test pupae from lot III. (See p. 374 for history of lots mentioned.)

ever, coincide almost exactly with the velocities for the larva in the apple as derived by entirely different methods (see Table V), up to 80° F. The top of the curve for the larva in the apple is about four velocity units lower at the maximum (see broken-line peak in Fig. 24.) This is in accord with expectation, as the larva in the center of the apple would probably not be warmed to the same extent as the larva in the cocoon, during the brief period of daily maximum temperature.

(D) VELOCITIES AS AFFECTED BY FACTORS OTHER THAN TEMPERATURE AND HUMIDITY.

The foregoing considerations of the development of the codling moth have been presented with reference to temperature and humidity as if no other factors operated to modify the results. It remains to consider how other factors modify the velocity values based on temperature and humidity data. The following are known to be of importance: (1) variability of temperature and humidity, (2) rainfall which soaks the larvae or pupae, (3) wind or air movement, (4) quality and intensity of light, (5) food, (6) mechanical stimuli, (7) seasonal march of temperature and humidity.

(1.) Variability of Temperature and Humidity in Weather Conditions.

Variability of weather conditions has to be considered, first, from two view-points: (a) variation of temperature and humidity in the form of daily rhythm, as contrasted to constant temperatures; (b) rising and falling of general temperature for the day, as shown by higher or lower maxima, minima, and means, under actual weather conditions.

(a) All available data on pupae, taken together, indicate that the length of the stage under variable temperatures is approximately 7 per cent shorter than under constant temperatures, although no experiments were especially designed to verify this difference. Such experiments, to give results comparable with those under actual weather conditions, would have to include temperatures outside the straight-line limits. The crucial experiments AD and AW (Fig. 15), with temperatures varying slowly within the straight-line limits, showed the same acceleration as the weather conditions. In some exceptional experiments, however, with small numbers of individuals, when the temperature rose suddenly and dropped again within a few hours, the velocity seemed to be decreased as compared with that for the corresponding constant temperatures. Although this retarding effect was obscured by other variations in conditions, the fact deserves mention, and the exceptional data are listed here: In one case, the temperature varied 4°–10° F. during 2 hours at mid-day, being constant most of the other hours, and the velocity was decreased 9 per cent. In another case (two lots of presumably uniform material in the 1917 experiments), with a rise of 15°–20° F. at mid-day, which is of the order of magnitude of the out-door rise in our region, the velocity differed by 12 per cent as follows: in constant conditions, with temperature 69.5° and humidity 80 per cent, the pupal time was 13.1 days; in variable conditions, with mean temperature 69.5° and mean humidity 82 per cent, showing a rise of 18° F. at mid-day, the time was 14.7 days. This decrease in velocity, correlated with the sharp mid-day rise followed by a rapid return to normal, suggests acclimation, temperature regulation, or a lag in the warming of the pupal body. No experiments with a sharp fall in temperature followed by a quick return to normal have been tried.

The effect of the normal daily variations of out-door temperatures, when corrected to the velocity curve and compared to the constant-temperature results, amounts to 7–8 per cent more rapid development than that under constant temperatures, for the pupae. The egg data suggest a difference of about 7 per cent, and the larval data about 8 per cent. In every stage, development is more rapid under the normal out-door variations.

(b) The effect of rising or falling mean daily temperature is reflected in the developmental total for the pupal stage and probably also for the other stages. Fig. 28 shows rainfall, minimum and maximum temperatures, and the relative rate of development for the groups of pupae, eggs, and larvae indicated for 3 years, 1915-17. A curve drawn so as to connect the mean centers for the period covered by the thirty pupae from pupation to emergence, rises and falls with the daily temperatures, suggesting that rising temperatures retard development and falling temperatures stimulate it. This may be explained on the basis of acclimation (Jacobs '19). Presumably, the velocity of development does not increase or decrease as rapidly as temperature changes. A close inspection of Fig. 28 shows that, as a rule, when the number of rises in temperature exceeds the number of drops, the developmental total is high, and vice versa. There are some exceptions to this, but these are due to the combining of several groups that pupated on different days. Taking merely the groups that pupated on the same day, there is usually not very much difference in time; it appears that they string out when rising temperatures come at the end. The correlation in general is good, but more and detailed study will be necessary to make clear its exact meaning. Doubtless direct measurement of CO_2 given off in relation to changes of temperature would be significant. It is not clear but that phenomena such as are shown by Lehenbauer ('14) may be the cause. He found that the maximum rate in relation to temperature varies with the length of exposure.

(2.) Rainfall and Submergence in Water. (See Figs. 3 and 28.)

