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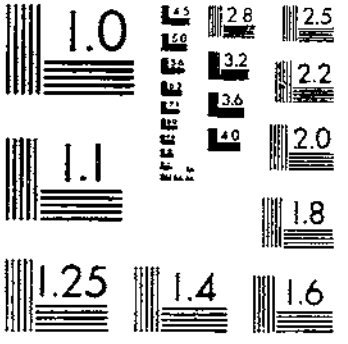
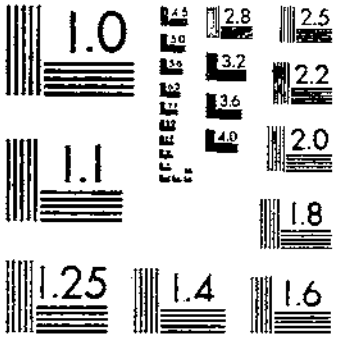


MICROCOPY RESOLUTION TEST CHART
NATIONAL BUREAU OF STANDARDS-1963-A



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LIFE HISTORY, HOST PLANTS, AND MIGRATIONS OF THE BEET LEAFHOPPER in the Western United States

By *William C. Cook*

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Acknowledgments

This bulletin includes the studies of many entomologists—Federal, State, and privately employed men—over a period of about 35 years.

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State entomologists: California—H. M. Armitage, H. J. Greene, and H. H. P. Severin; Idaho—R. W. Haegele; Oregon—Joe Capizzi; Utah—E. D. Ball and G. F. Knowlton; and Washington—E. C. Klostermeyer and H. S. Telford.

E. A. Schwing, entomologist for the Spreckels Sugar Company in California for many years, made suggestions for the central California work.

When one of these contributors is mentioned in this bulletin without any citation to a publication, reference is made to letters, unpublished manuscripts, or reports. Full credit for the particular work cited goes to such a worker.

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LIFE HISTORY, HOST PLANTS, AND MIGRATIONS OF THE BEET LEAFHOPPER IN THE WESTERN UNITED STATES

By WILLIAM C. COOK,[1] *Entomology Research Division, Agricultural Research Service*

Shortly before 1900, growers of sugarbeets in the Western States were alarmed by a new and serious disease that killed small beet plants outright and severely damaged larger ones. Because of the effects on the plants the disease has been named curly top. It has appeared in some seasons and not in others and has varied in its severity in different areas.

The erratic occurrence of curly top was mysterious until Ball (*3*)[2] pointed out that the condition was related to feeding by the beet leafhopper.[3] Ball (*4*) demonstrated later that the leafhopper was coming into cultivated fields from desert areas where it had overwintered, and he discussed several such areas in the West. He also realized that the breeding areas would have to be studied and the nature of the flights determined.

Later a disease of tomatoes, garden beets, snap beans, and other crops and ornamental plants was found to be caused by the curly top virus and carried by the beet leafhopper.

Since there was no direct control for the disease at that time, the first objective was to study the life history of this leafhopper and to discover and delimit its desert breeding areas, primarily for predicting the probable number of leafhoppers to be expected in certain cultivated areas. This prediction would govern the acreage of beets to be planted and the time of planting (Carter *6*).

As the studies progressed, it became obvious that the hosts of the leafhopper were largely range weeds, and plant ecological studies were made to determine the conditions under which the weed hosts might be replaced by nonhost plants (Douglass and Hallock *22*, Fox *26*, Lawson and Piemeisel *44*, Piemeisel *45*, Piemeisel and Chamberlin *46*, Piemeisel and Lawson *47*). At the same time, studies in California and Idaho indicated the possibility of actually controlling the leafhoppers in their breeding grounds by spraying their host plants (Armitage *2*, Cook *7*, *10*, Douglass et al. *25*). In 1958, the Bureau of Land Management, U.S. Department of the Interior, started seeding large breeding areas of the beet leafhopper in southern Idaho with perennial grasses to reduce the stands of leafhopper host plants.

All these methods of attack, particularly those to control or to predict leafhopper populations, must include studies on the ecology of the leafhopper in its desert habitat. As Ball (*4*) pointed out, the breeding grounds had to be found

[1] Retired 1962.

[2] Italic numbers in parentheses refer to Literature Cited, p. 119.

[3] *Circulifer tenellus* (Baker). This insect is also known in several areas as the white fly. As no other leafhopper is mentioned in this bulletin, the beet leafhopper will usually be referred to as the leafhopper.

and mapped, methods of quickly measuring plant density and leafhopper populations developed, and the leafhopper movements followed so as to relate specific breeding areas with specific areas of cultivated crops.

General résumés of the seasonal history, host plants, breeding areas, migrations, and control measures have been published (Cook *9*, Douglass and Cook *18*, *19*). More detailed studies of the Columbia Basin area (Hills *38*) and of the New Mexico-Texas area (Romney *48*) are also available. However, conditions have changed considerably in those areas since the original studies were made and some amendments seem necessary. Many papers also have been published regarding particular phases of the problem in the Snake River Plain of Idaho and Oregon, but no general statement of the situation there is available.

It is the purpose of this bulletin to bring together the unpublished basic data, combine them with reviews or abstracts of published papers, and present in detail the life history, host plants, breeding areas, and migrations of the beet leafhopper. This insect is second only to the migratory grasshoppers in its annual movements, and the economic problem of the leafhopper and curly top damage is still present after about 60 years of intensive studies.

SOME DEFINITIONS

Because of the complicated annual cycle of the leafhopper, certain terms have been defined to designate various types of host plants, breeding areas, and movements of the insect.

Host Plants.—Those plants on which the leafhoppers can live from egg to maturity are called *breeding hosts*. These may be again subdivided according to their period of succulence into *spring hosts* and *summer hosts*. Plants that sustain the leafhoppers when no breeding hosts are present but will not permit extensive breeding are called *holdover hosts*. At times of general movements, leafhoppers may be found on many other plants, but these are not considered host plants.

Breeding Areas.—Leafhopper host plants usually occur in patches or continuously over large areas, which are termed *breeding areas* or *breeding grounds*. If only spring broods of the leafhopper are produced in a breeding area, it is called a *spring breeding area*, if only the summer broods are found, it is a *summer breeding area*, and if both are usually found there and leafhoppers are present most or all the time, it is a *permanent breeding area*.

Leafhopper Flights.—The flight of leafhoppers from spring to summer hosts is termed the *spring movement*, whereas the reverse flight is the *fall movement*.

METHODS OF ESTIMATING LEAFHOPPER POPULATIONS

Sweep-Net Counts

In the earlier studies a standard sweep net with an opening about 15 inches in diameter and a depth of 18 to 24 inches, on a handle about 32 inches long, was used to estimate leafhopper abundance. A single sweep was the swing of the net through about a 90-degree arc while the rim was in contact with host plants. From 1 to 100 sweeps

constituted a single sample, depending on the density of the leafhopper population. It was soon apparent that the numbers of leafhoppers captured varied with meteorological and physical factors.

Romney (*49*) published a detailed study in which he compared samples taken with the sweep net with samples taken in the same area with a cylinder method, which probably captured most or all leafhoppers present. These data were all taken on a stand of perennial pepperweed in New Mexico during midsummer. He found that the number captured was affected chiefly by temperature and wind velocity. A change in the ambient temperature from 80° to 105° F. increased the number captured in the net by 200 percent, whereas an increase in wind velocity of about 4 miles in wind ranging from 1 to 8 miles per hour caused a drop of about 50 percent in the total catch.

Sweep-net captures also vary with the growth habit of the plants being sampled. A plant with pliable stems will bend when hit with the net, tending to thresh out the insects, whereas a plant with stiff stems resists such action. In many cases the net rim cannot penetrate into the interior of stiff plants, where many leafhoppers are found in hot weather.

In spite of its known disadvantages, the sweep net is still valuable for obtaining rapid estimates of leafhopper populations and is used extensively. Romney's cylinder method, although very accurate, proved too time consuming for general field work.

Hand-and-Knee Counts

In early leafhopper studies the population in beetfields was estimated by workers crawling along on their hands and knees, disturbing the beet plants ahead of them, and counting the dislodged leafhoppers. When using other methods of estimation, it was found that only a small part of the leafhoppers was counted on hands and knees, and the method was abandoned.

Cylinder Counts

Hills (*37*) described a cylindrical cage 1 square foot in area and about 18 inches high, open at both ends. The cage frame of light metal was sharpened on the lower side and covered with muslin. A pitchfork handle was fastened to the side of the cage. The cage was set down over the host plants with the lower rim in the topsoil, and the vegetation was disturbed with the hand so that any leafhoppers present flew up on the cloth side where they could be counted. Dorst (*15*) used a loop handle instead of the more awkward pitchfork handle. A transparent plastic lid was added for use in hot weather, when the leafhoppers were very active. Later Hills (*39*) described a blowtorch heater for activating the leafhoppers in cold weather. The modified Hills sampler has become standard in later work on the leafhopper.

Methods Based on Spraying

E. A. Schwing, when entomologist for the Spreckels Sugar Company, showed that it was possible to activate sluggish leafhoppers with a pyrethrum fly spray and to count them as they jumped. In the method finally developed for use on adults during the winter in California and Arizona, the sampler walked slowly along in a bent-over position, spraying just ahead of his feet, watching a strip of vegetation immediately in front

of him, and counting the leafhoppers as they jumped. The length of the strip was paced off after the examination, and, assuming the strip to be 1 foot wide, the results were recorded in leafhoppers per square foot. This was useful only for adults, as the nymphs were too small to be easily seen.

For nymphs on low-growing annuals, a sampling pan (Lawson et al. *43*) was devised. This was essentially a dark metal pan having 8- to 10-inch sides with a hole of definite area cut out of the bottom. When the pan was set down over vegetation, the operator disturbed the plants, causing the nymphs to jump into the pan, where they could be counted. Areas of 1/8-, 1/4-, and 1/2 square foot were used under varying conditions.

None of these methods were very useful on vegetation taller than about 1 foot. For tall vegetation, Lawson et al. (*43*) developed two devices, a sampling fork and a sampling spear. They were sprayed with pyrethrum-oil to form a trap for leafhoppers and inserted under the tall vegetation, which was then thoroughly sprayed with pyrethrum-oil to dislodge the leafhoppers. Those falling into a marked area of 1/4, 1/2, or 1 square foot on the spear or fork were counted. The spear was used under large plants with a central stem and the fork was used in denser, closer growing plants, where it could be more easily inserted and retrieved than the spear.

Hatching of Eggs From Host Plants

Between 1932 and 1943, different methods of estimating the number of eggs laid in host plants were tried. In one series of tests G. T. York collected host plants in the field, cleared and stained them, and counted the eggs that had been laid in the tissue. This method was reasonably accurate, but very time consuming and could not be adapted for general field studies. York and H. E. Wallace made another series of tests, in which the host plants were taken to the laboratory and the roots kept in moist cotton while the leafhopper nymphs hatched. This method also had serious drawbacks and was finally abandoned.

In 1941, die-cut samples of vegetation from breeding areas were potted and taken to the greenhouse, where they were caged and held until any eggs present had hatched. Counts of the nymphs hatched gave the potential reproduction, and field samples taken at the same time gave the nymphs actually present. This method was used through the spring of 1943 and gave valuable information on nymphal mortality.

DETECTING AND TRACING LEAFHOPPER MOVEMENTS

The beet leafhopper is so small that it is not easily seen when flying, and few actual flights have been seen and recorded. Ball (*4*) recorded an evening flight into the cultivated areas of the Sevier Valley, Utah. E. W. Davis witnessed the end of a flight into the same area on May 3, 1927. The flying insects were captured in a net and identified. No beet leafhoppers were present in the valley before the flight, but 41 leafhoppers per 50-sweep sample were found afterward. On October 18, 1935, Davis and H. E. Dorst witnessed

a flight into the St. George, Utah, area. Here again the insects were seen dropping from the air and were captured in a sweep net. These last two flights occurred between 5 and 6 p.m.

Severin (*51*) made several observations of California flights. Lawson et al. (*42*) watched individual leafhoppers and described their mode of flight.

All these accounts agree that in true flight the beet leafhopper flies with whatever wind is present, taking an erratic but definite course.

Because of the difficulty of following leafhopper flights visually, several indirect methods of tracing movements were used.

Sampling Stations

Most of the work of following migrations was done by repeated sampling at specific stations. Such stations were chosen before the flights occurred, when few or no leafhoppers were present, and were sampled at frequent intervals. The variations in leafhopper populations were assumed to measure the time and intensity of the movements. Variations between stations along a supposed line of movement were used to measure the direction and intensity of flight along the particular line.

Data of this kind are subject to more than one interpretation, and a large amount of such data is necessary before definite conclusions can be drawn. However, in spite of these drawbacks, sampling stations furnished most of the data used in tracing migrations.

Dorst and Davis (*16*), using artificial sampling stations, planted small plots of spring host plants in country along the supposed line of flight of leafhoppers where few or no wild hosts were available. These plots, planted in the fall and maintained by irrigation, were swept daily by cooperators during the spring movements, and all insects found were forwarded to a central point for determination. By using these plots, leafhoppers were traced across the Escalante Desert in southern Utah into the Sevier Valley and northern Utah.

Traps

Various types of traps have been tried and used rather extensively at times for tracing leafhopper movements. Fulton and Chamberlin (*28*) operated air-maze traps in southern Idaho to capture migrating leafhoppers. Their use to indicate leafhopper movements is described by Annand et al. (*1*). In general, this trap captured too few leafhoppers to justify its extensive use.

Lawson et al. (*42*) developed two types of net traps and described the results obtained with them. In the earlier version a cone of screening, about 18 inches in diameter at the forward, or open, end and tapering to 3 inches at the rear, was mounted on the front fender of an automobile. A cheesecloth bag was tied on the small end of the funnel to receive the intercepted insects. This trap collected only leafhoppers in motion and probably only those in actual migratory flight, as it took leafhoppers flying above the road as the car passed. It was only operative when the car was traveling at fairly high speed. For a stationary trap, to sample one location, the same workers mounted two nets at opposite ends of a 12-foot steel arm, which was then rotated at about 3 r.p.m. As in

the car traps, cheesecloth bags received the flying insects. Both types of traps were very useful.

Marked Leafhoppers

Dyed leafhoppers have been used to a limited extent. The principal difficulty was in coloring sufficient insects to make up a detectable part of the total population. About 250,000 leafhoppers were dyed and released in the mouth of a canyon in central California during the fall movements of 1941. During the next 2 weeks about 45 dyed leafhoppers were recaptured, some of which had gone 3½ miles and one male 11 miles up the canyon from the point of liberation. This test, unsatisfactory from the standpoint of returns, did indicate that leafhoppers drifted up the canyons for some time during the fall.

In the spring of 1954, according to H. J. Green, several thousand beet leafhoppers were marked with radioactive phosphorus by H. L. Wilson, of the California Department of Agriculture, in cooperation with R. C. Dixon and R. A. Flock, of the University of California. No recoveries were made from these liberations.

Leafhoppers were also dyed experimentally in southern Idaho in about 1958, but no results are available.

Color Forms of the Leafhopper

Severin (*50, pl. 2*) illustrated color forms of the adult leafhoppers, ranging from nearly lemon yellow in the summer to a greenish gray with dark markings on the elytra during the cooler months. Harries and Douglass (*34*) found that these color forms were related to the temperatures under which the late instars of the nymphs were reared. At 105° F. the color was pale yellow, at 100° greenish yellow, from 95° to 90° greenish or pale green, and below 85° darker areas appeared on the wings, which became larger as the temperature decreased. In general, the overwintering females are the darkest, the spring broods are intermediate with smaller dark areas and more greenish, and the summer forms are usually very pale green or all yellow. These color forms are useful in field work, as the appearance of a new color form in considerable numbers indicates either the development of a new brood of adults or a movement from some other area.

Sex Ratio of Migrants

Severin (*50*) first published data showing that the female leafhoppers migrated from the breeding areas in the spring in greater numbers than the males, leaving in the foothills an excess of males that amounted to nearly 90 percent of the total population by the end of the spring migratory period. He also showed a high proportion of female leafhoppers on sugarbeets and various weed hosts in the cultivated areas, amounting to about 92 percent of the population, just after the spring movements. No attempt was made to correlate the proportion of males with the distance flown. The method has been rather widely used by many workers for following suspected migration routes, but very few, if any, of the results have been published.

Fat Content of Migrants

Fulton (*27*) described a method of determining the chloroform extractives content of small samples of leafhoppers. Fulton and Romney (*29*) used the method for indicating three possible routes of

migration in the spring. These studies were supported by sample counts, showing that decreasing leafhopper numbers were parallel to decreasing chloroform extractives, but no sex ratios were given. Cook (*8*) described a simplified method by which many more lots of leafhoppers could be tested. This method was used once to try to trace movements from the San Joaquin Valley into the Sacramento Valley of California, with fair results. The fat content helped to substantiate the conclusions drawn from the sampling methods.

ESTIMATION OF HOST-PLANT STANDS

Methods had to be developed to estimate the area occupied by host plants and the density of the host-plant cover in order to calculate the total leafhopper population of a particular area.

Host-plant areas were estimated chiefly in two ways. Where areas were large and the general area occupied was known in advance, transects were run at as regular intervals as possible and the host-plant areas recorded as miles passed on each transect. In this method it was assumed that the measured miles of roadside hosts bear the same relationship to the total miles traveled that the actual area of hosts does to the total area involved. Actual areal surveys of critical areas have indicated the validity of the assumption.

In some cases where the host-plant area was readily accessible, closed transects were run around the area, and the included area was measured on a map with a planimeter.

Both of these methods are rather crude, but they indicate the relative areas occupied by different plant species in a particular year or by the same plants in different years.

Plant density usually was estimated by a pacing method. A point is marked on the toe of one boot and a record is made each time that point touches a host plant of the species being studied. The number of contacts made in taking 100 paces gives the percent density. After considerable practice with this method, a careful operator can usually estimate the plant density visually without making the counts. The accuracy is not high but sufficient for this type of field work.

LIFE HISTORY

The female leafhoppers are fertilized in the fall, and the males die during the winter. No true hibernation occurs, and the insect is active whenever the weather is warm. In the spring the eggs are laid in various annual host plants, not necessarily the same species as those on which the adults pass the winter. After five or six immature stages, a brood of spring adults appears. One or two broods develop on the wild desert vegetation, and those adults then leave these areas to seek summer host plants. Two or more further broods develop during the summer. The final fall brood, produced as the summer hosts are maturing, again flies in search of host plants. If rainfall has been sufficient, the leafhoppers settle down to pass the winter on newly germinated annuals, but if the

fall is dry, they may have to subsist on various perennial or fall annual herbs or shrubs until the winter annuals germinate.

Number of Broods

Ball (*4*) regarded the beet leafhopper as a single-brooded insect, the long-lived adults of which aestivated in the summer and then hibernated through the following winter before laying their eggs. Stahl (*54*) postulated two broods in southern Idaho and probably more in the coastal areas of California. Knowlton (*41*) thought at least two broods occurred annually in Utah. Haegele (*30*) stated that there were two complete broods and a partial third in southern Idaho in 1926. Harries and Douglass (*34*), after a detailed laboratory and field study of the leafhopper, concluded that it normally had three broods per year in southern Idaho. Work at the Modesto, Calif., laboratory of the U.S. Department of Agriculture during 1933–36 indicated that one or two broods were produced in the spring breeding areas, with at least three further broods on summer hosts. Hills (*38*) found three broods annually in the central Columbia River area of Washington and Oregon. Studies by H. E. Dorst and E. W. Davis indicated three broods in northern Utah and five broods in the northeastern Arizona-Nevada desert. V. E. Romney, O. A. Hills, W. A. Shands, and M. F. Bowen found five broods in the Arizona desert in favorable years and three in unfavorable years.

To summarize this information, the leafhopper apparently has three broods annually in the northern part of its range, four to five broods in central California and the southern desert, and possibly an additional brood near and south of the Mexican border.

Breeding Host Plants

The desert habitat of the beet leafhopper has a severe climate. The host plants on which the leafhopper breeds are almost entirely annuals that will germinate whenever sufficient heat and moisture are available, grow rapidly for a short time, mature, and die. The leafhopper must find these plants in order to oviposit in them, and then the nymphs must be able to reach the adult stage before the plant dries up. The leafhopper is well equipped to cope with these conditions. The nymphs can develop on many different plants, so that the drying of the original plant may only cause them to move to another more succulent plant of the same or a different species in order to find food and mature. Since the nymph cannot fly, the distance it can move between plants is rather limited, and many nymphs die when their food plants dry up.

By the time the winged form appears, the plant is usually mature, but, in some cases, a second brood may develop in the same plants, from eggs laid by the first-brood adults. The urge to migrate is so strong, however, that the leafhoppers will at least move to another plant of the same species, or, if need be, to another species, sometimes miles away. This means that a population of leafhoppers being studied may be in one place one week and somewhere else the next week, or it may have changed host plants without moving any great distance.

Because of the short period of succulence of most of its breeding host plants, the leafhopper leads a precarious existence most of the

time. Since summer hosts are rather long lived, the leafhopper will usually remain on one host species from spring (April to June in different places) until fall (September to November). During this period the principal hazard is that of premature drying of its host. Conditions are more severe in the southern desert than in most other breeding areas. A period of heat and drought forces the leafhoppers to leave in late spring and seek host plants in cooler, moister areas. Summer rains, usually starting in July, germinate summer annuals, and the leafhoppers can then repopulate the desert.

From the time the summer hosts mature in the fall until the leafhopper is again on them the following spring, many hazards are present. If fall rains have not germinated the overwintering annuals, the leafhopper must pass some time on holdover hosts, on most of which a high mortality occurs. After the winter annuals germinate, a dry period may follow and the plants dry up before maturity, forcing the leafhoppers back on to holdover hosts. If the annuals maintain themselves, the leafhoppers may suffer heavy mortality during the winter from unfavorable weather conditions. After the eggs have been laid and have hatched, the nymphs may be forced to other plants to mature. Sometimes drought in the early spring, combined by drying winds, has completely dried the annuals over large areas before the leafhopper nymphs could mature and caused complete mortality. These hazards, and other particularly local ones, have been studied extensively.

Holdover Hosts

The need for holdover hosts varies greatly in the different areas where the beet leafhopper breeds. In Washington, Oregon, Idaho, and northern Utah the period of feeding on fall perennials is very short. In some years rain sufficient to germinate winter annuals has fallen before the summer hosts mature, so that no holdover hosts are needed, but when the fall is dry, a month or more may be spent on them.

Fox (*26*) discussed the southern Idaho situation, which is typical of the northern area, for the period 1928–32. In 1928 and 1930, general germination of host plants was noted on November 10 and October 8, respectively. In 1929, scanty early germinated host plants dried up and the leafhoppers were kept on holdover hosts for some time. In the other 2 years, the leafhoppers were mainly held on holdover hosts until freezing weather. No comparable study of the northern Utah area is available, but conditions are similar to those in southern Idaho, and holdover hosts assume a similar importance. In the central Columbia River area the fall rains are more reliable than in Idaho, and holdover hosts are rarely needed. In central California the leafhoppers usually spend from 2 to 5 weeks on holdover hosts in various parts of the breeding area.

Several studies have been made of the effects of this feeding on holdover hosts on the vitality and mortality of the leafhoppers.

Winter Mortality

After the fertilized female has safely transferred from holdover hosts to winter annuals, there is a period of 1 to 3 months before the weather warms and eggs can be laid. During this time the female is subject to mortality

from many causes. In the northern part of the range low temperatures may inactivate her for days or weeks. Harries and Douglass (*34*) showed that death from low temperature is due to inability to feed and may be largely due to lack of moisture as well. In central California, temperatures are seldom lethal, but foggy weather and high humidity between foggy periods, as shown by Harries and Douglass (*34*), may destroy many leafhoppers. In the southern desert the principal cause of mortality is the drying of host plants.

HOST PLANTS

Because of severe environmental fluctuations, the leafhopper has become adapted to a wide range of host plants. Knowlton (*41*) listed 108 species of plants from which the leafhopper was captured in northern Utah. Of these, 36 were breeding hosts, 17 were holdover hosts, and the remainder were plants on which the leafhopper was found only during migrations. Severin (*51*) listed 39 species taken from the field from which he had bred leafhopper nymphs. The nymphs were unable to mature on many of these plants. Douglass and Hallock (*21*) made field and plot studies of 43 host plants in southern Idaho.

To shorten the lengthy lists by elimination, the author listed from the literature, from unpublished reports, and from field notes 99 possible leafhopper host plants, belonging to many families. This list was then submitted to all active workers on the beet leafhopper, and the plants were roughly graded as to their importance as host plants in particular areas. Many of these proved of rather limited importance and were dropped. The remainder have been combined into a tripartite list of winter and spring, summer, and holdover hosts that are of considerable importance in the Western States.

Over 25 species of winter and spring hosts are listed and only about 10 summer hosts. The list of fall holdover hosts is short, chiefly by elimination. The leafhoppers will stay on any perennial or annual that is succulent at the time they are forced from their summer hosts. As there are many such plants, most of those of only local importance are not listed here but may be considered in the discussion of individual breeding areas.

Winter and Spring Hosts

Common name	*Scientific name*
Family CHENOPODIACEAE	
Patata	*Monolepis nuttalliana* (Schult.) Greene
Russian-thistle	*Salsola kali* var. *tenuifolia* Tausch.
Smotherweed	*Bassia hyssopifolia* (Pall.) Kuntze
Family CRUCIFERAE	
Blistercress	*Erysimum repandum* L.
Pepperweeds	*Lepidium densiflorum* Schrad., *lasiocarpum* Nutt., *latipes* Hook., *nitidum* Nutt., *thurberi* Wooten
Perfoliate pepperweed	*Lepidium perfoliatum* L.

Common name	*Scientific name*
Family CRUCIFERAE—Continued	
Perennial pepperweed	*Lepidium alyssoides* A. Gray
Green tansymustard	*Descurainia pinnata* var. *filipes* (A. Gray) Peck.
Flixweed	*Descurainia sophia* (Lam.) Webb
Tumblemustard	*Sisymbrium altissimum* L.
Hedgemustard	*Sisymbrium irio* L.
Spectacle-pod mustard	*Dithyrea wislizeni* Engelm.
African mustard	*Malcolmia africana* (L.) R. Br.
Bladderpod	*Lesquerella gordonii* (Gray) Wats.
Family GERANIACEAE	
Redstem filaree	*Erodium cicutarium* (L.) L'Her.
Whitestem filaree	*Erodium moschatum* (L.) L'Her.
Family RESEDACEAE	
Wild mignonette	*Oligomeris linifolia* (Vahl) McBr.
Family BORAGINACEAE	
Nievita	*Cryptantha* spp.
Pectocarya	*Pectocarya* spp.
Family PLANTAGINACEAE	
Desert plantains	*Plantago bigelovii* Gray, *erecta* Morris, *insularis* var. *fastigiata* (Morris) Jeps., *purshii* Roem. & Schult., *pusilla* Nutt.

Summer Hosts

Common name	*Scientific name*
Family CRUCIFERAE	
Perennial pepperweed	*Lepidium alyssoides* A. Gray
Family CHENOPODIACEAE	
Russian-thistle	*Salsola kali* var. *tenuifolia* Tausch.
Halogeton	*Halogeton glomeratus* (Bieb.) C. A. Mey.
Lambsquarters	*Chenopodium album* L.
Nettle-leaf goosefoot	*Chenopodium murale* L.
Beets	*Beta vulgaris* L.
Bractscale	*Atriplex bracteosa* Wats.
Fogweed	*Atriplex expansa* Wats.
Redscale	*Atriplex rosea* L.
Australian saltbush	*Atriplex semibaccata* R. Br.
Family AMARANTHACEAE	
Tidestromia	*Tidestromia lanuginosa* (Nutt.) Standl.
Family COMPOSITAE	
Chinchweed	*Pectis papposa* Harvey & Gray ex. Gray
Trianthema	*Trianthema portulacastrum* L.

Holdover Hosts

Common name	*Scientific name*
Family CRUCIFERAE	
Perennial pepperweed	*Lepidium alyssoides* A. Gray

Common name	*Scientific name*
Family CHENOPODIACEAE	
Perennial saltbushes:	
Chamiso	*Atriplex canescens* (Pursh) Nutt.
Shadscale	*Atriplex confertifolia* (Torr. & Frem.) (S. Wats.), *corrugata* S. Wats.
Quail-brush	*Atriplex lentiformis* (Torr.) S. Wats.
Desert sage	*Atriplex polycarpa* (Torr.) S. Wats.
Spiny saltbush	*Atriplex spinifera* Macbride
Family ZYGOPHYLLACEAE	
Creosotebush	*Larrea tridentata* (DC.) Coville
Family COMPOSITAE	
Sagebrush	*Artemisia tridentata* Nutt.
California sagebrush	*Artemisia californica* Less.
False tarragon	*Artemisia dracunculoides* Pursh
Rabbitbrushes	*Chrysothamnus* spp.
Snakeweeds	*Gutierrezia* spp.
Lepidospartum	*Lepidospartum squamatum* (Gray) Gray

BREEDING AREAS

The beet leafhopper is widely distributed over the Western United States by its migratory habits. Some leafhoppers can be found almost anywhere that their hosts occur. However, the need for a succession of host plants restricts the abundance somewhat, and certain definite areas where leafhoppers breed in the spring, summer, or both are recognized as breeding areas.

Douglass and Cook (*19*) gave the following six major breeding areas, which will be generally followed in this bulletin: (1) Central California; (2) great southern desert of California, Arizona, Nevada, and Utah; (3) Rio Grande area of New Mexico and Texas; (4) northern Nevada, northern Utah, and western Colorado; (5) Snake River Plain of Idaho and eastern Oregon; and (6) central Columbia River area of Oregon and Washington. These areas differ in climate, host-plant complex, and leafhopper seasonal history.

CENTRAL CALIFORNIA

Topography, Climate, and Plant Ecology

Central California includes the Great Valley and some adjacent areas between it and the coast. This valley is a large, nearly flat plain almost completely surrounded by mountains. The Sacramento River drains the northern part and the San Joaquin River the southern part. The entire valley is over 300 miles long and averages 50 miles in width. The only opening in the Coast Ranges, which border it on the west, is at San Francisco Bay, where the two rivers join and enter the sea. (Fig. 1.)

The summers have frequent maxima above 100° F. between June and September, and the winters are cool. Frosts may occur between October and March, but the lowest temperatures recorded are about 10° in the Sacramento

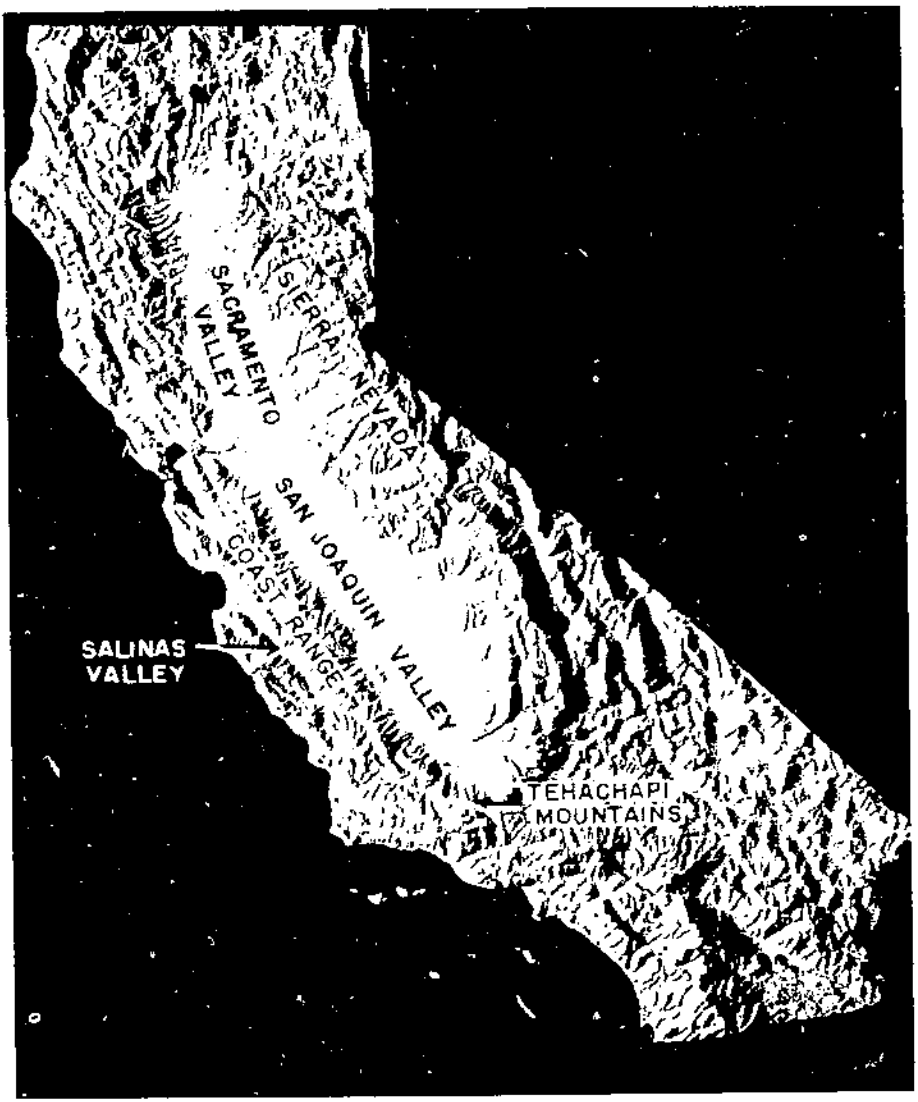

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FIGURE 1.—Relief map of California.

Valley and about 15 in the San Joaquin Valley. The annual rainfall decreases rather gradually from about 25 inches in the northern Sacramento Valley to less than 5 inches in the southwestern desert valleys. Most of the rain falls between December and March, and from June to September it is practically rainless.

The valleys west of the San Joaquin Valley are cooler in summer, with morning fogs and evening ocean breezes.

Since protracted periods of freezing weather rarely or never

occur in the Great Valley, overwintering leafhoppers can become active for at least part of each day during the winter. Some seasons have long spells of foggy weather, with temperatures of 40° to 50° F., which either kill many of the leafhoppers or force them to move into higher areas above the fog. The eggs are laid during February and March and the first spring brood usually matures in April. A partial second brood sometimes develops before the annuals dry up, and the adults move out late in May. The fall holdover period on perennials is very important.

The plant ecology of the San Joaquin Valley, as related to the host plants of the beet leafhopper, has been discussed by Piemeisel and Lawson (*47*) and that of the summer weed hosts by Lawson and Piemeisel (*44*). A large part of the Great Valley bottom is now irrigated and cultivated, but it was formerly occupied by grassland throughout the Sacramento Valley and the northern San Joaquin Valley. The largest part of the San Joaquin Valley bottom had various types of desert shrub and alkali land communities. Proceeding upward from the bottom, the grassland and desert types pass into shrub or tree savanna, and then into forest, which encircles the Great Valley at higher elevations. The host plants of the beet leafhopper grow chiefly in the valley bottom desert formations and in the grassland and shrub (chaparral) formations of the foothills.

Previous Studies

The central California area has probably been more intensively studied over a longer period than any other part of the beet leafhopper range. Curly top was a limiting factor in sugarbeet production in California in 1899, and the leafhopper has been studied ever since Ball (*3*) announced a relationship between leafhopper feeding and "blight." The earlier studies have been summarized by Ball (*4*).

Severin, at the University of California, worked on the leafhopper problem from 1918 to 1932 and summarized his findings (*50, 51*). These two publications formed the point of departure for all later work. E. A. Schwing, entomologist for the Spreckels Sugar Company, studied the problem from about 1918 to 1940. The former Bureau of Entomology and Plant Quarantine of the U.S. Department of Agriculture established a laboratory at Davis, Calif., in 1929, under the late P. N. Annand. In 1933 it was moved to Modesto, Calif., to be nearer the breeding areas, and it remained active until 1943.

Breeding Areas

Spring Breeding Areas

Spring leafhopper breeding has been found chiefly in the foothill canyons and plains on the west side of the San Joaquin Valley just east of the main Coast Ranges. The rain shadow of these ranges reduces rainfall to small values along its inner side. As indicated by Severin (*51, fig. 1*), these areas extend along the inner side of the Coast Ranges from San Francisco Bay to the south end of the valley. Figure 2 shows the breeding grounds in detail.

