BIONOMIC STUDIES ON THE BEET LEAFHOPPER

F. H. HARRIES AND J. R. DOUGLASS

Bureau of Entomology and Plant Quarantine
Agricultural Research Administration
United States Department of Agriculture

TABLE OF CONTENTS

BIONOMIC STUDIES ON THE BEET LEAFHOPPER

INTRODUCTION

The beet leafhopper (*Eutettix tenellus* (Baker)) (Order Hemiptera, Suborder Homoptera, Family Cicadellidae) the only known vector of the virus of curly top disease, has been the most important pest affecting sugar beets in the Western States and has also been outstandingly important in limiting the production of beans, tomatoes, melons, and other garden crops, and many ornamental plants. Since the agent of transmission of the disease was announced by Ball in 1906, extensive investigation of the problem has included studies of the life history, biology, and host plants of the insect in relation to weather and climatic conditions in the more important areas of distribution as well as epidemiological research and the breeding of disease-resistant varieties of plants.

Bionomic studies of the beet leafhopper have been especially difficult because of the rapid fusion or overlapping of successive generations, long migrations, and more or less local shifting movements, and the difficulty of determining and measuring effects of the more significant variables in the environmental complex. Such studies have also been complicated by seasonal variation in the time of germination and maturation of different wild host plants and their sequence, abundance, and distribution. Owing to the involved ecological relations and the difficulty of studying certain phases of the effects of weather and climatic factors by methods other than analytical, experiments were conducted to serve as a practical basis for field studies and as an aid in interpreting problems of development, activities, abundance, and distribution of the insect.

The investigations on which this paper is based were conducted as a part-time project from 1932 to 1937, inclusive, at Twin Falls, Idaho, in cooperation with the Bureau of Plant Industry, Soils, and Agricultural Engineering and the Idaho Agricultural Experiment Station. The study was initiated by P. N. Annand, to whom appreciation is expressed for direct supervision during earlier phases of the work. The writers are also indebted to W. C. Cook for his interest in the studies and many helpful suggestions given during the progress of the work and preparation of the manuscript. Other assistance given in various ways by R. A. Fulton, C. F. Henderson, J. C. Chamberlin, A. O. Larson, D. E. Fox, and M. F. Bowen is gratefully acknowledged.

PREVIOUS STUDIES

The beet leafhopper was announced to be the vector of curly top disease of sugar beets by Ball (4) in 1906, who also recorded early observations on its life history and wild host plants (5, 6). Ball (6) concluded that only one generation of the beet leafhopper occurs annually, but Stahl (87) and later investigators (14, 29, 41, 49) have correctly reported the occurrence of two or more generations annually in the more important areas of distribution. A detailed account of the life history of the leafhopper in California, supplemented by studies of the life cycle in observation cages was given by Severin (82, 83).

Carter (14) extensively analyzed the beet leafhopper problem with special reference to the ecology of the insect in southern Idaho. Annand *et al.* (2) discussed movements of the leafhopper from different desert breeding areas in southern Idaho and emphasized the importance of extensive and thorough surveys in the fall and spring as a closer check on the distribution, abundance, and development of the insect relative to economic conditions determined by the magnitude and time of the spring movement to the cultivated areas.

Seasonal development, natural enemies, and host-plant relations of the insect in northern Utah were discussed by Knowlton (49, 50). Hills (41) studied seasonal development of the leafhopper and effects of weather conditions on its abundance in south-central Washington and northeastern Oregon. Studies of types of vegetation in the San Joaquin Valley of California and effects of overgrazing and intermittent farming on the distribution and abundance of seasonal weed hosts of the beet leafhopper were reported by Piemeisel & Lawson (72) and Lawson & Piemeisel (53). Fox (24) described the occurrence of the beet leafhopper and associated insect species on secondary plant successions in southern Idaho with reference to studies by Piemeisel (71) of the changes in weedy plant cover that follow the abandonment of cleared sagebrush lands. Romney (76) discussed the breeding areas and economic distribution of the beet leafhopper in New Mexico, southern Colorado, and western Texas, and methods of its control on beets grown for seed in Arizona and New Mexico (77). The life history, bionomics, and control of the leafhopper were discussed by Cook (16, 17).

METHODS

Groups of eggs for the different experiments were obtained by placing mature females on sugar-beet plants in small cages designed to fit snugly around the petioles. After 12 hours the cages were removed and portions of the plant in which the eggs were embedded were marked with ink. Toward the end of embryonic development, cages were replaced on the plants to confine the young nymphs. The same

cages were used to confine single adult females in experiments on oviposition. Transfer of the females to fresh plants was accomplished by shaking the cage lightly until the insects would come to rest on the side of the container, when it was slipped off an exposed plant and onto a fresh one. One of these cages, which was designed and used by Charles F. Henderson in related studies, is shown in Figure 1A.
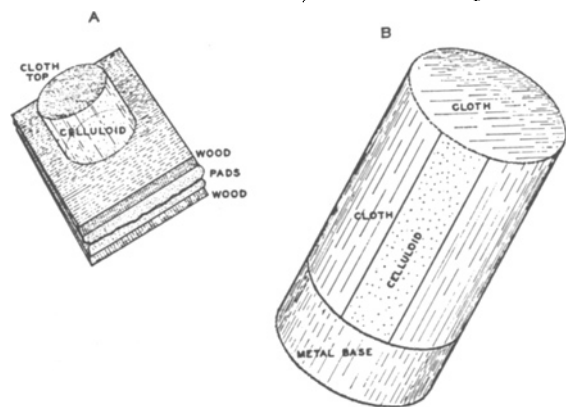

FIG. 1. Cages used to confine the beet leafhopper for studies under controlled conditions: A, For studies of egg and preovipositional stages; B, for studies of the nymphal stage.

Cages used in studies of nymphal development (Fig. 1B) were made of thin, fine-meshed cloth over a supporting frame of celluloid attached to a metal band. These were placed over the beet plant and pressed into a layer of clean sand covering the surface of the soil so that both leaves and petioles of the plant were available for feeding. Both types of cages were designed to provide a maximum circulation of air and thus to minimize any effect of evaporation on temperature and humidity conditions within the cages.

The cabinets in which the cages were placed have been described elsewhere (2a). The temperature of the cabinets was controlled within approximately $\pm 0.2°$ F. and the relative humidity within ± 1 percent. Continuous records of conditions within the cabinets were obtained with hygrothermographs, and temperature and humidity within the cages were checked with a thermometer and small dewpoint tube after methods described by Smith (86). Temperature changes and various periods of exposure at different temperatures were obtained by transferring the insects from one chamber to another at definite intervals. The relation of the temperature of the plants to air temperatures and the amount of temperature lag following transfers from higher to lower temperatures and vice versa were checked by means of small thermocouples inserted carefully in the plant tissue to insure placement of the junctions below the cuticle. The influence of temperature lag was apparently negligible, since differences of only a few degrees over periods of 2 to 6 minutes were detected, and these effects were evidently rather closely compensating in alternate transfers. Possible cooling effects of evapo-

ration were minimized by watering the plants sparingly from below in saucers.

Egg deposition, hatching, attainment of the adult stage, and first egg deposition occurred under the same experimental conditions as were maintained for the corresponding embryonic, nymphal, and preovipositional periods. The eggs were deposited during a 12-hour period, 9 a.m. to 9 p.m. or vice versa, and hatching was recorded daily at 9 a.m. and 9 p.m. in timing the embryonic period. The nymphs hatched or reached the adult stage over a 24-hour period and were observed daily at 9 p.m. in measuring the time required for the corresponding nymphal and preovipositional stages.

In studies of oviposition the eggs were counted as follows: The plant petioles were labeled with small string marking tags and immersed in a saturated solution of chloral hydrate, which was heated almost to the boiling point and then permitted to cool. The same solution was used repeatedly. This treatment rendered the plant tissue transparent and usually stained the eggs a light green. The eggs were counted by examining the plant material in a clear, concentrated solution of chloral hydrate under a binocular microscope. A photomicrograph of eggs in the plant tissue after treatment is shown in Figure 2.
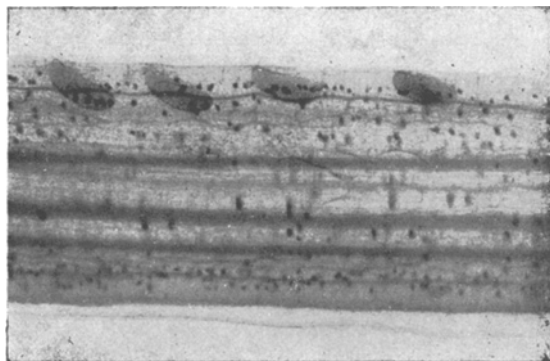
FIG. 2. Photomicrograph of eggs of the beet leafhopper in a beet plant after treatment with chloral hydrate.

Population samples on the desert plots were taken at random according to the following procedure: The observation plot was divided into smaller sections, 15 feet square, by placing numbered stakes at the corners. Beans, previously numbered to correspond with the numbers of the smaller plots, were drawn from a carton to determine the general distribution of the samples over the larger plot. From another series of beans numbered 1 to 15, two numbers were drawn to determine the coordinates of the position in the smaller plot where the sample was to be taken.

Samples were taken at the predetermined positions by throwing down a cage held within a circular die mounted on the end of a pitchfork handle. The sampling cage was a cylinder of transparent celluloid that was capped with fine-meshed cloth and mounted on a cylindrical sheet-metal base for insertion within

the cutting die. To remove the samples the die was forced into the soil to a depth of about 5 inches by means of a rotary motion. During the winter, and at other times when the soil was moist, the contained sample could be removed undisturbed by lifting the die. At other times, to avoid disturbing the contained soil and roots of the plants, it was necessary to remove the soil from one side of the position with a trowel and to insert and hold a metal disk beneath the sample while it was removed from the die.

The samples were placed in a delivery truck and brought to the laboratory for examination under a strong light. When necessary the samples were watered in a shallow metal tray when placed in the truck. Nymphs and adults were removed from the sampling cages by means of a suction tube and were recorded according to the nymphal instars and sex and seasonal color forms of the adult. After examination the samples were incubated for a week at 92° F. to permit hatching of the eggs and were then reexamined to determine the number of eggs that had been present on the date of sampling. From 20 to 50 samples were taken at weekly intervals during the summer and 40 to 50 samples were taken every 2 weeks during the winter. These methods and the apparatus were developed and used in cooperation with D. E. Fox, who was studying the seasonal abundance of the beet leafhopper relative to that of some of its more important predators and other associated arthropods (36a).

BRIEF OUTLINE OF THE LIFE HISTORY

In southern Idaho the beet leafhopper overwinters in the adult stage chiefly in sagebrush areas and abandoned dry-farming sections where there are mustards or other suitable host plants. The insects are active and feed during the winter whenever the temperatures permit. The overwintering females are fertilized in the fall, and most of the males die during the winter. Preoviposition development is completed during the winter, and egg laying usually begins early in March. Leafhoppers of the first, or spring, generation develop in the same areas chiefly on flixweed (*Descurainia sophia* (Lam.) Webb) and green tansymustard (*Descurainia pinnata* subsp. *filipes* (Gray) Detling) and usually reach the adult stage by the end of May. The influx of adults of the spring generation to the cultivated areas begins at this time, and the movement reaches a peak 1 to 3 weeks later, depending chiefly on temperature conditions affecting maturation of the insects in the contributing breeding areas.

In this season temperatures permit rapid ovarian development, and the insects begin egg laying on arrival in the beet fields or within a few days thereafter. One generation or one and a part of another mature in beet fields during the remainder of the season.

During the spring movement of leafhoppers to cultivated areas, weedy sections in the deserts and in abandoned and cultivated farms are also populated.

Russian-thistle serves as the most important breeding host during the summer. Maturation of the second generation, or the third or overwintering generation of the season, occurs on Russian-thistle late in September and in October, when cooler weather produces the darker markings that characterize the overwintering adults. Another dispersal occurs as the third generation matures, and the leafhoppers again appear in the overwintering and spring breeding areas, where they enter the winter on fall-germinated mustards or less favorable plants that serve as hold-over food hosts.

STUDIES OF THE EGG AND NYMPHAL STAGES

DEVELOPMENT

Effects of constant temperatures

The incubation periods at different constant temperatures are given in Table 1. The time-temperature relationships for duration of the egg stage and the relative effect of different temperatures on the rate of development are illustrated in Figure 3.

The data show that the rate of embryonic development is rather closely proportional to the temperature between 65° and 93° F. and is well represented within

FIG. 3. Development of the beet leafhopper at different constant temperatures: A, Duration of the egg stage; B, rate of embryonic development.

TABLE 1. Duration of the egg stage of the beet leafhopper at different constant temperatures and 50% relative humidity.

Temperature (°F.)	Eggs observed	Time required	Index rate of development	Thermal increment
	Number	Days		Day-degrees
105	121	6.37± 0.06	15.70	299
100	547	5.51± .02	18.15	231
95	1,258	5.63± .01	17.76	208
93	552	5.74± .03	17.42	201
92	532	5.77± .04	17.33	196
90	603	6.27± .02	15.95	200
85	1,274	7.41± .01	13.50	200
80	511	9.23± .03	10.83	202
75	791	11.93± .02	8.38	202
70	270	17.40± .06	5.75	208
65	280	26.35± .06	3.80	183
60	32	43.84± .30	2.28	85

this range of temperature by a linear regression line. The values for the rate of development are indices equal to 100 divided by the time. The equation for the regression line, when fitted by the method of least squares, is $100/D = -29.1171 + 0.5014\ T$, in which $100/D$ is the rate of development and T is the temperature in Fahrenheit degrees.

In Figure 3 the straight line is extended to the zero line of the time scale, and this intersection at 58.07° F. indicates the threshold temperature where development theoretically ceases as the temperature is lowered. Actually the minimum temperature seems to be between 55° and 50°, but much of the value of the regression line data at higher temperatures depends on the point selected for zero development, as the thermal increments approach a constant value only when temperatures are measured from this level.

This was shown by Krogh (51) from the linear relation, $v = k.x$ between temperature (x) and the rate of development (v). Since the rate of development is expressed as the reciprocal of the time ($v = 1/y$), the equation may be written, $1/y = k.x$, or $1/k = x.y$, in which the product of time and temperature is a constant. In the same way the equation $100/D = -29.1171 + 0.5014\ T$ can be expressed as $100/0.5014 = D(T - 29.1171/0.5014)$ or $D(T - 58.07) = 199$ day-degrees. The product of the calculated duration (D) and temperature counted above 58.07° F., or $T - 58.07$, gives the same number of day-degrees for any point on the regression curve.

The thermal increments for the observed duration of the egg stage show that approximately the same number of day-degrees are required for embryonic development at different constant temperatures from about 65° to 95° F. (Table 1). At higher and lower temperatures the observed values deviate in opposite directions from the regression line (Fig. 3) and the thermal increments (Table 1) show corresponding departures from the calculated thermal constant of 199 day-degrees.

The duration of the nymphal stage of development at different constant temperatures is given in Table 2. Time-temperature relations for the nymphal period and the relative effect of different temperatures on the rate of development are illustrated in Figure 4.

The regression lines in Figure 4 have the equations $100/D = -13.2290 + 0.2255\ T$, and $100/D = -12.8095 + 0.2180\ T$, for males and females, respectively. In the time-temperature form the equations become $D(T - 58.67) = 443$ day-degrees and $D(T - 58.76) = 459$ day-degrees, respectively. Males complete the nymphal stage in about 3.5 percent less time than is required by the females. The regression equations for averages of the values for both sexes are $100/D = -12.9897 + 0.2214\ T$, and $D(T - 58.67) = 452$ day-degrees.

Approximately the same number of day-degrees (Table 2) are required for nymphal development at different constant temperatures from 65° to 93° F. The observed values for rates of development at
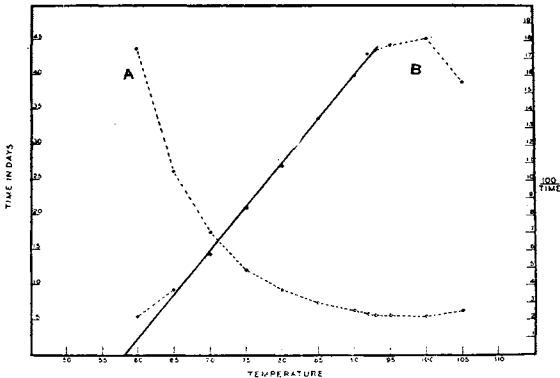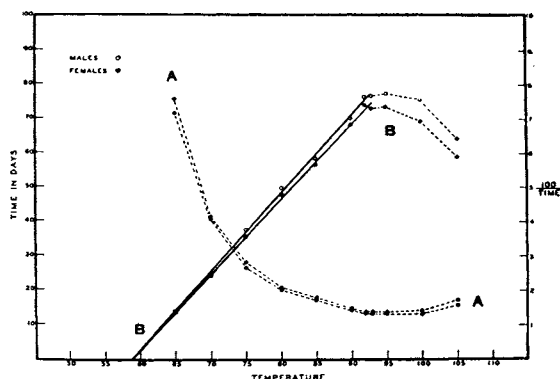

FIG. 4. Development of the beet leafhopper at different constant temperatures: A, Duration of the nymphal stage; B, rates of the nymphal development.

higher and lower temperatures deviate in opposite directions from the regression line (Fig. 4) and the thermal increments (Table 2) show corresponding departures from the calculated thermal constant of 452 day-degrees.

The thermal requirements for development from egg to adult, therefore, include 452 day-degrees above 58.67° F. for the nymphal stage plus 199 day-degrees above 58.07° for the egg stage, or a total of about 650 day-degrees. In round numbers these may be considered as 450, 200, and 650 day-degrees, respectively.

Embryonic periods of $6.05\pm.02$, $12.49\pm.04$, $17.09\pm.13$ and $25.99\pm.11$ days at 90°, 75°, 70°, and 65° F., respectively, for eggs of light colored adults collected during the summer do not show any marked differences from those just discussed and probably indicate that the thermal increments for development do not differ in progeny of the different seasonal color forms. Duration of the developmental stages of progeny of overwintered females collected from several of the Western States was also about the same when compared at the same time at 90° and 50% relative humidity. The embryonic periods were $6.31\pm.02$, $6.41\pm.02$, $6.41\pm.03$, and $6.27\pm.02$ days for progeny of adults from California, Colorado, Arizona, and Idaho, respectively, and the nymphal stage in the same order required $14.27\pm.11$, $14.58\pm.12$, $14.63\pm.11$, and $14.50\pm.07$ days.

Nymphs of the beet leafhopper were observed to molt five times when confined singly in small cages, and measurements of nymphs in different stages of development also indicate that there are five instars which may be reliably distinguished by the width of the head capsule. The weight prior to the final molt increases with lower temperatures and the nymphs are definitely larger, but frequency distributions of the head width of nymphs reared at 100° and 75° F. did not merge or indicate that there would be any overlapping of the measurements of successive stages developed at different temperatures. Averages of the head width in successive instars at the two temperatures are shown in Table 3. The ratio of increase

TABLE 2. Time required for the development of nymphs of the beet leafhopper at different constant temperatures and 50% relative humidity.

