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INTRODUCTION

THE ALFALFA WEEVIL, *Hypera postica* Gyll.,[4] was first discovered in lowland middle California in 1932. The extent and direction of its spread from its original areas are shown on the map in figure 1. The expansion of the area of infestation has been slight in view of the rapidity of spread of the insect that has been reported from other parts of the United States. Along some parts of the periphery of the area of infestation a slow rate of spread may possibly be the result of absence of suitable and abundant host plants. But in one sector of the periphery of the infested area—in the northwestern San Joaquin Valley—the boundary cuts across a continuous area devoted to the cultivation of alfalfa, where any insect preying on alfalfa might be expected to be disseminated rapidly and continuously from field to field. As may be seen from figure 1, no such spread has been observed. There appears to be no good reason why the southward spread of the insect is checked here unless it encounters a climatic barrier. Southward in the San Joaquin Valley summer temperatures become steadily higher; and all investigations of the alfalfa weevil indicate that high temperatures check the activity of the adult weevil and eventually inhibit its activity altogether.

The existence of an apparent climatic limit to the southward spread of the weevil in the San Joaquin Valley, and the reasonable conclusion that the climatic barrier encountered is high summer temperature, are the considerations that have prompted the investigation reported in this paper. Since the weevil is of rather recent introduction in California, it appeared that some light might be thrown on this question by a study of the temperatures obtaining in its original habitat in the Old World, with particular attention to the southern limit of its distribution there. The conclusions arrived at through this comparative study of the dis-

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[4] Formerly called *Phytonomus variabilis* Hbst.; see footnote 6, p. 83, in the accompanying paper (Michelbacher, 1940).

tribution of the insect and the temperatures that obtain along the limits of the areas infested by it are finally used in an attempt to predict approximately its possible future spread in California.

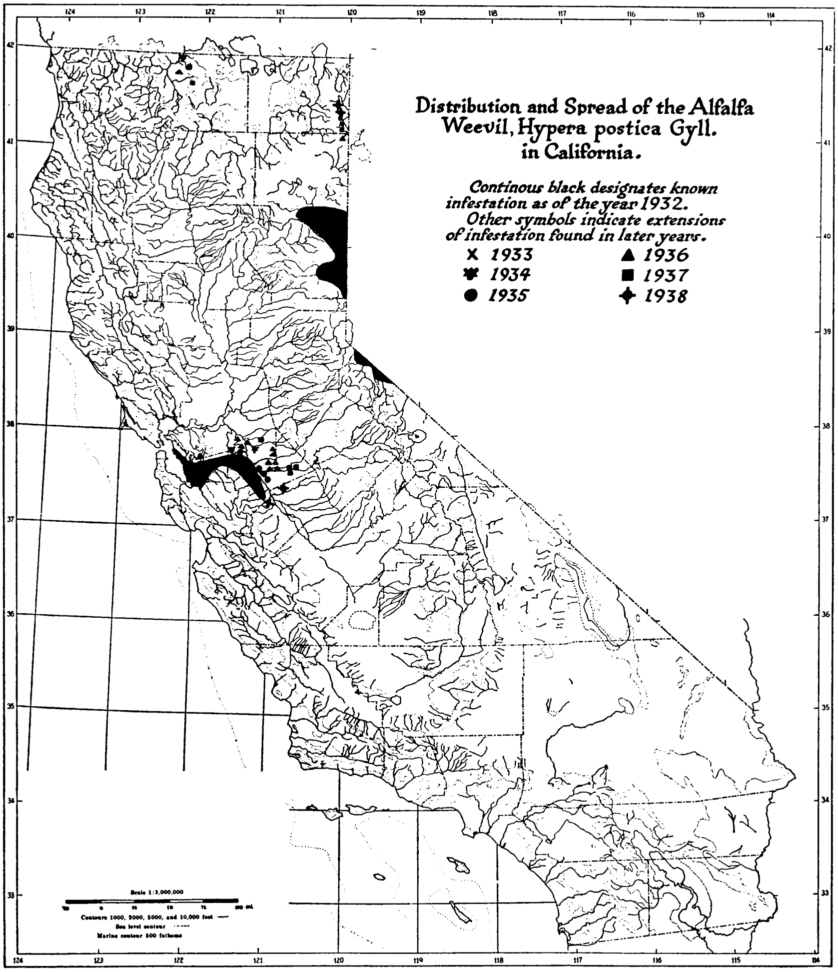

Fig. 1.—Areas in California infested by the alfalfa weevil in 1932 and the spread of the insect since that year.

SEASONAL ACTIVITY OF THE ALFALFA WEEVIL IN RELATION TO TEMPERATURE

A review of the seasonal history and habits of the alfalfa weevil appears necessary for an understanding of the climatic relations of its activity in California and elsewhere. Probably the most important consideration is that a female weevil on emerging from its cocoon is not sexually mature; several months must pass before it is capable of laying eggs. The length of this diapause is variable and is greatly influenced by temperature. Snow (1928)[5] conducted a careful investigation and found that the shortest time necessary for adults to reach sexual maturity is at least 4 months. Yakhontov (1934) gives the time as 55 to 60 days where the temperature does not fall below 12° C or rise above 25°. Observations in California indicate that some individuals reach sexual maturity within a 2-month period. Snow's work was done in the Great Basin, where sexual maturity is probably retarded by the high temperature to which the weevils are subjected upon their emergence from the cocoons.

In lowland middle California the first generation comes early, and consequently the emergence of new adults occurs before really hot weather sets in. The majority of the adults emerge in April, some even earlier. Therefore, the temperatures prevailing immediately after their emergence are highly satisfactory, and the length of the diapause is relatively short. The earliness of the first generation can probably be best appreciated by noting that the larval peak is reached in lowland middle California (fig. 4) at about the time that temperatures favorable for adult activity are beginning to occur in the Great Basin. In the intermountain region, which includes the Great Basin, most of the adults emerge in June and July; and the temperatures that obtain during these months and for a time thereafter are sufficiently high to lengthen greatly the diapause, and therefore a number of months must pass before sexual maturity is reached. Except for the fact that the alfalfa weevil is slow to reach sexual maturity, it would probably be a more serious pest in California and possibly elsewhere than it actually is.

Although the study of the weevil at this station has been in progress only since 1932, there is already considerable evidence that many adults of the first brood of larvae reach sexual maturity and lay eggs before the summer is past. Overwintering adults usually lay most of their eggs on the first crop of alfalfa, although a certain number lay eggs on the second crop. By the time the third crop starts its growth, however, the overwintering adults have nearly depleted their egg supply and larvae are very difficult to find. Toward the end of June there may be a marked increase in the larval population; in certain fields the larval population has at times exceeded that of the first crop. This increase can be accounted for only by supposing that some of the adults of the current season's generation have reached sexual maturity and are giving rise to a second

[5] See "Literature Cited" for complete data on citations, which are referred to in the text by author and date of publication.

generation. This occurs for a certainty in the cooler parts of lowland middle California, as is shown by experiments in which larvae, caged outdoors, pupated, emerged, and produced progeny during the same season (Michelbacher and Essig, 1935).

Probably the second generation makes it possible for the alfalfa weevil to establish relatively large populations in certain fields. Apparently exceptionally favorable conditions are necessary for this to occur. For example, a field with a comparatively low population density may change to one with a high density if weather conditions are such that a large number of adults of the current season's brood are able to reach sexual maturity before hot weather sets in. These adults must, moreover, reach sexual maturity and begin depositing eggs at the time when a new crop of alfalfa starts its growth; for if this condition is not fulfilled, the alfalfa will be cut and the new generation of weevils will die by cultural kill before they have had a chance to complete their development. This is what usually occurs; and by the time the next crop of alfalfa starts its growth, temperatures have risen high enough to send nearly all the adults into estivation. If a field once becomes heavily infested, however, favorable circumstances thereafter are likely to permit the expansion of the weevil population to a density that will be destructive as long as the field is left in alfalfa.

Because of their much later emergence in lowland middle California, we are inclined to believe that relatively more adults of the second brood survive the summer than do the adults of the first brood. It seems highly possible that there must be a certain mortality among the adults of the early brood before the adults of the second generation have emerged. Also, the first brood gives rise to the second, and therefore many of the individuals of the first brood must begin the summer in at least a partially depleted condition. The adults of the second brood may be comparable to the first and only brood of adults that occurs in the Great Basin; for in both cases they emerge at about the same time of the year. The only marked difference is that in California the adults have to withstand higher summer temperatures than in the Great Basin.

CLIMATIC CONDITIONS UNDER WHICH THE ALFALFA WEEVIL EXISTS

Summer Temperature as a Limiting Factor.—The aim of the present paper—to estimate from the present climatic distribution of the alfalfa weevil its probable future spread—is similar to that of an earlier paper by Cook (1925). Since, however, this paper is concerned with a smaller and climatically more homogeneous area than Cook discussed, the procedure is more detailed and has been determined by close observation of the seasonal history of the insect in lowland middle California. This paper deals, moreover, with the southern limit of dispersal of the insect, with which Cook, for lack of observational data, did not concern himself. His immediate acquaintance with the weevil was gained in the northern part of the intermountain region of the United States, where cold and wet spring weather and low winter temperatures are demonstrably limiting factors in the survival of the weevil. He was led, therefore, to attach great weight to precipitation as a climatic factor, since a moist habitat favors certain entomophagous fungi that attack the larvae of the weevil. This line of reasoning led him to conclude that almost the whole of California, with its dry summers, was destined to become an area of "normal occurrence" of the insect. He did, however, consider it possible "that the high temperatures of southern California and Arizona may prove fatal to larvae."

Any climatic limitations on the spread of the weevil in lowland middle California must be imposed by summer temperatures, not by precipitation. We have therefore ignored precipitation in interpreting present distribution and future spread of the weevil in California. Our method of handling climatic data is much closer to Yakhontov's (1934) than to Cook's. Like Cook, Yakhontov knows best the northern limit of the weevil (in the U. S. S. R.), but he has shown that this northern limit may very well be defined by temperatures alone.