During the "pre-pupal" period in hibernated larvae, submergence in water appeared in some cases to have little or no effect, while in other cases it accelerated development. Townsend has shown that submergence must be frequent to have any effect. None of Glenn's larvae were submerged or exposed to rain; so, rainfall had only an indirect effect through humidity. Hibernation in dry conditions lengthens the *pupal* period. This is shown in the 1918 experiments and in Glenn's 1915 material after an unusually dry late winter and early spring. The average time was nearly

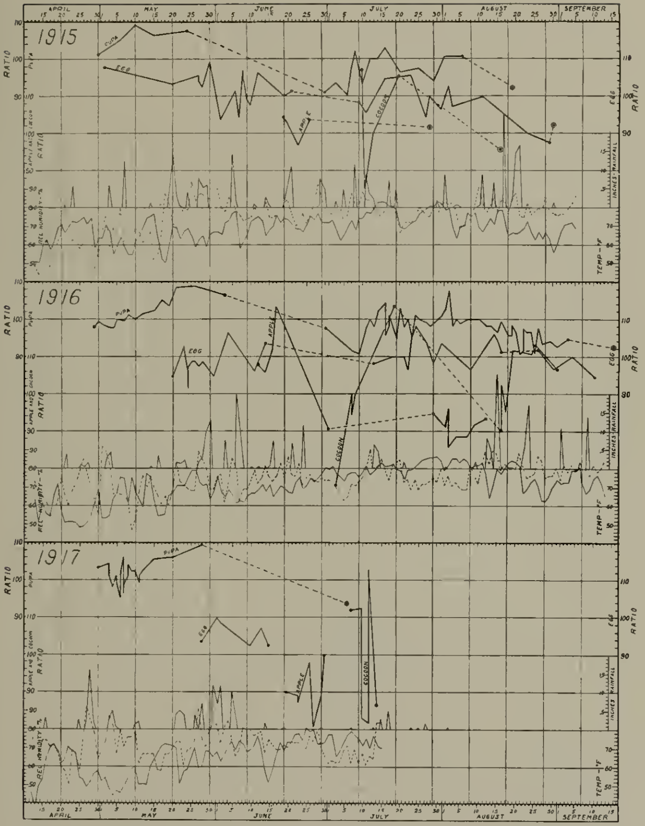

Fig. 28. Showing rainfall and mean temperature and humidity for the summer of 1915, 1916, and 1917 at Olney, Illinois. (See Table XI.) The pupa, egg, apple, and cocoon curves are plotted with reference to a standard or average time as follows:—The standard or average is plotted as 100; pupal scale, upper left; egg scale, middle right; apple and cocoon scale, lower left. The data are plotted on the median date of the first and last occurrence in each group of 30 pupae, 50 eggs, and 10 larvae in the apple and in the cocoon, a dot marking the first and the last dates of each series. Correlations of time (length of stages) with rainfall and rising and falling temperatures are indicated.

a day longer when the temperature remained the same or when, if different, it was reduced to the same velocity value. Heavy rainfall lengthens time in the apple (Fig. 28). Little or no rainfall shortens it.

(3.) Air Movement and Evaporation.

A large series of larvae were subject to various rates of evaporation measured by the porous cup atmometer. Mortality was high, and complete losses in certain evaporation rates rendered some sets useless. The excellent success attending the use of the porous cup atmometer with plant work has not attended our efforts. The reason for this is that higher temperature, which accelerates development, increases evaporation; while increased rainfall and humidity, which accelerate development, decrease evaporation. Although high mortality and failure to pupate render conclusions uncertain, the relative number of individuals emerging and the length of their pupal life may be taken as some evidence of the effects of evaporation when other conditions are considered. Accordingly, the data are shown: In 1917, temperature 79°, humidity 75 per cent, evaporation 4.3 cc. per day seemed most favorable. In 1918, temperature 58°, humidity 60 per cent, evaporation 30 cc. per day seemed most favorable. In 1919, first generation, temperature 80.2°, humidity 70 per cent, evaporation 8.4 (lowest) cc. per day seemed most favorable. In 1919, second generation, results were contradictory. In 1920 first results were contradictory, due to mortality. In 1920, one set, the shortest time was with 66.8 cc. evaporation, but this also showed the greatest failure to pupate. The 1920 second generation showed temperature 82°, humidity 77 per cent, evaporation 28.5 cc. to be best on the whole, although one rate was higher and four were lower. It appears that higher failure to pupate and higher mortality are accompanied by *shortest pupal life* under conditions of very rapid evaporation.

TABLE XXVIII. *Showing the emergence of moths from hibernated larvae (1920-21).*

All were kept at the same temperature during hibernation (37-48°) until March 15th, when the temperature was raised to 73.5° F.

	Soaked Humidity 100%				Dry Humidity 90%	
Collected.	Sept. 15.		Sept. 28.		Sept. 28.	
No. Spinnings	No.	Time	No.	Time	No.	Time
1(	(41	29.5	4	26.4	8	30.9
(	(53	30.6	4	26.4	8	30.9
2(	(75	28.7	40	27.7	56	28.0
(	(89	31.1	42	28.2	60	28.8
3(	(81	26.4	3	23.7	28	26.9
(	(81	26.4	3	23.7	29	27.3

(4.) Quality and Intensity of Light.

(a). *Intensity*. As compared with diffused daylight, the length of the pupal stage is longest in the dark. This is uniformly true in our experiments. Isely and Ackerman ('23) have shown that light checks egg-laying of the codling moth, and that temperatures above 62° after sundown are essential to laying.

