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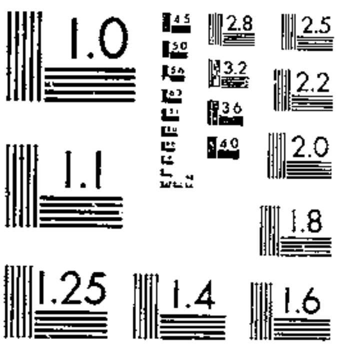

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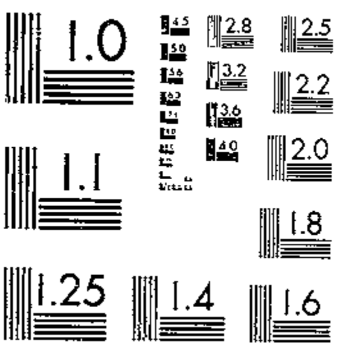

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TECHNICAL BULLETIN No. 618 JUNE 1938

# BIOLOGICAL STUDIES ON THE LEAFHOPPER EMPOASCA FABAE AS A BEAN PEST

By

DWIGHT M. DELONG

Formerly Specialist in Bean Leafhopper Studies
Division of Truck Crop and Garden Insect Investigations
Bureau of Entomology and Plant Quarantine



UNITED STATES DEPARTMENT OF AGRICULTURE, WASHINGTON, D. C.

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# BIOLOGICAL STUDIES ON THE LEAFHOPPER EMPOASCA FABAE AS A BEAN PEST[1]

By Dwight M. DeLong[2]

*Formerly specialist in bean leafhopper studies, Division of Truck Crop and Garden Insect Investigations, Bureau of Entomology and Plant Quarantine*

CONTENTS



## INTRODUCTION

The potato leafhopper (*Empoasca fabae* Harris) is undoubtedly the most important pest of potato occurring over a large area in the eastern part of the United States. It also attacks many other types of plants, including several of the legumes. Bush beans have been injured severely in Ohio during the last few years. In 1924 and 1925, while the author was attempting to carry on experiments for the control of the Mexican bean beetle in southern Ohio, this leafhopper became so abundant as to destroy entire plots of young beans intended for control experiments on the Mexican bean beetle (*Epilachna varivestis* Muls.). N. F. Howard, in charge of these experiments, then suggested that a special study be made of the potato leafhopper as a bean pest in this area and that an attempt be made to devise a method of control. Biological and control studies were therefore carried out during 1926, 1927, and 1928. In the latter part of the summer of

[1] Received for publication October 20, 1937.
[2] Separated from service April 2, 1933.

1928 and during 1929 a special study was carried on concerning the action of bordeaux mixture as an insecticide. In 1930, through the kindness of J. E. Graf and P. N. Annand, observations were made throughout the Western States and on the Pacific coast in connection with studies of the beet leafhopper (*Eutettix tenellus* Baker). Notes were made especially upon occurrence, economic injury, relative abundance in populations, and the ecological factors that are correlated with relative abundance.

This bulletin contains the more important data and conclusions obtained from these 5 years of study of the potato leafhopper with special reference to its attacks upon the bean plant.[3]

## PREVIOUS WORK

Since 1841, when the species was described by Harris (*28, p. 186*)[4] as a bean pest, this leafhopper has attracted attention and discussion because of its widespread economic damage. From the standpoint of generic or taxonomic treatment three papers should be mentioned. Gillette (*23*) made a pioneer study in 1898. Hartzell (*30*) revised the genus in 1923, and more recently the present author (*8*), in 1931, attempted to put the genus on a more sound taxonomic basis by the use of internal genital structures. This phase of the subject to date may be found by reference to this latter bulletin and three subsequent papers (*11, 12, 14*).

From the economic and biologic points of view many workers have published articles regarding *Empoasca fabae* since its early description. Le Baron (*37*), in 1853, recognized this insect as an apple pest and redescribed it as *Tettigonia mali*. In all probability, in many published records following Le Baron this species is confused with other apple leafhoppers, and some of these records are probably still in doubt. Washburn (*51, 52, 53, 54, 55, 56*), from 1903 to 1910, worked upon the biology of *E. fabae* on apple in Minnesota and found a three-brooded condition with a partial fourth brood indicated. Webster (*57, 58, 59, 60*), from 1908 to 1910, reported a four- or five-brooded condition in Iowa and thought the winter was passed in the egg stage. Garman (*22*), in 1908, reported on the biology on apple in Kentucky. Lathrop (*36*), in 1918, did the first work on separating biologically the different species of *Empoasca* on apple. In 1919 Ackerman (*1*) also worked on the biology of these forms on nursery stock.

Osborn (*41*), in 1896, was the first to note that *Empoasca fabae* was a potato pest. In 1920 Ball and Fenton (*2*), and Kotila (*35*) in Michigan, discussed its relation to tipburn; Fenton and Hartzell (*18*) worked on its biology; and Parrott and Olmstead (*43*) on its injury to potatoes and on control. In 1921 Hartzell (*29*) worked on biology, and Dudley (*15*) on biology and control; and in 1922 Eyer published two papers (*16, 17*) on the relation of hopperburn to *E. fabae*. In 1923 Fenton and Hartzell (*19*) published a complete discussion of their previous work, summarizing practically all of the work to that time. They reported a two-brooded condition on potato in Iowa.

[3] This manuscript was first submitted in October 1931. Since its publication has been delayed, certain data obtained during 1932 and 1933 have been included. Also references have been included concerning some investigations performed or completed by other workers several years after the completion of the work reported herein.

[4] Italic numbers in parentheses refer to Literature Cited, p. 57.

Davis (*5*), in 1893, discussed *Empoasca fabae* as a celery insect in Michigan, and Forbes and Hart (*21, pp. 425–427*), in 1900, reported it as a sugar-beet insect in Illinois and as a four-brooded species.

In 1922 Beyer (*3, 4*) worked upon the bean as a host plant in Florida and reported upon the biology and control of *Empoasca fabae* and its relation to hopperburn. In 1928 DeLong (*7*) reported upon the biology and control in Ohio, and in 1931 (*9*) upon the distribution in the United States of *E. fabae* and other economic species which had previously been confused with it. In 1935 DeLong and Caldwell (*13*) discussed hibernation studies in Ohio.

Gossard (*24*), in 1892, was the first to report *Empoasca fabae* as a pest of clover, the infestation occurring in Iowa. In 1912 Osborn (*42*) discussed it as a pest of cereal grains and forage crops, stressing especially injury to soybeans, alfalfa, cowpeas, and clover. Likewise Garman (*22*), in 1908, and Washburn (*52*) in the same year, reported *E. fabae* upon forage crops and other legumes. Hollowell, Monteith, and Flint (*31*), in 1927, reported injury to clover; and Granovsky (*25*), in 1928, reported upon this leafhopper in relation to alfalfa yellows in Wisconsin. In 1929 Monteith and Hollowell (*40*) discussed the general symptoms and conditions upon legumes. In 1930 Granovsky (*26*) reported upon the nature of damage to alfalfa; and Poos and Smith (*46, 48*), in 1931 discussed the types of feeding caused by the different related species of *Empoasca*, and comparative oviposition and development upon different host plants.

In 1932 Poos (*45*) discussed the biology of *Empoasca fabae* and closely related species. Smith (*47*), in 1933, described the nature of the sheath material in the feeding punctures produced by this leafhopper; and Johnson, in 1933 and 1934 (*32, 33*), described the nature of the injury to forage legumes.

## THE INSECT

### SYNONYMY

*Empoasca fabae* is known in literature under a variety of specific names. This is probably due to the fact that it was early recognized as an economic pest over a large area, but by isolated investigators or groups of workers who were working independently; and also undoubtedly in part to the large number of economic host plants upon which it feeds and its variability in color and color markings.

As far as can be ascertained it was first described by Harris in 1841 (*28*) under the genus *Tettigonia*. In 1853 (*37*) it was redescribed as *mali* by LeBaron, still as a member of *Tettigonia*. In 1864, when Walsh (*50*) erected the genus *Empoasca*, he apparently redescribed it under three different names, owing to its color variations, as *viridescens*, *consobrina*, and *malefica*, the last named under the genus *Chloroneura*. The types were destroyed in the Chicago fire, and Walsh's species cannot be verified. The original descriptions do not distinguish them specifically.

In 1884 Forbes (*20*) redescribed it as *albopicta* in the genus *Empoa*. Again, in 1898 Gillette (*23, p. 741*) redescribed it in part as *pallida*, from a series of specimens taken from cotton and placed in alcohol, which had caused the green color to disappear, leaving pure white insects. Also in his paper he referred certain of the color forms to *flavescens* F., a European species, which does not occur in North America as far as can be determined from material examined. Therefore, a large number of American references to *flavescens* by Gillette and

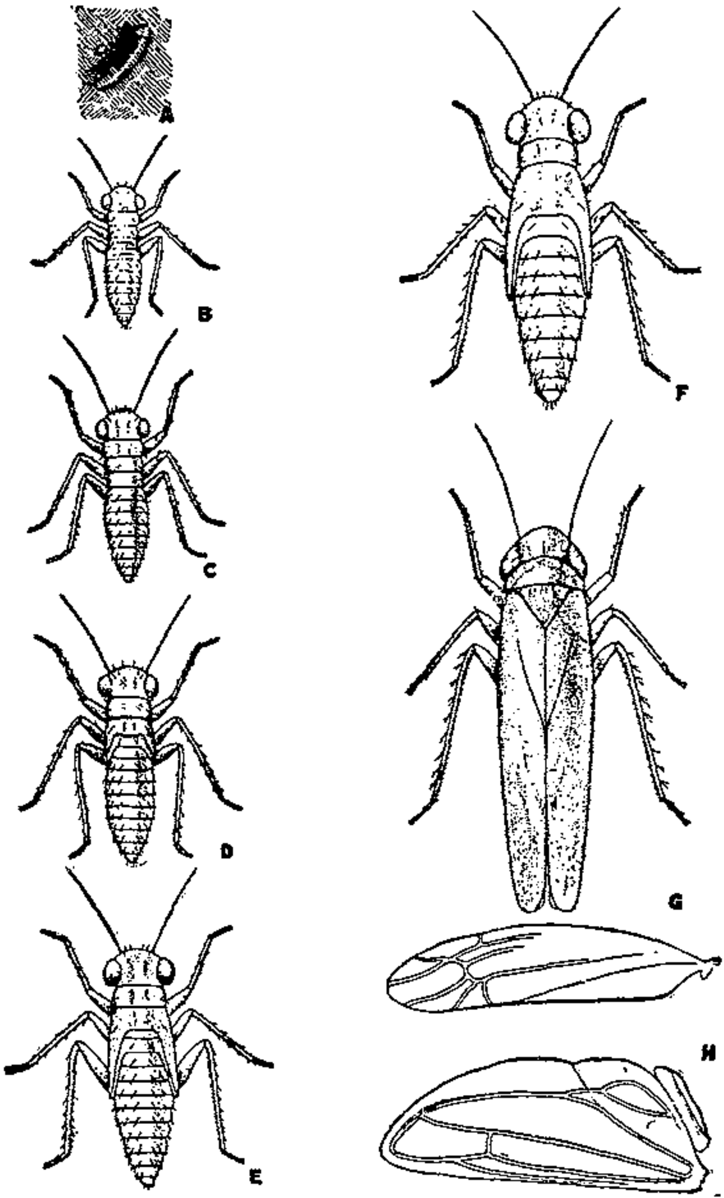


FIGURE 1.—Stages in the growth of the potato leafhopper (*Empoasca fabae*): *A*, Eggs in tissue of leaf; *B–F*, stages of the nymphs; *G*, adult; *H*, forewings and hind wings of adult.

workers who followed him have actually dealt with *fabae* or with one of the other closely related species. These records will probably never be correctly placed unless specimens have been retained.

### TECHNICAL DESCRIPTION OF EMPOASCA FABAE

Pale green, usually with a row of white spots on anterior margin of pronotum. Length 3.5 mm (fig. 1).

Vertex bluntly angled, a little longer on middle than next eye and about one-third wider between eyes than length at middle.

*Color.*—Yellowish to pale green, markings variable; vertex frequently with pale or dark-green spots; pronotum usually with a row of six or more pale spots along anterior margin, sometimes missing or indistinct; elytra greenish subhyaline.

*Female genitalia.*—Last ventral segment moderately produced and roundedly truncated.

*Male genitalia.*—Valve produced and rounded or bluntly angled; plates triangularly tapered to pointed apices, which are frequently upturned; lateral processes of the pygofers rounded on inner margins and broadened on apical half, then concavely rounded to narrow attenuated tips, which are slightly curved inward; spines of tenth segment broad, with tips narrowed and directed downward. This combination of characters will distinguish *Empoasca fabae* from closely related species (fig. 2).

### CLOSELY RELATED ECONOMIC SPECIES PREVIOUSLY CONFUSED WITH EMPOASCA FABAE

For many years the potato leafhopper (*Empoasca fabae*) has been considered as the only important species of *Empoasca* occurring on truck crops in the United States. This assumption has probably been due to the fact that the species of the genus *Empoasca* closely related to the potato leafhopper are so similar in color, markings, size, and appearance that upon the basis of these external characters they could not previously be separated with any assurance into specific groups. In fact, several species have not previously been recognized or described because these characters, previously used for designation, were not distinctive.

Furthermore, authentic field observations in certain areas have been almost entirely lacking. This fact, together with an inadequate supply of material, has undoubtedly delayed recognition of these forms. Recent field and laboratory studies have revealed the fact that at least four species are of major importance on truck crops in the United States. In the past these have all been designated as the potato leafhopper and placed under the scientific name of either *Empoasca fabae* or *E. flavescens*. The latter species is European, and no authentic American records have thus far been established.

Previous studies by the author have indicated that these species are distinct morphologically. This has been confirmed by the writer and other workers by biological studies and studies of the types of economic injury produced by different species. Heretofore only color and external characters have been used in classification of the species of this genus, and these are not sufficiently constant or distinctive to use for specific separation. Excellent characters for separating and distinguishing these species have been found in the genital chamber of the male. These chitinized structures are usually designated as internal genitalia. The lateral processes and the dorsal spines of the pygofers have indicated excellent characters for separation. These have been discussed and illustrated in a bulletin by the author (*8*).

By the use of these chitinized structures of the genital chamber and by field observations throughout a large portion of the United States, it has been found that in addition to the potato leafhopper (*Empoasca fabae*) at least three other species are major pests of truck crops in the United States. They are *E. filamenta* DeL., *E. abrupta* DeL., and *E. arida* DeL. Further field studies may later prove *E. cerea* DeL. also to be a major pest of truck crops.

## EASTERN SPECIES PREVIOUSLY CONFUSED WITH EMPOASCA FABAE

Previous discussions of the potato leafhopper by other workers have referred to wild host-plant records in connection with the discus-

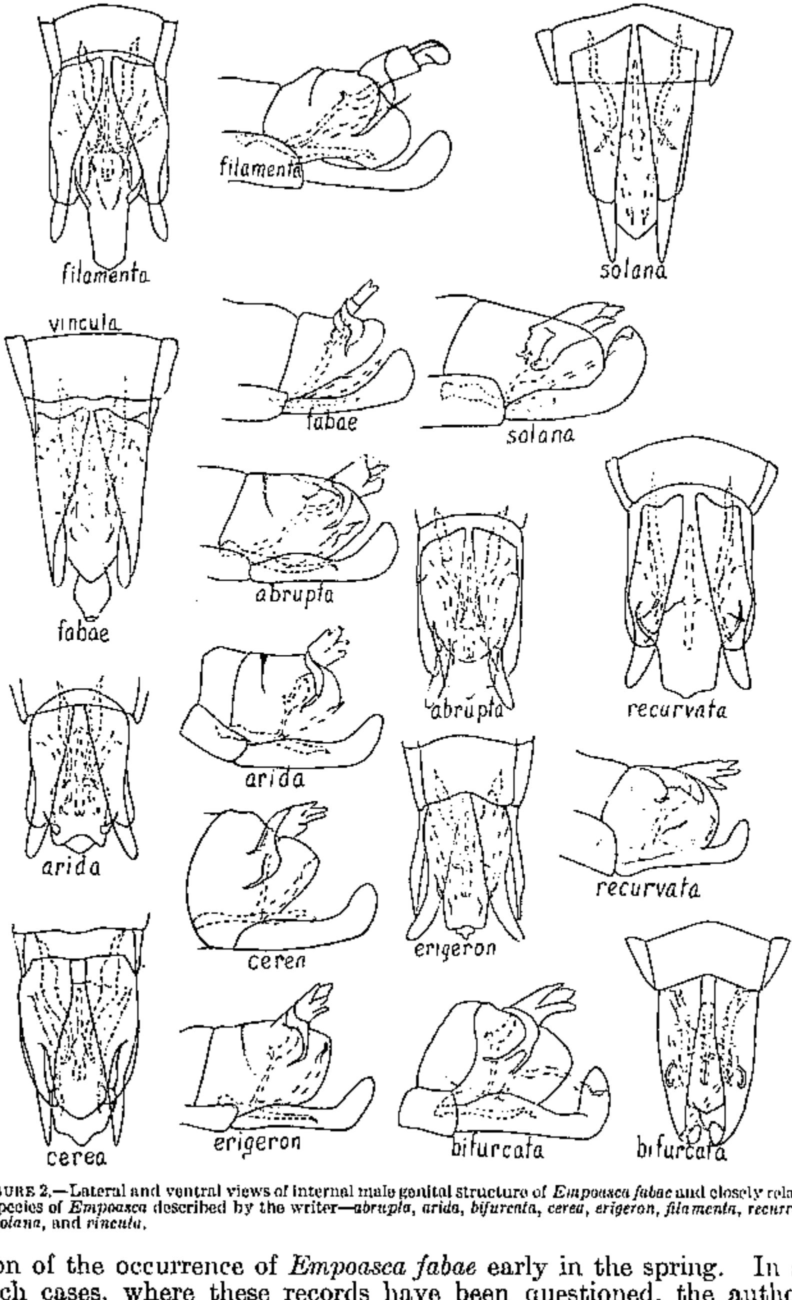


FIGURE 2.—Lateral and ventral views of internal male genital structure of *Empoasca fabae* and closely related species of *Empoasca* described by the writer—*abrupta, arida, bifurcata, cerea, erigeron, filamenta, recurvata, solana,* and *vincula.*

sion of the occurrence of *Empoasca fabae* early in the spring. In all such cases, where these records have been questioned, the authors did not examine or use genital characters for identification. It is apparent from data collected during the last 5 years that such records have been concerned chiefly with *E. erigeron* DeL., *E. bifurcata* DeL., and *E. recurvata* DeL., instead of *E. fabae* Harris. *E. erigeron* occurs on *Erigeron annuus*, *E. canadensis*, and similar wild host plants, overwintering in the egg stage in the old plant stems. It hatches late in April or early in May and is on the wing early in the spring at the same time or slightly before *fabae* is active in the field. *E. bifurcata* occurs upon *Coreopsis* sp., tansy, and related plants, overwintering in the egg stage, and both of these species have for years been confused with *E. fabae*. All specimens taken from dock in Ohio have proved to be either *E. erigeron* or *E. bifurcata*, usually the former. Also *E. recurvata*, which hibernates as an adult in Ohio, and *E. solana* DeL. have probably been confused with *fabae*. Therefore, unless material observed for published records by these workers has been retained and can be examined for identification at the present time, these data cannot be depended upon as authentic records of the spring occurrence or activity of *E. fabae*. Personal observations in the field early in the spring have shown that when a green leafhopper of the genus *Empoasca* appears upon a wild host plant, it cannot be assumed, as has been the custom in the past, that it is *E. fabae*, even though it resembles *E. fabae* very closely in external characters. Furthermore, all material collected from these wild plants and examined has proved to be one of the other species mentioned above.