Temperature (°F.)	INSECTS REARED		TIME REQUIRED		INDEX RATE OF DEVELOPMENT		THERMAL INCREMENT	
	Males	Females	Males	Females	Males	Females	Males	Females
	Number	Number	Days	Days			Day-degrees	Day-degrees
105..............	210	193	15.59±0.17	17.03±0.19	6.41	5.87	722	788
100..............	288	256	13.23± .11	14.44± .11	7.56	6.93	547	596
95..............	245	241	12.96± .10	13.63± .11	7.72	7.34	471	494
93..............	325	316	13.02± .10	13.74± .11	7.68	7.28	447	471
92..............	307	285	13.14± .08	13.52± .08	7.61	7.40	438	450
90..............	209	214	14.32± .10	14.67± .10	6.98	6.82	449	458
85..............	280	244	17.10± .11	17.68± .12	5.85	5.66	450	464
80..............	164	149	20.07± .12	20.89± .15	4.98	4.79	428	444
75..............	228	235	26.69± .19	28.28± .16	3.75	3.54	436	460
70..............	171	165	40.44± .24	41.17± .25	2.47	2.43	458	463
65..............	53	33	70.91± .53	75.42± .81	1.41	1.33	449	471

in head width seems fairly constant in accordance with the principle of Dyar (21) as is shown by comparison of the observed means with the corresponding values calculated by least squares. Estimated by least squares, the average increase in width of the head capsule is 26 to 27 percent in successive instars. Other studies (Harries & Henderson 37) show that the head width of successive instars increases about 25 percent but only about 5.5 percent from the fifth instar to the adult.

TABLE 3. Average width, in millimeters, of the head capsule of successive instars of the beet leafhopper reared at 100° and 75° F. and 50% relative humidity.

Instar	100° F.		75° F.	
	Observed	Calculated	Observed	Calculated
1................	0.326±0.001	0.331	0.328±0.004	0.333
2................	.422± .005	.420	.428± .005	.420
3................	.544± .006	.532	.532± .005	.529
4................	.678± .006	.673	.667± .005	.667
5................	.838± .005	.853	.836± .009	.841

Average durations of the different nymphal instars at 90° F. and 50% relative humidity are shown in Table 4. As noted by Carter (14), the first and last instars are of longer duration than are the intermediate stadia.

TABLE 4. Average duration of the different stadia of the beet leafhopper in laboratory rearings at 90° F. and 50% relative humidity.

Stadium	Nymphs observed	Average duration
	Number	Days
1................	45	3.38± 0.10
2................	44	2.29± .11
3................	43	2.39± .11
4................	41	3.07± .14
5................	38	3.76± .20

The average weight approximately doubles in successive instars, and at the end of the nymphal stage it is more than twenty times that at hatching. The daily increase in weight at 90° F. and 50% relative humidity is shown in Table 5. These data, illustrated in Figure 5A, define a typical sigmoid curve of growth in which the daily increment or rate of growth increases with increased weight of the insect during the major portion of the stage and then declines as the
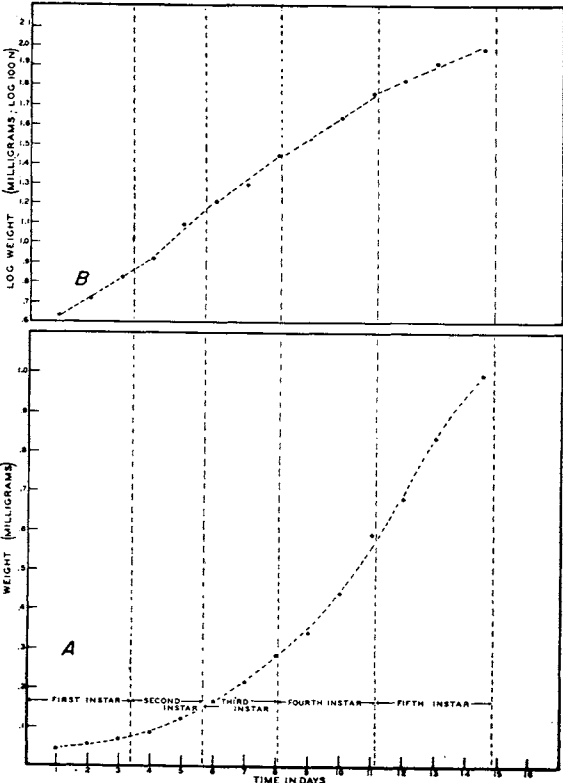

FIG. 5. Nymphs of the beet leafhopper during development at 90° F. and 50 percent relative humidity: A, Average daily weight; B, logarithms of weights.

adult stage is approached. When logarithms of the weights are plotted against time to illustrate the ratio of increase in weight during the nymphal stage, the growth curve appears to consist of 5 linear segments of different slope, indicating that growth occurs at different rates in successive periods which evidently correspond to the different instars (Fig. 5B). Weight of the nymphal and adult stages was observed and recorded by weighing lots of 50 nymphs or 10 adults at about the same hour each day. Similar S-shaped curves were shown by Brindley (10) for larval growth of the Mediterranean flour moth (*Ephestia kühniella* Zell.) and the confused flour beetle (*Tribolium confusum* Duv.) at a constant temperature.

TABLE 5. Daily increase in weight of the beet leafhopper, nymph to adult stage, at 90° F. and 50% relative humidity.

Age	Individuals weighed	Average weight	Growth ratio
Days	*Number*	*Mg.*	
1............	300	0.043	....
2............	350	.053	1.23
3............	400	.067	1.26
4............	400	.084	1.25
5............	400	.126	1.50
6............	500	.168	1.33
7............	450	.198	1.18
8............	400	.279	1.41
9............	500	.335	1.20
10............	550	.448	1.34
11............	650	.592	1.32
12............	500	.680	1.15
13............	550	.835	1.23
14.5[1]........	260	.994	1.19

[1] In adult stage.

Temperature coefficients

Although it seems doubtful that there is any fundamental basis for relating simple equations to physiological processes that may be the resultant of many reactions, both chemical and physical, such expressions are often of considerable interest because of their general descriptive value. Effects of temperature show many contrasts in the descriptive value and theoretical significance of different analytical expressions. In general, many of the data define curves of increasing slope in which the rate of activity appears to be some type of exponential function of temperature (20, 26, 33, 34, 40, 46, 51, 65, 74, 75, 84, 92) while other results indicate that the rate of activity is closely proportional to temperature as would be described by a straight line (9, 34, 51, 56, 68, 78, 85, 93).

In Figures 6 and 7 data on duration of the egg and nymphal stages are related to different expressions advanced by Krogh (51), van't Hoff (43), Arrhenius (3), and Belehrádek (7). The data are plotted according to graphs of the equations in linear form, and the extent of agreement is shown by the approach of the values to lines of best fit calculated by the method of least squares.

A quantitative expression of the idea that completion of a definite period of development requires a definite amount of heat expressed in temperature summations was presented by Sanderson & Peairs (78) in 1913. In 1914 Krogh (52) and Blunck (9) described the same relationship, which is often referred to as Blunck's or, more commonly, as Krogh's law. According to this principle, as expressed by Krogh's formula ($V_{t10} = V_t + K_{10}$), the increase in rate of development is proportional to the rise in temperature. Close agreement of data on the egg and nymphal stages with the Krogh equation was discussed previously as a basis for summing temperatures, but is illustrated in Figures 6 and 7 for comparison with that of other analytical expressions.

FIG. 6. Data on duration of egg stage of the beet leafhopper at different temperatures plotted with reference to the analytical expressions of A, Krogh; B, van't Hoff; C, Arrhenius; and D, Belehrádek.

According to the equation of van't Hoff, the rate of activity is a simple exponential function of temperature in which the ratio of increase in rate is constant and is expressed as Q_{10}, or in terms of a difference of 10 Centigrade degrees in temperature. The logarithm of rate is therefore proportional to the temperature in the linear form of the equation. When the data are plotted in this way in Figures 6, B, and 7, B, for the egg and nymphal stages, respectively, the distribution of points does not approach linearity for any appreciable range in temperature and from the curvilinear trend of the values relative to the calculated lines it is evident that Q_{10} decreases progressively with higher temperatures and cannot therefore be a constant for the processes.

The equation of Arrhenius associating rate of chemical reactions with temperature has also been widely used in describing the effect of temperature

on biological processes. In the linear form of the equation the logarithm of rate is proportional to the reciprocal of the absolute temperature. Figures 6, C, and 7, C, show that the data are not in agreement with the formula for any appreciable range in temperature.

Belehrádek (7) has related the effect of temperature on certain biological processes to an influence of protoplasmic viscosity on rates of diffusion at different temperatures, by the formula $y = a/x^b$ where y is time, x is Centigrade temperature, and a and b are constants. In this equation the logarithm of time is proportional to the logarithm of temperature in the linear form, $\log y = \log a - b \log x$. In some instances as was pointed out by Belehrádek, agreement of data with the equation sometimes depends on a correction made by counting temperatures above the biological minimum for the process instead of zero Centigrade. In such cases where the temperature scale is so adjusted, the rate of activity $(1/y)$ becomes more proportional to temperature as the value of the constant b approaches one, and when b equals one the equation becomes identical with that of Krogh (Belehrádek 7). In fitting the present data there was no substantial agreement with the equation until temperatures were counted from levels considerably above zero Centigrade. The best agreement seems to be obtained when b approaches a value of one in counting temperatures above 58° F. or near the theoretical developmental zeros indicated by intersection of the regression lines with the temperature axis in Figures 6A, and 7A. The close agreement shown in Figures 6D, and 7 D may therefore be only incidental, because the rate of development is closely proportional to temperature, but Belehrádek (7) suggested that the Krogh expression is a special case of the more general equation relating physiological processes to temperature.

Effects of alternating temperatures

Duration of the embryonic period under alternating high and lower temperatures is given in Table 6, together with the theoretical time that should be required on the basis of data shown in Table 1 for full-time development at each of the two temperatures. The time theoretically necessary for development in alternate exposures to two different temperatures was computed as follows: Since the egg stage was completed in 5.51 days at 100° F. and in 6.27 days at 90°, the sum of the percentages, 12/24 × 100/5.51 plus 12/24 × 100/6.27, for alternate exposures of 12 hours daily at each temperature represent 17.05 percent of the developmental time per day and the theoretical time necessary for development is, therefore, 100/17.05, or 5.86 days.

Comparison of the observed and calculated values shows that the egg stage was generally completed in less time than that theoretically necessary, or that development was relatively faster under alternating temperatures than at thermally equivalent constant temperatures. The amount of acceleration averages about 5 percent under the different conditions, but appears to be influenced by the temperatures involved, since a marked trend is shown toward greater acceleration as the range between the higher and lower temperatures increased.

Data on duration of the nymphal stage under alternating temperatures are shown in Table 7, together with the time theoretically required for development on the basis of results obtained at constant temperatures (Table 2), computed as previously described for similar data on the egg stage. Nymphal development was also completed in less than the expected time, with an average acceleration of about 8 percent apparently resulting from the alternate changes in temperature.

Reference to Figures 3 and 4 or Tables 1 and 2 shows that temperatures between 95° and 100° F. are relatively noneffective and should not be included in the summation. The inhibitory effect of still higher temperatures must also be taken into account when appreciable accumulations occur above 100°, and in this case the summation may be roughly adjusted by subtracting the number of day-degrees above 100 from the effective total summed between 58° and 95°. This adjustment for the higher temperatures, in the example of data on the effects of constant and alternating temperatures in Tables 1, 2, 6, and 7, brings the values much nearer the respective constants of 200 and 452 day-degrees for the egg and nymphal stages as is shown by the following summations:
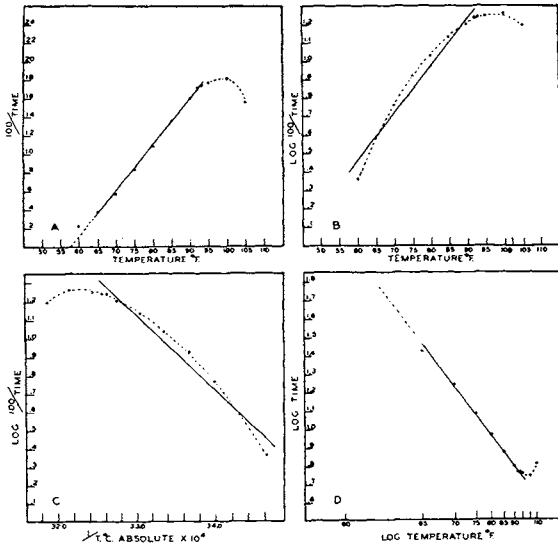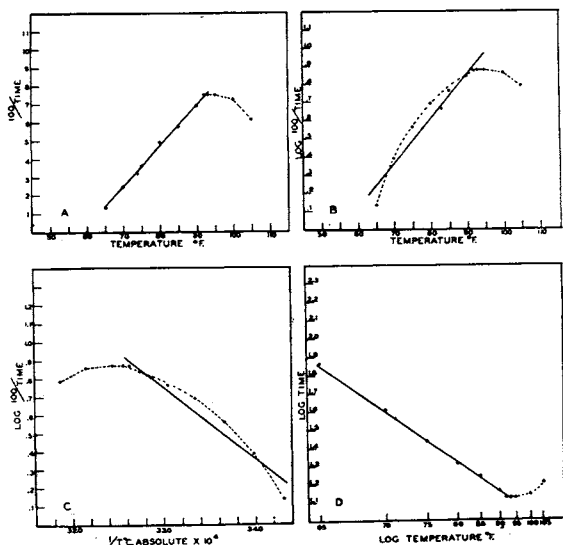

FIG. 7. Data on duration of the nymphal stage of the beet leafhopper at different temperatures plotted with reference to the analytical expressions of A, Krogh; V, van't Hoff; C, Arrhenius; and D, Belehrádek.

	EGG STAGE		NYMPHAL STAGE	
°F.	Day-degrees		°F.	Day-degrees
105	203		105	511
100	203		100	503
100-90	200		100-95	442
100-85	196		100-80	440
100-65	188		100-75	451
100-40	187			

TABLE 6. Duration of the egg stage of the beet leafhopper at alternating constant temperatures, together with the calculated time based on constant-temperature values. . Relative humidity was about 95% at 40° F. and 50% at all other temperatures.

12 HOURS DAILY AT EACH TEMPERATURE

Alternating Temperatures (°F.)	Eggs observed	Time required	Calculated time	Deviation	Thermal increment
	Number	Days	Days	Percent	Day-degrees
100 and 90	320	5.82±0.02	5.86	− .68	215
100 and 85	294	6.13± .02	6.32	−3.01	211
100 and 65	97	8.58± .05	9.11	−5.82	210
100 and 40	90	10.13± .02	11.02	−8.08	212
95 and 90	212	5.70± .02	5.93	−3.88	196
95 and 85	514	6.14± .02	6.40	−4.06	196
92 and 80	249	6.69± .03	7.10	−5.77	187
92 and 65	436	8.93± .02	9.47	−5.70	182
93 and 40	849	10.67± .01	11.48	−7.06	186
90 and 85	356	6.54± .02	6.79	−3.68	192
90 and 70	427	8.74± .02	9.22	−5.21	192
90 and 65	429	9.53± .03	10.13	−5.92	185
90 and 60	267	10.12± .03	10.97	−7.75	171
85 and 75	247	9.21± .03	9.14	+ .77	202
85 and 70	113	10.01± .03	10.39	−3.66	194
85 and 65	234	10.93± .04	11.56	−5.45	185
80 and 75	353	9.88± .02	10.41	−5.09	192

8 HOURS DAILY AT HIGH TEMPERATURE AND 16 HOURS DAILY AT LOW TEMPERATURE

80 and 60	231	19.06± .07	19.49	−2.21	164
90 and 60	52	13.42± .07	14.63	−8.27	160
90 and 50	150	16.15± .05	18.81	−14.14	172

TABLE 7. Duration of the nymphal stage of the beet leafhopper at different alternating constant temperatures when held for 12 hours daily at each temperature. Relative humidity was about 95% at 40° and 50% at all other temperatures.

Temperature (°F.)	INSECTS REARED		TIME REQUIRED		CALCULATED TIME		DEVIATION		THERMAL INCREMENT	
	Males	Females	Males	Females	Males	Females	Males	Females	Males	Females
	Number	Number	Days	Days	Days	Days	Percent	Percent	Day-degrees	Day-degrees
100 and 95	85	91	11.71±0.14	12.64±0.17	13.26	14.25	−11.69	−11.30	455	490
100 and 85	101	113	13.50± .15	14.56± .14	14.91	15.90	− 9.46	− 8.43	457	491
100 and 70	71	56	18.35± .20	19.52± .23	19.92	21.37	− 7.88	− 8.66	483	512
95 and 90	73	81	12.73± .15	13.52± .17	13.79	14.35	− 7.69	− 5.78	430	456
95 and 85	82	74	13.28± .10	14.04± .14	14.96	15.65	−11.23	−10.29	416	439
95 and 70	90	93	17.72± .19	18.01± .18	19.61	20.49	− 9.64	−12.10	422	428
95 and 40	88	90	25.12± .20	25.77± .22	25.92	27.26	− 3.09	− 5.47	456	467
93 and 80	178	194	15.71± .14	16.44± .14	15.80	16.58	− 0.57	− .84	437	456
92 and 75	165	152	16.80± .11	17.21± .11	17.61	18.28	− 4.60	− 5.85	417	426
93 and 65	161	131	19.99± .12	20.85± .18	22.03	23.20	− 9.26	−10.13	407	422

Effects of time of exposure to different temperatures

In the effects of alternating temperatures on embryonic development, a definite trend toward greater acceleration is shown as the range between the higher and lower temperatures increased (Table 6). Cook (15) has shown in studies of cutworm larvae that the effect of alternating temperatures is determined by the time of exposure to different temperatures as well as by the temperatures involved. In alternately subjecting the cutworm larvae to different temperatures for various periods of exposure, Cook found that the amount of acceleration increased with greater differences in temperature within a range of 8° to 32° C. and with shorter daily exposures of 8 and 4 hours at the higher temperature.

Data in Table 8 indicate that the percentage of embryonic development of the present species also increases with decrease in time of exposure from 20 to 8 hours daily at the higher temperature. Further

studies of this phase of the effect of temperature on embryonic development of the beet leafhopper (35) have shown that in exposures of 4, 8, 12, 16, and 20 hours daily at 90° F. alternating with exposures for the remainder of each 24-hour period at 80°, 70°, 60°, or 50°, the percentage of acceleration increased with shorter exposures at the higher temperature and with greater differences between the higher and lower temperatures. Inasmuch as the daily period of higher temperatures tends to shorten with increase in the daily range of temperature occurring in the spring and fall, both factors of temperature and time of exposure would apparently act to the advantage of the species in permitting more development than would otherwise occur in the cooler seasons of the year.