Among investigators of the weevil there is general agreement on the gross relations of its activity to temperature. Moderately cool weather is favorable to its activity. There is no definite hibernation; it is active when warm and quiet when cold (Reeves, Miles, *et al.*, 1916; Yakhontov, 1934). According to Sweetman (1929) the weevil becomes active when the temperature rises to about 10° or 12° C. Regarding the upper temperature limit of its activity. Sweetman and Wedemeyer (1933), working under controlled conditions, found that the upper limit of the range of temperature favorable to oviposition is approximately 28° C. Yakhontov (1934) states that the insect does not become active until a temperature of 12° C is reached, and that a temperature of 25° limits the activity of the adult. His investigations showed that 55 to 60 days are required for the development of the internal reproductive system, and that a temperature higher than 12° C but lower than 25° is necessary for this development. In working out the climatic limitations of the insect he found it necessary to add to the period required for the weevil to pass through the developmental stages (from the egg to the emergence of the adult) a period of 55 to 60 days to allow the adults sufficient time to reach sexual maturity. He computed the period suitable to the weevil as beginning when the daily mean temperature reaches 10° C. This is apparently a rather satisfactory starting point, since, with such a mean temperature, the temperature during a part of the day will ordinarily be in excess of 12° C. The temperatures selected by Yakhontov come close to defining the range within which the adult weevil is active and are used here in a slightly modified form as the basis of our attempt to determine the southern limit of distribution of the insect.

The temperatures used by Yakhontov and those which must be used in the investigation of the distribution of any organism in relation to climate are climatologic temperatures, not controlled laboratory temperatures. That is to say, they are observed in standardized ventilated shelters several feet above the ground. Observations thus made obviously do not record the temperature of the air within the stand of alfalfa infested by the insect, the temperature of the plants, nor the temperature of the bodies of the insects themselves. The temperatures actually experienced in the field by the insects are not known. It cannot be doubted, however, that at midday and in summer the temperatures to which insects are subjected in stubble fields are higher than the observed climatologic temperatures. The upper temperature limit of activity of the insect reported from laboratory investigations is therefore higher than the upper limit of activity as reported from comparisons of the distribution of the insect with that of climatologic temperatures.

Construction of Temperature Graphs.—In order to form a judgment concerning the length of time favorable to the activity of the weevil at any climatologic station it was necessary to put the ordinarily published monthly means of temperature into a form in which time intervals between the dates of attainment of critical temperatures might be read with a nominal accuracy of one day. To this end mean temperatures were plotted by months on coördinate paper[6] on which the axis of abscissas is divided into single days. Abscissas of the monthly means were the middles of the successive months. Continuous smooth curves were then drawn with reference to these plotted points in such a manner that the mean temperature of any month represented the mean ordinate of the curve drawn through the segment of the chart corresponding to the month in question. Such smooth curves are of course only an approximation to curves of mean daily temperature but are as close approximations as may be obtained for all but exceptional climatologic stations. From such curves the approximate mean daily temperature of any day in the year

[6] Coördinate paper by Keuffel and Esser no. 358–142 was used for this study.

and the interval in days between the attainment of any pair of critical temperatures may be read.

Even an approximation to the mean temperature of any day takes no account of the daily range of temperature. Yet the daily range of temperature is of great importance in an investigation of such an insect as the alfalfa weevil, particularly in fixing a date for the beginning of its activity in late winter or early spring. This insect has no definite period of hibernation, but becomes active in the warmer hours of the day even when the mean temperature of the day would indicate that it remains inactive. In order to take account of this peculiarity of the insect, use was made of mean maximum temperatures as well as of mean temperatures. On the temperature chart drawn for each station curves of mean maximum temperature were drawn in the same manner as of mean temperature. The temperature interval represented by the vertical distance between the two curves at any date is then approximately half the daily range on that date, and if the daily march of temperature be considered symmetrical, 12 hours have temperatures between the mean and the maximum.

A horizontal line was then drawn on the chart at a temperature of 12.5° C (54.5° F). The beginning of the period of activity of the weevil in the spring was taken as the date corresponding to the point on this horizontal line that is equidistant vertically from the curves of mean temperature and mean maximum temperature. Again assuming a symmetrical daily march, this is the first date in the spring when the temperature is above 12.5° C during 6 hours of the day. The end of the active period in autumn was fixed in the same manner. In figures 5 to 9 the segments of both temperature curves lying within the period of assumed activity of the weevil are drawn; the graphs are cut off on the left and on the right at the extremities of the season of activity in the graphs referring to stations where winter temperatures fall low enough to produce a winter interruption.

In fixing the limits of the period of activity of the weevil that are determined by high temperature, mean temperature alone was used; where a summer interruption of activity is indicated in figures 5 to 9, it begins where the rising curve of mean temperature reaches the ordinate of 25° C (77° F) and ends where the curve falls below this ordinate. This procedure implies that the weevil becomes inactive when 12 hours of the daily period (assuming a symmetrical daily march) have temperatures above 25° C. Before this point is reached, however, the activity of the adult weevil is certainly greatly reduced. When the beginning and end of the parts of the year during which temperature permits the adult

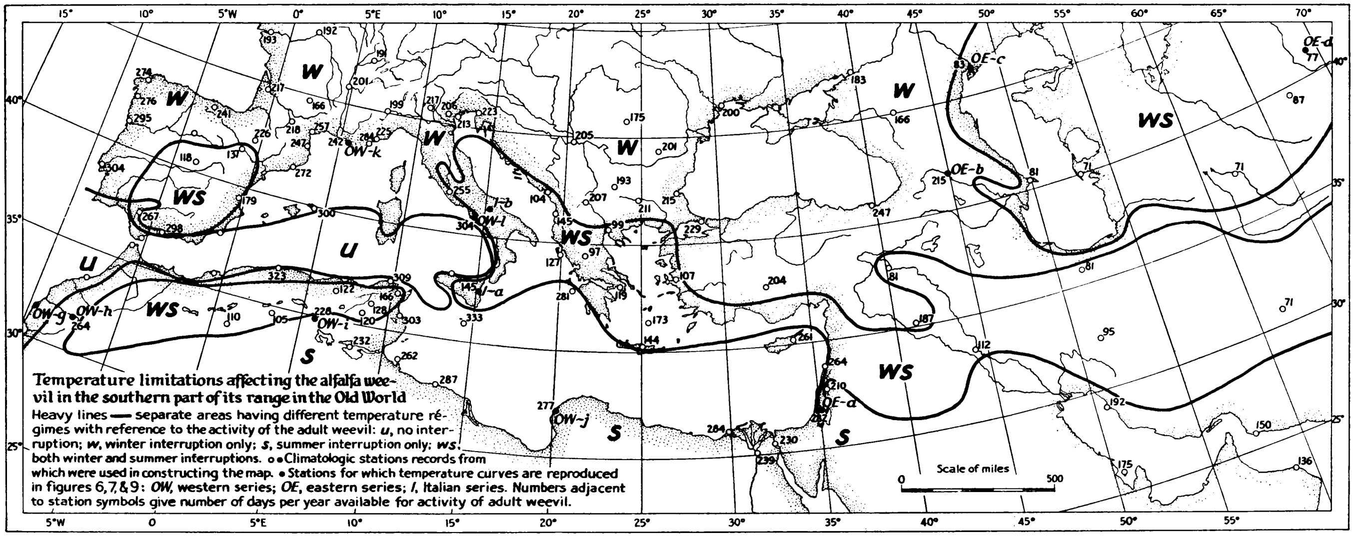

Fig. 2.—The four types of temperature regime under which the alfalfa weevil exists in the Old World. The small letters on the map that accompany the different series, such as the "*a*" in "*OW-a*," refer to the stations shown in figures 6, 7, and 9.

weevil to be active were thus fixed, it was easy to scale off from the chart the length of the period of activity in days.

Classification of Climatic Types.—The classification of types of annual

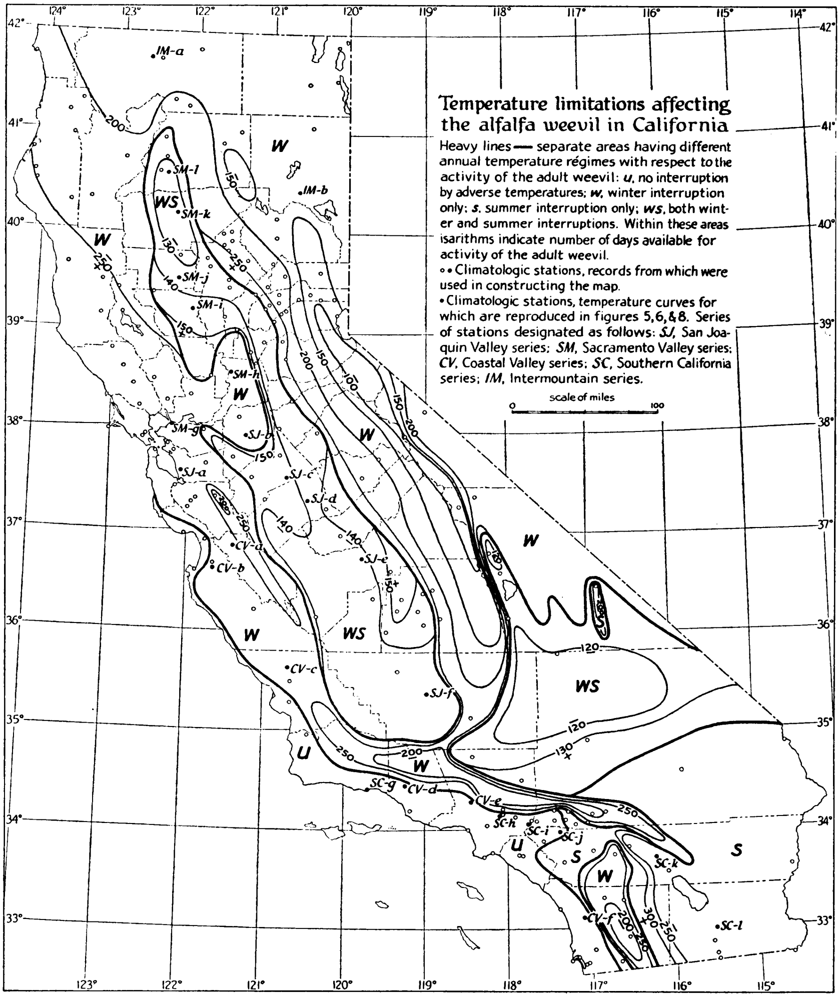

Fig. 3.—The four types of temperature regime in California under which the alfalfa weevil exists. The small letters on the map that accompany the different series, such as the *"a"* in *"SJ-a,"* refer to the stations shown in figures 5, 6, and 8.

march of temperature given below, and the regional distinctions shown in figures 2 and 3, are based on the procedure just described, a chart having been drawn for each of the several hundred stations identified on the two maps. In figures 5 to 9 sections of a few of the charts are reproduced, which are cut off on the time axis at the beginning and end of the periods that may be considered favorable to the weevil, and on the temperature axis by the ordinates of 12.5° and 25° C. Data were accessible to permit a detailed representation of temperature regimes in California, but only for a much less detailed representation of the parts of the Old World to be compared with California. The length of the period available for the activity of the adult alfalfa weevil is therefore represented on the map of California, figure 3, by isarithms[7] of number of days, but in figure 2 only by numbers entered next to the station symbols.