## CHARACTERS DISTINGUISHING EMPOASCA FABAE AND CLOSELY RELATED SPECIES

The use of the internal genital characters for distinguishing both the economic species and the species occurring on wild host plants in the eastern United States that have previously been confused with *Empoasca fabae* have been discussed in detail by the author in a previous bulletin (*8*). Without repeating portions of this detailed discussion, the illustrations (fig. 2) of the characters used for their separation and a brief statement concerning these characters will greatly aid the field worker in distinguishing them.

The western economic species can be distinguished in the ventral view of the lateral processes by the long, slender, tapering, filamentous processes in the case of *Empoasca filamenta*. In the case of *E. abrupta* these processes are abruptly narrowed and produced as slender fingerlike processes on the outer margins. *E. arida* is characterized by the curved hooked portions near the apex on the outer margins with the apices extending inwardly, and *E. cerea* is distinguished by lateral processes which are narrowed at about one-third their length and tapered, forming long attenuated tips.

Of the eastern species previously confused with *Empoasca fabae*, the slender fingerlike processes on the outer margins of the lateral processes of the pygofers will easily distinguished *E. erigeron*. In the case of *E. recurvata* these processes in lateral view are curved sharply upward and forward at the apex. *E. bifurcata* is conspicuously different by having the bifurcate dorsal spines on the tenth segment and the long, vermiculate, laterally crossed, "spear-headed" lateral processes of the pygofers. The lateral processes of *E. solana* in ventral view are abruptly narrowed, appearing twisted and slightly attenuated at the tip. In lateral view they appear terminally narrowed, concavely curved upward, forming a slightly hooked, narrowed apex.

## DISTRIBUTION AND ABUNDANCE

Contrary to previous opinion, recent study has proved that *Empoasca fabae* is not generally distributed throughout the United States. In fact, there are certain large areas in which it has not been and cannot be found and there are other areas where it is very scarce or difficult to find. *E. fabae* is generally distributed over the Eastern States, where it is found usually in abundance and becomes injurious (fig. 3). It extends westward through South Dakota, Nebraska, Kansas, and Oklahoma and is found in eastern Colorado, southeastern Wyoming, and eastern Texas. During the summer of 1930 the writer collected it in small numbers in the lower altitudes of California, at Centerville, Spreckels, Salinas, Watsonville, King City, San Jose, San Bruno, Turlock, Bakersfield, Santa Margarita, and Santa Cruz,

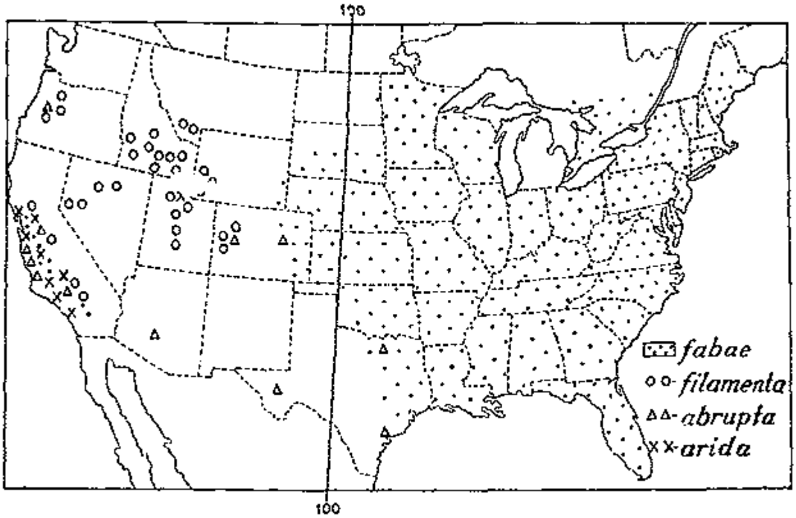


FIGURE 3.—Map showing distribution of *Empoasca fabae*, *E. filamenta*, *E. abrupta*, and *E. arida* in the United States.

and it was first authentically reported for that area by the author in 1931 (*9*). Each record in the West is on the basis of a very few specimens. Nothing could be found approaching in any way economic populations, and no damage of importance was found. Records are not complete for Arizona and New Mexico, where *E. fabae* may occur in numbers similar to those of California, but all specimens examined from these localities have proved to be other species of *Empoasca*. From the standpoint of abundance and populations, it is probably safe to say that it is an important pest in the Eastern, Middle Western, and North Central States.

## ECONOMIC IMPORTANCE

Under natural conditions *Empoasca fabae* feeds and can complete its life cycle upon a large number of different types of wild and cultivated host plants. Sufficient observations have not been made to present a completed list of such plants, but they include, in addition to wild hosts, fruit trees like the apple; truck crops like bean, potato, eggplant, and rhubarb; forage crops like alfalfa, clover, and sweetclover; and ornamentals like dahlia. Upon most of these plants severe economic damage may occur, the type of damage or injury being specific for different types of plants. A condition known as hopperburn is probably most serious and constitutes the characteristic type of injury upon potato, eggplant, rhubarb, horsebean, and dahlia. Stunting and dwarfing are common types of injury and the tight curling of the leaves or rosette condition is a characteristic type of injury upon the bean. Young apple trees are especially injured by this leaf-curling condition. Alfalfa is injured in such a manner that it produces a characteristic yellowing, while clover and alfalfa are often reddened by severe feeding.

FIGURE 4.—Typical hopperburn injury on a potato plant.

## TYPES OF INJURY

### HOPPERBURN

The term "hopperburn" has been applied to a diseased condition produced on potato and other plants by the feeding of adults or nymphs of *Empoasca fabae*. This condition is characterized by distortion of the leaf veins and a consequent yellowing of the tissue around the margin and at the tip of the leaf (fig. 4). This is soon followed or accompanied by a rolling or curling upward and rolling inward of the margins as the leaf changes from yellow to brown and becomes dry and brittle. Although hopperburn usually begins with a spot at the tip of the apical leaflet the discoloration and curling rapidly spread until the whole leaf is dry and dead. The portion which remains green longest is a central area along the midrib, especially at the base near the petiole. When the insect infestation is heavy the entire plant is usually killed in a short time.

Experiments carried on by Fenton and Hartzell (*19*) and by Eyer (*17*) have shown that inoculations made in the potato plant by solutions of sterile distilled water, or dilute alcohol, containing macerated bodies of adults or nymphs cause the same or a very similar condition to that produced by permitting leafhoppers to feed upon these plants.

Fenton and Hartzell are also responsible for the statement that the larger nymphs are of greater importance in producing hopperburn than either the adults or smaller nymphs. Hopperburn has been observed commonly upon eggplant, rhubarb (fig. 5), and dahlia. Beyer (*3*) has recorded this condition upon beans in Florida, and in 1929 there was a serious infestation of *Empoasca fabae* on horsebeans

FIGURE 5.—Rhubarb leaves showing marginal hopperburn.

at Birmingham, Ala., in connection with which hopperburn was conspicuous. A similar condition [5] was observed at Columbus, Ohio, in 1935. No authentic record of hopperburn on beans in the Northeastern States is available.

### STUNTING, DWARFING, AND LEAF CURLING

A condition resembling hopperburn was observed on the bean plant once during the last 5 years, and this case was considered to be doubtful. A planting of pole beans in northern Ohio had developed a type of injury very similar to hopperburn where the leafhopper population was very large. The normal condition, which has been observed over the Eastern States in general, is a marked curling or rolling under of the leaves combined with an unusual roughening, crinkling, or rugose appearance of the leaf tissue (fig. 6). This is followed by

[5] Determined by R. H. Davidson.

yellowing and bronzing and a general weakening and dying of the plant. Combined with this is usually a stunting and dwarfing of the leaves and plants. The leaves curl so tightly that a tight rosette condition of the leaves is very common (fig. 7).

Certain fields have been observed during this investigation where the plants attained approximately one-tenth only of their normal size, owing to this type of leafhopper injury (fig. 8).

Field experiments have shown that where bean plants are protected by screen cages from leafhopper infestation these types of injury do not occur (fig. 9). It is apparent from these observations that soil and climatic conditions are not responsible for causing this injury except as they tend to favor the accumulation of leafhopper populations.

It is apparent also that this injury is caused either by the feeding or the egg deposition of the leafhoppers or by both processes. Almost

FIGURE 6.—Curling of bean leaves due to injury by *Empoasca fabae.*

all feeding and egg-laying punctures are made on the under surfaces of the leaves of the plants, under normal conditions, and these are usually in the midrib or larger veins of the leaf, although sometimes in the petioles or stems. It is apparent that some material injected into the plant during one or both of these processes or the mechanical injury due to the punctures causes a reaction which inhibits growth. The failure of the cells on the under surface of these veins to grow normally and multiply and the continued normal growth of the cells on the upper surface apparently cause the curling under and the rolling of the leaf. Attempts were made to produce this injury mechanically with a sterilized needle. The leaves were pricked in the same place that they would normally be injured by the leafhoppers but only negative results were obtained.

Young apple trees are frequently injured in a similar manner, especially in nurseries, with the curling under and rolling of the leaves.

PIGMENTATIONS OF CLOVER AND ALFALFA

Yellowing occurs in alfalfa, and reddening is common in clover, as a result of leafhopper feeding, and certain other symptoms occur in common also in these plants as in other legumes. Dwarfing may occur in the leaves, stems, and petioles, while the floral development

FIGURE 7.—Severe curling of leaves on pole beans due to injury by *Empoasca fabae.*

may be reduced or arrested. The leaves may be curled downward, as in the case of the bean, and the discoloration usually follows the veins and midrib of the leaf. The leaves may become brown and curl as in hopperburn in cases of severe infestation. These conditions upon alfalfa have been studied and reports presented by Granovsky (*25*, *26*), Monteith and Hollowell (*40*), Poos (*44*), Poos and Smith (*46*, *48*), Smith (*47*), and Johnson (*32*, *33*).

According to the theories of Fenton and Hartzell (*19*) and Eyer (*17*) a specific toxin is injected into the plant, which causes hopperburn. Recently Smith and Poos (*48*) and Smith (*47*) have shown that *Empoasca fabae* feeds by puncturing the phloem, causing it to be torn and distorted, and plugging occurs in the xylem tubes in portions of the midribs and stems. Consequently, they have advanced the theory that the disorganization of the phloem disturbs the normal plant processes above the point of attack, and as a result the plant may produce substances which cause the pigmentation or hopperburn. Also, plugging of the xylem seems to cause a delay in translocation or a piling up of materials beyond the point of attack, due to the interference of the downward movement in the phloem. Johnson (*32*) has reported chemical analyses which show that con-

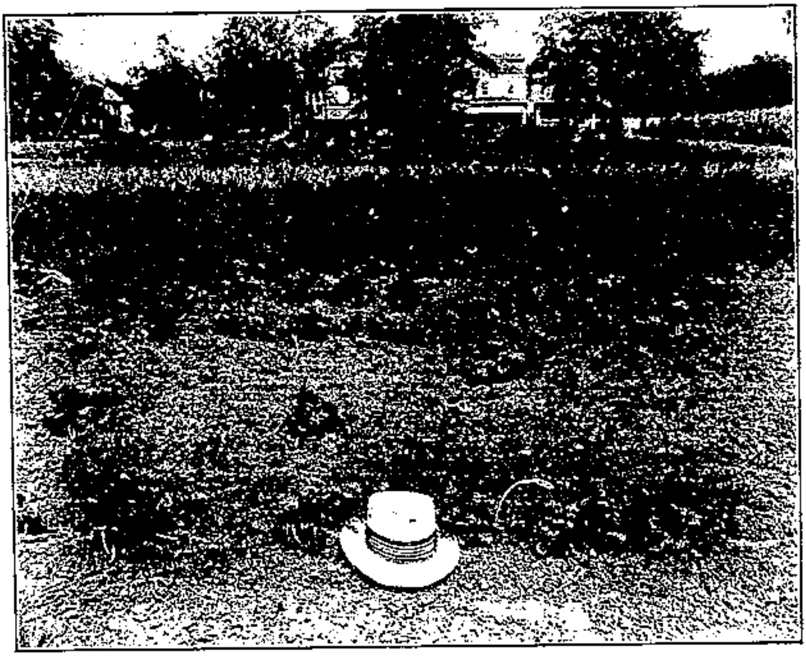

FIGURE 8.—Severe stunting of beans in a field due to injury by *Empoasca fabae*.

gestion of carbohydrates occurs in leaves of alfalfa and clover plants infested with this leafhopper.

## ECONOMIC DAMAGE

All types of injury that have been mentioned cause marked losses in terms of yield. In the case of hopperburn on potatoes the normal number of tubers are usually produced, but they are so small that they are ordinarily not worth harvesting and are almost an absolute loss from the standpoint of production. In average cases of light infestation 30- to 50-percent losses are usually suffered.

In view of the fact that certain varieties of beans are infested more heavily than others, the yields will vary with the variety. As a rule, when beans are attacked the first blossoms will produce pods, but the plant does not produce other blossoms. Also it is quite common for the pods produced to be very short, with few beans in the pod. In a few cases fields of bush beans have been observed where the few long pods produced were as long as the height of the plant because of the marked dwarfing of the plant after the young bean pods were formed. In most cases, however, the pods are short and only a few are produced on a plant.

In the case of crops like alfalfa and clover the actual loss of leaf surface by dwarfing, yellowing, or reddening and browning is a direct loss in pasturage or hay yield. Johnson (*34*) has shown that alfalfa yellowed by leafhopper attack contains only one-half the carotene that is present in green alfalfa and "is, therefore, only about one-half as rich in potential vitamin A activity." This represents a further

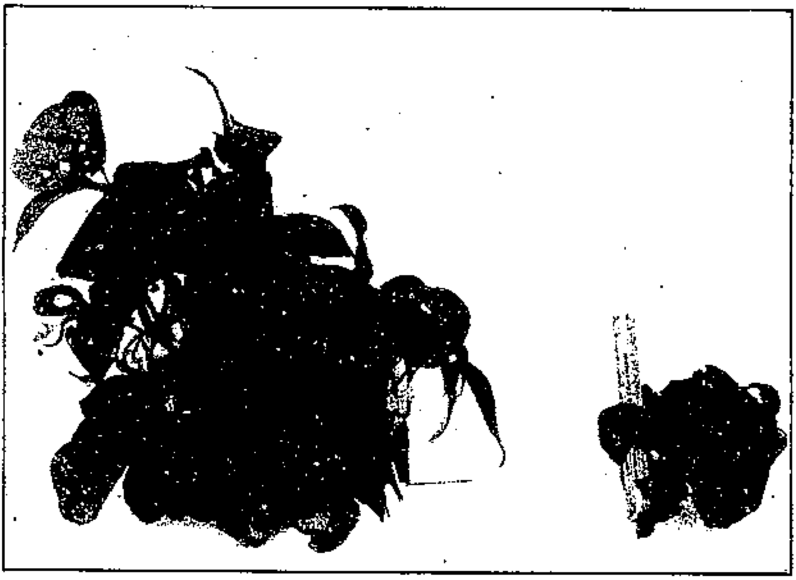

FIGURE 9.—Comparative growth of normal beans and those stunted by attack from *Empoasca fabae*. The plants were grown in the same field, but the one on the left was protected from leafhopper attack. The ruler shown by the right-hand plant is 6 inches long.

serious annual loss that must be attributed to the activities of the potato leafhopper.

## DISTRIBUTION IN RELATION TO CLIMATIC AND PHYSICAL FACTORS

### ALTITUDE

If the known distribution of *Empoasca fabae* (fig. 3) is correlated with altitude (figs. 10 and 11), it will be noted that with the exception of the Appalachian Mountains the eastern part of the United States is what may be termed a low-altitude area (2,000 feet elevation or less). In most of this territory where agriculture is predominant over enormous acreages the elevations are much lower. Most of this territory east of the Mississippi does not exceed 1,000 feet in elevation. Westward from the Mississippi River there is a gradual rise in elevation through Missouri, Kansas, and Colorado to Denver, where the elevation is approximately 5,300 feet. Although *E. fabae* occurs in scattered numbers up to elevations of approximately 4,600 feet, there are no infestations, and the insect is apparently of no economic importance at points 3,000 feet or more in elevation. West of Denver the elevation increases very rapidly to 11,000 or 12,000 feet over the high passes of the Rocky Mountains and then drops rapidly onto a high intermountain plateau area interspersed with numerous mountain ranges. At no place does this plateau drop below approximately 4,000 feet, and the major portion is 5,000 feet or more above sea level. This area extends from the high Rockies west to the Sierra Nevada, and north and south through Colorado, Wyoming, Montana, Idaho, Utah, Nevada, and a large part of New Mexico and Arizona. Throughout this high-altitude area not a single specimen of *E. fabae* has been found on cultivated or wild host plants. The species completely drops out of the insect-population picture at approximately 4,600 feet elevation east of the Rockies and is not found again until the low-altitude areas of the Pacific coast are reached. Here the populations are very meager

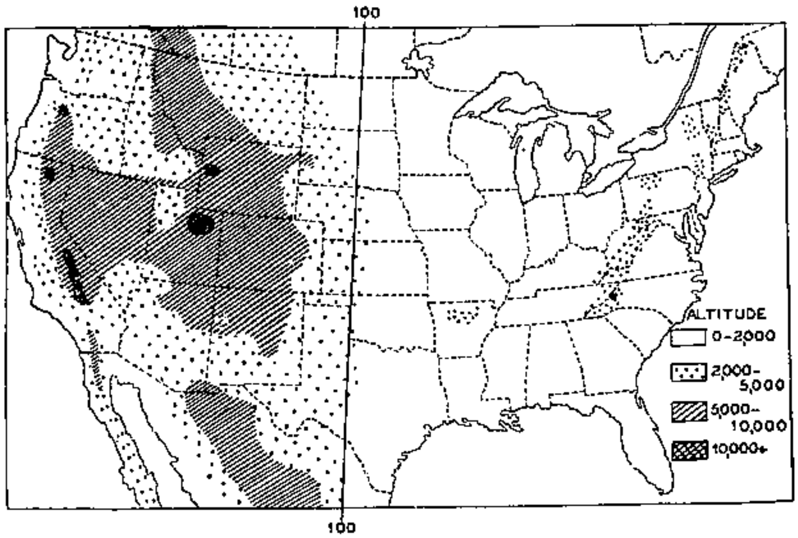


FIGURE 10.—Map showing the general elevations of the United States.

and scattered, and about the same numbers exist as were found east of the Rocky Mountains at a 4,600-foot elevation.