TABLE 8. Duration of the egg stage of the beet leaf-hopper under varying periods of exposure to high and low temperatures and 50% relative humidity at both temperatures.

HOURS OF EXPOSURE AT		Eggs observed	TIME		Deviation
90° F.	65° F.		Required	Calculated	
		Number	Days	Days	Percent
24	0	603	6.27± 0.02	.....	......
20	4	395	7.39± .03	7.18	+2.92
16	8	170	8.25± .03	8.40	−1.79
12	12	229	9.67± .03	10.13	−4.54
8	16	149	12.11± .05	12.74	−4.95
4	20	54	16.44± .12	17.17	−4.25
0	24	280	26.35± .06	.....	......

In other studies of differential effects of temperature on development of the beet leafhopper (36) a single change from a higher to a lower temperature resulted in completion of the egg and nymphal stages in a shorter time than could be expected. This effect evidently was not due to a direct stimulus, since a reverse change between the same two temperatures usually resulted in an increase in the time required rather than a decrease. Apparently there are at least two different growth phases within the egg and nymphal stages that are unequally affected by different temperatures, and these time differences indicate that the rate of development at a lower temperature is relatively less in the earlier part of the embryonic and nymphal periods and greater in the later portions, in comparison with the rates at a higher temperature, than is indicated by the average rates based on the time required for completion of the entire stages at each temperature. Therefore, the time necessary for development under alternating or variable temperatures cannot be computed accurately from durations of the entire stages at different constant temperatures.

The relatively more rapid development at lower temperatures in the later nymphal stages apparently would enable more of the larger nymphs, which occur abundantly late in the fall, to complete development than would otherwise reach the adult stage in which the insect passes the winter.

Effects of varying temperatures

Except at temperature extremes, the egg and nymphal stages have been shown to require the accumulation of approximately an equal number of effective day-degrees for development at any constant temperature, but the total effect of normally varying temperatures cannot be measured accurately on this basis because of the factor of acceleration shown in comparisons of the relative effect of constant and alternating temperatures. The direct summing of effective temperatures in day-degrees must therefore be recognized as a method of approximation, since effects of differences in temperatures involved, in time of exposure to different temperatures, and in phases of development completed at different temperatures are too complex to be taken completely into account.

Summations recorded with a thermograph under varying temperatures in a greenhouse insectary, during periods represented by the average duration of the egg and nymphal stages in groups of insects of the same age, are in fairly good agreement with the specified thermal constants. The area on the thermograph chart under the recorded line between 58° and 95° F. was measured with a planimeter and computed in day-degrees. During these experiments the daily temperatures were generally fluctuating between 55° and 90° and occasionally between 50° and 100°. Results of successive tests, for egg and nymphal stages as compared with the respective constants of 199 and 453 day-degrees, are shown as follows:

EGG STAGE		NYMPHAL STAGE	
Insects reared per test	Day-degrees	Insects reared per test	Day-degrees
860	198	184	413
174	191	236	434
153	219	181	411
		244	455
		118	405

The weighted average for tests on the egg stage falls very close to the thermal constant of 199 day-degrees, and that for the nymphal stage shows an acceleration of about 6 percent, which is a fairly common deviation in previous results obtained under alternating temperatures.

Effects of seasonal temperatures

During 1934 and 1935 studies of seasonal development were carried on by sampling representative plots in the desert breeding areas. In the spring of 1934 the plot was located near Wendell, Idaho, in a fairly uniform stand of flixweed. When drying of the mustard or spring host plants occurred, sampling was continued on another plot located in an adjacent stand of Russian-thistle, *Salsola kali* var. *tenuifolia* Tausch (Fig. 8). Hygrothermograph records were taken under an instrument shelter placed on the ground with the heat sensitive element elevated about 5 inches above the surface of the soil. Recordings of temperatures between 58° and 95° F. were measured with a planimeter and computed in day-degrees for comparison with seasonal development of the leafhopper. Soil-surface temperatures and records of

FIG. 8. Second plot at Wendell, Idaho, showing stand of Russian-thistle and subdivision by stakes placed at the corners of the smaller plots.

precipitation were also obtained during the progress of the studies.

The spring of 1934 was exceptionally early, and the spring generation of leafhoppers matured much earlier than normally. Egg laying of the overwintered insects began early in March. Nymphs of the spring generation had begun to appear when sampling was started on April 18. The light-colored adults of the spring generation began to appear about April 28, and the beginning of the migration or influx of these adults to the cultivated areas was noted about the same time. Standard-shade air temperatures recorded at the laboratory in Twin Falls, Idaho, during maturation of the spring generation in 1934 totaled only about one-half the necessary day-degrees between 58° and 95° F., but summation of soil-surface temperatures were about equal to the required amount.

During the spring, temperatures recorded in the shade are evidently inadequate as a measure of the actual environment, since the day-degree summations up to the date of the spring movement rarely total more than one-half of the necessary amount for development through the egg and nymphal stages. In this season of the year the insects seem especially subject to soil-surface temperatures, which generally range much higher than air temperatures and are more than sufficient to account for the seasonal development observed. The host plants are usually very short during the egg and early nymphal stages in the spring, and on cold days, and sometimes when air temperatures are near or below the minimum for development, nymphs are observed to obtain much higher temperatures exposed to full sunlight on the plants or barren areas of soil.

Adults of the spring generation were most numerous about May 15. Eggs and nymphs of the

second generation were most abundant about May 20 and June 5, respectively, and between these dates the accumulation of effective temperatures at 5 inches above the ground was approximately equal to the required sum of 200 day-degrees for duration of the egg stage. Adults of the second generation were approaching maximum abundance by the middle of July and the required sum of effective temperatures, or about 450 day-degrees, was accumulated between June 6 and July 11.

There was considerable overlapping of the second and third generations, but the presence of a third generation of the season was clearly indicated by the abundance of eggs and small nymphs in the last half of July following maturation of the second generation adults. Nymphs of the third generation were most abundant about the end of July, following accumulation of the necessary increment of 200 day-degrees for the egg stage during the last half of the month, and reached the adult stage late in August and early in September, after approximately the required sum of 450 day-degrees for nymphal development had been recorded during August.

During maturation of the second generation from about May 15 to July 15, and the third generation between July 15 and August 31, there was a slight excess of recorded temperatures that would about account for preoviposition development of the second generation, but otherwise the progress of seasonal development seemed to check at least as closely with the recorded thermal increments as the peaks of abundance could be determined in estimating the average duration of the stages.

Temperatures accumulated after the end of August, when the third generation matured, were sufficient for a partial fourth generation. However, owing to the

early spring and the effects of extreme drought and higher-than-normal temperatures during the summer, the Russian-thistle was maturing and drying prematurely during September, and the appearance of eggs and nymphs of a fourth generation on the plot was apparently prevented by unfavorable condition of the host plants.

The population studies were continued during 1935 on a plot near Berger, Idaho, where there was a fairly uniform stand of spring host plants, mostly flixweed, and a sufficient admixture of Russian-thistle for plant succession to carry the leafhoppers through the season. In this year spring development of the leafhopper was about 2 weeks later than usual, but temperatures during the remainder of the summer were about normal.

Oviposition of the overwintered adults in 1935 began during the first part of May, and the eggs were most numerous about May 20. Nymphs began to appear about May 10 and were most abundant around the first of June. Adults of the spring generation were first noted about June 5, when the movement began, and reached a maximum toward the middle of June. As in the preceding year, the first nymphs of the spring generation matured well before the necessary accumulation of effective air temperatures had been recorded, but records of soil-surface temperatures exceeded the required summation during the same period.

Insufficient data were obtained on the occurrence of eggs during the remainder of the season, but nymphs of the second generation began to appear early in July and were most abundant toward the end of the month. Maturation of the second generation was delayed by lower than normal temperature accumulations during the first half of July. Increments of temperature recorded between peaks of abundance of nymphs of the first and second generations on about June 1 and August 1, respectively, were near the estimated amount necessary for a generation. Apparently the peak of abundance of the second-generation adults came about September 1, or after the accumulation of approximately 450 day-degrees during August.

Nymphs of the third generation appeared during the latter half of August and were reaching maximum abundance about the middle of September, or when about 200 day-degrees necessary for development in the egg stage had been accumulated following the peak of abundance of the second generation adults. Adults of the third generation began appearing in late September and were becoming most abundant in October during colder weather. Only about two-thirds of the necessary temperature accumulation for maturation of nymphs of the last generation was recorded after September 1. Many larger nymphs were present with the advent of colder weather, but many or most of these seemed to complete development with the aid of higher soil-surface temperatures.

In 1935 population samples were also taken in beet fields at weekly intervals during the season. The movement of leafhoppers of the spring generation to beet fields began about June 5, when the first insects were reaching the adult stage in the desert. The number of adults reaching the beet fields increased slowly at first and then more rapidly to about June 25 and the increase coincided generally with the progress of maturation of the spring generation in the desert breeding areas. Ovarian dissections and cage tests indicated that the leafhoppers began ovipositing within 2 or 3 days after arriving in the beet fields. Nymphs were abundant in the latter part of July. Adults of this generation produced in the beet fields reached a peak of abundance in late August and early September, as the corresponding second generation of the season was maturing on wild host plants in the desert areas. Only one complete generation of leafhoppers developed in beet fields during the season, and few if any adults of another generation appeared before harvest of the beets in October.

Considerably greater accumulations of effective temperatures for development are obtained in the actual environment than are recorded between 58° F. and 95° by the standard shade thermograph (5 feet above the ground). Also, temperatures at different levels above the ground are apparently not closely enough correlated to establish an accurate basis for summing standard-shade temperatures for this purpose. Comparisons of standard-shade temperatures, accumulated above 40°, 45°, 50°, and 55° on the thermograph charts, indicate, however, that such temperatures should be summed above levels of 45° to 50° to correspond most closely with those near the ground or between 58° and 95° in the actual environment of the insect.

Summations of standard shade temperatures between 50° and 90° F. at Twin Falls, Idaho, from thermograph records available since 1926 have given the following seasonal accumulations:

Year	Day-degrees	Year	Day-degrees
1926	2,700	1932	2,400
1927	2,300	1933	2,600
1928	2,600	1934	3,300
1929	2,500	1935	2,600
1930	2,700	1936	2,700
1931	2,900	Mean	2,664

This method seems to underestimate the actual temperatures during the spring, according to dates of the maturation and movement of adults of the first generation to the cultivated areas, but tends to overestimate the effective seasonal totals as compared with those taken near the ground in 1934 and 1935 during sampling studies of seasonal development on the desert plots.

The 11-year average of 2,664 day-degrees is about equal to the estimated sum required for three generations, including preovipositional development of the first and second generations, and is nearly the same as that shown above for 1935, when maturation of the third generation seemed fairly complete. The seasonal accumulations thus seem to check fairly well with field observations that there are 3 generations

annually in southern Idaho, the last generation some-times maturing late in the season and perhaps limited by a deficiency of annual temperatures.

The beet leafhopper was reared through several successive generations in the green house and appar-ently will continue to reproduce indefinitely under favorable temperature conditions. The number of generations occurring annually appears, therefore, to be determined by the seasonal temperature accumula-tions in the different areas of distribution. As many as. 15 to 16 developmental cycles, through the egg, nymphal, and preovipositional stages, would be pos-sible annually under experimental conditions of about 95° F., but since the relatively long oviposition period permits some of the earlier progeny to mature before the last eggs are deposited, the minimum would seem to be about 8 and the average number of cycles about 12. Since considerably more than half of the eggs are deposited during the first half of the oviposition pe-riod, an average of about 12 cycles seems to be a conservative estimate of the number of complete gen-erations possible annually under the most favorable experimental conditions for rapid development. Ap-parently, temperatures in the hotter areas of the Southwestern States would produce 6 to 8 complete generations annually, although their identity is lost later in the season because of overlapping or fusion of the succeeding generations.

Effect of Temperature on the Time of Migration

The first influx of beet leafhoppers to the cultivated area has generally been considered as marking the date of migration. The major part of the movement usually occurs considerably later, and its progress co-incides generally with maturation of the spring gen-eration. The movement increases slowly at first and then more rapidly, and reaches a peak usually 1 to 3 weeks later, depending on weather conditions, chiefly temperature affecting the rate of maturation of the insects in the contributing breeding areas.

From the time egg laying begins in the spring the leafhopper requires an accumulation of about 650 day-degrees between 58° and 95° F. to reach the adult stage. The major portion of the movement cannot occur much before this total is obtained. The thermal constant of 650 day-degrees is based on mean durations of the egg and nymphal stages in groups of the same age, and when development occurs at different constant temperatures. Because of the accel-erative effect of varying temperatures, and difference in the minimum and average times for development under the same conditions, the beginning of the movement could be expected somewhat in advance of the date indicated by the specified thermal increment necessary for maturation of the spring generation. Frequency distributions of durations of the stages under the same conditions show that the minimum is uniformly about 15% less than the mean, regardless of temperature. Estimating the acceleration at from 5 to 10% on the basis of data on development at alternating temperatures, and under varying temper-atures in the insectary, the total reduction of 20 to

25% would correspond to from 75 to 80% of the normal temperature increment, or about 490 to 520 day-degrees.

Comparison of the observed migration dates and soil-surface temperatures at Twin Falls for the years 1927-34, for which complete records are available, shows an average accumulation of about 513 day-degrees above 58° and below 95° F., after March 1 and preceding the beginning of the movements (Table 9). In comparison with standard shade temperatures measured in the same way for the years 1927-36, the migrations always began considerably before the amount necessary for development to the adult stage had been recorded. This illustrates the inadequacy of standard shade temperatures as a measure of the actual environment of the insect especially during the spring when the host plants are very short. In this connection, Carter (14: 12; Tables 3, 4) has shown that soil-surface temperatures generally exceed those of standard shade throughout the year and that the maximum temperatures at 6 inches above the ground were consistently higher during the winter and spring months than those of the soil surface or at any other level. Also, during the spring on bright calm days when the heat of reflection is greater and less rapidly dissipated, the insects may be observed feeding, or resting on exposed areas of the soil, under favorable to optimum temperatures when standard shade tem-peratures are well below the minimum for develop-ment or even for physical activity.

Evidently it is such increments of favorable tem-peratures that enable the insect to complete ovarian development during the winter months and thus the time when egg laying begins in the spring may be determined. When day-degrees of effective soil-surface temperatures from different dates back to November 1 of the preceding year are included in the summation, the correlation between the observed migra-tion dates and the recorded temperatures is not improved (Table 9).

Although the thermal requirements for develop-ment can be determined rather accurately under con-trolled conditions, the intraenvironmental differences in temperature make it difficult to correlate closely seasonal development with the available thermograph records. On the basis of correlation with the actual environmental temperatures, standard shade temper-atures summed above 45° F. are also compared in Table 9 with the observed dates of the initial migra-tions. This level seems near the appropriate base for summing standard shade temperatures since sums above 50° average about two-thirds of the necessary accumulation for maturation of the spring generation, and above 40° the required increment is exceeded by about the same amount. By including the day-degrees accumulated during the period December through February, the average deviation of the temperature summation from the 10-year mean is reduced from 65 to 48 day-degrees, indicating only a slight improve-ment in the estimate of the mean. Inclusion of the data for November does not improve this estimate.

By taking 670 day-degrees above 45° F. (Table 9)

TABLE 9. Summations of standard shade temperatures above 45° F. and of soil-surface temperatures above 58° and below 95° from different dates to the time of the spring migration of the beet leafhopper to the cultivated areas.

STANDARD SHADE TEMPERATURES ABOVE 45 ' F.

Year	Migration date	Day-degrees of Temperature Counted from				
		March 1	February 1	January 1	December 1[1]	November 1[1]
1927	June 13	703	707	709	717	778
1928	May 14	461	462	464	472	555
1929	June 9	705	705	705	706	754
1930	May 24	580	621	622	678	732
1931	do	648	650	650	650	695
1932	June 13	765	765	765	766	819
1933	June 6	639	639	644	648	710
1934	April 28	578	634	646	679	739
1935	June 5	672	676	676	677	777
1936	May 25	704	707	707	707	708
	Average	646	656	659	670	727
	Average deviation	65	55	54	48	48

SOIL-SURFACE TEMPERATURES ABOVE 58° AND BELOW 95° F.

1927	June 13	496	496	496	496	...
1928	May 14	406	406	406	406	422
1929	June 9	690	690	690	690	696
1930	May 24	460	477	477	478	482
1931	do	631	631	631	631	653
1932	June 13	615	615	615	615	615
1933	June 6	405	405	405	405	414
1934	April 28	401	427	427	432	485
	Average	513	518	518	519	538
	Average deviation	99	95	95	95	100

[1] Of the previous year.

as the mean accumulation of standard-shade temperatures to the date of migration, the correspondence between the dates when this total is attained and those of the observed migrations is represened by a correlation coefficient of 0.957, adjusted for the number of cases. This agreement is illustrated in Figure 9. In the present series of observations the standard error of estimate of 4.27 days was exceeded once in the 10-year period (Fig. 9). This was in 1928, when the initial movement apparently began about 10 days before it could be expected according to the standard shade temperature records.

Despite the high correlation coefficient, the initial movement cannot be anticipated reliably on the basis of standard shade temperatures. This seems to be due largely to the effect of sunlight or differences in the vertical temperature gradient above the ground in different years. At least this seems to account for much of the wide discrepancy in 1928, since soil-surface temperatures in this year were about equal to those in 1933 and 1934 and were exceeded only 22% by those in 1927, when in standard shade temperatures the accumulation was 53 percent greater (Table 9). Carter (14, Table 7), in terms of recorded area on the thermograph charts above 60° F. to the initial movements, shows an accumulation of 22.1 square inches in soil-surface temperatures through May 14, in 1928, or a deficiency of about 11%

as compared with 24.9 square inches through June 13, in 1927.

According to the correlation coefficient, 0.957, about 92% of the variation in the time of migration may be accounted for by the thermal accumulations during the spring. Since this leaves about 8% of the
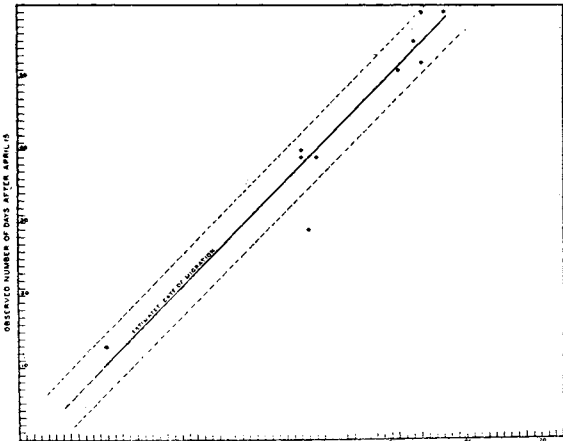

FIG. 9. Relation of estimated date determined from the standard shade temperature summations to the observed time of migration of the beet leafhopper. The dotted lines indicate the standard error of estimate of ± 4.27 days.

variation attributable to other factors, including the
unreliableness of standard shade temperatures as a
measure of the actual environment, evidently temper-
ature is the most important variable governing the
time of migration.