(b). *Color*. A series of experiments on color gave inconsistent results. Red, blue, and green were less favorable, in all cases, than darkness or Mazda lamp light through daylight glass. See Table XIIIg (p. 372).

(5.) Food.

It is a well-known fact that the larvae develop in picked apples more quickly than in apples on the tree and in some varieties of apples than in others, but no analysis of the cause has been made. (See Glenn '22.)

(6.) Mechanical Stimuli and Number of Spinnings.

Some investigators have maintained that the time to pupation is increased by the number of spinnings and the large amount of mechanical stimulation due to opening the cocoons several times for observations. The results shown in Table XXVIII are on larvae that had spun one, two, or three times in the fall, but were not disturbed in the spring. The second item includes all that came through, while the first is only to May 20.

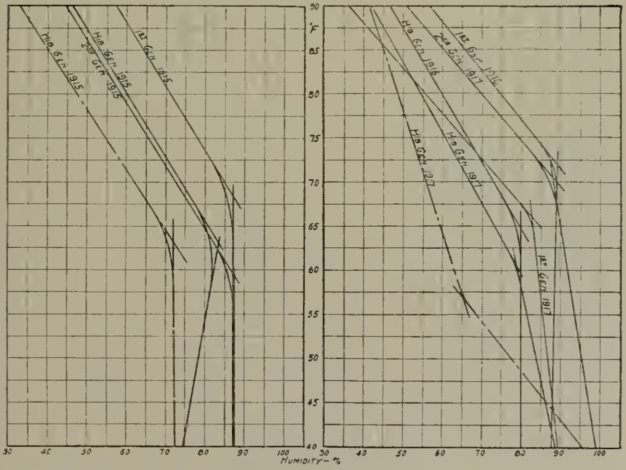

Fig. 29. The average daily march of temperature and humidity 1915-17 at Olney.

If number of spinnings has any effect, the evidence indicates that it decreases the length of stages. In an experiment in 1920 there was no difference in the length of pupal life related to number of spinnings. A decrease in time might be inferred from Bishop's ('23) work on the honeybee larva. In the codling moth, it may be assumed that the increased acidity due to several spinnings helped to complete processes which are essential to rapid development, and which take place over a long period.

(7.) Seasonal March of Temperature and Humidity.

Fig. 29 shows the average daily variation of temperature and humidity for the different generations at Olney. The curves are roughly drawn through the plotted records of temperature and humidity as shown in Fig. 17, and they represent the conditions encountered by several sets of pupae. Although slightly different from the curves which would result from the use of data unselected from a biological point of view, they serve to indicate the marked difference between different seasons and thus emphasize the reason for taking humidity into account.

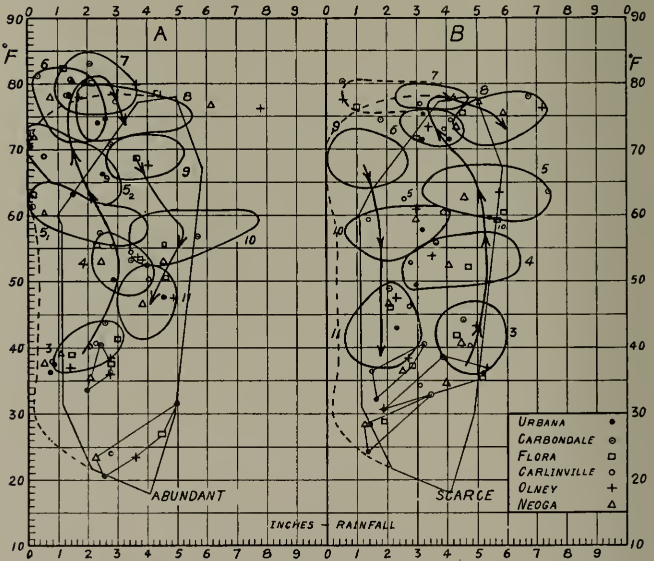

Fig. 30. Ball-Taylor diagrams and hythergraph of scarce and abundant codling-moth years in Southern Illinois localities.

Experiments on combinations of temperature and humidity, where the series is limited, should follow the general trend of the weather of the region and of the season to be studied. This plan will save much time and unnecessary experimentation, provided hygro-thermograph records have been kept; otherwise, some means of using vapor-pressure tables will have to be devised. The changes in humidity do not follow the trend shown by air warmed by other means.

Fig. 30 shows complete data for the Ball-Taylor rainfall-temperature charts, or hythergraphs, for "abundant" and "scarce" years at six localities, with the amount of variation. The conclusions from this study have already been expressed in PART TWO, pp. 350-355, where the parts are shown separately in Fig. 3-7.