North of Los Banos, breeding is confined to the bottom and south slope of dry washes. About 2,000 to 3,000 acres have been sufficiently populated with leafhoppers each winter to require control treatment. The proximity to large

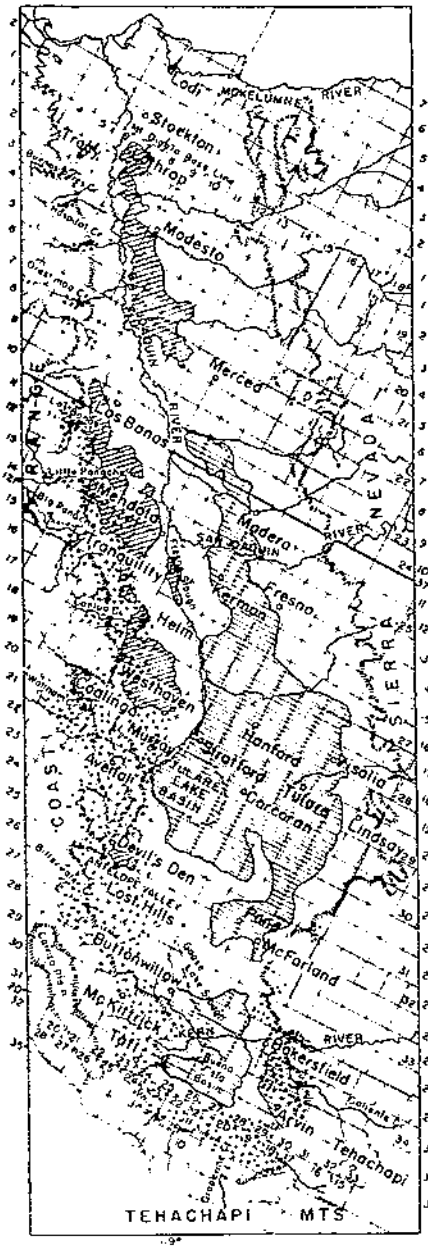

FIGURE 2.—Spring and summer breeding grounds of beet leafhopper in San Joaquin Valley. Summer breeding grounds (lined) are mostly in valley bottom and spring breeding grounds (dotted) lie farther west. (From Lawson and Piemeisel 44.)

areas of curly top-susceptible crops makes the area highly important. From Los Banos south, breeding has been found almost anywhere within the area outlined. High populations of leafhoppers often develop between Los Banos and Devils Den, which produce heavy long-distance movements into the Sacramento Valley. South of Devils Den the leafhoppers do not appear to move into the Sacramento Valley, but are important as far north as Merced and occasionally fly into the coastal areas of southern California.

Rarely, if ever, are high populations of leafhoppers produced in the entire breeding area at one time. The rainfall gradient from north to south is sufficient to control the annual distribution of the leafhoppers. In wet years the northern area produces few leafhoppers, whereas the southern area may have enormous populations; in dry years the southern area may be too dry for leafhopper reproduction, whereas the northern area will be well populated. In most seasons at least moderate populations of leafhoppers may be found in the central area.

In the smaller areas west of the Coast Ranges, leafhopper breeding is sporadic, depending on abnormally dry winters and the presence of considerable quantities of summer hosts to populate the foothills. At the upper end of the Salinas Valley leafhoppers in several canyons occasionally become important and migrate to nearby crops. Some breeding has also been detected in the Carrizo Plain and Cuyama Valley, both to the southwest of the San Joaquin Valley. Local breeding also occurs in some of the higher and drier

valleys of southern California, affecting locally grown crops.

Summer Breeding Areas

As indicated in figure 2, the summer host plants of the beet leafhopper are in the San Joaquin Valley bottom, but the most important summer host areas are on the west side of the valley, where they are in or very close to spring breeding areas. Figure 2 indicates the situation between 1931 and 1937. Since that time farming and grazing conditions have changed greatly, and larger areas of summer hosts are in the southwestern part of the valley.

Seasonal History

Overwintering and Spring Breeding

When winter rains germinate the annual vegetation, the surviving leafhoppers leave the holdover hosts and spread out on the annuals. At first, and later if germination is scanty, the leafhoppers remain fairly close to the holdover hosts, but when germination becomes general they will drift away. In the northern and central parts of the breeding area, cold or foggy weather usually forces the leafhoppers up on south slopes.

Cook (*12*) showed that soil surface temperatures in very low, sparse vegetation on south slopes would reach 58° F., the point of minimum activity of the leafhoppers, when thermometers in a nearby standard shelter registered 45°. This temperature advantage on the south slope enabled the leafhoppers to develop and lay their eggs when standard shade temperatures were below their minimum for activity. Ball (*5*) overlooked this point when trying to prove that a generation of leafhoppers could not be produced in the desert breeding areas in the spring.

These slopes, so favorable for leafhopper breeding in early spring, become too hot and dry later in the season, and the maturing leafhoppers may find suitable vegetation for egg deposition in the canyon bottom or even on the plains outside the canyons in which they lay eggs for a second brood.

Occurrence of Second Spring Brood in Desert

Only occasionally does a large second brood of leafhoppers develop in the spring breeding area, but when it does, the resulting leafhopper populations are much higher than those following movements of the first brood. In 1940, surveys in February showed a very low population of overwintering females, and further surveys in March and April indicated the development of a very small brood of leafhoppers. These moved out into the lowlands late in April, leaving almost no leafhoppers in the original areas. Late in that month, nymphs started to appear in desert locations not occupied earlier, and these nymphs matured and moved out during May. This movement between May 10 and 20 raised leafhopper populations in the cultivated areas to the highest levels found between 1931 and 1943.

Nymphal Mortality on Spring Annual Host Plants

In California several attempts were made to determine the preferred host plants and the nymphal mortality more accurately than could be done by field observations. An experiment in 1942 gave some excellent data on spring

mortality under at least average spring conditions.

For this purpose a cylinder of heavy sheet metal was devised, sharpened at the lower end and with a heavy rim and handle at the upper end. This could be worked down into moist soil to a depth of about 5 inches. The cylinder of soil and plants so separated could then be transplanted into a 6-inch flowerpot and transported. Such samples taken from the actual breeding spots were held in the greenhouse until the eggs contained in the plants had all hatched, so that the nymphs could be counted. The number of nymphs counted in the sample gave a minimum estimate of the number of eggs laid there, as some eggs undoubtedly failed to hatch and some young nymphs were missed or died before the count was made.

An area of breeding host plants (largely *Plantago insularis* var. *fastigiata*) was found near Taft, Calif., in January 1942 with about five to six adult leafhoppers per square foot. Sets of 16 plant samples were taken from this small area on January 20 and 29, February 11 and 25, and March 9. The adult population was estimated on the first two sampling dates, but quantitative samples of the field population were made at all later dates. By adding the number of nymphs hatched in the greenhouse, from a particular set of samples, to the field population of adults and nymphs found on the same date, the total can be compared with the field population to indicate the nymphal mortality. The pertinent data are found in table 1.

The greenhouse samples for January 20 contained no eggs that hatched, those for January 29 a few, and the bulk of the hatching came from the February samples, indicating that most of the eggs were laid before February 25. The disappearance of the overwintering adults in March is normal, as is the finding of the first spring brood adults at the end of March.

The potential population indicates a fairly high rate of egg deposition, as the data show a

TABLE 1. *Field and greenhouse plant samples from south slope near Taft, Calif., January–March 1942, combined to indicate spring nymphal mortality of beet leafhopper per square foot*

Sampling date	Field population			Greenhouse nymphs	Potential population	
	Adults	Nymphs	Total		Total	Percent of highest
	Number	*Number*	*Number*	*Number*	*Number*	*Percent*
Jan. 20	[1] 5–6	0	[1] 5–6	0		
Jan. 29	[1] 5–6	0	[1] 5–6	4.5		
Feb. 11	2.0	0	2.0	70.5	72.5	100
Feb. 25	.7	10.0	10.7	56.5	67.2	93
Mar. 9	0	28.5	28.5	17.0	45.5	63
Mar. 17	0	31.2	31.2	[2]	31.2	43
Mar. 31	[3] 6.5	9.5	16.0	[2]	16.0	22

[1] Population estimated.
[2] No samples taken as vegetation was drying.
[3] Light-colored spring generation.

production of about 14 nymphs per female. The vegetation started to dry in mid-March, with consequent concentration of nymphs and adults on the greener plants. For this reason, and also because it was getting too late for oviposition, no samples were taken to the greenhouse on March 17 and 31.

The potential population is undoubtedly underestimated, but in spite of this a total mortality of 57 percent by March 17 is indicated. The field population on March 31 is undoubtedly far too low, as adults had been emerging for some time and they tend to leave the spot where they emerged.

In the same season, three sets of eight samples each were dug early in March from the best available breeding areas in four parts of the Great Valley for the hatching of nymphs. Similar computations were made, based on an estimate of overwintering female leafhoppers in January and of spring nymphal populations early in March. These, with the nymphs hatched from greenhouse samples, yield data for potential and actual populations (table 2), in which each figure is based on samples taken from three locations within the general area.

The data in table 2 give a fairly good picture of the relative suitability of the various areas for spring reproduction in 1942. Heavier than normal rainfall for several years had increased the amount of nonhost plants and greatly reduced the areas of breeding hosts in the northern and central parts of the valley while increasing the breeding hosts in the southern part of the valley. Consequently, spring mortality was nearly total for the few nymphs that hatched in the northern canyons and only averaged about 40 percent in the southern areas.

Summer Broods

Determination of the exact number of summer broods in this area is difficult because of overlapping of generations. Severin (*50*) showed in a chart four generations of beet leafhoppers per

TABLE 2. *Overwintering beet leafhopper populations per square foot (Jan. 29–Feb. 10) and spring nymphal populations (Mar. 17–31) compared with corresponding potential nymphal populations from greenhouse samples taken March 9–10, 1942, central California*

Area in Great Valley	Overwintering adults	Potential spring nymphal population			Actual spring nymphal population [1]	
		Field	Actual hatch in greenhouse	Total	Total	Percent of potential
	Number	*Number*	*Number*	*Number*	*Number*	*Percent*
Northern hills	0	0	2.3	2.3	0	0
North central	.6	5.2	35.7	40.9	5.6	13.7
South central	.9	3.9	19.0	22.9	13.7	60.1
Southern	2.9	21.3	19.7	41.0	26.0	63.4

[1] Southern area sampled Mar. 17 and others Mar. 30–31 to find nymphs mostly in middle instars.

year, including two summer generations. His tabular data gave ample time for the development of another summer generation.

In the summer of 1931, H. C. Donohoe, of the former U.S. Bureau of Entomology and Plant Quarantine, collected a series of weekly sweep-net samples in the beetfields of the Sacramento Valley. At each stop 10 sets of 50, 25, or 10 sweeps each were taken, the number of sweeps depending on the size of the leafhopper population. The study, started in June, missed most of the first generation in the beet plants. Since variations over the whole territory were too great to be averaged because of differing dates of spring leafhopper movements and differing growing conditions, seven fields in the Sacramento Delta area were chosen as a typical example. The average number of leafhoppers found in 50 sweep-net samples for each date is plotted logarithmically in figure 3.

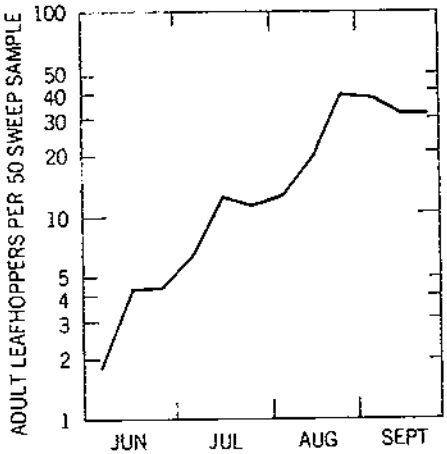

FIGURE 3.—Average number of adult leafhoppers per 50 sweeps found in 7 beetfields in Sacramento Delta of California during summer of 1931 (data by H. C. Donohoe).

The leafhopper population increased almost at a logarithmic rate from the first sample until about September 1, when the growth slackened because of the maturing of the beet plants. There were three periods when the number of adults captured reached a peak and remained steady for a week or two before resuming its general progress. These came around June 20, July 20, and August 30, and indicated the period of maximum emergence and emigration of adults of three summer broods. These findings were also substantiated by some sampling done by G. T. York on summer weed host plants at Modesto, Calif., in 1934 and 1935.

In the summer of 1934, L. C. Stanford, of the former U.S. Bureau of Entomology and Plant Quarantine, extensively reared beet leafhoppers in cheesecloth cages tied on naturally growing plants of bractscale and Russian-thistle at the Modesto laboratory. The tests overlapped in time, as they were designed to even out the work of handling the leafhoppers. Four 1-generation tests were completed on bractscale, for which the heat requirement, calculated as day-degrees between 58° and 93° F., averaged about 680 day-degrees. This checks closely with the value of 650 day-degrees found by Harries and Douglass (*34*) in Idaho. Using 680 day-degrees as a measure, there is ample time for three summer generations between mid-May and late August or early September in most years. When there are two broods in the foothills, the progeny of the second spring brood probably produce only two further broods before autumn.

More recent work by H. L. Wilson, California Department of

Agriculture, indicates two complete generations during the summer, which, with the spring and fall broods, total four generations per year. This varies in different localities and seasons.

Utilization of Fall Holdover Hosts

Since the fall, or overwintering, brood of leafhoppers usually matures during October, when the summer host plants are maturing, the adults must seek other sources of food. As shown by Lawson et al. (*42*), the leafhoppers travel on the wind, which is usually light and variable at that time of year. The general wind drift carries them south and west from the cultivated and abandoned areas, where summer hosts are drying, into the open range. Here they must seek sustenance from any available plant, of which there are only a few at that time of year. The bottom of the dry canyons usually contains perennial shrubs of various species that are still succulent (fig. 4), and there are a few late fall annuals that can also support the leafhoppers. Some of the annuals are in the canyons, but many of them are on the benches between the canyons.

Extensive field observations of newly germinated annuals and the effect of rainfall immediately preceding germination indicated that at least 0.75 inch was needed to start germination in October, but if fall rains were further delayed, 0.50 inch or more would initiate the process in November, or 0.25 inch in December or January. These figures reflect the lessened evaporation in the late fall and winter, making the use of moisture more efficient at those times. Lighter rains than these might cause limited germination of annuals where water accumulated, but such germination was spotty and of little value. In some seasons heavy early rains caused widespread germination of annuals, but drought periods that

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FIGURE 4.—Mouth of Cantua Creek on west side of San Joaquin Valley late in August, showing perennial vegetation in creek bottom. Dark-colored plants are largely lepidospartum and desert sage.

TABLE 3. *Dates of fall movement and of germination of winter annuals and periods on holdover hosts for beet leafhopper breeding areas of central California, 1912–43*

Area in San Joaquin Valley	Approximate date of fall movement	Date of germination of winter annuals			Period on holdover hosts	
		Earliest	Latest	Average	Average	Range
					Days	*Days*
Northern	Oct. 15	Sept. 12	Jan. 14	Nov. 18	34	0–91
Panoche	Oct. 25	Oct. 1	Jan. 15	Nov. 22	28	0–82
Coalinga	Nov. 1	Oct. 7	Jan. 12	Nov. 27	26	0–73
Kern County:						
Lowlands	Nov. 1	Sept. 30	Jan. 13	Nov. 30	29	0–74
Plains	Nov. 1	Sept. 26	Jan. 29	Nov. 30	29	0–90
Foothills	Nov. 5	Sept. 26	Jan. 29	Dec. 5	30	0–85

followed killed the newly sprouted plants and forced the leafhoppers back onto perennials. This was definitely observed in 1939 and probably also occurred in 1918.

Weather records were obtained from many stations on the dry west side of the San Joaquin Valley and analyzed to estimate the approximate time of germination of winter annuals. The Standard Oil Company of California furnished temperature and rainfall records for their pipeline pump stations for 1912–43 and also the Shell and Union Oil Companies for shorter periods. A few U.S. Weather Bureau stations furnished records.

For the purposes of this study, the winter and spring breeding areas of the San Joaquin Valley have been divided from north to south into six areas, designated as Northern, Panoche, Coalinga, and Kern County, with the last subdivided into lowlands, plains, and foothills. The approximate dates of fall movements into these areas, the earliest, latest, and average dates of germination of winter annuals, and the ensuing holdover periods on perennials are shown in table 3.

As indicated in this table, the leafhoppers averaged from 26 to 34 days on holdover hosts in different parts of the valley, with a range of 0 to 91 days.

Host Plants

Winter and Spring Hosts

The following plants, arranged as to their relative importance, have been found to be winter and spring host plants of the beet leafhopper in central California:

IMPORTANT HOSTS

Common name	*Scientific name*
Desert plantains	*Plantago erecta, bigelovii, insularis* var. *fastigiata*
Pepperweeds	*Lepidium nitidum, latipes*
Redstem filaree	*Erodium cicutarium*
Herniaria	*Herniaria cinerea* DC.
Hollisteria	*Hollisteria lanata* Wats.

MINOR HOSTS

Common name	*Scientific name*
Whitestem filaree	*Erodium moschatum*
Filaree	*Erodium botrys* (Cav.) Bertol.
Tropidocarpum	*Tropidocarpum gracile* Hook.
Redmaids	*Calandrinia* sp.

The first plants to germinate in the fall are usually the filarees, whose seeds will germinate at rather high temperatures. Pepperweeds usually appear next, and as the weather cools, desert plantains come up. Early drying of pepperweeds in many years forces the leafhopper nymphs to other plants, such as the filarees and plantains. As these winter annuals mature, other plants that germinate late and grow slowly during the early spring take over. These include herniaria, hollisteria, tropidocarpum, and redmaids. The second spring brood is usually produced on filaree and on these last plants. The periods when these plants are generally succulent in relation to leafhopper broods are shown in figure 5.

Desert Plantains. — *Plantago erecta* and *bigelovii* occur together throughout the northern and central parts of the Great Valley and are not easy to distinguish in the field. Consequently, both have been recorded in field notes as *erecta*. *P. insularis* var. *fastigiata* is different in its ecology.

Plantains of the *erecta* group are very small, rarely over 4 inches in height. Usually they grow in dense stands, where the individual plant generally has six leaves or less and one or two flower heads. These stands are often so thick as to crowd out all other plants, and the resulting pure stands have a characteristic gray appearance, which makes them visible for some distance (fig. 6).

P. insularis var. *fastigiata* is found in the south-central and southern parts of the San Joaquin Valley and in the great southern

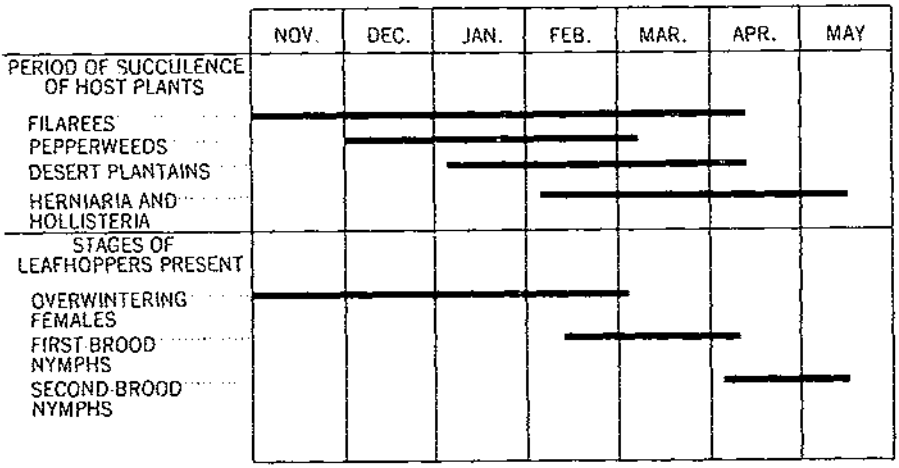

FIGURE 5.—Period of succulence of important spring host plants in relation to leafhopper broods.

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FIGURE 6.—Typical dense stand of *Plantago erecta*.

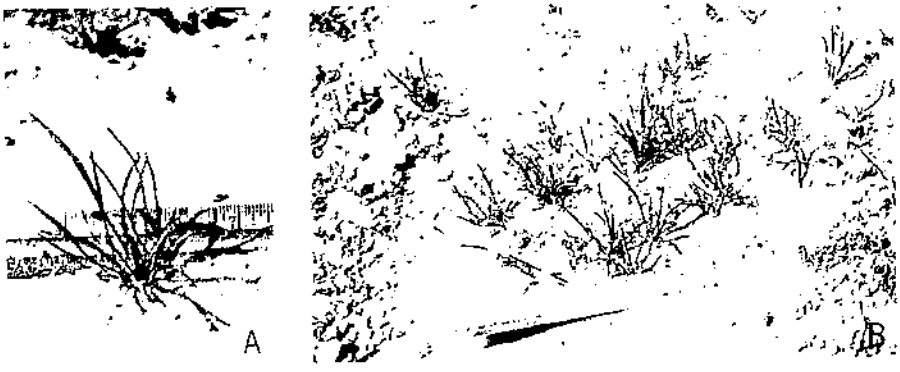

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FIGURE 7.—*Plantago insularis* var. *fastigiata*: *A*, Single plant; *B*, characteristic open stand.

desert. Unlike the *P. erecta* type, *fastigiata* usually occurs in rather open stands, in which the individual plants are well separated (fig. 7). It is a relatively deep-rooted annual, and can continue in a green, succulent condition after most other annuals have dried.

The seeds of desert plantains have a gelatinous outer coating, which imbibes water and becomes gluey after a rain, adhering to small stones and pieces of soil or plant debris. As the soil dries, this coating also dries, attaching the seed firmly to whatever it hap-

pens to contact. The seeds germinate only at relatively low temperatures, and young seedlings are rarely found before January, even when fall rains come early.

The plantains are well distributed over the breeding areas. They occupy the driest and warmest slopes in the foothills, and are also found on the flats and plains outside the foothills. On these plains, where there is less heat and more moisture than in the foothills, they grow more slowly, and leafhoppers leaving the foothills early in the spring often stop and lay part of their eggs in these later patches of plantain, producing a second partial generation about a month later than the first generation.

The plants are attractive to the leafhoppers if measured by the populations of overwintering females found feeding on them. They are short plants and generally favorable in growth habit. Their period of succulence is long, and they are often among the last host plants to dry in the spring. They consistently occur from year to year. When found in mixed stands, the plantains make up such a small part of the whole stand as to be negligible. Since those of the *P. erecta* group sometimes grow too thickly for beet leafhopper reproduction, they have very low populations. *P. insularis* var. *fastigiata* rarely grows thickly and is almost always a favorable host plant.

Pepperweeds.—Two species of *Lepidium* are highly important host plants of the beet leafhopper in this area. *L. nitidum,* in particular, is abundant and widespread and is highly attractive to the overwintering female leafhoppers (fig. 8).

L. nitidum is a small, usually much-branched annual growing

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FIGURE 8.—Single plant of *Lepidium nitidum.*

from 1 to 6 inches in height. Like the desert plantains, its seeds are coated with a gelatinous layer, which imbibes water. The seeds will not germinate until fall, but usually sprout in November, soon after the first rain falls. Under very dry conditions these plants will mature a single pod with two seeds. Such depauperate forms are often found on south slopes that are too dry for other plants. The pepperweeds can endure competition, and small, stunted plants may be scattered through rather heavy stands of bromegrass (*Bromus rubens* L.) or rank filaree. Pepperweeds will be the first plants found on bare slopes or flats. They usually mature and dry in late February or March, and before the leafhopper nymphs can mature, they must complete their development on other hosts. Also, pepperweed that has started to flower seems less attractive to female leafhoppers than that in the early or rosette stage. If the plant is flowering in January, the leafhoppers when ovipositing will often pass it by in favor of other less mature host plants.

On the other hand, if the fall rains are late, so that pepperweed does not sprout until late December, it will be in a very attractive condition at the right time and

will receive a large share of the total eggs laid. Even when it matures early, many eggs are laid in it. In many instances, careful search through the eighth or quarter square foot of other host plants being sampled in March will reveal a few dead or dying pepperweed plants, from which many of the nymphs found may have hatched.

Lepidium latipes is not so common or widespread as *nitidum*, but tends to occur with it in mixed stands. It is about equally attractive to the female leafhoppers, and is a good host wherever it is found in the breeding areas.

In brief, the pepperweeds are very attractive to the leafhoppers, have a desirable growth habit, are widely distributed in the particular spots where they are likely to be found by the leafhoppers, occur in open stands, are almost always abundant, and occur consistently. They often are mixed with other leafhopper host plants, but this does not seriously affect their value to the leafhopper, as the nymphs can move from drying pepperweeds to other more succulent hosts without traveling far.

Alfilerias or Filarees. — Jepson (*40, p. 591*) listed five species of *Erodium* as occurring in California. Three of them—*cicutarium*, *moschatum*, and *botrys* — are found in the leafhopper breeding areas. *E. moschatum* usually occupies higher, more moist ground, but occasionally invades the lower slopes. *E. botrys* is very abundant in the Sacramento Valley and in the northern San Joaquin Valley, but has not been of any great importance as a leafhopper host.

Redstem (*cicutarium*) and whitestem (*moschatum*) filarees may occur in mixed stands. They cannot be separated until the seeds form. Late-season studies have indicated that whitestem filaree is not abundant in the breeding areas, and is only a minor leafhopper host.

Redstem filaree was listed by Severin (*51*) as the most important spring host plant in the foothill areas. Although later studies have shown that it was not so important as Severin thought, it still remains a highly useful member of the host-plant complex. It was apparently introduced very early from the Mediterranean region, and it is now well adapted in many Western States. Unlike the pepperweeds and plantains, some of its seed will germinate whenever moisture is sufficient, as in June 1931, when local cloudbursts supplied nearly an inch of moisture to parts of the San Joaquin and Salinas Valleys. Within a week these areas were green with newly germinated filaree. It is ordinarily the first plant to germinate after the fall rains commence. For this reason, it is highly important to the leafhoppers, as it usually supplies the first succulent food they receive after leaving their summer hosts.

The growing plant first forms a rosette, usually from 3 to 6 inches in diameter, with the leaves lying almost flat along the soil surface (fig. 9). In a dry season or in dry locations a few blossoms are produced on stems arising from the rosette, and a few seeds are set. When moisture is plentiful several long stems arise from the rosette, at first erect, then gradually becoming semiprostrate. They may grow 3 feet long and branch profusely. If the stand of filaree is at all thick, the tangled mass of stems will grow 12 to 18 inches high. Such tangled mats are not favorable for leafhoppers, and very few nymphs will be found in

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FIGURE 9.—Typical plant of redstem filaree.

them. However, such mats grow in the moister places, and when the stunted plants on south slopes and similar locations dry up, the leafhopper nymphs are often forced onto the heavy growth, and enormous populations may be found there near the time of the spring movements. Such aggregations of adults and nymphs on this plant have greatly enhanced its reputation as a host.

Filaree has another valuable characteristic in certain seasons. If rains are scanty, the scattered plants on dry spots will fold their leaves into a tight vertical bunch to reduce transpiration and exist with little further growth for some time. If rain comes late before the plant is dead, new succulent growth develops, which is very attractive to the adults of the first spring brood of leafhoppers, and they will lay many eggs in it to produce a second brood in the desert.

In 1927 and 1940, the filaree, growing rankly over many parts of the foothills, was almost completely wiped out by the attack of an aphid closely related to the pea aphid. Within a few days, areas of many square miles where rank filaree had been growing were brown and dry. However, the filaree in many places puts out basal shoots of new growth, and in 1940 many leafhoppers laid their eggs in this growth and thus contributed toward the large second brood of that year.

Filaree is apparently attractive to the overwintering females. It has a period of succulence generally sufficiently long to mature a complete brood, and in many instances will mature a partial second brood. It is the most generally distributed plant in the desert. It often occurs in pure scattered stands, which are very attractive to leafhoppers, and often in heavy stands mixed with bromegrass, which do not attract this insect. In brief, under certain conditions it is an excellent host, under others, worthless.

Herniaria. — Herniaria, a tiny plant with small leaves, grows in rather heavy stands on the northern foothills of the Great Valley, but it is not abundant south of Fresno. It germinates in early spring rather than in late fall or winter as the previously mentioned host plants. During March the tiny seedlings may be found in the cotyledon stage, growing thickly in the breeding areas. In April the plant starts to grow, and by the middle of May it is full size, which may be 3 or 4 inches in height. The plants are normally dry by the end of May.

The plant is too small at the time the overwintering females are ovipositing to receive any of the eggs, but it is sufficiently attractive to the first spring brood to receive many of its eggs. The growth habit (fig. 10) is suitable for the leafhoppers at this time of year. It occurs generally in rather thin stands, which may be mixed

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FIGURE 10.—Single plant of *Herniaria cinerea.*

with other plants but in many cases are nearly pure. Its distribution is rather general over the northern foothills, especially on hilltops and south slopes. The chief disadvantage is inconsistent occurrence. The factors controlling its abundance from year to year are not known, but it will appear rather suddenly and for a year or two be abundant over large areas, only to disappear just as suddenly.

Hollisteria. — Although hollisteria belongs to a different family, it is very much like herniaria in its general habits. It is also a small grayish-green annual that germinates early in the spring. The fully developed plants may be somewhat larger than those of herniaria, and because the stem internodes are longer, the plant is more open. It is also mature and dry by the first of June.

Hollisteria is distributed over the southern San Joaquin Valley and is abundant on the plains near Middlewater and in the hills and canyons as far north as Fresno. Like herniaria, it occurs erratically from year to year. Occasionally heavy populations of second-brood leafhoppers develop in it, as in the spring of 1937, when a large second brood developed over a rather large area.

Tropidocarpum. — This is a rather small yellow-flowered mustard (fig. 11). It is an excellent host plant and very attractive to the leafhoppers, which may be found feeding on it before they are ready to lay their eggs. Unlike pepperweeds, it usually remains succulent long enough for the nymphs to mature. It is low growing and rather sprawly, often covering an area 8 or 9 inches in diameter with its nearly prostrate stems and leaves. Frequently it is found mixed with filaree and pepperweeds; the three plants possibly cover 50 percent of the ground area. The combination may produce large leafhopper populations.

In 1934, counts were made of the plant cover in 23 locations in the desert breeding areas, scattered from north to south. Twelve of these locations yielded one or more plants of tropidocarpum in ten ¼-square foot samples. It thus appears to be rather gener-

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FIGURE 11.—Single plant of *Tropidocarpum gracile.*

ally distributed, although rarely abundant. The plant is rather consistent and tends to occupy the same general areas year after year.

Relative Importance of Spring Hosts. — It is difficult to find a quantitative basis for rating the relative importance of these plants. They often occur in mixed stands, from which only detailed study can determine the true host plants. Their relative importance varies in different years, depending on their stage of growth when the leafhoppers are ready to lay their eggs. Their type of growth varies with the rainfall, so that a location producing only a few stunted plants in one season may have a fair cover of normal plants in the next.

To present their relative importance in general terms, all the quantitative samples taken during March, April, and May during the survey have been classified as to host plant and area sampled and have been averaged. Samples other than survey samples were disregarded, as they gave undue prominence to some particular plant or plants being studied. Each sample is in itself the average of 10 or more subsamples. Since the field notes gave only generic terms for the host plants, species could not be segregated. The northern area reaches from Altamont Pass east of Oakland to a point due west of Fresno, the central area extends from this point south to the north line of Kern County, and the southern area is south of the Kern County line (table 4).

Of the three host plants tabulated, the desert plantains had the highest spring populations of leafhoppers. This superiority was due considerably to the presence of *P. insularis* var. *fastigiata* in the central and southern areas. The pepperweeds were not too accurately represented, as they usually matured during March, and few later samples were taken on them. Filarees, although very abundant and consistent, were not as good host plants as either of the others. The filarees had slightly higher leafhopper populations in the central and southern areas than in the north, a reflection of lower rainfall and sparser stands of smaller plants toward the south. The central and southern areas were far more productive of

TABLE 4. *Total number of samples on indicated host plants of first spring brood beet leafhoppers and average number of leafhoppers per square foot in 3 areas of San Joaquin Valley, 1934–43*

Host plant in samples	Northern		Central		Southern		All areas	
	Samples	Leafhoppers	Samples	Leafhoppers	Samples	Leafhoppers	Samples	Leafhoppers
	Number	*Number*	*Number*	*Number*	*Number*	*Number*	*Number*	*Number*
Desert plantains	67	4.67	126	13.46	133	12.99	326	11.46
Pepperweeds	22	1.01	62	11.09	13	6.75	97	8.22
Filarees	53	4.01	121	5.79	60	7.33	234	5.78
All plants	142	3.86	309	9.98	206	10.94	657	8.96

leafhoppers than the north. Differences between the central and southern areas were slight.

These data, in general, give the overall spring host-plant picture, which changes from year to year as the weather changes. In 1933, H. E. Wallace and G. T. York collected samples of vegetation from occupied breeding areas in the northern San Joaquin Valley, bleached them with household bleach, cleared them in gasoline, and counted the leafhopper eggs. In 10 samples, containing 1,700 plants, they found 102 eggs in desert plantain and only 10 in filaree, showing a strong preference for plantain in that place and season.

In that same season W. C. Cook and F. R. Lawson sampled the leafhopper populations of three closely adjacent locations near Coalinga in the central area, using a pan-type sampler. After the leafhoppers were counted, the plants in the sample were pulled up and counted. The samples from the three places were dominated by pepperweeds, redstem filaree, and goldfields (*Baeria chrysostoma* F. & M.), respectively. The results are given in table 5.

In this set of samples there were over four times as many leafhopper nymphs in the location dominated by pepperweeds as in the other areas. On the following day the same workers sampled a south slope dominated by desert plantains and an adjacent bottom area dominated by pepperweeds. The plantain area averaged 12.4 nymphs per square foot and the pepperweed area 26.0 nymphs. The latter produced more leafhoppers in both instances.

In the spring of 1935, G. T. York obtained 19 host-plant samples from various breeding areas, segregated the host plants by species, and held them with their roots in moist cotton until any eggs laid in them had hatched. His samples covered the breeding area as far south as Coalinga. The numbers of nymphs he found are shown in table 6.

These samples were taken too late for the maximum number of nymphs from the pepperweeds, but as pepperweeds made up just over 10 percent of the host-plant cover, they were not very important. Nearly three-fourths of the nymphs were produced on the plantains.

These examples show the variations in utilization of the principal host plants in different places and seasons.

Changes in Annual Vegetation After Wet Years. — During the

TABLE 5. — *Relationship of nymphal populations of beet leafhopper to plant cover, Coalinga, Calif., April 1933. (Figures in italics show highest percentage for each plant species.)*

Dominant plant species	Leafhoppers per square foot	Plant cover			
		Pepperweeds	Redstem filaree	Goldfields	Miscellaneous
	Number	*Percent*	*Percent*	*Percent*	*Percent*
Pepperweeds	142.4	*71.1*	7.1	20.0	1.8
Redstem filaree	29.3	4.1	*52.9*	36.3	6.7
Goldfields	30.8	2.2	3.1	*76.1*	18.6

TABLE 6.—*Relationship of nymphal populations of beet leafhoppers to host-plant species, as shown by laboratory rearings, spring 1935*

Host plant	Number of samples	Leafhopper nymphs		Host plants	
		Number	Percent of total	Number	Percent of total
Plantains	19	95	73.7	1,715	38.1
Filarees	19	12	9.3	1,040	23.1
Pepperweeds	8	1	.8	525	11.6
Other host plants [1]	12	21	16.2	1,227	27.2

[1] Included 9 other plants, none of which made up 4 percent of host-plant cover.

period 1929–34, rainfall in the San Joaquin Valley was consistently below normal. The average for 9 to 12 weather stations in the breeding areas was 5.57 inches from July 1 through June 30. Vegetation was probably at a low point, as such droughts were not too common. Starting in the fall of 1934 and continuing through the spring of 1942, heavier-than-normal rainfall occurred, averaging 9.14 inches for the same stations. This had a very definite effect on the annual vegetation, which has been discussed from the standpoint of stock range by Talbot et al. (*55*) for the general range area of the San Joaquin Valley.

In 1933–34, counts of the plants on samples taken for leafhopper nymphs were made at 20 locations in the San Joaquin Valley. These plant counts were filed and almost forgotten until, in 1942, the changes in vegetation had become so obvious that it seemed desirable to resample the vegetation. Two sets of samples were taken in 1942. The first set was taken as close as possible to the area where the 1933–34 samples had been taken to check the changes in those particular spots. Many of these spots had developed such heavy growth in 1942 that they would no longer support leafhoppers. The best nearby spots of breeding area, comprising the second set, were also sampled to find out under what conditions the leafhoppers were forced to breed. In all instances from 5 to 20 samples were taken, and the plants were sorted and identified in the field. About 20 locations in the general breeding area were sampled. The plant cover is shown in table 7.

The plant cover is shown for almost identical locations in 1933–34 and 1942. Heavy rainfall that reduced the leafhopper host plants from 200 to about 160 per square foot would not have been serious except that nonhost plants increased 10 times, to nearly 700 per square foot. Vegetation of this density is too heavy for beet leafhopper reproduction, especially when most of the plants are nonhost grasses.

Comparing the second and fourth columns of table 7 will give some idea of the actual conditions under which the leafhoppers were breeding in the two seasons. Filarees and pepperweeds had decreased in 1942, whereas plantains and herniaria had increased. Grasses were over 10 times as abundant in 1942 as in 1933–34, but the presence of 200 grass

TABLE 7.—*Plant cover in beet leafhopper breeding spots in 1933–34 compared to cover in same spots and also in nearby favorable breeding spots in 1942, San Joaquin Valley*

Plant species or group	Plants per square foot in same spots in—		Plants per square foot from best nearby breeding spots (1942)
	1933–34	1942	
	Number	*Number*	*Number*
Filarees	67	42	39
Plantains	66	86	96
Pepperweeds	55	9	19
Herniaria	4	22	16
Tropidocarpum	6	0	0
Redmaids	2	0	1
Total host plants	200	159	171
Grasses	15	613	200
Miscellaneous annuals	52	74	53
Total nonhost plants	67	687	253
Total plant cover	267	846	424

plants per square foot was not so serious here as the 600 on the old breeding areas. The increases in plantains and herniaria insured a host-plant succession, and a second brood was noted in at least three seasons. Field notes in 1942 indicate the presence of much grass in nearly all parts of the breeding area.