Spring temperatures are especially important, be-
cause the extent of crop damage is determined by
the time of occurrence as well as by the magnitude
of the movement. This is because the plants are
more susceptible to effects of the virus when infected
in earlier stages of growth.

Temperature accumulations at Twin Falls, Idaho,
for weekly intervals during the different years of
study by the laboratory have been illustrated in
Figure 10 in comparison with a smoothed curve
approximately representing the mean summation of
temperatures in successive weeks during the 12-year
period. Serious curly top injury to sugar beets
occurred in 1926, 1928, 1930, 1931, and 1934, when
the date of movement was advanced by greater than
normal accumulation of effective temperatures for
development of the spring generation of leafhoppers,
as is shown by the blackened area above the curve
preceding the average date of migration. Temper-
ature deficiencies from the average increments are
similarly illustrated by cross-hatched areas below the
curve. Good yields of sugar beets were obtained in
1927, 1929, 1932, and 1935, when the spring temper-
ature accumulations were below normal and the initial
movements occurred after the average date. Since
1935 newly developed strains of sugar beets resistant
to curly top have been planted and the yields have
fluctuated much less widely in different years.

Effects of humidity

Being inserted within the tissue of the plant, eggs
of the beet leafhopper seem to be relatively inde-
pendent of atmospheric moisture. As shown in Table

10, duration of the egg stage at different relative
humidities and a constant temperature is about the
same; and there is no regular order of variation that
would indicate any effect of atmospheric moisture on
the rate of development at 85°, 90°, and 100° F.

The data show very little difference in length of
the nymphal stage for either males or females under
eight different percentages of relative humidity at
92° F., but at 100° for both sexes the rate of devel-
opment decreased as the relative humidity increased
from 10 to 50 and to 90%. Under the distinctly
unfavorable 90 percent relative humidity at 100°,
where only 9 of 500 specimens completed the stage,
there was a definite retardation in the rate of devel-
opment. When the temperature was lowered to 70°,
the stage lengthened for both males and females with
an increase from 50 to 80% relative humidity. Only
two conditions of relative humidity are compared in
this case and the results are not very presumptive,
but the time differences are statistically significant
for both sexes.

In general the development of insects seems to be
more rapid at the higher relative humidities. The
egg stages of *Prodenia litura* (F.) (Janisch 47) and
Microbracon hebetor (Say) (Maercks 57); larval
stages of the bean weevil (*Acanthoscelides obtectus*
(Say)) (Menusan 62), *Tribolium confusum* Duv.
(Holdaway 44), and *Tineola bisselliella* (Hum.)
(Griswold & Crowell 28); and pupal stages of *Win-
themia quadripustulata* F. (Hefley 39), *Pyrausta
nubilalis* (Hbn.) (Caffrey & Worthley 13), *A. ob-
tectus* (Say) (Menusan 62), and the yellow mealworm
(*Tenebrio molitor* L.) (Payne 67) were observed to
require less time for development in moist than in
drier air at the same temperature. Wigglesworth
(94) cites other examples of this and also some cases
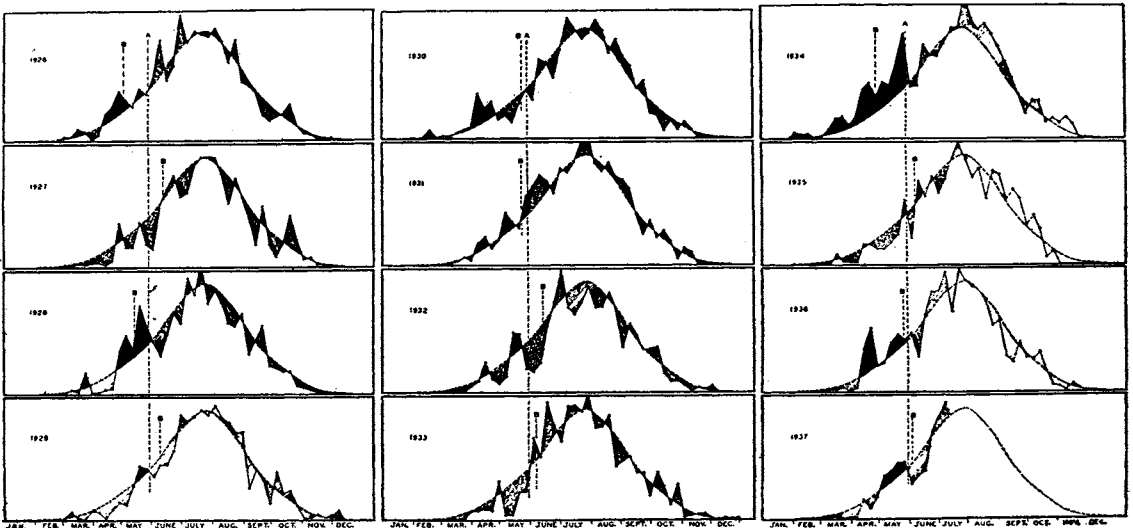where the rate of development was retarded at very

FIG. 10. Thermal summations in day-degrees of standard shade temperatures above 50° and below 90° F. for
weekly intervals, 1926-1937, Twin Falls, Idaho: A, Average date of migration for the 12 years; B, date of migration
for each year.

TABLE 10. Duration of the developmental stages of the beet leafhopper under different temperature and humidity conditions.

Temperature (°F.)	Relative humidity	Egg Stage		Nymphal Stage			
				Reared		Time required	
		Reared	Time required	Males	Females	Males	Females
	%	Number	Days	Number	Number	Days	Days
100	10	...	...	179	173	13.98±0.11	14.08±0.10
	20	154	5.67±0.04	...	...	...	...
	50	547	5.51± .02	288	256	13.23± .11	14.44± .11
	80	204	5.85± .04	...	...	...	...
	90	...	...	4	5	13.00±....	16.00±....
92	20	...	...	300	300	12.86± .07	13.62± .07
	30	...	...	250	271	13.35± .10	13.83± .09
	40	...	...	370	334	13.02± .07	13.68± .08
	50	...	...	307	285	13.14± .08	13.52± .08
	60	...	...	472	411	13.05± .07	13.66± .08
	70	...	...	170	170	13.39± .14	13.84± .15
	80	...	...	218	190	13.18± .09	13.85± .10
	90	...	...	161	130	13.10± .15	13.52± .18
90	30	405	6.50± .03	...	...	...	...
	50	358	6.05± .02	...	...	...	...
	60	264	6.37± .03	...	...	...	...
	80	320	5.94± .02	...	...	...	...
85	30	105	7.56± .05	...	...	...	...
	50	599	7.54± .05	...	...	...	...
	50	1,274	7.41± .01	...	...	...	...
	70	309	7.59± .05	...	...	...	...
70	50	...	...	171	165	40.44± .24	41.17± .25
	80	...	...	36	40	43.53± .54	45.05± .49

high humidities. Certain other insects, such as *Toxoptera graminum* (Rond.) (Headlee 38), *Heliothrips haemorrhoidalis* (Bouché) (Rivnay 75), and onion thrips (*Thrips tabaci* Lind.) (MacGill 60), appear to be quite independent of atmospheric humidity.

Effects of light

The egg stage was slightly longer in total darkness than under about 80 foot-candles of continuous illumination, but it was found that this difference evidently resulted from an inhibiting effect of darkness on emergence from the egg after embryonic development was completed. The emergence of leafhoppers completing embryonic development during the hours of darkness would thus tend to be delayed until stimulated by sunlight and rising temperatures in the morning, and the effect of light would evidently account for much of a diurnal rhythm in which most of the eggs were observed to hatch during the early morning and daytime.

The eyes of the embryonic nymph in its later stages of development are to some extent exposed to light, inasmuch as they are readily discernible from the exterior of the plant. The poles of the egg, when in the oviduct, correspond in orientation with those of the female in accordance with the law of Hallez (30), so that the cephalic end of the egg, being last to leave the ovipositor, is always less deeply embedded and is ordinarily covered with only the relatively transparent cuticle of the plant when ready to hatch.

The effect of light on hatching was studied under controlled conditions by turning the lights off and on at definite intervals and covering the windows in top of the cabinets with a blanket during periods of darkness. The results are illustrated in Figure 11 by plotting the number hatching in two lots of eggs, held at 80° F., that were alternately exposed to darkness and an illumination of about 80 foot-candles. In both lots most of the eggs hatched while the lights were on regardless of whether this period occurred during the daytime or at night.

Effects of light factors were not critically or extensively investigated, but the indications were that the rate of nymphal development is not influenced appreciably by differences in illumination or by ultraviolet radiation. In these tests temperature and humidity were held constant, and higher intensities of illumination could not be used because of the heat factor. A sun lamp suspended within the cabinets directly over the insect cages was used as the source of ultraviolet radiation. The cages were similar to those used in other experiments (Fig. 1) except that the tops were closed with cellophane. At the distance used, 30 inches, the lamp was rated at about one-third that of midday midsummer sunlight as a source of ultraviolet in the portion of the spectrum that is ordinarily biologically effective.
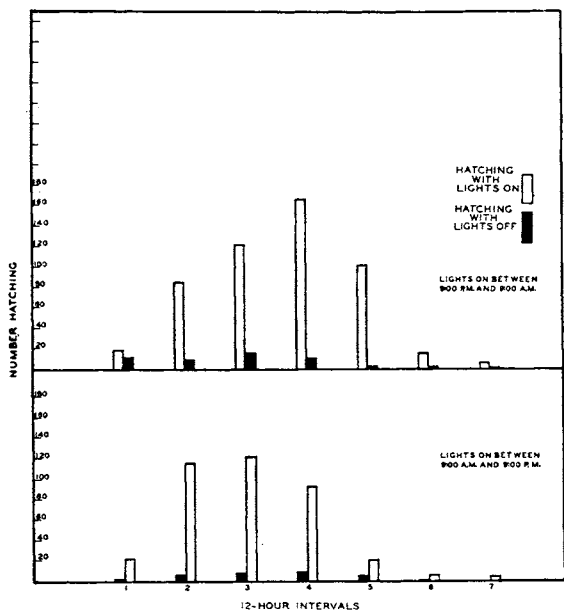
FIG. 11. Number of beet leafhopper eggs hatching in two lots during alternate intervals of illumination and darkness.

At 92° F. and 50% relative humidity the duration of the nymphal stage under continuous exposure to ultraviolet radiation was 13.37 ± 0.10 days for 251 nymphs and under similar exposure to 80 foot-candles of illumination with no ultraviolet, 13.32 ± 0.07 days for 592 nymphs. In another test at 90° and 50% relative humidity, the nymphal stage was 15.16±0.15 days in total darkness and 15.22±0.16 days under continuous lighting of about 40 foot-candles. The difference in time was not significant in either case.

Effect of host plants

The beet leafhopper has been collected from a large number of plant species. Many of these serve only as temporary food plants, but, nevertheless, an imposing list of breeding host plants has been recorded. The more important breeding plants include filaree, *Erodium* sp. (Geraniaceae); many species of saltbush, *Atriplex* spp.; Russian-thistle (*Salsola pestifer* A. Nels.); *Bassia* sp. (Chenopodiaceae); blistercresses, *Erysimum* spp.; peppergrasses, *Lepidium* spp.; and tansymustards, *Descurainia* spp. (Cruciferae).

Haegele (29) listed tumbling orach (*Atriplex rosea* L.), Russian-thistle, *Bassia hirsuta* (L.) Aschers, tumblemustard (*Sisymbrium altissimum* L.), and green tansymustard (*Descurainia pinnata* (Fourn.) Howell subsp. *filipes* (Gray) Detling) as the principal host plants in Idaho. It was later emphasized by Carter (14) that the leafhopper requires a sequence of these plants in which Russian-thistle and tumbling orach are the principal summer and fall breeding plants, and the mustards *S. parviflora* (Lam.) Webb., *D. pinnata* subsp., *filipes* and *Sisymbrium altissimum* are the most important breeding hosts in the spring and

carrying-over hosts for the overwintering adults in the fall and winter. Similar conditions in northern Utah were reported by Knowlton (49) except that *Erysimum repandum* L., *Lepidium perfoliatum* L., and *Erodium cicutarium* (L.) L'Her. were listed as additional host species of importance in this region.

Studies of the nutrition of insects have shown that elementary food substances such as nitrogen or vitamins may influence the rate of growth. Development of the boll weevil (*Anthonomus grandis* Boh.) was observed to be more rapid in young bolls than in old ones (Fenton & Dunnam 23) and to decline as the size of the boll increases (Isely 45). Isely suggested that the observed differences in growth rate may have been due to changes in the nitrogen content of the plant, as it was shown that the percentage of nitrogen declined progressively from squares to large bolls. Peterson & Hauessler (70) observed that development of the oriental fruit moth (*Grapholitha molesta* (Busck)) was more rapid in peaches than in apples. The larval period of the Indian-meal moth (*Plodia interpunctella* (Hbn.)) was found to be shorter on figs than on prunes or raisins (Hamlin, Reed, and Phillips 32). Hodge's experiments (42) on growth of the differential grasshopper (*Melanoplus differentialis* (Thos.)) have shown that the rate of development of this species was considerably more rapid on some food plants than on others. Seamans & McMillan (81) reared the pale western cutworm (*Agrotis orthodonia* Morr.) on wheat, oats, barley, rye, alfalfa, sugar beets, sweetclover, and several weed hosts. They showed that development was more rapid on the grains and alfalfa than on the weed host plants.

Under experimental conditions considerable difficulty was experienced in maintaining weed host plants in good condition, and frequent transfers of the leafhoppers to fresh plants were necessary. Experimental factors evidently contributed to an excessively high mortality, and for this reason the results may not provide a fair comparison of the viability of nymphs on the different host plants employed.

As shown in Table 11, the plant is evidently not an important factor in the duration of the egg stage, but the time required for development of nymphs varies considerably on different host plants. Many of these data do not show significant differences in the time required for development, but a trend toward slower growth is indicated on less favorable plants, where a high mortality was observed.

MORTALITY

Effects of temperature and relative humidity

Mortality in the egg stage was difficult to determine since the eggs could not be counted at the beginning of the experiments, and at the termination of the tests hatched and unhatched eggs could not be reliably distinguished by the technique used. An unfavorable effect of the temperature extremes of 105° and 65° F. was plainly indicated, however, by the number of nymphs that died with the heads protruding from the plant tissue.

TABLE 11.   Duration of the egg and nymphal stages of the beet leafhopper on different host plants at 90° F. and 50% relative humidity.

Host Species	Egg Stage		Nymphal Stage	
	Insects observed	Time required	Insects observed	Time required
	Number	*Days*	*Number*	*Days*
Sugar beet, *Beta vulgaris* L.............................	603	6.27±0.02	423	14.50±0.07
Tumblemustard, *Sisymbrium altissimum* L..................	202	6.35± .03	...	....
Red stem filaree, *Erodium cicutarium* (L.) L'Her..........	...	....	14	15.00± .58
Russian-thistle, *Salsola Rali* var. *teniufolia* Tausch..........	112	6.28± .04	..	....
Flixweed, *Sophia parviflora* (Lam.) Webb..................	485	6.29± .02	35	15.63± .20
Blistercress, *Erysimum bakeri* (Greene) Rybd.............	...	....	19	16.00± .25
Wild lettuce, *Lactuca serriola* f. *integrifolia* Bogenh........	...	....	16	16.62± .53
Peppergrass, *Lepidium alyssoides* Gray....................	...	....	15	17.13± .52

The nymphal mortality observed in studies of development at different constant temperatures and 50% relative humidity (Table 2) are shown in Figure 12A. The mortality ranged from about 25 to 39 percent at moderate temperatures, but there were marked increases at the more extreme temperatures. Temperatures in a range of about 75° to 93° F. seem most favorable, but large survivals at 95°, 100°, and 105° indicate considerable tolerance of high temperatures, which is consistent with the insect's occurrence in abundance under high temperatures in the desert environment. It was observed that mortality in the nymphal stage at alternating constant temperatures was affected little by sudden temperature changes of rather wide range.

In some years, in Idaho and other northern areas of distribution, the standard shade temperature may fall below 50° F. for considerable periods in March and April during maturation of the spring generation. Such periods of cold, wet weather, which greatly retard development for 1, 2, and 3 weeks or more, appear to be unfavorable for survival of the embryonic and nymphal stages.
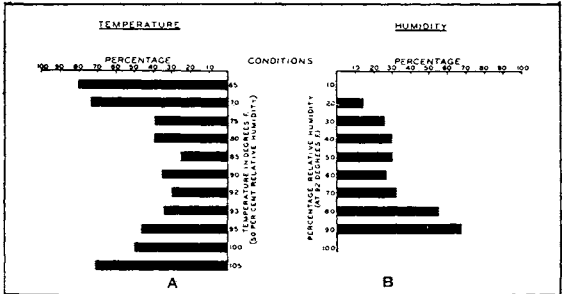

FIG. 12. Mortality of beet leafhopper nymphs: A, Under different temperatures with a constant relative humidity of 50 percent; B, under different percentages of relative humidity, but at a temperature of 92° F.

Other experiments were conducted, in which three periods of exposure to four different conditions of temperature and relative humidity were superimposed on three different stages of development in all combinations, giving 3 × 4 × 3, or 36, different treatments. In these experiments the eggs in early,

medium, and late periods of development, and nymphs of the first, third, and fifth or last instars were exposed for 1, 2, and 3 weeks at temperatures of 40° and 50° F. and relative humidities of 30 and 80% at each temperature. Each experiment on eggs and nymphs consisted of six tests on different dates.

Small potted sugar beet plants were used in studies of the egg stage, since flixweed, the most common spring host plant, did not remain in good condition under the reduced illumination in the cabinets for the period of more than 4 weeks necessary to complete some of the tests. The groups of eggs were obtained by confining 5 ovipositing leafhoppers on different plants for 24 hours at 90° F. Plants containing these eggs were then assigned at random to the different treatments. The nymphs, reared at 90° F., were confined in groups of 25 on flixweed plants and then assigned at random to the different treatments.

The analysis of variance of results for the egg stage shows a significant difference in mortality of the different periods of embryonic development, and a highly significant effect of time of exposure, mortality increasing with later stages of development and with longer periods of low temperatures.

Analysis of variance of data on the nymphs shows highly significant effects of all three factors in which mortality increases with lower temperature, longer exposure, and with earlier stages of development. These effects are illustrated by the following averages of data for the different treatment groups:

°F	% Mortality
50	39.2
40	53.2
Difference required for significance	4.7

Time of exposure, weeks	
1	35.8
2	45.6
3	57.2
Difference required for significance	4.1

Instar	
First	79.4
Third	37.1
Fifth	22.0
Difference required for significance	5.4

Highly significant interactions are also shown between temperature and stage of development, time of exposure and stage of development, and temperature and time of exposure. According to these effects, high nymphal mortality results from relatively shorter exposures with increasingly lower temperatures.