Within the range of distribution of the alfalfa weevil four types of annual temperature regime are distinguished: (1) Type *u* has no interruption of activity of the weevil in the course of the year; that is, the winter temperatures do not go low enough nor the summer temperatures high enough to exceed the limits defined. (2) Type *w* has winter interruption only. (3) Type *ws* has both winter and summer interruptions. (4) Type *s* has summer interruption only.

In type *u* the length of the annual period of activity is obviously 365 days. In types *w* and *s* the length of the annual period entered in figures 2 and 3 is the total number of days during which temperatures remain between the limits assumed to be critical for the weevil. In type *ws* there are two periods that fall within these limits, one in the spring and one in the fall. Since the spring period is of greater significance, the length of the period of activity in days, shown in figures 2 and 3 in the areas marked *ws,* is the length of the period of activity in spring and early summer. This is not intended to imply that the fall period is of no importance, for the sexual organs of the weevil are probably undergoing slow development at that time. To what extent this occurs is unknown, because the weevil has not been studied by us where there is a marked summer interruption. But there is not a great deal of activity during fall, and if the spring and fall periods were added to calculate the annual period of activity, the total would not be comparable with that in areas where there is no summer interruption. It would seem, however, that the fall period would become increasingly important as the summer interruption becomes shortened and the winter interruption lengthened.

It is doubtful whether any simple expression of temperature derived from ordinary climatologic records defines adequately the range of tolerance of any organism. The best that can be expected is that gradations of favorable or unfavorable conditions be defined and critical boundaries approximately located. We do not claim to have done more than that in

[7] *Editor's note.*—"Isarithm," sometimes spelled "isorithm," is a line drawn on a map or chart connecting points having equal numerical values of any quantity.

constructing figures 2 and 3. Since the quantities used in constructing the maps refer only to a range of temperature within which the alfalfa weevil can survive, and since the regional distinctions made are in terms of time rather than of temperature, extremes of heat and cold that kill the insect outright are not taken into consideration. These lethal conditions will be

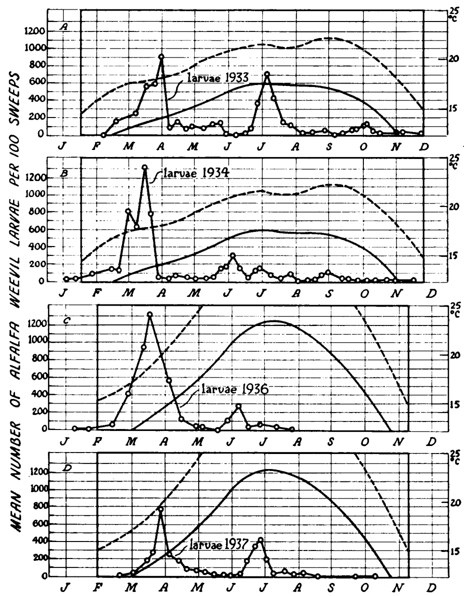

Fig. 4.—Average larval counts of the alfalfa weevil in the southern San Francisco Bay area in 1933 and 1934 and in the northern end of the San Joaquin Valley in 1936 and 1937, plotted for comparison with curves of mean (solid lines) and mean maximum (broken lines) temperature for two climatologic stations: *A* and *B*, Alvarado; and *C* and *D*, Stockton.

taken into account in the sections "Type *w* with Long Winter Interruption," "Type *ws* with Long Winters," and "Type *s* Climates Having a Summer Interruption but No Winter Interruption."

Relation of Larval Population to March of Temperature in Two Localities in Lowland Middle California.—The relation of the larval population in specific years to the average march of temperature in two localities in the infested area of lowland middle California is shown graphically in figure 4. The temperature curves drawn in *A* and *B* of figure 4 refer to Alvarado, a station near the eastern shore of the southern arm of San Francisco Bay; those in *C* and *D* to Stockton, situated at the northern end of the San Joaquin Valley. Alvarado has the characteristic cool summers and mild winters of the Bay area; Stockton has a more continental annual march of temperature but one less extreme than is found farther south in the San Joaquin Valley. The larval populations plotted in figure 4 are averages of all the larval counts obtained by sweeping a number of alfalfa fields in each of the two areas—the southern San Francisco Bay area and the northwestern San Joaquin Valley—the climates of which are represented by the temperature curves for the two stations.

Larval populations in the southern San Francisco Bay area in 1933 and 1934 are used because they represent conditions obtaining before the larval parasite *Bathyplectes curculionis* (Thoms.) was firmly established in the Bay area. In 1933 the winter was cold; in 1934 it was mild. In 1933 larvae were not found in the Bay area until well after the beginning of the season of activity of the adult weevil as defined by mean temperatures. In 1934 they were found before the beginning of the assumed period of activity. The average between the dates of first appearance of the larvae in these two years comes close to the average date of beginning of adult activity as defined. While the larval population is not large toward the end of the year in the Bay area, temperatures remain favorable for the development of the sexual organs of the adults. The larval curves for both years show that there at least two broods of larvae and that adults are reaching sexual maturity throughout the season of activity. Later peaks, after the first rise of the larval curve to a maximum, are probably greatly reduced by frequent cutting of the alfalfa. Moreover, after the first crop is harvested, the alfalfa in different fields is likely to be cut at different dates, so that the average larval populations plotted represent averages of counts made in fields where the alfalfa is in different stages of growth. Such an averaging eliminates pronounced maximums (other than the first maximum in the spring) that might appear if the later growth periods between cuttings were uniform for all fields and were as long as the period required for the first crop to mature.

In the northwestern San Joaquin Valley, the season of 1936 followed a mild winter, that of 1937 a cold winter. (In 1933 and 1934 the weevil populations in the San Joaquin Valley were very small.) Here again, the average of the dates of appearance of larvae in the two years falls at about the beginning of the season of activity as defined by mean temperatures at Stockton. In each of the two years a second peak in the larval curves indicates the occurrence of a second brood. But after this second maximum the curve drops to insignificant levels, which indicates that the summer temperatures of the northern San Joaquin Valley are more effective in restricting the activity of the adult weevil than are the lower temperatures experienced at the same time of the year in the neighborhood of San Francisco Bay. The agreement found between the seasonal march of larval population and the annual march of temperature in these two districts in lowland middle California gives us confidence in our definition of limiting temperatures.

TYPE *u*, CLIMATES HAVING NEITHER WINTER NOR SUMMER INTERRUPTION

From what is known of the habits of the weevil, areas having an annual march of temperature such as type *u* should be very favorable for it. According to data available, the weevil is found in only one area having this type of climate; namely, the northwestern coast of Africa and the extreme coastal strip of the western Mediterranean area (see fig. 2). The march of temperature in this area is illustrated in figure 6, *g*, by the curve for Mogador, Morocco. Our information on the destructiveness of the weevil in this general area is scanty, but according to J. M. Mimeur,[8] the weevil is well distributed throughout Morocco and causes damage only locally and occasionally. This fact would lead us to believe that there are factors other than climate that limit the activity of the insect. Possibly a climate of this type is very favorable to the parasites of the weevil. Or the brood or broods of the insect may be so dispersed through the year as to minimize its destructiveness.

A fairly large area lying entirely in southern California has a climate that falls into type *u* (see fig. 3 and fig. 5, *d* to *j*). Here, however, winter temperatures are lower and summer temperatures higher than in coastal Morocco, and at the present time the weevil is not known to occur in this area in California.

TYPE *w*, CLIMATES HAVING A WINTER INTERRUPTION BUT NO SUMMER INTERRUPTION

In the United States and over a large part of the Old World the weevil is most likely to be destructive in climates that fall into type *w*. It comprises a rather large variety of climates, and over a wide range of these the weevil finds conditions favorable. It can be roughly divided into two subtypes. The first has a relatively short winter interruption; the second, a long winter interruption.

Type w with Short Winter Interruption.—The first subtype of *w*, characterized by a short winter interruption, is found over a large part of central coastal California (fig. 3 and fig. 5, *a* to *c*) and in some places about the Mediterranean (fig. 2, fig. 6, *l* and fig. 7, *a*). This is the type of

[8] Letter to A. E. Michelbacher, April 28, 1938.

climate found in the infested area of lowland middle California in the several counties adjacent to San Francisco Bay and in the northwestern San Joaquin Valley. Much alfalfa is produced in this infested area, and

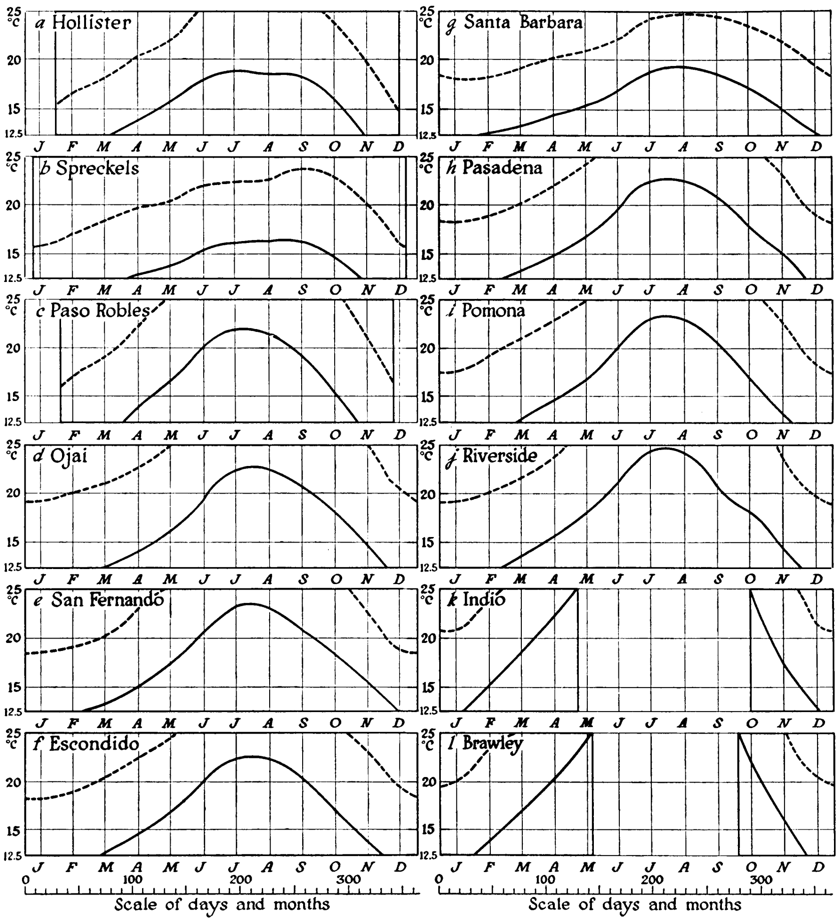

Fig. 5.—March of mean (solid lines) and mean maximum (broken lines) temperature during season or seasons permitting activity of the adult alfalfa weevil: *a* to *f*, stations in coastal valleys in the southern half of California (designated *CV* in fig. 3) in order from north to south; *g* to *l*, stations in southern California (designated *SC* in fig. 3) in order from the coast inland to Imperial Valley.