Since rainfall is heavier in the northern part of the San Joaquin Valley than in the south, a general increase in rainfall shifted vegetation zones to the south, as shown in table 8, where the samples are segregated according to the collection area.

TABLE 8.—*Analysis of annual plant cover in favorable breeding areas in different parts of San Joaquin Valley in 1933–34 as compared with that in 1942*

Area and type of plants	Plants per square foot		Change
	1933–34	1942	
Northern foothills:	*Number*	*Number*	*Number*
Hosts	412	322	−90
Nonhosts	104	223	+119
Panoche:			
Hosts	147	103	−44
Nonhosts	37	305	+268
Coalinga:			
Hosts	162	167	+5
Nonhosts	124	322	+198
Southern plains:			
Hosts	189	79	−110
Nonhosts	6	363	+357
Southern foothills:			
Hosts	86	184	+98
Nonhosts	59	49	−10

In both sampling seasons the plant density decreased rather regularly from north to south, in conformity with decreasing seasonal rainfall. In 1933–34, host plants made up more than half the total plant cover in all areas, but by 1942 three of the five areas contained more nonhosts than hosts.

Since in 1933–34 the plant cover in the northern area was too heavy for optimum leafhopper reproduction and that in the south was too light, the three middle sections produced most of the leafhoppers. By 1942, the heavy grass cover was present everywhere except in the southern foothills. In 1933–34, the three central sections had an average total

plant cover of 175–300 plants per square foot, of which 150–200 were host plants. Assuming this to be the optimum condition for the leafhopper, the only area to fulfill the specifications in 1942 was the southern foothills with 233 plants per square foot, of which 184 were host plants. In all the other areas there were more plants, with nearly as many or more nonhosts as hosts. Very few leafhoppers were produced in 1942 anywhere except in the southern foothills.

The spring host-plant complex in central California may be summarized as follows:

The beet leafhopper may lay eggs and the nymphs may mature in many species of annual range plants (Severin *51*), but only a few of these are important because of the leafhopper populations produced. Many plants are excellent hosts for the leafhopper, but they may be unattractive to the female, may mature at the wrong time, may be widely but sparsely distributed, or may, on the contrary, be concentrated on one area or a few small areas.

The important spring host plants in central California are plantains, pepperweeds, and filarees, in about that order. Other hosts, such as herniaria and hollisteria, will help to produce a second brood in certain years, at which times their importance is great, but they may be of little value for a series of years between these second-brood situations.

Apparently a plant density of 200 to 300 plants per square foot, of which two-thirds are leafhopper host plants, will produce optimum breeding conditions. This critical density occurring in different parts of the breeding area in different seasons makes it difficult to assign importance to any particular breeding area except in terms of distance from susceptible cultivated crops. Leafhopper populations fluctuate from year to year, depending on how prevalent the optimum conditions are and how many leafhopper adults found their way to those areas during the fall and early winter.

Late-Spring and Early-Summer Breeding Hosts

The late-spring and early-summer breeding hosts germinate in the fall, winter, or spring, but chiefly in the spring, and mature by midsummer to a point where the leafhoppers cannot breed on them. The importance of these plants is secondary to that of the true summer hosts, which remain green until fall. Severin (*51, pp. 287–296*) discussed these and the more important plants.

A group of short-lived annual saltbushes (*Atriplex* spp.) occurs in many parts of the Great Valley, but none of them have high leafhopper populations and they mature late in June. These include the species *cordulata* Jepson, *coronata* Wats., *phyllostegia* (Torr.) Wats., *parishii* Wats., and *cordulata* var. *tularensis* Jepson. They occur in the lower, more alkaline parts of the Great Valley, and their stands are scattered. The total acreage is small.

The annual mustards (*Brassica* spp.) may germinate either in late fall or early spring. They and the pigweeds (*Chenopodium* spp.) occur chiefly as weeds in cultivated crops. Their period of attractiveness is short, and their growth soon becomes woody.

All these plants except the annual saltbushes occur chiefly in irrigated fields, where they will hold leafhoppers during May and June. When cultivation removes

the weeds, the leafhoppers may move to any susceptible crops present, transmitting curly top to them.

Summer Hosts

Only such plants as are present and attractive when the leafhoppers fly from their spring host plants and remain succulent long enough to mature the last brood in October will be considered as summer host plants. The chief plant species are sugarbeets, Russian-thistle, fogweed, bractscale, and smotherweed.

Sugarbeets grow from February through November in the Great Valley and provide excellent conditions for leafhopper multiplication. Samples taken in sugarbeet fields at approximately weekly intervals during 1931 (fig. 3 and p. 19) showed that the leafhopper population increased at a logarithmic rate from the time the migrant leafhoppers reached the fields in May until about September 1. The generation produced in September was smaller in numbers, and these leafhoppers began to leave the beets as they developed wings. Some of them apparently remained in the beetfields until November.

Smotherweed is of minor importance in central California. It occurs chiefly as a weed of barnyards and ditchbanks. It is widely distributed, but the total acreage is small.

Russian-thistle, fogweed, and bractscale are the summer hosts of greatest importance in central California. The distribution and ecology of these plants have been covered in detail by Lawson and Piemeisel (*44*). These authors do not, however, give much information regarding their utilization by the beet leafhopper.

Russian-Thistle.—Russian-thistle occurs throughout western North America, where it is one of the most widespread and abundant annual weeds. The species apparently approaches its southern limit in the Southwest, as it is not a serious pest in the Imperial Valley of California. It has recently spread throughout the cultivated areas of southern Arizona, but ranks as a poor leafhopper host there. It occurs in disturbed and overgrazed land in central California.

During 1931–42, Russian-thistle in the San Joaquin Valley varied from about 125,000 acres in 1931 to less than 10,000 acres in 1941 and 1942. Since that time it has again increased. According to Harold Green, entomologist for the California State Department of Agriculture, it appears that 150,000 to 250,000 acres of Russian-thistle in the San Joaquin Valley have been treated for leafhopper control each year from 1960 to 1965, so there must have been a still larger total acreage.

In central California, Russian-thistle seed will germinate any time except midwinter if sufficient moisture is present. Heavy stands followed the inundation of a large area of lowland in June 1931. Normally the bulk of the seed germinates during February and March. The plant starts to mature seed in August and remains attractive to leafhoppers until the last main stem has dried in November.

Under favorable conditions isolated plants may grow as high as 5 feet and be 6 feet in diameter (fig. 12). Entire fields of this plant that range up to 4 feet high are fairly common in some seasons. When the growth is thicker, an almost solid stand from 8 to 18 inches in height results. In

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FIGURE 12.—Heavy growth of Russian-thistle near Mendota, Calif., in 1933.

either type of stand high populations of leafhoppers can develop.

The leafhoppers infest the Russian-thistle at the time of their spring movements, and the population increases to about 25 to 30 leafhoppers per square foot during June. The hot weather of July and August reduces the population, largely because of mortality of newly hatched nymphs, but with cooler weather in September and October the population again builds up, reaching a high point of about 75 leafhoppers per square foot by mid-October. The thistle dries early in November and the leafhoppers leave.

The importance of Russian-thistle as a host plant for the final fall generation of leafhoppers is so great that a survey, covering from 30 to 80 fields scattered over the known thistle area, was made almost every year in mid-October. For the period 1933–42, the samples averaged 62 leafhoppers per square foot. The highest population was 179 per square foot in 1934 and the lowest was 16 in 1940 and 1942.

Large, healthy thistle plants may carry enormous populations of leafhoppers. In 1934, when general populations were very high, three sets of five samples each, taken at random from three large fields, averaged over 1,000 leafhoppers per square foot. The plants in these fields averaged 3 feet in height, with a stand density of 50 to 75 percent. Such fields produced enormous numbers of leafhoppers.

Fogweed or Silverscale. — Fogweed is found in many places in the central valley of California, chiefly in locations with a relatively high water table and with considerable alkali in the surface soil. It occurs almost entirely in disturbed land and has been able to maintain itself indefinitely in the grainlands around Tulare Lake.

The seed of fogweed germinates late in the winter, usually in February or early March. The small plants grow very little until the grain is harvested, when they are about a foot high. After the grain is cut the plants grow rapidly, reaching 3 feet in height by September (fig. 13). The plant matures and dries soon afterward. This drying usually takes place before the fall brood of leafhoppers develops and results in a high nymphal mortality or a forced movement to other plants. In certain seasons and locations, however, fogweed has been known to remain succulent and attractive to the leafhoppers until late October and then produces a large population of fall-brood leafhoppers. This variation has not been fully explained, but undoubtedly is caused, at least in part, by variations in available water.

Fogweed varied greatly in abundance during 1930–43, when it was closely observed. About

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FIGURE 13.—Fogweed plant in stubble field.

165,000 acres were found in 1931, but never more than 50,000 acres during the rest of the period, reaching a low of about 10,000 acres in 1941 and 1942. During this period, the acreage of fogweed was related to the fluctuating supply of water in Tulare Lake, a large part of which is a reservoir in wet years but is farmed in dry years. The acreage of grain near and in the lake was determined by the available water.

In general, leafhopper populations on fogweed were larger in the southern San Joaquin Valley than in the northern part. The seasonal fluctuations in population followed the same general pattern as those on Russian-thistle, with an early peak in June and a late, slightly higher peak in October. With fogweed, however, part of this fall peak is illusory, because large fields may dry, leaving only roadside fogweed in succulent condition, which causes the leafhoppers to concentrate, and it is these concentrations that would have to be sampled.

Bractscale.—Bractscale has been found throughout the San Joaquin Valley in locations similar to those occupied by fogweed. It is less tolerant of alkali in the soil than fogweed and more like Russian-thistle. Most stands of bractscale have been found east of the San Joaquin River, and its distribution west of the valley bottom is limited to very small disturbed areas in the foothill ranges.

Bractscale germinates in the late winter, and has a seasonal history like that of fogweed. Generally it matures later than fogweed, and is often succulent sufficiently late in the season to mature the fall generation of leafhoppers.

In 1930 and 1931, bractscale was very abundant, with about 114,000 acres in 1931. This area decreased rapidly to less than 10,000 acres in 1935, and bractscale was a relatively scarce barnyard, fence-row, and ditchbank weed for the remainder of this study, probably because of shifts in agricultural crops and techniques. (See Lawson and Piemeisel 44.)

Many field samples of bractscale were taken during its years of abundance, and the leafhopper populations found followed the general trends of those on Russian-thistle and fogweed, except that the populations on bractscale were at no time as high as on the other plants.

Relative Importance of Summer Hosts.—The importance of a host plant in the economy of the leafhopper depends on many factors. The more obvious of these may be summed up in the statement that the plant must be in the right place at the right time and be attractive to the female leafhoppers for oviposition.

Populations of leafhoppers found on the three most important summer hosts—Russian-thistle, fogweed, and bractscale—are shown in figure 14. Since the critical period in the economy of the leafhopper comes in the fall, Russian-thistle ranks far above the others in this respect. This plant is also found in the critical areas in or near the overwintering quarters of the leafhopper. Fogweed ranks second because of its general distribution in the valley bottom, whereas bractscale, with a more local distribution and poor host-plant qualities in the fall, ranks third.

Fall Holdover Hosts

Species Involved. — Although many species of perennials are found in the wash bottom, only a few are both abundant and widespread in the areas where the leafhoppers exist. In the northern part of the San Joaquin Valley, chrysopsis (*Chrysopsis villosa* (Pursh) Nutt.) occupies much of the wash bottom, with occasional patches of lepidospartum, alkali heath (*Frankenia grandifolia* C. & S.), alkali blite (*Suaeda moquini* Greene), and saltgrass (*Distichlis spicata* (L.) Greene). Ascending the canyons, other species such as California sagebrush, wild buckwheat (*Eriogonum fasciculatum* Benth.), and snakeweed (*Gutierrezia californica* (DC.) T. & G.) become more common. On the hillsides are found such perennials as licorice (*Glycyrrhiza lepidota* Pursh) and horehound (*Marrubium vulgare* L.) and such annuals as tarweed (*Hemizonia* spp.) and bluecurl (*Trichostema lanceolatum* Benth.), sometimes covering rather large areas. In the central part of the San Joaquin Valley, chrysopsis is replaced by desert sage, wild buckwheat becomes more abundant, and rattleweed (*Astragalus leucophyllus*

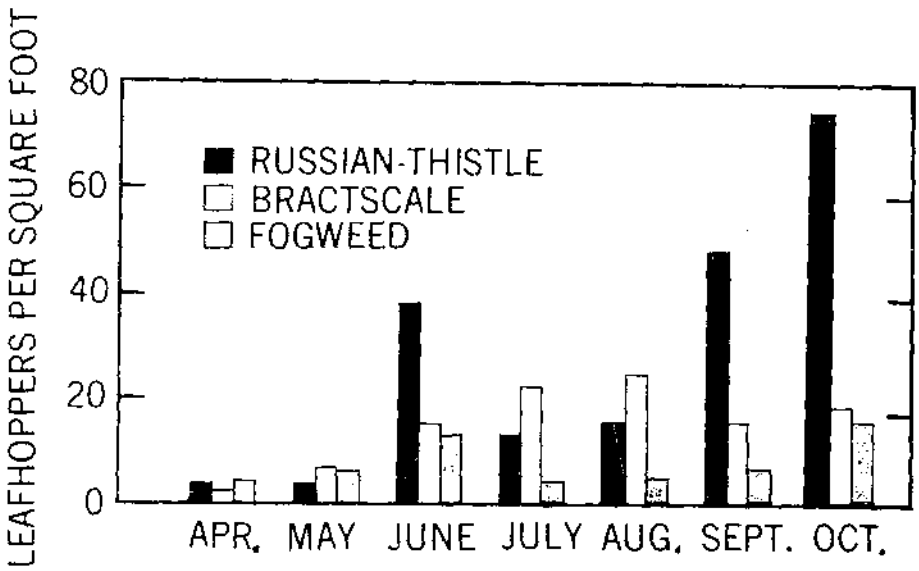


FIGURE 14.—Leafhopper populations per square foot on three principal summer hosts in central California, 1931–40.

T. & G.) begins to become common. In the southern part of the area, desert sage is by far the most abundant holdover host, with lepidospartum and isocoma (*Isocoma veneta* (H. B. K.) Greene) as minor hosts.

The relative abundance and attractiveness to the leafhopper of the principal fall holdover hosts in central California, where samples were taken on all holdover hosts for many years, were tabulated. Plant species on which the largest number of samples were taken are as follows:

Plant species	*Number of samples*
Desert sage	479
Lepidospartum	422
Bluecurl	310
Snakeweed	181
Alkali heath	149
Tarweed	140
Alkali blite	98
Rattleweed	88
Chrysopsis	71
Isocoma	36

These data should not be confused with the general abundance of these species in central California, as some abundant species were usually too dry to sample late in the fall (chrysopsis) or occurred in areas only briefly visited by the leafhoppers (spiny saltbush, alkali blite).

Plant species with the greatest average leafhopper populations in the fall are as follows:

Plant species	*Leafhoppers per square foot*
Burro fat (*Isomeris arborea* Nutt.)	26.8
Pickleweed (*Allenrolfea occidentalis* (Wats.) Ktze.)	19.9
Creek senecio (*Senecio douglassii* DC.)	19.0
Desert sage	6.2
Spiny saltbush	5.0
Lepidospartum	4.2
Jimsonweed (*Datura meteloides* DC.)	3.5
Rattleweed	3.3
Flax (*Linum usitatissimum* L.)	3.1
Alkali blite	2.8

These data emphasize attractiveness to the leafhopper rather than availability. The first three species occur sparingly in the habitats sampled, although pickleweed covers thousands of acres in the valley bottom.

Both tabulations emphasize that the leafhopper will try to feed on any green plant that is available in the fall, and the utilization of certain host plants is due as much to their location as to their suitability for maintaining the leafhoppers. Australian saltbush and quail-brush are both excellent host plants when leafhoppers are confined on them, but, although both species are fairly common in the areas where these insects seek holdover hosts, very few leafhoppers are found on them in central California.

To further emphasize the wide variety of host plants on which the leafhoppers may feed during the fall, H. E. Wallace tied cages containing 25 to 50 leafhoppers each on willow, pine, fig, and almond trees on the grounds of the Modesto laboratory during the fall of 1935. When the cages were examined in January, 69 days later, the mortality was as follows:

Host plant	*Mortality (percent)*
Willow	33.0
Pine	44.4
Fig	47.5
Almond	86.3

The leaves dropped from the deciduous trees during this experiment, but the leafhoppers maintained themselves on the green stems. This would indicate that almost any plant can maintain them in the fall for a considerable period under central California conditions.

Mortality of Leafhoppers on Holdover Hosts.—In the fall of

1933, H. E. Wallace tied cheesecloth bags containing 25 beet leafhoppers each on naturally growing perennial plants in canyons on the west side of the San Joaquin Valley. The host-plant species selected were those where leafhoppers had been found to congregate in the fall. In a northern canyon, 20 cages each were placed on lepidospartum, snakeweed, chrysopsis, California sagebrush, and wild buckwheat. Because some of the important hosts did not occur so far north, 10 cages each were placed on Australian saltbush and desert sage in an area 50 miles farther south. Some or all of the cages were removed weekly by cutting off the stem of the plant, the leafhoppers counted into a pipet, and the survivors recaged on another branch of the same plant. Another set of cages was tied on the same plants to supply leafhoppers for fat determinations. The mortality in this test is given in table 9.

This mortality varied greatly on different holdover host plants. Lepidospartum and snakeweed are very important hosts wherever they are found, whereas desert sage is the only available holdover plant in much of the southern San Joaquin Valley. The others are of rather minor importance. Although Australian saltbush was one of the most favorable plants, leafhoppers rarely fed on it in large numbers during the fall. A direct comparison of the mortality between the first five and the last two plants cannot be made because of the differing locations.

At the time that the counts were made, samples of leafhoppers from other cages were taken for fat samples and shipped to R. A. Fulton at the Twin Falls, Idaho, laboratory. All the leafhoppers in some of these cages were dead after 4 weeks, and no more were available for fat analysis until the test was terminated on December 22, after 10 weeks, when samples were taken from the surviving leafhoppers in the mortality test cages. The remaining live leafhoppers were taken to the laboratory and caged on filaree for 12 days, when final fat samples were taken. The fat content

TABLE 9.—*Mortality of beet leafhoppers on holdover hosts in San Joaquin Valley in fall of 1933 (data from H. E. Wallace)*

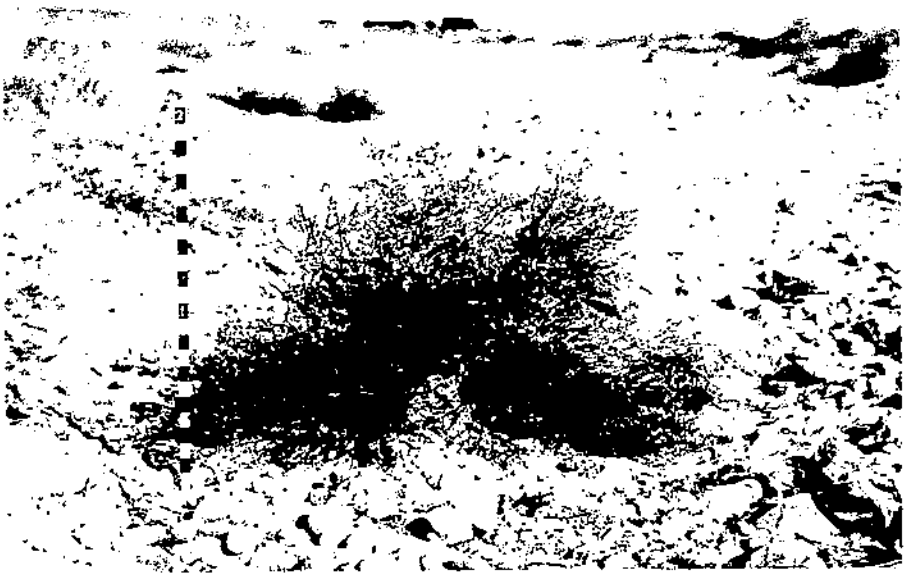
Locality and host plant	Mortality at end of indicated exposure in weeks				
	1	5	7	8	10
Northern San Joaquin Valley:	*Percent*	*Percent*	*Percent*	*Percent*	*Percent*
Lepidospartum	3.2	7.0	8.4	8.9	12.3
Snakeweed	5.2	9.7	12.4	13.4	17.7
Chrysopsis	7.2	11.8	14.8	16.6	23.8
California sagebrush	1.6	21.7	31.1	32.8	38.9
Wild buckwheat	11.2	41.8	81.2	86.5	92.6
Central San Joaquin Valley:					
Australian saltbush	0	1.6	7.5	10.9	(1)
Desert sage	3.0	36.8	44.7	47.4	63.8

[1] Australian saltbush, a prostrate plant, and cages were trampled by livestock between 8th and 10th weeks.

TABLE 10.—*Fat content of beet leafhoppers held for varying periods on naturally growing perennials in San Joaquin Valley in fall of 1933*

Host plant	Fat, as percent of dry weight, on date indicated						
	Oct. 13	Oct. 19	Oct. 26	Nov. 2	Nov. 9	Dec. 22	Jan. 1 [1]
	Percent	*Percent*	*Percent*	*Percent*	*Percent*	*Percent*	*Percent*
Russian-thistle	[2] 41.7						
Lepidospartum		36.1	34.2	33.5	35.9	11.5	12.6
Wild buckwheat		33.1	26.2	22.6	13.4	9.1	
Chrysopsis		33.1	26.6	24.1	23.1	10.2	13.4
Snakeweed		27.9	27.4	22.2	15.5	11.2	16.8
California sagebrush						8.2	24.5
Australian saltbush						20.1	19.7

[1] Survivors on Dec. 22 were held until Jan. 1 on filaree at laboratory.
[2] Fat content of leafhoppers as obtained to start experiment.



BN-26258

FIGURE 15.—Lepidospartum plant in wash bottom.

determined by Fulton is given in table 10.

The decline in the fat content of the leafhoppers is fairly indicative of their loss of vitality and consequent mortality. Note that the fat content increased slightly from December 22 to January 1 in all but one case when the survivors were caged on filaree.

Cook (*11*) followed up this finding and substantiated it. He showed that leafhoppers held on holdover hosts lost vitality, which varied with the host plant and the length of time they were caged.

This paralleled the mortality on the same host plants, as found by H. E. Wallace. Measurements of fat content also confirmed Wallace's finding. In tests where leafhoppers were held on holdover hosts for 30 days and then moved to winter annuals or sugarbeets (Cook *13*), the leafhoppers regained some of their lost fat and vitality and were about equal in both respects to others held on favorable annual hosts for the entire period.

Although the leafhopper can exist for some time on any one of a considerable number of perennial and annual holdover host plants, lepidospartum and desert sage are of greatest economic importance in central California. Lepidospartum (fig. 15) is found in patches in wash bottoms, where some underground water may be available. These patches are in strategic locations, and the leafhopper will find them as it moves up from the valley bottom. It is an excellent holdover host, as the leafhoppers lose their vitality and fat content very slowly when confined on it.

Desert sage (fig. 16) is not nearly so good a host plant as lepidospartum, but it is very important, as it is widespread on the plains outside of the canyons and on the sides of the washes. Thus, lepidospartum is important because it occurs in particularly strategic locations, whereas desert sage is important because it is widely distributed.

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FIGURE 16.—Desert sage plant.

GREAT SOUTHERN DESERT

The great southern desert is the most extensive desert area in North America. It extends about 500 miles from the California Sierras to southeastern Arizona and from southern Nevada and southwestern Utah to northern Mexico. On the topographic map (fig. 17) all the area shown below 3,000 feet is desert, as is much of that between 3,000 and 5,000 feet. This is all included in the southern desert shrub vegetation type of Shantz (*52*).

The southern desert lies between two great rainfall types, the southern Great Plains type on the east, where most of the rain falls during the summer, and the Pacific type on the west, where most of the rain comes in the winter. As a consequence, there is a definite rainfall gradient across the area from east to west. Most of the desert in Arizona has periods of rainfall in both winter and summer. Winter rains come from December to February, and summer rains, often locally heavy thunderstorms, come in July and August. The northern part of the desert in Utah and Nevada has

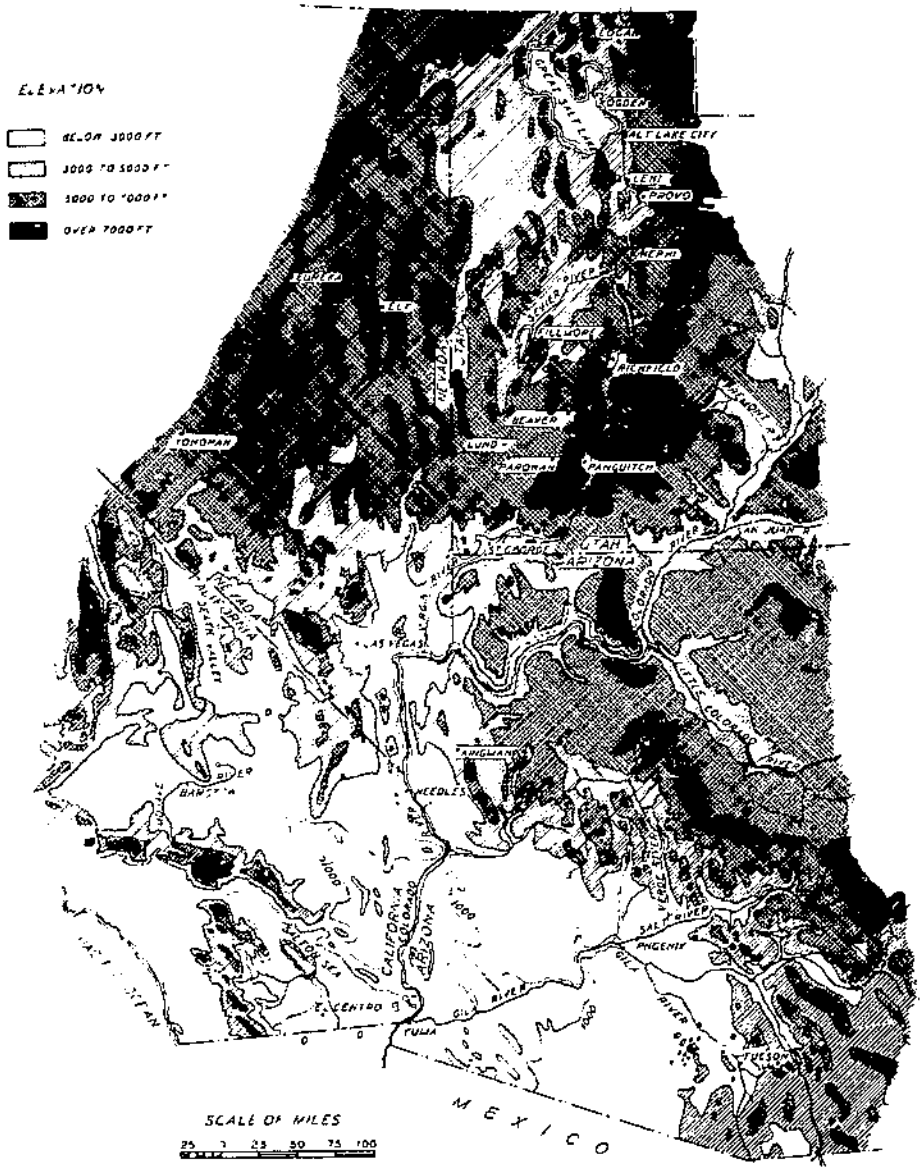


FIGURE 17.—Topographic map of great southern desert and adjacent areas in western Utah, eastern Nevada, southeastern California, and western Arizona.

slightly more winter than summer rainfall. Farther west in the California desert area the summer rains become less reliable and finally fail altogether. Records from 31 weather stations in Arizona, 11 in Utah and Nevada, and 13 in California have been averaged and plotted to show these differences in climatic type (fig. 18).

In the area where summer rains

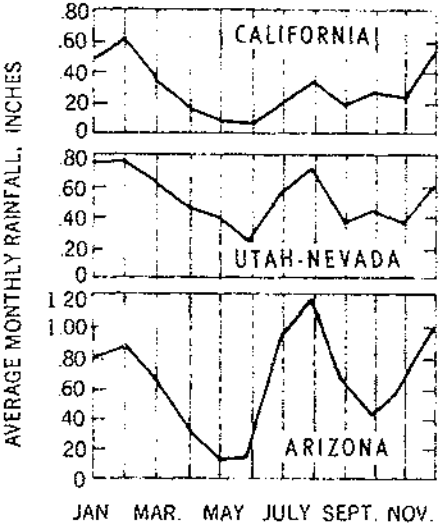


FIGURE 18.—Average monthly rainfall for 31 weather stations in Arizona, 11 in Utah and Nevada, and 13 in California. (From U.S. Dept. Agr. Ybk. (1941).)

are more or less reliable, several summer annuals germinate in July and remain green until fall. In the western part of the desert these annuals are lacking, and the only summer host plants are weeds around the irrigated parts of the desert.

In addition to this variation in seasonal rainfall, there is an important difference in the total amount received. The Arizona, Utah-Nevada, and California stations averaged 7.49, 6.24, and 3.51 inches, respectively.

Besides being scanty, the rainfall in these desert areas is very erratic. A year of heavy rainfall may be followed by 2 or 3 years of little or no rainfall, or vice versa. In the years of heavy, widespread rains, annual vegetation will germinate over a large part of the desert and may support large populations of the beet leafhopper. In very dry years the annual vegetation, where present, is confined to small patches around the base of desert shrubs and may be entirely absent over large areas. Under such conditions few beet leafhoppers are produced.

Work on the leafhopper in the southern desert was undertaken to locate the sources of beet leafhoppers that invaded the beetfields of central Utah and western Colorado. Studies were made in central Utah by E. W. Davis in 1927 and in the Grand Junction area of western Colorado by W. A. Shands in 1930. These led independently to the discovery of two widely separated parts of the southern desert breeding area in 1928 and 1934, respectively. The work of Davis and H. E. Dorst in Utah located the source of the leafhoppers infesting central Utah in the tongue of desert running south and west from St. George, Utah, and spreading into the main desert as far as Kingman, Ariz., and Needles, Calif. W. A. Shands, V. E. Romney, and M. F. Bowen, working farther east, traced the leafhoppers from western Colorado backward into the Arizona desert around Phoenix.

It was thought for some time that the two breeding areas were unrelated, but further studies showed that one large breeding area is involved. The Wasatch Range of the Rocky Mountain system divides Utah on the north-south line. Leafhoppers bred in the eastern part of the desert usually move northward to the east of that range, and those from the western part move west of the Wasatch Range.

Breeding Areas

In discussing the amount and distribution of rainfall over the

great southern desert (p. 40), the weather stations were grouped as follows: Arizona, Utah-Nevada, and California. These same groupings serve to separate three parts of the desert breeding area, which differ considerably in their host-plant complex and leafhopper seasonal history. The variations are gradual, and no definite lines can be drawn. In general, the Colorado River separates the California and Arizona areas, and the Utah-Nevada area extends southward into California and Arizona about as far as Needles, Calif., and Kingman, Ariz.

Host Plants

The host-plant situation in the great southern desert is even more complex than in central California. Seeds of many plants are plentiful, but may lie dormant for many years until temperature and moisture are favorable. Under such conditions the plants may germinate profusely, but they may never mature because of lack of rainfall following germination. This happens much more frequently here than in central California. An additional hazard is high wind, which carries sand and fine gravel along the surface and may cut off the plants at the ground level. Another hazard is the irregularity of the plant stands. Summer annuals may produce a large fall brood of leafhoppers in an area where winter germination is scanty, and the leafhoppers have to search elsewhere for hosts, usually with a heavy mortality.

The fall or winter rains that germinate the winter annuals may start any time between October and February. The earlier the host plants are germinated, the more favorable are the overwintering conditions for the leafhopper. Since these and other hazards keep down leafhopper populations in this area, it is only rarely that high leafhopper populations are found in the spring over large areas.

Winter and Spring Annual Hosts

The most important winter and spring annuals in this area were the pepperweeds, patata, desert plantains, redstem filaree, tansymustards, nievitas, and bladderpod.

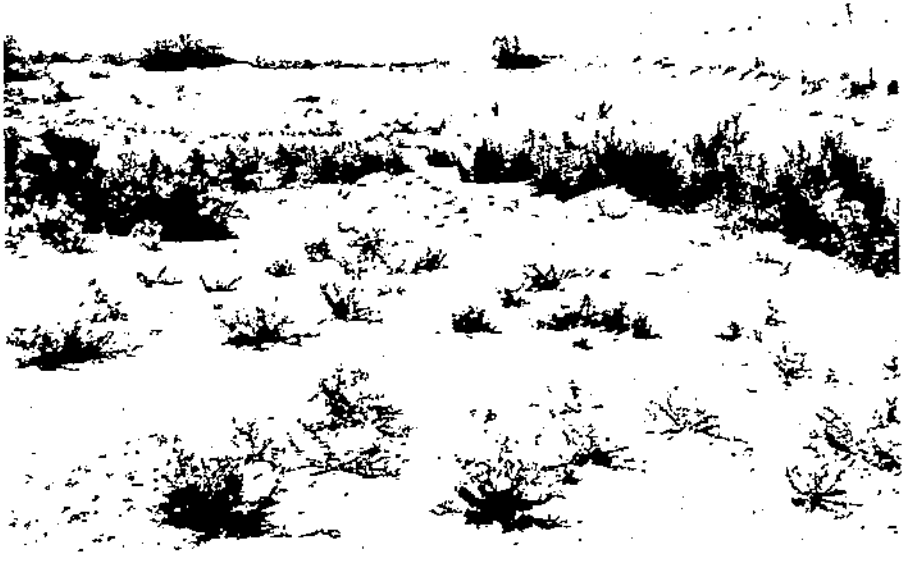
The pepperweeds had the widest distribution of any winter annual over the area as a whole. *Lepidium lasiocarpum* (fig. 19, *A*) was most abundant, with an occasional *L. medium* Greene. These plants occurred in varying proportions in all parts of the desert. At elevations above 4,000 feet in the Utah-Nevada and California areas, stands of *L. densiflorum* were common. In southeastern Arizona *L. thurberi* replaced the others (fig. 20). In some years stands of this plant occupied nearly half the total area in this section. Pepperweeds are among the most favorable breeding host plants of the leafhopper, and the overall population density of this insect in many areas can be judged from the abundance and condition of these plants.

Patata (fig. 19, *B*) was the second most important annual for overwintering and development of the first spring generation in the central Arizona area. The 1937 survey, including 345 random stops, showed that stands of this plant occupied about 1,665 square miles, with an average density of 10.9 percent. The plant was also found in scattered patches in southeastern Arizona.


A


B

[illegible]



BN 2021 and BN 2240

Boll weevil damage in Pima cotton, Arizona. *A*, Apache 1. Square shed; *B*, Star Cross all. Photographed in 1961.

Desert plantains were third in overall abundance and they served as important breeding hosts for the beet leafhopper in the Utah-Nevada and California areas, where extensive stands were found without intermixture of mustards or other preferred plants. The most common desert plantain was *Plantago insularis* var. *fastigiata*, with some *P. purshii*. *P. erecta* occurred in the northern Utah-Nevada area.

Redstem filaree was very abundant and widely distributed except in the southern California desert area. This plant should not be classed among the preferred host plants in most of the Arizona area, but E. W. Davis and H. E. Dorst found it to be of great importance in the Utah-Nevada area. It often remained green longer than the mustards and supported large populations of leafhoppers, which hatched on the intermixed mustards and were forced to move when they dried. It was often an important host plant for the second spring generation.

The tansymustards in the southern desert were largely *Descurainia pinnata* (Walt.) Britton, with some *D. obtusa* (Greene) O. E. Schulz and *D. sophia*, all of which were about equally attractive to the leafhopper. These plants were fairly abundant in the Arizona area and common in the other areas.

Several species of nievita occurred. *Cryptantha angustifolia* (Torr.) Greene was the most abundant, with some *C. micrantha* (Torr.) Johnston and *C. maritima* (Greene) Greene. The principal range of these plants was in the California desert area, where they served as hosts for the second spring generation of leafhoppers during May.

Bladderpod has a rather extended range in Arizona, but occurred mostly in sparse stands. It was a good spring breeding host when not mixed with pepperweeds or patata.