Hythergraphs form a basis for interesting speculation as to the original home of the codling moth. The heavy line in Fig. 31 shows the average monthly temperature and rainfall for a typical year in three apple-growing districts in south-eastern Europe. The large area (enclosed by the solid line) in each part of the figure indicates the limits of average data for all the great apple-

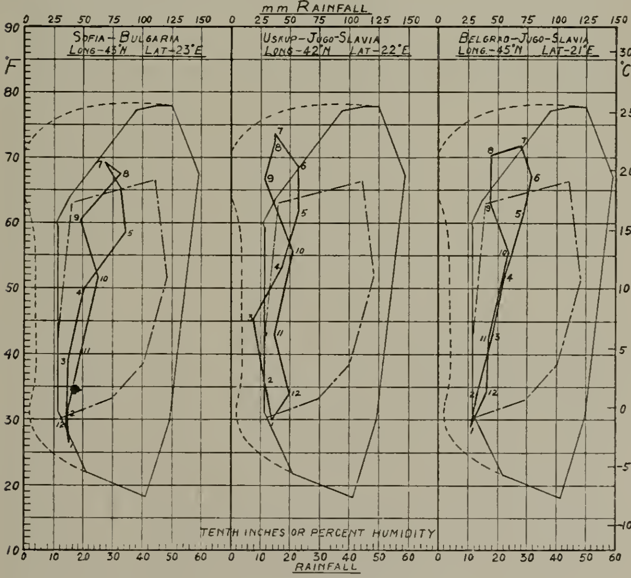

Fig. 31. Hythergraphs for apple-growing regions.

growing regions of the world* except the irrigated districts of the western part of the United States, which are shown by the extension of this large area by dotted lines at the left. The inner area (enclosed by the dot-dash line) in each part of the figure indicates the limits of average data for European countries alone, which may be considered as the most favorable conditions because extremes of temperature and rainfall are thus excluded. The Sophia data fall generally within these medial conditions; while the data for the other two localities, which are at a higher altitude, do not. It is probable that a complete analysis of the climatic relations of the apple and the codling moth would help to settle the question of the origin of the moth. On the hypothesis that this origin was in the territory around the eastern Mediterranean, where conditions fall within the small area shown in Fig. 31, the difference between a "scarce" and an "abundant" year in Illinois is explicable. Since the hythergraph for southern Illinois does not always fall entirely within this area of favorable conditions, both winter and summer temperatures sometimes reaching extremes, the codling moth is abundant here only in years when these general limits are not exceeded. At least, the important effects of autumn and winter rainfall, as pointed out in this paper, suggest the Mediterranean region as the original habitat of the codling moth.

(E) EXPERIMENTAL METHODS.

In the experiments reported in this paper many important innovations were employed, especially in the controlling and recording of variable conditions of temperature, humidity, air movement, and evaporation. Most experimental work has formerly been done with constant temperatures. We know of no other attempts to use variable temperatures of an interpretable type, with factors all recorded, as a means of bridging the gap between constant-temperature experiments and actual weather conditions. The chambers for constant-temperature work are unique in that they allow the use of several humidities at the same temperature. This feature is essential, because variation in stock necessitates the running of a large series started at the same time from the same stock. This is a very important feature for climate-simulation work.

A. GENERAL EQUIPMENT.

1. *Building*. This work was done in the Vivarium of the University of Illinois. The greater part of the work was carried on in a glass-roofed house of greenhouse construction. The room was provided with center-roof and side ventilators, and a door at the end. To facilitate air circulation, three fans were placed on the bottom of the side ventilator on the south. The room was heated by steam radiators regulated by a Johnson automatic temperature control, as described by Harding and Willard ('16).

2. *Apparatus*. The constant-temperature experiments were conducted with the apparatus regularly used in the Vivarium, which will be

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* The following countries were included in this category: Great Britain, Spain, France, Germany, Denmark, Australia, Tasmania, Canada, and the United States.

described in a forthcoming book.* The apparatus for variable-temperature-experiments consisted of five chambers of a type shown in perspective in Fig. 32. The three smaller chambers (C, D, and E), which were 25½ inches long by 20¾ inches wide by 42 inches high, were designed first; when found to be too small, they were supplemented by two other chambers (F and G), which were 39 inches by 20 inches by 48 inches. These smaller chambers were of two kinds: two, (C and D), with glass slides; ane one, (E), with opaque sides. The water tank above chamber D was provided with a glass bottom and glass sides so as to admit skylight through the water. Water from the general supply flowed in through the tank and out through a waste pipe so as to maintain a water level two inches below the top of the water tank. This made it possible to control the supply of cold running water to keep down the temperature of the main chamber on hot summer days. The main chamber was provided with a wooden shelf, as shown in Fig. 32, leaving an opening from below the shelf up into the main body of the chamber when the door was closed. The coils which turned on the heat during the night were under this shelf (ordinarily the sun caused the temperature to rise to about 100° F. on summer days). To ventilate the cages, the chamber was supplied with humidified air from a compression tank. The wall of the chamber contained four small pipes ending in a slender hose-end on the inside and in a small (⅛-inch) cock on the outside, for the purpose of conducting the atmometer leads, or suction leads, through the wall. The dark chamber (E) was of the same size as the glass-sided chamber and was provided with the water tank above, but received the light only from above, and was intended to demonstrate the effects of light under the same temperature conditions. Difficulty was usually experienced in maintaining a temperature similar to that in the other chambers, which tended to rise higher during the day. The same mean temperature, however, was obtained in this chamber as in the others, although it was done by raising the minimum during the period of the night instead of by raising the maximum at mid-day.