adjacent to it are other large alfalfa-growing sections. There is some variation in climate over the area, in terms of the length of the winter interruption. Near San Francisco Bay the winter interruption is very short, and summer temperatures are rather low; except for the short winter interruption the annual march of temperature is similar to that of type *u* (compare Alvarado, fig. 8, *a;* Mogador, fig. 6, *g;* and Santa Barbara, fig. 5, *g*). In the northwestern San Joaquin Valley, on the other

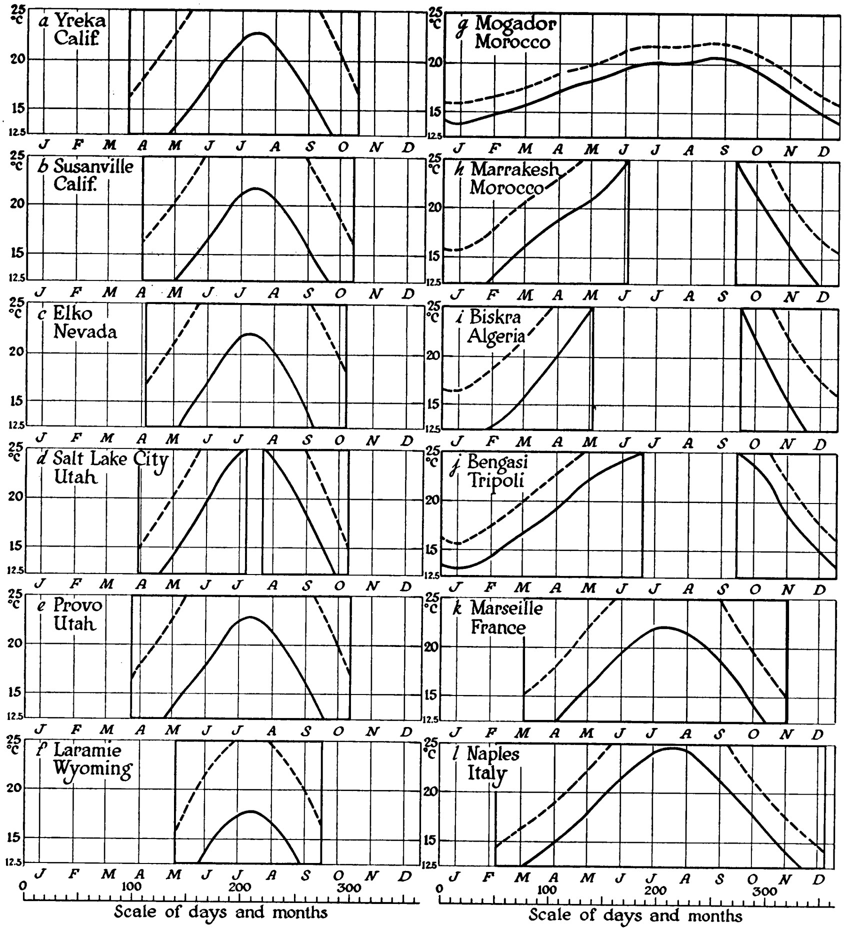

Fig. 6.—March of mean (solid lines) and mean maximum (broken lines) temperature during season or seasons permitting activity of the adult alfalfa weevil: *a* to *f*, intermountain series (the two California stations designated *IM* in fig. 3); *g* to *l*, western Old World Series (designated *OW* in fig. 2).

hand, the winter interruption is longer and the summer temperatures higher; its climate grades into type *ws,* characterized by both a winter and a summer interruption.

The weevil must have been present in lowland middle California for many years before its discovery in 1932, since when first found it was already distributed over a rather wide area traversed by two ranges of hills. One of these ranges, the Altamont Hills, is rather wide and barren. Yet before the discovery of the insect (made accidentally) not a single complaint had been received of any damage done by it. Our observations of the alfalfa weevil have been limited to the seven years it is known to have been present in lowland middle California. Owing to differences in climate, the behavior of the weevil has been different here from what it has been in other parts of the United States where it occurs—specifically in the Great Basin. This behavior is probably not, however, much different from its behavior in parts of the Old World.

Near San Francisco Bay the weevil probably reacts to climatic conditions in much the same way as it does along the northwestern coast of Africa and in the western Mediterranean area. There it is reported as doing damage only locally and occasionally, which report agrees with our observations here. Before the establishment of *Bathyplectes curculionis,* one severely damaged field could usually be found each year and sometimes several. Since the parasite became established, even these small losses have been greatly reduced, but possibly when final equilibrium is reached between the parasite and the weevil, fields will occasionally be found that have been damaged.

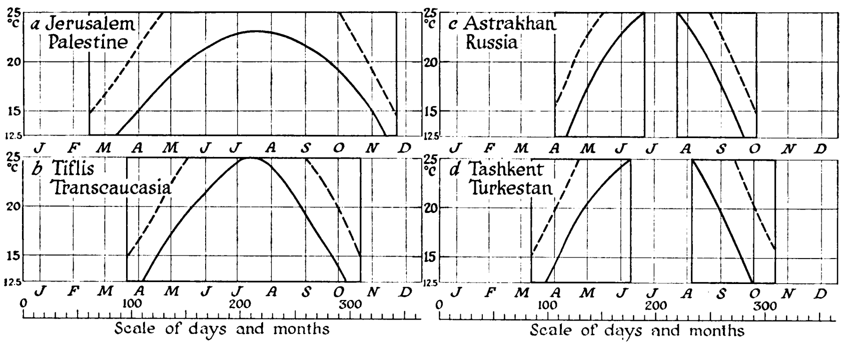

Fig. 7.—March of mean (solid lines) and mean maximum (broken lines) temperature during season or seasons permitting activity of the adult alfalfa weevil: eastern Old World series (designated *OE* in fig. 2).

In the northwestern part of the San Joaquin Valley very little damage has been observed. In fact, unless the weevil had been rather closely observed, the conclusion could easily enough have been reached that it is not a pest. The climate here is very similar to that found in parts of Italy and Palestine. This fact is rendered evident by a comparison of the temperature curves for Stockton (fig. 8, *b*), with those for Naples (fig. 6, *l*) and for Jerusalem (fig. 7, *a*). The response of the weevil to climate in all the areas represented by these stations must be rather similar. Bodenheimer (1930) reported that the weevil was present in Palestine, but that it was not considered a serious pest. Bodenheimer has, however, recently written[9] that since 1930 a more careful study of the weevil has been conducted and that it has been found to be a more serious pest than it was at first thought to be. Such an observation appears to agree rather closely with the observations made in lowland middle California. Certainly the weevil should not be considered a serious pest in the San Joaquin Valley. Since 1933, when the observations began, really serious injury has been noted in only one field, although in several others damage to the first crop has been noticeable. Injury may occur in one field while other fields in the same locality are relatively free from the insect. It has not been uncommon to find the density of the weevil in a heavily infested field ten or more times as large as in adjoining, more lightly infested fields.

At the southern edge of the infested area in the San Joaquin Valley only very light infestations have been encountered. The weevil was found near Gustine, Merced County, as early as 1933, but has always been scarce. No doubt it is encountering here a climate not very favorable to its development. The annual march of temperature near Gustine, probably very similar to that at Denair (fig. 8, *c*), represents the southern extremity of climates in the San Joaquin Valley that have, according to our interpretation, a winter interruption but not a summer interruption of activity of the adult weevil. Farther south summer temperatures become higher and the summer interruption appears (fig. 8, *d* to *f*). The same transition appears in the Sacramento Valley in a south to north direction (fig. 8, *g* to *l*). The difference in latitude between the southern San Joaquin Valley and the northern Sacramento Valley (compare Bakersfield, fig. 8, *f*, with Redding, fig. 8, *l*) expresses itself more distinctly in the length of the winter interruption than in the length of the summer interruption.

Type w with Long Winter Interruption.—The second subtype of *w*, characterized by a long winter interruption, is found in the intermountain region of the United States, including northeastern California (fig. 6, *a* to *f*). Representative stations in the Old World are Marseille, France, (fig. 6, *k*), and Tiflis, Transcaucasia (fig. 7, *b*).

In the United States the weevil reaches its highest degree of destructiveness in climates of this subtype. It produces a single and rather even brood. Egg deposition tends to occur within a relatively short period, so that the larvae attack the alfalfa in large numbers at the same time. This mass feeding is the principal cause of serious injury to the alfalfa.

[9] F. S. Bodenheimer, letter to A. E. Michelbacher, April 13, 1938.

This climatic type extends to the northern limit of distribution of the weevil in the United States, which limit is set by severe winter temperatures that persist for several months. Laramie, Wyoming (fig. 6, *f*), lies

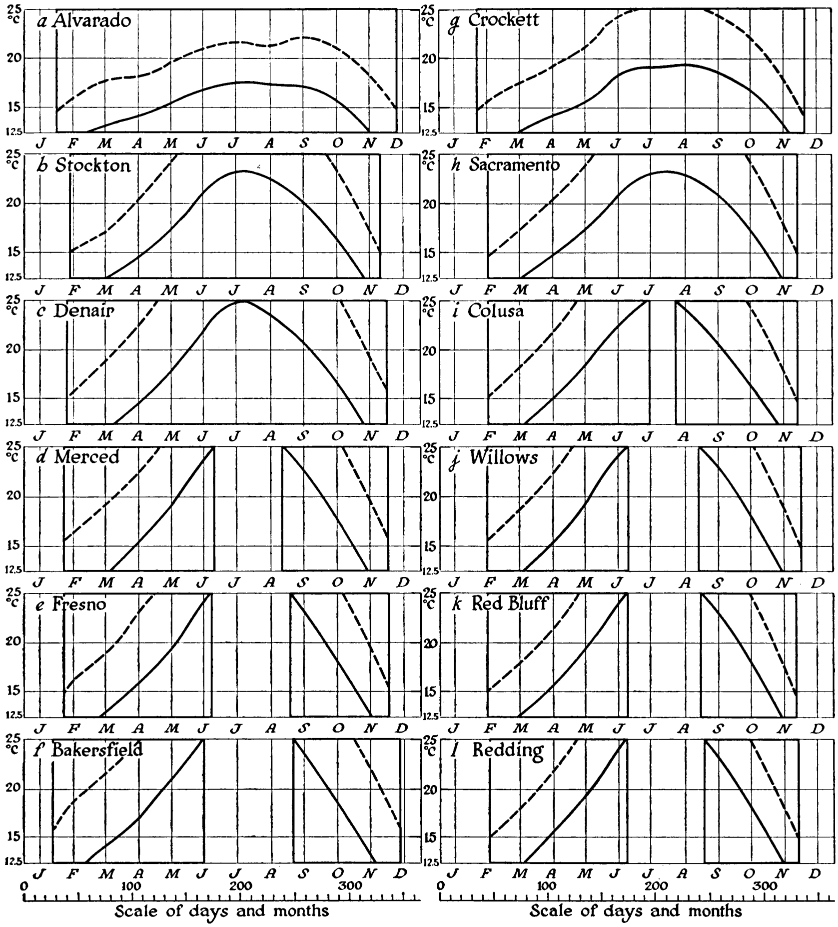

Fig. 8.—March of mean (solid lines) and mean maximum (broken lines) temperature during season or seasons permitting activity of the adult alfalfa weevil: *a* to *f*, San Joaquin Valley series (designated *SJ* in fig. 3); *g* to *l*, Sacramento Valley series (designated *SM* in fig. 3). The order of the stations in each series is from the San Francisco Bay area (Alvarado is not in the San Joaquin Valley proper) up to the respective valleys and so in the direction of increasing continentality.