### HUMIDITY AND PRECIPITATION

Field and laboratory observations indicate that high relative humidity is a very important factor in the survival of the insect. Relative humidity is closely correlated with precipitation. Even in arid regions of the West the relative humidity is much higher in the irrigated districts, and leafhopper populations are more abundant there than in districts not irrigated. A typical index to the relative humidity throughout the United States is shown by the map (fig. 12), giving the average relative humidity at 8 p. m. during July. It can be determined at a glance that the relative humidity is high in the Eastern States and low in the Western States and that it almost continuously increases from the Pacific to the Atlantic Oceans. The occurrence of *Empoasca fabae* is almost entirely east of the zone of 40-percent relative humidity, and the area in which it is able to build economic populations is bounded approximately on the west by the zone of 50-percent relative humidity. The one hundredth meridian falls generally between the 45- and the 50-percent relative humidity lines, and this has usually been considered the approximate line separating the arid and humid regions of the United States. This has already been referred to (*9*) as representing the approximate

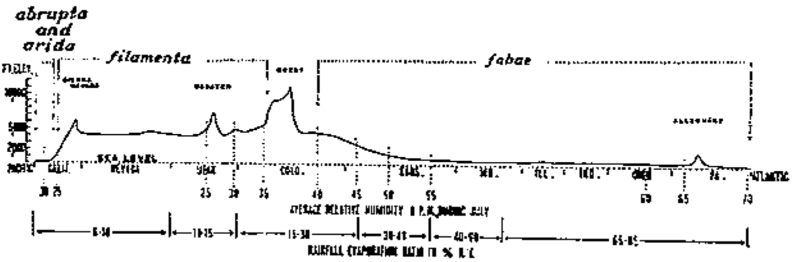


FIGURE 11.—Profile section of the United States from Philadelphia to San Francisco, showing approximate altitude, zones of similar average relative humidity at 8 p. m. during July, rainfall-evaporation ratio zones, and the principal areas of distribution of the important truck-crop species of *Empoasca*.

western boundary of the area in which *E. fabae* assumes an economic status.

If the annual precipitation in inches is considered for the United States, it is noted (fig. 13) that the areas of high precipitation correspond rather closely to the areas of high relative humidity, whereas the arid regions show comparatively small amounts of rainfall. The line showing on the map the western boundary of the average annual rainfall of 25 inches corresponds closely to the 50-percent relative humidity zone in the central part of the country. Although the amount of annual rainfall may be quite important, the amount of rainfall during the growing season is apparently more important in

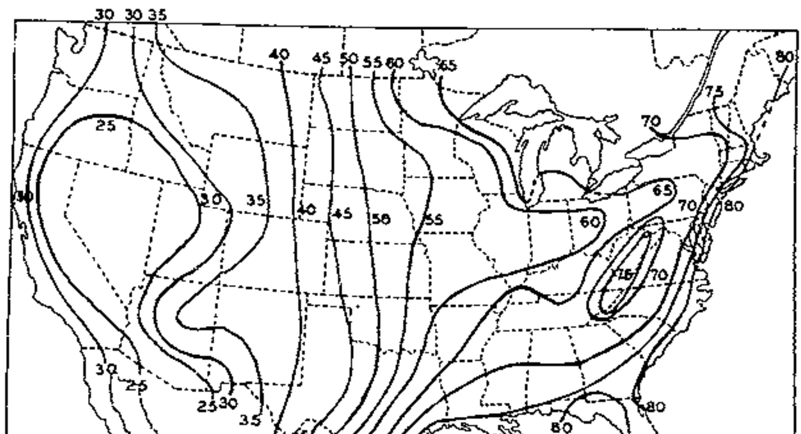


FIGURE 12.—Zones of similar average relative humidity in the United States made from records taken at 8 p. m. during July.

this insect problem than the annual rainfall. The map showing the rainfall from April to September (fig. 14) shows the western limit of the area occupied by *Empoasca fabae* to correspond with the 18-inch line, while most of the West shows 12 inches or less for this period.

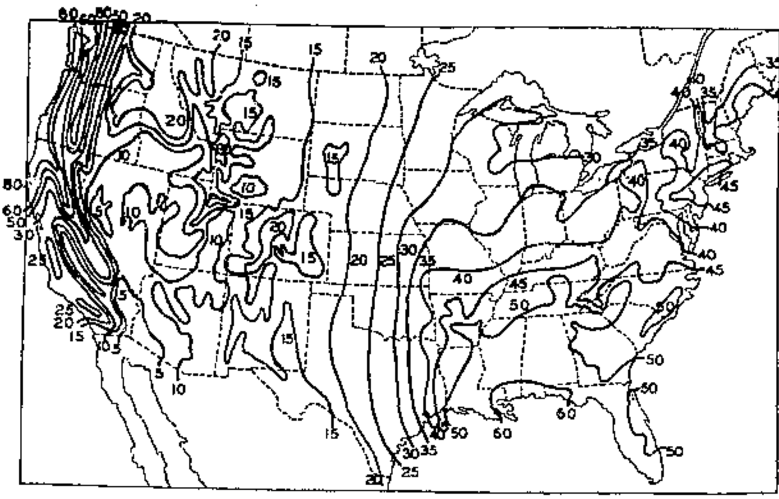

FIGURE 13.—Average annual precipitation in inches for various areas of the United States.

The rainfall map for March, April, and May (fig. 15) shows the western limit to have approximately 8 inches, while most of the western area has less than 6 inches of rainfall.

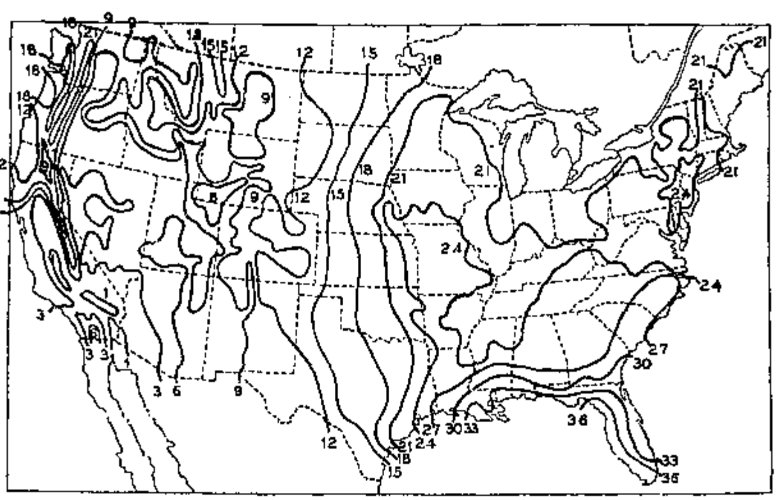

FIGURE 14.—Average precipitation in inches for various areas of the United States, from April to September, inclusive.

### RAINFALL-EVAPORATION RATIO

The rainfall-evaporation ratio is obtained by dividing the total precipitation by the total evaporation. Climatic factors which especially influence evaporation and consequently this ratio, are rainfall, relative humidity, temperature, and wind velocity. This ratio is in itself an excellent index to the relative importance of several other factors and is a prime indicator of plant distribution, according to

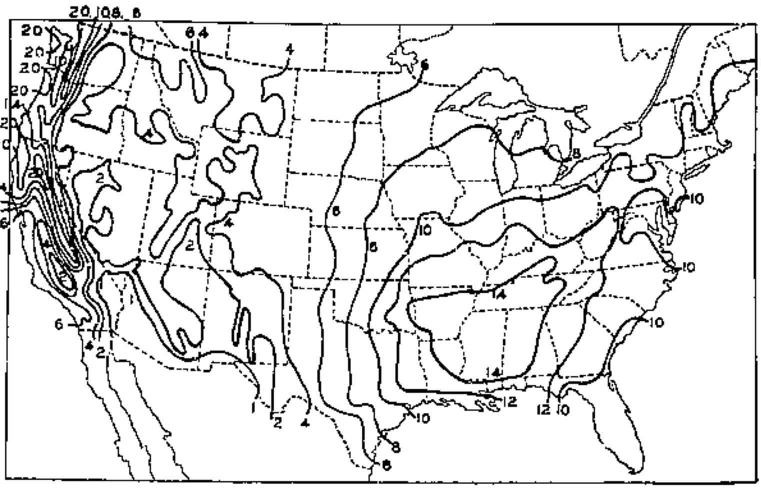

FIGURE 15.—Average precipitation in inches for various areas of the United States, from March to May, inclusive.

Transeau (*49*) and Livingston and Shreve (*38*). In view of the fact that these plant-feeding insects are so dependent upon the presence of certain types of food plants, the rainfall-evaporation ratios in certain

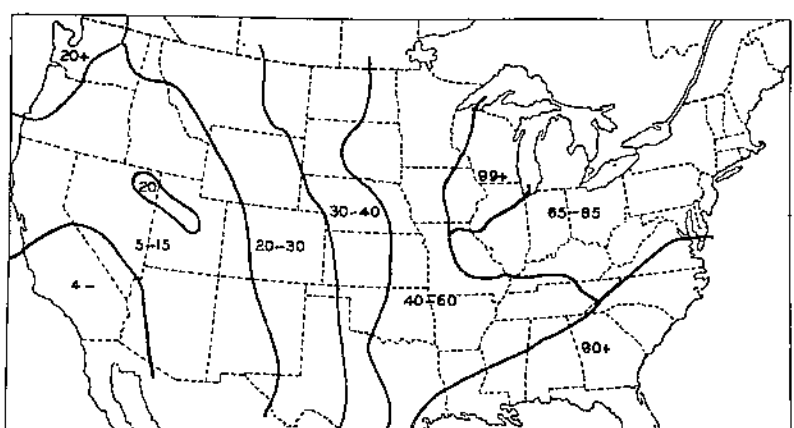


FIGURE 16.—Areas of approximately similar percentages of rainfall-evaporation, as expressed in ratio of rainfall divided by evaporation.

areas of the United States might be cited here to show their relationship to this distribution. Since the evaporation data have been taken by different methods and by so many different workers they show quite a variation in certain areas, but the general zones (fig. 16) are quite marked and correspond very well with the data already presented. The 40-percent rainfall-evaporation ratio line is approximately the western border of the area in which *Empoasca fabae* is an economic pest. Other areas in the Eastern States show a ratio as high as 100 percent, and this condition seems to be favorable for rapid development and the building up of large populations.

#### TEMPERATURE

High temperature alone is apparently not a factor in limiting the distribution of *Empoasca fabae*—at least there is no definite correlation, since high temperatures occur in both the eastern and western parts of the country, and the leafhopper is able to produce enormous populations in the Eastern States when the temperature is high, provided the precipitation and relative humidity are normal. Under California conditions where the temperature is high and the humidity low with a deficient rainfall, *E. fabae*, even though present, apparently cannot build populations of any size. At least none has ever been recorded, and personal observation failed to reveal any during 1930 in the more important crop areas.

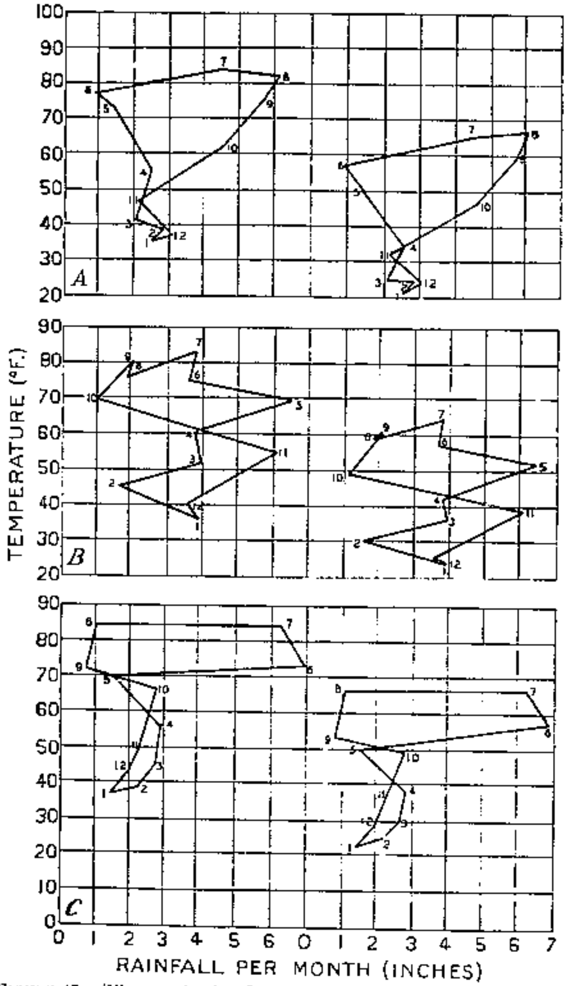


FIGURE 17.—Climographs for Columbus, Ohio: *A*, For 1926; *B*, for 1927; *C*, for 1928. The figures indicate the months of the year, the curve at the left of each set shows the mean maximum temperature, and that at the right the mean minimum temperature.

#### DATA PRESENTED BY THE CLIMOGRAPHS

The climograph has been used to a large extent by scientific workers in recent years to compare climates of various localities, or areas, by using temperatures and precipitation and constructing a graph showing monthly conditions. In most cases the mean monthly temperatures and the monthly precipitation are plotted on a graph.

In view of the fact that leafhoppers are affected rather definitely by low temperatures, it has seemed advisable to use data for maxima and minima instead of for the mean. This gives two graphs for each locality and year with the same precipitation in each case.

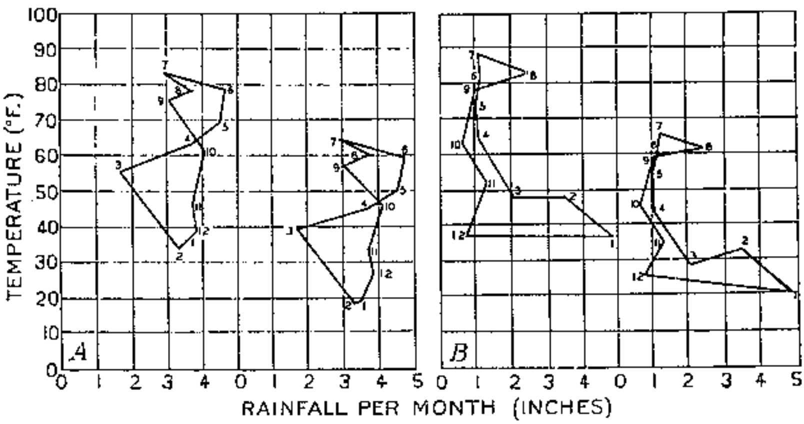


FIGURE 18.—Climographs for Columbus, Ohio: *A*, For 1929; *B*, for 1930. The figures indicate the months of the year, the curve at the left of each set shows the mean maximum temperature, and that at the right the mean minimum temperature.

The climograph data for Columbus, Ohio, are given for specific years, from 1926 to 1930 (figs. 17 and 18), together with a mean for 48 years (fig. 19). The varied data at Columbus, especially for the drought year 1930 in comparison with normal years, are of interest in the explanation of the distribution and abundance of *Empoasca fabae* in other areas.

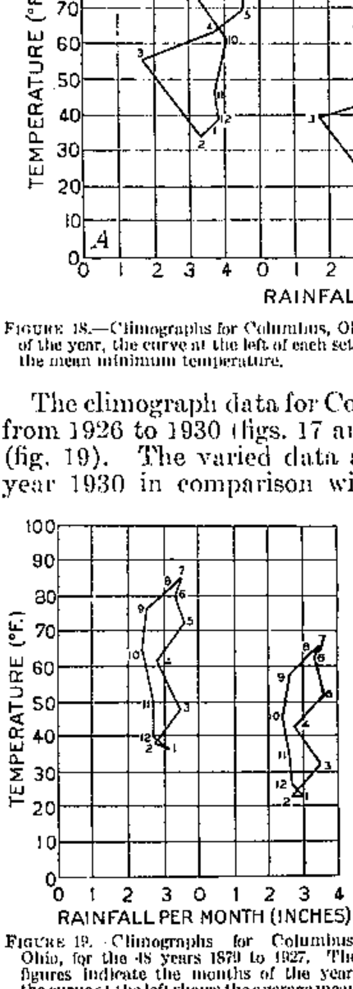


FIGURE 19.—Climographs for Columbus, Ohio, for the 48 years 1879 to 1927. The figures indicate the months of the year, the curve at the left shows the average mean maximum temperature, and that at the right the average mean minimum temperature.

Although mean minimum temperatures may be of importance as regards winter survival of *Empoasca fabae*, all the data obtained would point to spring and early summer rainfall as probably the most important factor determining its distribution and abundance. Observations have shown that heavy and rather continuous rainfall does not interfere with the species in any way, and the populations are not reduced. Extremely heavy rainfall apparently reduces populations somewhat, but not to such an extent as does a deficiency of rainfall. A certain amount of rainfall is essential during the growing season if populations are to be retained or increased.

During the summer of 1926 the rainfall at Columbus, Ohio, was only an inch or slightly over for each of the months May and June. In July, however, more than 4 inches of rain fell. This year was a good leafhopper year, but populations produced were not so large as in previous or succeeding years. In 1927, May had about 6½ inches of rainfall, and June and July each had in excess of 3½ inches. This was a serious leafhopper year. In 1928, although May showed only 1½ inches, June had approximately 7 inches and July in excess of 6 inches. This was an excellent leafhopper year also. The year 1929 ran closer to a normal year with each month from April to September inclusive having 3 inches or more of rainfall, while May and June had 4½ inches. The leafhopper populations were large, and economic damage was marked in Ohio in 1929.

In 1930 there was a decided drought in Ohio. Only three times previously in 77 years had the average annual precipitation for the State fallen below 30 inches. The average annual precipitation for Ohio is 37.49 inches. In 1856 the total was 28.46 inches; in 1894, 29.75 inches; in 1895, 28.46 inches; and in 1930, 27.00 inches (only 21.60 inches for Columbus).

More important from the standpoint of insect populations is the distribution of this rainfall. For the first 7 months of the year the precipitation in 1930 (17.87 inches) was just slightly in excess of the precipitation for a like period in these other 3 years. The total rainfall in Ohio for the 4 months' crop-growing season (April to July inclusive) in 1930 was only 7.78 inches (Columbus 4.85 inches). In 1930 less rain fell in Ohio during April, May, June, and July than was previously recorded for these 4 months for 77 years. The leafhopper is ordinarily an important pest in Ohio, but in 1930, under these conditions, it was not recorded or observed as an economic pest upon any crop in Ohio, and the populations were so small that sufficient material for experimental work could not be obtained in the field.

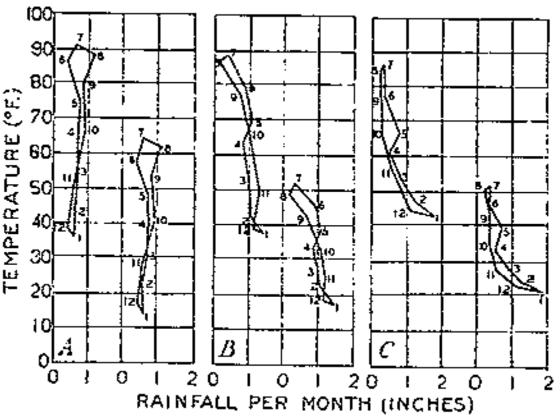


FIGURE 20.—Climographs showing the maximum and minimum mean temperatures for the points and periods indicated: *A*, for Grand Junction, Colo., for 37 years; *B*, for Twin Falls, Idaho, for 30 years; *C*, for Reno, Nev., for 32 years.

In the climograph curve for Columbus in 1930 (fig. 18, *B*), it will be seen that the numbers 4, 5, 6, and 7, denoting the months April to July, run almost in a straight line at approximately the 1-inch rainfall line. This is quite similar to the type seen in the curves of Grand Junction, Colo., Twin Falls, Idaho, and Reno, Nev. (fig. 20). In each of these curves the rainfall curve for these months usually falls within the 1-inch line. The rainfall condition in Ohio in 1930 approached the condition found in these other areas where *Empoasca fabae* is not found. In Denver, Colo., and Salt Lake City, Utah (fig. 21), the rainfall curves for the same 4 months are greater than in Ohio for 1930, but apparently *E. fabae* cannot build populations at these localities with this amount of precipitation and the other climatic factors that prevail.