The humidifying device which treated the air supplied to these chambers, is shown in Fig. 33, consisted of a galvanized-iron cylinder so constructed as to stand pressure of from five to ten pounds. Air at reduced pressure entered this cylinder at the right. In the top of this cylinder was a Schutte-Koerting head which sprayed cold water into the space through which the air passed, so as to nearly saturate the air at the temperature of the water, which was about 16° C. during the summer months. The surplus water from the humidifying chamber flowed out through a ball-float cock (steam trap—Harding and Willard, '16, p. 214). The air passed over the galvanized-iron cylinder through a condensation separator, which removed any water. This humidifying process supplied air nearly saturated at the temperature of the running water, and the humidity for any temperature above or below this could readily be calculated. This

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* Experimental Animal Ecology, to be published in 1927 by Williams & Wilkins Co., Baltimore, Md.

was experimentally ascertained for a period of several weeks in July, 1919, by allowing the air after leaving the humidifier to pass through a hood which was slipped over the sensitive parts of a Friez hygro-thermograph. The air was passed through a block tin pipe coil surrounding the temperature-sensitive part, before passing into the hood entrance. This apparatus then recorded the temperature and the humidity of this air

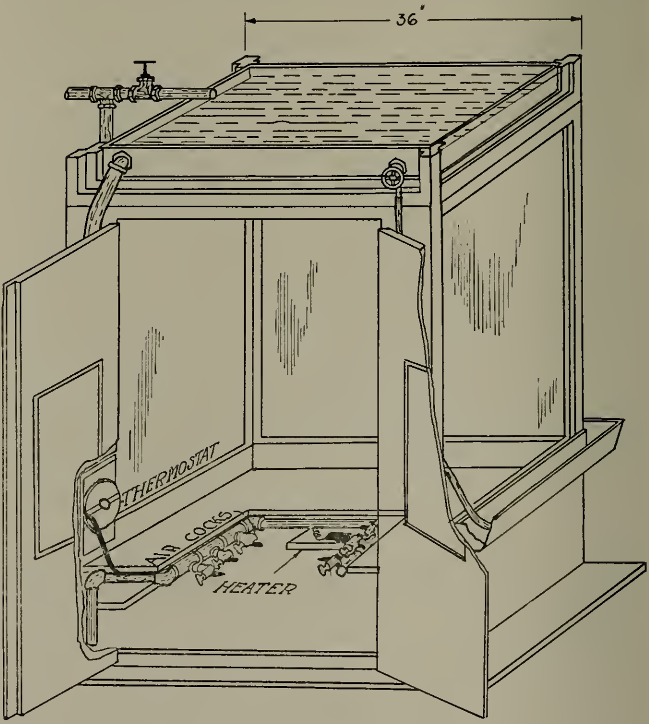

Fig. 32. Showing the unit F for simulating daily rhythm, (U. I. V.). Cooling water tank at the top with high drain at the left and siphon valve at the right to remove all water in cleaning. The C-shaped shelf, air cocks, and one thermostat with heater also appear in the drawing.

when raised to a given degree above the temperature of the water. These results indicated that the air was generally above 90% of saturation, so that the calculations on that basis were approximately correct.

Compressed-Air Supply. Air was supplied at a pressure of 60–80 pounds through pipes from a large piston compressor at the University power-house, about 200 yards from the Vivarium. It appeared to be satisfactory air, although doubtless a better supply should be sought for very refined work. It contained nothing which could be injurious, except a rather large amount of carbon dioxide in some samples. There was a slight odor from the oil used in the pump, which was decomposed under pressure. This odor was not present when the best grade of oil was used, and particularly in the summer time when a large amount of air was drawn. For nearly all of the work the pressure was reduced to 3–5 pounds, the reduction being accomplished by a Mason pressure-reducing valve. This valve has an advantage over others which have come to our attention, as it gives practically constant pressure regardless of fluctuations in the initial pressure and in the rate of flow through the valve.

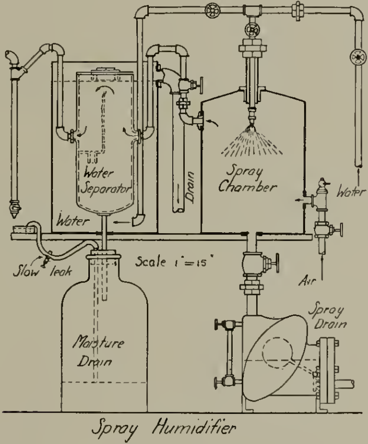

Fig. 33. Showing an assembled spray humidifier (N. H. S.). Air comes into contact with finely divided water at a low temperature in the spray chamber and passes to the separator where any droplets of water are removed by baffles.