Nymphal mortality increases with lower temperatures and the time of exposure to cold, and both factors have relatively greater effect on the smaller nymphs. With increase in cold, shorter exposures have relatively greater effect on nymphal mortality. Difference in relative humidity at these low temperatures seems to have no appreciable effect on nymphal mortality.

An increased mortality in the egg stage was observed under conditions of high humidity in combination with high temperatures. At moderate temperatures differences in relative humidity had no appreciable effect.

Differences in relative humidity at high temperatures have a marked influence on mortality in the nymphal stage, however. The results included in Table 12 show a progressive increase in mortality as the relative humidity increases from 20 to 90% at 92° F., the correlation coefficient being +0.88. Similar results are shown by data obtained at higher and lower temperatures. Decidedly low relative humidity furnishes a well-defined optimum of atmospheric moisture. Higher percentages of saturation are especially unfavorable at higher temperatures, and at 100° a relative humidity of 90% is near the maximum permitting development through the nymphal stage. It seems probable that these effects result directly from humidity since no evidence of bacterial or fungous infection was observed.

The present results show that relatively low humidities are most favorable, and in this respect the beet leafhopper differs from many other species that have been studied. Relatively high percentages of saturation were found to be more favorable for all stages of the bean weevil (Menusan 62); larvae of the boll weevil (Isely 45); all stages of *Trichogramma minutum* (Riley) and eggs of Angoumois grain moth (*Sitotroga cerealella* (Oliv.)) (Lund 55); and larvae of the onion thrips (MacGill 60). Further data and conclusions, showing low humidities most favorable in the case of different insects or stages, may be found in papers by Peterson (69), Elwyn (22), Davies (18), Zwölfer (95), and Sweetman & Wedemeyer (89).

The data on nymphal mortality in Table 12 have the same correlation with the saturation deficiency as with relative humidity, since these measures are inversely proportional at the same temperature. The results, therefore, cannot be compared to any purpose with differences in saturation deficiency at the same temperature. Nymphal mortality at different temperatures and the same relative humidity decreases from 71 percent at 105° F. to about 30% in the range of 92° to 85°, and then increases with lower temperatures, while the saturation deficiency decreases pro-

TABLE 12. Mortality of beet leafhopper nymphs under different relative humidities.

PROGENY OF OVERWINTERING ADULTS

Temperature (°F.)	Relative humidity	Mortality
	%	%
92	20	14.29
	30	25.57
	40	29.60
	50	29.94
	60	26.42
	70	32.00
	80	54.67
	90	63.62
100	10	41.33
	90	98.20

PROGENY OF SUMMER ADULTS

90	30	34.60
	50	37.70
	60	58.60
	80	61.10

gressively from the highest temperature to the lowest (Fig. 12). It is evident, therefore, that the combined effects of temperature and humidity on nymphal mortality cannot be expressed in terms of the saturation deficiency.

STUDIES OF THE ADULT

COLORATION

Coloration in the adult stage becomes generally darker as the temperatures at which the insects develop grade downward. At higher temperatures the color ranges from pale yellow at 105° F. to greenish yellow at 100°. Between 95° and 90° the adults are greenish or pale green, and darker areas begin to appear on the wings at 85° to 80°. Color forms having more and darker areas on the wings, vertex, and pronotum are produced at 80° to 75° and at lower temperatures. When reared at high, moderate, or lower temperatures, the insects show a gradation of color characteristic of the "summer, spring, and overwintering forms" in California as described by Severin (82).

Adults of the spring brood in southern Idaho are generally greenish, but in some years they are often marked with darker areas on the wings and are difficult to distinguish from the overwintered insects. During the warmest part of the summer many pale-green and some yellowish individuals are found which resemble those reared at the higher controlled temperatures. Insects that attain the winged stage during colder weather later in the season always bear the dark-colored markings that characterize the overwintering form.

Effects of temperature on coloration of the adult are determined in the last instar probably during

formation of the wings and hypodermis preceding the final molt. This evidently explains the sudden appearance, during cool periods in the spring, and following the first cool weather in the fall, of adults having dark wing markings.

There is considerable random variation in color markings of the nymphs, but those reared at lower temperatures are generally darker especially in the later stages of development. Nymphs hatching from eggs incubated at 60° to 65° F. are grayish white in color, whereas those from eggs kept at moderate or higher temperatures are white.

Coloration appears not to be affected within the adult stage as suggested by Ball (6), since no modifications in color were produced by the exposure of the darker overwintered adults to high temperatures or by subjecting the light-colored summer adults to low temperatures for prolonged periods.

Darker adults could be expected in the field when the maximum temperatures drop below 80° F. for several days in succession, but it is difficult to evaluate exact conditions of varying temperatures necessary to produce a distinct division into dark and light forms, because coloration is influenced by both the time of exposure and the degree of cold in relation to different stages of nymphal development. This is also more complicated by the fact that the color forms intergrade and individual variation may also occur under the same conditions.

Coloration of the adult does not seem to be influenced by any other factors, such as light, atmospheric moisture, sexual development, or age.

The effect of temperature in color aberrations of Lepidoptera is well known, and Knight (48), Genieys (27), Schlottke (79), Parker (66), and Marcovitch & Stanley (59) have shown in other orders that low temperatures produce darker colored adults than higher temperatures.

SIZE

Some seasonal variation occurs in the size and weight of the adult leafhoppers. The lighter-colored adults produced during warmer weather are generally smaller than the darker adults of the overwintering generation that mature in the fall. Larger adults were also produced at lower temperatures under controlled conditions. Males are almost invariably smaller than females that develop at the same temperatures. This difference in weight between the sexes becomes more pronounced with ovarian maturation in the females.

The average weights on the first day of the adult stage for males and females reared through the nymphal stage at different temperatures and 50% relative humidity are shown in Table 13.

Other observations indicating that larger insects are produced at lower than at higher temperatures have been recorded by Standfuss (88), Dewitz (19), Schlottke (79), Titschack (90), Alpatov & Pearl (1), and Menusan (64).

TABLE 13. Average weight, at emergence, of adults of the beet leafhopper reared through the nymphal stage at different constant temperatures and 50% relative humidity.

Temperature (°F.)	Males	Females	AVERAGE WEIGHT	
			Males	Females
	Number	Number	Mg.	Mg.
100	70	70	0.794	1.069
90	130	130	.841	1.146
85	100	80	.865	1.143
80	100	100	.891	1.196
75	120	130	.897	1.230
70	100	100	.903	1.274

SEX RATIO

The sexes are about evenly divided in numbers, with perhaps a slight normal excess of males. The percentage of females was 48.5 in 12,199 adults reared in different experiments. No consistent effect of temperature or humidity on the sex ratio was noted.

Marked differences in the proportion of male and female adults are usually observed in the field. Males require less time for development, and the majority of the first adults to appear in the breeding areas are males. The females apparently have a greater tendency to move when reaching the adult stage, and in such areas the preponderance of males usually continues, whereas in areas populated by dispersal movements the females usually occur in greater numbers. The greater mortality of males increases the sex ratio during the winter, and in southern Idaho almost all the overwintered leafhoppers are females.

FERTILIZATION

Fertilization seems to occur soon after the adult stage is reached and generally before avarian maturation. Copulation was observed on the first, second, and third days following emergence at 95° F. The mating of older insects was not observed. Females that emerged within a 24-hour period at 90° and that were segregated at the end of this period, laid fertile eggs. Repeated fertilizations are evidently not necessary, since different lots of females used as a source of eggs and nymphs continued to produce fertile eggs throughout life. The observation of Severin (82) that the eggs of virgin females do not hatch was also verified.

THE PREOVIPOSITION PERIOD

Effects of temperature

The length of the preoviposition period ranges from 5 to 6 days in midsummer to 6 or 7 months during the winter. With the occurrence of lower temperatures in the fall there seems to be little, if any, preoviposition development of the darker overwintering form appearing at this time. Development appears to be suspended by the decreased temperatures in the fall and to be resumed following exposure to more extreme cold. This serves to delay oviposition over the winter until conditions permit survival and

development of the next generation. This ovarian quiescence appears to be induced only by seasonal temperature changes in the fall, since both summer and overwintering forms always complete the preoviposition period rapidly under controlled conditions at temperatures above 90° F.

Ovarian maturation, like embryonic and nymphal development, is most rapid at about 95° F. (Table 14). Some leafhoppers of both forms complete ovarian maturation at decreased temperatures without exposure to extreme cold, but an increasingly greater proportion of them seem unable to complete development as the temperature is lowered. As was described by Carter (14: 4, 24), the rate of development does not follow the straight-line relationship and ovarian maturation cannot be correlated with ordinary temperature summations.

TABLE 14. Duration of the preoviposition period of the beet leafhopper at different constant temperatures and 50% relative humidity.

SUMMER FEMALES

Temperature (°F.)	Females	Time required	Index rate of development
	Number	Days	
105.........	25	5.32±0.28	18.80
100.........	47	4.66± .22	21.46
95.........	25	3.96± .26	25.25
94.........	15	3.87± .18	25.84
92.........	24	5.00± .23	20.00
90.........	52	5.31± .19	18.83
85.........	45	9.93± .32	10.07
80.........	47	13.83± .31	7.23
75.........	50	16.74± .59	5.97
70.........	29	25.07± .50	3.99

OVERWINTERING FEMALES

100.........	11	2.64± .14	37.88
90.........	32	3.28± .08	30.49
85.........	31	4.13± .20	24.21
75.........	17	5.06± .16	19.76
70.........	12	8.50± .28	11.76
65.........	18	14.56± .86	6.87
60.........	21	21.76± .68	4.60

Overwintering females that had been exposed to outdoor temperatures during October, November, and December were able to complete ovarian development at constant temperatures of 60° and 65° F., whereas females of the summer form that had not been exposed to the outdoor temperatures were not able to complete development at these constant temperatures. At higher temperatures the preoviposition period for the overwintering form was shorter than for the summer form, being only a third as long at 75° F. Exposure to cold was evidently a contributing factor, but it is probable that some ovarian development in the overwintering females had taken place before the exposure to constant temperatures.

Durations of the preoviposition period in alternate

12-hour exposures to high and lower temperatures, with some comparisons of relative effects of constant and alternating temperatures on the rate of ovarian development, are shown in Table 13. The time theoretically necessary for development in alternate exposures on the basis of results obtained at constant temperatures was computed as described for data on the egg stage.

TABLE 15. Duration of the preoviposition period of the beet leafhopper (summer form) at alternating constant temperatures and 50% relative humidity.

Temperature (°F.)	Females	Time required	Calculated time	Deviation
	Number	Days	Days	%
110 and 90........	11	7.09±0.27	....	....
100 and 90........	19	4.05± .23	4.96	−18.35
100 and 75........	16	6.12± .25	7.29	−16.05
100 and 70........	27	6.59± .40	7.86	−16.16
90 and 85........	26	7.38± .35	6.92	+ 6.65
90 and 75........	16	7.31± .23	8.06	− 9.31
90 and 70........	16	9.94± .32	8.76	+13.47

The differences shown in the relative effect of constant and alternating temperatures on the preoviposition period are rather variable, but there is considerable indication that temperature changes produce an acceleration, as occurs in embryonic and nymphal development, because results of most of the tests show a gain in time. It is also shown that leafhoppers of the summer form complete the preoviposition period in a relatively short time in exposures to 90° and 100° F. in combination with lower temperatures. It seems also that ovarian maturation would occur under extremely high maximum temperatures in the field because development was completed in alternate exposures to 110° and 90°. Ovarian maturation was not attained, however, in continuous exposure to 110°.

Effects of humidity

Humidity has an effect on duration of the preoviposition period similar to that described for the nymphal stage. The retarding effect of temperatures above the optimum is slightly accentuated by increase in atmospheric moisture. As is shown in Table 16, at 100° F. the length of the stage apparently in-

TABLE 16. Duration of the preoviposition period of the beet leafhopper under different humidity conditions.

Temperature (°F.)	Relative humidity	Females	Time required
	%	Number	Days
100..........	10	37	4.19± 0.18
	50	47	4.66± .22
	90	17	4.71± .37
92..........	40	18	4.78± .26
	50	24	5.00± .23
	80	20	5.00± .36
	90	22	5.18± .22

creases with the increase in relative humidity. The data obtained at 92° also show a slight trend of the same sort, but there are no significant differences.

Effects of light

A test of the effect of light on the duration of the preoviposition period was conducted at 90° F. and 50% relative humidity. Insects that developed through the nymphal and preoviposition periods during continuous exposure to the sun lamp were compared with other insects that were reared through the same stages in total darkness. The length of the preoviposition period for the group under the sun lamp was 4.00 ± 0.18 days, and for the group reared in total darkness, 3.73 ± 0.20 days. The difference is not significant.

Fertilization does not seem to have a marked effect on the rate of ovarian maturation. At 90° F. and 50% relative humidity, 5.31 ± 0.26 days was required for preovipositional development of fertile females and 5.57 ± 0.26 days for virgin females. No significant difference is shown.

OVIPOSITION

Effects of constant temperatures

The leafhoppers used in studies of oviposition were collected in the field, or taken from outdoor cages during the winter, when in the preoviposition stage of development and were held at 90° F. until oviposition began. Excluding those already laying or found to deposit eggs on the first day, a sufficient number beginning egg laying on the same day were divided at random into different groups and placed under different temperatures in controlled cabinets. The total number of eggs laid by each female was ascertained in studies of fecundity. The rates of oviposition under different experimental conditions, however, were not determined until after allowing an adjustment period of 3 days to minimize any effects of previous temperatures, and then the records were taken for only 7 or 10 days in the first part of the oviposition period when egg laying was more uniform among individuals, and the mean rate was more constant over a period of time. The females were always confined singly in cages placed over the petiole and basal portion of the leaves of small potted sugar beet plants, and males were included with them during the preoviposition period at 90°, except in the case of overwintering females, which are normally fertilized in the fall.

The effect of temperature on fecundity of the leafhopper was not investigated throughout the possible gradient, but the oviposition period and the total number of eggs deposited were found to decrease rather sharply at temperatures above 90° F. (Table 17). Egg production seems to be directly limited by higher temperatures, since laying ceases in about 1 day at 115° and in 4 days at 110°, although the females usually live several days longer. Some eggs were also deposited at 120°, but the adults succumbed

TABLE 17. Effects of high temperatures at 50% relative humidity on the length of the oviposition period and the total number of eggs deposited by the beet leafhopper.

Temperature (°F.)	Females	Eggs Deposited		Oviposition Period	
		Average	Maximum	Average	Maximum
	Number	Number	Number	Days	Days
115	25	4.80± 0.93	17	1.08±0.19	3
110	31	34.61± 3.39	70	4.26± .20	6
100	50	132.86±11.57	324	15.52±1.14	32
90	100	229.97±14.92	541	25.71±1.93	79

in a few hours. The maximum temperature for continued formation and deposition of eggs is near 105°.

When held at 90° F., a group of 67 females deposited 270.45 eggs per female after being removed from outdoor cages in January and February 1932, and an average of 229.97 eggs per female was obtained from a lot of 100 overwintered females in 1934. Maximum depositions of 675, 641, 541, 526, and 508 eggs per female were recorded. Frequency distributions of the data are shown in Figure 13.
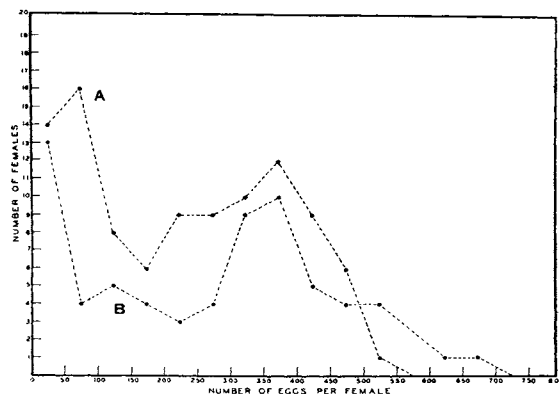

FIG. 13. Frequency distributions illustrating the fecundity of 100 overwintered females of the beet leafhopper: A, In the spring; B, of 67 females removed from outdoor cages in January and February.

The modes of the distributions indicate that the majority of overwintered females may deposit between 300 and 400 eggs under favorable conditions. Probably owing to the occurrence of individuals weakened by exposure to winter conditions, a relatively high mortality early in the tests of females laying fewer than 100 eggs, reduced the average abnormally below the modal number. Stahl (87) observed a maximum deposition of 247 eggs by 1 female and Severin (82) reported an average of 350 eggs from 5 females.

Records of the effects of temperature on the rate of oviposition include data on the egg laying of the light-colored or summer-form adults in August, of the darker overwintering generation late in September (Table 18), and of overwintered adults in March and April (Table 19).

Table 18. Oviposition of summer and fall generations of the beet leafhopper at different constant temperatures and 50% relative humidity.

Temperature (°F.)	Summer-Form Adults in August			Overwintering Adults in September		
	Females	Eggs	Rate of egg laying[1]	Females	Eggs	Rate of egg laying[1]
	Number	*Number*		*Number*	*Number*	
90.....................	16	875	7.81±0.68	18	1,231	9.77±0.56
80.....................	13	456	5.01± .51	19	818	6.15± .37
70.....................	15	282	2.69± .31	17	343	2.88± .27
60.....................	15	153	1.46± .19	15	147	1.40± .10
55.....................	15	72	.69± .11	14	83	.85± .15

[1] The average daily deposition per female during a 7-day period.

Table 19. Oviposition of beet leafhopper of the overwintering generation in the fall and in the spring at different constant temperatures and 50% relative humidity.

Temperature (°F.)	Overwintering Adults (September and October)			Overwintering Adults (March and April)		
	Females	Eggs	Rate of egg laying[1]	Females	Eggs	Rate of egg laying[1]
	Number	*Number*		*Number*	*Number*	
100.....................	21	1,011	6.88±0.47	20	1,712	12.23±0.87
90.....................	18	1,231	9.77± .56	45	3,647	11.58± .42
85.....................	20	945	6.75± .43	14	840	8.57± .54
80.....................	19	818	6.15± .37	16	696	6.21± .57
75.....................	18	526	4.17± .27	25	878	5.02± .36
70.....................	17	343	2.88± .27	25	549	3.14± .24
65.....................	19	282	2.12± .15	25	391	2.23± .18
60.....................	15	147	1.40± .10	19	184	1.38± .26
55.....................	14	83	.85± .15	15	46	.44± .16
50.....................	13	54	.59± .13	15	9	.09± .08

[1] The average daily deposition per female during a 7-day period.

There was a progressive acceleration in the laying rate in all cases as the temperature increased from 55° to 90° F. The oviposition rate of insects of the overwintering generation in the fall was also generally higher than that of the summer-form adults (Table 18), and the rate of egg laying of overwintering insects in the fall was generally exceeded by that of the overwintered females in March and April, after exposure to severe winter temperatures (Table 19). The maximum rate occurred at 90° to 100° F., where the average female laid from 8 to 12 eggs daily. This rate may be maintained for a considerable time, as is shown by an average of about 9 eggs per day for about 26 days by a group of 100 females held at 90° (Table 17). Exceptional females may deposit as many as 30 eggs in a 24-hour period at temperatures of 90° to 100°. With higher temperatures the rate of oviposition is more briefly stimulated and declines more rapidly.