The climographs for San Jose, Bakersfield, and Lodi, Calif. (fig. 22), are of the same general type and show the extreme condition of practically no rainfall for July, August, and September with considerable rainfall during the winter months. The occurrence of the leafhopper in these California areas is probably due to irrigation, but it is very scarce and apparently cannot build populations under such conditions. Similarly, in Ohio in 1930 it was present, but could not multiply.

The average for a period of 48 years for Columbus, Ohio (fig. 19), is shown, since this is probably a typical average of areas where *E. fabae* can be expected to cause economic damage. The rainfall averages for every month are between 2½ and 3½ inches. The climographs for Ames, Iowa, Madison, Wis., and Topeka, Kans., for periods of 40 and 35 years (fig. 23), show the reverse of the California condition—that is, the light rainfall occurs during the winter months, while the months including the growing season each have 3 or more inches of rainfall. A condition of this kind is favorable to large leafhopper populations, as previous investigations by Fenton and Hartzell (*19*) have shown.

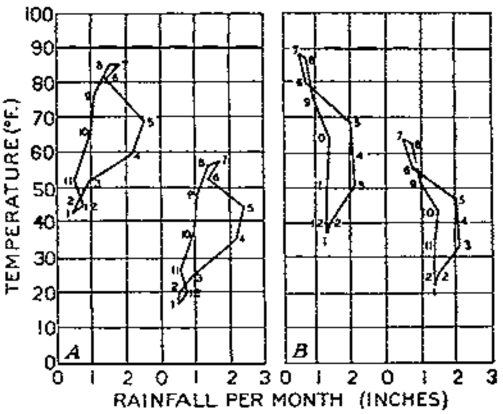

FIGURE 21.—Climographs for Denver, Colo., and Salt Lake City, Utah, showing maximum and minimum mean temperatures: *A*, for Denver for 35 years; *B*, for Salt Lake City for 30 years.

The climograph showing an average condition for 30 years at Gainesville, Fla. (fig. 24), is included for comparison with other areas. The leafhopper increases to populations of economic importance in this area, as shown by Beyer. The climograph shows from 3 to 6 inches of rainfall each month of the year.

It seems apparent that the climograph is an excellent index to the suitability of a locality for the potato leafhopper, and that this insect, even though it occurs there, will not be a factor of any importance in areas where the average precipitation for each of the months of the growing season is below 2 inches. Irrigation may change this condition, but observations would indicate that up to the present it has not changed it.

In connection with control studies in the field during 1932 and 1933 certain observations were made concerning the effect of climatic conditions on populations in the field. In 1932 an abundance of precipitation (3 inches late in June and almost 4 inches during the first week of July) (fig. 25) produced an average high population of from 550 to 600 leafhoppers per 100 trifoliate leaves. This population remained about the same until July 19, when a temperature of 95° F., which occurred after 12 days with occasional light rains, caused the death of large numbers of nymphs; so that after this temperature had prevailed for 3 days the populations decreased to about 75 per 100 trifoliate leaves and continued to decrease during the next few days.

Beginning with July 21, the rainfall over a period of a week totaled more than 2 inches, which seemed to be the important factor in causing the populations to build up rapidly and far surpass the populations found early in July.

Late in June 1933 and early in July, as shown in figure 26, a total of 1¼ inches of rainfall over a period of 9 days apparently caused the populations of leafhoppers to increase rather rapidly. As a result, on July 18 there was an average of 815 leafhoppers per 100 trifoliate leaves of bean foliage in the field, but a later deficiency in rainfall (there was only a half inch of precipitation in 18 days) combined with maximum temperatures of from 95° to 99° F. from July 20 to 23, inclusive, caused the nymphs to die in enormous numbers on the undersides of the leaves of the bean plants in the field. The transpiration caused a portion of the leaves to shrivel and to become dry and parched on the majority of the plants. On July 24 and 25 a half inch of rainfall combined with cooler temperature caused the populations to increase slightly, but these never increased to numbers of any size during the remainder of the season because of continued deficiency of rainfall.

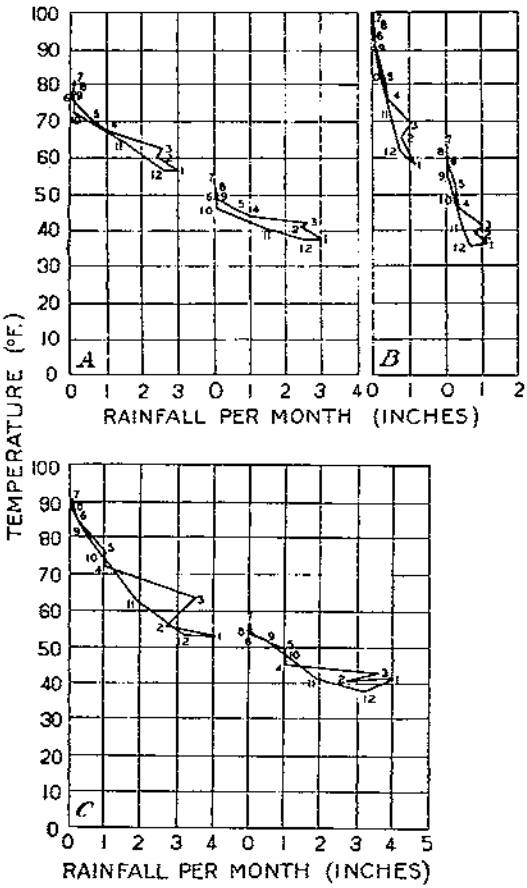


FIGURE 22.—Climographs showing the averages of the mean maximum and the mean minimum temperatures of, *A*, San Jose, Calif., for 16 years; *B*, Bakersfield, Calif., for 22 years; and *C*, Lodi, Calif., for 12 years. The left-hand curve in each set of graphs shows the maximum and the curve at the right the minimum temperatures; the numbers on the curves indicate the months of the year.

A map (fig. 27) showing the life zones as established by Merriam (*39*) on the basis of the summation of temperatures is included for comparison with the maps showing the distribution of *Empoasca fabae*, rainfall, humidity, and rainfall-evaporation. It can be seen at a glance that there is no correlation of the life-zone map with any of the other maps, whereas all of the others show a marked correlation between them. In other words *E. fabae* is distributed rather abundantly through each of the Transition, Upper Austral, Lower Austral, and Lower Austral gulf-strip life zones in the Eastern States, but in the far West it occurs only very sparsely in the Transition Zone in the coastal portion of California, and its abundance is in no way correlated with these life zones as they are found in different areas of the United States. This is true of the leafhoppers in general, as has been pointed out by the writer (*6, p. 114*).

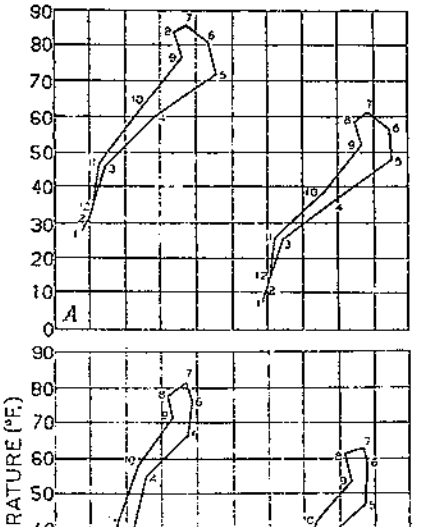


FIGURE 23.—Climographs showing the averages of the mean maximum and the mean minimum temperatures of, *A*, Ames, Iowa, for 40 years; *B*, Madison, Wis., for 40 years; and, *C*, Topeka, Kans., for 35 years. The left-hand curve in each set of graphs shows the maximum and the curve at the right the minimum temperatures; the numbers on the curves indicate the months of the year.

## DISTRIBUTION OF OTHER ECONOMIC SPECIES OF EMPOASCA IN RELATION TO CLIMATE AND PHYSICAL FACTORS

In connection with this discussion regarding the climatic factors influencing the distribution of *Empoasca fabae*, it is interesting to note the relationship of these same factors to the distribution of the three other species of special economic importance, *E. filamenta*, *E. arida*, and *E. abrupta* (fig. 3). The conditions which are apparently most unfavorable for *fabae* are seemingly most favorable for *filamenta*, which is found abundant in the areas where *fabae* cannot be found. The area occupied chiefly by *filamenta* is the arid region with a rather high elevation. It occurs abundantly throughout western Colorado and Wyoming, southern Montana and Idaho, Utah, Nevada, and Oregon, chiefly on potatoes, sugar beets, and beans. It is practically the only species of *Empoasca* that occurs in this region on economic crops; and it might be designated as an intermountain leafhopper to distinguish it from the others, since its area of importance is between the eastern range of the Rocky Mountains and the Sierra Nevada of California. While a western species occurring under arid conditions, it is apparently a high-altitude species and is found abundantly upon crops growing at from 4,000 to 6,000 feet elevation, but it seems to be scarce at altitudes of less than 1,000 feet. It has been collected in several localities in California upon a variety of truck and field crops, but always in very small numbers except upon sweetpotato in one area. There is, therefore, no indication that it is important economically in California, and its status is similar to that of *E. fabae* in the California area. In many respects its distribution is very similar to that of the beet leafhopper (*Eutettix tenellus*) and it is probably second to this insect in abundance in this area. It occurs almost entirely within the zone of 30-percent average relative humidity for 8 p. m. during July. The rainfall-evaporation ratio is from 5 to 15 percent, and the average annual rainfall is 10 inches or less for this area, which comprises the most extended arid region in the United States. *E. filamenta* has not been found east of the Rocky Mountains.

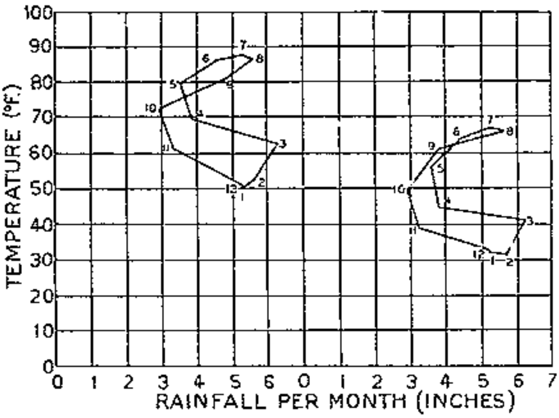


FIGURE 24.—Climographs showing the averages of the mean maximum and of the mean minimum temperatures of Gainesville, Fla., for 35 years.

*Empoasca arida* and *E. abrupta* occur for the most part in the lower-altitude areas of California, where they are able to build enormous populations. *E. fabae* also occurs here, but cannot multiply to large numbers. Lack of rainfall and low relative humidity are apparently optimum factors for survival and reproduction of the two former species. Although

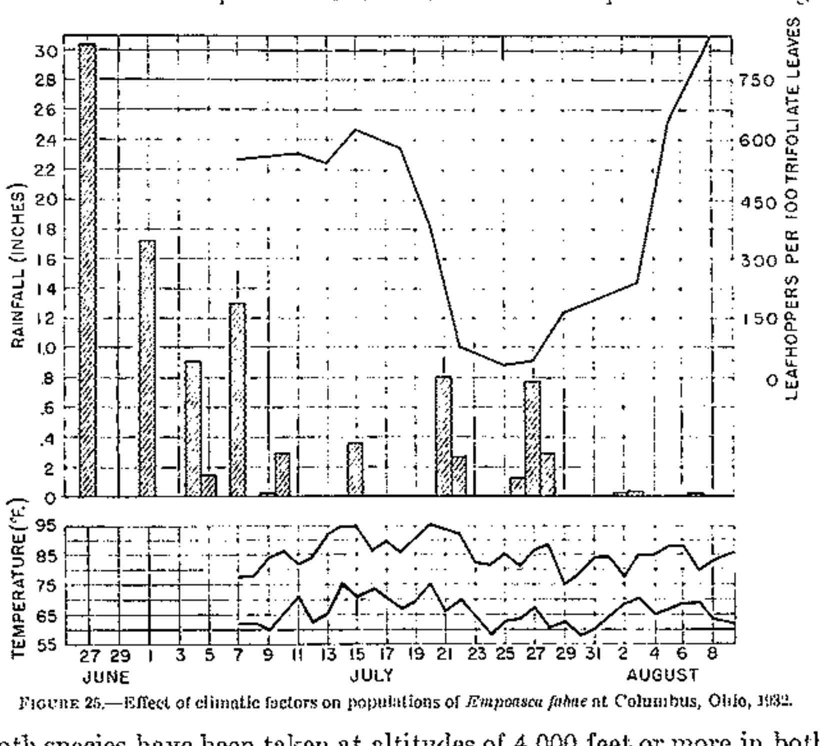


FIGURE 25.—Effect of climatic factors on populations of *Empoasca fabae* at Columbus, Ohio, 1932.

both species have been taken at altitudes of 4,000 feet or more in both Utah and Colorado, apparently neither of them can build populations at these higher altitudes, and records were obtained by scattered specimens only.

The areas, therefore, in which these species occur and become abundant are distinct and are well defined by climatic and physical

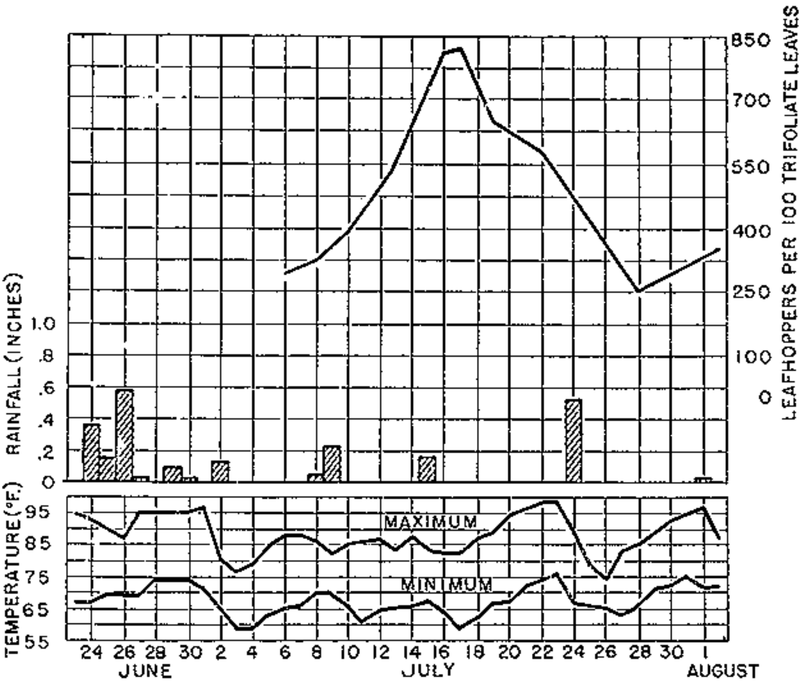


FIGURE 26.—Effect of climatic factors on populations of *Empoasca fabae* at Columbus, Ohio, 1933.

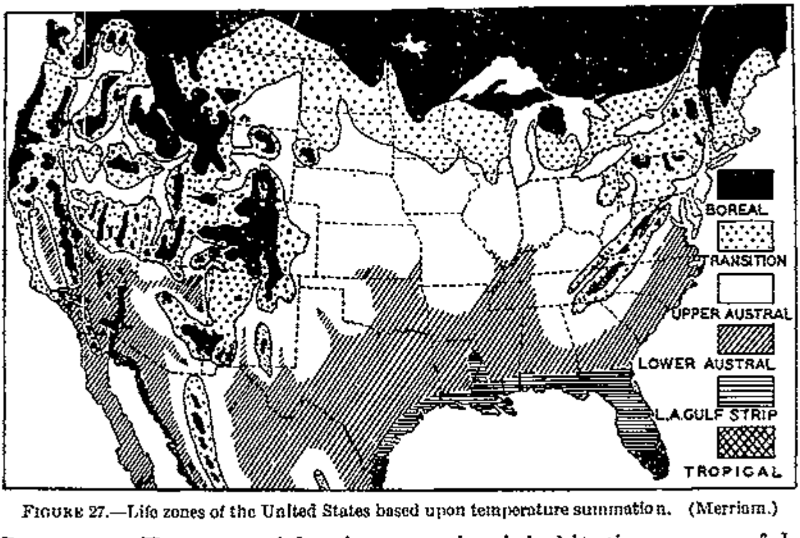


FIGURE 27.—Life zones of the United States based upon temperature summation. (Merriam.)

differences. *Empoasca fabae* is a species inhabitating areas of low altitude, high humidity, and high precipitation. *E. filamenta* inhabits areas of high altitude, low humidity, and low precipitation, while *E.*

*abrupta* and *E. arida* are more successful in areas of low altitude, low relative humidity, and low precipitation. These conclusions are drawn from the data presented above and the following facts: In California all four species occur together, but only *abrupta* and *arida* are important; in Utah *filamenta* and *arida* occur together, but only *filamenta* is important; in western Colorado *filamenta* and *abrupta* occur together, but only *filamenta* is abundant; and in eastern Colorado *abrupta* and *fabae* occur together, and neither one is important or abundant.

The foregoing conclusions were reached by collecting and studying some 27,600 specimens of leafhoppers of the genus *Empoasca* on economic crops in the Western States. Some 15,000 of these were determined by boiling and examining the chitinous internal male genitalia. On the basis of some 18,000 specimens collected in California, the proportionate abundance of each species would indicate

FIGURE 28.—Interior view of screened insectary at Columbus, Ohio

that they occur on economic crops in general in about the percentages given: *E. abrupta* 58.2, *E. arida* 28.3, *E. filamenta* 11.4, *E. fabae* 1.1, and *E. cerea* 1.0.

In Idaho, Utah, and Colorado (west of the eastern range of the Rocky Mountains) *Empoasca filamenta* comprises 99.7 percent of the *Empoasca* population and *E. abrupta* 0.3 percent on similar economic plants.

## BIOLOGICAL STUDIES

### METHODS, TECHNIQUE, AND EQUIPMENT

Biological studies were conducted at Columbus, Ohio, in a screened insectary measuring approximately 10 by 12 by 30 feet (fig. 28). The lower portion was boarded to a height of approximately 3 feet, and the upper portion was entirely screened except for a small room 3 feet square in the northwest corner, which was used as a transfer room to prevent the escape of adults during the time they were being transferred from one plant to another, and which is described later. The insectary was covered by a gable roof. It was on the Ohio State

University farm, at a point where it was not affected by other buildings. Shelves placed at heights of 3½ and 5 feet were used for plants or cages under observation. A large table in the center was also used for a portion of these cages. During these studies a continuous record was obtained by a hygrothermograph which was checked daily by maximum-minimum thermometers and a sling psychrometer. Similar records were obtained for comparison from the Weather Bureau station of the Ohio State University, which was about 100 yards from the insectary.

In view of the fact that adults could not be successfully carried through hibernation, or found in hibernation, and that spring studies proved that the early nymphs upon wild host plants were not *Empoasca fabae*, the life-history study each year was started with the first adults of *E. fabae* that appeared in the field. A certain number of pairs were mated, and when second- and third-generation forms became quite numerous, it was frequently necessary to discontinue detailed study of certain pairs of previous generations. The records for some pairs in each generation are therefore incomplete.

### METHODS OF ESTIMATING POPULATIONS IN THE FIELD

During this study three methods, especially, have been used in an effort to measure or estimate relative populations of this leafhopper. The common method was employed, especially in studies made in the Western States, of counting the entire catch obtained by 100 full sweeps of a standard sweep net having a finely woven cloth bag. While this gives an index to the various species present in any crop or area, so many factors of a variable nature may enter into this method, as previously discussed by the writer (*10*), that a doubtful degree of accuracy is obtained. A second method used is similar and might be criticized on the same basis. It consists of sweeping with the same type of net all the plants that are growing in a definite number of feet of row in a field or crop, then killing and examining all the specimens secured.