B. MEASUREMENT OF TEMPERATURE, HUMIDITY, AND AIR MOVEMENT.

Most of the earlier temperature records were made with standard thermographs placed adjacent to the bottles containing the codling moths or placed in the cages containing insects inhabiting plants. In the latter work a Leeds and Northrup resistance thermometer recorder, carrying ten resistance thermometers, was used. These thermometers are approximately 1 by 8 cm. and can be inserted into small cavities or places in soil or in the branches of a food plant. They are by far the most accurate of all thermometers on the market, being correct to 0.2° (the unavoidable error is due to shifting of the paper). This recorder, furthermore, has the great advantage of eliminating the difficulty which results from having the thermometer in one place and the animals in another with a degree or two difference in temperature, as is usually the case. Where thermographs were used an effort was made to eliminate this difficulty by taking regular readings of a mercury thermometer.

Humidity was recorded by Friez hygrographs (human hair type) which were checked weekly with a sling, or by daily readings of wet and dry bulb thermometers enclosed in a tube.

Evaporation was measured by the Livingston atmometer. The rate of air flow was measured by use of the diaphragm chambers and Ellison gage (Hamilton '17). The flows are readily measured by this method, but it offers no adequate means of maintaining the flow as constant. In practice, flows were set principally by the use of screw compression clamps on rubber hose. In some cases, mercury valves were installed, which consisted merely of a U-tube containing a small amount of mercury. A slight rise in pressure would push the mercury around in the U-tube and allow some air to bubble out. Generally, the flows were simply set by the compression cock at intervals of a few days, and the mean of the readings taken as indicating the rate of flow.

Instrument records. The record sheets from the thermograph and hygrothermograph, except where temperatures were practically constant, and in many cases where they were not, were treated according to a definite routine plan. The means for each two hours of the day were first determined by inspection, a clerk being employed to write with a lead pencil the mean number of degrees and the mean per cent of humidity for the two hours in the proper space immediately below the graphs. Each sheet was then checked by another clerk, corrected if any mistakes were found, and returned for inking. The person doing the checking often did the inking, so that the presence of the two-hour means in ink indicated that the work had been checked over by a second person. The sheets were then gone over a second time and means for half-days computed. These half-days were taken as from eight to eight, and the mean was composed of the sum of six two-hour means. These were then written on the sheets in lead pencil with the eight o'clock hours indicated by vertical lines. The period from eight to eight was taken because in the variable temperatures the temperature begins to rise at eight A. M., reaches a maximum about two P. M., and falls during the following six hours to a point near the average for the night. We made our observations the first thing in the morning and the last thing in the evening, usually beginning at eight or earlier, and ending as late as six or six-thirty, and sometimes seven, in the evening, when the experiments were gone over twice a day. While carrying with it the possibility of a very slight error in the total temperatures, any phenomenon occurring so as to be first noted in the morning observation was recorded as having taken place at 8:00 A. M. Any phenomenon noted in the afternoon observation was recorded as having taken place at 8:00 P. M. With this division of mean temperatures for half days, it was easily possible to compute the means for any number of days with an adding machine, as a one-week period would contain only fourteen items. The humidities were treated in a similar fashion. The accounting was greatly simplified by this routine clerical work, which proved to be on the whole very satisfactory, although done by students who were paid very little.

In experiments with very variable temperature, the sheets were given a third type of inspection. The daily temperature and humidity curves were inspected, and notation was made of the night humidity and the night temperature, which under most of our experimental conditions was intentionally kept at a constant level. The hour at which this low level was ordinarily reached in the evening and at which the temperature began to rise in the morning was noted, and this temperature was called the base temperature, as under the experimental conditions and often under outdoor conditions the points marking this low level approach a straight line. This base temperature had a corresponding base humidity. The base temperature for each day was then noted by inspection and recorded on a separate sheet, together with the absolute maximum and absolute minimum and the amount of elevation above the base for each day. In Tables XVIII, XIX, and XXVII these data are presented in full, for they proved to be significant criteria of the climatic factors influencing the rate of development.

Standard Atmometers. The atmometer used was the Livingston porous cup atmometer, obtained from the Plant World, Tucson, Arizona. The standardized cups ordinarily obtained, after use ranging from one to three months, depending upon air conditions, were standardized. For this purpose a wheel having a diameter of 38 inches was fastened in a horizontal position on a table and turned at the rate of approximately one revolution per second by a belt from a ½ h. p. motor making 1,200 R. P. M. The upper side of the wheel bore twelve upright posts, giving it a capacity of twenty-four atmometers at one time, although only twelve were commonly run at a time. These were standardized against a fresh atmometer, and then scoured, emeried, and re-standardized, and used until the standard fell to 0.50 or rose to 1.00, after which they were used as irrigators in the chinch-bug work. It was desirable to have this piece of apparatus on account of the large number of atmometers installed.

The device cost only $50, but it required some supervision, as it was made too large throughout. At the present time it would be cheaper to purchase the standardized turn-table direct from the Plant World, all ready to use, but of a smaller size.