In Figure 14, it is seen that the oviposition rate is not proportional to temperature as would be described by Krogh's formula, but the rising portions of the curves are apparently of the exponential type commonly described by other analytical expressions. In the range of 60° through 90° F. the same data have been fitted to the equations of van't Hoff (B), Arrhenius (C), and Belehrádek (D). Apparently a better fit is obtained with the first two equations. In
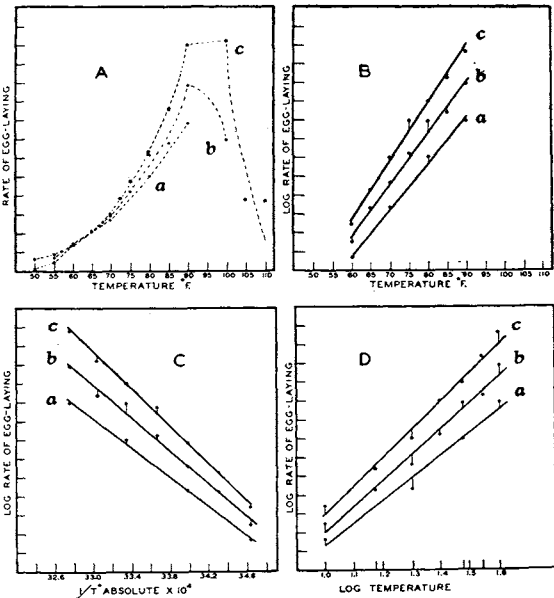

Fig. 14. Rates of egg laying of beet leafhoppers of (a), the summer form in August; (b), the overwintering generation in September; and (c), in March and April when plotted: A, directly against temperature; and according to the equations of B, van't Hoff; C, Arrhenius; and D, Belehrádek.

this case, as was pointed out in a previous discussion of temperature coefficients for insect oviposition (Harries 34), it seems that the percentage increase in rate is closely proportional to the increase in temperature and may be described as well by the more simple van't Hoff formula or preferably by the analogous expression, $y = Ae^{bx}$, which may be used without regard to any theoretical implications associated with the former equation.

Oviposition occurred at temperatures as low as 45° F., but the eggs may have been completely formed in previous exposure to higher temperatures. In this connection Bliss (8) has pointed out in studies of other species of leafhoppers that oviposition may be conditioned directly by temperatures at the time of egg laying and indirectly by the effect of previous temperatures on ovarian maturation of the eggs. The lowest temperature for continued oviposition seems to be near 50°, but this minimum appears subject to some seasonal variation because leafhoppers previously exposed to cold late in the fall and in the winter lay appreciably more eggs at this temperature than those collected in the summer and early fall or after warm weather in the spring. Although some eggs are deposited at more extreme temperatures, continuous oviposition occurs from a slightly lower minimum or through about the same range of temperature as embryonic and nymphal development.

Effects of alternating temperatures

Comparisons of the effects of constant and alternating temperatures were made by exposing different lots of overwintered females continuously to different constant temperatures, or alternately at 12-hour intervals to two constant temperatures. The two sets of tests were run simultaneously. Average rates of egg laying were based on individual records during a 10-day period, after allowing for an adjustment interval of 3 days under the same conditions.

Considerable individual variation occurred in the

TABLE 20. Oviposition of overwintered beet leafhoppers in March and April under alternate 12-hour exposures to different temperatures and 50% relative humidity.

Alternating temperatures (°F.)	Females	Eggs laid in 10 days	Daily Rate of Egg Laying		Deviation
			Observed	Calculated	
	Number	Number	Number	Number	%
105 and 90.....	20	1,890	9.45± 0.82	7.44	+27.02
100 and 90.....	14	1,464	10.46± .67	11.60	− 9.83
95 and 90.....	20	1,849	9.25± .47	9.90	− 6.57
90 and 85.....	19	1,788	9.41± .52	8.10	+16.17
90 and 80.....	17	1,352	7.95± .52	8.52	− 6.69
90 and 75.....	20	1,887	9.44± .36	9.40	+ .43
90 and 70.....	17	1,595	9.38± .63	6.75	+38.96
90 and 65.....	20	1,823	9.12± .39	7.05	+29.36
90 and 60.....	20	1,535	7.67± .43	6.77	+13.29
90 and 55.....	16	539	3.37± .24	4.82	−30.08
90 and 50.....	17	607	3.57± .39	4.65	−23.23
80 and 65.....	18	742[1]	5.89± .39	5.68	+ 3.70
75 and 65.....	20	915	4.58± .29	4.97	− 7.85

[1] In 7 days.

rate of egg laying, and, owing probably to the limited number of insects that could be handled simultaneously the results (Table 20) are rather inconclusive. Since the number of plus and minus deviations are approximately equal, the rate of egg laying is not affected by temperature changes, at least not sufficiently to be demonstrated within the range of experimental error.

Effects of humidity

Studies of oviposition under different conditions of atmospheric moisture were conducted during November and December 1933 with leafhoppers of the overwintering generation that were collected late in the fall. Rates of egg laying were based on individual records of the females for a 7-day period at different humidities, after being held for an adjustment period of three days under the same conditions. All the insects were taken from the same group and were used during the first portion of the oviposition period. The results (Table 21) indicate that the rate of egg laying is not appreciably affected by differences in relative humidity. Since few of the ovipositing females died during the experiments, no significant effect of humidity on mortality of the adults was shown within the 10-day exposure to different conditions.

TABLE 21. Oviposition of the beet leafhopper under different conditions of relative humidity with the temperature held at 90° F.

Relative humidity %	Eggs laid by 50 females in 7 days	Daily rate of egg laying
	Number	
20.............	5,089	14.54±0.64
30.............	4,936	14.10± .35
40.............	4,589	13.11± .32
50.............	5,152	14.72± .42
60.............	5,179	14.79± .46
70.............	4,923	14.07± .28
80.............	4,737[1]	13.81± .64
90.............	5,254	15.01± .52

[1] 49 females.

Menusan (63) found that the bean weevil deposited the greatest number of eggs at a relative humidity of 90%. Opposite results were found by Schubert (80) for the beet bug (*Piesma quadratum* (Fieb.)). Other references have been reviewed by Richardson (73) and Uvarov (91).

Effects of light

Oviposition of the leafhopper was not studied extensively in relation to light factors, since preliminary experiments indicated that light did not have any marked effect. A daily rate of 14.83 ± 0.59 eggs was observed under conditions of total darkness. A comparable rate of 14.74 ± 0.65 eggs per day was obtained during continuous exposure to about 40 footcandles of illumination from ordinary light bulbs, and a rate of 15.57 ± 0.64 under ultraviolet radiation

provided by continuous exposure beneath a sun lamp. The experiments were conducted simultaneously at 90° F. and 50% relative humidity with insects from the same group. The average oviposition rates are based on the number of eggs deposited by 23 to 25 females during a 10-day period. These results show no significant differences attributable to light.

Effects of age

Data obtained in studies of 100 overwintered females at 90° F. and 50% relative humidity (Fig. 15) show that the rate of egg laying gradually declines with age although it is fairly constant during the period of 2 to 3 weeks in which the majority of the eggs are deposited. Oviposition of individual females is continuous at different temperatures and is not subject to cyclical or periodic variations.

Most of the females for which oviposition records were obtained died without showing a definite lapse in egg laying. The average postoviposition period for a group of 100 females was less than 2 days, which indicates that oviposition continues throughout adult life and that egg-depleted individuals would never comprise an appreciable percentage of the population.

Effect of host plants

To obtain some comparison of oviposition on different host plants, laying individuals from the same collection of spring-generation migrants from beet fields in June 1936 were placed on potted sugar beets, beans, and tomatoes, and on several common weed hosts that were transplanted into flower pots from outdoors. The plants were held in the greenhouse for a sufficient time before the tests for any eggs that may have been present to incubate. Tests on different plants were made at the same time at 80° F. and 50% relative humidity. The leafhoppers were transferred to fresh plants each day, and the eggs were counted by clearing the exposed plants in chloral hydrate. The average numbers of eggs per female laid during a 7-day period by 14 to 16 individuals on each species of plants are shown as follows:

	Eggs deposited
Sugar beet	30.1
Tumbling orach	4.2
Tomato	2.6
Russian-thistle	1.7
Flixweed	1.2
Bean	.2
Smotherweed	.2

It is well known that sugar beets are one of the best hosts and that beans and tomatoes are among the poorest, as is indicated here. Unless the adaptation to certain plants must be more gradual, it is difficult to account for the small number of eggs in the weeds, since flixweed and Russian-thistle are favorable hosts and considerable numbers of newly hatched nymphs have been observed on both smother-weed (*Bassia hyssopifolia* (Pall.) Kuntze) and tumbling orach in the field.
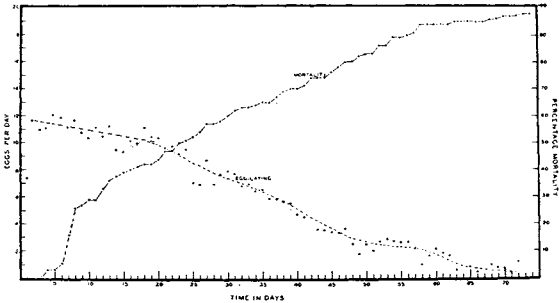

FIG. 15. Average daily oviposition and cumulative mortality of 100 overwintered beet leafhoppers at 90° F. and 50 percent relative humidity.

LONGEVITY AND MORTALITY

Effects of temperature

Leafhoppers collected from wild host plants in the fall were used in studies of the effects of temperature and other factors on the length of adult life. Data on the average survival of some groups of adult females at different temperatures from 30° to 115° F. are given in Table 22. These insects were collected and placed under controlled conditions in November, and small potted sugar beets were used as host plants at all temperatures. Data obtained at below 90° are not strictly comparable with those at higher temperatures, since tests in the two portions of the gradient were not conducted at the same time. It is shown, however, that the length of life decreased to a few days at 110°-115°, was greatly extended with lower

TABLE 22. Average length of life of overwintering females of the beet leafhopper when collected in November and placed under different temperatures.

Temperature (°F.)	Relative humidity	Females	Length of life
	%	Number	Days
115	50	26	2.24±0.23
110	50	32	9.56± .75
100	50	50	16.12±1.15
90	40	100	28.18±2.00
60	50	100	82.86±2.52
50	50	100	73.78±2.84
40	50	100	50.42±2.90
30	..	100	9.66± .42

TABLE 23. Comparison of average length of life of male and female beet leafhopper adults at different temperatures.

Temperature (°F.)	Relative humidity	LENGTH OF LIFE, DAYS	
		Males	Females
60	50%	13.78±1.17	82.86±2.52
50	50%	14.01± .73	73.78±2.84
40	50%	18.31± .70	50.42±2.90
30	..	6.70± .20	9.66± .42
15	..	3.20± .17	14.68± .83
10	..	4.49± .31	11.94± .45

temperatures and decreased metabolism down to 60°-50°, and then decreased markedly again when physical activity and feeding were suspended in exposures at 30°.

Results given in Table 23 show that the females live considerably longer than the males at the same temperatures. Relative values for males and females at the same temperature are strictly comparable, but not those at different temperatures, since the tests were conducted at different times.

Effect of host plants

The length of adult life also seems to be affected by the species of food plants, since females on flixweed survived longer than others from the same collections that were started at the same time on sugar beets. Averages of the length of life on flixweed at 50°, 40°, and 30° F. were 82.55 ± 2.61, 86.54 ± 4.00, and 10.41 ± 0.37 days, respectively, in comparison with the corresponding averages on sugar beets at the same temperatures shown in Table 23.

Effects of evaporation and moisture obtained in feeding

During dispersal movements feeding is interrupted when the leafhopper is airborne or distributed where there are no host plants. The insect survives only a very short time without feeding, but the length of life increases considerably with lower temperatures and higher relative humidity, as is shown in Table 24. Similar effects of temperature on the survival of unfed leafhoppers are shown by data in Table 25.

Closely related to the effect of humidity is the

TABLE 24. Longevity of overwintering unfed females of the beet leafhopper under different conditions of temperature and humidity.

Temperature (°F.)	Relative humidity	Saturation deficiency	Length of Life (in days)	
			Average	Maximum
	%	Mm.		
	100	0.0	1.94±0.08	3.0
	90	3.7	1.38± .04	2.5
	70	10.7	1.23± .04	1.5
90	50	17.9	.94± .03	1.5
	30	25.0	.84± .03	1.0
	10	32.2	.77± .03	1.0
	0	35.8	.59± .03	1.0
	100	.0	3.02± .09	5.0
	90	1.9	2.35± .19	5.0
	70	5.6	1.92± .10	3.5
70	50	9.3	1.49± .06	3.0
	30	13.0	1.54± .04	2.0
	10	16.7	1.28± .05	2.5
	0	18.6	1.05± .07	2.5
	100	.0	10.56± .84	19.0
	90	.9	7.16± .49	11.5
	70	2.7	3.82± .34	8.5
50	50	4.6	4.13± .25	6.5
	30	6.4	3.40± .23	6.0
	10	8.2	2.96± .23	5.5
	0	9.1	2.74± .20	4.5

TABLE 25. Longevity of overwintering females of the beet leafhopper at different temperatures and about 50% relative humidity without host plants and with and without water for feeding.

Temperature (°F.)	Length of Life (in days)			
	With distilled water		Without water	
	Mean	Maximum	Average	Maximum
115	0.64±0.22	1.00	0.06±0.01	.08
110	2.60± .16	4.00	.18± .01	.21
100	4.04± .25	7.00	.35± .01	.54
90	4.04± .33	6.50	1.03± .03	1.50
85	5.28± .34	9.00	1.00± .02	1.50
80	5.95± .70	11.50	1.31± .06	2.00
75	7.60± .65	12.00	1.50± .05	2.00
70	12.28±1.03	24.00	2.30± .11	4.00
65	19.00± .92	33.00	2.87± .15	5.00
60	25.56±1.35	35.00	2.96± .16	4.00
50	31.44±3.33	61.00	4.28± .20	6.00
40	37.62±1.95	80.00	6.40± .65	12.00

matter of the quantity of water available to the insect, either as a part of its food or in the form of contact moisture. As is shown in Table 25, the time of survival without host plants was considerably extended at all temperatures when the insects were supplied with distilled water. The decrease in time of survival of unfed leafhoppers with lower humidities at the same temperature (Table 24) seems to be due largely to the rate of water loss, since Table 26 shows that the survival time was about the same under different humidity conditions when the insects were given distilled water.

TABLE 26. Longevity of overwintering females of the beet leafhopper at 70° F. under different humidity conditions when fed on distilled water.

Relative humidity %	Saturation deficiency (Mm.)	Length of Life (in days)	
		Average	Maximum
90	1.9	4.12±0.22	7
80	3.7	3.80± .23	8
70	5.6	3.74± .17	8
50	9.3	4.28± .28	11
40	11.2	3.66± .23	8
30	13.0	4.64± .33	11
10	16.7	4.76± .39	13

During migration and dispersal movements, and also when the seasonal sequence of favored host plants is unfavorable because of premature drying or delayed germination, almost any species of plant may be used at least as a source of moisture, and it seems probable that such unfavorable food plants as sage brush, *Artemisia tridentata,* Nutt. serve chiefly in this way as temporary or hold-over hosts. Since Table 25 shows that the length of life without host plants may be increased to as much as 80 days at 40° F. when the insects were supplied only with water, late fall or winter precipitation may also be an important factor

in extending survival when there is delayed or sparse germination of winter host plants.

According to Dalton's law the rate of evaporation from a water surface is proportional to the saturation deficiency of the air. Buxton (11), working with the yellow mealworm, found that water was evaporated from the insect in proportion to the saturation deficiency of the air for a short time and emphasized (12) the importance of this measure of the environment with data on insects by Parker (66) and others. Mellanby (61) found that this was nearly the case with bedbugs.

On the other hand, in studies of 3 species of African locusts, Hamilton (31) obtained different results under almost the same saturation deficiency at different temperatures. Leeson (54) found no direct relation between the survival of unfed fleas and the saturation deficiency at different temperatures, and Maercks (57), with eggs of *Microbracon hebetor* has shown that relative humidity, and not saturation deficiency, determined the temperature limits for a given mortality. Maercks (58) also concluded that the processes involved in loss of water by living insects are too complex to be expressed by a simple physical law. Wigglesworth (94) states that the rate of water loss is governed largely by saturation deficiency, but cites a number of exceptions where insects lose more water in proportion to the saturation deficiency at higher temperatures and less than the expected amount in very dry, or moist, air; he discusses a number of factors, both physical and physiological, that cause such departures from the rule.

Table 24 shows that longevity of unfed leafhoppers increased with higher relative humidity and lower saturation deficiency at each of the three different temperatures. The general increase in length of life at all humidities as the temperature decreased from 90° F. to 70° and to 50° shows that temperature has an independent effect which cannot be expressed in combination with that of atmospheric moisture in terms of the saturation deficiency or evaporating power of the air. According to Wigglesworth (94), this could be due to a more rapid loss of water vapor from the tracheal system with increased respiration, or to greater permeability of the cuticle to water and an increasing rate of diffusion in still air, as the temperature rises. At each temperature (Table 24) the time of survival is disproportionately longer in saturated atmosphere than at lower humidities or greater saturation deficiency. Similar examples are cited by Wigglesworth (94), including instances where certain insects are apparently able to absorb moisture from the air at high humidities. However, the possibility exists in the present case that some moisture may have been condensed and imbibed or that hygroscopic excrement was reingested.

Different humidity conditions for tests shown in Tables 24 and 26 were obtained in sealed desiccators with solutions of sulfuric acid. The leafhoppers were given distilled water by the same methods described by Fulton and Chamberlin (25), in which small mesh-capped cages were placed on feeding dishes capped with animal mesentery.

Effects of low temperatures

The effects of low temperatures in causing mortality evidently depend on the length of exposure as well as on the degree of cold. Continuous exposures under controlled conditions produced complete mortality of groups of overwintering females in approximately 20 days at 30° F., 15 days at 20°, 11 days at 15°, 6 days at 10°, 2 days at 5°, less than 12 hours at 0°, and less than 5 hours at −4°. The average survival is roughly one-half these specified exposures. These results also seem to agree fairly well with those of Carter (14: 63, 64; Tables 28-33), who found that the overwintering females rarely survived 4-hour exposures to −2° F., −10°, and −14° in a commercial refrigeration plant, or when chilled to 0° or lower in laboratory apparatus.