A third method seems to give a greater degree of accuracy. This consists in counting the nymphs present upon 25 or 50 trifoliate leaves picked at random and consisting of an equal proportion of leaves from the same relative level on each plot. Graphs are then constructed upon the basis of the number of nymphs per 100 trifoliate leaves.

During its development an individual nymph will move about considerably upon a bean plant, especially upward, but nymphs very seldom leave the plant. On the other hand, the adults are very active and move freely from plant to plant and from row to row, and, as evidence shows, they may also move freely from field to field. Counting the nymphs and disregarding the adults is therefore believed to give the best index to relative populations. Furthermore, if the adults are present in different numbers in separate plantings, the egg deposition and subsequent hatching during the period under study will usually give a better indication of numbers than an attempted count of the shifting and active adults.

### INSECTARY AND FIELD RECORDS COMPARED

The insectary condition is not a natural environment and, as a consequence, insectary records of the activity or behavior of an insect do not duplicate, at least in detail, the field record. By correlating the climatic factors in each case as closely as possible with the biological development and then comparing the field and insectary conditions, an approximate knowledge of field behavior can be gained. Also, it should be stated that it is practically impossible with present known methods to gain a complete continuous record of an individual potato leafhopper under field conditions, so it seems advisable to make the insectary study and the comparison as mentioned above.

Spring hatching on economic plants in the field could always be checked with the insectary hatching, and growth and development to the adult could be checked in the same way during the time of this brood. But the broods overlap to such an extent that observations of this type in the field were of no value after about July 1. In order to check the egg laying, development, etc., after that time, it was necessary to use plants raised under cover, expose them under a screened cover in the field to fertile females, and then note hatching and development as closely as possible by leaving the leafhoppers among the field plants but under a screened cage. A plant of this type set in the field without a screened cover will become infested or contaminated within a few hours by eggs, which will be concealed in the plant tissue, or by active hopping nymphs. The time required for incubation and that for hatching were the same in the field as in the insectary with the exception of minor differences of a few hours during periods of fluctuating temperature. The insectary results are therefore considered as representative for this species under Ohio conditions.

In order to carry on biological studies with the potato leafhopper a number of routine duties must be performed which are not necessary with certain other types of insects that are larger and have different habits.

In the first place, these insects are so small that it is necessary to handle them very carefully and keep them under suitable coverings for observation in order to prevent their escape and to obtain a continuous record of their activities. If one of these escapes from its cage it is practically impossible to recapture or identify it. Furthermore, they are very frail and easily injured, and they should be handled as little as possible, and very carefully when handling is necessary. Special methods and technique are therefore required in handling.

In the second place, the eggs are laid singly and in small numbers daily and are inserted into the tissues of the plant. In order to obtain egg records, preoviposition data, etc., it is necessary to handle a large number of plants, and when records are being obtained upon several females over periods of several days or weeks a great number of plants must be used. Because of lack of space for plants and lack of time for handling, the number of individual records that could be obtained is not as large as would be desired.

### LIFE-HISTORY CAGES

An improvised glass cage used for rearing was quite satisfactory. Wide-mouthed chemical salt bottles 7 to 8 inches in diameter, the diameter of the mouth being about 3 inches, were used to make these cages. By the use of a heating-element wire and an electric current with sufficient resistance to heat the wire to redness, the bottoms could be cut off of these jars very easily and neatly (fig. 29). The jars thus made could be pushed slightly into the dirt inside the edge of the pot containing the plant under study. The tops were covered with cheesecloth (fig. 30). The advantage of this type of cage is that the bottom is as large as any part of the jar, and the plant is not disturbed when the cover is removed. These jars proved economical and satisfactory in that, so far as could be ascertained, not a single specimen was lost during the entire study owing to excess humidity collecting on the inside of the jar. Field cages were constructed of 40-mesh copper screen wire (fig. 31).

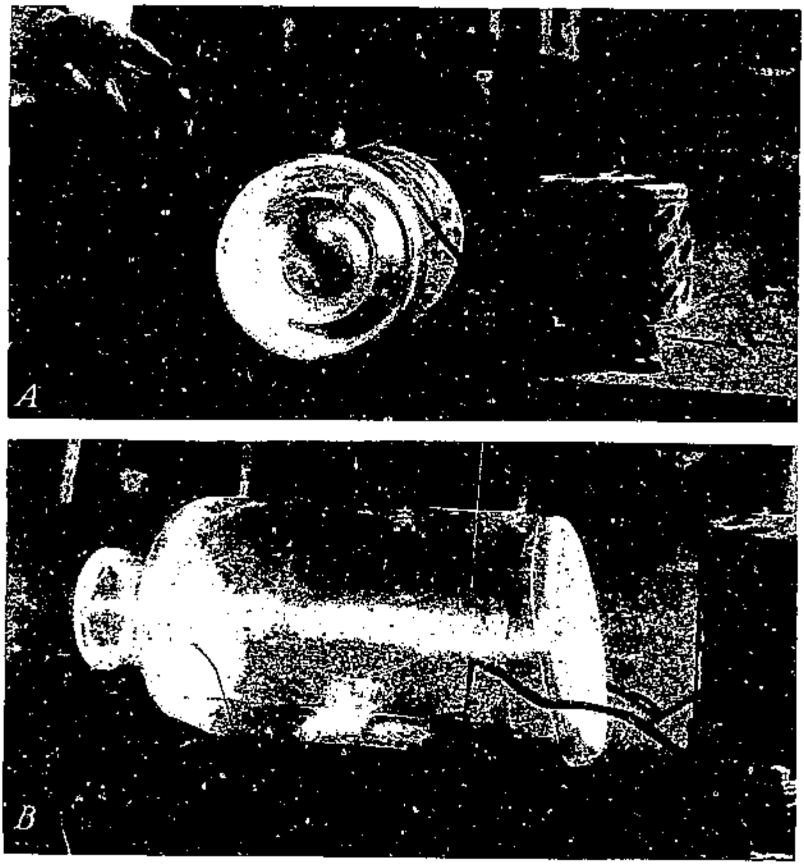


FIGURE 29.—Method of making bell-jar cages from large chemical salt jars: *A*, Electric wire and resistance set-up used to cut the bottoms from the jars; *B*, a bell jar with the bottom which has been cut off.

PLANTS USED FOR BIOLOGICAL STUDIES

In order to obtain plants free from eggs it was necessary to plant seed each day and to raise plants out of doors under protected conditions. Individual plants were potted and used for individual records. Each plant was exposed to the feeding and egg laying of a single female leafhopper or a pair for a certain number of hours, after which the plant was kept in a protected place and the hatching record obtained. After the nymphs had emerged they were kept under covers, and the dates for developmental stages were recorded. If a plant died, the egg records were lost, as hatching seldom occurred under such a condition. The proper raising, potting, and handling of plants was, therefore, an important routine in obtaining successful records in the biological studies.

TRANSFERRING INDIVIDUALS

In order to transfer a female from one plant to another for egg deposition a special room was used similar to those used for parasite work. The room was 3 feet square and provided with a small window. The bench used for transferring, as well as the door, was covered with a black hood, to prevent reflection of light. The insect was not touched or handled during the entire operation. As the insect responds positively to rather bright light, a small camel's-hair brush was used to agitate the leaf upon which it was resting and cause it to hop upon the side of the glass jar toward the light. This was accomplished by tilting the glass over slightly away from the operator and toward the source of light. While the leafhopper was on the glass jar this was carefully, but quickly, removed and placed over a new plant for the next record. This avoided injury to the insect and also afforded opportunity for obtaining a continuous record on egg laying by an individual. These covered plants were kept in the screened insectary previously described, where as much light as possible was available without direct sunlight.

FIGURE 30.—Improvised glass bell-jar breeding cage for *Empoasca fabae* in use.

NOTE FORMS AND RECORD SHEETS

A complete record was kept of the source and history of each female. The number of the plant and the dates between which the female was present upon it for oviposition were also recorded, and a complete record of each of these plants was kept on a separate life-history chart. These data were then summarized. The method of designating the individual insects employed in life-history studies on the Mexican bean beetle (*Epilachna varivestis* Muls.) was used in this work.

### THE WINTERING CONDITION

The problem of how and where this insect winters is the most perplexing one encountered during the present study. Three possibilities are offered: (1) That the insect passes this period as an adult in hibernation; (2) that it spends the winter in the egg stage upon a wild host plant and develops to maturity before migrating to economic food plants; and (3) that it cannot live over winter in the Northern States but migrates from southern areas in the spring. The evidence that has been obtained by field study and observations regarding each hypothesis will be presented briefly.

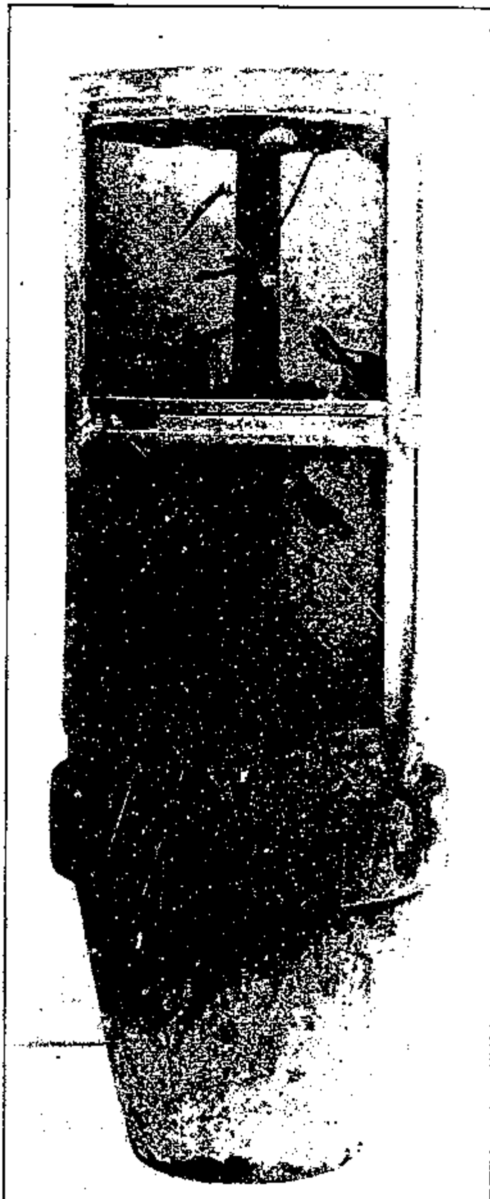

FIGURE 31.—Cage of fine-mesh screen used for outdoor biologicl studies of *Empoasca fabae*.

In regard to the first possibility, adult hibernation, the evidence that has been obtained has all been negative. Attempts made in Ohio by the author and other workers to carry these insects through hibernation in fallen leaves, crop remnants, and similar debris in protected places have proved unsuccessful to the extent that not a single individual survived. Furthermore, for a period of 8 years attempts to find or recover *Empoasca fabae* in hibernation under natural conditions have proved unsuccessful. All specimens of *Empoasca* that have been recovered in hibernation have been identified as of some other species. *E. fabae* is by far the most abundant in numbers of any species of *Empoasca* occurring in the Eastern States, and if it hibernates successfully under conditions similar to those favorable to other hibernating leafhoppers, it should be found by chance at least more quickly than any other species. But investigation has shown that *recurvata* De-

Long, *infusca* DeLong, *birdii* Goding, *curvata* Poos, *bicorna* DeLong and Caldwell, *spira* DeLong and Caldwell, *hama* DeLong and Caldwell, *lata* DeLong and Caldwell, *recta* DeLong and Caldwell, *ditata* DeLong and Caldwell, *vergens* DeLong and Caldwell, *distracta* DeLong and Caldwell, and *pyramidata* DeLong and Caldwell, a number of which are species of minor abundance and the only ones of the genus *Empoasca* known to hibernate as adults in this area, have been found in Ohio along with hibernating species of *Erythroneura* during January, February, March, and April, but no specimens of *E. fabae* could be found either here or in similar habitats. Furthermore, if this insect passes the winter as an adult, it would be expected to come out of hibernation at approximately the same time as other hibernating leafhoppers, such as *Empoasca recurvata* and species of *Erythroneura, Dikraneura, Eugnathodus, Agallia, Euscelis, Phlepsius, Thamnotettix, Platymetopius, Polyamia,* and *Deltocephalus*. Observations have shown, however, that the earliest specimens of *E. fabae* appear at least a month later than these hibernating species.

Several records have been published regarding the early occurrence of adults of *Empoasca fabae* upon wild host plants in the spring when they have supposedly come from hibernation. These observations and records have been made by investigators who have stated that they did not use the genital characters to identify their material and could not distinguish *E. fabae* from the other closely related species of *Empoasca* that have the same external appearance and that normally live upon these wild hosts. An examination of specimens occurring in Ohio upon dock (*Rumex* sp.) and other wild host plants in the spring has revealed that all of them are either *E. erigeron*, or *E. bifurcata*, or *E. recurvata*.

The second possibility is that the insect overwinters in the egg stage upon a wild host plant and there completes its development, then migrates to economic plants later in the spring. The time of its first appearance in the field would be a factor favoring this possibility. As indicated above, it occurs in the field much later than other forms that hibernate. But detailed search in the field during the early part of the season for a period of 8 years upon many types of wild host plants has failed to give any positive evidence that *Empoasca fabae* winters in the egg stage upon wild host plants. *E. erigeron* and *E. bifurcata* are known to pass the winter in this way, and the eggs hatch late in April or early in May. Although these species are in minor abundance as compared to *E. fabae*, they are found commonly in the spring upon wild host plants in the nymphal stage, but nymphs of *E. fabae* cannot be found. If *E. fabae* overwinters as an egg, the fact that it is in great abundance later in the season should make it easily found early in the season in the nymphal stage on either wild or cultivated host plants. Examination of crop remnants has also failed to give any positive evidence regarding its overwintering as an egg.

In view of the fact that specimens of *Empoasca fabae* have not been successfully carried through hibernation or found in hibernation and that no evidence can be obtained regarding the passing of the winter in the egg stage upon either a wild or a cultivated host, and in view of the late appearance in great abundance of the adults in the spring, there is a strong possibility of the truth of the third theory, that the insects pass the winter or survive only in areas of milder climate and migrate into Ohio and similar States at a later date as adults. The only evidence for this is the strong negative evidence presented in regard to the other two possibilities and the fact that leafhoppers of this species appear in cultivated fields exactly as other migrating leafhoppers appear in other areas on economic crops. Migration flights are usually marked by the abrupt appearance of large numbers in cultivated fields and late in the season, the insects apparently migrating from a breeding ground elsewhere.

The work of Beyer (*3, 4*) in Florida shows that this leafhopper breeds in that State on castor-bean and other wild host plants during the entire winter. Material from the Gulf States collected during the winter months shows definitely that *Empoasca fabae* breeds in these areas during the winter on alfalfa and similar crops and that the populations become large in March and April. This adds evidence to the migration theory.

### APPEARANCE IN THE SPRING

*Empoasca fabae* appears upon cultivated hosts in the spring of the year, usually rather late in May or early in June in central Ohio, the date varying with climatic conditions.

Detailed observations were not made early in 1926. But the average temperature in April (44.4° F.) was unusually low. May was normal (60.7°), and the temperature for June (66.1°) was a little below normal. The rainfall in April (1.42 inches) was quite deficient, and that for May (0.96 inch) was even more so. This apparently did not greatly delay the spring appearance and the normal development of the first generation. On June 14 large numbers of nymphs appeared in a field on bean plants. Some of these were in the last instar and changed to the adult stage on June 21. On June 18 the average nymphal population in this field was five or six per leaf.

In 1927 the temperature from January 17 to March 21 was persistently and at times markedly above the normal. In general the temperature in April (average 50.9° F.) was normal, May, with an average of 60.4°, was normal, and June, with a temperature of 65.5°, was about 5° deficient. In spite of this deficiency in June the temperature for the period January 1 to June 10 was 277° in excess of the normal. For the same spring, precipitation in March (3.97 inches), April (3.80), May (6.48), and June (3.63) was in excess each month with almost twice the normal precipitation in May. Under these conditions (a decided excess of both temperature and precipitation) the bean plant developed in the field more rapidly than the potato plant, although the potato plants had pushed through the ground before the beans were planted. In spite of this earlier appearance of the potato the leafhoppers had begun to infest the two-leaved bean plants on May 25, and on June 7 averaged two or three adults per bean plant, and the nymphs were hatching. On this same date the potatoes, which were almost a foot high, were examined and five adult leafhoppers were found on 100 plants. The occurrence here seemed entirely accidental. On June 15 field observations showed that each bean plant had a population of from 8 to 10 adults and many nymphs in the second and third instars, whereas a maximum of 10 adults were found on 75 potato plants. On June 22 an abrupt migration to potatoes increased the infestation to 20 or 25 adults per plant, but no nymphs were present and no hopperburn. On June 24 and 25 the nymphs upon bean were emerging as adults, and no nymphs were found upon potato until after July 1.

In 1928 a generally cool spring was recorded in central Ohio. In March both temperature and precipitation were subnormal. In April the temperature (average 46.5° F.) was lower than normal and the rainfall was slightly deficient. May was generally cool and dry with a subnormal temperature (average 59.1°) and a decided rainfall deficiency amounting to 1.77 inches. According to the monthly weather report for Ohio, June 1928 was next to the wettest and fourth from the coolest June in Ohio in 46 years; the precipitation of 6.79 inches being 3.04 inches above normal, and the average mean temperature of 65° being 4.6° below normal. In spite of a heavy rain the rainfall from January 1 through June was 3 inches below that of the same period in 1927, while the temperature on June 10 was deficient by 196° compared with the normal and 473° below that for the same period in 1927. Under these cool conditions potatoes grew and developed very rapidly, but beans made slower growth. The first scattered population of leafhoppers was found on beans on June 1. On June 4 and 5 leafhoppers appeared on both bean and potato plants at Columbus in small numbers. On June 6 the leafhoppers were not so abundant upon either bean or potato as they had been the previous season on May 25 on bean. From this point the populations built up very slowly but about equally upon both crops. It was apparent from examinations on June 6 that the cool weather was ideal for rapid growth of the potato plants, which were blossoming and were far ahead of the previous season, while the beans, which were just putting out the first trifoliate leaves, had apparently been arrested in development by the same conditions. An examination of later-planted potatoes, which were only about 6 inches high, showed no leafhopper populations.

In 1929 the month of March, with a temperature of 47.4° F., was 5° above normal, and the precipitation for the month (1.76 inches) was quite deficient. Although quite variable, April, with a temperature of 54.4°, showed an excess of 4.6° above normal and a precipitation of 3.71, which was a considerable excess. May had a temperature of 59.7°, which was approximately normal, and a rainfall of 4.55, which was approximately 1 inch above normal. June had a temperature of 68.7°, which was about normal, and a rainfall of 4.76 inches, which was 1.46 inches in excess of normal. These data showed an almost exactly normal temperature for the first 6 months and an excess rainfall of 2.57 inches. The season would seem, therefore, to have been almost intermediate between 1927, which was greatly in excess in both temperature and humidity, and 1928, which was deficient in both temperature and humidity. The reactions of the leafhoppers to host plants were more like their activities during 1927 than in 1928, except that the interval between appearance on the two plants was not so great.