about at this limit in the United States. In such an area the long severe winter reduces the time favorable to the weevil to a point where the pest is unable to survive. Even in areas subjected to serious weevil attack, cold winters lessen the damage done in the succeeding seasons. Reeves (1927), writing of the Great Basin, stated that during the first nine years of the history of the weevil in America it was very destructive and that during this time temperatures were for the most part abnormally high throughout the egg-laying season in April and May. He observed the same conditions in later years when serious damage was done by the insect.

TYPE *ws*, CLIMATES HAVING BOTH A WINTER AND A SUMMER INTERRUPTION

Climates of type *ws* are found throughout the greater part of the interior lowlands of California (fig. 3 and fig. 8, *d* to *f* and *i* to *l*). The type is continental rather than coastal, and in the Old World appears along the northern shore of the eastern, more continental, basin of the Mediterranean, in the Near East, and in the Aralo-Caspian depression (fig. 2, fig. 7, *c* and *d*, and fig. 9). It, too, can be divided into two subtypes. One subtype has long and moderately severe to very severe winters; the other has rather mild winters.

Type ws with Long Winters.—The first subtype of *ws,* characterized by long winters, is found in the Aralo-Caspian depression (see graphs for Astrakhan and Tashkent, fig. 7, *c* and *d*). Both stations have long and severe winters and also summers sufficiently warm to produce, according to definition, a summer interruption of activity of the weevil. The nearest to these among the American stations represented is Salt Lake City (fig. 6, *d*), where, however, the summer interruption is very short. In the American Great Basin, however, the winters are not so cold nor the summers so hot as in its counterpart in the Old World.

Yakhontov (1934) reports that the alfalfa weevil is not a serious pest about Astrakhan. From a comparison of winter temperatures at Astrakhan with those at other continental stations, both in the United States and in the Old World (table 1), the weevil should not be expected to be serious; Astrakhan's winter temperatures must be close to the lower limit endured by overwintering adult weevils. This evidence is of no great value, however, since the same low winter temperatures reduce the cultivation of alfalfa itself to insignificance. In Turkestan, however, the weevil is a serious pest. Tashkent, our representative station for Turkestan (table 1), has notably milder winters than Astrakhan. Our conclusion, therefore, is that in climates of this subtype of *ws,* severe winter temperature is the critical factor that limits activity of the alfalfa weevil. Detailed observations of the behavior of the weevil have not been made in climates of this subtype in the United States.

Type ws with Mild Winters.—This subtype of *ws,* characterized by mild winters, is found in the San Joaquin and Sacramento valleys (fig. 8,

TABLE 1

COMPARISON OF TEMPERATURES IN AREAS WHERE THE ALFALFA WEEVIL IS A PEST WITH THOSE WHERE WINTERS ARE TOO SEVERE FOR ITS SURVIVAL

Station	January		February		March		April		June		July		August		September	
	Mean °C	Mean maximum °C	Mean °C	Mean maximum °C	Mean °C	Mean maximum °C	Mean °C	Mean maximum °C	Mean °C	Mean Maximum °C	Mean °C	Mean maximum °C	Mean °C	Mean maximum °C	Mean °C	Mean maximum °C
Astrakhan,* U.S.S.R.	−7.00	− 4.3	−6.3	−3.2	−0.3	4.3	9.3	14.4	22.8	26.9	25.5	29.6	23.7	28.4	17.6	21.8
Tashkent, Turkestan	−1.30	3.6	1.6	7.0	8.0	13.4	14.3	19.8	25.8	32.4	27.6	34.6	25.4	33.3	19.5	28.0
Tiflis, Transcaucasia	0.00	4.2	2.5	7.0	6.6	11.8	11.8	16.2	21.4	26.8	24.5	30.1	24.1	30.0	19.2	25.0
Laramie,* U.S.	−5.40	0.6	−4.9	0.8	−1.3	4.8	3.2	9.8	13.7	21.5	17.3	25.1	16.6	24.4	12.0	19.9
Provo, U.S.	−3.11	3.6	0.0	7.0	4.8	12.3	9.3	18.1	18.1	28.7	22.3	32.8	21.1	31.8	15.8	26.6
Salt Lake City, U.S.	−1.60	2.6	1.0	5.2	5.3	10.3	9.9	15.3	19.7	26.3	24.5	31.3	23.7	30.2	18.0	24.5
Elko, U.S.	−4.70	3.7	−1.5	6.5	3.0	11.5	7.3	16.1	17.1	27.3	21.4	33.1	19.9	31.7	13.9	25.8
Susanville, U.S.	−0.90	4.2	1.5	7.6	4.7	11.3	8.6	16.3	16.9	25.8	21.2	30.6	20.5	29.7	15.7	24.3
Yreka, U.S.	1.00	6.6	3.8	10.1	6.4	14.0	9.4	18.1	17.8	28.1	22.0	33.1	21.2	32.2	16.2	26.6

* Areas having too severe winters for the survival of the weevil.

d to *f* and *i* to *l*) and in Italy (fig. 9). Information on the behavior of the weevil in this subtype is rather meager. The insect is reported as being present in parts of southern Europe belonging to this subtype, notably in Italy. Little information is available on the amount of damage it does, although Martelli (1911) reported extensive damage done by the pest in 1909 at Campobasso in east-central Italy. Lucas (1849) reported the weevil as being taken in the following places in Algeria: Melah, near Lake Tonga, and in the vicinity of Lacalle. These places for the most part fall into the subtype being discussed. In California the weevil has not penetrated into any area having both a winter and a summer interruption although in the northwestern San Joaquin Valley there is no barrier between the area of present occurrence and the more continental part of

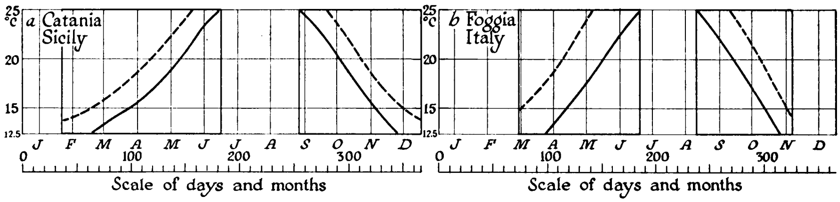

Fig. 9.—March of mean (solid lines) and mean maximum (broken lines) temperature during seasons permitting activity of the adult alfalfa weevil: Italian series (designated *I* in fig. 2). Compare figure 6, *l*.

the Valley. Winter and spring temperatures should be favorable in the parts of the interior valleys of California assigned to type *ws;* the only important element of the climate that might be detrimental is the hot, dry summer. Perhaps the length of time during which the weevil has been under observation in California is as yet insufficient to permit a definitive judgment concerning the distance it may be expected to penetrate into the more continental parts of the valleys. Yet evidence indicates that their climate is not very favorable to it and that there is not much likelihood of its becoming a serious pest in them. Apparently the long, hot summers increase the length of the diapause to a point where the environmental resistance becomes very great.

In figure 9 temperature curves for two Italian stations belonging to the second subtype of type *ws* are reproduced. They are very similar to the curves shown for interior stations in the San Joaquin and Sacramento valleys (fig. 8, *d* to *f* and *j* to *l*). The principal difference is that the maximum temperatures occurring in the summer are notably higher at the California stations (table 2). We therefore consider high summer temperatures the limiting factor in the second subtype of type *ws,* as low winter temperatures are in the first.

TABLE 2

COMPARISON OF TEMPERATURES FOR STATIONS IN SOUTHERN EUROPE AND IN THE INTERIOR OF THE SACRAMENTO AND SAN JOAQUIN VALLEYS

Station	January		February		March		April		June		July		August		September	
	Mean °C	Mean maximum °C	Mean °C	Mean maximum °C	Mean °C	Mean maximum °C	Mean °C	Mean maximum °C	Mean °C	Mean Maximum °C	Mean °C	Mean maximum °C	Mean °C	Mean maximum °C	Mean °C	Mean maximum °C
Catania, Sicily	10.80	13.6	11.4	14.2	13.5	16.0	15.7	18.6	23.4	26.7	26.4	30.1	26.3	30.1	24.4	27.5
Foggia, Italy	6.40	10.0	7.5	11.1	10.2	15.2	13.5	18.2	22.6	28.5	26.0	31.9	25.7	31.2	22.0	26.7
Merced, U.S.	7.80	12.8	9.8	16.4	11.8	19.1	15.2	22.5	23.6	32.5	26.9	36.1	25.9	35.1	22.5	31.3
Fresno, U.S.	7.83	12.4	10.8	16.3	12.9	18.9	15.9	23.1	24.1	32.9	27.7	37.2	26.9	36.3	23.0	31.7
Bakersfield, U.S.	8.40	14.7	11.4	18.8	13.7	21.3	17.0	24.7	25.3	34.5	28.8	37.9	27.6	37.1	23.3	32.9
Willows, U.S.	7.40	11.7	9.7	15.5	12.2	18.5	15.2	22.3	23.9	32.5	26.9	36.1	26.1	34.7	23.0	30.7
Red Bluff, U.S.	7.33	11.6	9.9	14.8	12.3	17.8	15.2	21.4	23.9	31.4	27.5	35.9	26.5	35.1	22.8	30.4
Redding, U.S.	7.30	12.1	9.7	14.9	12.2	17.9	15.4	21.9	24.0	31.3	27.7	35.8	27.1	35.2	23.1	30.5