Wild mignonette (fig. 21) occurred irregularly. It might be very abundant one year and completely absent the next. The reasons for these fluctuations are not known. In 1937, this plant was not easily seen during March in the Phoenix, Ariz., area, but by May its stands were estimated to occupy some 1,000 square miles, and it was found to be a very important host plant, as it remained green long enough for two generations of the leafhopper to develop. In 1939, wild mignonette was common in the Phoenix area and in the Imperial Valley of California, and occurred in spotted patches over the rest of the Cali-

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FIGURE 21.—Wild mignonette: *A*, Stand on bottom land near Blythe, Calif., in 1940; *B*, single plant; such individual plants may produce as many as 5,000 leafhoppers.

fornia desert. In 1940, it was very abundant throughout its range. The largest beet leafhopper populations per unit area recorded for the southern desert have been found on this plant, although its usually scattered distribution and irregular occurrence limited its importance.

Other plants of minor importance as spring breeding host plants for the beet leafhopper in the southern desert included *Pectocarya heterocarpa* Johnston, which was abundant and of some importance as a host plant in the Utah-Nevada and California areas, where it helped mature the second spring generation during May. Other plants were *Microsisymbrium laciophyllum* (Hook. and Arn.) O. E. Schulz, *Lupinus arizonicus* (S. Wats.) S. Wats., and hedgemustard. A popcorn flower (*Plagiobothrys* sp.) is associated with desert plantains in the Imperial Valley and often carries large leafhopper populations.

In years of favorable rainfall, spectacle-pod mustard occurs along the sandy riverbeds near Phoenix. Although the area is comparatively small, the close proximity to the cultivated areas and the potential productivity of this plant as a leafhopper host make it at least of local concern. In April 1953, an estimated 6 square miles of spectacle-pod mustard along the Salt River bed near Phoenix contained an average leafhopper population of 492 nymphs and 8 adults per square foot.

Composition and Density of Winter Annual Cover.—To obtain information on the distribution and abundance of the winter annuals where the leafhoppers bred, V. E. Romney and M. F. Bowen sampled many places in the southern desert between 1937 and 1940, recording the plants present and the density at each stop. An attempt was made to estimate, at least roughly, the number of square miles involved in these host-plant stands. For the purpose of this analysis, the Arizona area was subdivided into southeast Arizona, including the area around Safford and Douglas, and the Phoenix area, taking in the remainder of Arizona as far as Kingman.

Table 11 shows that in favorable seasons the 72,200 square miles of desert may support nearly 60,000 square miles, or five-sixths the total area, of leafhopper host plants. As shown, southeast Arizona and Utah-Nevada had host-plant areas exceeding their total extent because of more than one host in a particular area. These mixed stands were more prevalent at slightly higher elevations than the others, indicating somewhat higher rainfall.

Characteristic stands of winter and spring host plants are shown in figure 22.

The same data used for table 11

TABLE 11.—*Total area of southern desert and estimated area occupied by beet leafhopper host plants in favorable winter and spring seasons, 1937–40*

Breeding area	Total area	Area occupied by host plants
	Square miles	*Square miles*
Phoenix, Ariz.	29,000	21,700
Southeast Arizona	7,000	7,900
Utah-Nevada	15,500	17,000
California	20,700	12,950
Total	72,200	59,550

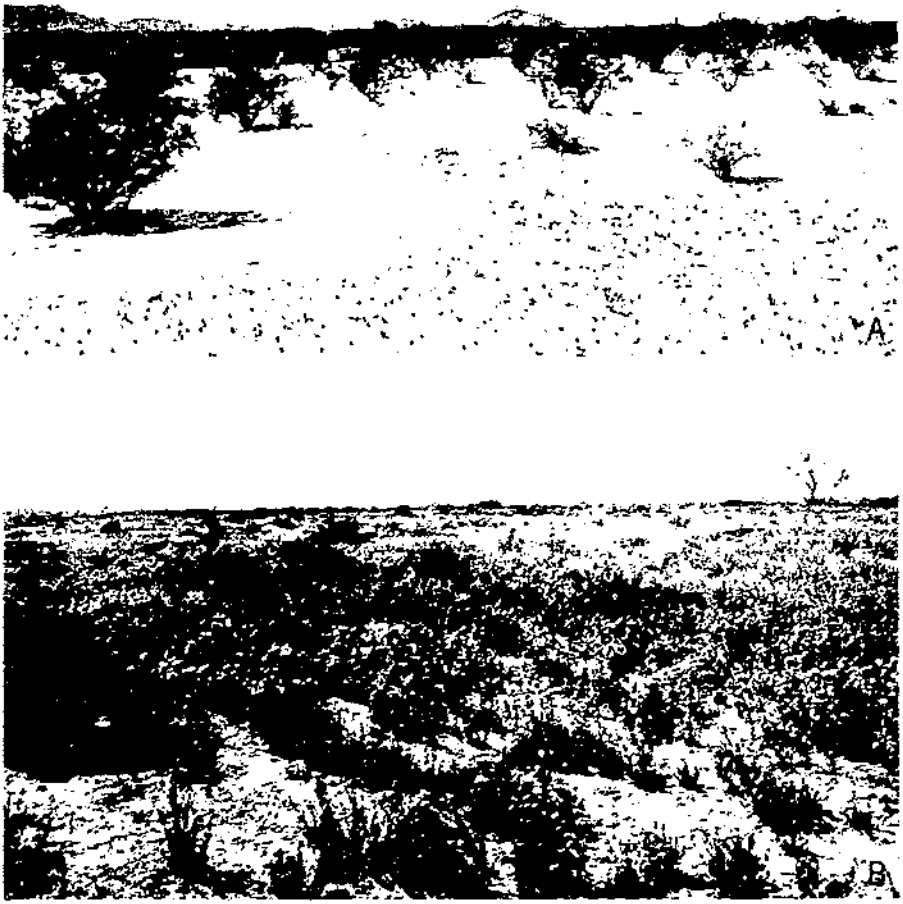

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FIGURE 22.—Winter and spring host plants in Phoenix, Ariz., area: *A*, Filaree and desert plantains among creosote bushes; *B*, nearly pure stand of spectacle-pod mustard along Salt River bed.

have been recombined in table 12 to show the relative importance of the individual host plants in the various areas.

In table 12 the stands are subdivided according to the host plants present, and the percentages of the total host-plant stands occupied by each species or group are calculated for each area. The stand density, or ground cover, for the different host plants is indicated. The pepperweeds were most abundant in southeast Arizona and Phoenix areas, but much less important in the California

TABLE 12. *Total beet leafhopper host-plant area occupied by stands of particular species or groups and their range in density of ground cover*

Host plant	Total host-plant stands in area indicated				Ground cover
	Phoenix, Ariz.	Southeast Arizona	Utah-Nevada	California	
	Percent	*Percent*	*Percent*	*Percent*	*Percent*
Pepperweeds	39.6	45.6	31.2	14.7	0-2.3
Desert plantains	29.0	8.9	19.4	30.9	0-8.5
Redstem filaree	13.4	25.3	20.6	30.9	0-21.5
Tansymustards	7.4	16.5	7.6	6.2	0-2.8
Nievitas	0	0	15.9	17.0	0-3.0
Bladderpod	10.6	3.7	5.3	.3	0-1.5

desert. The desert plantains were very important in the California and Phoenix areas, but less important elsewhere. Redstem filaree was rather evenly distributed, but somewhat less abundant in the Phoenix area, which has a low altitude, than in the higher areas. The tansymustards were abundant in southeast Arizona only; nievitas were important in the Utah-Nevada and California areas and bladderpod only in the Phoenix area. Patata was not included in these stand estimates, although it was a very important spring host plant in the Phoenix area.

Abundance of Winter Annuals in Relation to Rainfall.—Precipitation in the fall and early winter of 1936–37 was about 19 percent above normal, whereas in 1937–38 in the same area for the corresponding period it was 40 percent below normal. This greatly affected both the areas occupied and the stand density of the winter annual host plants. The central Arizona area was sampled from January to late March in both years; stops were made at 3-, 5-, or 10-mile intervals. At each stop the composition and density of the annual vegetation were estimated, and the total area occupied, in square miles, was projected from these basic data. The equivalent solid stand was obtained in each case by multiplying the total area covered by the percent density. The changes from 1936–37 to 1937–38 were calculated on the solid stand data. The basic data and calculations are given in table 13.

The only host plant showing a positive change from 1936–37 to 1937–38 was filaree, possibly because its greater drought resistance enabled it to continue growing in 1938 after competing annuals had died. The ground cover for all species combined was reduced from 5 to just over 4 percent, and the total area occupied from 31,600 to 22,900 square miles. Although filaree was apparently the least affected, patata, tansymustards, and bladderpod were most severely affected, with reductions of about 90 percent in their total plant population.

A similar study was made near Kingman, Ariz., in which the dry season 1935–36, with 3.18 inches of rainfall, was contrasted with the wet season 1938–39, with 6.36 inches. The data are given in table 14.

TABLE 13.—*Host-plant abundance in central Arizona in wet season of 1936–37 as compared with dry season of 1937–38*

Host plant	Wet season (1936–37)			Dry season (1937–38)			Solid stand change from 1936–37 to 1937–38
	Total area	Ground cover	Equivalent solid stand	Total area	Ground cover	Equivalent solid stand	
	Square miles	*Percent*	*Square miles*	*Square miles*	*Percent*	*Square miles*	*Percent*
Pectocarya	8,400	7.2	605	6,000	6.4	384	−36.5
Redstem filaree	2,900	9.4	273	2,900	11.2	325	+19.0
Desert plantains	6,300	4.2	265	4,700	2.7	127	−52.1
Pepperweeds	8,400	2.3	193	6,800	1.2	82	−57.5
Patata	1,700	10.9	185	1,000	2.1	21	−88.6
Tansymustards	1,600	2.8	45	100	2.0	2	−95.6
Bladderpod	2,300	.8	18	1,400	.2	3	−83.3
Total or average	31,600	5.01	1,584	22,900	4.12	944	−40.4

TABLE 14.—*Host-plant abundance in Kingman area of northwestern Arizona for dry season of 1935–36 as compared with wet season of 1938–39*

Host plant	Dry season (1935–36)			Wet season (1938–39)			Solid stand change from 1935–36 to 1938–39
	Total area	Ground cover	Equivalent solid stand	Total area	Ground cover	Equivalent solid stand	
	Square miles	*Percent*	*Square miles*	*Square miles*	*Percent*	*Square miles*	*Percent*
Pectocarya	1,000	12.4	124	2,800	3.8	106	−14.6
Pepperweeds	800	.3	2	2,300	.4	9	+350.0
Redstem filaree	1,600	13.4	214	2,200	15.5	341	+59.3
Desert plantains	300	1.4	4	1,100	4.9	54	+1,350.0
Tansymustards	300	2.6	8	800	.3	2	−75.0
Total or average	4,000	8.8	352	9,200	5.6	512	+45.4

In the northwestern Arizona study there was a heavier ground cover of host plants in the dry year, but the total square miles of hosts, either the whole area covered or the computed solid stand, were much less. There were heavier stands of pectocarya and tansymustards in the dry season, but these were greatly reduced in area. Redstem filaree appeared in both studies to be less affected by shifts in rainfall than most of the other host plants.

It is interesting to compare these desert areas, with their plant stands covering from 4 to 10 percent of the area, to the heavy growth in the San Joaquin Valley of California, with its 200–

500 plants per square foot in a solid stand (table 8).

Leafhopper Populations on Winter Annuals. — To estimate the population of overwintering females in the southern desert, sampling surveys were made from January to March during 1936–42. Most of the counts were made by the hand-and-knee method. Not all the desert was sampled in any one season, and the intensity of sampling varied greatly. However, the data in table 15 indicate the general magnitude of the overwintering populations found.

This table, although not a compilation for each area for the whole period, shows that adult populations varied from place to place and from time to time. In general, the Arizona areas produced more prolific leafhopper breeders than the California areas, as might be expected from their slightly higher rainfall. Also, populations varied greatly from year to year within any area, as shown for central Arizona, which had 0.6 leafhopper per 100 square feet in 1938 against 3.83 leafhoppers in 1936. Furthermore, populations over the entire area varied greatly in different seasons. In this table, 1936, 1939, and 1942 were seasons of relatively high leafhopper numbers, whereas 1938 was very low in the areas sampled.

Summer Annuals

In those areas where summer rains are fairly reliable, a group of annuals germinates in July or August and remains succulent as long as moisture is available, which may be as late as November. These summer hosts are most

TABLE 15.—*Numbers of overwintering beet leafhoppers found in various parts of southern desert during 1936–42*

Year and area sampled [1]	Total samples	Samples infested	Adults per 100 square feet
1936:	*Number*	*Percent*	*Number*
Arizona, central	386	78	3.83
Arizona, southeastern	19	100	9.00
Utah-Nevada	21	71	2.56
1937:			
Arizona, central	329	57	1.18
Arizona, southeastern	13	31	.38
1938:			
Arizona, central	265	33	.60
California, northeastern	12	33	.58
California, southern	17	6	.01
1939:			
Arizona, southeastern	57	49	2.07
Utah-Nevada	38	42	1.42
California, northeastern	36	58	1.03
California, southern	37	19	.35
California, northwestern	29	7	.21
1942:			
Arizona, southeastern	16	31	.55
California, northeastern	35	31	1.84
California, southern	35	26	3.51

[1] Compass directions refer to parts of desert, not necessarily to parts of States.

abundant in southern Arizona and become less abundant to the west and north as summer rains become less reliable. The Utah-Nevada area and the northern part of California may contain scattered patches of these hosts in favorable years.

The principal summer hosts in central Arizona are chinchweed, tidestromia, trianthema, and some annual saltbushes. Chinchweed is the most abundant and widespread of this group, tidestromia occurs over the northeastern two-thirds of central Arizona, and trianthema and the annual saltbushes are found in the southern part of the desert. Characteristic stands of tidestromia and trianthema are shown in figure 23.

In the Utah-Nevada area the

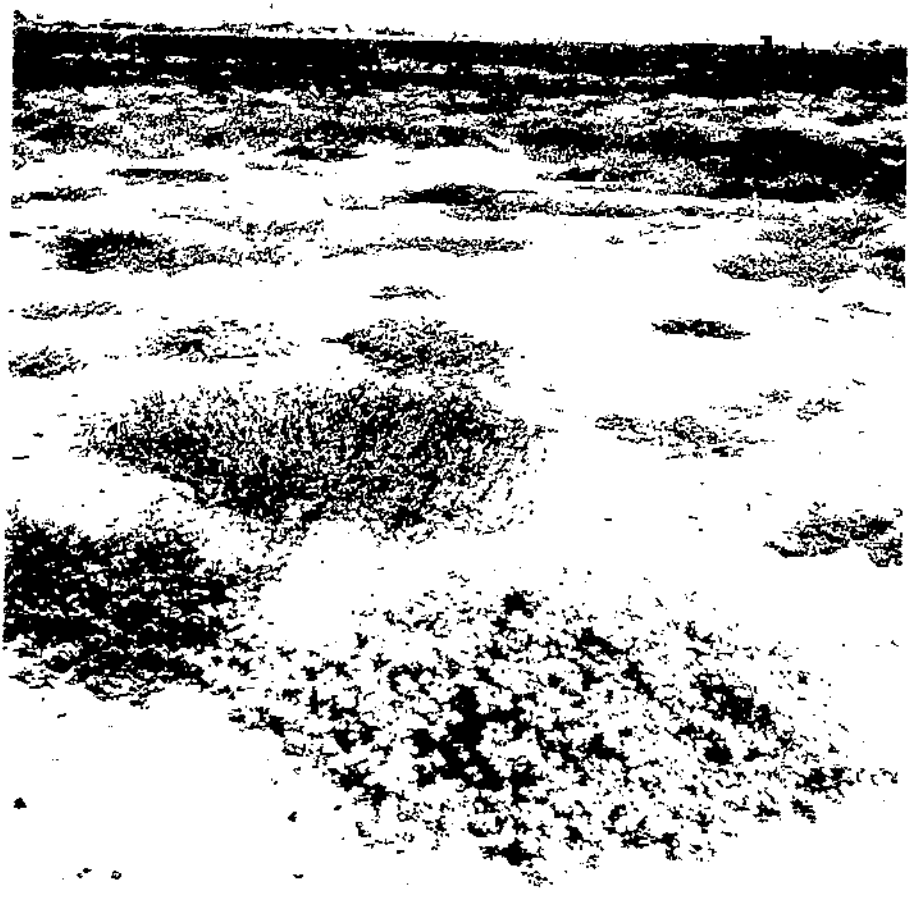

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FIGURE 23.—Summer and fall host plants near Phoenix, Ariz., in September: White mound in foreground is tidestromia, darker plants around it are trianthema, and taller dark plants in upper right background are Russian-thistle.

only important summer hosts are chinchweed, spiderflower (*Cleome lutea* Hook.), Russian-thistle, and redscale. Of these, chinchweed and spiderflower occurred in the open desert and the others around the small irrigated areas. Chinchweed germinates with the late summer rains and matures in October, spiderflower is an early summer plant maturing in May, and Russian-thistle and redscale germinate in the spring and remain succulent until fall.

Holdover Hosts

Since the southern desert is so large, with such great variations in rainfall and elevation, many holdover hosts have been used by the leafhopper. Some of these hosts and the desert area where each is useful are as follows:

Species	Desert area		
	Arizona	*Utah-Nevada*	*California*
Creosotebush	X	X	X
Bursage (*Franseria dumosa* Gray)	X	X	X
Desert sage	X	X	X
Chamiso	X	X	X
Seepweeds (*Dondia* spp.)	X	X	X
Arrowweed (*Pluchea sericea* (Nutt.) Cov.)		X	X
Quail-brush		X	X
Burrobrush (*Hymenoclea salsola* Torr. & Gray)		X	X
Desert thorn (*Lycium* spp.)	X		
Spurge (*Euphorbia polycarpa* Benth.)	X		
Globemallow (*Spaeralcea emoryi* Torr.)	X		
False tarragon		X	
Rabbitbrushes		X	
Snakeweeds		X	
Pepperweed (*Lepidium fremontii* Wats.)		X	
Goldenweed (*Applopappus acradenius* (Greene) Blake)		X	

As in California, mortality among leafhoppers may become high if they are forced to remain on some of these hosts for long periods.

Southern Arizona Desert

The southern Arizona desert has both winter and summer rainfall, with corresponding groups of annual plants. Periods on holdover hosts come between May and July, and in many years again in November and December. Some of the winter annuals remain succulent into May, and studies over a period of years indicated that the areal extent of these late annuals may be at least as important in producing a large population of spring leafhoppers as the number of leafhoppers that overwintered. In other words, it is possible for a small number of leafhoppers surviving in early spring to build up a high population by May if succulent vegetation is abundant at that time. Two generations of leafhoppers develop in the spring if vegetation is favorable into May, but only one generation is found in dry years.

Generations on Winter Annuals

It is difficult to deduce the number of generations from overall population trends as the plant stands thinned and contracted during the spring, concentrating the leafhoppers. Consequently, an analysis of the percentage of the

nymphs in the various stages was made in conjunction with measures of total population density.

Nymphs were collected with a 1/8-square-foot sampling pan at approximately semimonthly intervals from many points well scattered over the Phoenix area. These nymphs were then grouped and the percentage of each instar was determined. During the spring seasons of 1935 and 1937 partial stands of the pepperweeds remained alive well into May over the areas included in the study. The data concerning nymphal populations for these two seasons are given in table 16.

In this type of sampling study a gradual increase in the number of fourth and fifth instars indicates the maturing of a brood. When this is followed by a large increase in the number of first instars, another brood is starting.

The data for 1935 are not clear cut for the first spring generation. There were two peaks of fifth instars before April 22, indicating a break in egg laying probably due to cold weather in February. The second generation started near April 20, as shown by the large proportion of first and second instars, and matured late in May. Favorable host-plant conditions made it possible to start a third generation early in June, but these perished from heat and drying of their hosts.

In 1937, sampling was started later, so that any irregularities in the broods of the first generation did not appear. The first spring generation matured about April 15 and the second near the middle of May.

Generations on Summer Annuals

Similar studies of beet leafhopper nymphal size and abundance were made on summer host plants during 1934–41. On the basis of nymphal size, the data showed

TABLE 16.—*Distribution of beet leafhopper nymphs in samples taken in Phoenix, Ariz., area Feb. 21 through June 5, 1935, and Apr. 17 through May 14, 1937. (Figures in italics show highest percentage for each date.)*

Survey date	Total nymphs	Nymphal instars in percent of total				
		1	2	3	4	5
1935	*Number*	*Percent*	*Percent*	*Percent*	*Percent*	*Percent*
Feb. 21–28	174	12.7	*39.1*	30.4	11.5	6.3
Mar. 18–22	281	10.7	11.4	24.2	24.2	*29.5*
Mar. 29	325	11.4	17.5	*28.3*	20.6	22.2
Apr. 8–15	340	8.8	13.5	16.8	22.7	*38.2*
Apr. 22–26	420	*43.2*	35.2	12.6	5.2	3.8
May 14–18	800	10.0	15.3	12.6	21.1	*41.0*
May 27–29	448	15.2	16.1	11.1	15.4	*42.2*
June 5	109	*24.8*	23.8	19.3	15.6	16.5
1937						
Apr. 7–9	216	4.2	12.9	25.4	*29.4*	28.1
Apr. 13–15	214	1.4	8.4	16.3	30.4	*43.5*
Apr. 26–27	243	*35.8*	29.2	17.3	9.9	7.8
May 6–10	620	3.7	14.7	27.1	*35.6*	18.9
May 12–14	461	2.4	7.8	16.1	30.4	*43.3*

that from two to three generations of the beet leafhopper developed on such summer annuals as chinchweed, tidestromia, and trianthema. Two generations occurred every year and a third only when new stands germinated in early September. During dry seasons the summer annuals may dry before the second-generation nymphs complete their development, but on such occasions the nymphs shift onto many plants to complete their development, the more important of which include spurges, globemallows, annual saltbushes, and wild buckwheats.

Data from these and similar sampling studies, together with much more field work in the area, led to the conclusion that two spring and three summer generations may develop during favorable years, whereas only one spring and two summer generations develop in dry, unfavorable years. These relationships are shown in figure 24.

Holdover Host Plants in Arizona Desert

In the list of holdover host plants in the southern desert (p. 53), eight species are important in the Arizona desert area. In a field experiment, V. E. Romney caged leafhoppers on all these species in the fall. After an exposure of 80 days the leafhopper mortality exceeded 95 percent on all except bursage, where it was about 85 percent. Apparently suitability and attractiveness to the leafhoppers did not coincide, as the adult leafhoppers were usually found feeding on spurge and globemallow rather than on bursage.

Utah-Nevada Area

Like the Arizona area, the Utah-Nevada area also belongs to

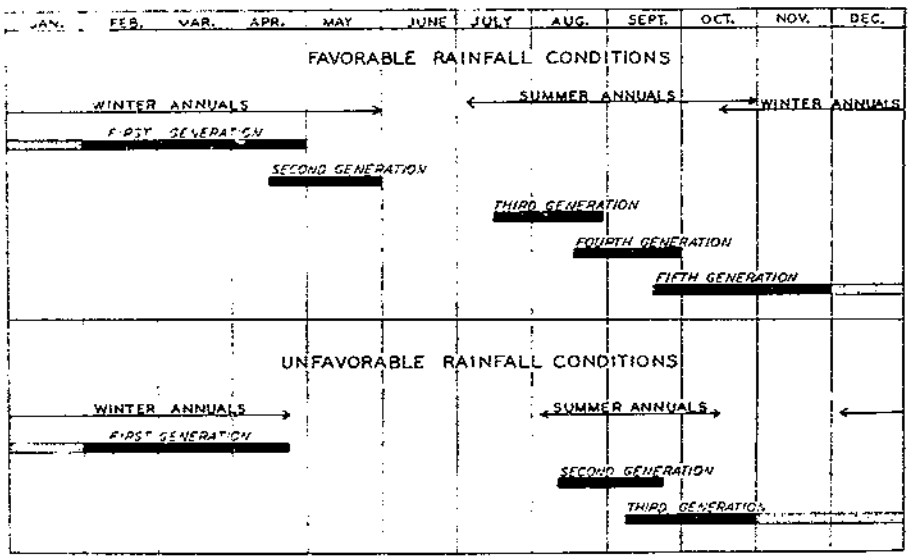

FIGURE 24.—Seasonal occurrence and number of generations of beet leafhopper, as indicated by size and abundance of nymphs, in Phoenix, Ariz., area during year with favorable rainfall conditions compared with dry season. Dotted bars represent overwintering adults and black bars the nymphs of given generations.

the creosotebush formation, but it has less rainfall. Large, flat valleys merge into gentle slopes, ending abruptly in steep mountainous formations. These valleys range from 5 to 50 miles in width and from 5 to 100 miles in length (fig. 17). Cross channels cut by cloudburst rainfall provide many small slopes of various sizes and exposures. These breeding areas are shown in figure 25.

The normal monthly temperature and precipitation from three

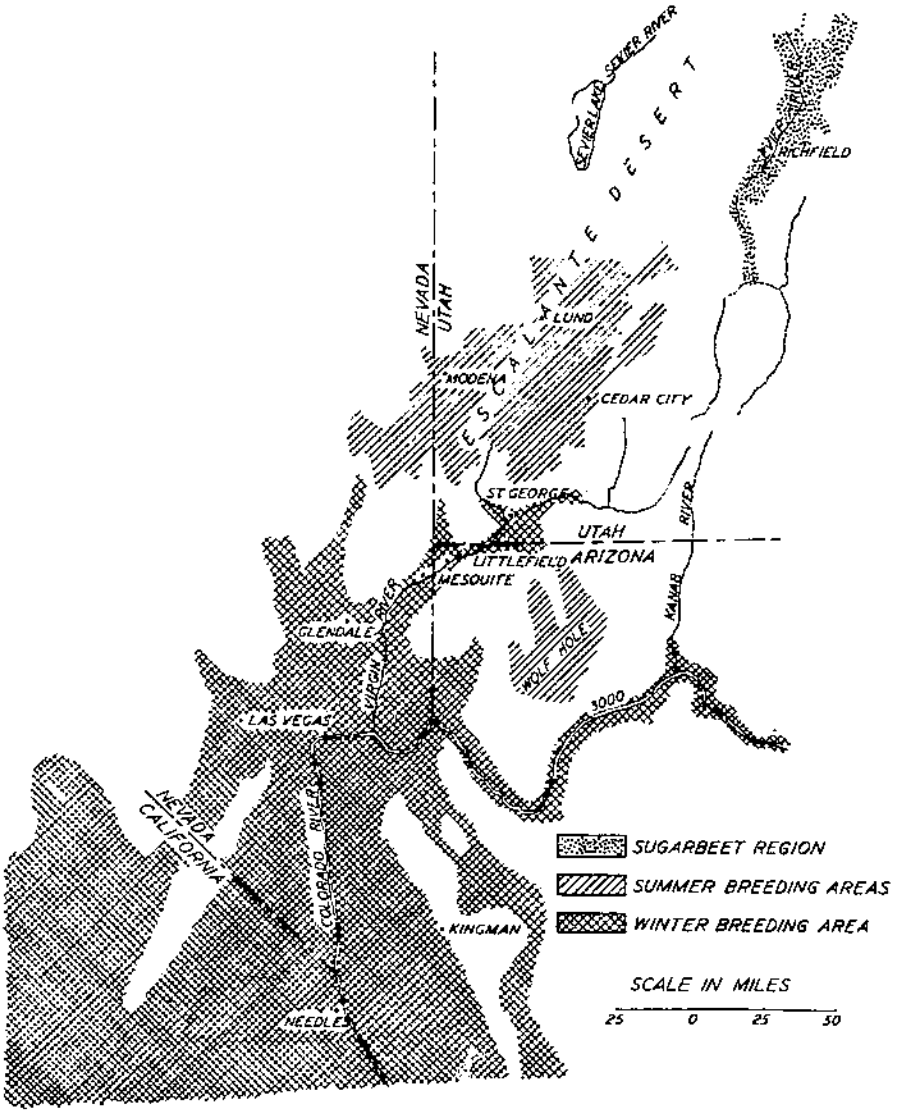

FIGURE 25.—Southern end of cultivated area in Utah and northern part of great southern desert, indicating both summer and winter breeding areas of beet leafhopper.

selected stations within the Utah-Nevada breeding area are given in table 17. St. George, Utah, (altitude 2,800 feet) represents the northernmost extension of this area; Logandale, Nev., (altitude 1,400 feet), approximately 7 miles southeast of Glendale, represents the central part; and Needles, Calif., (altitude 480 feet) represents the southern part.

The average annual temperature increases from 59.5° F. at St. George to 71.8 at Needles, whereas at the same time the precipitation decreases from 8.84 to 4.62 inches, so that conditions become much hotter and drier toward the southern part of the area.

As is generally the case in desert areas, the precipitation is exceedingly variable. The Weather Bureau records at Needles have been kept since 1892. During this period the annual precipitation has varied from 0.87 to 13.25 inches. At St. George, where records have been kept since 1890, the annual precipitation has varied from 3.55 to 18.71 inches. Logandale is intermediate.

Winter temperatures are mild throughout the area, the lowest temperature ever recorded being −11° F. at St. George, 6° at Logandale, and 18 at Needles.

During this study, snow cover has not been of any importance with one exception. In January 1937, approximately 15 inches of snow fell at St. George, 3 inches at Logandale, and 3 inches at Las Vegas. Although this snow cover lasted only about 30 days, it was present during the low temperatures mentioned previously and thus afforded protection to overwintering beet leafhoppers.

Seasonal History

Temperatures are high enough to permit activity of the insect almost every day during the winter, and many nymphs survive, along

TABLE 17. *Average monthly temperatures and precipitation at 3 weather stations in southern winter breeding area of beet leafhopper*

Month	St. George, Utah		Logandale, Nev.		Needles, Calif.	
	Temperature	Precipitation	Temperature	Precipitation	Temperature	Precipitation
	F.	*Inches*	*° F.*	*Inches*	*F.*	*Inches*
January	37.9	0.97	44.2	0.92	51.7	0.58
February	43.3	1.09	50.4	.65	57.4	.56
March	50.2	.82	56.4	.55	63.5	.41
April	58.0	.58	63.9	.27	70.8	.20
May	67.1	.43	71.9	.16	78.8	.11
June	76.5	.25	81.0	.13	87.5	.08
July	82.6	.90	87.2	.45	94.1	.35
August	80.9	1.02	85.3	.56	91.9	.75
September	71.8	.67	83.3	.30	83.4	.32
October	59.6	.80	65.8	.55	71.0	.25
November	47.5	.56	53.5	.35	59.3	.35
December	38.0	.75	44.6	.54	53.0	.66
Annual average or total	59.5	8.84	65.6	5.43	71.8	4.62

with the females that matured in the winter breeding area and those that moved in from summer breeding areas late in the fall. Data from collections made throughout the year indicate that about five broods of leafhoppers are produced, as in Arizona.

As the winter annuals dry, the leafhoppers either move to available summer hosts in the same area or may move long distances to other summer breeding grounds. In the latter area they breed until September, when the last fall brood moves back into the winter area.

Because of the scarcity of summer annuals, the population of leafhoppers produced during the summer and fall within the Utah-Nevada winter breeding area is very small. If these were the only leafhoppers to be considered, the following spring broods would be so small as to be of only local importance. However, this small indigenous population is so completely overshadowed by fall migrants from an outside source that the resulting spring brood is often so large as to cause economic damage at a distance of more than 200 miles from the breeding area.

Winter temperatures are high enough in the southern California desert area to allow an early spring brood to mature there and move north in time to mingle with overwintering females in the Utah-Nevada area. This early spring brood is ordinarily so small because of the extremely dry conditions in the California desert that it is of little importance, but in years of high rainfall and large leafhopper populations, such as in 1940, it may become extremely important. In these exceptional years the progeny of the migrants from the southern part of the breeding area may constitute a large proportion of the total spring migrants. Both the fall and spring movements into this area from outside sources confuse the situation and increase the liability of a heavy leafhopper population being produced in the spring.

Annual Breeding Host Plants

In the Utah-Nevada breeding area, as in Arizona, rains occur chiefly in the late summer and again during the winter; consequently, both winter and summer annuals occur.

Winter and Spring Annuals.—Many species of winter annuals have been observed in this area, but only five have been important host plants of the beet leafhopper. These are redstem filaree (fig. 26), desert plantains (fig. 7), wild buckwheat (*Eriogonum trichopes* Torr.) (fig. 27), flixweed (fig. 26), and wild mignonette (fig. 21). All except flixweed and filaree were native desert plants.

Most of the beet leafhoppers upon which data for this part of the desert are based were collected with a sweep net, which does not accurately sample low-growing annuals. Consequently, data for low-growing annuals are limited to a much smaller number of hand-and-knee counts and some counts with a pan sampler in the later years of investigation. Any of these annuals are capable of producing several nymphs per plant, and their importance in any given season depends on the area occupied and the density of the stand.

These annuals have been closely observed as host plants of the beet leafhopper, with the result that filaree was shown to be the most consistent winter host plant in the higher parts of the breeding area. At lower elevations filaree is

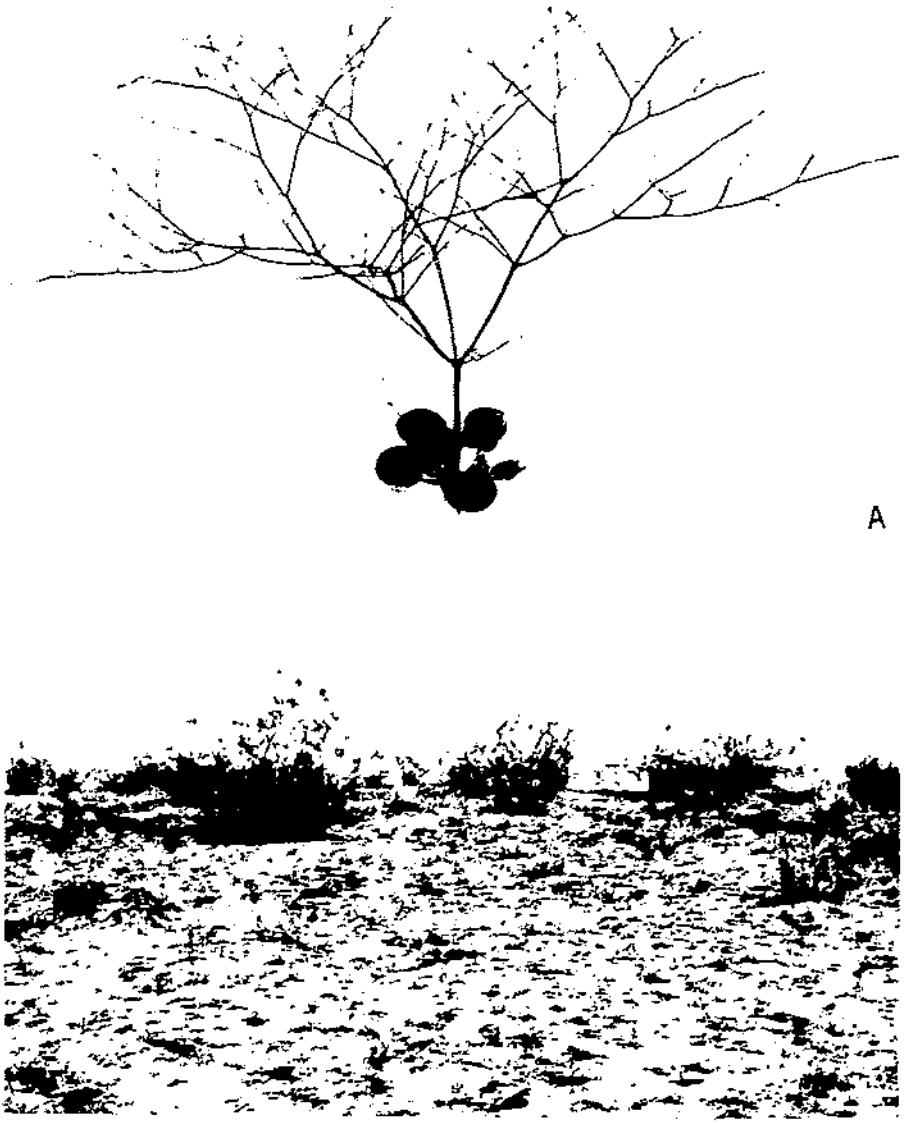

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FIGURE 27.—Wild buckwheat in Utah-Nevada area: *A*, Single plant in bloom; *B*, scattered stand around creosotebushes near St. George, Utah, in July.

mixed with desert plantains, and at still lower elevations it is completely replaced by this plant. These two plants probably produce nine-tenths of the spring migrants in the area.

Wild buckwheat occurs in coarse, well-drained soils of flat, unbroken areas. The maximum acreage occupied by this plant is less than one-tenth that of either filaree or desert plantains. Flix-

weed occurs mainly in small patches around creosotebushes, and wild mignonette is found scattered in alkali flats or along roadsides. Although the last two annuals are widely distributed, their total acreage is very small.

These annuals germinate with the first fall rains and their length of life depends on the amount and distribution of subsequent precipitation. If the rainfall is adequate to produce normal maturity before drying, desert plantains will mature and dry most rapidly, followed by filaree, flixweed, wild buckwheat, and wild mignonette in about the order named.