Measurements were made of sugar and osmotic pressure [6] in these plants in an attempt to find if these materials or plant processes showed any correlation to insect attractiveness. The data obtained are given for comparison in table 1. In the tests given here and all other tests made upon young bean and potato plants it was shown that the bean

[6] Both were measured by the standard methods. Sugars were determined by the refractometer method and osmotic pressure estimated in atmospheres was determined by undercooling the plant sap below the freezing point and determining osmotic pressure by the standard tables prepared from the formula $O.\ P. = 12.06\Delta - 0.021\Delta^2$ of Harris and Gortner (27).

plant is much higher in sugar content when it first breaks through the ground than is the potato plant, and in most tests is much higher proportionately in the bean than in those tests shown in the table. The leafhoppers are never attracted to the potato until it has attained a considerable size, whereas they are attracted immediately to the bean. There is apparently some product or factor associated with growth which attracts the leafhopper to potato at a later date. It is interesting to note in this connection that Fenton and Hartzell (*19, p. 425*), in discussing the influence of the date of planting of potatoes upon the development of hopperburn, make this statement:

> This was due to the fact that the female leafhoppers preferred partly grown plants for oviposition and were not attracted at the time of the spring flight to smaller vines which had developed from tubers planted later.

In connection with their work they apparently made no observations upon the appearance of *Empoasca fabae* on the bean, but did observe the late appearance on potato or the preference for older potatoes when there was a choice between plants of different ages.

In 1930, the drought year in Ohio, some very interesting observations were made, but chiefly in connection with population studies. The temperature was in excess for every month except March, when it was only slightly deficient, so that by June 30 an excess of 462° had been accumulated. In contrast to this, the rainfall had been conspicuously deficient during March, April, May, and June, until the accumulated deficiency was slightly more than 6 inches. Under these conditions the leafhopper migrated to bean and became rather abundant, with populations of from 10 to 12 adults per trifoliate leaf on June 25 to 28, but it never became abundant upon potato, owing to the continued drought and its effect upon either the potato plant or directly upon the leafhopper.

If we may judge from these data and observations in the field during these varied seasons, it would seem that climatic factors and their effect upon different types of plant growth were determining factors in regard to host preference and spring activity in the field. Under normal conditions or when the season is advanced, this leafhopper is attracted first to leguminous hosts and later goes to potato and other species of *Solanum*. In a cool or late spring the insect seems to be attracted to potato much sooner than it normally would be, and there is only a short time intervening between its occurrence upon legumes and upon potato.

Data recorded during the spring of 1931 are included here in order to show the normal sequence of species of *Empoasca* in Ohio. From April 11 to May 5 specimens of *E. recurvata* were taken in hibernation in ravines, privet hedges, etc. Nymphs of *E. bifurcata,* which overwintered as eggs, were abundant on *Coreopsis* sp., an ornamental of the family Compositae, on May 15. These became adults on May 20 and 21. During the same period nymphs of *E. erigeron* were abundant on *Erigeron* spp., and they became adults about May 20. On May 21 the first specimens of *E. fabae* were found on alfalfa and on May 22 on *Baptisia australis,* an ornamental legume, and they appeared on bean at about the same time. This late-spring appearance of *E. fabae* in the field, which has been shown consistently throughout these records of spring occurrence from 1926 to 1931, inclusive, has been discussed more fully under the heading The Wintering Condition.

TABLE 1.—*Osmotic pressure and sugar content of potato and bean plants and populations of Empoasca fabae at Columbus, Ohio, 1929*

| Date plant was sampled | Size and condition of plants | | Leafhopper appearance and abundance | | Osmotic pressure | | | | Sugar content | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | | Total leaves | | Ground leaves | | Total leaves | | Ground leaves | |
| | Potato | Bean | Potato | Bean | Potato | Bean | Potato | Bean | Potato | Bean | Potato | Bean |
| *1929* | | | | | *Atmospheres* | *Atmospheres* | *Atmospheres* | *Atmospheres* | *Per cent* | *Per cent* | *Per cent* | *Per cent* |
| May 16 | About 6 inches high | Just pushing through ground. | None | None | 6.71 | | | | 2.18 | | | |
| May 23 | | Small 2-leaved plants | do | do | 7.18 | 5.81 | | | 1.93 | 2.85 | 4.63 | 6.25 |
| May 31 | About 10 to 12 inches high. | Large 2-leaved plants | do | Averaged 2 adults per plant. | 6.22 | 7.57 | 9.42 | 9.29 | 3.94 | 4.64 | 6.74 | 7.44 |
| June 6 | | First trifoliate leaves | do | Adults abundant | 7.83 | 8.19 | 9.15 | 8.28 | 6.78 | 5.71 | 8.56 | 7.33 |
| June 13 | 15 to 18 inches high | With only 1 large trifoliate leaf. | Adults abundant; no nymphs. | Adults and nymphs[1] abundant. | 6.88 | 6.92 | 7.71 | 7.63 | 8.59 | 7.09 | 9.06 | 9.23 |
| June 20 | | Beans blossoming | Adults abundant | Adults and nymphs abundant. | 7.67 | 7.15 | 9.07 | 8.48 | 7.43 | 8.56 | 9.54 | 12.94 |
| June 28 | | | (2) | | 6.76 | 7.28 | | | 6.64 | 7.54 | | |

[1] Several in third and fourth instars.
[2] Heavy migration of adults to potato June 25.

### MATING IN RELATION TO EGG PRODUCTION

Mating normally occurs within 48 hours after emergence. It was apparent from the observations made that fertile eggs cannot be deposited and that the insect cannot reproduce unless mating takes place. Reared females have been kept for weeks unmated, and no fertile eggs were produced by them. As soon as they were mated they produced eggs normally and in approximately the same time after mating that eggs would have been produced had mating taken place as soon as the female emerged. One mating is apparently sufficient for the fertilization of eggs during the entire life of the individual. Females isolated after mating produced on an average the same number of fertile eggs as those caged with males. If fertile females are given repeated opportunity to remate by introducing newly emerged males, the normal number of eggs produced is not changed.

Experiments have demonstrated that a male or female from any brood may mate normally with the opposite sex from any other brood. The time of occurrence in the season of any individual, rather than the brood to which it belongs, is the most important factor. Since broods overlap greatly in the field there are always individuals present for mating.

### PREOVIPOSITION

In order to obtain preoviposition records, the nymphs were isolated during the last instar and each nymph reared to the adult stage in a separate container. They were then mated and placed upon a previously protected plant. Sometimes these adults were left on one plant for a period of 3 or 4 days, and in some cases the insects were transferred daily. The preoviposition records discussed later were checked or established by known fertile females which were under observation for life-history studies and were transferred at least daily. In such cases the date of egg laying was known and there could be no question about the length of the preoviposition period. The preoviposition period was counted in every case from the time the female reached the adult stage and regardless of the date she was mated. A number of observations and matings have shown that the period of preoviposition is determined by the time of mating. If two females are mated at the same time, as a rule, both will produce fertile eggs on the same day, although one may be newly emerged and the other 20 days old but previously unmated.

The biological work would indicate that where mating occurs within a few hours after emergence, as undoubtedly happens in the field, the preoviposition period is from 3 to 5 days. This factor must be considered, therefore, in the data presented here regarding the length of time elapsing prior to oviposition.

During 1926 preoviposition for 40 individuals showed an average of 6.4 days with a minimum of 3 days and a maximum of 11 days. In 1927 preoviposition records for 54 individuals gave an average of 6.6 days with a minimum of 3 and a maximum of 19 days. In 1928 records for 31 females gave an average of 5.57 days with a minimum of 3 and a maximum of 14 days. In view of the statement made above concerning mating, it is probable that the average is lower than these figures would indicate.

Fenton and Hartzell (*19, p. 387*) are the only previous workers to give preoviposition records. They cite preoviposition records for three females ranging from 18 to 29 days and averaging 23.3 days.

### EFFECT OF TEMPERATURE UPON PREOVIPOSITION

Under cage conditions a rather definite correlation has been shown between the duration of the preoviposition period of *Empoasca fabae* and the average temperature prevailing during that period, although some variability in this general trend has occurred in the instance of individuals that did not mate immediately or soon after emergence. In such instances it appeared that the prevailing temperatures exerted only a secondary influence. When mating occurred as soon as the insect emerged, however, as is usually the case, the duration of the preoviposition period appeared to be short, ranging from 3 to 8 days, and to have a definite correlation with temperature. The data obtained on the preoviposition period during 1926 and 1927, and for which temperature records are available, are shown in table 2.

TABLE 2.—*Relation of temperature to the duration of the preoviposition period of the potato leafhopper under cage conditions at Columbus, Ohio, during 1926 and 1927*

| Specimens observed 1926 | Preoviposition period | Average temperature during preoviposition period | Specimens observed 1927 | Preoviposition period | Average temperature during preoviposition period |
|---|---|---|---|---|---|
| *Number* | *Days* | *°F.* | *Number* | *Days* | *°F.* |
| 1 | 3 | 75.1 | 1 | 3 | 76.6 |
| 3 | 4 | 75.8 | 10 | 4 | 77.9 |
| 8 | 5 | 76.4 | 5 | 5 | 76.0 |
| 14 | 6 | 71.2 | 11 | 6 | 72.0 |
| 5 | 7 | 70.7 | 8 | 7 | 70.0 |
| 4 | 8 | 70.0 | 3 | 8 | 66.4 |
| 1 | 9 | 72.5 | 4 | 9 | 68.8 |
| 1 | 10 | 75.7 | 6 | 10 | 72.3 |
| | | | 1 | 11 | 65.1 |

### OVIPOSITION

The number of eggs laid by a female could not be accurately ascertained in view of the fact that the eggs are very small and are inserted in the tissue of the plant. They were inserted almost entirely in the main veins on the under surface of a leaf or in the petiole, or upon the upper portion of the stems of very young bean plants used in the cages. In the following discussion, therefore, the eggs referred to are in reality only those that produced nymphs.

There is a considerable variation in the total number of eggs that individuals lay, the number of days over which eggs are laid, and the number of eggs laid per day. A few outstanding extremes as well as the averages might be mentioned specifically. In 1926 one second-generation female produced 226 eggs in 47 days, or an average of 4.8 eggs per day. Another female of the same generation produced 166 eggs in 29 days, or an average of 5.7 eggs per day. One produced 153 eggs in 26 days, or an average of 5.9 eggs per day. The highest record for 1 day was established by a female that laid 8 eggs in a 24-hour period. On the other hand, one female laid 25 eggs in 23 days, or an average of only 1.1 eggs per day. An average of 2.8 eggs per day was produced by all females of all generations in 1926. These records are based on the activities of 51 females laying a total of 2,327 eggs.

In table 3 is given a summary of the time spent in the preoviposition and incubation periods of the four broods and the time of nymphal development by *Empoasca fabae* in 1926.

TABLE 3.—*Minimum, maximum, and average time spent in the various stages by the potato leafhopper, Empoasca fabae, at Columbus, Ohio, in 1926*

| Period | First brood (June 15–July 22) | | | | Second brood (June 21–Sept. 2) | | | |
|---|---|---|---|---|---|---|---|---|
| | Cases | Minimum | Maximum | Average | Cases | Minimum | Maximum | Average |
| | *Number* | *Days* | *Days* | *Days* | *Number* | *Days* | *Days* | *Days* |
| Preoviposition | | | | | 12 | 5 | 11 | 6.6 |
| Incubation | 176 | 7 | 12 | 8.7 | 624 | 7 | 11 | 8.4 |
| Nymphal development | 40 | 10 | 15 | 12.4 | 133 | 10 | 19 | 12.5 |
| Total | | 17 | 27 | 21.1 | | 17 | 30 | 20.9 |

| Period | Third brood (July 27–Oct. 11) | | | | Fourth brood (Aug. 28–Oct. 3) | | | |
|---|---|---|---|---|---|---|---|---|
| | Cases | Minimum | Maximum | Average | Cases | Minimum | Maximum | Average |
| | *Number* | *Days* | *Days* | *Days* | *Number* | *Days* | *Days* | *Days* |
| Preoviposition | 17 | 3 | 10 | 6.0 | 11 | 5 | 9 | 7.0 |
| Incubation | 920 | 7 | 18 | 10.2 | 244 | 10 | 19 | 13.2 |
| Nymphal development | 90 | 10 | 22 | 14.5 | 6 | 22 | 22 | 22.0 |
| Total | | 17 | 40 | 24.7 | | 32 | 41 | 35.2 |

TABLE 4.—*Minimum, maximum, and average time spent in various stages by the potato leafhopper, Empoasca fabae, at Columbus, Ohio, in 1927*

| Period | First brood (May 25–Aug. 25) | | | | Second brood (June 26–Nov. 2) | | | |
|---|---|---|---|---|---|---|---|---|
| | Cases | Minimum | Maximum | Average | Cases | Minimum | Maximum | Average |
| | *Number* | *Days* | *Days* | *Days* | *Number* | *Days* | *Days* | *Days* |
| Preoviposition | | | | | 14 | 3 | 7 | 5.1 |
| Incubation | 551 | 8 | 16 | 10.7 | 722 | 8 | 15 | 9.8 |
| Nymphal development | 141 | 10 | 20 | 14.0 | 225 | 12 | 24 | 14.2 |
| Total | | 18 | 36 | 24.7 | | 20 | 39 | 24.0 |

| Period | Third brood (July 24–Oct. 7) | | | | Fourth brood (Aug. 27–Oct. 9) | | | |
|---|---|---|---|---|---|---|---|---|
| | Cases | Minimum | Maximum | Average | Cases | Minimum | Maximum | Average |
| | *Number* | *Days* | *Days* | *Days* | *Number* | *Days* | *Days* | *Days* |
| Preoviposition | 19 | 4 | 11 | 6.3 | 21 | 4 | 19 | 7.8 |
| Incubation | 365 | 8 | 16 | 11.0 | 185 | 8 | 15 | 10.3 |
| Nymphal development | 154 | 8 | 24 | 18.0 | 28 | 15 | 25 | 17.1 |
| Total | | 16 | 40 | 29.0 | | 23 | 40 | 27.4 |

In 1927 one female taken from early beans in the field on May 25 remained alive for 92 days and deposited 195 eggs during this period, making an average of 2.1 eggs per day. A higher record was obtained for a second-generation female which emerged as an adult on June 29, was mated on the same date, and was kept under observation for 91 days. She produced 216 eggs in 85 days or an average of 2.5 eggs per day. These are the longest periods of egg laying recorded during this study. In 1927 all observations showed 579 oviposition days with a total of 1,334 eggs, and an average of 2.3 eggs per day for all females of all generations. A condensed summary of the life-history data for 1927 is given in table 4.

In 1928 the greatest number of eggs were obtained from a female of the second generation that emerged on July 4, was mated on the same date, and was kept under observation for 49 days. She began to lay eggs in 3 days, and during the 46 days of egg laying produced 240 eggs, or an average of 5.2 per day. During the same season a female taken in the field on early beans on June 9 was kept under observation for 42 days, but was accidentally injured in handling at the end of this period. During the 41 days of egg laying she produced 173 eggs, or an average of 4.2 eggs per day. The data for oviposition and female egg records were not so complete for 1928 as for the two previous seasons; the number of oviposition days was 397 and the number of eggs laid was 1,200. This gives an average of 3.0 eggs per day laid by all females of all generations during 1928. A condensed summary of the data for 1928 is given in table 5.

For the three seasons the average was 2.7 eggs per day for all of the females under observation.

TABLE 5.—*Minimum, maximum, and average time spent in various stages by the potato leafhopper, Empoasca fabae, at Columbus, Ohio, in 1928*

| Period | First brood (June 5–July 21) | | | | Second brood (July 4–Sept. 4) | | | |
|---|---|---|---|---|---|---|---|---|
| | Cases | Minimum | Maximum | Average | Cases | Minimum | Maximum | Average |
| | *Number* | *Days* | *Days* | *Days* | *Number* | *Days* | *Days* | *Days* |
| Preoviposition | | | | | 12 | 3 | 14 | 6.0 |
| Incubation | 371 | 7 | 14 | 9.5 | 603 | 7 | 14 | 8.6 |
| Nymphal development | 73 | 8 | 15 | 11.4 | 127 | 9 | 24 | 11.9 |
| Total | | 15 | 29 | 20.9 | | 16 | 38 | 20.5 |

| Period | Third brood (July 26–Sept. 9) | | | | Fourth brood (Aug. 20–Oct. 5) | | | |
|---|---|---|---|---|---|---|---|---|
| | Cases | Minimum | Maximum | Average | Cases | Minimum | Maximum | Average |
| | *Number* | *Days* | *Days* | *Days* | *Number* | *Days* | *Days* | *Days* |
| Preoviposition | 11 | 3 | 9 | 5.4 | 8 | 4 | 8 | 5.4 |
| Incubation | 346 | 7 | 23 | 10.5 | 149 | 8 | 22 | 13.8 |
| Nymphal development | 55 | 10 | 17 | 13.1 | 8 | 16 | 26 | 22.5 |
| Total | | 17 | 40 | 23.6 | | 24 | 48 | 36.3 |

## RELATION OF TEMPERATURE TO OVIPOSITION

The relationship of temperature to egg laying has not been shown in detail in view of the fact that egg laying seems to occur normally over a rather wide range of temperature. High temperatures up to 90° F. or slightly higher have not affected the normal activities of *Empoasca fabae* in any way, nor has it prevented or arrested egg laying. On the other hand, a sudden drop in temperature, even though not extremely great, or a fairly low temperature for a period of several hours or days, inhibits egg laying. The following actual records are cited to illustrate these low-temperature effects:

In 1928 the maximum temperatures from June 20 to 25 ranged from 76° to 83° F., while the minimum ranged between 60° and 65°. On June 26 the temperature dropped suddenly to a maximum of 66° with a minimum of 59°. On this date no eggs were laid by any of the females under observation. On August 12 the maximum temperature dropped to 76° from a previous maximum of 80°, and the minimum dropped from 63° to 56°, and no eggs were laid on this date. The average temperature of 66° for this date did not seem to be sufficiently high for the egg-laying activity. On September 17 a similar condition occurred when a previous maximum temperature of 85° dropped to a maximum of 71°, and a previous minimum of 60° dropped to 54°, no eggs were deposited on this date. Again on September 23 the temperature dropped from a previous maximum of 70° to a maximum of 59° and remained at 58° or 59° during the 3 succeeding days. The minimum temperature ranged from 35° to 46° for the same period. No eggs were laid by females under observation during this period.

The maximum and minimum temperatures are given here since they seem to be the controlling factors. If the temperature goes sufficiently high during a 24-hour period or a portion of it so that the insect becomes normally active, egg laying will usually occur. On September 4, 1928, the minimum temperature was 51° F. but the maximum of 70° permitted egg laying for this date, although it was probably very close to the conditions mentioned above when no egg laying occurred. A sudden drop in temperature during a rather warm period will frequently reduce activity and prevent egg laying for a short period. A sudden rise in temperature may occur for a short time during a rather cold period and eggs will be deposited when the average temperature is relatively low.

### INCUBATION

Incubation records were somewhat difficult to obtain with any degree of accuracy because of the concealment of the eggs in the plant tissues. The only way records could be obtained was by exposing an uninfested plant to females for oviposition for a certain period of time. It was usually necessary to expose them for 24-hour periods and to estimate the incubation period upon this basis. They are figured, therefore, in whole days instead of fractional periods.

In 1926 the minimum incubation period was 7 days for the first three broods and 10 days for the fourth brood. The maximum time in the different broods ranged from 11 to 19 days. The averages for the four broods were 8.7, 8.4, 10.2, and 13.2 days, respectively, and for the entire season the average was 9.9 days for 1,964 observations.

In 1927 the minimum incubation period was 8 days in all four broods, while the maximum in each brood was 15 or 16, and the averages for the four broods were 10.7, 9.8, 11.0, and 10.3, respectively. These gave an average for the season of 10.4 days for 1,823 observations.