TABLE 3

COMPARISON OF TEMPERATURES FOR STATIONS IN NORTH AFRICA AND IMPERIAL VALLEY

Station	January		February		March		April		June		July		August		September	
	Mean °C	Mean maximum °C	Mean °C	Mean maximum °C	Mean °C	Mean maximum °C	Mean °C	Mean maximum °C	Mean °C	Mean Maximum °C	Mean °C	Mean maximum °C	Mean °C	Mean maximum °C	Mean °C	Mean maximum °C
Marrakesh, Morocco	11.4	15.8	12.9	17.9	16.1	20.6	18.8	22.4	24.5	30.4	28.0	34.8	30.3	36.2	24.9	30.0
Biskra, Algeria	10.7	16.6	13.1	18.8	15.5	21.4	19.9	25.6	29.9	35.7	34.6	40.3	32.8	39.0	29.1	34.7
Bengasi, Tripoli	13.2	15.8	14.4	17.5	16.7	19.9	19.1	22.6	23.9	27.0	25.6	28.3	26.2	28.9	25.6	28.9
Indio, U.S.	12.1	20.9	15.1	23.8	18.3	26.4	22.3	30.1	31.0	38.9	34.1	41.4	33.3	40.8	29.9	38.1
Brawley, U.S.	11.4	20.1	14.1	23.3	16.9	25.6	20.4	29.4	29.1	39.2	32.3	41.1	32.0	40.6	28.4	37.8

TYPE *s*, CLIMATES HAVING A SUMMER INTERRUPTION BUT NO WINTER INTERRUPTION

Climates of type *s* are found in the Imperial Valley of California (fig. 5, *k* and *l*) and in northern Africa (fig. 6, *h* to *j*). The weevil is reported to occur throughout northern Africa. De Lepiney and Mimeur (1932) reported its presence in many localities in Morocco, including the vicinity of Marrakesh (fig. 6, *h*). Willcocks (1922) reported it from Egypt as a pest on berseem (Egyptian clover) ; but the rapid growth of the host plant, close feeding by cattle, or frequent cutting of the crop prevents it from causing appreciable damage. He reported further that he had seen only one or two instances of serious injury and that these were in fields where the clover was making a poor growth. A. E. Hassan[10] writes that the alfalfa weevil is present throughout the Nile Valley and is found in the oases of the western desert. He states that little alfalfa is grown in the area mentioned, but that he considers the weevil a serious pest especially during the breeding season from January to April. Fletcher (1917) reported the weevil as occurring in India at Pusa, Lyallpur, and in the Punjab but that it is not considered a pest. This area falls into type *s*.

In northern Africa injury by the weevil is probably for the most part restricted to areas close to the coast and at higher elevations. Certainly there are no published reports of its causing serious losses, nor should one expect to find it abundant in the hot, dry interior of northern Africa. Along the coast and at higher elevations lower summer temperatures obtain than in Imperial Valley (table 3) or, for that matter, in many other parts of southern California. In the interior valleys of southern California at any rate, the daily and yearly fluctuations of temperatures are much greater than in coastal northern Africa. These more extreme fluctuations are probably more hostile to the weevil than the temperature conditions under which it exists in northern Africa. We believe, therefore, that it will not be able to adapt itself to the climate of Imperial Valley and that even in localities having temperatures such as are observed at Riverside (fig. 5, *j*), which station just falls within type *u*, it will find survival rather difficult on account of the high summer maximums.

CONFUSION OF SPECIES

Recently (spring of 1939) *Hypera brunneipennis* (Boh.), a very close relative of the alfalfa weevil, *H. postica* Gyll., has been found in the Yuma Valley of Arizona and in the adjacent part of California. The two

[10] Letter to A. E. Michelbacher, April 18, 1938.

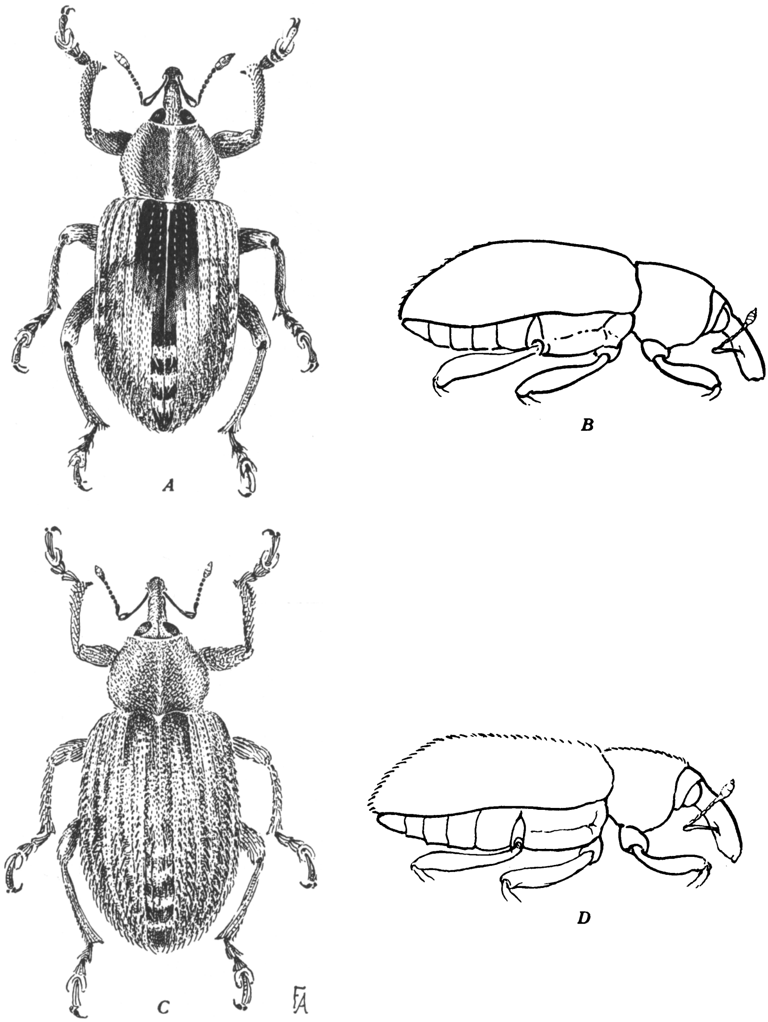

Fig. 10.—*A,* Dorsal view, and *B,* lateral view, of the adult alfalfa weevil, *Hypera postica* Gyll.; *C,* dorsal view, and *D,* lateral view, of adult *H. brunneipennis* (Boh.).

species are very much alike[11] (see fig. 10), but *H. brunneipennis* is larger with proportionately broader prothorax, is flatter in side view, has a more even and not so pronounced color pattern, slightly more erect setae, and the elytra is broader, evenly oval, and not so parallel in front as in *H. postica.*

[11] The authors are indebted to Professor E. C. Van Dyke for the comparisons of the two species as here given.

Hypera brunneipennis, known by the common name of Egyptian, or Ethiopian, alfalfa weevil, is reported from Egypt and Sicily (Schoenherr, 1834; Csiki, 1934). It is probably widespread in northern Africa although it is not known to occur in Europe, for Capiomont (1868) stated that all specimens labeled as *brunneipennis* were *H. murina.* He gave the distribution of *brunneipennis* as Egypt, Abyssinia (Ethiopia), and Hindustan. Very probably it has been mistaken, in part, for *H. postica* and referred to that species in the literature dealing with the occurrence of the alfalfa weevil in Africa. Both species occur in northern Africa,[12] but because *H. brunneipennis* is an insect apparently well adapted to climates having hot summers, it no doubt extends into the hotter regions. Because it is already found in Yuma Valley, there is little doubt that it will find the Imperial Valley and other desert regions with hot summers where alfalfa is grown suitable for its survival. Recently specimens have been received from Egypt, which M. T. Sayed[13] reports as being the common species occurring there.

In reply to an inquiry about the distribution of *Hypera postica,* L. L. Buchanan writes the following:

> As far as I can find, the National Museum Collection [Washington, D. C.] contains no specimens of *Hypera postica* from northern Africa, India, Persia, or any of the neighboring Asiatic countries. It should be remembered, however, that the Museum Collection from these regions is relatively very limited, and the absence of a species does not necessarily have any significance.
>
> In looking over the undistributed and unarranged material I did find a few specimens of *Hypera* which were previously overlooked and which may be of some interest to you. One of these is supposedly from Syria, and bears a label "*ponticus* Cap."; it seems to me to belong to *Brunneipennis* Boh. A set of five specimens are from Mostaganem, Algeria, and are labeled "Algerian variety of *Ph. varius*"; these I feel confident are *Hypera murina* F., a species which rather closely resembles *brunneipennis* but has a somewhat differently shaped prothorax, different ♂ genitalia, etc. Lastly, a few unidentified specimens from northwestern India (labeled "Punjab and U. Provinces") were located. These agree very well with *brunneipennis.*[14]

PARASITISM AND CLIMATE

Parasitism must be taken into account in any discussion of the climatic limitations of the alfalfa weevil. Climatic conditions favorable to the weevil may also be exceptionally favorable for one or more of its parasites. It is therefore conceivable that the weevil may be more destructive,

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[12] Specimens of *Hypera postica* were received from Le Kef, Tunisia, during the winter of 1939 (after this paper went to press), so there can be but little doubt that this species exists throughout the cooler regions of northern Africa. Also during 1939, specimens of *H. postica* have been received from several localities in Palestine.

[13] M. T. Sayed, letter to A. E. Michelbacher, August 31, 1939.

[14] L. L. Buchanan, letter to A. E. Michelbacher, July 17, 1939.

or at least more abundant, in a climatic zone other than its optimum if the conditions in the zone in question are not optimum for maximum parasitism. Nicholson (1937) has cited this principle, but without giving any examples of its application.

In California our observations have yielded evidence of such a phenomenon. When the weevil was first found in lowland middle California, it was most abundant at Pleasanton, Alameda County, and in adjacent areas near San Francisco Bay. The populations encountered in the infested part of the San Joaquin Valley were rather small in comparison with those found near the Bay. In 1933 and 1934 the United States Department of Agriculture Bureau of Entomology and Plant Quarantine introduced the larval parasite, *Bathyplectes curculionis* (Thoms.), into the infested areas. The parasite readily became established and is evidently more effective about Pleasanton and in the Bay area in general than in the San Joaquin Valley.