During the winter the insects are evidently protected to a considerable extent against low or subzero minimum temperatures because the soil-surface temperatures rarely reach levels low enough for sufficient time to approach lethal exposures as determined under experimental conditions. This is shown in Figure 16, where corresponding standard shade and soil-surface daily minimum temperatures during the winter are compared for a 10-year period, 1925-26 to 1934-35, at Twin Falls, Idaho. Although subzero temperatures occurred rather frequently and were as low as −20° F. in January 1930 and February 1933, the temperature of the soil rarely fell below 5° and never reached 0°.

Carter (14: 65, 66, 110) pointed out that the surface of the soil is well protected against extremes of low temperature and that for three winters the soil-surface temperatures did not reach the lethal minimum temperatures determined experimentally. On this basis he was unable to account for differences in survival in hibernation cages and the overwintered or spring populations in 1926-27 and 1927-28 as a direct effect of low temperature, either as extreme cold for a short time or longer durations of more moderate low temperatures. He concluded, however, that "the more frequent the occurrence of temperatures below zero Fahrenheit, the greater the reduction in overwintering populations."

In the action of subfreezing temperatures previously discussed, shorter exposures are lethal or equal periods are more lethal as the temperature decreases, but this seems to depend to a considerable extent on the occurrence of continous or unbroken exposures, because higher fluctuations of however slight duration appear to counteract the effects of intensity and duration of cold. This effect was observed when two portions of a collection of overwintering females were exposed at the same time in a cabinet at 10° F. The mortality in continous exposure of one group was estimated by removing and discarding a sample of 50 insects each day, while the
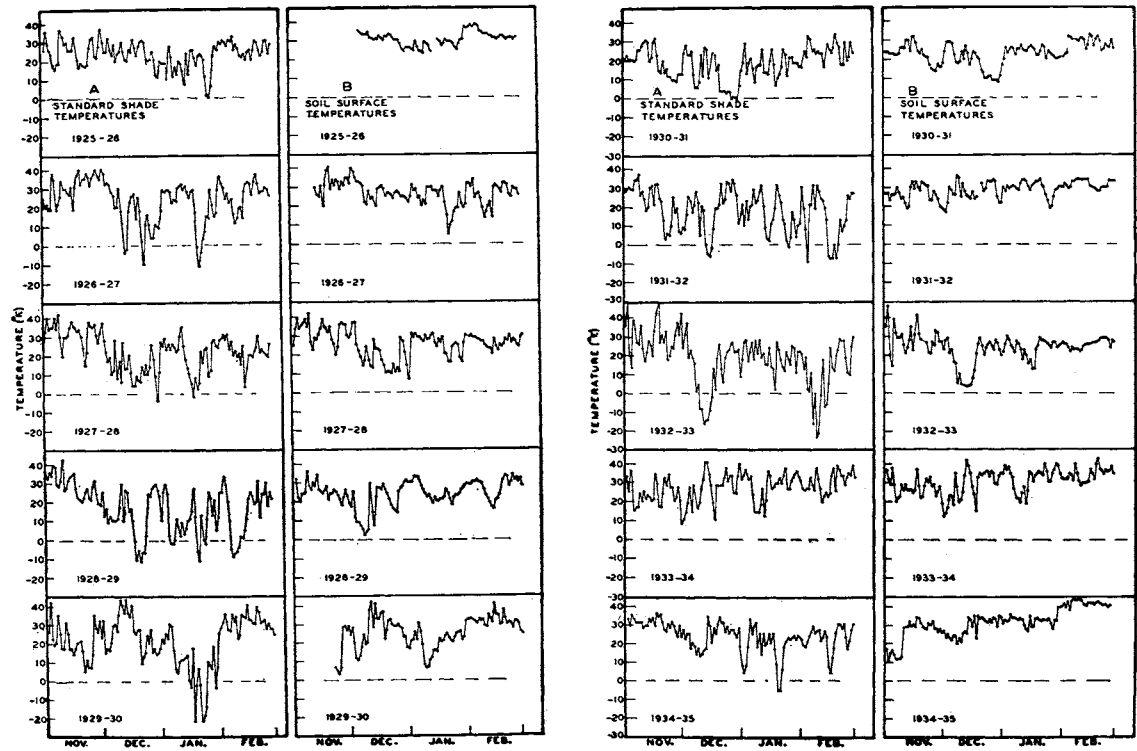
FIG. 16. Comparisons of standard shade and soil-surface daily minimum temperatures for the years 1925-35 at Twin Falls, Idaho.

other group was removed from the chamber for 5 to 10 minutes daily and then replaced after sufficient warming to permit slight life movements by the survivors, so that mortality on successive days could be determined. In continuous exposures the average survival was 4.74 ± .23 days, while the second group withstood a much longer exposure of 11.94 ± .45 days or a significantly longer total time under the same conditions.

In further studies using both methods of procedure and observation, it was found that effects of the intensity of subfreezing temperatures were counteracted by broken exposures so that the time of survival at lower levels was about the same as at 30° F., where death apparently results from desiccation or only indirectly from cold in preventing physical activity for feeding. The average survival in broken exposures at different temperatures is shown as follows:

°F	Days
30	10.16 ± 0.31
25	10.77 ± .30
20	11.22 ± .27
15	10.11 ± .28
10	10.79 ± .23

In exposures broken 5 to 10 minutes daily for examinations, the longevity was also about the same under different relative humidities at 10° F. and the corresponding saturation deficiencies, as is shown by the following results:

% Relative humidity	Saturation deficiency mm.	Days
70	0.5	12.46 ± 0.60
50	.8	13.16 ± .66
30	1.1	12.22 ± .70
10	1.4	13.18 ± .54

Inasmuch as death apparently comes from loss of moisture by the insects under these conditions, the similar survival with small differences in saturation deficiency at the same temperature seems significant and the results at 10°, 15°, 20°, 25°, and 30° likewise seems reasonable, because there is so little difference in evaporating power of the air at these low temperatures.

Differences in the effect of broken and continuous exposures on the survival at different temperatures are illustrated in Figure 17 by the increase in divergence of the mortality curves at each level as the temperature decreased. Curves showing the effect of continuous exposure are based on different samples of 250 insects taken from the cabinet each day after the different time intervals and then discarded. Curves labeled "broken exposures" are based on data for the same group of 200 females at each temperature that were removed from the cabinet for 5 to 10 minutes on successive days for examination.

The effect of cold periods during the winter therefore appears to depend to an important extent on the daily maximum temperatures, since the intensity of subfreezing temperatures, at least down to 10° F.,
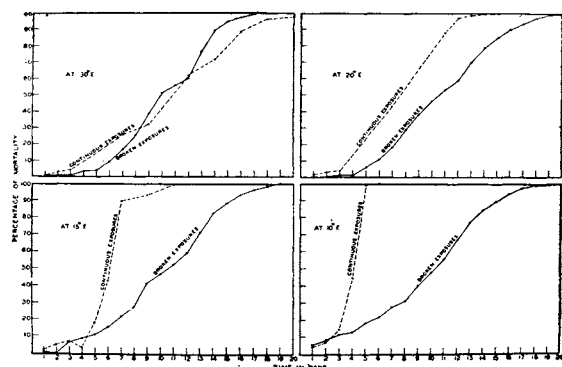
FIG. 17. Relative effects of broken and continuous exposures to cold on mortality of overwintering females of the beet leafhopper in February.

have little effect when relaxed by the diurnal temperature fluctuations. During the winter the leafhoppers are active as temperatures permit, and feeding at intervals is evidently necessary for survival, since the average period endured under controlled temperatures just below the minimum for feeding is only 10 to 11 days and death apparently results from desiccation under these conditions. Extended periods when the ground is covered with snow, or the soil-surface maximum temperatures do not rise above 32° for 1 to 2 weeks or more to permit feeding or imbibition of moisture, would seem to be very unfavorable for survival.

Effects of contact moisture in exposure to cold

In laboratory studies of the effect of contact moisture in exposure to cold the mortality was greater on moist than on dry soil, and the percentages of survival were still lower when the insects were exposed to low temperatures and then warmed to activity under a covering of snow or ice. Overwintering females from outdoor cages when held for 24 hours at 10° F. sustained mortalities of 7.0% when exposed on dry sand, 46.0% on moist sand, and 88.6, 91.2, and 90.4% on moist sand and under 1, 2, and 3 inches of snow, respectively. Similar results, with mortalities of 28, 46, and 93% were obtained in another experiment when overwintering females were exposed at 10° on dry sand, moist sand, and moist sand under about 1 inch of snow, respectively. In these experiments the water drained away and the insects were warmed slowly to activity after the cold exposures. The insects used in the tests were strictly comparable, and the experimental treatment was the same except for the difference in moisture conditions.

Complete mortality occurred when the insects were frozen in ice at 10°.

The effect of winter precipitation on mortality of overwintering leafhoppers has not been adequately investigated in the field, but in comparisons of winter survival in outdoor cages that were kept covered, or exposed by removing the tops during snowfalls, Carter (14: 60, 61, 62) found that mortality of the insect was increased by contact moisture in wet soil and precipitation.

It seems doubtful, therefore, that high percentages of the overwintering females are very often eliminated at one time by the occurrence of extremely low temperatures or by less severe temperatures for longer periods. Ordinarily winter mortality seems rather to be a gradual wearing down process in which lower temperatures of longer duration, snow cover for extended periods, precipitation, and alternate freezing and thawing chiefly contribute.

Effects of winter conditions observed in sampling studies in 1934-35

Population-sampling studies were continued during the winter of 1934-35 on the Berger plot. The data obtained on the occurrence of overwintering females based on 50 unit samples (except for 49 on March 6-9) taken on two proximate days are illustrated in Figure 18 in relation to the soil-surface minimum temperatures recorded during the winter. The actual estimates with their standard errors are listed as follows:
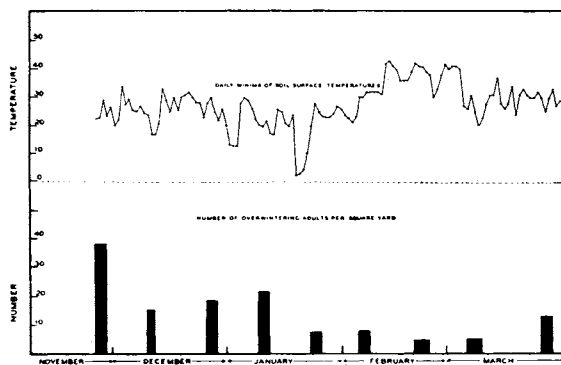

FIG. 18. Number of overwintering females of the beet leafhopper per square yard associated with the daily minimum soil-surface temperatures, Berger, Idaho, 1934-35.

Date of sampling	Female adults per square yard
November 26-28	38.23 ± 6.90
December 10-11	15.53 ± 3.44
December 26-28	18.82 ± 3.76
January 9-11	21.65 ± 5.11
January 23-25	7.53 ± 2.53
February 5-7	8.00 ± 2.16
February 20-23	4.71 ± 1.62
March 6-9	5.27 ± 1.79
March 26-28	12.71 ± 2.52

From November 28 to December 10 the data show a decrease of about 60% in the number of overwintering females, or a statistically significant reduction of 22.70 ± 7.71 per square yard according to the difference in means. Apparently no appreciable mortality occurred during December and the first part of January. Later in January a further significant reduction in number occurred following a cold period, when minimum temperatures near 0° F. were recorded for two nights in succession (Fig. 18). This increase in mortality was evidently produced by low temper-

atures, since experimental work has shown that exposures to 2°-3° for several hours, obtained by refrigeration, will kill some of the leafhoppers. Late in February and early in March there is another decrease in numbers, which is not statistically significant, however. After some warm weather in March a significant increase occurred that was evidently due to an influx of overwintered females to the observation plot from other points in the vicinity where there were less favorable host plants. Precipitation during the winter was below normal, and the light and temporary snow covers could have afforded little protection from subzero minimum temperatures or caused any appreciable mortality in preventing feeding for sufficient time. Precipitation of 0.58 inch was recorded for December, but this came after the decrease in population shown for December 10 and 11, and apparently had no effect on mortality. In January, February, and March the precipitation was 0.30, 0.29, and 0.03 inch, respectively.

SUMMARY

Studies of the beet leafhopper were conducted at Twin Falls, Idaho, during the years 1932-37. The investigations consist chiefly of laboratory tests of effects of temperature and other factors on development, oviposition, and mortality of the insect with population-sampling studies of its seasonal development and abundance in the field during two seasons.

The average duration of the egg stage ranges from 5.5 days at 100° F. to 43.8 days at 60°. Duration of the nymphal stage increases from 13.0 days at 95° to 75.4 days at 65°. Males complete the developmental stages in slightly less time than is required by the females. Development is very slow at 55° and apparently the minimum effective temperature is between 55° and 50°. Rate of development in the egg and nymphal stages is closely proportional to the temperature between 65° and 95°. In this range of temperature thermal increments of about 200 and 450 day-degrees summed between 58° and 95° are required for completion of the egg and nymphal stages, respectively.

The nymphal stage consists of 5 instars that may be reliably distinguished by the width of the head capsule. The mean headwidth increases about 25 percent between molts, the ratio of increase being fairly constant through successive stages in accordance with Dyar's principle. The duration of the different instars at 90° F. vary from 2.3 to 3.8 days, with the first and the last stages being significantly longer than any of the others at this temperature. The nymphal weight approximately doubles in successive instars and increases from about .04 milligram at hatching to approximately .9 to 1.0 milligram just preceding the final molt. The curve of nymphal growth at a constant temperature is typically sigmoid, but apparently consists of 5 different segments, indicating that the growth ratio differs slightly in the various instars.

In alternate daily exposures to high and low tem-
peratures and under naturally varying temperatures the rate of development is accelerated in comparison with effects of equivalent constant temperatures. The amount of acceleration under variable temperatures apparently differs with the temperatures involved, with the time of exposure at different temperatures, and also with the stages of embryonic and nymphal development completed under different temperature conditions.

Population sampling in 1934 and 1935 shows that 3 generations matured each year. Studies of the annual temperature accumulations over a 10-year period indicate that there are usually 3 generations in southern Idaho, with the last generation sometimes maturing rather late in the fall and possibly limited somewhat in size by insufficient temperatures.

The spring movement to the cultivated areas in May or June begins slowly at first and then increases more rapidly to a peak in from 1 to 3 weeks later, depending on temperatures affecting maturation of the spring generation of leafhoppers in the contributing breeding areas. A high correlation between dates of the beginning of the movement in different years and the recorded temperature increments indicates that temperature is the most important variable governing the time of migration. In years of early migrations advanced by higher spring temperatures curly top injury to sugar beets has usually been severe, while beet yields have generally been good when the migration was delayed by lower temperatures.

The rate of embryonic development is apparently unaffected by differences in relative humidity. Nymphal development is slightly retarded with high humidity at unfavorably high temperatures.

Apparently light factors have no important effect on the rate of embryonic and nymphal development. Hatching is stimulated by light after completion of development, and the embryonic period may thus be extended slightly by the occurrence of darkness.

The host plant is not an important factor in the duration of the egg stage, but considerable variation is shown in the time required for nymphal development on different host plants, development being slower on less favorable plants.

Mortality in the egg stage was greater at both temperature extremes for development. Nymphal mortality increases with higher and lower temperatures and with higher humidity. The effects of temperature and humidity on mortality of the immature stages cannot be expressed satisfactorily in terms of saturation deficiency.

In studies of the effects of moderate temperatures just below the minimum for development, differences from 30 to 80% relative humidity at 40° and 50° F. seem to have no appreciable effect on mortality in the egg and nymphal stages. Mortality in the egg stage increases with longer exposures at these temperatures and probably with the decrease in temperature. The late embryonic stages are most susceptible to the effects of cold. Nymphal mortality increases with

lower temperature and with the time of exposure to cold, and both factors have relatively greater effect on the smaller nymphs. With increase in cold, shorter exposures have relatively greater effect on mortality.

The seasonal color forms are determined by temperature conditions. The first adults of the overwintering form appear suddenly after the first cool nights in the fall, and sometimes darker adults of the spring generation that are produced by cooler weather are difficult to distinguish from those of the overwintered generation. As temperatures at which the nymphs are reared grade downward, coloration of the adults ranges from yellowish green at 105° and 100° F. and light green at 95° to darker green at 90° and 85° with darker areas appearing on the wings, vertex, and pronotum at 80° and 75° and lower temperatures. Coloration seems to be largely determined during later stages of nymphal development and probably mostly during formation of the wings and hypodermis preceding the final molt.

Size and weight of the adults is also influenced by temperature. Adults maturing in the fall and spring are generally slightly larger than those appearing during the summer. When reared under experimental conditions the adult weight increases with successively lower temperatures. Female adults are also slightly larger than the males at the same temperatures.

The sexes are about evenly divided under all conditions of temperature and humidity.

Fertilization occurs early in the adult stage and the females continue to lay fertile eggs throughout life although mating was never observed after ovarian development was completed. Fertilization is not necessary for egg laying and apparently has no effect on ovarian development or duration of the preoviposition period.

Average duration of the preoviposition period ranges from about 4 days at 90° F. or 4 to 6 days in summer, to 4 to 6 months during the winter and is apparently governed largely by the maximum temperatures. With the appearance of the darker colored adults of the overwintering generation early in the fall, ovarian development is suspended by the decreasing maximum temperatures, or is at least greatly retarded by smaller increments of higher temperatures. After exposure to more extreme cold has occurred the insect is enabled to complete ovarian development during the remainder of the winter under increments of higher soil-surface maximum temperatures. The rate of preovipositional development seems to be unaffected by differences in relative humidity, except for a very slight retardation with high humidity at high temperatures.

Oviposition begins at about 50° F., the rate is accelerated to about 90°-100°, and then declines at higher temperatures. Effects of the temperature gradient are represented by S-shaped graphs in which data for the rising portion of the curves are well described by van't Hoff formula or analogous expressions where the ratio of increase in rate of egg laying is proportional to the difference in temperature. The oviposition rate is apparently not accelerated by varying temperatures in comparison with results at constant temperatures. The rate of egg laying seems to be unaffected by the quality and intensity of light or by differences in atmospheric moisture. Oviposition continues toward the end of adult life, but the rate of egg laying declines gradually with increasing age. The majority of overwintered females may deposit between 300 and 400 eggs each, and a maximum of 675 eggs was recorded for one individual.

The length of adult life decreases to a few days at 110°-115° F., is greatly extended with lower temperatures and decreased metabolism down to 60°-50°, and then decreases markedly again when physical activity and feeding are suspended in exposures at 30°. Females live considerably longer than males at the same temperatures. The length of adult life is apparently affected by host plants since the insects survived significantly longer on flixweed than on sugar beets. The adult survives but a short time without water either as part of its food or in the form of contact moisture. The time of survival without water increases with lower temperatures and higher humidity and is apparently determined by the rate of water loss from the insect, but the effect of both temperature and humidity factors cannot be expressed satisfactorily in terms of the saturation deficiency. The time of survival is considerably extended when the insects are fed on distilled water, and many unfavorable food plants may serve chiefly in this way as temporary or hold-over hosts in providing moisture.