C. Special Methods.

Special methods and special equipment will be discussed here. The larvae studied were placed in corrugated papers with celluloid covers and backed up by small pieces of wood, after the manner used by Mr. Glenn. In fact, we secured some of his observation cases and merely selected a container which would hold them, modifying them only slightly (Fig. 34). The sticks used were 4 inches (10 cm) long and one inch (2.5 cm) wide. The celluloid covers were supported by wood 2–2.5 mm thick, allowing a space between the celluloid and the wood back. We mounted the back of the piece of wood in order to make two of them approach a cylindrical form. Two were commonly placed face to face, and when only one was used it was provided with a dummy front piece of wood without the pasteboard. The bottles used for most of the experiments were of 250 cc capacity with an inside diameter of about 2¼ inches (56 mm) and an outside diameter of a little less than 2½ inches (61 mm). A pair of sticks with their larvae were dropped into a bottle and the two taken together made an elliptical cylinder with a diameter of one inch by ⅞ inch. Each one of these bottles was provided with a two-hole rubber stopper. Air was introduced through a tube inserted into one of these holes in the rubber stopper, the tube ending at the lower edge of the stopper, and air left the bottle through a tube extending to the bottom. Thus the tube extending to the bottom tended to push the elliptical cylinder to one side and it rested immediately beneath the incoming air which flowed down over the larvae container to the bottom and out. Leaving the bottle, the air was conducted through a small tube into another bottle of the same kind, from which the bottom had been removed by a skilled glass-worker. This bottle rested over a Livingston porous cup atmometer, which is a little more than one inch in diameter and just a little larger than the bottle used as a larvae-container. Thus the apparatus for experimentation was so arranged that the air flowed through the bottle and then over the atmometer at approximately the same rate at which the evaporation was measured. These containers were mounted on pieces of board about 3 inches by 6 inches (7.5 cm by 15 cm). See Fig. 34. The bottle containing the larvae rested on the board and was held in place by three or four slender nails driven into the board. The atmometer, with the recording attachment at its lower end, was supported on a piece of soft aluminum tubing, ⅛ inch inside diameter, bent into the form of an elbow, inserted through a flat stopper, a channel being cut in the lower side so that one arm of the aluminum tubing rested in this, flush with the underside. This was nailed to the end of the board opposite to that to which the bottle was placed. Above this three corks 1½ inch (3.7 cm) by approximately one inch (2½ cm) in diameter were placed on the edge of the large flat cork and fastened there with long slender nails so that the circumference was divided into three.

Additional slender nails were shoved into the top of this cork to hold the bottomless bottle in position over the atmometer. In this manner, units for measuring evaporation and controlling the conditions of the air surrounding the larvae were made up in numbers and used in all experiments in which the rate of evaporation is given. A number of experiments were made with larvae in the celluloid-fronted cases already described. When a saturated atmosphere was desired, they were dropped into a bottle which contained an open vial of distilled water. Evapora-

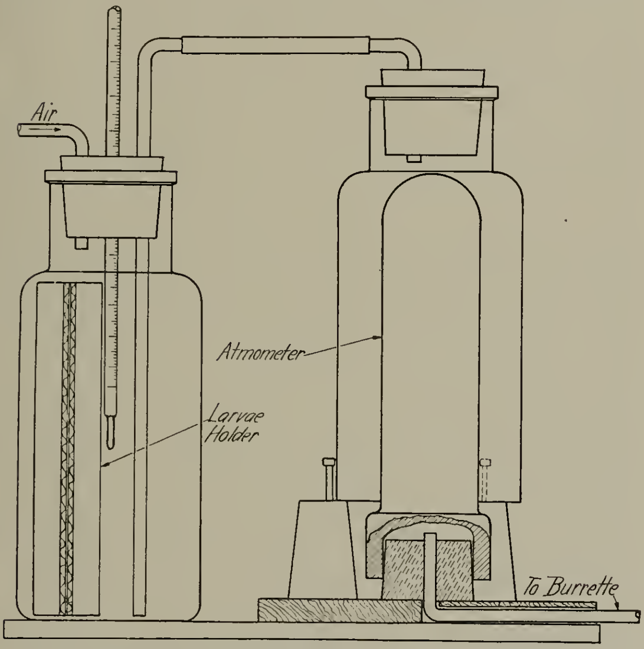

Fig. 34. Showing the arrangement of the bottle, thermometer, larva holder, and atmometer used in the experiments on the codling-moth larvae and pupae. In some cases egg-bearing leaves were fastened to the larva containers.

tion from this water made a practical saturation, as indicated by the almost continual presence of condensation on the walls. Experiments of this type were not ventilated. The rate of flow of air through the experimental bottles was determined by the use of the Ellison differential gage and diaphragm chambers. A 2 mm. aperture and 5 mm. reading were used in the standard experiments, but the rate of air flow was not checked up as closely as it should have been in the earlier experiments, because various difficulties with the equipment rendered it impracticable to make frequent measurements. This commonly gave a flow of a little more than one mm. per second through the bottle. A series of variable-temperature experiments was run with paired larval containers simply placed out of doors, or in a greenhouse, or in the experimental case where various chinch-bug experiments were being made and many data were being reported. The experiments with light were made with single containers under conditions as described on p. 427 Table XIIIg (p. 372).