Summer Annuals.—In the Utah-Nevada area the important summer host plants were found to be Russian-thistle, redscale, spiderflower, and chinchweed. Russian-thistle and redscale normally germinate in March and remain in excellent condition until September. Spiderflower germinates late in winter or early in the spring and matures in April or May. Chinchweed germinates with the summer rains and matures in October.

Russian-thistle and redscale occur almost entirely in fallow fields or roadsides in the small irrigated areas. The maximum amount of Russian-thistle found during this study was about 1,600 acres, whereas the acreage of redscale was smaller.

Spiderflower is scattered in desert wastes adjacent to cultivated land. Its abundance fluctuates greatly from year to year, but it is of minor importance.

Chinchweed occurs in patches in this part of the desert, and in years of heavy summer rainfall may cover thousands of acres. It is an excellent breeding host and would produce large numbers of leafhoppers except that normally very few leafhoppers are in the area when it is succulent.

The relative abundance and importance of these summer hosts is shown by the following tabulation of sweep-net samples taken over a 9-year period:

Species	*Number of samples*	*Leafhoppers per 50 sweeps*
Russian-thistle	590	75.8
Redscale	27	197.3
Spiderflower	43	24.1
Chinchweed	11	89.9

Russian-thistle is by far the most frequently sampled, whereas chinchweed is infrequently found. Based on the leafhopper populations, redscale is the best host, followed in order by chinchweed and Russian-thistle.

The seasonal development of leafhopper populations on Russian-thistle is shown by a redistribution of these samples.

Month	*Number of samples*	*Leafhoppers per 50 sweeps*
January	0	0
February	3	38.7
March	8	16.5
April	53	32.2
May	111	75.0
June	90	101.8
July	83	78.5
August	62	76.4
September	65	75.4
October	95	94.2
November	20	10.1
December	0	0

The leafhopper population on Russian-thistle gradually increased during the spring and reached a peak in June, after which it decreased. The second increase found in October was due to the presence of fall migrants from outside. These migrants

were dark overwintering forms, and could be easily separated from the indigenous leafhoppers, which were still light-green summer forms. The drying of the thistle during October forced the leafhoppers to other plants.

The total area occupied by summer host plants in the Utah-Nevada area is so small that the fall populations of leafhoppers produced would only lightly populate the large areas of winter hosts that germinate later. Consequently, the chief source of overwintering leafhoppers must lie outside this area.

Perennial Breeding Host Plants

In the Utah-Nevada area, where the temperatures are not so high in the summer as in southern Arizona and California, the leafhoppers have been found breeding on two perennial hosts, false tarragon and croton (*Croton longipes* Jones). Both plants remain succulent during much of the summer and maintain summer leafhopper populations. False tarragon is not so widely distributed as croton, but it is an important host where it occurs. The stands of both of these plants are so scattered that it is difficult to estimate their real importance. Judging from the fall populations found in the general area, they do not produce very many leafhoppers.

Utilization of Holdover Hosts

The relative abundance and value to the leafhopper of the holdover hosts in the Utah-Nevada area may be obtained from the following tabulation of sweep-net samples taken on these plants from 1929 to 1933, in which the perennials are arranged in the order of their leafhopper populations:

Species	Number of samples	Leafhoppers per 50 sweeps
False tarragon	9	147.6
Croton	27	18.6
Rabbitbrushes	55	11.3
Chamiso	70	8.2
Snakeweed	64	7.4
Arrowweed	62	7.2
Seepweed	50	6.0
Creosotebush	125	3.8
Quail-brush	17	3.7
Pepperweed	6	2.5
Burrobrush	31	1.5
Goldenweed	14	.5
Bursage	16	.3

Creosotebush and bursage are the most widely distributed of the plants listed. Creosotebush is probably the most important holdover host because it occurs almost everywhere, and the leafhoppers can feed on it at any time of year in case of necessity. Bursage apparently holds very few leafhoppers, but this may be partly due to the method of sampling. Bursage is a low, rounded, compact bush with stiff stems, and a sweep net could not reach into the interior of the shrub. On the other hand, creosotebush is a very open, high shrub, with flexible stems, which is easily sampled. Because of V. E. Romney's finding (p. 55) that leafhopper mortality is very low on bursage, this plant may be of more importance than is indicated in this tabulation.

Arrowweed and quail-brush grow only in bottom lands with a high water table. Seepweed occurs chiefly in alkali flats. The other plants listed occur in mixed stands in flats or as patches in washes.

E. W. Davis and H. E. Dorst tied cheesecloth bags containing female leafhoppers on a creosotebush near Logandale, Nev., in the fall of 1931 (fig. 28). Three lots of about 150 females each were placed on different sides of the

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FIGURE 28.—Cloth cage for leafhopper mortality study in place on creosotebush.

same plant on October 11. Samples of the insects were taken for fat determination at the start and at four later dates. The leafhoppers were counted and the mortality was computed on the three last dates. The data obtained are given in table 18.

The high mortality among the leafhoppers on December 19, combined with the low fat content at that time, indicates that the maximum period of time they can remain on creosotebush at that time of year is not much over 69 days.

Effect of Rainfall on Host Plants and on Leafhopper Populations

The critical point of the beet leafhopper cycle in this breeding area, as elsewhere, occurs during the fall and early winter, when the leafhoppers live on holdover plants.

In some years precipitation does not occur until December or January, and the summer annuals dry during the early part of October. In such years the leafhoppers are forced to live for a long time on perennial holdover hosts. In some years sufficient precipitation occurs to permit the germination of the winter annuals before the summer annuals have matured.

This point can best be illustrated by rainfall charts of the fall, winter, and spring months at Logandale, Nev., as shown in figure 29. The seasons 1927–28 and 1928–29 were chosen because of the extreme contrasts both in rainfall and in populations of beet leafhoppers.

In 1927–28, a year of heavy beet leafhopper populations, the

TABLE 18. *Changes in fat content and mortality of beet leafhoppers held on creosotebush at Logandale, Nev., 1934*

Date (1934)	Time on creosotebush	Source of leafhoppers for fat determination	Fat content (chloroform extractives)	Leafhopper mortality
	Days		*Percent*	*Percent*
Oct. 11	0	Outside cages	39.5	
Oct. 26	15	do [1]	22.8	0
Nov. 14	34	Inside cage	22.6	0
Dec. 19	69	Inside cage	14.4	30
		do	9.3	88

[1] Sample taken to see whether handling leafhoppers in caging them had affected their vitality.

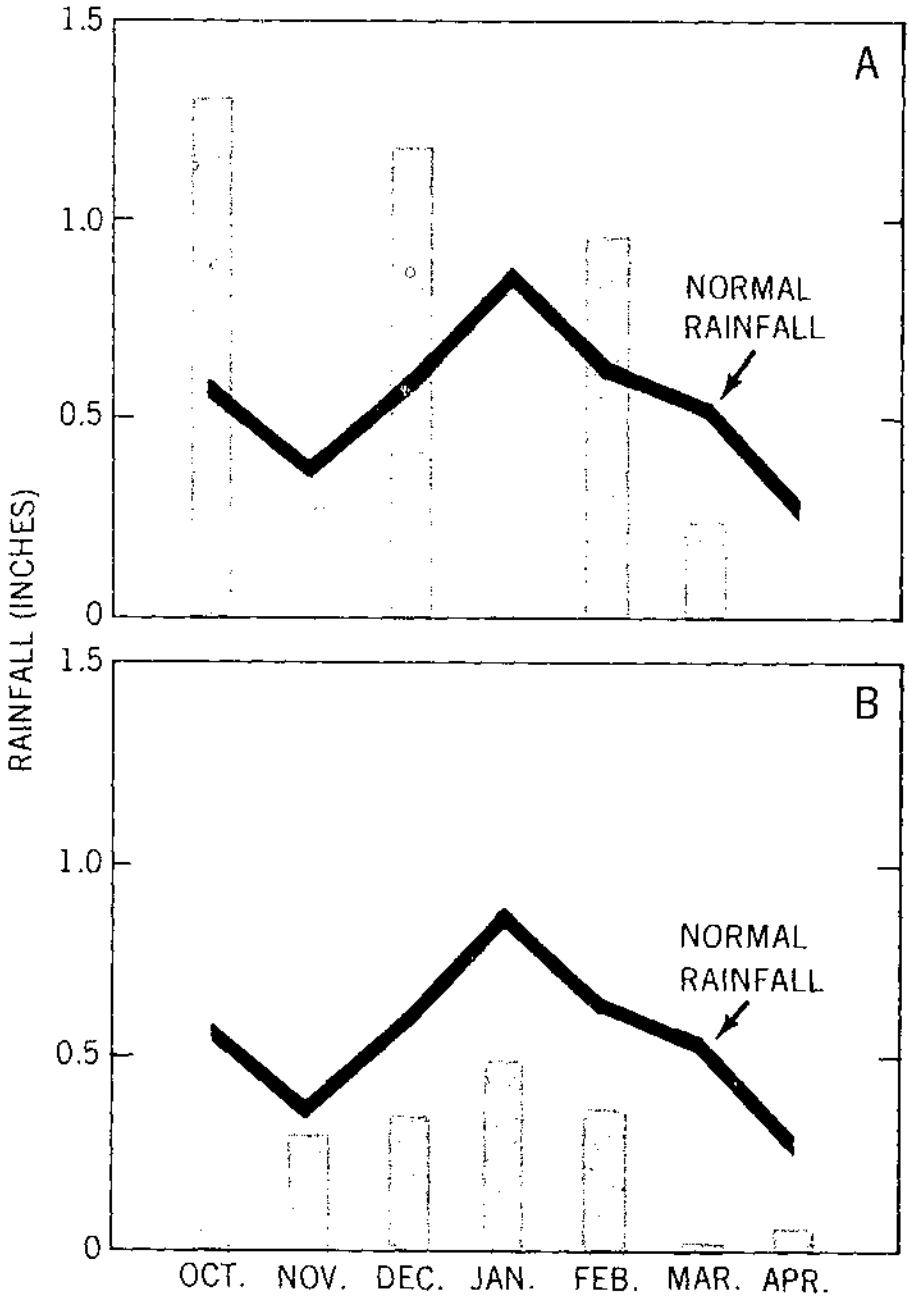

FIGURE 29.—Monthly rainfall charts for October-April at Logandale, Nev., in (*A*) season of high leafhopper populations (1927–28) and (*B*) season of low leafhopper populations (1928–29).

precipitation was above normal in October, December, and February, so that the winter annuals germinated early and remained in excellent condition during the winter. Leafhoppers were able to move, therefore, from the perennial holdover hosts to the winter annuals during October. Consequently, there was little reduction of population in the fall, and by the time the plants matured in the spring of 1928 a very high population of leafhoppers had been produced.

In 1928–29, a year of light beet leafhopper populations, the precipitation from October to April was below normal each month. The winter annuals did not germinate until late November and then only in a very small area. Consequently, the beet leafhopper population was so reduced by forced feeding on perennials that only low populations were produced in the small area of annuals found in the spring of 1929.

The conditions shown in figure 29 were extreme, but they indicate a relationship between winter rainfall and spring population. This relationship has been found sufficiently dependable to be used to estimate the spring population when the incoming fall population, the date of sufficient rainfall to germinate winter annuals, and the amount and distribution of subsequent precipitation are known.

California Desert Area, or Mohave Desert

The California desert area, or Mohave Desert, has not been studied so thoroughly as either the Arizona or Utah-Nevada areas. Most of the information has been obtained from a few survey trips in years when it seemed probable that host-plant conditions were favorable for the leafhoppers. H. E. Wallace and G. T. York studied the western end of the desert from Riverside in 1929–32, E. W. Davis and W. C. Cook covered the area rather thoroughly in March 1940, and V. E. Romney made similar sampling trips in several years. The development of a California State program for control of the beet leafhopper has led to further study of the desert by Harold J. Green, of the California Department of Agriculture, and his associates in 1955–62.

The central part of the Mohave Desert is practically devoid of summer host plants. To the north of Needles, Calif., an area of chinchweed occurs in some years, and in and near the irrigated areas are considerable patches of Russian-thistle. H. J. Green (unpublished reports) has mapped from 10,000 to 25,000 acres of Russian-thistle along the western edge of the desert, just east of the Sierras and from the Santa Ana River southward. Russian-thistle also occurs in the Antelope Valley around Lancaster and Palmdale, in Lucerne Valley, and along the Mohave River between Victorville and Barstow.

E. W. Davis and H. E. Dorst found that leafhoppers from the Wolf Hole area of northwestern Arizona would travel southwest into the northern Mohave Desert in the fall, and W. C. Cook and Davis found in 1940 that leafhoppers from a source in that direction had traveled down the Colorado River at least as far as Blythe, Calif. H. J. Green and his coworkers (unpublished reports) obtained good evidence that leafhoppers from the Russian-thistle areas along the east side of the Sierras traveled southeast in the fall, and were an important source

of overwintering and spring leafhopper populations on wild hosts around the Imperial Valley.

These sources of infestation account for the finding of spring populations of leafhoppers around the periphery of the desert. However, it is only rarely, when unusually heavy fall rains germinate winter hosts over the whole area or a large part of it, that the central area becomes infested in the fall.

In the fall of 1939, heavy rains fell over a large part of the Mohave Desert, and these were followed by several rains during the winter. They germinated and nourished a good cover of annuals over a large part of the desert. E. W. Davis and W. C. Cook made an extended sampling trip over the area in March 1940, taking samples at 95 well-scattered locations from the Imperial Valley to St. George, Utah. At each stop, records were made of the vegetation present. They give a general idea of the prevalence of various breeding host plants in that season. The following tabulation gives the number of stops at which the principal host plants were mentioned. The sum is greater than 95 because of mixed stands at many locations.

Species	*Number of stops*
Desert plantain	54
Filaree	28
Wild mignonette	8
Pectocarya (?)	10
Wild buckwheat	7
Other species	11

The desert plantain was *P. insularis* var. *fastigiata*. The specific identification of pectocarya was doubtful and not checked later. The "other species" included smotherweed, pepperweed (*L. nitidum*), tansymustards, Russian-thistle seedlings, and bladderpod. At that particular time plantain was by far the most abundant and widespread host plant. Most stands were estimated at 5 to 25 percent, but an occasional stand of plantain was recorded as 50 percent or even as a solid stand.

The distribution of leafhoppers found on this trip is shown in figure 30. The large area with high leafhopper populations extended almost directly down the Colorado River from the Escalante Desert, which is north of St. George, Utah, and from the Wolf Hole area, which is south of the same city. Another smaller area of high populations lay along the eastern side of the Sierras near Indio, Calif. As the later studies of H. J. Green and his coworkers have shown, this southern area was probably populated from Russian-thistle areas just north and west of where the spring population was found.

Collections of adults from two places near Indio contained 162 males and 62 females, indicating that a generation had matured already, as the overwintering population in places so far south rarely contains males in March. Four collections taken from areas of high population from Blythe, Calif., northward yielded 59 males and 409 females, all light-colored forms. These adults must have moved into the more northern areas from the south very recently, as few large nymphs were found. These collections indicate that two things were happening. The temperature in the southern part of the desert was sufficiently high to mature a generation by the middle of March, and this brood moved northward, where they mingled with leafhoppers that had wintered there, to increase the size of the spring brood

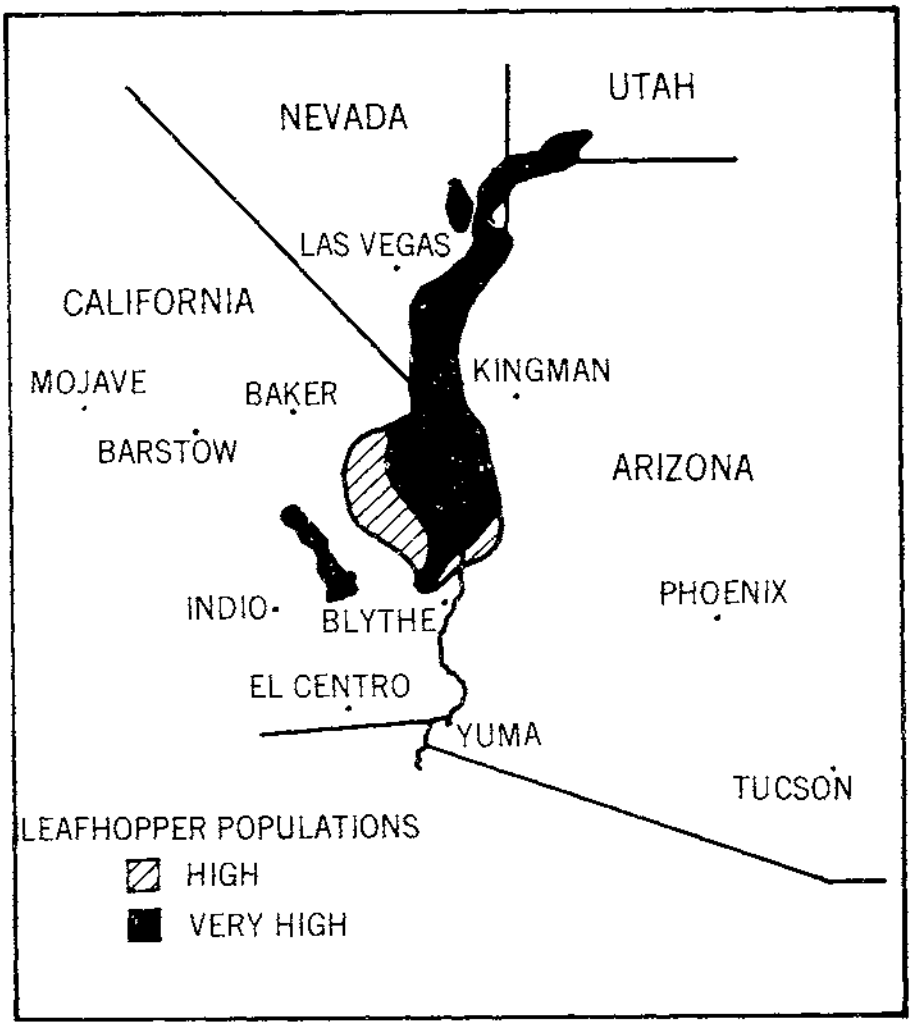

FIGURE 30.—Distribution of leafhoppers over California desert area in March 1940.

in that area. In a later trip from Phoenix, Ariz., V. E. Romney found large numbers of leafhoppers breeding north of the California areas where E. W. Davis and W. C. Cook found them in March, showing production of a heavy second brood there. The chief food plant of the second brood was filaree at higher elevations.

To further confuse the general situation, there is some indication that leafhopper breeding may continue through the winter in the Imperial Valley and northern Mexico to produce a still earlier brood.

The California desert area in general does not have so many holdover host plants as do the Arizona and Utah-Nevada areas because of more severe climate.

Large areas support only meager stands of creosotebush and bursage. Along the dry washes and seeps, desert sage, chamiso, seepweeds, arrowweed, and quailbrush can be found. No studies have been made on the relative importance of these plants.

Escalante Desert of Southwestern Utah

The Escalante Desert lies to the west of the Wasatch Range and includes the major part of Iron, Beaver, and Millard Counties, Utah. However, the part described here as a summer breeding area lies within a triangle roughly formed with Modena, Lund, and Cedar City as corners (fig. 25). The altitude of this area is approximately 5,000 feet, and the vegetation belongs to the northern desert shrub formation (*52*).

The original vegetation has been greatly altered because of dry farming and persistent overgrazing. The perennials found, in order of abundance, were sagebrush, rabbitbrush, shadscale, and greasewood (*Sarcobatus vermiculatus* (Hook) Torr.). Perennial grasses persist to some extent in the southern part, but were rapidly being replaced by Russian-thistle. Annual bromegrass occurs, becoming more abundant to the north.

Climatic Conditions

Temperature and precipitation records have been taken at Modena since 1901 and at Cedar City since 1905. The normal monthly temperatures and average precipitation there are given in table 19.

Winter temperatures at Modena are rather low, and the extreme minimum of −32° F. was recorded in 1937. In 1932, 1933, 1935, and 1936, beet leafhoppers overwintered on experimental plots where host plants were growing at Modena and Nada. The average monthly minima at Modena during the winters of 1931–32 and 1932–33 ranged from

TABLE 19. *Normal monthly temperature and average precipitation at Modena and Cedar City, Utah*

Month	Modena		Cedar City	
	Temperature	Precipitation	Temperature	Precipitation
	F.	*Inches*	*F.*	*Inches*
January	26.7	0.85	31.1	0.86
February	31.2	.98	35.0	1.22
March	38.2	1.03	40.5	1.18
April	46.0	.89	48.0	1.20
May	53.5	.79	56.7	.92
June	63.4	.32	67.2	.43
July	70.6	1.08	73.5	1.38
August	69.2	1.29	71.1	1.45
September	60.0	.78	63.3	1.02
October	48.0	.74	51.6	1.27
November	36.4	.59	41.1	1.01
December	28.1	.83	30.9	.94
Average or total	47.6	10.17	50.8	13.18

5.3° to 8.5° and were near the lowest for the period from 1919 to 1935. This shows that the overwintering of beet leafhoppers is possible in this section, provided host plants are present. It would appear from table 19 that there should be sufficient precipitation and high enough temperatures in this area to germinate fall annuals, but only once from 1925 to 1935 were any fall annuals observed and then only in a small area in the fall of 1928.

Summer Annuals

Blistercress, Russian-thistle, and redscale constitute over 95 percent of the annual cover. Since these annuals usually germinate early in April, samples can normally be taken from early spring to late fall.

The seasonal trend of leafhopper populations in this area from 1930 to 1936, inclusive, is shown for these three host plants in figure 31, in which the average number of leafhoppers per 50 sweeps each month is plotted for the season.

Blistercress dries in June and serves only as a spring host. Russian-thistle and redscale last through the summer and support high populations of the beet leafhopper as late as September. The sharp drop in these populations on Russian-thistle from August to September may be due partially to the limitation of the sweep-net method of collecting. Russian-thistle is succulent in August and the net passes readily through the plant, whereas in September it is stiff and woody and only the outer surface is reached by the net.

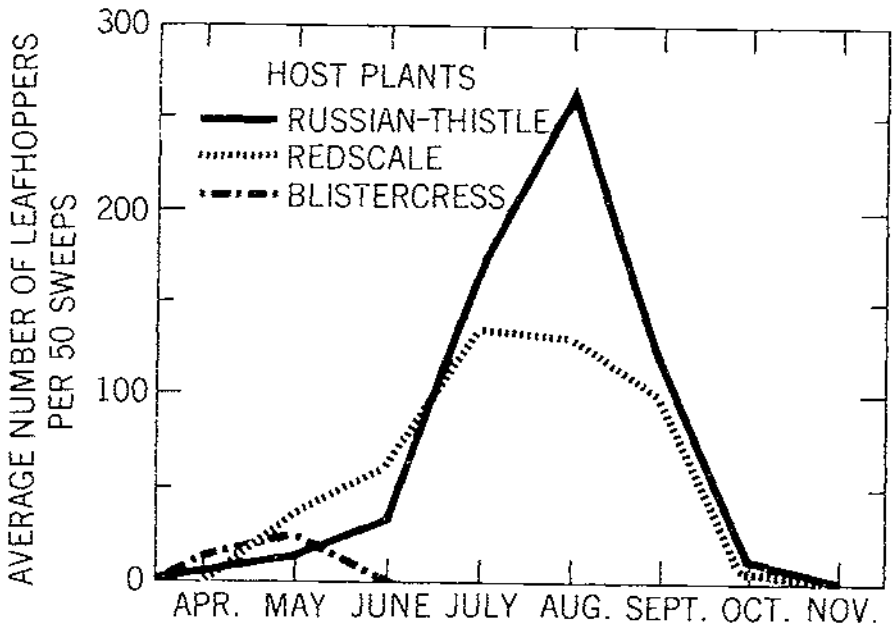

FIGURE 31.—Average number of leafhoppers per 50 sweeps from three principal breeding host plants in Escalante Desert, 1930–36.

However, even if the drop in population is real, a high population still remains on this plant in September. Populations on redscale decline slightly from July to September and are slightly below those on Russian-thistle in September. The fall migration starts early in October, and all beet leafhoppers have left this area by November.

Blistercress is distributed in the northern Escalante Desert, where 1,000–2,000 acres of this plant occur.

Russian-thistle is by far the most abundant summer annual in this desert. In 1934, 1935, and 1936, surveys were made of the Russian-thistle area in the southern part of the desert and 178,000, 190,000 and 232,000 acres, respectively, of this plant were recorded.

Redscale in this area does not exceed 2,000–3,000 acres and is scattered in small patches.

Wolf Hole Area

The Wolf Hole area is located in the high plateau starting about 35 miles south of St. George, Utah, and extending toward the Colorado River (fig. 25). The vegetation on this plateau also belongs to the northern desert shrub formation and lies in the upper part of the sagebrush association. Most of it still contains sufficient grass to make it excellent for grazing. Large areas of this sagebrush and grassland in the flats and near waterholes have been so excessively overgrazed that very little grass remains. In the overgrazed areas as much as 400,000 acres of Russian-thistle have been recorded. In some years this plant produces large numbers of migrant beet leafhoppers.

Like the Escalante Desert, the Wolf Hole area is of practically no importance as a winter breeding area.

RIO GRANDE AREA

The Rio Grande area, the only large breeding area of the beet leafhopper east of the Continental Divide, lies around the Rio Grande and Pecos Rivers in western Texas and in southeastern New Mexico. According to Shantz (*52*), it is still part of the southern desert shrub formation. The vegetation resembles that of southern Arizona, but mesquite (*Prosopis glandulosa* Torr.) is more abundant and the larger cacti are absent.

Romney (*48*) studied the area from 1928 to 1934. He found that the beet leafhoppers were breeding on perennial pepperweed, which occupied about 2,000–2,500 square miles in a territory of about 8,000 square miles. The breeding area was also mapped.

This perennial pepperweed starts sprouting from the crown in the fall, flowers and seeds in the late spring, and becomes partially dormant during the summer. Romney (*48*) found leafhoppers breeding during all seasons on this pepperweed. At the same time that the old plants resprout from the crown, the seed that was dropped in the spring starts to germinate. Romney found this newly germinated plant much more favorable for leafhopper breeding than the resprouted stems, and he was able to demonstrate a relationship between the amount and condition of newly germinated plants in the fall and leafhopper damage the following spring.

In addition to the large area of

perennial pepperweed, Romney also mapped some smaller areas of annual mustards lying along the Rio Grande north of El Paso, Tex., and in the Big Bend area farther south. In these areas spectacle-pod mustard and a tansymustard, *Sophia halictorum* Cockerell, served as spring host plants. Other host plants of minor importance in both areas were *Cheirinia bakeri* (Greene) Rydb., *Lepidium lasiocarpum*, and *Abronia fragrans* Nutt. ex Hook. Romney estimated that about 90 percent of the total spring leafhopper population was produced on perennial pepperweed.

Leafhoppers produced in the spring in these areas moved to the north and east, causing some damage in areas as far away as southeastern Colorado and southwestern Kansas. The damage was much less at a distance than close to the known breeding areas.

In 1953, a severe epidemic of curly top, which is carried only by the beet leafhopper, occurred in southwestern Kansas, and this led to a further study of the Texas-New Mexico breeding areas. J. R. Douglass, W. E. Peay, and other workers found during 1954–58 that the breeding areas outlined by Romney were very dry because of several dry years, and that leafhopper breeding had extended out onto the High Plains of New Mexico, Oklahoma, and Texas, where no leafhoppers had previously been found. In this new area the host plants were annuals, and a cycle between mustards and Russian-thistle kept the leafhoppers breeding.

In 1954, the leafhoppers were found just east of the original area and also extensively farther east and north, extending into southwest Oklahoma. In 1955, the breeding area had shifted west and south, but was still far outside the original area. The same general areas were occupied in 1956, but leafhopper populations were lower. In 1957, the leafhopper was widespread but rather light. In 1958, the most concentrated breeding occurred in western Texas-southeastern New Mexico, some distance east of the original area. The outbreak appeared to have subsided by 1960, but the perennial pepperweed areas had not recovered, and breeding was still found east and north of them.

In 1957, J. R. Douglass, W. E. Peay, and J. I. Cowger, Plant Pest Control Division, U.S. Department of Agriculture, (unpublished report) tabulated as follows the frequency with which each host-plant species was found in a total of 211 stops in the southern Great Plains during February and March:

Host	*Times recorded*
Tansymustard	90
Tumble and town mustard (*Sisymbrium altissimum* L., *irio* L.)	76
Patata	59
Russian-thistle	51
Pepperweed (annual)	48
Filaree (common)	29
Pepperweed (perennial)	20
Pigweed	17
Kochia sp	14
Undetermined plant	14
Borage	13
Deadnettle (*Lamium* sp.)	11
Bladderpod	10
Filaree (Texas)	9
Spinach (*Spinacia oleracea* L.)	9
Spectacle-pod	8
Saltbush	7
Verbena	7
Shepherds-purse (*Capsella bursa-pastoris* (L.) Medic.)	7
Plantain	6
Turnips (*Brassica rapa* L.)	5
African rue (*Peganum harmala* L.)	4
Blistercress	4
Falseflax (*Lesquerella* sp.)	3
Flax	2
Red beets	2
Dwarf phlox (*Phlox* sp.)	1
Stickleaf (*Mentzelia* sp.)	1

Host	*Times recorded*
Buckwheat	1
Kale (*Brassica oleracea* var. *acephala* DC.)	1
Swiss chard (*Beta vulgaris* var. *cicla* L.)	1

This outbreak is described in detail to emphasize that the breeding areas of the leafhopper are not fixed in either area or location, and new ones may develop from time to time. The cause of this one was probably the breaking up of much grassland in the High Plains during World War II for the growing of wheat and cotton. The drought that lasted through most of the 1950's caused this land to be abandoned, and it quickly developed a weed cover, which included many leafhopper host plants.

Romney (*48*) stated that Russian-thistle ranks fifth among summer host plants in the area and commented: "Russian-thistle serves as an important spring host of the beet leafhopper in some breeding areas, but in New Mexico and Texas it germinates early in the spring and is limited to cultivated districts, where the use of irrigation water leads to a rank growth, which invariably sponsors low leafhopper populations. Its very limited distribution within the breeding areas is another factor which places it fifth in importance as a summer and fall host."

J. R. Douglass and W. E. Peay (unpublished report) stated: "From August 19 to 30, 1956, a study was made of the distribution of beet leafhoppers and curly top in the eastern part of Colorado and New Mexico and in western Kansas, Nebraska and Texas . . . Kochia (*Kochia scoparia* (L.) Schrad.) and Russian-thistle (*Salsola kali* var. *tenuifolia* Tausch.), the principal summer weed hosts in the above areas, were abundant on idle and waste lands from the Edwards Plateau of Texas north to the Platte River Valley of western Nebraska and westward to the Rocky Mountains."

This last statement shows how the host-plant complex changed between 1931, when Romney's studies were completed, and 1956. There are also indications that the perennial pepperweed area has become much larger than it was when Romney studied it.

BELT OF NO WINTER BREEDING

Very few, if any, leafhoppers pass the winter in the Escalante Desert of southwestern Utah, and spring host plants are relatively scarce. For this reason, Dorst and Davis (*16*) depended on artificially developed plots of host plants to indicate movements of the leafhoppers. Few winter annuals are in the Utah-Colorado area. Cursory examinations of south-central Nevada have also revealed an area where winter hosts are scarce. The cause of this plant distribution is not known, but it is probably connected with fall temperature and rainfall. This would indicate that a belt running from western Colorado across Utah and Nevada south of Grand Junction, Colo., and Reno, Nev., but north of the sharp drop that divides the northern desert from the great southern desert, is practically free of leafhoppers during the winter and is repopulated early in the spring.

North of this belt lie the areas of northern Utah and Nevada, the Snake River Plain, and the Columbia River Basin, where the leafhopper survives the winter.

NORTHERN NEVADA, NORTHERN UTAH, AND WESTERN COLORADO

Northern Nevada

Spring breeding of the beet leafhopper has been found chiefly near the Carson and Humboldt Sinks and Pyramid Lake, all in northwestern Nevada. The leafhoppers overwinter on tansymustard and pepperweed and produce a spring generation on these plants. It matures at about the same time as the second generation on the lower Colorado River desert. Russian-thistle is also present in the Walker Lake area farther south, but no studies of overwintering have been made, and it is questionable whether there is much spring breeding in that area. The fall holdover hosts in western Nevada are chiefly sagebrush and rabbitbrush, and the period on such hosts is usually short.

The areas supporting the leafhoppers are small and scattered, and the total leafhopper population is usually only of local significance. In certain years, however, it is possible, although not very probable, that leafhoppers from along the Humboldt River in northern Nevada may invade the Snake River Plain of southern Idaho.

Northern Utah

Winter Breeding Areas

The northern Utah winter breeding areas of the beet leafhopper are located in the Great Salt Lake Basin and lie in the northern desert shrub formation at an altitude of slightly over 4,000 feet. Eleven small separate areas are delimited in the area between Santaquin on the south and Garland on the north and are grouped somewhat differently from the areas described by Knowlton (*11*). The cultivated districts extend north and south in the same territory adjacent to the various breeding areas. When damaging beet leafhopper populations are found in these cultivated districts, they are in most years directly traceable to 1 or more of the 11 distinct breeding areas. The locations of these breeding areas in relation to the cultivated districts are shown in figure 32.

Approximately 80 percent of the Utah sugarbeet acreage lies in the northern part of the State. The major part of the leafhopper populations in this beet district comes from the northern Utah winter-breeding areas. The geographical distribution of the breeding areas and their proximity to specialized cultivated crops necessitate discussing each area individually.

No weather data are given here since climatic conditions are essentially similar to those described by Carter (*6*) for the Twin Falls, Idaho, area.

Utah Lake Group.—West Mountain lies east of the south tip of Utah Lake, adjacent to the shore. The breeding area occupies about 10 square miles of the south end of West Mountain. Beet leafhoppers from this area need to travel only 5 to 10 miles to the Santaquin-Provo cultivated areas.

The *west Utah Lake area* is south of Lehi and occupies approximately 25 square miles between Lake Mountain and Utah Lake. This area is from 7 to 12 miles from and contributes leafhoppers to the cultivated areas of

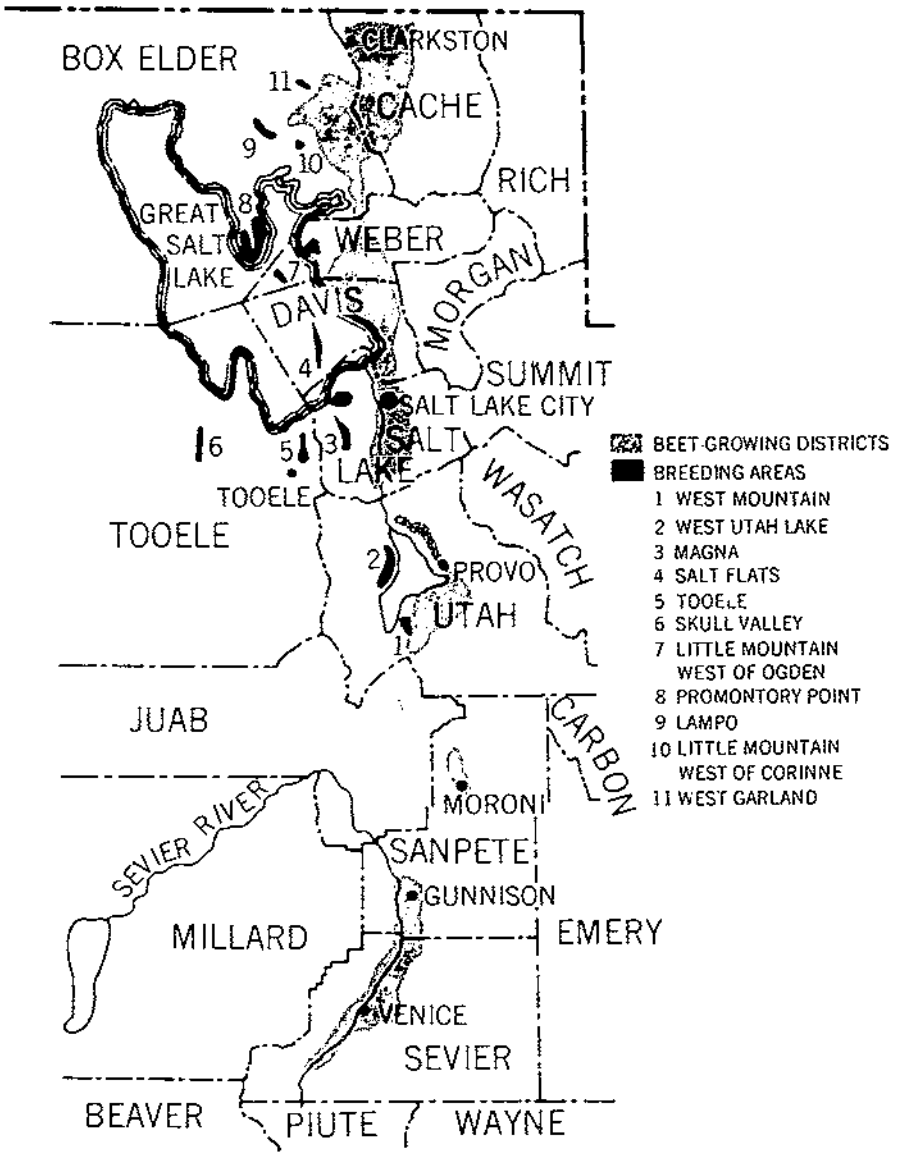

FIGURE 32.—Principal local breeding areas and beet-growing districts of northern Utah.