Effects of subzero temperatures on mortality of the overwintering females depends on the degree of cold and the time of continuous exposure, shorter exposures being lethal or equal exposures more lethal as the temperature decreases. The insects seem highly protected against subzero air temperatures because the soil-surface temperatures rarely reach lethal extremes near 0° F., or low enough levels for sufficient time to approach highly lethal exposures as determined under experimental conditions. Also, the effects of periods of extreme cold would appear to be greatly lessened by temperature rises of however slight duration during the day because under experimental conditions, broken exposures for 5 to 10 minutes daily to permit perceptible life movements counteract the intensity factor of cold so that the time of survival at 25°, 20°, 15°, and 10° is about the same as at 30° where death apparently results only directly from desiccation. Extended cold periods when the ground is covered with snow or the soil surface maximum temperatures do not rise above 32° F. for 1 or 2 weeks or more to permit feeding or imbibition of moisture, would seem to be very unfavorable for survival. Contact moisture as well as thawing and freezing in ice also increases the lethal effects of experimental exposures to cold, and winter precipitation seems generally unfavorable for survival.

Population sampling studies of overwintering leaf-

hoppers on a plot in the desert breeding area show a significant increase in mortality following a cold period in January when the soil surface temperature approached 0° F. for two nights in succession.

LITERATURE CITED

(1) **Alpatov, W. W., & Raymond, Pearl.** 1929. Experimental studies on the duration of life. XII. Influence of temperature during the larval period and adult life on the duration of the life of the imago of Drosophila melanogaster. Amer. Nat. **63:** 37-67.

(2) **Annand, P. N., J. C. Chamberlin, C. F. Henderson, & H. A. Waters.** 1932. Movements of the beet leafhopper in 1930 in southern Idaho. U. S. Dept. Agr. Cir. **244:** 1-24.

(2a) **Annand, P. N., & F. H. Harries.** 1940. Temperature-humidity controlled cabinets for the study of insects. U. S. Bur. Ent. and Plant Quar. ET-**159:** 1-6.

(3) **Arrhenius, Svante.** 1915. Quantitative laws in biological chemistry. London. 1-164.

(4) **Ball, E. D.** 1906. The beet leafhopper (Eutettix tenella). Utah Agr. Expt. Sta. Ann. Rpt. (1904-05) **16:** XVI.

(5) 1917. The beet leafhopper and the curly-leaf disease that it transmits. Utah Agr. Expt. Sta. Bul. **155:** 1-55.

(6) 1934. The number of generations of the beet leafhopper under natural conditions. Jour. Econ. Ent. **27:** 945-959.

(7) **Belehrádek, J.** 1930. Temperature coefficients in biology. Cambridge Phil. Soc. Biol. Rev. **5:** 30-58.

(8) **Bliss, Chester I.** 1927. The oviposition rate of the grape leafhoppers. Jour. Agr. Res. **34:** 847-852.

(9) **Blunck, Hans.** 1914. Die Entwicklung des Dytiscus marginalis 1. Vom Ei bis zur Imago. 1. Teil. Das Embryonalleben. Ztschr. f. Wiss. Zool. **111:** 76-151.

(10) **Brindley, Tom A.** 1930. The growth and development of Ephestia kuehniella Zeller (Lepidoptera) and Tribolium confusum Duval (Coleoptera) under controlled conditions of temperature and relative humidity. Ann. Ent. Soc. Amer. **23:** 741-757.

(11) **Buxton, Patrick A.** 1930. Evaporation from the meal-worm (Tenebrio: Coleoptera) and atmospheric humidity. Roy. Soc. London, Proc., (B.) **106:** 560-577.

(12) 1932. Terrestrial insects and the humidity of the environment. Cambridge Phil. Soc. Biol. Rev. **7:** 275-320.

(13) **Caffrey, D. J., & L. H. Worthley.** 1927. A progress report on the investigations of the European corn borer. U. S. Dept. Agr. Bul. **1476:** 1-154.

(14) **Carter, W.** 1930. Ecological studies of the beet leafhopper. U. S. Dept. Agr. Tech. Bul. **206:** 1-114.

(15) **Cook, William C.** 1927. Some effects of alternating temperatures on the growth and metabolism of cutworm larvae. Jour. Econ. Ent. **20:** 769-782.

(16) 1941. The beet leafhopper. U. S. Dept. Agr. Farmers' Bul. (1886) 1-21.

(17) 1943. Evaluation of a field-control program directed against the beet leafhopper. Jour. Econ. Ent. **36:** 382-385.

(18) **Davies, W. Maldwyn.** 1928. The effect of variation in relative humidity on certain species of Collembola. Brit. Jour. Expt. Biol. **6:** 79-86.

(19) **Dewitz, J.** 1913. Physiologische Untersuchungen auf dem Gebiet der Schädlingsforschung. 2. Uber Wachstumschemmungen bei Insektenlarven. Naturw. Ztschr. f. Forst u. Landw., **11:** 431-440.

(20) **Dunham, W. E.** 1930. Temperature gradient in the egg-laying activities of the queen bee. Ohio Jour. Sci. **30:** 403-410.

(21) **Dyar, H. G.** 1890. The number of molts of lepidopterous larvae. Psyche **5:** 420-422.

(22) **Elwyn, Adolph.** 1917. Effect of humidity on pupal duration and on pupal mortality of Drosophila ampelophila Loew. Amer. Mus. Nat. Hist. Bul. **37:** 347-353.

(23) **Fenton, F. A., & E. W. Dunnam.** 1929. Biology of the cotton boll weevil at Florence, S. C. U. S. Dept. Agr. Tech. Bul. **112:** 1-75.

(24) **Fox, D. E.** 1938. Occurrence of the beet leafhopper and associated insects on secondary plant successions in southern Idaho. U. S. Dept. Agr. Tech. Bul. **607:** 1-43.

(25) **Fulton, R. A., & J. C. Chamberlin.** 1934. An improved technique for the artificial feeding of the beet leafhopper with notes on its ability to synthesize glycerides. Science **79 (2050):** 346-348.

(26) **Fries, E. F. B.** 1926. Temperature and frequency of heart beat in the cockroach. Jour. Gen. Physiol. **10:** 227-237.

(27) **Genieys, Paul.** 1925. Habrobracon brevicornis Wesm. Ent. Soc. Amer. Ann. **18:** 143-202.

(28) **Griswold, Grace H., & Mary F. Crowell.** 1936. The effect of humidity on the development of the webbing clothes moth (Tineola bisselliella Hum.). Ecology **17:** 241-250.

(29) **Haegele, Rowland W.** 1927. The beet leaf-hopper (Eutettix tenellus Baker). A survey in Idaho. Idaho Agr. Expt. Sta. Bul. **156:** 1-28.

(30) **Hallez, Paul.** 1886. Loi de l'orientation de l'embryon chez les insectes. Acad. Sci. Compl. Rend. **103:** 606-608.

(31) **Hamilton, Andrew G.** 1936. The relation of humidity and temperature to the development of three species of African locusts—Locusta migratoria migratorioides (R. & F.), Schistocerca gregaria (Forsk.), Nomadacris septemfasciata (Serv.). Roy. Ent. Soc. London, Trans. **85:** 1-60.

(32) **Hamlin, J. C., W. D. Reed., & M. E. Phillips.** 1931. Biology of the Indian-meal moth on dried fruits in California. U. S. Dept. Agr. Tech. Bul. **242:** 1-26.

(33) **Harries, F. H.** 1937. Some effects of temperature on the development and oviposition of Microbracon hebetor (Say). Ohio Jour. Sci. **37:** 165-171.

(34) 1939. Some temperature coefficients for insect oviposition. Ent. Soc. Amer. Ann. **32:** 758-776.

(35) 1943. Some effects of alternating temperatures and exposure to cold on embryonic development of the beet leafhopper. Jour. Econ. Ent. **36:** 505-509.

(36) 1944. Differential effects of temperature on the development of the beet leafhopper. Jour. Agr. Res. **69:** 127-136.

(36a) **Harries, F. H., & D. E. Fox.** 1937. An apparatus for all-season sampling for the study of insects. U. S. Bur. Ent. and Plant Quar. ET-**113:** 1-2.

(37) **Harries, F. H., & C. F. Henderson.** 1938. Growth of insects with reference to progression factors for

successive growth stages. Ent. Soc. Amer. Ann. **31**: 557-572.

(38) **Headlee, T. J.** 1917. Some facts relative to the influence of atmospheric humidity on insect metabolism. Jour. Econ. Ent. **10**: 31-38.

(39) **Hefley, H. M.** 1928. Differential effects of constant humidities on Protoparce quinquemaculatus Haworth, and its parasite, Winthemia quadripulstulata Fabricus. Jour. Econ. Ent. **21**: 213-221.

(40) **Heller, J.** 1930. Sauerstoffverbrauch der Schmetterlingspuppen in Abhängigkeit von der Temperatur. Ztschr. f. Vergleich. Physiol. **11**: 448-460.

(41) **Hills, O. A.** 1937. The beet leafhopper in the Central Columbia River breeding area. Jour. Agr. Res. **55**: 21-31.

(42) **Hodge, Charles, IV.** 1933. Growth and nutrition of Melanoplus differentialis Thomas (Orthoptera, Acrididae) 1. Growth on a satisfactory mixed diet and on diets of single food plants. Physiol. Zool. **6**: 306-328.

(43) **Hoff, J. van't.** 1884. Etudes de dynamique chimique. Amsterdam. (English translations by E. Cohen and T. Ewan in 1896: 1-286. Amsterdam and London.)

(44) **Holdaway, F. G.** 1932. An experimental study of the growth of populations of the "flour beetle" Tribolium confusum Duval, as affected by atmospheric moisture. Ecol. Monog. **2**: 261-304.

(45) **Isely, D.** 1932. Abundance of the boll weevil in relation to summer weather and to food. Ark. Agr. Expt. Sta. Bul. **271**: 1-34.

(46) **Janisch, P. E.** 1927. Das Exponentialgesetz als Grundlage einer Vergleichenden Biologie. Berlin. 383.

(47) 1930. Experimentelle Untersuchungen über die Wirkung der Umweltfaktoren auf Insekten. I. Die Massenvermehrung der Baumwolleule Prodenia littoralis in Ägypten. Ztschr. f. Morph. u. Ökol. der Tiere **17**: 339-416.

(48) **Knight, H. H.** 1924. On the nature of the color patterns in Heteroptera with data on the effects produced by temperature and humidity. Ent. Soc. Amer. Ann. **17**: 258-273.

(49) **Knowlton, G. F.** 1932. The beet leafhopper in northern Utah. Utah Agr. Expt. Sta. Tech. Bul. **234**: 1-64.

(50) 1937. Biological control of the beet leafhopper in Utah. Proc. Utah Acad. Sci. **14**: 111-139.

(51) **Krogh, A.** 1914. On the influence of the temperature on the rate of embryonic development. Ztschr. f. Allg. Physiol. **16**: 163-177.

(52) 1914. On the rate of development and CO_2 production of chrysalides of Tenebrio molitor at different temperatures. Zeitschr. f. Allg. Physiol. **16**: 178-190.

(53) **Lawson, F. R., & R. L. Piemeisel.** 1943. The ecology of the principal summer weed hosts of the beet leafhopper in the San Joaquin Valley, California. U. S. Dept. Agr. Tech. Bul. **848**: 1-37.

(54) **Leeson, H. S.** 1932. The effect of temperature and humidity upon the survival of certain unfed rat fleas. Parasitology **24**: 196-209.

(55) **Lund, H. O.** 1934. Some temperature and humidity relations of two races of Trichogramma minutum Riley (Hym. Chalcididae). Ent. Soc. Amer. Ann. **27**: 324-340.

(56) **Ludwig, D.** 1928. The effects of temperature on the development of an insect (Popillia japonica Newman). Physiol. Zool. **1**: 358-389.

(57) **Maercks, H.** 1933. Der einfluss von Temperatur und Luftfeuchtigkeit auf die Embryonalentwicklung der Mehlmottenschlupfwespe, Habrobracon juglandis Ashmead. Arb. Biol. Reichanst. Landw. u. Forstw. **20**: 347-390.

(58) 1933. Wird der Wasserhaushalt der Insekten durch das Daltonsche Gesetz bestimmt. Anz. f. Schädlingsk. **9**: 66-68.

(59) **Marcovitch, S., & W. W. Stanley.** 1930. The climatic limitations of the Mexican bean beetle. Ent. Soc. Amer. Ann. **23**: 666-686.

(60) **MacGill, E. I.** 1931. The biology of Thysanoptera with reference to the cotton plant. VII. The relation between temperature and humidity and the life cycle. Ann. Appl. Biol. **18**: 574-583.

(61) **Mellanby, K.** 1932. Effects of temperature and humidity on the metabolism of the fasting bed-bug (Cimex lectularius), Hemiptera. Parasitology **24**: 419-428.

(62) **Menusan, H., Jr.** 1934. Effects of temperature and humidity on the life processes of the bean weevil, Bruchus obtectus Say. Ent. Soc. Amer. Ann. **27**: 515-526.

(63) 1935. Effects of constant light, temperature, and humidity on the rate and total amount of oviposition of the bean weevil, Bruchus obtectus Say. Jour. Econ. Ent. **28**: 448-453.

(64) 1936. The influence of constant temperatures and humidities on the rate of growth and relative size of the bean weevil, Bruchus obtectus Say. Ent. Soc. Amer. Ann. **29**: 279-288.

(65) **Miller, D. F.** 1929. Determining the effects of change in temperature upon the locomotor movements of fly larvae. Jour. Expt. Zool. **52**: 293-313.

(66) **Parker, J. R.** 1930. Some effects of temperature and moisture upon Melanoplus mexicanus mexicanus Saussure and Camnula pellucida Scudder (Orthoptera). Mont. Agr. Expt. Sta. Bul. **223**: 1-132.

(67) **Payne, N. M.** 1932. Duration of the pupal stage of Tenebrio molitor Linnaeus at constant and at alternating temperatures (Coleop.: Tenebrionidae). Ent. News **43**: 6-7.

(68) **Peairs, L. M.** 1927. Some phases of the relation of temperature to the development of insects. W. Va. Agr. Expt. Sta. Bul. **208**: 1-62.

(69) **Peterson, A.** 1920. Some studies on the influence of environmental factors on the hatching of the eggs of Aphis avenae Fabricius and Aphis pomi deGeer. Ent. Soc. Amer. Ann. **13**: 391-400.

(70) **Peterson, A., & G. J. Haeussler.** 1928. Some observations on the number of larval instars of the oriental peach moth, Laspeyresia molesta Busck. Jour. Econ. Ent. **21**: 843-852.

(71) **Piemeisel, R. L.** 1932. Weedy abandoned lands and the weed hosts of the beet leafhopper. U. S. Dept. Agr. Cir. **229**: 1-23.

(72) **Piemeisel, R. L., & F. R. Lawson.** 1937. Types of vegetation in the San Joaquin Valley of California and their relation to the beet leafhopper. U. S. Dept. Agr. Tech. Bul. **557**: 1-28.

(73) **Richardson, Charles H.** 1925. The oviposition response of insects. U. S. Dept. Agr. Bul. **1324**: 1-17.

(74) **Rivnay. E.** 1935. Ecological studies of the greenhouse thrips, Heliothrips haemorrhoidalis, in Palestine. Bul. Ent. Res. **26**: 267-278.

(75) **Rogers, Edith.** 1929. The effect of temperature on the oxygen consumption of an insect, Melanoplus differentialis. Physiol. Zool. **2**: 275-283.

(76) **Romney, V. E.** 1939. Breeding areas and economic distribution of the beet leafhopper in New Mexico, southern Colorado, and western Texas. U. S. Dept. Agr. Cir. **518**: 1-14.

(77) 1943. The beet leafhopper and its control on beets grown for seed in Arizona and New Mexico. U. S. Dept. Agr. Tech. Bul. **855**: 1-24.

(78) **Sanderson, E. D., & L. M. Peairs.** 1913. The relation of temperature to insect life. N. H. Expt. Sta. Tech. Bul. **7**: 1-125.

(79) **Schlottke, E.** 1926. Über die Variabilität der Schwarzen Pigmentierung und ihre Beeinflussbarkeit durch Temperaturen bei Habrobracon juglandis Ash. Ztschr. f. vergleich. Physiol. **3**: 692-736.

(80) **Schubert, W.** 1927. Biologische Untersuchungen über die Rübenblattwanze, Piesma quadrata Fieb., im Schlesischen Befallgebiet. Ztschr. f. Angew. Ent. **13**: 129-155.

(81) **Seamans, H. L., & E. McMillan.** 1935. The effect of food plants on the development of the pale western cutworm (Agrotis orthogonia Morr.). Jour. Econ. Ent. **28**: 421-425.

(82) **Severin, H. H. P.** 1930. Life-history of beet leafhopper, Eutettix tenellus (Baker) in California. Calif. Univ. Pubs., Ent. **5**: 37-88a.

(83) 1933. Field observations on the beet leafhopper, Eutettix tenellus, in California. Hilgardia **7**: 281-350.

(84) **Shapley, H.** 1920. Thermokinetics of Liometopum apiculatum mayr. Natl. Acad. Sci. Proc. **6**: 204-211.

(85) **Shelford, V. E.** 1927. An experimental investigation of the relations of the codling moth to weather and climate. Ill. Nat. Hist. Survey Bul. **16**: 311-440.

(86) **Smith, R. C.** 1931. A study of temperature and humidity conditions in common types of insect rearing cages. Jour. Agr. Res. **43**: 547-557.

(87) **Stahl, C. F.** 1920. Studies on the life history and habits of the beet leafhopper. Jour. Agr. Res. **20**: 245-252.

(88) **Standfuss, M.** 1896. Handbuch der Paläarktischen Gross-schmetterlinge fur Forscher und Sammler. Jena 1-392.

(89) **Sweetman, H. L., & J. Wedemeyer.** 1933. Further studies of the physical ecology of the alfalfa weevil, Hypera postica (Gyllenhal). Ecology **14**: 46-60.

(90) **Titschack, E.** 1925. Untersuchungen über den Temperatureinfluss auf die Kleidermotte (Tineola biselliella Hum.). Ztschr. f. Wiss. Zool. **124**: [213]-251.

(91) **Uvarov, B. P.** 1931. Insects and climate. Ent. Soc. London, Trans. **79**: [1]-247.

(92) **Wadley, F. M.** 1931. Ecology of Toxoptera graminum, especially as to factors affecting importance in the northern United States. Ent. Soc. Amer. Ann. **24**: 325-395.

(93) **Wardle, R. A.** 1930. Significant variables in the blowfly environment. Ann. Appl. Biol. **17**: 554-574.

(94) **Wigglesworth, V. B.** 1939. The principles of insect physiology. New York.

(95) **Zwölfer, W.** 1933. Studien zur Ökologie, insbesondere zur Bevölkerungslehre der Nonne, Lymantria monacha 1. Vermehrungspotential und Sterblichkeit der Entwicklungsstufen in ihren Beziehungen zu Temperatur und Luftfeuchtigkeit. Ztschr. f. Angew. Ent. **20**: 1-50.