During the season of 1928 the minimum was 7 days for the first three broods and 8 days for the fourth brood, while the maximum ranged from 14 to 23 days. The averages for the four broods were 9.5, 8.6, 10.5, and 13.8 days, respectively. These gave an average of 9.8 days for the 1,469 observations of the season.

For the three seasons of 1926, 1927, and 1928 the average incubation period for 5,256 observations was 10.0 days.

#### RELATIONSHIP OF HUMIDITY AND TEMPERATURE TO LENGTH OF INCUBATION PERIOD

During the incubation period the humidity may be considered as a constant factor, as the egg is in the plant tissue and is in a condition of

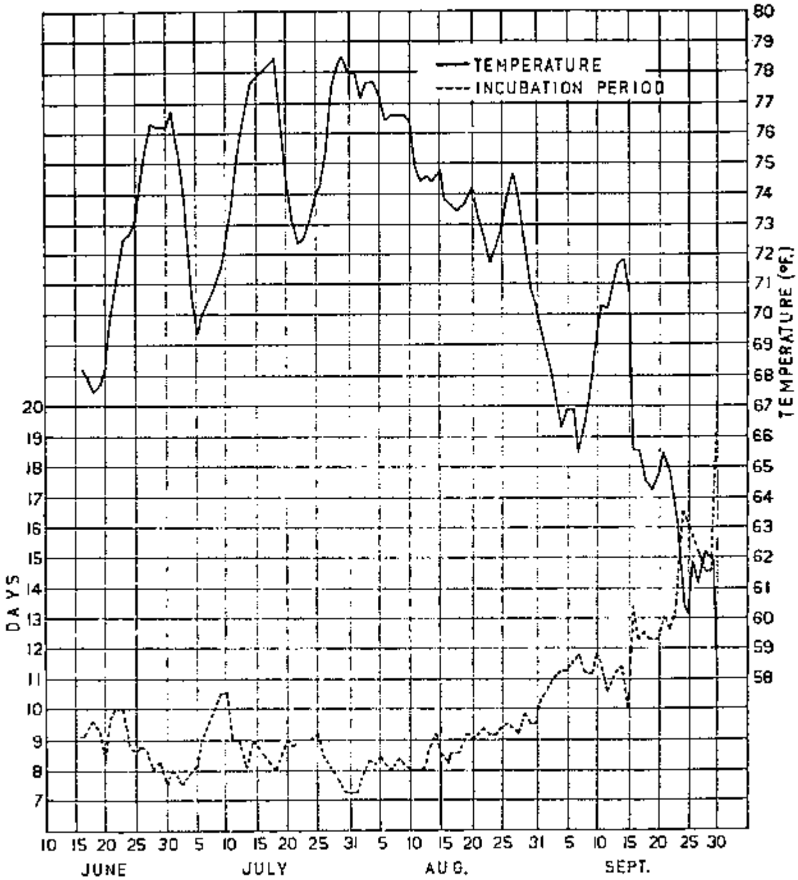


FIGURE 32.—Average incubation period of eggs of *Empoasca fabae* as correlated with temperature. Each point on the temperature curve corresponding to a given date is the average temperature for the average incubation period of all eggs deposited on that date. Columbus, Ohio, 1926.

saturation. If the egg is dissected out of this plant tissue it soon collapses and no eggs thus treated hatched. So while humidity is no doubt a primary factor, it can be considered a constant one, and atmospheric humidity need not be considered further, so long as it remains high.

Variations in temperature, however, show a decided effect upon the number of days necessary for the completion of the incubation period. The correlation between temperature and number of days spent in incubation during 1926, 1927, and 1928 is shown in figures

32, 33, and 34. In these diagrams each point in the incubation curve corresponding to a deposition date represents the average period of time required for incubation for all eggs deposited on that day. Similarly, each point on the temperature curve is the average temperature during the average incubation period after the date of deposition. For example, the average incubation period for eggs deposited on July 20, 1926 (fig. 32), was 9 days, and the temperature indicated on the temperature curve for July 20 is 74.5° F., which is the average

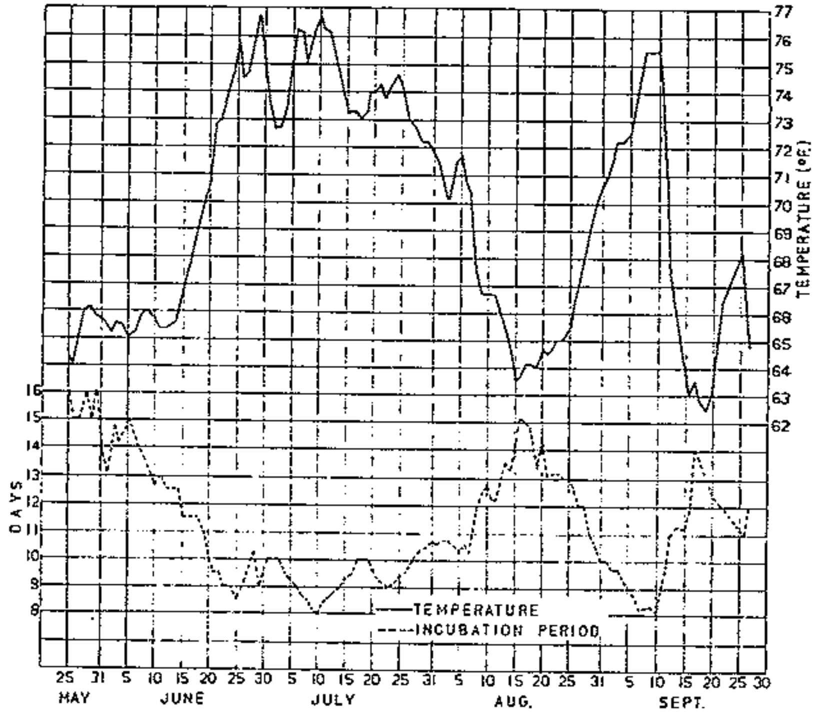


FIGURE 33.—Average incubation period of eggs of *Empoasca fabae* as correlated with temperature. Each point on the temperature curve corresponding to a given date is the average temperature for the average incubation period of all eggs deposited on that date. Columbus, Ohio, 1927.

of all temperatures recorded for the 9 days from July 20 to July 28, inclusive.

These diagrams show that the rapid incubation of the egg is to a marked degree dependent upon rather high temperature. In summer, with temperatures that are rather high and continuously so, the egg will hatch in from 7 to 10 days after deposition. During colder portions of May, June, August, September, or October, the incubation period may extend to 23 days. In one case, in October 1927, not shown on the diagram, the incubation period was 25 days.

In 1927 a rather cold period prevailed during the latter part of May and early in June, again from August 10 to 25 and in the early part of September. The longer number of days required for incubation at these periods is quite characteristic. In seasons like 1926 and 1928, when the fluctuations in temperature remain within a rather high range of degrees, this great variation in the incubation period is not so marked until in September.

The minimum temperature rather than the average temperature may be the most important factor, and development for a certain period may be either inhibited or retarded by cold, and the hatching delayed.

On August 12, 1928, the minimum temperature dropped to 56° F. and hatching was delayed. Again on September 18 a drop of temperature to a minimum of 50° prevented hatching on this date, and

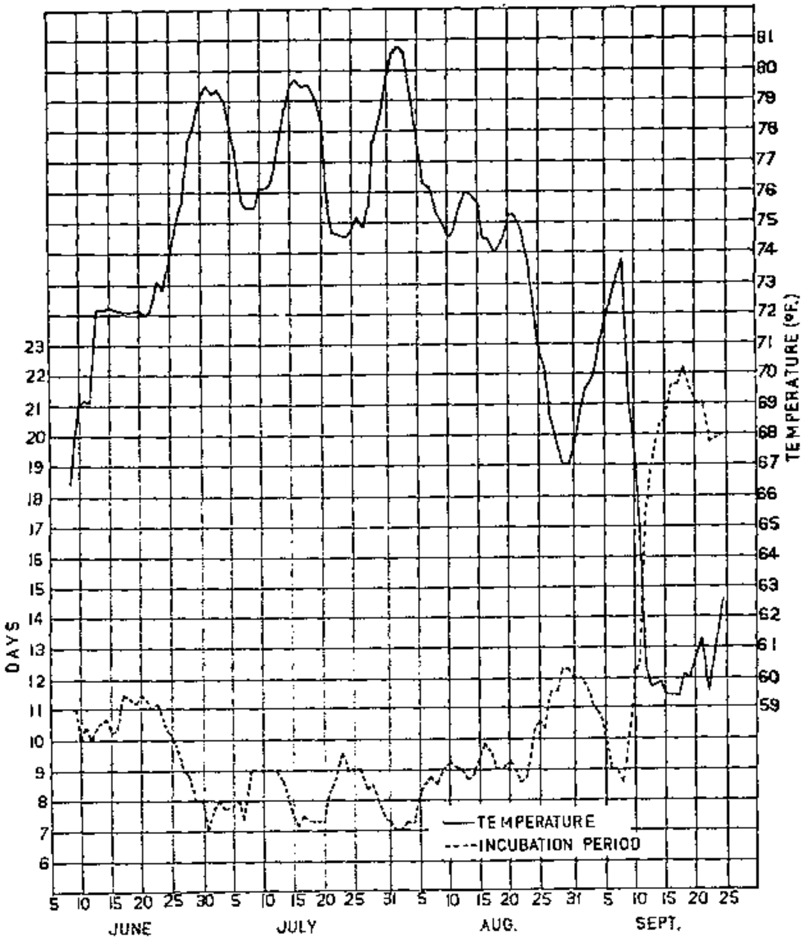


FIGURE 34.—Average incubation period of eggs of *Empoasca fabae* as correlated with temperature. Each point on the temperature curve corresponding to a given date is the average temperature for the average incubation period of all eggs deposited on that date. Columbus, Ohio, 1928.

from September 23 to 29 in a series of days with minimum temperatures ranging from 36° to 48° hatching was prevented for several days.

#### HATCHING

The entire process of hatching was observed many times during this study. Although the time required for the entire hatching process varied considerably at different times, the series of movements were quite uniform. In June, July, and the early part of August most of the nymphs emerged before 9 a. m. Late in August and in September most of the them did not emerge until nearly noon. The difference in temperature at this season, with cool nights and hot days, seemed to favor hatching later in the day.

On September 1, 1926, four individuals were observed hatching upon the main stem of a young bean plant below the first two original leaves. The four eggs were about a millimeter apart, and they hatched from top to bottom in sequence as though the eggs had been laid in that order. The process of hatching of each individual required about one-half hour, and they began the hatching process about 10 or 15 minutes apart.

The head of the nymph is pushed through the plant epidermis and remains in that position for about 20 minutes. The large red eyes are conspicuous and show quickly after the head first appears. After remaining in this position for some time without any apparent change except a slight enlargement of the head, the remainder of the hatching process is completed rather rapidly. The body is rapidly pushed out for a distance of about two-thirds of its length (fig. 35, *A*). Then by a backward-and-forward swaying motion the insect continues to

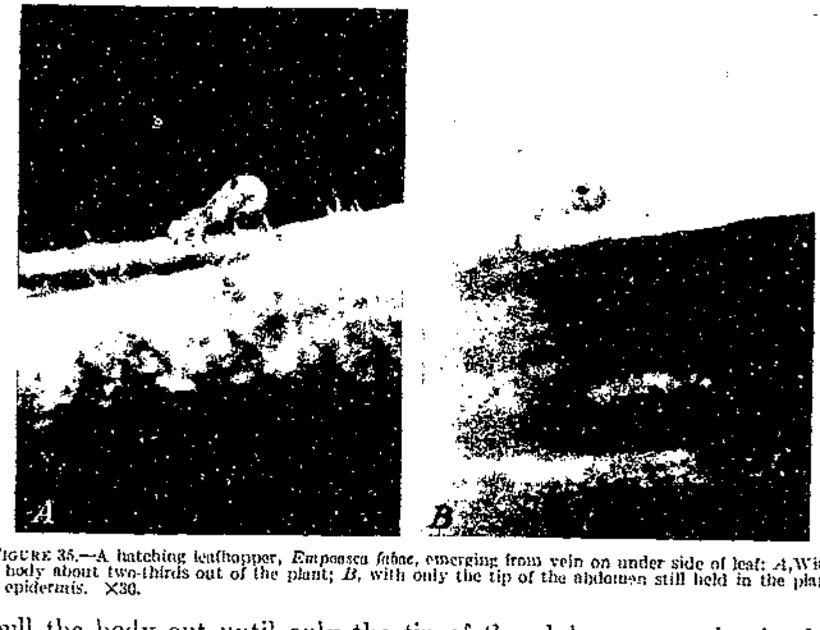


FIGURE 35.—A hatching leafhopper, *Empoasca fabae*, emerging from vein on under side of leaf: *A*, With body about two-thirds out of the plant; *B*, with only the tip of the abdomen still held in the plant epidermis. ×30.

pull the body out until only the tip of the abdomen remains in the plant tissue (fig. 35, *B*).

During the process of hatching as described, the insect emerging from the plant has remained dorsal side downward with the legs extended tightly along the ventral side of the body to the tip of the abdomen. Now by curving or arching the body dorsally or downward very strongly, the first pair of legs are freed and exercised, then the second pair, and finally the third pair are freed and vigorously exercised in like manner, but only after a considerable amount of swaying and bending of the body. As soon as the legs are free, the body is quickly bent forward, the legs hold firmly to the leaf vein, and by a prying motion the tip of the abdomen is pulled from the plant tissue. In a few seconds the nymph becomes active and wanders off to feed upon the under surface of a leaf, in some instances moving around quite a while before feeding, but as a rule attempting to feed almost immediately.

Many nymphs are unable to free the legs and in some cases are unable to free the abdomen and die without completing emergence.

### NYMPHAL DEVELOPMENT

The time required for nymphal development during these studies varied considerably with the temperature, and there was a variation for the different broods. In 1926 the minimum number of days from the hatching of the egg to the adult was 10, which was the minimum in the first three broods. The maximum was 15 in the first brood, 19 in the second, and 22 in the third. In the fourth brood only six individuals were reared to adults and each of these required 22 days. The average number of days for nymphal development was 12.4 days in the first brood, 12.5 in the second, 14.5 in the third, and 22 in the fourth. For all the individuals reared during the entire season the average was 12.9 days.

In 1927 the minimum varied considerably, being 10 days in the first brood, 12 in the second, 8 in the third, and 15 in the fourth. The maximum showed 20 days in the first brood, 24 in the second and third broods, and 25 in the fourth. The average numbers of days for the four broods, respectively, were 14.0, 14.2, 18.0, and 17.1. For the entire season this gave an average of 15.4 days.

In 1928 the minimum time for nymphal development ranged from 8 days in the first brood to 16 in the fourth. The maximum time required ranged from 15 days in the first brood to 26 in the fourth; while the averages for the four broods were 11.4, 11.9, 13.1, and 22.5 days, respectively. The average for the season was 12.3 days.

The average number of days for the nymphal development for the three seasons was 14.02.

A limited number of observations were made of the length of time spent in the different instars. During 1926 some data were obtained for all instars for the first three broods. These showed a considerable amount of variation for individuals, but the averages are probably rather close to the mean. These averages in days are 2.6, 2.3, 2.3, 2.5, and 4.7 for the five instars, respectively.

### RELATION OF TEMPERATURE TO NYMPHAL DEVELOPMENT

Previous discussion has indicated that precipitation and high humidity are more important than certain limits of temperature in explaining the distribution of *Empoasca fabae* and its ability to produce large populations. In areas, however, which possess these primary factors, temperature is undoubtedly an important secondary factor affecting the rate of development. Assuming, therefore, that humidity is above a certain minimum requirement, there is a definite correlation between temperature and rate of development. Figures 36, 37, and 38 show this correlation for the years 1926, 1927, and 1928, respectively. Each point on the curve of nymphal development is the average time required for all nymphs hatching on that date from any generation to complete their development to the adult stage. Each point on the temperature curve is the average of all daily mean temperatures to which the larvae hatching on a given date were subjected during their average nymphal developmental period. For instance, 12 days was the average developmental period for all nymphs hatching on July 5, 1927, and the corresponding point on the temperature curve is 75° F. This temperature was obtained by averaging all the daily mean temperatures for 12 consecutive days, beginning with July 5.

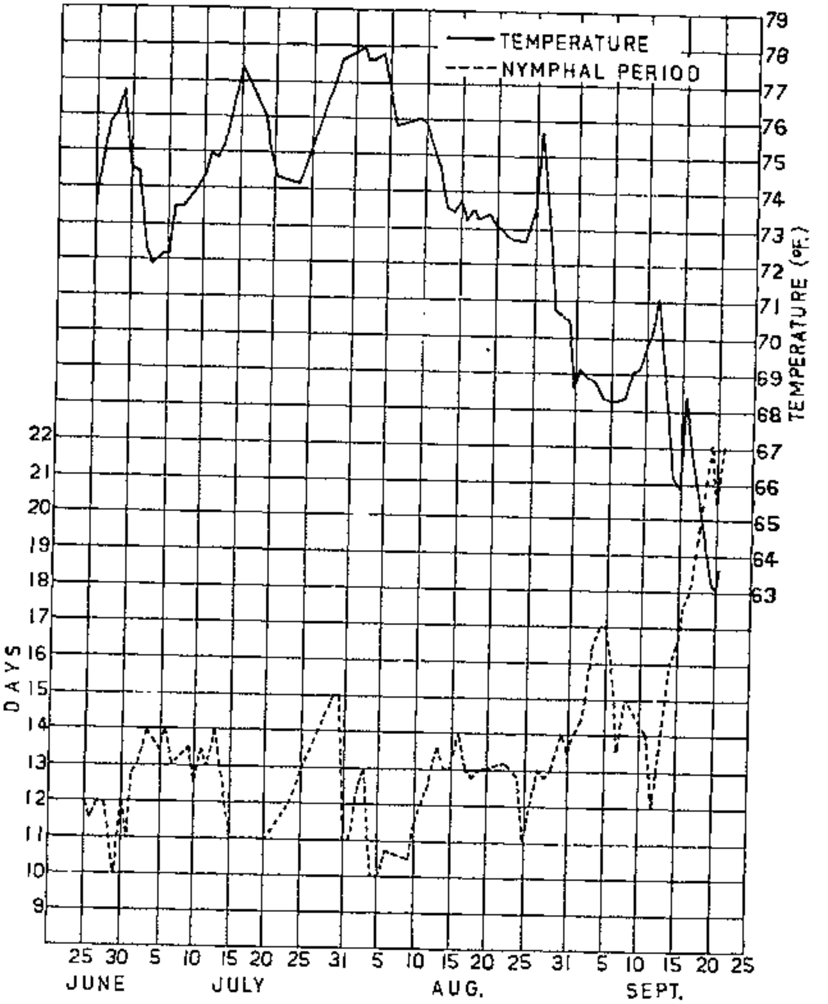


FIGURE 30.—Average developmental periods of nymphs of *Empoasca fabae* compared with the average temperatures for the respective developmental periods at Columbus, Ohio, season of 1926.

## NUMBER OF BROODS

These studies have revealed four distinct broods of *Empoasca fabae* during each season, with one complete generation, a second almost complete, a partial third, and a smaller partial fourth generation (fig. 39). The generations overlap greatly, and there is no definite break in infestation upon bean plants in the field at any particular time except when the beans begin to age and the leaf hoppers consequently seek younger plants.