Lehi and vicinity. This area may possibly contribute leafhoppers also to the northern part of the Santaquin-Provo cultivated areas, but no evidence of this distribution was obtained during the study.

Magna Group. — The *Magna area* extends from the Great Salt Lake south along the east side of

the Oquirrh Mountains to the vicinity of Harriman and occupies approximately 10 square miles. It is from 1 to 15 miles from the cultivated areas of Magna, Midvale, and Riverton.

The *Salt Lake Flats area* occupies about 15 square miles of the flats between Salt Lake City airport and Saltair. Antelope Island is nearby. The east slope of the Antelope mountain range, or approximately 15 square miles of the island, is a breeding area. It is from 3 to 15 miles from the cultivated area between Salt Lake City and Kaysville.

The *Tooele area* lies north of the city of Tooele. The breeding area contains about 15 square miles and occupies a narrow strip along the west side of the Oquirrh Mountains and the adjacent flats to the west. The area is from 10 to 12 miles from the cultivated areas of Salt Lake County.

Skull Valley is located in central Tooele County and contains a breeding area of approximately 10 square miles. It includes a narrow strip in the north part of this valley along the west side of the Stansbury Mountains. This area is approximately 25 miles from any beet- or tomato-growing areas.

During recent years there has been no indication that the leafhopper movement from Tooele or Skull Valley has damaged any of the present beet- or tomato-growing sections of Utah.

Beets were grown in Tooele County at Grantsville and vicinity at one time, but their culture was abandoned, probably because damage resulted from the beet leafhoppers that moved from the two breeding areas previously mentioned.

Promontory Group. — *Little Mountain area west of Ogden* is on the extreme west part of the mainland that adjoins the Great Salt Lake and occupies approximately 10 square miles. It is not over 6 to 8 miles from the cultivated area of Hooper. Fremont Island is of similar size and is located south and west of Little Mountain.

The *Promontory Point area* is on the southern part of the peninsula that extends into the Great Salt Lake from the north and occupies approximately 30 square miles. This lies about 12 to 14 miles from the nearest beet and tomato areas in Davis and Weber Counties.

Lampo Group. — The *Lampo area* contains about 25 square miles and is from 8 to 10 miles from the cultivated areas of Penrose, Thatcher, and Tremonton.

The *Little Mountain area west of Corinne* contains approximately 5 square miles and is about 8 miles northwest of Corinne. It is from 3 to 8 miles from the beet and tomato areas of Corinne, Bear River City, and Honeyville.

The *west Garland area* of approximately 5 square miles occupies the south slopes of the foothills to the west of Garland. The area is adjacent to beet- and tomato-growing areas near Garland.

Host Plants

Annuals in Summer Breeding Areas. — The principal summer host plants in the northern Utah areas are Russian-thistle and beets. Small areas of Russian-thistle lie adjacent to winter breeding areas and beets are not far distant. Consequently, very little mortality of the beet leafhopper occurs during the fall migration. Observations have shown that populations of the leafhopper on summer hosts are usually sufficient to produce from 1 to 10

females per square foot on the winter annuals after the fall movement.

Perennial Holdover Hosts.—Perennial holdover hosts are rarely required in this area. However, in the occasional dry years when the beet leafhopper must use these plants, the principal holdover species are sagebrush, pickleweed, seepweed, and greasewood.

Winter Annuals.—Redstem filaree is the principal overwintering and spring annual in the area of Magna, Salt Flats, Little Mountain west of Ogden, Promontory Point, Little Mountain west of Corinne, and west Garland, and is found to some extent in all the winter breeding areas of northern Utah. Blistercress is the principal overwintering and spring annual in the west Utah Lake, Tooele, and Skull Valley breeding areas. African mustard is the principal overwintering and spring host in the West Mountain and Lampo breeding areas. Blistercress and African mustard are both introduced wild mustards. These mustards and filaree usually germinate in the fall or early winter and mature in late spring. The area occupied by these annuals has not been constant from year to year. The acreage of African mustard increased in the Lampo area and that of blistercress in Skull Valley during these studies.

Winter Mortality

In 1931–32 and 1932–33, E. W. Davis and H. E. Dorst placed outdoor cages similar to those used by Carter (*6*) in Idaho over healthy plants of blistercress in Skull Valley, about 40 miles west of Salt Lake City. The cages had two compartments, one of which could be closed against the weather and the other left open for rain or snow. About 150 female leafhoppers were liberated in each half of 10 cages late in the fall. Distant-reading thermographs recorded weather conditions in the cages. The cages were left undisturbed until the following March, when they were opened and the surviving leafhoppers counted. At this time the host plants were found to be in good condition in both compartments of all cages. The survival in the two seasons is given in table 20.

TABLE 20. *Survival of adult female beet leafhoppers caged on blistercress in Skull Valley, Utah, during winters of 1931–32 and 1932–33*

Season and compartment	Placed in cages	Recovered from cages	Survival
1931–32:	*Number*	*Number*	*Percent*
Exposed	1,510	502	33.3
Covered	1,520	159	10.5
Total	3,030	661	21.6
1932–33:			
Exposed	1,503	70	4.6
Covered	1,503	45	3.0
Total	3,006	115	3.8

In 1931–32, the air temperature did not dip below zero until the middle of January, after which there were two short periods of subzero temperature. Snow cover was light or absent. In 1932–33, subzero weather came in December and February. The December cold snap came when there was no snow cover, whereas a continuous snow cover was maintained through most of January and February, as indicated by the soil thermographs. In 1931–32, the soil surface temperature was rather variable, whereas in 1932–

33 it averaged close to 30° F., with minor fluctuations.

Leafhopper survival in the exposed compartments was higher than in the covered compartments in both years, but the most noteworthy result was the great seasonal difference in survival, which was over five times as great in 1931–32 as in 1932–33. Probably the long continued exposure to low temperatures in 1932–33 was as instrumental in causing mortality as the sharp temperature drop in December. These results foreshadow the conclusions of Harries and Douglass (*14*) reported 15 years later.

This variation in winter survival was reflected in the number of leafhoppers in the spring brood that were found in the beetfields of nearby Salt Lake County. In 1932, when winter survival was high, the average was about 18 leafhoppers per 100 beet plants in mid-April, whereas in 1933, after low winter survival, the average at the same time was about 1 leafhoppers per 100 beet plants. The drop in spring population was somewhat less than proportional to the winter mortality in the two seasons.

Development of Spring Brood

Ball (*5*) stated definitely that it was impossible for a generation of the beet leafhopper to mature in the desert areas before the spring movement to beets, and that the adults which moved into the beets in the spring were the same ones which had left the preceding autumn. That he was mistaken in this statement has been demonstrated many times by field workers, but most of the evidence has been indirect and possibly misinterpreted.

Ball's assumption was based on monthly average temperatures taken in standard shelters. The temperatures near the soil surface, where the leafhoppers are breeding, run much higher. Cook (*12*) showed that sufficient heat was received at the soil surface on a south slope in the central San Joaquin Valley to mature adult leafhoppers before the first adults appeared in the valley bottom. Unfortunately too few leafhoppers were on this particular slope to make possible regular sampling of the developing population.

Collections by H. E. Dorst in northern Utah in the spring of 1936 give evidence that a brood is also produced there in the spring on overwintering hosts before migrations occur. Two independent but related lines of evidence are presented, one based on dissection of females for eggs and the other based on collections of nymphs at short intervals from stations in the breeding areas. Both lines of evidence are affected by temperature.

Measurements of standard shade (Weather Bureau shelter) and soil surface temperature were recorded on a south slope at Promontory Point, Utah. The rod of the soil thermograph was covered with a thin layer of soil of the same texture as that in which the plants were growing, so that the temperature recorded by the soil thermograph was a close duplication of the temperature in the habitat of the beet leafhopper.

Figure 33 presents air and soil thermograph records for the week ending May 4, 1936, on a south slope at Promontory Point. This is a representative week and illustrates the difference between standand shade temperature and the temperature where the leafhopper is feeding. The minimum temperatures in standard shade

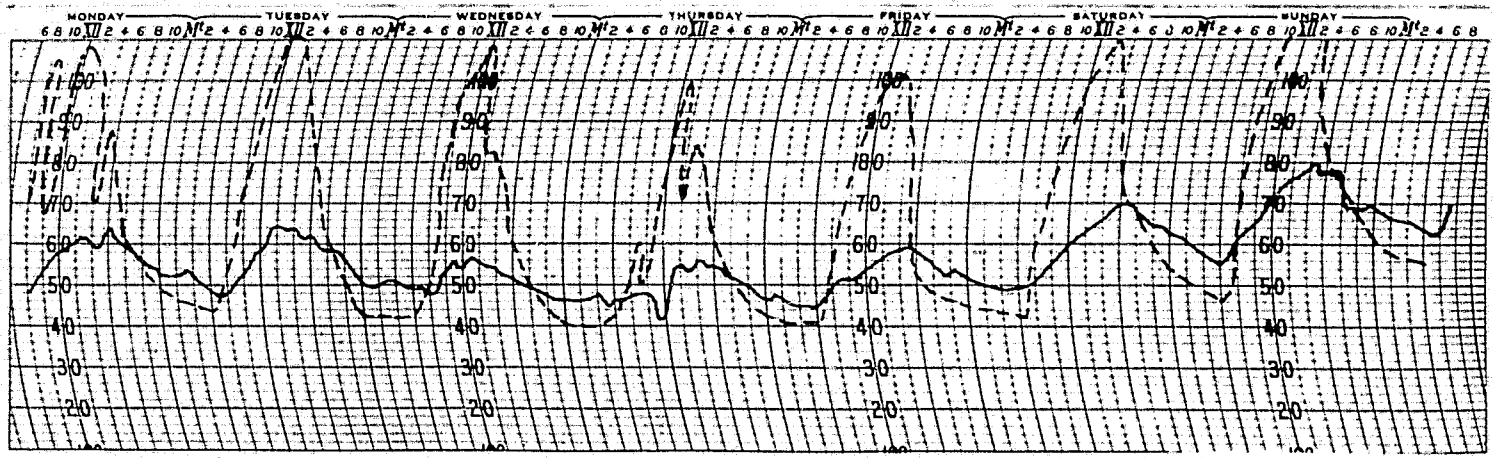

FIGURE 33.—Thermograph records for week ending May 4, 1936, at Promontory Point, Utah. Solid line represents air temperature in shade and broken line the soil surface temperature.

and at the soil surface are very similar, but the difference in the maximum recordings in the shade and at the soil surface illustrates the effect of direct radiation on the soil surface.

The dark overwintering females develop mature eggs as soon as warm weather starts in the spring and continue to do so for the rest of their lives. On the other hand, newly emerged females do not contain mature eggs during the first few days of their adult lives, but generally mature some eggs after a few days. Hence the presence of light or semilight females, without mature eggs, in the late spring indicates the emergence of the first spring brood. At the time the spring forms start to appear, the few dark overwintering females left are worn and frayed and easily distinguished from the freshly emerged spring forms, regardless of their coloration.

Egg Development Study.—This study embraced four adjacent slopes. Two of these faced south and southwest and the other two east and southeast. Because there was little difference within the pairs as listed, the results have been grouped.

Dissection of females started during the last part of February 1936, coincident with the first activity of the beet leafhopper in the spring. Collections of 15 or 20 females were made with a Hills' sampler at 3- or 4-day intervals on filaree, Russian-thistle, and African mustard. Dissections were made under a binocular microscope.

Table 21 shows the results of dissecting females from the selected slopes. Since the number of eggs per female varied only slightly within a dissected group, the number of eggs recorded under each date is the average (to the nearest whole number) of 15 to 20 individuals of each color form found in each area on the date given. The blanks in the table previous to March 12 indicate that no collections were made because of no spring host plants at these locations. Blanks after March 12 indicate that although collections were made, certain color forms were not found in sufficient numbers for dissection. The newly emerged light forms could easily be separated from older light forms by the unexpanded translucent abdomen and somewhat smaller size. This separation has been made in table 21 to show roughly the time of their first appearance and the length of time required for the development of mature eggs.

There was no egg development in the first females collected from the south and southwest slopes, but by March 2 one or two immature ovules were found in nearly every female.

The dark overwintering individuals had disappeared by the last of May. Semilight forms suddenly appeared in all the areas on April 16. Their origin is unknown, but the fact that they appeared a few days after migrating adults were taken in the Escalante Desert (p. 91) and at about the same time that similar forms appeared in the Sevier Valley strongly indicates that they came from the southern breeding area.

The data in table 21 also show that newly emerged females appeared on the south and southwest slopes on May 11 and 14, but did not appear on the east and southeast slopes until June 1. South and southwest slopes received more heat from the sun during the warmest part of the day than the east and southeast slopes. The

TABLE 21.—*Average number of mature eggs per female beet leafhopper collected in northern Utah winter breeding areas during spring of 1936*

Date	Eggs per female leafhopper found on—							
	South and southwest slopes				East and southeast slopes			
	Dark overwintering	Semilight	Light	Newly emerged	Dark overwintering	Semilight	Light	Newly emerged
Feb. 24	0							
27	[1] 1							
Mar. 2	[1] 1							
5	1							
9	2							
12	3							
15	4				1			
19	4				2			
23	6				3			
26	6				4			
30	7				5			
Apr. 2	7				5			
6	7				5			
9	9				5			
13	9				7			
16	10	2			8	3		
20	9	5			9	5		
23	6	8			8	7		
27	6	9			7	9		
30	7	11			8	10		
May 4	5	11			6	9		
7	5	12			6	10		
11	5	9		0	5	8		
14	4	8	5	0	4	8	7	
18		7	7	0	4	7	7	
21		7	10	2	2	6	10	
25			8	6	3	5	8	
28			10	6		4	7	
June 1			8	7		6	8	0
4			6			3	5	0
10		4		8				4
15								0

[1] Some eggs found, but less than one mature egg per female

light forms, which emerged from the south and southwest somewhere in the area, appeared May 11–14 on all slopes.

Table 22 shows the time of appearance of these forms in the cultivated fields. The data in this table are average populations of beet leafhoppers per 100 square feet in seven beetfields near the local breeding areas. Dark overwintering leafhoppers were present until May 13, semilight individuals were present at the time of the first count, and light forms became numerous about May 21, which is about 11 days later than they first appeared on the local breeding grounds (table 21).

Nymphs were found in the beets before May 21. Since they were not sufficiently developed to pro-

TABLE 22.—*Populations of dark, semi-light, and light beet leafhoppers per 100 square feet in 7 beetfields in Box Elder County, Utah, in spring of 1936*

Date	Dark forms	Semi-light forms	Light forms
Apr. 27	6.7	1.3	0.3
May 1	2.0	2.6	0
5	2.0	2.0	0
8	.7	2.0	0
12	0	3.3	0
13	.6	4.6	.3
15	0	5.1	0
18	0	5.0	.9
21	0	2.3	3.4
25	0	6.0	12.0
28	0	5.7	20.9
June 10	0	0	[1] 20.0
12	0	0	[1] 28.5
15	0	6.7	[2] 49.3

[1] Based on counts in two fields only.
[2] Based on counts in three fields.

duce light adults by that date, the light forms must have come from the nearby breeding area.

Nymphal Development Study.—For this study, nymphs of the beet leafhopper were collected during the spring of 1936 in the same locations and from the same host plants as the females that were dissected for eggs. Six samples were taken at random every 3 or 4 days at each location with a pan sampler, which covered one-half square foot. The nymphs were removed from the sampler and classified according to instar under a binocular microscope.

Three of the five stations sampled were south slopes and their records of nymph development were so similar that they have been combined. Figure 34 gives the number of insects in each stage collected during the spring.

Only first-instar nymphs were found on April 20. Second-instar nymphs appeared on April 23 and third-instar nymphs on April 27. The peak of abundance of first-instar nymphs was on April 28 and of last-instar nymphs about May 14. Light adults were first seen on May 14.

Harries and Douglass (*34*) showed that an accumulation of about 650 day-degrees of temperature between 58° and 92° F. is necessary to mature adults from newly laid eggs. This accumulation of soil surface temperature was reached on May 11 on one of the south slopes studied, so that the first light adults could have developed from eggs laid early in March. This is further substantiated by the finding (table 21) that many of these light forms contained no mature eggs on May 11.

As with the adults discussed previously, temperature had a considerable effect on the rate of nymphal development. In addition to the data given for the south slopes, collections were made at the same times at one station each on the east and the southeast slopes. Development was similiar on the last two slopes, so the results have been combined. Also, the population curves for the several instars were similar to those shown in figure 34, except that the peaks of abundance were at later dates. The fifth instar may be taken as representative of the nymphal development. The seasonal abundance of the fifth-instar nymphs collected on the south and the east and southeast slopes is illustrated in figure 35. The south slopes were 18 days earlier in producing the earliest fifth-instar nymphs and the peak of nymphal population.

Summer Broods

When it is considered that overwintering females lay eggs for

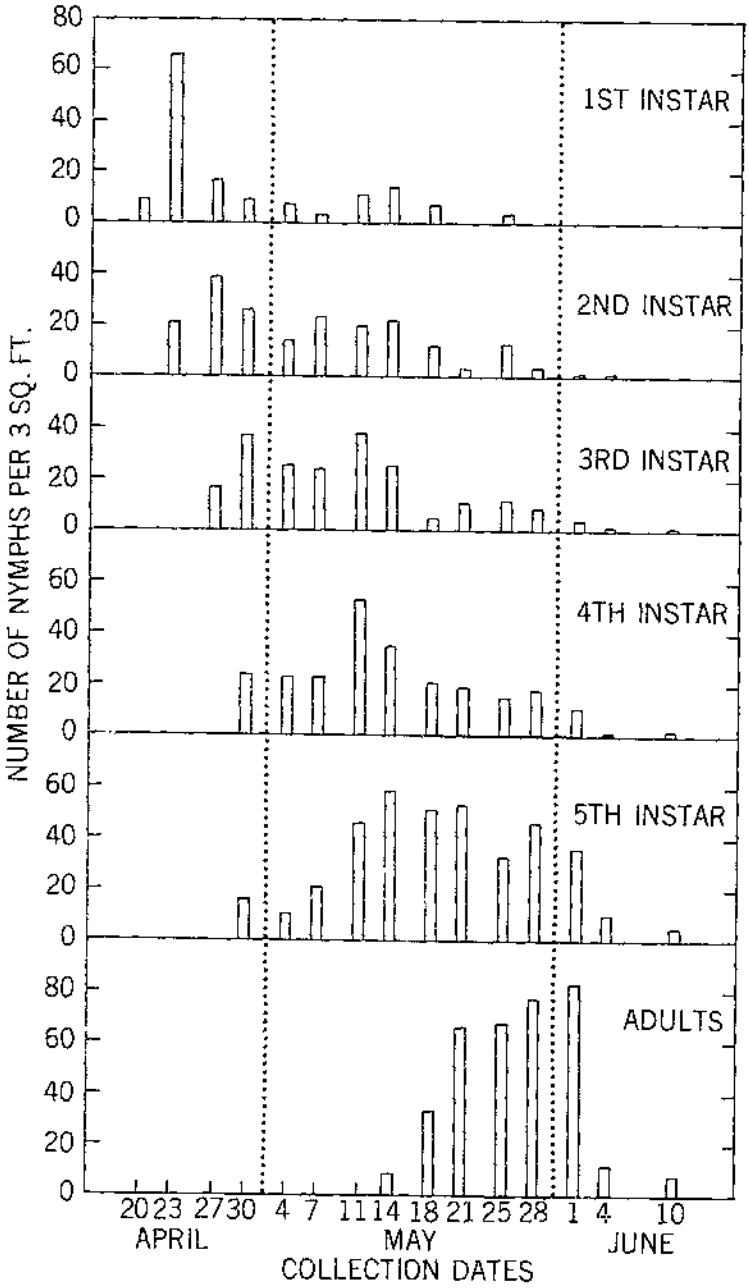

FIGURE 34.—Number of beet leafhopper nymphs per 3 square feet, segregated into various stages, as collected on representative south slopes in northern Utah during spring of 1936.

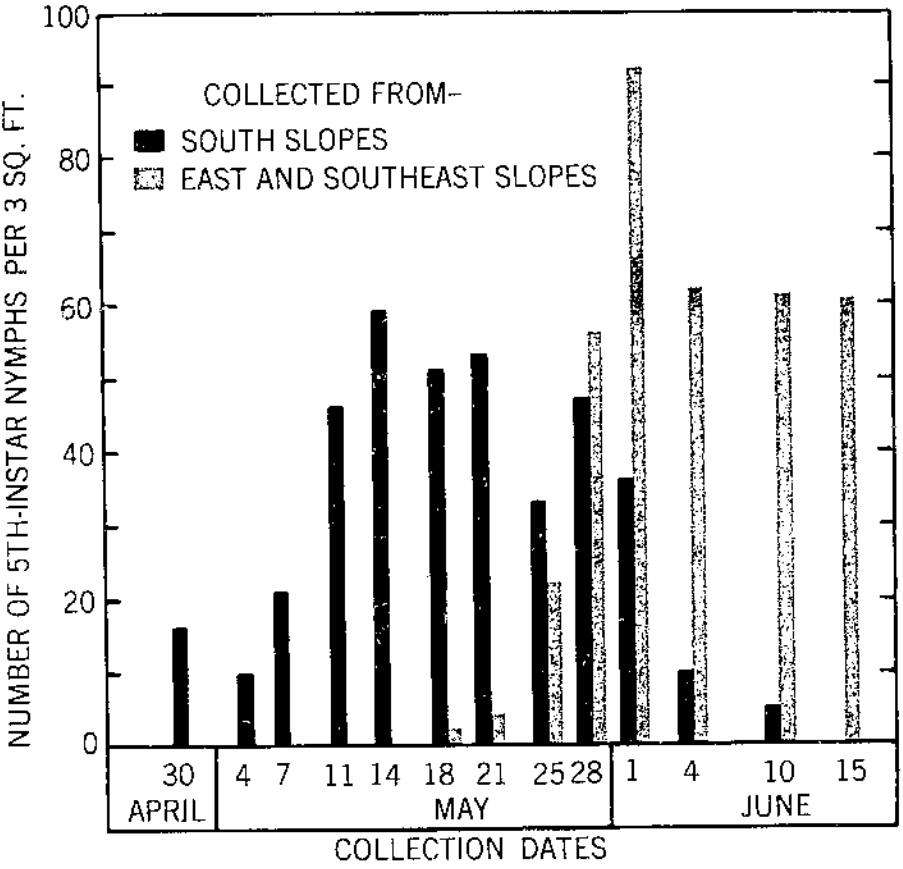

FIGURE 35.—Number of fifth-instar nymphs of beet leafhopper per 3 square feet on south slopes compared with number on east and southeast slopes at same time.

over 2 months; that semilight forms usually appear in April from the southern area and lay eggs for at least 6 weeks in both the northern winter breeding area and the cultivated area; that progeny from the overwintering females appear before the semilight forms die; and that the emergence of light spring forms is greatly affected by local conditions of slope and temperature; it can be seen that later broods become a hopeless tangle, and it is impossible to separate them in field collections.

Also, the temperature in the beetfields in the summer is lower and leafhopper development is slower than on short annuals during the spring, a point discussed by Carter (*6*). Field collections and rearing experiments seem to indicate that two summer broods are produced in the beet areas after the local migration.

Breeding Areas in Eastern Utah and Western Colorado

The spring-summer areas of the beet leafhopper in eastern Utah

and western Colorado were located and studied during 1930–38. They have been comparatively unimportant as a source of beet leafhopper infestations into the eastern Utah and western Colorado sugarbeet-growing districts. From the spring of 1931 to 1938, inclusive, data indicate that these local breeding areas were important in contributing to the beetfield leafhopper infestations only during the spring of 1934 and may have contributed to some extent during the seasons of 1935 and 1938; thus only during 1 year of the 8 studied were these areas important to the agricultural districts.

The high leafhopper productivity in the spring of 1934 was apparently caused by the preceding warm winter, the warmest in 43 years, combined with early germination of Russian-thistle. These spring-summer breeding areas are usually populated during April and May by first- and second-generation beet leafhoppers from warmer areas. The population of overwintered beet leafhopper adults in the northern breeding areas was usually very low or absent in April, but their progeny and that of first migrants from the south developed nearly simultaneously. On the basis of nymphal size and adult sex ratio it was evident that leafhoppers often remained in the northern desert breeding areas during the summer and did not augment populations in the agricultural districts.

Winter annuals such as blistercress and tumblemustard occurred only in limited patches within the eastern Utah-western Colorado breeding areas. This lack of favorable overwintering plants together with low winter temperatures is apparently responsible for either very low survival or complete mortality of the beet leafhopper during the winter.

Spiderflower germinated in March and produced one and a partial second generation of beet leafhoppers before drying in May or June. The plant occurred mostly adjacent to agricultural districts, and beets near such areas were damaged by leafhoppers that were forced from the plant stands because of drying. It was sufficiently abundant to be of importance in only one season in eight.

Russian-thistle was the chief spring and summer breeding host plant for the leafhopper in this area. The annual cycle of both plant and insect is similar to that described for the California and Utah-Nevada desert areas, except that the plant is sometimes killed by drought in spring or early summer.

The leafhoppers are on holdover hosts from October or November until spring. The principal holdover hosts are snakeweed, shadscale, and *Atriplex corrugata*. Of these plants, snakeweed seems to be preferred, and in some areas large numbers of leafhoppers have been found on it early in the winter. Survival, however, has always been low.

In 1937, O. A. Hills selected a patch of snakeweed near Moab, Utah, which had a high leafhopper population late in the fall. Samples of the leafhopper population were taken twice each month between November 11, 1937, and March 3, 1938, by means of the sampling cage. In cold weather a specially designed heater (Hills *39*) was used to activate the leafhoppers for counting. The female leafhoppers declined from 31.7 in November to 1.3 per plant in March. As can be seen from figure 36, most of

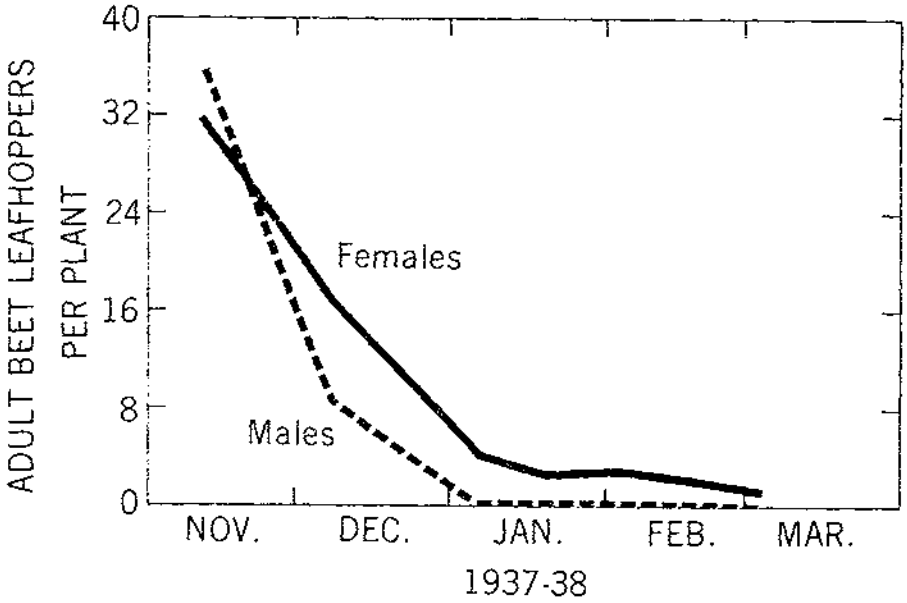

FIGURE 36.—Population changes of beet leafhopper on snakeweed near Moab, Utah, during winter of 1937–38.

the mortality came between November and early January. The number of dead specimens found under the plants indicated that the insects had not moved to other plants.

The winter of 1937–38 was considerably above normal in temperature in the Moab area, so that survival would probably have been even less under normal or subnormal temperatures. Since snakeweed was considered to be a preferred host among the important host plants, it can be seen that winter survival in the eastern Utah-western Colorado breeding areas must be very low.

SNAKE RIVER PLAIN

The Snake River Plain was intensively studied for many years. Stahl (*54*) reported on life-history investigations of the beet leafhopper in the area during 1913–14, and a laboratory was established at Twin Falls, Idaho, in 1925, which was still active in 1965. During that period many detailed investigations were reported, including the life history and seasonal history of the leafhopper, its migratory movements, and the host-plant complex.

Following the pioneer work of Carter (*6*), which outlined the problem, Harries (*32*, *33*) and Harries and Douglass (*34*) studied the physiological life history of the leafhopper in relation to its environment. Fox (*26*), Piemeisel (*45*), and Piemeisel and Chamberlin (*46*) discussed various phases of the host-plant succession and its relation to leafhopper population. Douglass and Hallock (*21*, *22*) reported on experimental studies of various host plants and on the distribution of Russian-thistle. Henderson (*35*,

36) studied important parasites of the beet leafhopper in that area and their synchronization with the life history and movements of the leafhopper.

The annual rainfall over the Snake River Plain varies from less than 10 to about 12 inches. In most places it is insufficient for dryland farming, and irrigation is required. Most of the scanty rainfall occurs from November through May, when temperatures are low and moisture is of greatest value. July and August are the driest months. Fall rains are usually sufficient to germinate the winter annual cover in October, but this germination may be delayed until November.

This area was originally covered with sagebrush and grass, and was in the northern desert shrub formation of Shantz (*52*). The land lying near the Snake River has mostly been irrigated and is farmed intensively. Surrounding the irrigated area is a much larger area, most of which has never been plowed and which contains sagebrush and annual grasses. In the most overgrazed areas the grasses have almost completely disappeared, leaving a cover of weedy annuals, many of which are good host plants for the beet leafhopper. If the land is not cultivated, heavily grazed, or burned over for several years, downy bromegrass (*Bromus tectorum* L.) will replace the weeds. Bromegrass is not a leafhopper host, but it grows very thickly and matures early in the summer, presenting a serious fire hazard. Consequently, large areas of bromegrass are burned over almost every summer and revert to their preceding weed cover. Piemeisel (*45*) and Piemeisel and Chamberlin (*46*) have discussed these changes in considerable detail.

Seasonal History

The fertilized female leafhoppers overwinter on annuals around the base of sagebrush and other shrubs. Carter (*6*) emphasized that in Idaho the overwintering leafhoppers must have food for survival, as the insects become active whenever temperature permits. He presented evidence that the leafhoppers could not endure subzero temperatures for more than a few hours. His outdoor tests indicated that snow cover protected them during the coldest weather in the Twin Falls area. Harries and Douglass (*34*) confirmed Carter's findings, but found further that the effects of cold could be greatly modified by breaking the exposure and warming the insects, if only for a few minutes each day. Temperature may thus be important—as a short cold snap without protection, which kills many leafhoppers from exposure, or as a protracted period of cold weather when the leafhoppers have no opportunity to feed.

The surviving leafhoppers lay their eggs in March or early April in the annual plants on which they overwintered. One generation produced here matures in May or June. At that time the annuals on which they bred are maturing and drying, and the leafhoppers move from them to other hosts. If summer annuals are present in the area, many of the leafhoppers will remain there, but usually most of them move into nearby cultivated areas, where they infest many crops. Two summer generations are usually produced. The adults of the second summer generation leave the drying summer hosts for holdover hosts or newly germinated winter annuals (Harries and Douglass *34*). The period on

holdover hosts is usually short, and in many seasons the winter annuals have already germinated when the leafhoppers leave their summer hosts. Mortality in the fall and winter is very important in preventing excessively high spring brood populations in this area (Douglass et al. *24*).

Host Plants

Douglass and Hallock (*21*) made greenhouse and plot studies of 13 species of leafhopper host plants in southern Idaho. In their summary they stated: "In burned, overgrazed or deteriorated rangeland the most important host plants were flixweed, perfoliate pepperweed and tumblemustard. In the sagebrush areas green tansymustard was the most important. . . . The largest nymphal populations were produced on fanweed in early summer, patata in midsummer and smotherweed in late summer. There was no significant difference between the nymphal populations developing on cut-leaved nightshade, redscale, Russian-thistle and smotherweed during late summer."

This citation only shows the relative usefulness of these plants and does not mention their abundance. If their distribution and abundance are considered, flixweed, perfoliate pepperweed, tansymustard, and tumblemustard are the most important spring hosts and Russian-thistle the most important summer host.

In recent years halogeton, an introduced poisonous weed, has become abundant in southern Idaho and northern Utah. Tests have shown it to be about equal to Russian-thistle in producing and maintaining fall populations of leafhoppers. Its importance cannot be estimated at present. It is still spreading, but serious attempts to control it are being made (Douglass et al. *23*, Hallock and Douglass *31*).

The most abundant holdover host plants in this area are sagebrush, rabbitbrush, and shadscale.

CENTRAL COLUMBIA RIVER AREA

The central Columbia River area embraces land on both sides of the Columbia River in central Washington and Oregon and extends into the newly irrigated section known as the Columbia Basin Project. It lies in the dry sagebrush plains east of the Cascade Mountains, where the annual rainfall is 10 inches or less. Much of the lower and better land is now irrigated, but there are scabland areas and higher hills that are not profitably irrigable, many of which bear leafhopper hosts.

The area was studied by Hills from 1930 through 1933, and his findings have been published (*38*). Hills' publication gives the essential facts regarding the life history and host plants of the leafhopper and should be consulted for detailed information. He postulated three broods of leafhoppers per year, one each in spring, summer, and fall as in the Snake River Plain. Hills found redstem filaree and tumblemustard to be the principal winter and spring hosts and Russian-thistle the chief summer host. Holdover host plants are rarely necessary, and the leafhoppers usually move directly from summer to winter annuals. In the rare dry autumn

seasons sagebrush and rabbitbrush serve as holdover hosts.

The chief breeding areas, as mapped by Hills (*38*), lay on both sides of the Columbia River in Washington and Oregon. The area north of the river was largely overgrazed range and dry farmed land, and part of that to the south was occupied by irrigated farms.

Recent studies in the area by E. C. Klostermeyer and E. F. Dailey, of the Washington Agricultural Experiment Station, and by Joe Cappizzi, of the Oregon State Department of Agriculture, indicate that the picture has changed considerably. Since the original breeding areas have been more carefully farmed and grazed, leafhopper host plants are rare except where a summer fire has destroyed the grass cover. The opening of a large area to irrigation in central Washington has greatly increased the distribution and aoundance of both spring and summer host plants, which are found on roadsides, ditchbanks, and scabland fields scattered through the irrigated area. This makes the problem local, as it is only a short distance from spring to summer hosts.

As during the earlier studies, Russian-thistle is the chief summer host. Perfoliate pepperweed has become abundant and now ranks rather high as a spring host. The principal spring hosts are tumblemustard, flixweed, perfoliate pepperweed, and filaree, in about that order, in the Washington area, whereas filaree is somewhat more abundant and important south of the Columbia River in Oregon.

MIGRATIONS

Several methods have been used in tracing the migrations of the beet leafhopper or in deducing their direction and extent, but, in general, greatest reliance has been placed on serial samples from the same or nearby locations taken at frequent intervals during the migrations.

The only definite summer migration was in the Arizona desert, where summer hosts were repopulated during July. Fall migrations have been studied in California (Lawson et al. *42*, Severin *51*) and in southwestern Utah. The spring migrations were by far the most extensive and important and have been studied in detail in several places (Annand et al. *1*, Dorst and Davis *16*, Douglass et al. *20*, Fulton and Romney *29*, Lawson et al. *42*, Severin *51*).

Repopulation of Summer Hosts in Arizona Desert

Between drying of spring host plants and germination of late summer hosts, conditions in the Arizona desert were so hot and dry that all leafhoppers were forced to leave. When the summer hosts finally germinated, they were immediately repopulated with leafhoppers from some outside source. This source remained somewhat of a mystery until, in the summer of 1938, a widespread sampling survey of the newly germinated summer hosts showed that the highest populations of leafhoppers and the highest percentage of males in the population were both found toward the southeast.

A further search led to the discovery of an area around Douglas,

Ariz., about 150 to 200 miles southeast of the central Arizona desert, at an altitude of 3,000 feet or more, where a late-maturing pepperweed, *Lepidium thurberi*, was producing leafhoppers. This discovery led to a more detailed study in 1939. In that season, when adequate rains had only fallen on about two-thirds of the potential host area, some 1,600 square miles of this host plant were found and sampled five times between March 7 and August 9. The results are given in table 23.