As a result of depredations of the parasite, the weevil populations now found in the Bay area are smaller than those found in northwestern San Joaquin Valley, a condition that is the reverse of that which obtained before the parasite was introduced. The relation of the parasite to the weevil is discussed by Michelbacher (1940). Further observation is needed to determine whether the present relative frequency of the insect in the two areas will be permanent. If the trends of the weevil populations were studied without any attention to parasitism, however, the conclusion might be reached that the climate of the northwestern part of the San Joaquin Valley is more favorable to the weevil than that of the areas close to San Francisco Bay, with their cooler summers and more moderate winters. Such is evidently not the case.

We have noted that the maximum destructiveness of the weevil has been observed in areas having rather short growing seasons, such as the Great Basin and Turkestan. Short growing seasons tend to bring about mass feeding by weevil larvae with resulting heavy losses. It has been suggested that in more moderate climates, such as those about San Francisco Bay and in the western Mediterranean, the destructiveness of the weevil has been slight because the brood or broods are scattered and drawn out over a long season of activity, so that there is not the same opportunity for mass attack as in climates having a shorter season of activity. Reeves (1917) reported that H. S. Smith, who studied the weevil along the coast of Italy, was of the opinion that one of the reasons why the weevil, though present in considerable numbers there, is of no consequence as a pest is that the generations are more or less spread out so that feeding continues through several months instead of being concentrated into a few weeks. Certainly, in climates having mild winters and cool summers, feeding continues through a good portion of the year, partly because the lifetime of a single generation is prolonged, and partly because the climate permits more than one generation a season. However, even under such conditions some damage may be done by the weevils attacking the alfalfa en masse.

A mild summer and a long season of activity may not only favor a certain parasite but may also favor parasitism in general because the host is accessible through a large portion of the year and parasitism therefore probably more effective.

SPREAD OF THE ALFALFA WEEVIL IN LOWLAND MIDDLE CALIFORNIA

In spite of the fact that the southern limit of infestation cuts across one of the most important areas of alfalfa production in the state, in seven years, as previously mentioned (p. 103), the spread of the weevil beyond the area found to be infested in 1932 has been slight. In 1933 the weevil was found about 2 miles northwest of Gustine, Merced County; this find represented an air-line extension of only about 6 miles since the preceding year. Since that time the weevil has shown no evidence of building up in population in the vicinity of Gustine; in some years it has been very difficult to find. In 1938 a few specimens of the weevil were collected near Hilmar, Merced County; this find established an extension of the area of infestation but did not carry the weevil south of where it had already been found for several years.

The greatest spread of the weevil has been eastward and northward, but no jumps of noteworthy magnitude have been recorded. In some places where the insect has been collected it has been very scarce. Quite possibly it existed in such places for some time before it was first collected, so that these finds may not record recent jumps. Yet conditions in the San Joaquin Valley would seem in general to be favorable to rapid spread of the weevil. Not only are quantities of alfalfa grown, but in some areas under favorable conditions there is a luxurious growth of bur clover (*Medicago hispida*), a very suitable host plant and one that should aid the weevil in its spread from one field to another.

Reeves (1927) reported the dispersion of the weevil at the rate of 10 to 20 miles a year, with little regard to natural aids or hindrances. Newton (1933) recorded that in Colorado it had spread at an average rate of about 6 miles a season. Hagan (1918) estimated an average spread of 20 miles a year but was of the opinion that under very favorable conditions the rate might be as high as 50 to 60 miles.

If the weevil had spread in the San Joaquin Valley at the rate of only 10 miles a year, it should now be found at least 60 miles from the boundary of the infested area as determined in 1932. The greatest spread observed is hardly half this distance, and the spread south in the San Joaquin Valley is not more than a tenth of the distance in spite of the fact that the southern periphery of the known infestation is in the midst of a large alfalfa-growing section. Since, in spite of apparently ideal conditions for rapid dissemination, no such dissemination has taken place, we judge that the insect is reaching an unfavorable climatic zone. We have suspected this since the time when the weevil was first discovered in the San Joaquin Valley, but because of the large populations observed in scattered fields throughout the infested area from Tracy, San Joaquin County, to Patterson, Stanislaus County, we have not felt justified in drawing definite conclusions before the insect was observed through a series of years. Small populations occur throughout the infested area, but only in scattered fields does the population rise to a level at which some injury results.

In the spring of 1939[15] the larval population was the largest yet encountered in the San Joaquin Valley. In most fields an increase in numbers over the preceding year was observed, and in several the injury done, bordered on economic damage. Yet in spite of this general increase in population we were unable to demonstrate any extension of the infested area.

The most serious damage observed was in a single field near Patterson, Stanislaus County. Although this field is situated not far from the southern boundary of the infestation, the first crop of alfalfa in 1936 was almost completely destroyed. The infestation was so heavy that the growth of the second crop on half the field was delayed four weeks. This occurrence was unusual; but if such a population can develop near the southern border of the infested area, it is difficult to understand why the weevil is not able to penetrate farther south in the San Joaquin Valley. Nevertheless, no marked jumps have been noted; and over the infested area as a whole it is difficult to find fields in which the insect is actually doing damage.

Failure of the weevil to advance farther southward is a curious phenomenon which may, nevertheless, have a parallel along one part of the boundary of its distribution in the Old World: in Turkestan, U. S. S. R. —represented in our collection of temperature curves by Tashkent,

[15] During the spring of 1940 (after this paper went to press) a serious outbreak of the alfalfa weevil occurred in 5 or 6 fields just south of Tracy. Outside of this one small area of heavy infestation the weevil population was very small, being no larger than in previous years and in some cases smaller.

figure 7, *d*. On the basis of our analysis of its temperature limitations in the United States, the weevil should not exist here at all, and in fact this area is certainly close to both the northern and southern boundaries of weevil distribution in central Asia.[16] Yet the weevil not only survives, but even inflicts noteworthy damage in this area. Here then, as in the San Joaquin Valley of California, large weevil populations are apparently built up very close to a climatic barrier. That the insect should be more destructive near such a barrier than in the climates presumably most favorable to its survival is a strange paradox. As a further, though less striking, example, perhaps the Great Basin may be compared with lowland middle California. We merely note this paradox, without trying to offer a complete explanation. Our information, both on the behavior of the weevil and on the temperatures that obtain along the boundaries of the Asiatic area of infestation, is too scanty to permit us to discuss the favorable and unfavorable conditions encountered there by the weevil.

The conclusion that climate limits further rapid spread in the San Joaquin Valley could be more easily accepted if the weevil had shown signs of more rapid dissemination about the country adjacent to San Francisco Bay, where summers are cool. All evidence indicates that the climate in the Bay area is very favorable. The failure of the weevil to spread more rapidly than it has may be the result of scarcity of alfalfa fields, but this fact by itself hardly seems an adequate explanation. The larval parasite, *Bathyplectes curculionis,* may also be a factor.[17] The fact

[16] The weevil is, in fact, absent from most of the Aralo-Caspian depression, evidently on account of the shortness of the season favorable to its activity between the cold winter and the hot summer. Yakhontov's (1934, fig. 3, p. 32) map shows the weevil as occurring in Turkestan only in the foothill country at the eastern edge of the Aralo-Caspian depression. The northern boundary, according to Yakhontov, swings sharply southeastward from the vicinity of Leningrad to the mouth of the Volga, is resumed at the northeastern extremity of the Caspian Sea, and extends eastward through Kazakstan to Lake Balkhash. The more southerly position of the boundary in the east is the consequence of the increasing severity of winter temperatures toward the interior of the continent. Summer temperatures become higher, as well, toward the eastern extremity of the boundary, both because of increasing continentality and because of lower latitude.

[17] On April 11, 1940 (after this paper went to press), a thorough survey was made south of the known infestation adjacent to the San Francisco Bay. Although no alfalfa weevils were collected, four adult *Bathyplectes curculionis,* the larval parasite of the alfalfa weevil, were taken—one near Paicines, San Benito County, the southernmost point covered in the survey. The finding of the parasites may indicate that the weevil occurs here but in such small numbers that it has not yet been taken; for the area surveyed has a climate known to be favorable for extremely efficient parasitism. If the weevil does occur here, then the area of the infestation has been increased in an air-line distance by more than 60 miles. Of course the specimens of *Bathyplectes* collected may possibly have flown into the area from the alfalfa-weevil-infested area to the north, and although we hardly believe this to be the case, doubt will exist until specimens of the alfalfa weevil are actually collected. If the latter really occurs in this area, then some interesting light is shed on the occurrence of the pest in lowland middle California. In 1932, after the discovery of the weevil, an ex-

remains, however, that the slow spread of the weevil in the Bay area weakens somewhat the hypothesis of a climatic cause for the lack of expansion of the infestation southward into the San Joaquin Valley. However, the fact that the weevil has hardly been able to maintain itself near Gustine would indicate that it is meeting considerable environmental resistance, and we believe this resistance to be high summer temperature.

PROBABLE FUTURE SPREAD OF THE ALFALFA WEEVIL IN CALIFORNIA

There is always danger in attempting to predict what an insect will do in a new area. The attempt to do so could be undertaken with full prospect of success only if the necessary information were available from all other areas in which it occurs. Even then there would be difficulty in predicting the behavior of the insect in a new home in the absence of its usual parasites and predators. But the climatic limitations of an insect should be capable of definition if its distribution in its original habitat and the climatic conditions it encounters there were thoroughly known. The information at our disposal concerning the distribution and abundance of the alfalfa weevil in the Old World, and concerning the climates of the wide area of its distribution there, has fallen far short of what we should have liked to have. Statements in the literature concerning the distribution and abundance of the insect are too often couched in extremely general terms. Climatic data, particularly on mean maximum temperatures, are scanty for many parts of the wide area of distribution of the insect, especially for sparsely settled and scientifically backward areas. We cannot be certain about the comparability of all the data we were able to find. The southern limit of distribution of the insect in the Old World has not been defined accurately, nor the extent of damage done by it in northern Africa. The tracing of this southern limit is further complicated by the occurrence of *Hypera brunneipennis* in the vicinity of the southern limit of *H. postica*. Nevertheless, with the information obtainable, and with our knowledge of the behavior of the weevil in California, we are in a position to say something concerning its probable

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tensive survey of lowland middle California was made, and since it was not found around San Benito County then, the supposition is that the weevil was first established in the San Joaquin Valley. From there it spread to the Pleasanton area and then to the fields adjacent to the San Francisco Bay. It probably had just recently reached the San Francisco Bay area at the time of its discovery in the San Joaquin Valley and therefore it had not had sufficient time to spread south, even though the climate was favorable to the pest. *Bathyplectes* was introduced into the San Francisco Bay area in 1934, and because it became such an effective parasite, and since there were no extensive further surveys beyond this area, the spread of the weevil was obscured.

future spread in this state and concerning the likelihood of its becoming destructive in the large fraction of the area of California to which it has not yet spread.