In 1926 the first eggs were laid about June 1, and eggs of the fourth brood were still hatching on October 20. In 1927, under field conditions, the first eggs were laid about May 25, and on November 1 eggs were still hatching. Adults and second-, third-, and fourth-instar nymphs were still present on rhubarb in the field on December 1 after a minimum temperature of 25° F. had occurred. Most of the food plants of this insect had been killed at that time. In 1928 the

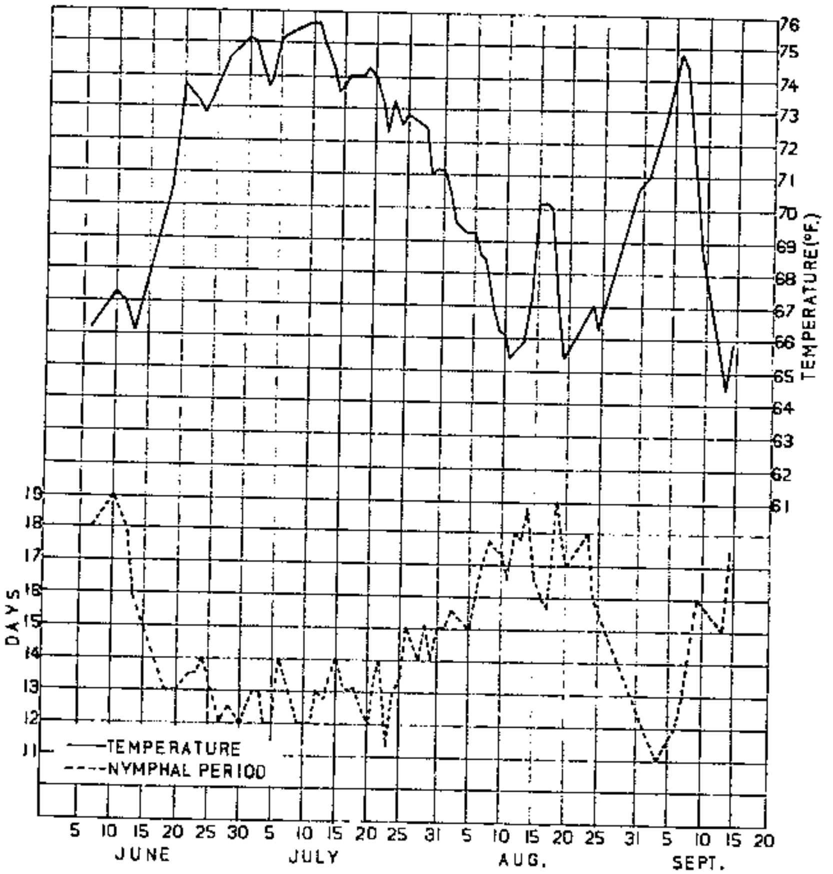


FIGURE 37.—Average developmental periods of nymphs of *Empoasca fabae* compared with the average temperatures for the respective developmental periods at Columbus, Ohio, season of 1927.

first eggs were laid in the field about June 6 to 8 and on October 13 eggs were still hatching in the field.

So long as temperature and other conditions remain favorable for development and activity, the adults of any given generation behave similarly to the adults of any other generation since they immediately mate and begin egg laying. When late adults of the first generation, adults of the second generation, and early adults of the third generation were mated on the same day, viable eggs were laid by each of these females at approximately the same time.

Fenton and Hartzell (*19, p. 394*), working with potato, state: During the three years that life history studies were conducted, attempts were made to rear a third generation, but in every instance the results were negative." In the light of the data obtained during

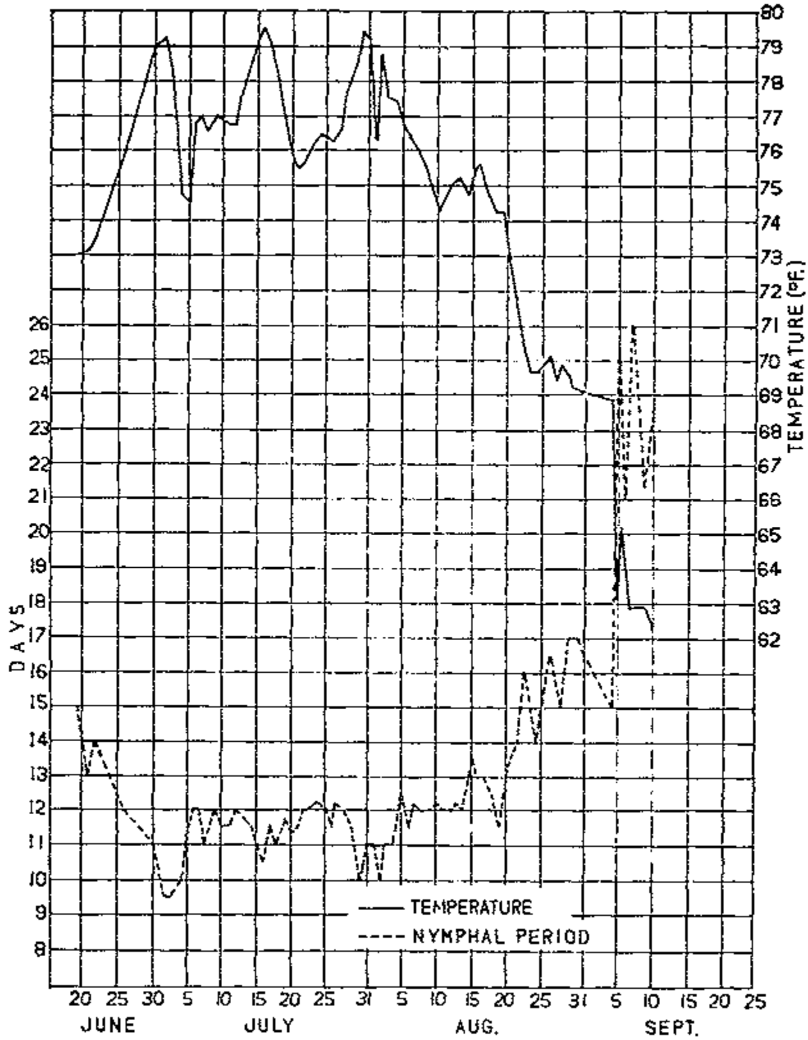


FIGURE 38.—Average developmental periods of nymphs of *Empoasca fabae* compared with the average temperatures for the respective developmental periods at Columbus, Ohio, season of 1928.

the present study and reported above concerning the behavior of the newly emerged adults, it is difficult to understand this negative result, unless the different host (potato) might explain this difference. Forbes and Hart (*21*) have already reported four broods in Illinois, Webster (*60*) reported four broods in Iowa, and Washburn (*52, 56*) reported three broods and probably four in Minnesota. It is doubtful that these workers confused this with *Empoasca maligna* Walsh

(*E. unicolor* Gillette), as Fenton and Hartzell suggest, because the latter species has only one generation a year. The writer believes, furthermore, that the present study is the first that has been reported in which the morphologic characters were ever used to identify the species both in the field and in the detailed biological studies.

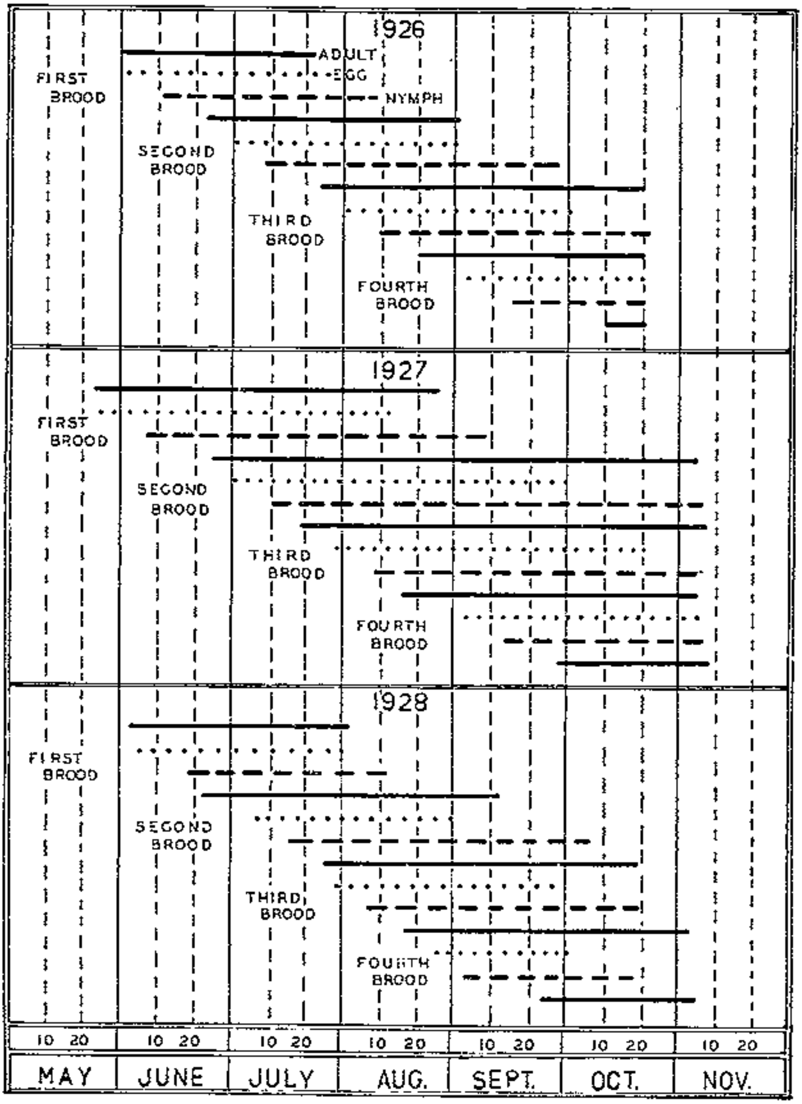


FIGURE 33.—Occurrence, duration, and number of broods of *Empoasca fabae* at Columbus, Ohio, during the seasons of 1926, 1927, and 1928.

### LONGEVITY

Longevity records for 71 females under observation in 1926 gave an average of 30.3 days, in 1927 an average of 34.1 days was obtained for 37 females, and in 1928 records for 18 females gave 33.6 days.

In view of the fact that a number of records of 8, 9, 10, and 12 days are included in the average for 1926, the average numbers of days recorded for 1927 and 1928 are probably nearer the normal. In each year some records are included where adults were known to have escaped or to have been killed, or where observations were discontinued because of insufficient time for detailed records.

The maximum records for longevity were obtained in 1927. On May 25 a female taken from the field was kept under observation until August 25, a period of 92 days. On June 29 a female emerged which was kept under observation until September 28, a period of 91 days. These two longevity periods are the longest recorded for this insect.

In 1926 the longevity record for 59 males averaged 33.5 days. In 1927 records for nine males gave an average of 33.3 days. Records kept for six males in 1928 gave an average of 33.6 days. No records have been obtained for males which will compare with the 91- and 92-day records for the females, but the average is shown to be as long.

### HABITS AND ACTIVITY

Both the adults and nymphs are very active and respond quickly to movements of the investigator, even when the plant is not disturbed. The normal place of feeding is underneath the leaf near the midrib or large veins and to a large extent upon the main stems or petioles of the leaves, especially when these are not exposed to bright light. This may be a response to one of several stimuli or a combination of these. It may be a positive geotropic response or a negative phototropic response, or may be a response to a condition of humidity, since the transpiration on the under side of the leaf is much greater than that on the upper surface and the humidity below is consequently higher. Measurements conducted during this study by G. W. Blaydes showed that on a normal bean leaf under field conditions the transpiration rate was much greater upon the under surface than upon the upper surface. If disturbed in any way, the hoppers usually walk sidewise and use this type of locomotion in going over the edge of the leaf from upper to lower surface or vice versa. This is especially true of the nymphs. The adults and frequently the larger nymphs jump or hop when disturbed and thus perform the characteristic type of locomotion for which they are named. If the leaf is turned upside down the nymphs usually orient themselves very quickly to this condition by running over the edge of the leaf to the upper surface, which is then underneath.

The adults in the field are continuously changing from plant to plant; and the nymphs change from one plant to another either by hopping or less frequently by migration, especially when plants mature or are destroyed by disease.

Both adults and nymphs feed from the leaves and stems of plants by puncturing the surface with their slender elongated needlelike mandibles. The maxillae, attached to each other, are then inserted, forming a sucking tube through which plant juices are taken into the pharynx, very much as in other Homoptera. The beak extends backward ventrally, between the fore legs. When feeding, the insect remains quiet, as a rule, with the beak inserted in the plant tissue for a considerable period of time. During this feeding process it pumps out an enormous quantity of plant sap and excretes a large quantity of liquid which is dropped upon the plant foliage or fruit. When a few of these hoppers are confined to a small area of leaf surface, they cause it to die in the course of 4 or 5 days. This demonstrates that the actual drain upon the plants caused by feeding is very severe.

## A COMPARATIVE STUDY OF EMPOASCA FABAE AND E. ABRUPTA UNDER OHIO CONDITIONS

During the summer of 1929, while the writer was still attempting to solve the problem concerning the number of economic species of *Empoasca* occurring in the United States and their relationship to *E. fabae*, permission was granted by the Bureau of Entomology to bring living specimens of *E. abrupta* (then known as *E. fabae*) into Ohio for attempted crossing with Ohio specimens. This study was carried on under the most careful conditions, and all specimens were killed at the termination of these experiments. The material of *E. abrupta* was obtained through the kindness of H. H. P. Severin, of the University of California, who collected the insects from potato. The material arrived from California on June 10, and eggs which had been deposited on sugar beet en route began hatching June 12. On June 27 several had matured to adults. A second brood was produced in July and the early part of August, and eggs for a third brood were hatching on September 1. The material remained on hand until October 10, when it was destroyed and the experiment terminated.

During the period from June 10 to October 10, unsuccessful attempts were made to mate newly matured males or females from California (*Empoasca abrupta*) with newly matured adults of the opposite sex from Ohio (*E. fabae*). From June 27 to September 15, 25 reared females from each lot of material were mated with males from the other lot. Not a single fertile egg resulted, although either species could be reared abundantly if the females were mated with their respective males under exactly the same conditions and in cages similar to those used for these attempted crossings.

In order to prevent error in these experiments, plants were grown in protected places to prevent egg deposition by leafhoppers before they were exposed to the females under study. In order to prevent fertilization soon after emergence, each individual nymph of either lot was isolated during the last instar and permitted to emerge as an adult in an individual container. Each was then examined to obtain the sex record, and mated with a newly emerged adult of the opposite sex from the other lot.

Certain coworkers had previously expressed the opinion that because of climatic factors hopperburn did not occur in California or the arid West. In view of the fact that an examination of the internal genital pieces had indicated a distinct species and unsuccessful attempts had been made to cross these two lots or species, experiments were performed to obtain comparable types of injury of the Ohio and California material under exactly the same conditions and in a region where hopperburn is abundantly produced.

The same number of fertile females of each species, ranging from 3 to 10 in different tests, were placed on each plant and permitted to feed and build populations without disturbance. The plants were selected from potatoes planted at the same time and of approximately the same size and condition. The leafhoppers were placed under

FIGURE 40.—*A*, Potato plant injured by a known population of *Empoasca fabae* under Ohio conditions; *B*, potato plant injured by a leafhopper population of the same number as caused the injury shown in *A*, but in this case the insect was *Empoasca abrupta*. The two plants were in similar condition and the tests were made at the same time and place in Ohio.

cages of 40-mesh copper screen wire (fig. 31) and were kept under conditions as nearly normal as possible. In from 12 to 15 days hopperburn appeared on the plants infested with populations of the Ohio form (*Empoasca fabae*) and it rapidly increased in severity (fig. 40, *A*.) No hopperburn was produced on any of the plants infested by the California species (*E. abrupta*), but an entirely different

FIGURE 41.—Bean leaf injured by *Empoasca abrupta* under Ohio conditions. Note the mottled appearance and absence of curling.

type of injury was produced, a stippling (fig. 40, *B*) which did not cause the leaf to curl or turn brown, but which resulted in the loss of chlorophyll and a speckled-white appearance. The injury appeared entirely different and was readily distinguished from hopperburn caused by *E. fabae*. The same difference was noted on bean plants (fig. 41).

These experiments show that *Empoasca fabae* and *E. abrupta* are not only morphologically different but biologically distinct, and have different feeding habits.

Following this attempted mating and the differentiation of economic injury by the writer, Smith and Poos performed similar experiments in 1931 and made microscopic examination of feeding punctures of these and other closely related species. In a recent report of this work (*48*) they have shown that *Empoasca abrupta, E. bifurcata, E. filamenta, E. maligna,* and *E. erigeron* feed by puncturing the lower epidermis of the leaf and then feeding upon the mesophyll tissue in all directions from this point. This is responsible for the production of the whitish spots (stippling) on the upper surface. In the case of injury by *E. fabae* the phloem cells are punctured, torn, and distorted, and in portions of the midribs and stems of potato, alfalfa, etc., plugging is evident in the xylem tubes. This difference in feeding undoubtedly accounts for the different type of injury.

## SUMMARY

It has been found that the potato leafhopper (*Empoasca fabae* Harris) has previously been confused with several other species, both economic and noneconomic, occurring in different areas of the United States.

*Empoasca fabae* feeds upon a variety of cultivated host plants and may cause several types of injury, such as hopperburn on potato, eggplant, dahlia, and rhubarb; stunting, dwarfing, and rosette formation on beans; and pigmentation on alfalfa and clover. These injuries are caused by its method of feeding. Severe losses are suffered by its feeding on these crops.

*Empoasca fabae* is primarily a low-altitude, humid-climate species, although it occurs in small numbers in low-altitude areas of the Pacific coast where rainfall is scarce. In order for it to build economic populations it is apparently necessary that there should be several inches of rainfall during the growing season.

Definite proof has not been obtained to show that *Empoasca fabae* passes the winter in the Northern States. The evidence points to a migration in the spring of the year from some more southern breeding ground. This has been assumed after failure to find it in hibernating quarters with other closely related forms, failure to carry it over when it has been placed in hibernation, and failure to find a wild host upon which it might breed. The late appearance in the field in the spring would indicate that, if it overwinters in the North, it must have been active upon some plant. Finally, the sudden appearance of large numbers of adults upon economic crops indicates migration from some other source.

*Empoasca fabae* always appears in the field late in the spring (about the middle of June in Ohio). Climatic factors and their effect upon the growth of different types of plants were apparently determining factors in regard to host preference and spring activity in the field.

When mating occurs normally the preoviposition period is from 3 to 5 days in duration.

The oviposition record can be estimated only on the basis of eggs that hatch. During the 3 years in which detailed records were obtained the average number of eggs produced per day per female, for

all females of all generations, was 2.8 in 1926, 2.3 in 1927, and 3.0 in 1928. Variations in temperature caused fluctuations in egg laying.

The average incubation period during the season of 1926 was 9.9 days, in 1927 it was 10.4 days, and in 1928 it was 9.8 days. The period of incubation, within normal growth temperatures, varies with the temperature.

Nymphal development also varies with temperature. The average time for development during 1926 was 12.9 days, in 1927 it was 15.4 days, and in 1928 it was 12.3 days.

During the 3 years of study four distinct broods were produced upon bean each season. The first was complete, the second practically complete, and the third and fourth were partial generations only.

Records showed longevity averages of 30 to 34 days for all females during the three seasons. The longest record obtained was that of a female that lived 92 days after capture in the field.

An attempt was made to mate *Empoasca fabae* and the California species *E. abrupta*. All records were negative, and no progeny were produced. In addition, different types of economic injury were consistently produced by each species.

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