The *L. thurberi* stands were found to be practically without an overwintered population of the leafhopper, as shown on March 7–8. This means that the plant would not serve as a breeding host until populated by flights of first-generation adults from areas producing them by late March or April. During the survey of April 21, first-generation adults were found to be fairly abundant and small nymphs were beginning to appear. This indicated that these plants had received an influx in early April from other desert breeding areas containing other species of pepperweed. The most likely sources were to the north and northwest. A survey made on May 23 showed that a large first generation was present on this plant, but it consisted mostly of nymphs, since the adult population was comparatively low and the proportion of males was also small. By July 7, leafhopper populations on *L. thurberi* averaged 513.6 per square foot. By August 9, practically all the leafhoppers had left. It was this July population that moved north and west, repopulating the desert breeding areas in late July 1939.

Severin (*50*) showed that females tended to migrate greater distances in California than males and, therefore, after a migration there were more males than females remaining in the breeding source. This same condition was found in the Arizona areas, where an excess of males was considered as good evidence that the area involved was the source of a migration. A survey was made on August 7–10, 1939, to determine the source of the reinfestation in other parts of the breeding area. The results are given in table 24.

The average number per 100 sweeps and the sex ratio indicate that the source was in the direction of the Douglas area, since a

TABLE 23. *Populations of beet leafhoppers found on* Lepidium thurberi *in southeastern Arizona during spring and summer of 1939*

Date of sampling	Stations	Samples	Leafhoppers per square foot			Male adults
			Adults	Nymphs	Total	
	Number	*Number*	*Number*	*Number*	*Number*	*Percent*
Mar. 7-8	9	[1]	[1]	0		
Apr. 21	5	61	5.0	.5	5.5	18
May 23	5	11	23.4	164.6	188.0	35
July 7	5	20	79.2	434.4	513.6	59
Aug. 9	5	25	.6	9.6	10.2	67

[1] Too early to measure spring reproduction. One female found in 900 lineal feet of host stands.

TABLE 24.—*Beet leafhopper adults per 100 sweeps and sex ratio of adults collected from summer host plants August 7–8, 1939, after semidesert areas had been reinfested by long-distance flights*

Approximate air-line distance from edge of Douglas, Ariz., area (miles)	Direction from Douglas area	Stops	Average adults per 100 sweeps	Total adults	Average proportion of males
		Number	*Number*	*Number*	*Percent*
115	Northwest	6	15.8	200	21.5
230	do	4	12.6	88	10.2
290	do	3	4.3	61	4.9
100	West	2	7.5	25	16.0
150	do	2	3.0	16	8.7
190	do	3	5.3	52	5.8

higher proportion of males was closest to that area. The data also indicated that larger numbers moved northwest than west. This is to be expected since the mountain ranges run northwest, and in order to go west they must cross several basins and small mountain ranges, which would not be difficult if winds were favorable, but apparently they were not.

During the previous summer (1938) similar data had been obtained. By late July the flight had extended northwest beyond Desert Center, Calif., about 350 air-line miles from the western edge of the Douglas area. Many leafhoppers migrating to the southeastern California areas, where summer hosts are limited, probably died after remaining for several months on undesirable food plants.

As may be noted, this study was done in 1939. By 1965, conditions had changed considerably in the Arizona desert. Since more summer hosts are available inside the irrigated areas, the Douglas area and *L. thurberi* need further study.

Fall Migrations

The fall migration from summer hosts to holdover or winter hosts is usually a gradual drift. Leafhopper populations build up slowly on the holdover hosts during the fall, with little evidence of rapid shifts in population. The mechanics of these movements in central California was discussed by Lawson et al. (*42*). They found no evidence of large numbers of leafhoppers moving farther than 20 to 30 miles from the summer hosts, and the leafhopper populations were highest in late fall on those patches of holdover hosts within a few miles of summer host plants.

Repopulation of Winter Hosts in Utah-Nevada Area

In repopulation of the southern desert during the summer, the total amount of summer host plants in the Utah-Nevada area was too small to produce sufficient leafhoppers and the area was so far from the southeastern area which repopulated the main Arizona desert that very few leafhoppers from that source reached it. Ball (*4*) stated: "The occurrence of curly-leaf in the Sevier Valley, where there is a low pass over the mountains, and again, in Salt

Lake Valley and Bear River Valley—close to low passes, suggests strongly that the Utah infections come from the Escalante Desert region, and the finding of beet leafhoppers fairly thick in several places in the Desert appears to confirm this. The only difficulty with this conclusion is that these hoppers in the desert may have been from swarms that flew in there from still more distant regions." The present studies confirm this last statement.

Extensive surveys showed that ordinarily the beet leafhopper did not overwinter in the Escalante Desert, owing apparently to the lack of suitable host plants. Collections were made in the Escalante Desert and Sevier Valley from 1927 through 1936, approximately every 10 days from early spring until after the migration. The dates of first appearance of the insect in both areas during this period are as follows:

	Escalante Desert	*Sevier Valley*
1927	May 6	May 3
1928	Apr. 14	[1]Apr. 24
1929	May 17	June 1
1930	May 1	[1]May 5
1931	Apr. 26	Apr. 22
1932	Apr. 14	Apr. 14
1933	Apr. 24	Apr. 17
1934	Mar. 22	Mar. 18
1935	Apr. 15	Apr. 15
1936	Apr. 10	Apr. 8
Average date	Apr. 21	Apr. 22

[1] Approximate; exact date not known owing to weather conditions.

These dates show that in most years the leafhoppers appeared in the Escalante Desert and in the beetfields of the Sevier Valley at about the same time, indicating that the leafhoppers in both areas had a common source, which was found to be the Utah-Nevada area.

The Escalante Desert, though not a direct source of leafhoppers for the spring migrations, has been found to be an important summer breeding area (p. 69), from which leafhoppers repopulated the Utah-Nevada desert areas in the fall.

In some places the summer breeding areas of the Escalante Desert and the winter breeding areas of the southern desert are only about 30 miles apart. However, summer areas lie at an altitude of 5,000 feet or more, whereas the winter areas are below 3,000 feet. This difference in altitude, with its parallel difference in temperature, causes dark leafhoppers to mature in the Escalante Desert, whereas those produced at the lower altitude are still light green. This difference enables easy separation of leafhoppers from the two sources. Furthermore, the area between the two types of breeding grounds is largely sagebrush and junipers (*Juniperus* spp.), on which leafhoppers are only found when migrating, and this fact also aids in the detection of movements.

The first records of the fall migration into the southern winter breeding area from the Escalante Desert were made early in October 1934. The migration had already started, but its peak was observed on approximately October 10.

In 1935, the fall migration into the southern breeding areas started during the middle of September and reached a peak about October 18. The movement was actually encountered near St. George, Utah, on October 18 at 5 p.m. The leafhoppers were moving in a southerly direction on a light breeze. Sweeps made in the open air with an insect net at shoulder height in the middle of the road gave five leafhoppers per 20 sweeps. Surveys were made to

ascertain routes of migration, but the only routes followed during these surveys that gave positive results were from the Escalante Desert. A large area of Russian-thistle in the Wolf Hole area in 1935 carried an extremely high population of leafhoppers, but no evidence was obtained that this area contributed any large number of leafhoppers to the winter breeding area north of Las Vegas, Nev.

The annual fall migrations from both the Escalante Desert and the Wolf Hole area were generally southwesterly during this study and the lines of movement were roughly parallel. The distance covered by a single fall migration and the magnitude of population changes are shown in table 25.

The relationship of these changes to topography are shown in figure 37. The map shows population increases at all collecting points. The areas of largest increase lie close to Littlefield, Ariz., near Mesquite, and near the point where the Muddy River and Meadow Valley Wash join the drainage of the Virgin River. All these places are on streams and washes, which drain southward from the Escalante plateau and form natural channels of air drainage, which are probably fol-

TABLE 25.—*Distance from summer breeding area and number of beet leafhoppers per 50 sweeps in Utah-Nevada winter breeding area before and after migration of October 17–18, 1935*

Location	Approximate distance from summer breeding area[1]	Population on—		Population change
		Oct. 15–17 before migration	Oct. 19–20 after migration	
Arizona, miles from Littlefield:	*Miles*	*Number*	*Number*	*Number*
8.8 north	36	0	6.0	+6.0
1.9 north	43	.5	6.0	+5.5
.7 north	44	6.5	35.0	+28.5
2 south	47	1.0	32.0	+31.0
9 south	51	1.5	8.5	+7.0
Nevada, miles from:				
Mesquite, 0.5 north	54	13.0	53.0	+40.0
Glendale:				
29 northwest	40	1.0	7.0	+6.0
13 northeast	55	0	10.0	+10.0
10 northeast	58	3.0	19.0	+16.0
6 northwest	56	4.5	9.5	+5.0
4 northwest	58	1.0	20.0	+19.0
4 south	60	11.0	19.0	+8.0
7.2 south	63	3.0	6.1	+3.1
7.3 south	63	2.5	6.9	+3.4
8.4 south	64	3.3	4.7	+1.4
11.5 southwest	74	.5	15.5	+15.0
24.3 southwest	87	.5	6.5	+6.0
Las Vegas:				
12 southeast	100	2.0	6.5	+4.5
17.5 southeast	105	0	3.5	+3.5

[1] Air-line miles, not distance traveled by leafhopper to reach place indicated.

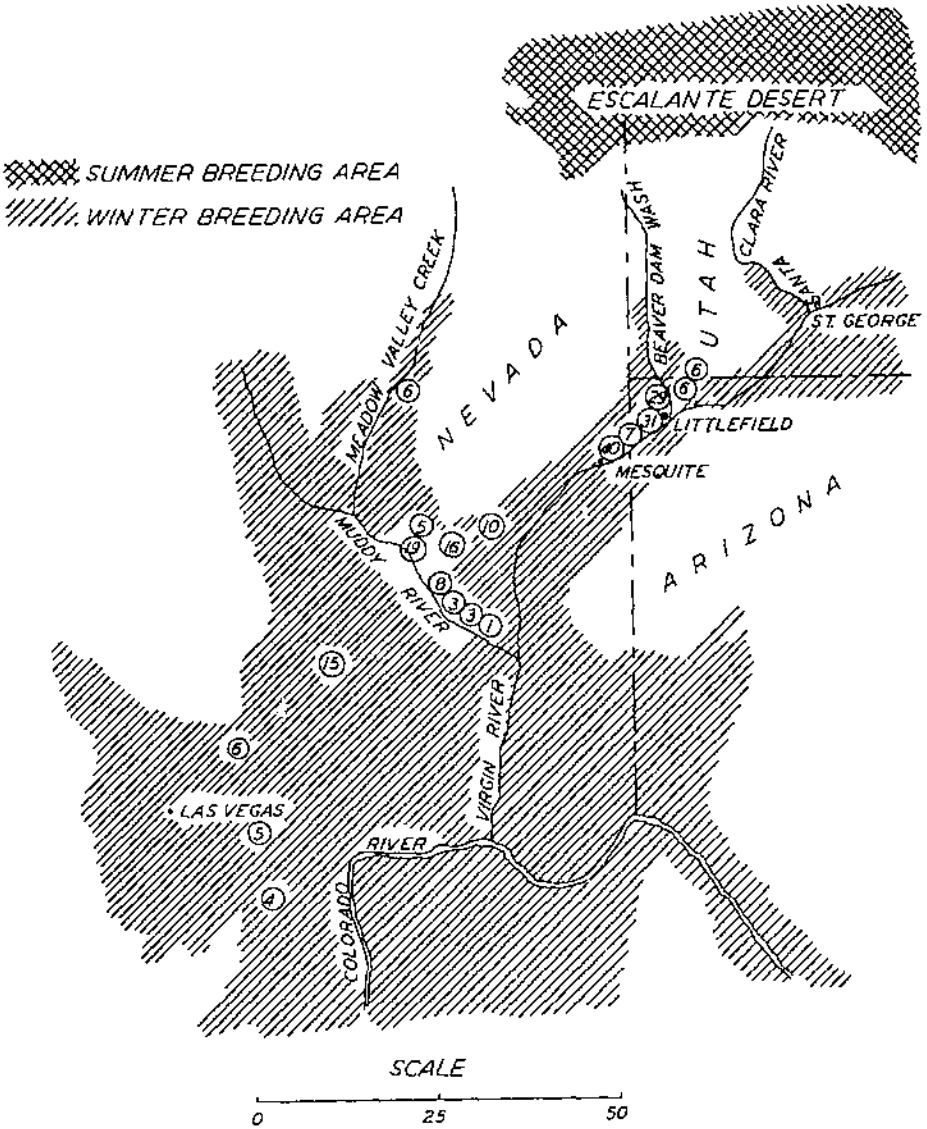

FIGURE 37.—Changes in beet leafhopper populations in southern winter breeding area caused by a fall migration between October 15–17 and October 19–20, 1935. Encircled numbers represent increases in leafhopper populations per 50 sweeps.

lowed by the migrating leafhoppers.

Increases from 3.5 to 6 leafhoppers per 50 sweeps were found near Las Vegas, which is about 100 air-line miles from the nearest point in the Escalante Desert breeding area.

In 1936, the leafhopper migration started on September 8 and

reached a peak on approximately September 21. No further direct observations of the fall migrations have been made in this area.

Local variations in topography and variations in host-plant condition result in such irregular local concentrations of migrating leafhoppers that any detailed conclusions as to routes traveled are impossible. The data indicate a general decrease in population with increasing distance from the summer breeding areas. Not only do the fall migrants increase the resident population in those parts of the winter breeding area already occupied, but some of them disperse over the entire winter breeding area, so that they are present in any part when winter annuals germinate.

Spring Migrations

Lawson et al. (*42*) attempted to determine the conditions under which the leafhoppers leave their hosts and the mechanics of their migrations in central California. They found that leafhoppers seem to have an inborn urge to migrate, which is evident with the maturation of each generation. This urge is related, in the female, to the preoviposition period, and few females containing ripe eggs migrate any distance.

The temperature threshold, below which flights do not take place, they found to be between 60° and 64° F. Most flights take place in the late afternoon, near and after sunset, but some activity is shown in the early morning at the same temperatures. The flights cease when the temperature drops below the threshold value. On a cool morning after a heavy flight, torpid leafhoppers can be found lying on the ground, or even in the road, as their flight was stopped by falling temperature. Evening flights will continue into the night if the temperature remains above their threshold. Undoubtedly many leafhoppers are borne aloft on air currents from which they cannot escape and continue to be carried at temperatures below their threshold.

These workers found that the conformation of the San Joaquin Valley and the winds that most often occurred in the spring at times favorable for flight combined to produce migrations from the breeding areas to the north and northeast into the valley bottom. Under other circumstances they found the leafhoppers moving up canyons and over passes into the Salinas Valley and west across the Coast Ranges. They did not try to trace any long-distance migrations, but believed that these would follow those described.

Central California

Severin (*51*) discussed the main features of the long-distance migrations from the San Joaquin to the Sacramento and Salinas Valleys, on the basis of observations made largely by E. A. Schwing and himself. He concluded that these movements occurred on calm, warm evenings, when the normal air circulation was disturbed or nullified by general weather conditions. He thought that the insects flew against light northwest winds in the San Joaquin Valley, but later work has shown this finding to be erroneous. The probable mechanics of these movements, worked out in detailed studies over many years, is about as follows:

The Great Valley of California, rimmed by high mountains, is usually considerably warmer than adjacent areas, so that the rising

warm air is replaced by currents flowing into the valley through every opening. The chief gap on the west side is the San Francisco Bay opening, which cuts the mountains down to sea level. At a higher level is Pacheco Pass, about 80 miles farther south, at an altitude of about 2,100 feet. The currents blowing through these openings block the movements of leafhoppers toward the northwest from the breeding areas, and usually are so strong as to completely bar northward movement, even on the east side of the valley.

With the approach of cyclonic storms from the north, a wind from the southeast may blow in the valley, partially neutralizing the normal circulation, and allowing the leafhoppers to travel to the northwest. The suction created by these winds, however, keeps the crosswinds in motion, only deflecting them toward the north. The net result of this circulation is that leafhoppers on the east side of the valley can move north and west on south winds, but those on the west side must cross the valley and then move north. If a south wind occurs on a warm evening and heavy populations of leafhoppers are ready to move, large numbers may be carried into the far northern end of the Sacramento Valley.

The populations of leafhoppers found in the east and west side areas of both the San Joaquin and Sacramento Valleys confirm this type of movement. They are always higher east of the rivers in both valleys, and, on the east side, the leafhoppers tend to pile up in the area around Fresno and again between Modesto and Merced.

These movements have been confirmed many times by field collections, but in most seasons the data were fragmentary. In the spring of 1940, the development of a large second brood of leafhoppers in the northern and central breeding areas gave an opportunity for detailed checking, which was utilized as fully as possible with available manpower.

M. F. Bowen and G. T. York, of the Modesto laboratory staff, took weekly or semiweekly samples during late April and May over routes covering the northern part of the San Joaquin Valley and the Sacramento Valley west of the river. The east side of the Sacramento Valley was not sampled until late in the season, because heavy rains had washed out roads and made travel very difficult. During these trips numerous samples were also taken for fat determination and analyzed at the Modesto laboratory.

Unpublished studies have shown that the average fat content of recently emerged females during the preoviposition period ranges between 15 and 20 percent of the dry weight. Migratory movements reduce this fat content, but the energy used is replaced in a short period of feeding on a good host plant. Thus, a drop in fat content during a series of samples at one station indicates the presence of migratory leafhoppers. This is usually followed by a rise unless further migrants arrive at such a rate as to hold the fat content constant. The drop in fat content is usually not large, as the migratory forms merely dilute the population already present. However, if migrants enter a previously unfested area, the fat content of those migrants is considerably below the normal average.

Since from 50 to 100 females are needed for a good analysis, it was not feasible to sample the very lowest populations, and this

lack of data tended to confuse the situation somewhat. In 1940, fat analyses from the areas as far north as Sacramento agreed in indicating a movement of leafhoppers from their foothill breeding areas into the valley and northward on about May 6 or 7 and continuing to about May 15. At this last date, a very heavy migration carried leafhoppers to the northern end of the Sacramento Valley in considerable numbers.

Population samples were much more definite. Table 26, in which the areas are arranged from south to north, shows that the highest leafhopper populations were found in San Joaquin weed areas east of the river on May 7–8, on beets west of the river in the same part of the valley on May 10–11, and in the Delta area on May 14–15. At this last date the peak population was also recorded in the Hamilton City and Chico beet area 100 miles farther north. In the areas designated as "southwest of Sacramento," "Sacramento to Knights Landing," and "Knights Landing to Hamilton City," all three of which were west of the Feather River, although the last one mentioned is east of the Sacramento River, peak populations, much lower than those around Hamilton City and Chico, were recorded about a week later.

Because of the high leafhopper populations around Hamilton City and Chico on May 14–15, a special effort was made to find and sample beets east of the Sacramento and Feather Rivers the following week. At this time eight fields south of Sacramento and east of the rivers averaged 40 leafhoppers per 100 square feet, and eight fields north of Sacramento and east of the routes followed earlier averaged 53 leafhoppers. These leafhopper populations were definitely much higher than in any other areas north of the San Joaquin River.

The best possible interpretation of these data is that a movement of leafhoppers left the northern part of the San Joaquin Valley and infested the southern beet areas between May 7 and 10. Another movement occurred about May 14, which carried large numbers of leafhoppers up the eastern side of the Sacramento Valley to the northern end, and this movement was followed by a drift westward across the valley, which increased leafhopper populations west of the river by May 20. These movements are indicated in figure 38.

Arizona Desert

Tracing the Migrations. — Surveys made during April and May from 1932 to 1938 showed that beet leafhopper populations increased on host plants from Grand Valley, Colo., toward the southern desert breeding areas in Arizona. The adult sex ratio also indicated these desert areas to be the source of northern infestations. A survey made on April 19–24, 1933, along a route on the western side of the migration circuits (fig. 39) showed that the average percentage of males was as follows: 3.2 in southeastern Utah, 11.7 over northern Arizona, and 81.3 in the Arizona desert breeding areas. These collections were made immediately after a heavy April dispersal had taken place.

The same season (May 19–25) after a large migration of second-generation adults over the same route and at the same locations had occurred, the following percentages of the adult population

TABLE 26. *Populations of beet leafhoppers per 100 square feet on various dates in 1940 during spring migration. (Highest populations found in each area are in italics.)*

Location	April				May								
	16	23	26–27	30–May 1	3–4	7–8	10–11	14–15	17–18	20–21	24–25	28–29	30–31
San Joaquin:													
East of river	80.0	245.4	------	391.6	------	*686.9*	------	447.5	------	------	------	------	------
West of river	7.0	25.7	22.7	41.7	152.7	191.0	*234.7*	196.7	166.3	158.0	85.0	56.0	------
Delta:													
South of river	------	.2	.6	.6	9.6	10.7	10.0	*13.4*	10.4	5.6	7.4	3.8	------
North of river	------	------	------	.3	3.1	2.3	5.6	*8.7*	6.3	6.8	4.9	2.8	------
Southwest of Sacramento	------	.4	.4	.8	.4	1.2	1.6	1.6	2.0	*2.4*	2.0	2.0	------
Sacramento to Knights Landing	------	------	------	.2	------	.4	------	1.0	------	*2.4*	------	------	1.2
Knights Landing to Hamilton City	------	.7	------	0	------	1.3	------	6.7	------	*13.3*	------	------	5.0
Hamilton City and Chico	------	------	------	.5	------	6.0	------	*44.5*	------	32.0	------	------	13.0
East of Sacramento and Feather Rivers and —													
South of Sacramento	------	------	------	------	------	------	------	------	------	40.0	------	------	------
North of Sacramento	------	------	------	------	------	------	------	------	------	53.0	------	------	------

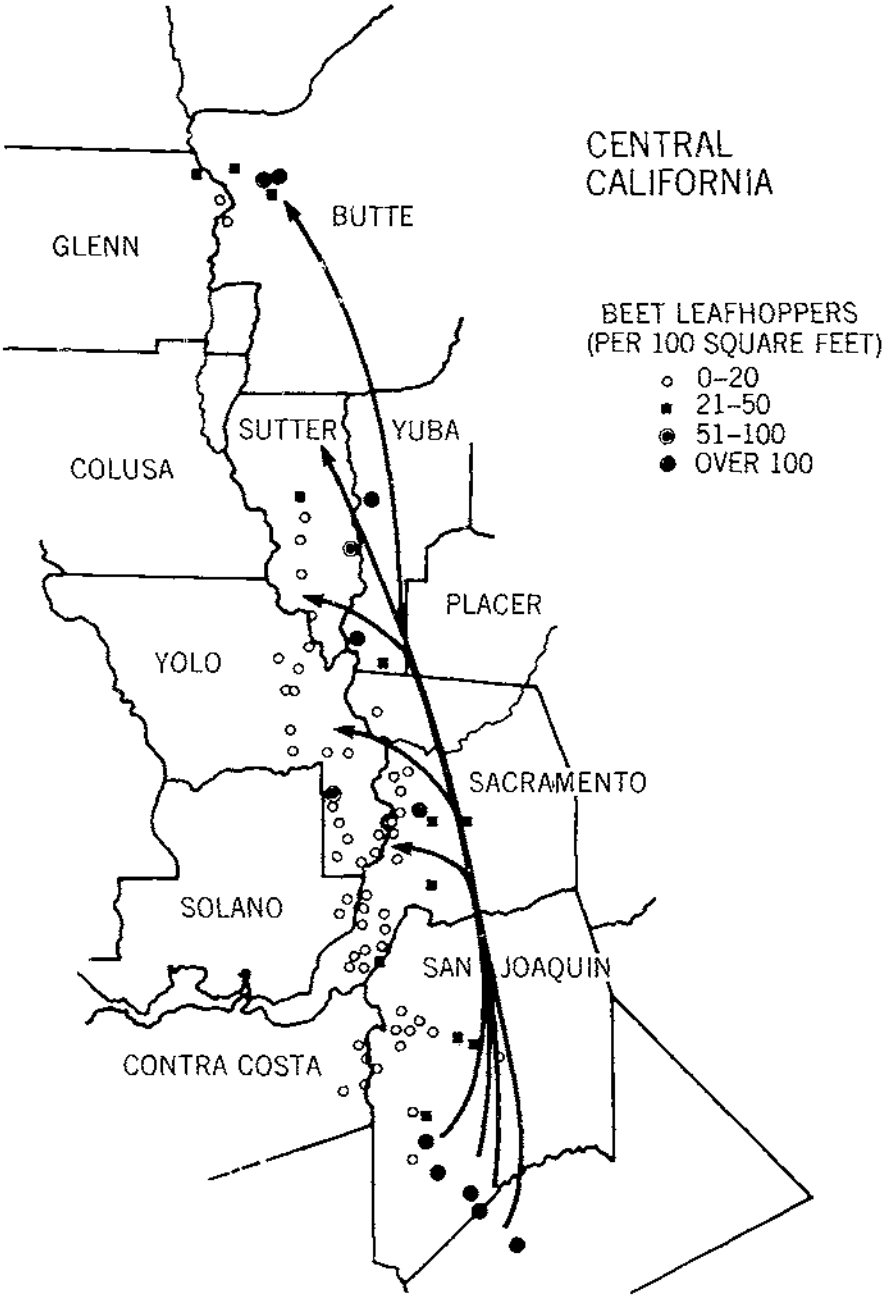

FIGURE 38.—Leafhopper populations per 100 square feet and probable routes of movement in Sacramento Valley of California in May 1940. Arrows indicate general direction of movement.

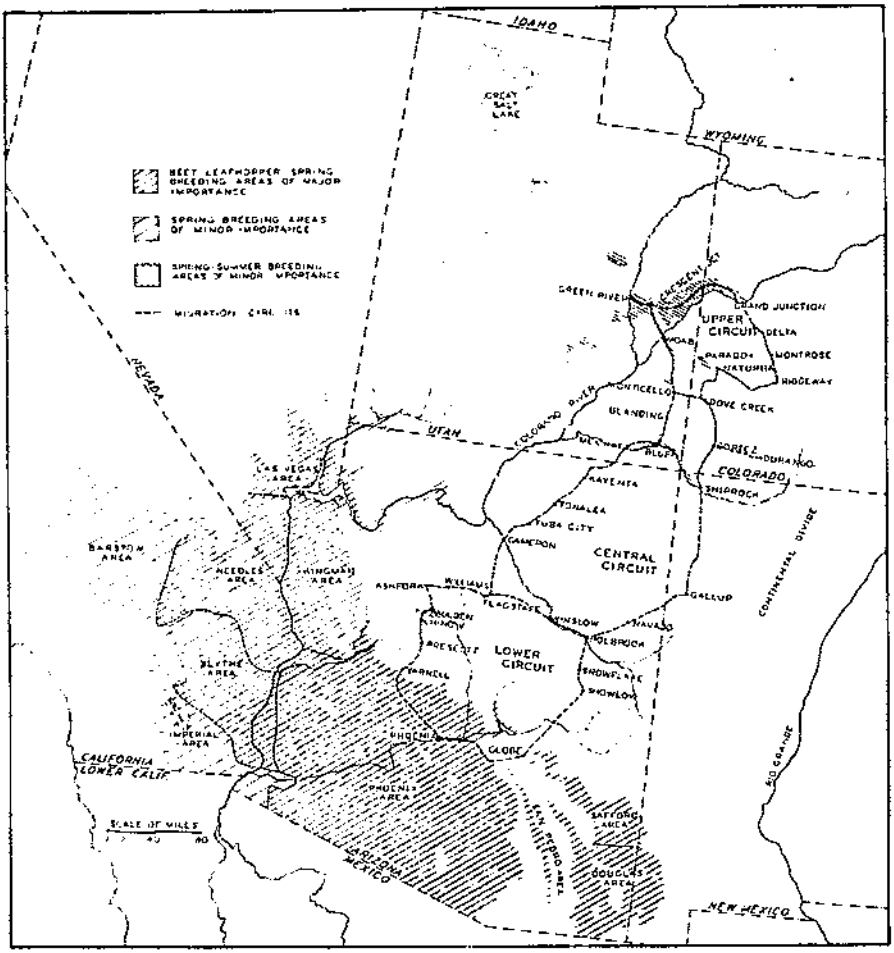

FIGURE 39.—Spring breeding areas of beet leafhopper in southern desert and circuits traveled in studying long-distance spring flights into western Colorado.

were males: 13.6 in southeastern Utah, 39.5 in northern Arizona, and 66.1 in the southern desert breeding areas.

Fulton and Romney (*29*) showed that the chloroform-soluble extractives of female beet leafhoppers, collected along the same migration route as was surveyed for sex ratio in 1933, decreased as distance from the breeding areas increased.

To further study beet leafhopper migrations from southern Arizona to western Colorado, existing roads were traveled periodically during April and May from 1936 to 1939, inclusive. The area was covered by three circuits, as shown in figure 39. These were designated as the upper, central, and lower circuits. Samples were taken with a sampling cage at regular intervals when Russian-thistle was available or wherever plants could be found. From

3 to 14 stops were made between each pair of towns shown in table 27.

April dispersals result from maturation and movement of the first generation in the southern desert, and May dispersals involve chiefly second-generation adults. The peak of emergence for each generation in the spring of 1937 was late April and late May, respectively.

As shown in table 27, migrant leafhoppers had reached about the northern limits of Arizona by April 22, and 5 days later small numbers had reached Grand Junction, Colo., with proportional increases at points toward the southern breeding areas. Studies at Grand Junction from 1930 to 1938 showed that two migration periods occurred most commonly, the first during the last 10 days of April and the second during the last 10 days of May.

Conditions in 1937 deviated a little from this by showing a comparatively heavy influx of leafhoppers all along the line from May 11 to 16. This large increase was apparently brought about mostly by second-generation leafhoppers being forced to migrate

TABLE 27.—*Average number of beet leafhopper adults found on Russian-thistle during 1937 spring surveys along west and east sides of 3 circuits shown in figure 39*

Locations between points	Leafhopper adults per 100 square feet on—			
	Apr. 19–22	Apr. 23–27	May 11–16	May 20–26
	Number	*Number*	*Number*	*Number*
WEST SIDE				
Grand Junction Crescent Junction		0.2	13.1	16.9
Grand Junction Moab		.1	25.6	110.0
Moab Monticello		0	14.6	85.0
Monticello Bluff	0	.9	45.6	
Bluff Mexican Hat	0	16.7	130.0	
Mexican Hat Kayenta	1.3	5.0	78.0	
Kayenta Tonalea	3.9	6.3	45.6	
Tonalea Cameron	56.7	102.5	461.7	
Cameron Flagstaff	13.0	57.0	308.0	
Flagstaff Ashfork	13.3		75.0	388.5
Ashfork Prescott	60.0		296.5	399.6
EAST SIDE				
Grand Junction Delta		0	2.2	52.9
Delta Montrose		0	6.0	48.6
Montrose Ridgeway		0	1.7	32.2
Ridgeway Naturita		0	1.9	2.5
Naturita Dove Creek		0	0	7.5
Cortez Shiprock		1.3	11.3	
Shiprock Gallup		2.9	18.2	
Gallup Navajo		4.5	23.9	
Navajo Holbrook		30.7	98.6	
Holbrook Showlow		24.0	229.0	299.8

prematurely as a result of drying of host plants in the southern breeding areas. Otherwise, studies have shown that large numbers of second-generation adults would not have moved until later. For example, in early May 1935, large numbers of adults were present in the southern breeding areas and wind conditions were favorable for dispersals, but they did not move until after May 20 because host-plant drying did not force them out as it did in 1937. Collections were not made around the central circuit in late May 1937, but data from the upper and lower circuits (table 27) showed that additional influxes occurred in late May, which is the usual time for large numbers to move.

In general, the data in table 27 indicate an increase in leafhopper populations toward the south, but there are exceptions such as from Mexican Hat to Kayenta and from Kayenta to Tonalea. Lower populations at these points do not necessarily mean that this territory was not in the main path of the dispersals, but rather indicates a lack of adequate food plants along the route or topographical conditions unfavorable for the deposition of migrating leafhoppers.

In 1937, the leafhopper populations on the east side of the circuits were lower than those on the west side. However, in two other seasons out of eight studied, larger numbers of leafhoppers were found on the east side of the circuits. In both of these seasons beet leafhoppers were more abundant in the Delta, Colo., district to the southeast than in the Grand Junction area. In all seasons there was a marked increase in leafhopper populations as one traveled from western Colorado into Arizona. A strip of territory about 100 miles wide, with the Colorado River in the middle, is considered to be the main route of dispersal in most seasons.

As a result of these studies and others from 1932 to 1938, it has been concluded that the migrations are of a blanket movement type, since when increases were recorded in Grand Valley there were proportional increases on Russian-thistle all along the line southward. The studies tend to indicate that most leafhoppers infesting a given host area or beetfield as a result of a sudden long-distance migration could have traversed the 400 to 500 miles without intermediate stops.

Weather Conditions as Related to Time of Migrations.—The periods during which long-distance beet leafhopper migrations occurred were checked with daily weather maps compiled by the U.S. Weather Bureau. A low-pressure area would usually progress eastward from the west coast through Tonopah, Nev., toward Denver, Colo. This condition was accompanied by winds mostly from the southwest at Phoenix, Ariz., blowing in a northeastward direction up the Colorado River drainage. The velocity of these winds during daylight hours usually ranged from 5 to 15 miles per hour 4 feet above the ground in the breeding areas, whereas in northern Arizona the same winds would blow from 20 to 30 miles per hour. From 1930 to 1938, most beet leafhopper influxes into beetfields in Grand Valley, Colo., occurred coincidentally with such windy periods.

During May 1937, leafhopper populations in the southern desert areas were fairly large. The weather maps compiled at Phoenix were examined daily during May to determine the time when

wind conditions were favorable for long-distance flights. As soon as conditions were found to be favorable, a survey was started around the lower circuit, as shown in figure 39.

A tanglefoot trap, fashioned somewhat after that described by Smith et al. (*53*), was placed at an elevation of 6,900 feet 10 miles west of Flagstaff, Ariz. A caretaker collected daily all leafhoppers that stuck to the tanglefoot screen during May 1937.

On the afternoon of May 9, 1937, wind conditions were favorable for a long-distance movement of the leafhopper. During the forenoon of May 10 while wind conditions were still favorable, seven adult beet leafhoppers were caught in a cone-shaped air dredge, which was attached to the automobile fender, over a distance of 88 miles south of Ashfork, Ariz. (fig. 39). This territory is mostly mountainous with some open grassland valleys. Records from the tanglefoot trap showed that four adults were caught on May 9 and on May 10 four more adults were taken. A heavy influx of beet leafhoppers occurred in Grand Valley, Colo., during May 8–10.

The second favorable period for leafhopper movement occurred on May 17–18. The air dredge was not used and the tanglefoot trap did not catch leafhoppers at that time, although a second May influx into Grand Valley occurred on May 18–19.

The third favorable windy period occurred on May 24–25. On May 25, six adults were caught in the air dredge over the same 88 miles south of Ashfork, and the tanglefoot trap caught four adults on May 24 and three on May 25. The trap did not show catches on any other dates during May. The peak in beet leafhopper numbers migrating to the Grand Valley beetfields was recorded during May 24–27. These data indicate that adult beet leafhoppers move during the windy periods.

Correlation of Breeding Area Conditions With Intensity of Initial Infestations of Leafhoppers in Beetfields of Western Colorado.—Beet leafhopper populations in the Phoenix, Ariz., area from the fall of 1934 to the end of the 1938 spring season were correlaced with leafhopper populations found each spring in the beetfields of western Colorado. Studies in the Phoenix area were made by surveys. Many well-scattered locations over most of the extensive breeding area were sampled each year at about the same time. The data obtained are given in table 28.

1934–35. Beet leafhopper populations on chinchweed in the fall of 1934 were high followed by large numbers per unit area on pepperweed at the population peak for the first spring generation, and also a second generation was large in May. Since considerable areas of pepperweed and wild mignonette were included in the 4,300 square miles of host plants for the second generation, all conditions were favorable for large populations in the spring of 1935. After the late May 1935 dispersals, there were on an average 210 adults per 100 feet of sugarbeet row in Grand Valley, Colo. This is a high initial infestation for the valley.

1935–36. In the fall of 1935, large numbers of leafhoppers were again found on chinchweed, but the peak of the first spring generation on pepperweed was low, and very few second-generation leafhoppers were produced. The apparent reason for the small numbers in the first spring gen-

TABLE 28.—*Host-plant conditions and beet leafhopper populations in fall and spring in Phoenix, Ariz., area (fig. 24) from 1934 to 1938 as related to infestations on sugarbeets in Grand Valley, Colo., after spring movement from Arizona*

Season	Phoenix area						Leafhopper adults per 100 feet of sugarbeet row in Grand Valley
	Stops in area with chinchweed present late in September	Leafhoppers per square foot on chinchweed	Holdover period	Area of host plants for first spring generation	Leafhoppers per square foot on pepperweed at peak of first generation	Area of host plants for second generation	
	Percent	*Number*	*Days*	*Square miles*	*Number*	*Square miles*	*Number*
1934–35	90	11.0	10–15	15,000	20.1	4,300	210.0
1935–36	100	18.2	75–90	7,000	2.1	200	16.3
1936–37	95	5.8	20–30	14,200	5.4	2,360	95.0
1937–38	61	7.4	55–70	8,349	2.9	500	95.0

eration was a long period of 75 to 90 days on holdover hosts in the fall, during which most of the leafhoppers died. Also, the areas and density of winter annuals were low because the rainfall was only 74 percent of normal. The spring hosts nearly all dried in April except for an estimated 200 square miles of filaree at the higher elevations. As a result of these conditions, the beetfields of western Colorado had very low infestations of leafhoppers in May.