These conclusions are expressed in the following paragraphs, and the climatic areas referred to are drawn in figure 11. Figure 11 is based on the data shown in figure 3 and on a comparison of the distribution of the weevil in the Old World, for which the southern part of the area of distribution of the insect is analyzed climatically in figure 2. In addition, conclusions based on the considerations expressed in the foregoing independently of our treatment of the annual march of temperature have been used, particularly in making estimates of the expansion of the weevil in the parts of the state having high maximum temperatures in summer. Errors made here in the estimate of possible future expansion of the area of infestation are probably all in the direction of giving the weevil the benefit of any doubt of its ability to invade hitherto uninfested country. The potential spread defined is to be looked upon as a maximum rather than as a minimum estimate.

The weevil should be able to survive in all the coastal valleys of California. In some of these it may occasionaly appear in destructive numbers but should not in general become a serious menace to alfalfa production. In areas having moderate climates the larval parasite, *Bathyplectes curculionis,* may be very effective in holding the weevil populations in check. The weevil should be able to maintain itself in the cooler parts of southern California, but we doubt very much that it will be a serious pest. Here and there a small amount of damage may be done. The weevil should spread northward in the Sacramento Valley at least to a point a little north of Sacramento; within this potential area of infestation some injury may occasionally be experienced.

Extensive damage may be expected in all parts of the state having type *w* climate with long winter interruption similar to that in the intermountain region (fig. 6, *a* and *b*). Fortunately only a very small part of the alfalfa grown in California is produced in such climates.

Information gained from investigation of the weevil to date indicates that areas having summer temperatures as high as those observed at Denair (fig. 8, *c*) or higher, that is, belonging to type *ws* with mild winters and high summer temperatures, are safe from serious attack by the weevil. Hence large parts of both the San Joaquin and Sacramento valleys should be unsuited to the pest and not in danger of serious attack.

We have no way of judging the effect of very hot, dry summers on the weevil but are inclined to believe that they are very unfavorable and are an important influence in limiting the distribution of the insect in California. The work of Sweetman and Wedemeyer (1933) showed that temperatures of 30° to 37° C are very injurious, especially when relative humidity is high. Since climatologic observations probably always record maximum temperatures lower than those actually experienced by the weevil among the plants on which it feeds, undoubtedly it would daily experience temperatures as high as Sweetman and Wedemeyer found injurious, especially in stubble, during the hot summers of the interior California valleys.

In figure 11 the heavier shading is used for the parts of the state in which greater damage from the alfalfa weevil may be expected. The first area, the one where the weevil is likely to be most destructive, is the part of the state having a type *w* climate with long winter interruption similar to that of the intermountain region. Although it covers a large fraction of the area of the state, it is of no great importance, since it is largely mountainous and only in small part suited to alfalfa culture.

The second is the coastal area; although it has a climate highly suitable to the weevil (*u* and *w* with mild winters), we do not expect the weevil to do serious damage there, because the study of the larval parasite *Bathyplectes curculionis* indicates that the climate of coastal California is also well suited to the activity of the parasite which will act as an important check on the weevil.

The third area includes the interior valleys of the state having only moderately continental climates, type *w* with moderately mild winters and higher summer temperatures than found in the coastal areas. This area includes a very large alfalfa-growing section. Under favorable conditions of culture the weevil may be somewhat destructive locally and occasionally in this area but will probably not become a serious pest. It is possible for the weevil to produce at least a partial second generation within a season. *Bathyplectes curculionis* does not appear to be as effective here as in the coastal area. Rapid growth and frequent cutting of the alfalfa are probably important factors in reducing damage by the weevil. The weevil is known to have been present in a part of the area since 1932, and during this time has not been a serious pest.

The interior valleys having hot summers (*ws* with high summer temperatures) make up the fourth area. The weevil has not penetrated into this area, but in the Old World it is reported from areas having a similar climate, so that on the basis of this evidence the spread into corresponding parts of California might be expected. But the situation is complicated by the fact that in the Old World the alfalfa weevil has evidently been confused in part with the closely related species, *Hypera brunneipennis*. This fact hampers our judgment concerning the possible future spread of *H. postica*. Judgment seems warranted, however, that even if the alfalfa weevil does establish itself in this area it will never become a serious pest. *H. brunneipennis* will probably in time find its way into the

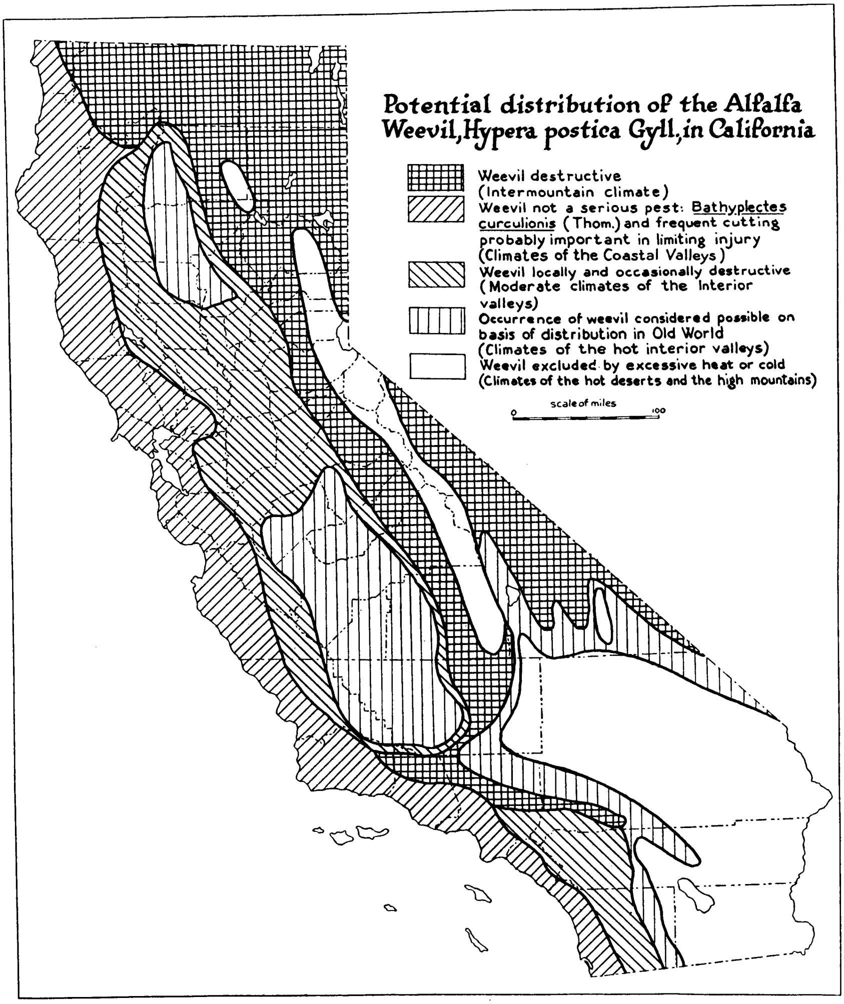

Fig. 11.—Greatest potential distribution of the alfalfa weevil in California.

area, and when it does, we expect that it will find the climate well suited to its development.

The fifth area shown in figure 11 includes both the higher mountain regions where the winter is too cold for the weevil to survive, and the hot deserts where high temperatures experienced through a good part of the year exclude it. Three climatic types are included: *w* with short summer period of activity of the weevil, *ws* with short spring period of activity, and *s* with short winter period of activity. *Hypera brunneipennis* is already known to occur in the last type. In the very small infested area to which it was limited when first discovered in the spring of 1939, it was found in large numbers, and all our evidence indicates that *H. brunneipennis* will find the hot deserts of California very favorable to its survival.

SUMMARY

Because the alfalfa weevil has failed to spread readily into the hotter portions of the San Joaquin Valley since its discovery in lowland middle California in 1932, we are inclined to the belief that the pest is encountering a climatic barrier.

From our observations and from studies made throughout the world where the weevil occurs, it appears that high temperature sends the adult weevils into estivation. Furthermore, high temperature retards or inhibits the maturing of the sexual organs. The temperature range favorable for sexual development appears to fall between the limits of 10° and 25° C. Using this temperature range as a basis, the portion or portions of the year favorable to adult-weevil activity have been plotted for stations in America and in a part of the Old World where the weevil is known to occur. By so doing the weevil was found to exist in areas having four distinct types of climate: (1) type *u* in areas where temperatures favorable to adult activity are present throughout the entire year; (2) type *w* where, owing to cold winters, there is a winter interruption in adult activity; (3) type *s* where, owing to hot summers, there is a summer interruption; and (4) type *ws* where both cold winters and hot summers cause a summer and a winter interruption.

Areas having a winter interruption (type *w*) are further divided into two subtypes: (*a*) those having a short winter interruption; and (*b*) those having a long winter interruption. In climates of the latter type the alfalfa weevil is very destructive. This is the result of the short growing season which brings about a mass attack of the weevil on the alfalfa. Climates of this type are characteristic of the intermountain region of the United States which includes northeastern California. In this subtype the principal adverse factor affecting the weevil is low winter temperature. In climates of the first subtype where the winter interruption is short, adult weevils are active early in the year and before midsummer there is time for one full generation and at least a partial second generation. Alfalfa is seriously attacked only occasionally. This subtype ap-

pears in California in the coastal valleys north of southern California, in the lower extremities of the San Joaquin and Sacramento valleys, and along the coast of the northern half of the state.

Areas having both a winter and a summer interruption (type *ws*) are also divided into two subtypes: (*a*) those having cold winters; and (*b*) those having relatively mild winters. The first subtype is represented by the continental stations in the Old World where the alfalfa weevil is destructive because of mass feeding by the larvae, and the factor that limits the weevil is cold and severe winters. In the second subtype with mild winters the limiting factor is high summer temperatures, as is also the case in the climatic type *s* where there is a summer interruption but no winter interruption.

Judging from the reported distribution of the alfalfa weevil in the hotter portions of its range in the Old World, the pest can apparently adapt itself to almost all the climates of California. Certainly the climates of the hot California deserts would appear to be favorable, but we hardly think that this is the case, for evidence is presented that would tend to indicate that a second species closely related to the alfalfa weevil is involved. The species *Hypera brunneipennis* was recently found in the neighborhood of Yuma, Arizona, and adjacent part of California. Very likely this species, which is adapted to hot climates, has been confused with *H. postica* in the hotter portions of the Old World and has been referred to the latter species. Judging from the behavior of the alfalfa weevil in California and the lack of reported damage in places such as Italy, we are inclined to believe that the pest will not be able to survive in the hotter portions of California.

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