D. Recording of Data.

Records of experimental work were copied on large sheets, legal size, 8½ by 14, printed with a special heading bearing the name of the survey and calling for the name of the observer in the upper right hand corner, with experiment number, date, and species immediately below this; while at the right of the center were the words "Subject of Experiments." Below this was the description of apparatus, and a line calling for notes on light and temperatures, together with previous history and condition of the stock. The lower 11 inches of this paper was ruled horizontally at quarter-inch intervals, with 21 vertical rulings at ⅜-inch intervals, and leaving a square space of one-half inch at each margin. Down the center of the page was a double blue ruling, which constituted one of the equidistant sets, and, on each side of this, three red rulings, which constituted three of the equidistant sets. This type of paper was found to be particularly useful where a large number of individuals had to be checked up, as the numbers were put at the heads of the vertical columns and the dates in the left-hand margins, the checkings in each square to show the condition of the individuals from day to day. The upper left-hand corner of this paper was clear of printing or writing for the equivalent of a triangle with its sides three inches. This left a space in which no writing was ever placed, which made easy the fastening together of the sheets with various types of clips without interfering with the writing of the notes. These were got up for the current experiments and placed on legal size board clips, which the investigator carried about with him as he observed the conditions of the experiments from day to day. The different chambers in which these experiments were going on were lettered, beginning with the large constant-temperature rooms, which were lettered A and B; then the variable units, lettered C, D, E, F, and G, as already noted; then the smaller units inside the constant-temperature rooms, lettered H, I, L, and V (the intervening letters having been used for temporarily installed incubators during the series of experiments in which they were so designated). With the maximum amount of experimental work going on, the entire alphabet was used in designating chambers and places in which animals were kept; and some such plan is needed for convenience of records and conversation with assistants and caretakers. When once adopted, these letters were allowed to stand in subsequent years for all the permanent pieces of the equipment. (For the meanings of other alphabetical designations, see p. 363.)

The records of the codling moth work were kept on the special ruled paper already mentioned, the heading being proportionally filled out; and the numbers were inserted on the celluloid above the individual larvae and corresponding numbers at the heads of the long columns on the experimental sheet. When the observer looked over the experiments morning and evening, he recorded the condition of each individual, as follows: A small check indicated that the larvae were present and alive; the letter P indicated that the larvae had pupated; E, that adults had emerged; D, that larvae had died; M, that they were missing; and K, that they were accidentally killed. The use of the check mark was very desirable, ordinarily, to indicate that the animal was actually observed, because later on, if there had been no such record kept, or if something new had occurred, one might otherwise wonder whether he had actually looked at it or not. The check marks avoided this form of doubt in working over the results. In counting the days which elapsed from the time of pupation to the time of emergence or any other period, clerks were first put to work ruling the sheets into days, where the observations were made twice a day, which was the case in all except the low temperatures. They were warned especially to look out for any irregularities of times when observations had been missed, as was sometimes necessary, particularly with the heavy program, and in some of the lower temperatures where little progress was made, which were ordinarily looked over twice a day. These clerks drew a horizontal red line across the paper, separating the days; then, starting with the data of pupation, for example, they checked each corresponding reading. Thus, if the pupation occurred in the forenoon, they checked each subsequent forenoon reading; if in the afternoon, each subsequent afternoon reading. All readings were checked to the first. At the same time, the clerks counted the number of days from the time of pupation until the time of emergence, or whatever other phenomenon was being observed; and the number of days which had elapsed was written at the bottom of the column or at the end of the record of the particular individual. This made it possible for any person to rapidly check the work of the clerks, who were found to have carried out this plan with a great deal of precision, having rarely made any errors.

SUMMARY OF CONCLUSIONS.

(1) Temperatures cannot be summed correctly for biological purposes unless readings are taken at intervals of one or two hours instead of daily and corrected for the effects of other conditions besides temperature so as to fit the true curve for velocity of development. Such correction, here called the *temperature-substitution* method, is possible only through preliminary experimentation or observation affording temperature and humidity data for the defining of *standard conditions.*

(2) The temperature-substitution method, when correctly used, translates the observed conditions into terms of the response of the organism, that is, into *developmental units,* which can be summed for biological purposes.

(3) The use of a *normal total* of developmental units for a stage in the life-cycle of an organism makes possible the calculation of *standard average time* for the stage. This permits estimation of the amount of individual variation in any given case and the effects of factors other than temperature and humidity which make the developmental total larger or smaller than normal.

(4) Autumn and winter rainfall influence the time of first pupation in spring and the length of the pupal stage.

(5) Ball-Taylor rainfall-temperature diagrams (hythergraphs) show characteristic differences between years when the codling moth is abundant and years when it is scarce.

(6) Rainfall influences the time which the larva spends in the apple and probably the length of other stages.

(7) The falling of the mean temperature from day to day in late summer is correlated with increased rate of development; the rising of the mean temperature from day to day in spring is correlated with decreased rate of development.

(8) The falling of mean temperatures, or at least minimum temperatures, has no apparent effect on the initiation of hibernation.

(9) The explanation of hibernation phenomena is probably to be sought in the activity of enzymes.

(10) There is no reliable basis for predicting the time of the first spring pupation.

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