1936–37. Fall leafhopper populations were low on chinchweed, and the number entering the winter was small in spite of a favorable short period (20–30 days) on holdover hosts. The first spring generation was small, but a second generation developed during May on 2,360 square miles of host plants, which included pepperweed and wild mignonette. The resulting infestation in western Colorado was moderate by late May.

During these three seasons there was a close correlation between the populations of leafhoppers found in the Arizona desert around Phoenix and the population of leafhoppers found in the Grand Valley of Colorado after the spring movements. In the following season (1937–38), however, the correlation failed almost completely.

1937–38. In the fall of 1937, leafhopper numbers were again fairly low on chinchweed (table 28). The holdover period was fairly long, and numbers at the peak of the first generation on pepperweed were low. The 500-square-mile host stand for the second generation was again filaree at the higher elevations, which supported very low populations by the middle of May. Practically no second generation was produced in the Phoenix area during May 1938, and yet the infestation into the western Colorado beetfields was moderately large. This con-

dition indicated that other areas, in addition to the Phoenix area, must be responsible for leafhopper infestations into sugarbeet fields of western Colorado. It was known that different conditions existed in breeding areas in southeastern Arizona as well as in southeastern California, and it was suspected that these other areas affected the Colorado infestations in the spring of 1938.

Following the poor correlation of spring populations in the Phoenix area with the Colorado leafhopper infestation of 1938, surveys were immediately extended to other breeding areas during late April. Beet leafhopper populations found during late April 1938 in southeast and northwest Arizona and northeast California are given in table 29. Many leafhoppers were found in the Safford and Douglas (southeast Ariz.) areas on pepperweeds, tansymustards, and bladderpod, part of which were second-generation nymphs. Many leafhoppers were also found in the Kingman (northwest Ariz.) and Needles (northeast Calif.) areas in late April 1938 on pepperweeds, tansymustards, redstem filaree, and pectocarya. Since the plants were in fairly good condition, these areas could have contributed to the Colorado infestation in the spring of 1938. An estimate of the extent of stands in square miles for each area was not made in 1938, but the amount of succulent plant stands was fairly extensive and many leafhoppers were produced in these areas after the Phoenix area plant stands had almost completely dried.

During the spring of 1939 and 1940, surveys were extended to the Imperial Valley, Needles, Blythe, and Barstow, Calif., areas (fig. 39) to determine their importance as beet leafhopper breeding areas. These data are given in table 29. The surveys were not over the same territory both seasons.

Plants productive in the Imperial Valley area on April 14, 1939, were desert plantains, wild mignonette, and sandverbena (*Abronia* sp.). One of the three plants was found at practically all systematic stops made in the area.

Sections surveyed on May 11–14, 1939, in the Needles (northeast Calif.) area showed large populations on pepperweeds and wild mignonette, with fair numbers on desert plantains and smaller numbers on nievitas. About the same time in the Blythe (southern Calif.) area such plants as pepperweeds, desert plantains, and nievitas were important in supporting adult and nymphal populations.

Sections surveyed on May 1–4, 1940, in the Needles (northeast Calif.) area showed comparatively large populations on all plants listed in table 29, except on redstem filaree and pectocarya, and this condition existed again at a time when host plants were dry in the Phoenix area. Parts of the Blythe (southern Calif.) area surveyed in 1940 showed desert plantains, nievitas, and wild mignonette to be the important plants. Most of the Barstow (northwest Calif.) area was surveyed in 1940. Pepperweeds, desert plantains, nievitas, wild mignonette, and sandverbena supported fairly large populations, whereas numbers on redstem filaree were low.

The comparative abundance of the various host plants for the 1939 and 1940 surveys are shown in table 12.

TABLE 29. *Beet leafhopper populations per square foot found on various spring hosts in southern desert during sampling surveys in 1938, 1939, and 1940*

Date and area [1]	Pepper-weeds	Tansy-mustards	Bladder-pod	Desert plantains	Nievitas	Redstem filaree	Wild mignonette	Pecto-carya	Sand-verbena
April 19-28, 1938:									
Arizona, southeast	2.8	6.4	3.3			0.04			
Arizona, northwest	3.2	5.9				.8		2.0	
California, northeast	7.9					.7			
April 14, 1939:									
California Imperial Valley				6.0			33.1		8.0
May 11–14, 1939:									
California, northeast	18.0			5.6	1.7		37.3		
California, southern	164.0			12.5	7.3				
May 1–4, 1940:									
California, northeast	72.6	17.0	72.0	21.1	23.5	2.6	190.0		12.0
California, southern				14.6	26.9		224.0		
California, northwest	48.5			14.7	12.0	1.3	132.0		6.5

[1] Directions refer to parts of southern desert, not necessarily to parts of States as a whole.

Utah-Nevada Area

It became apparent during early investigations in the Sevier Valley of Utah that beet leafhoppers had moved into sugarbeet fields from an outside source, probably the desert breeding areas. It was essential to define such areas before any control of the leafhopper in the desert could be possible. Therefore, tracing leafhopper movements from the breeding areas to the sugarbeet fields was of primary importance in determining which breeding areas were of economic significance.

Surveys had indicated that the spring migration of the leafhopper into the southern beet-growing section of Utah must be from a great distance, because the nearest winter breeding area was about 200 miles southwest of the beet-growing section and a large part of the intervening territory over which the migrations occur is desert. Consequently, there is an absence of suitable plants from which leafhoppers may be collected to detect movements. To overcome this deficiency, small experimental plots of host plants (Dorst and Davis *16*) were germinated in the fall by irrigation and maintained in a growing condition so that early in the spring the plants were growing vigorously and were of a suitable size to be sampled for leafhopper populations.

The principal mountain ranges in the area observed extend from north to south. The Virgin and the Santa Clara Rivers and their tributaries traverse the southern winter breeding area. These rivers have created openings through the mountain ranges, which offer routes of migration for the beet leafhopper. Some plots were established near these openings from the winter breeding area and on these suspected routes; other plots were placed to the west and northwest to check other possible routes and sources.

The most outstanding feature of the plot collections was their irregularity, which is in accord with data regarding migrations of the beet leafhopper obtained by other means. Migrations take place in favorable weather, but are checked by cold weather, heavy rains, or unfavorable winds. Data from the trap stations indicated that the leafhoppers covered considerable distances in a short time, as heavy increases might be found at points 150 miles apart on the same or successive dates.

The time of movement of the beet leafhopper is fundamentally governed by the time the broods mature in the breeding area. After the beet leafhoppers leave the breeding area, their movements are affected by weather conditions, especially wind and temperature encountered en route, which affect the direction and rate of travel of the leafhopper. For example, data from plots and field collections in 1933 showed that after the migration had begun, adverse winds stopped its progress, but with the reappearance of favorable winds the movement to the beet-growing area was resumed.

On a given route, the direction of migration may be indicated by the inverse ratio of the leafhopper density to the distance from the breeding area. To utilize this fact in demonstrating routes of migration in southern and central Utah, daily sweep-net collections from all plots have been assembled to form seasonal totals, and these totals averaged so as to give the number of beet leafhoppers

captured per season at each plot. These summarized data are shown in table 30.

Since it was necessary to place the plots where operators could be found for them, it was not possible to cover the territory adequately. More plots at intermediate points would probably have served to clarify the situation if they could have been so placed. So far as the data may be interpreted, the spring migration is probably a blanket movement over the entire desert, in which the density of leafhoppers is greatest along channels of natural air drainage or wind movement. The suspected routes described below follow such channels.

The arrangement of the stations in table 30 is roughly from south to north. To show the relationship of beet leafhopper movements to topography, these stations and the average seasonal catches, as given in table 30, are mapped in figure 40.

In general, the catches decreased from south to north, and relatively low catches were usually recorded north of Delta. The data indicate that the leafhoppers may reach the Sevier Valley by three routes. They may travel through Modena, Nada, and Beaver to a pass opposite the south end of the cultivated area near Sevier. In some seasons the leafhoppers may travel slightly farther west either through Modena, Nada, Milford, and Delta or by a route farther

TABLE 30.—*Total beet leafhoppers collected from plots in Utah for 1932–35 and average for each plot*

Location	1932	1933	1934	1935	Average
	Number	*Number*	*Number*	*Number*	*Number*
Modena		810		5,655	3,233
Glendale		2,304	236	2,142	1,561
Cedar City	112	380	118	917	382
Parowan		44	28	130	67
Panguitch		90	159		125
Nada	127	227	352	1,307	503
Beaver		53	192	1,090	445
Milford		90	132	133	118
Marysvale		224	79	231	178
Cove Fort			47	173	112
Sevier 1	42	221	79	229	143
Sevier 2		633		735	686
Fillmore			18	55	37
Hinckley	23				[1] 23
Delta	24		407	641	357
Scipio		38			[1] 38
Lyndyl	45	42	135	22	61
Eureka	4	3			4
Lofgreen	0				[1] 0
Fairfield			6	1	4
Lehi	6		87	10	34
Vernon	0				[1] 0
Iosepa		2	58		30
Tooele		20	81	19	40
Burmeister			363		[1] 363
Hooper	2	1	123	5	33

[1] Not included in fig. 40 because trap plots were only operated for one season.

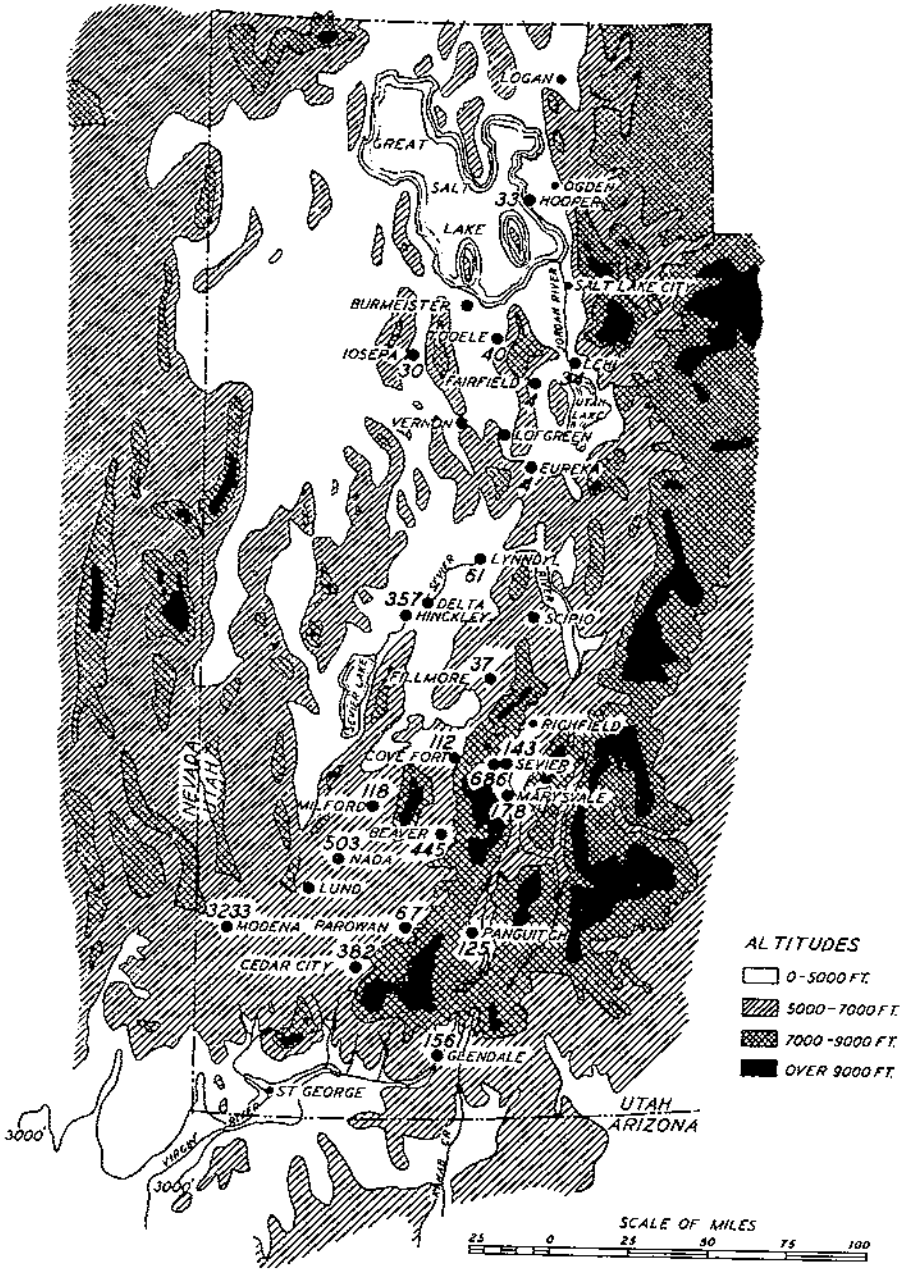

FIGURE 40.—Topographic map showing average collections of beet leafhoppers on plots during spring migrations of 1932–35.

west from Modena to Delta through an area in which it was impossible to maintain plots and no host plants occur upon which to check the possibility, finally entering the Sevier Valley at the north end and traveling up the river. The migrations on these routes may be augmented by leafhoppers coming from the lower areas through smaller openings between Modena and Cedar City. A third route is by way of the Virgin River through St. George and Glendale, reaching the headwaters of the Sevier River near Panguitch.

Ball (4) mentioned leafhoppers swarming near Panguitch. From this point they may follow the Sevier River northward into the beet areas. Table 30 shows the 1933 collections to be larger at Marysvale and Sevier than at Panguitch, indicating that some other route was followed by the leafhoppers. On the other hand, the 1934 collections are larger at Panguitch than at either Marysvale or Sevier, showing that the leafhoppers may have passed through Panguitch on their way to the Sevier Valley in this season.

The large catches of leafhoppers on the trap plot at Glendale illustrate the funneling effect that would drive the leafhoppers into that area from the west and southwest. A westerly wind would carry leafhoppers east from Glendale into a migration route leading to western Colorado. The contours in figures 17 and 40 illustrate this possibility.

These plot collections have shown that only small numbers of leafhoppers reach north Utah from the southern desert during the period of observation and that the leafhoppers may leave the desert on several routes. The irregularity in the number of leafhoppers captured between nearby stations may be due partly to the inadequacy of the sweep-net method, but probably largely to variations in local conditions. Such irregularities have been found wherever movements have been traced over rough country by any method.

The dates of the start and peak of the spring migrations into the Sevier Valley were determined for 4 years by the plot method, and for 5 additional years from the regular survey collections. These data are as follows:

Year	*Start*	*Peak*
1927	May 3	(1)
1928	Apr. 24 [2]	(1)
1929	June 1	(1)
1930	May 5 [2]	May 26
1931	Apr. 22	May 22
1932	Apr. 14	June 2
1933	Apr. 17 [2]	June 2
1934	Mar. 18	May 5
1935	Apr. 15	May 10

[1] No record.
[2] Exact date not known owing to weather conditions or absence of collector.

The start of the migration was very easily determined, because the beet leafhopper does not overwinter in the Sevier Valley area. The peaks are recorded as the time when the greatest increase was observed. It can be seen from this tabulation that the period from the start to the peak of the migration from the southern breeding area ranged from 21 to 49 days and that the date of the first spring migration varied between March 18 and June 1.

Northern Utah Breeding Areas

The major irrigated area in Utah occupies a narrow strip, which lies to the west of the Wasatch Range and extends from Joseph on the south to the State line on the north, a distance of

over 200 miles. Curly top damage, if the infestation was from one source, theoretically would be proportional to the distance from the source. The fact that damage is irregularly distributed through the northern areas indicates that several sources contribute. The distribution of leafhoppers in the beetfields of Utah after the spring movements are over indicates that each section is largely populated with leafhoppers from specific breeding areas and not from any breeding area that is common to the entire region.

Breeding grounds in northern Utah are small isolated areas of host plants at short distances from the cultivated areas. As a result, migrations of the leafhopper from these breeding areas affect chiefly nearby fields of beets, and the distribution of leafhoppers over northern Utah after the local migration is very irregular. Ordinarily the migrations from the southern winter breeding grounds are about a month earlier than the northern migrations from local breeding areas. This makes it possible to separate roughly the contribution of leafhoppers to the northern Utah beetfields from the two general sources by making population counts in the beetfields before and after the local migrations.

The records obtained in 1935 illustrate the distribution of the leafhopper in the beet area in years of normal long-distance migrations from southern Utah. Population determinations were made on May 24 after the peak of the long-distance migration had reached the beet-growing area and previous to the start of the migrations from the local breeding areas. The second population survey in 1935 was made on June 15, after the migrations from the local area had occurred. Surveys were made with the square-foot sampling cage. The leafhopper population was determined by taking between 100 and 200 square-foot samples in each of 98 fields on both surveys. (Fig. 41.)

The small peak of leafhopper abundance at Payson was caused probably by an influx of beet leafhoppers from the West Mountain breeding area; the peaks between Lehi and Farmington by migrations from the Magna group and possibly smaller adjacent breeding grounds; the peak at Hooper by movements from Little Mountain west of Ogden and Promontory Point; and the peak between Corinne and Garland by movements from local breeding areas around the north end of Great Salt Lake. To show these relationships more clearly, the general areas covered by migrations from the southern and northern winter breeding areas are indicated in figure 41, and the names of the local breeding areas have been so placed as to show their effect on local populations.

It is apparent from figure 41 that the contributions from the local breeding areas far outweighed those from the southern breeding area in the entire territory north of Santaquin.

To show variations between seasons, the beetfield populations were averaged by counties and arranged from north to south for 1931–40, as shown in table 31. The population data from 1931 to 1933 were obtained by the hand-and-knee method. After 1933, population data were obtained with the Hills sampler. From 10 to 50 square-foot samples were taken in each field, depending on the population present. Since comparative collections indicated that the population of leafhoppers

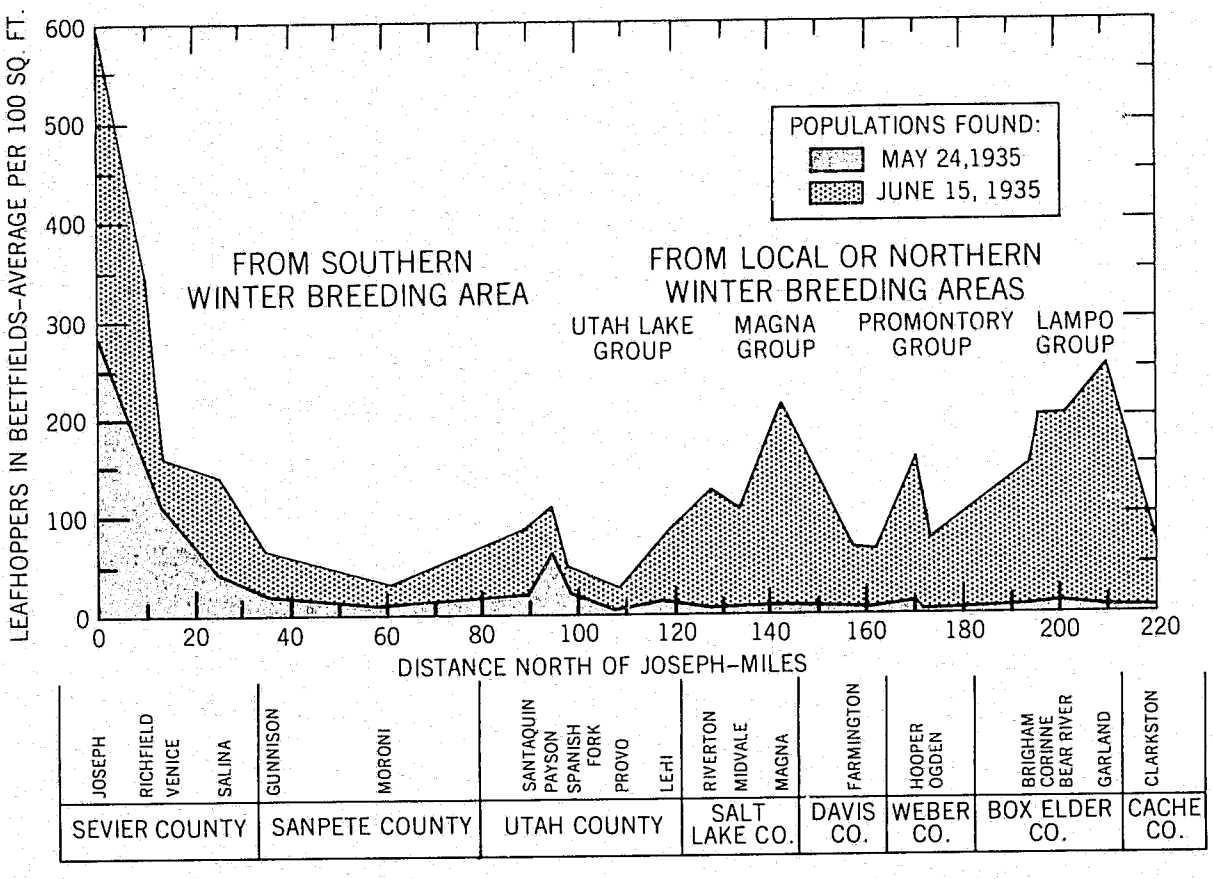

FIGURE 41.—Populations of beet leafhopper in various beet-growing sections of central Utah after early movement from southern breeding areas (May 24) and after local or northern movements (June 15), indicating breeding areas contributing these populations.

TABLE 31.—*Number of beet leafhoppers per 100 plants in beetfields of central and northern Utah after spring migrations*

County	1931	1932	1933	1934	1935	1936	1937	1938	1939	[1] 1940	Average
Cache	---	---	4.3	33.0	46.0	0.6	16.8	15.0	2.7	96.7	26.9
Box Elder	---	---	11.2	353.6	71.9	26.6	11.0	35.3	32.6	134.0	84.5
Weber	---	---	8.6	414.0	79.0	10.0	60.0	47.0	78.3	180.0	109.6
Davis	---	---	7.7	472.0	68.0	37.9	30.0	49.0	90.0	146.7	112.7
Salt Lake	146.2	18.1	4.3	586.4	153.7	44.6	75.0	118.0	80.0	126.7	135.3
Utah	38.7	11.2	3.4	348.8	75.5	19.7	106.7	37.6	48.0	126.7	81.6
Juab	103.2	15.5	---	228.0	94.5	---	90.0	15.0	---	190.0	105.2
Sanpete	97.2	34.4	19.8	58.0	45.1	3.6	192.5	22.0	2.0	120.0	59.5
Sevier	1,458.6	86.0	55.0	116.6	271.9	34.0	277.5	20.0	19.5	203.3	[2] 120.4
Average	---	---	14.3	290.0	100.6	22.1	95.6	39.9	44.1	147.1	93.1

[1] 1940 data taken before local movement occurred and represent almost entirely results of very heavy movement from southern breeding area.

[2] 1931 omitted in determining average for Sevier County (see text).

shown by square-foot samples was approximately 8.6 times that shown by the hand-and-knee counts, the counts for the years 1931–33 have been multiplied by this factor before they were entered in table 31.

In 1931, out of the 33 fields examined in Sevier County there were 27 fields in which the beet leafhoppers were too numerous to count. The population of these fields was arbitrarily placed at 200 leafhoppers per 100 beet plants (hand-and-knee count) and became 1,720 when the counts were corrected. However, the average for the 33 fields was 1,158.6. As the figure for this year is merely a corrected estimate, 1931 was omitted in figuring the average for Sevier County in table 31. Examination of the averages in this table shows that the smallest numbers of leafhoppers reached Cache County.

There are no local leafhopper breeding areas in Cache County, and the movement from the southern areas rarely reaches there. Average populations increased from 84.5 leafhoppers per 100 beet plants in Box Elder County to 135.3 leafhoppers in Salt Lake County. The breeding areas around Great Salt Lake consist of a large area north of the lake at a considerable distance from beets (Promontory Point, Lampo, west Garland), some very small areas east of the lake in close proximity to beets (Little Mountain west of Corinne, Little Mountain west of Ogden), and a large area south of the lake immediately west of the beet-growing area (Magna, Salt Lake Flats). The beet leafhoppers contributed by these breeding areas to the counties mentioned appear to vary directly as the size of the breeding area and inversely as their distance from the sugar-beet region.

Populations in Utah, Juab, and Sanpete Counties are similar to those in Box Elder and Weber Counties. These counties contain two small breeding grounds (West Mountain and West Utah Lake) and are between the areas normally affected by either of the main movements. They may receive leafhoppers from either breeding area. Sevier County receives its high populations almost entirely from the southern breeding area.

A comparison of the leafhopper population in Sevier County with that in the counties from Salt Lake north will show the relative magnitude of the southern and northern migrations in any season. The southern migration was heavier in 1931, 1932, 1933, 1935, 1937, and 1940, whereas the northern migration was heavier in 1934, 1936, 1938, and 1939. The abnormal year of 1934 stands out in table 31, as populations at all points north of Sanpete County except Cache County were higher than those in Sevier County.

The averages given indicate that 1934, 1935, 1937, and 1940 had relatively large beet leafhopper populations in the areas as a whole, whereas 1933, 1936, 1938, and 1939 had relatively small populations.

Snake River Plain Area

The spring breeding grounds in the Snake River Plain area lie to the west and northwest of the cultivated areas, and the leafhoppers drift on the prevailing westerly winds into the cultivated areas during May and June. Sometimes drying winds will force most of

the leafhoppers to migrate about the same time, but usually the movement is gradual, reaching a peak in late June. This is very similar to the migrations into northern Utah cultivated areas from their local breeding grounds. The particularly heavy spring movement of 1930 was discussed in detail by Annand et al. (*1*), and its pattern is typical of such local movements.

There is considerable evidence for an occasional spring migration of leafhoppers into southern Idaho from the southern desert, but such movements are rare. Such a movement was suspected in 1934, but the evidence was not sufficient to prove just where the leafhoppers originated. In 1958, the Snake River Plain received a very heavy early migration from a southern source. Earlier examination of local breeding areas and adjacent parts of northern Nevada ruled out any northern source, and leafhoppers were very abundant in the southern desert that spring. H. E. Dorst also reported a heavy movement of leafhoppers from the southern desert into northern Utah at about the same time as the Idaho movement. This evidence leaves little doubt that the source was the southern desert.

Spring Migrations Into Territory Not Normally Occupied

In seasons when the leafhoppers are particularly abundant in their spring breeding areas, favorable winds at just the right time may carry them far outside their normal range. Suspected migrations of this type occurred from the southern desert into southern Idaho.

Davis (*14*) reported the occurrence of the beet leafhopper and curly top in many areas west of the Cascade Range in Oregon, Washington, and British Columbia in August 1926. Carter (*6*) examined parts of these areas in the spring of 1927 and found no leafhoppers. Curly top has not been serious in any of these areas since that time. Carter (*6*) thought the climate too humid in winter and spring for the leafhoppers to survive, an opinion with which the present writer concurs. This is a clear-cut case of movement into the area in the spring, probably through the Columbia River Gorge from the central Columbia breeding area. Since east winds down that gorge in the spring are not common, the flight has not been repeated on a detectable scale. Carter also discussed the finding of leafhoppers and curly top in western Montana, probably from the Snake River area.

Douglass (*17*) discussed many of these unusual flights, particularly from the Rio Grande area into the Great Plains and as far north and east as Minnesota and Illinois. He also suggested a causal connection between the appearance of the leafhopper in Wyoming and central Montana and very early and heavy migrations in southern Idaho.

With any introduced insect there is always the possibility that it may suddenly adapt itself to conditions other than those under which it first became abundant. The alfalfa weevil occupied the Western States for many years before it migrated east. Now it is well adapted in what appears to be a much more humid environment than in the West. There is always the possibility that the beet leafhopper might do likewise and become adapted to farming conditions in the Eastern States.

Small colonies of the beet leafhopper have maintained themselves in Illinois and in Florida for some time (Douglass *17*). These have apparently found favorable microclimates, but show no signs of spreading into uninfested territory. Other than these two instances, all local infestations outside the normal distribution of the leafhopper have been sporadic, dying out after one or a few seasons. The recent shift in breeding area in west Texas was not an adaptation on the part of the insect, but rather a shifting of climatic conditions that made breeding possible in previously uninfested areas. Likewise, the shift of leafhoppers into the Columbia Basin is not an adaptation of the leafhopper, but a change in farming conditions that produced a more favorable host-plant succession.

There is no evidence that the leafhopper can permanently occupy any desert or semidesert territory outside that normally occupied.

Effect of Weather on Leafhopper Flights

To get an idea of the actual weather conditions accompanying migrations, the author obtained flight records from O. A. Hills for the Arizona movements, from H. E. Dorst for those from the southern desert to central and northern Utah, and from K. E. Gibson for the Snake River Plain. California records were already available from data of E. A. Schwing and the Modesto laboratory. About 44 dates were selected on which the beet leafhopper population showed rapid changes over a short period. These dates give a leeway of 2 to 7 days in most cases, as samples were taken at intervals of several days, and not every day. In the earlier years the dates were not so reliable as more recently.

Through the cooperation of Lester B. Larson, meteorologist, U.S. Weather Bureau in Walla Walla, Wash., the author was able to examine a series of historical daily weather maps covering practically the entire period. Out of the 44 available dates, 34 fell within 2 or 3 days of a favorable wind complex as shown on the maps. As noted earlier, in the Arizona-Colorado migrations, the passage of an area of low pressure across the middle of the Great Basin area usually brought, on its southeast quarter, strong winds from the Southwest. In central California the high mountain range to the east changed the surface direction to south or southeast and produced long-distance migrations into the Sacramento Valley. On most of the 10 dates where the favorable weather complex was not found, there was some question as to the exact dates of migrations, as the movements were small and their detection was difficult.

In a few recent instances, where weather maps were available for the 10,000-foot level, agreement between migrations of leafhoppers and the passage of low-pressure areas was even more marked than in the maps of surface winds, as the surface winds at particular stations appeared to be strongly affected by purely local conditions, whereas those at higher altitudes were not and probably gave a better picture of general conditions. The heavy movement of leafhoppers from southern Arizona into northern Utah and the Snake River Plain in 1958 accompanied a particularly well-developed wind circulation in the right direction, especially

as shown on the 10,000-foot altitude maps.

On the other hand, at least 2 years were known in which the leafhoppers in California did not reach the Sacramento Valley although they were numerous in the San Joaquin Valley. In those years many of the leafhoppers moved south and southeast over the Tehachapi Mountains into southern California, and that area had a rare outbreak of curly top. In those seasons, the daily maps showed no time during the maturing of the leafhoppers when winds were favorable for northward flights.

The leafhoppers are at the mercy of whatever wind is blowing when they are ready to move, and the extent and intensity of the movements depend on how many leafhoppers are ready to move on a particular wind and on how long and strong that wind blows. The combination of high leafhopper populations in spring breeding grounds and strong air currents at the proper time has probably caused most of the long-distance movements in which leafhoppers have been found outside their normal range.

NATURAL ENEMIES

Egg parasites as natural enemies of the leafhopper were discussed by Henderson (*35*, *36*) under Idaho conditions. The predaceous bug *Geocoris* was studied by York (*56*) in California. Publications by Severin and Knowlton, previously referred to, as well as others, have considered the natural enemies. In this study the natural enemies were not sufficiently effective to reduce large leafhopper populations and prevent outbreaks. Local populations have been reduced during wet weather, possibly from fungus diseases, but no studies have been made to justify this statement.

The leafhopper is undoubtedly an introduced insect from the Mediterranean region of Europe and Africa, and apparently none of its natural enemies were imported with it. It seems likely that some predator or parasite may be found in the native country of the leafhopper that might prove effective in western North America, but none are yet available.

DISCUSSION

The studies described in this bulletin have generally followed the outline first given by Ball (*4*). Much work has been done on the life history, host plants, breeding areas, and migrations of the leafhopper. It is evident that the leafhopper is adapted to any of the deserts or semideserts of western North America. In the Northwestern States the breeding areas are small and largely local in their effects. The individual areas may be but a few square miles in extent, as shown by the detailed study of northern Utah. The very smallness of these breeding areas makes the breeding of the leafhopper on ditchbanks and in fence rows, as well as in small temporarily fallow or abandoned fields, of considerable importance. This point was stressed by several workers in correspondence with the author.

The particular spots where leafhoppers may be found in any year are variable, as they are caused by overgrazing, range fires, or abandonment, and the annual conditions change. Leafhopper movements from such areas are usually very local, affecting chiefly agricultural crops grown within 50 to 100 miles to leeward of the breeding area. Unusually favorable conditions, such as a range fire covering a large area followed by favorable fall and winter conditions, may cause very high populations of leafhoppers, which will move to greater distances. (See Douglass *17*.)

Host-plant areas and the leafhopper breeding associated with them may shift widely in short periods under the effects of pseudocycles of wet and dry years. The pronounced shift from the northern to the southern part of the San Joaquin Valley in California during 1934–42 was discussed earlier. The fluctuations in annual cover in the southern desert are similar in nature. New breeding areas may be expected to develop wherever and whenever ecological conditions are favorable for leafhopper host plants, and these areas will shift or die out as conditions change. These shifts can only be appraised by annual study of the entire area. Unless this is done, the first warning of a shift in breeding areas is the appearance of leafhoppers and curly top in areas not usually infested, or the appearance of the insects in unexpectedly large numbers in areas usually moderately infested.

The movements of the leafhoppers are determined by the winds blowing at the time of migration, although there is some evidence that the insects may remain on spring host plants for some time awaiting a particular wind direction, unless driven off by drying of the host plants. In general, leafhoppers from a particular breeding area tend to travel to the same general destination every year, but this is subject to wind direction. For example, a large population of leafhoppers that developed around the Colorado River in California and Arizona might move northeast into western Colorado, north-northeast into northern Utah, or even (very rarely) north into southern Idaho.

South of the region in which leafhopper breeding is almost entirely found in local spots is a belt, in which few or no leafhoppers breed in the spring. Many factors must interact to cause this condition, but the chief factor is the lack of fall-germinated host plants to hold the adults through winter.

Still farther south, below this belt of no breeding, lies the vast southern desert extending from southern California eastward into Texas and from southern Nevada and Utah southward into Mexico. These breeding areas in the South offer a great contrast to those in the Northern States. The individual areas are very large, and in years with favorable rainfall may extend for many miles in all directions. Enormous numbers of leafhoppers can breed in these large areas. Their migrations may extend for 500 miles or more and blanket entire agricultural areas. Movements from the southern areas sometimes carry the leafhoppers far outside their normal range of distribution to start incipient and temporary infestations.

Leafhopper breeding areas in the Northern States are relatively fixed in position. In a spring survey of the general area, usually

most of the leafhoppers will be found within a few miles of the places where they occurred the preceding year. On the other hand, leafhoppers move around extensively in the southern areas, and their abundance in any particular year depends on favorable host-plant conditions. Breeding in any particular year may be several hundred miles from the places located the preceding year.

The beet leafhopper has a much wider range of host plants than many insects. Important breeding host plants include about 35 species belonging to 7 families. In addition to this wide host range, the leafhopper nymphs are able to transfer from a dying plant of one species to a succulent plant of another, even of another plant family, with relatively low mortality. Such transfers are common and enable the nymphs to survive where many other insects might perish.

In the northern areas almost all the important host plants are introduced weeds. These include redstem filaree, blistercress, African mustard, smotherweed, perfoliate pepperweed, and tumble-mustard among the spring host plants and Russian-thistle as a summer host. The host plants in the southern desert are largely native. Filaree and Russian-thistle are important all over the Western States, but most of the other host plants, such as the desert plantains, pepperweeds, chinchweed, tidestromia, and wild mignonette, are indigenous to the areas.

The chief characteristics of all these host plants is their aggressiveness and ability to colonize abandoned lands at the first opportunity. When some area is farmed and then abandoned, the annuals immediately take possession; when a series of dry years causes the stockmen to overgraze their ranges, annual weeds soon appear; a range fire may remove the grass and leave space for the annuals. The result is that the actual area occupied by weed hosts may change greatly in a short time. Such a shift has occurred in the central Columbia River area since 1935.

The leafhopper host-plant complex is not stable, but is constantly changing. Since 1945 the fireplant (*Kochia scoparia* (L.) Schrad.) has escaped cultivation and become of considerable importance as a leafhopper host (*31*). The introduced poisonous weed halogeton has taken over large areas in northern Utah, southern Idaho, and southern Oregon during the same period. It is not one of the most favored hosts of the leafhopper, but may become important because of its wide distribution. Perfoliate pepperweed has spread rather rapidly from Idaho into Oregon and Washington, and has become an important host in all these areas. It may be expected that other plants will be introduced from time to time, and some may prove to be good leafhopper hosts. If some plant should be introduced that could overwinter in a green condition in the present belt of no breeding and also was a favorable overwintering host plant, that belt might become of importance, as it contains a large area that is closer to the northern cultivated areas than the southern desert.

SUMMARY

The beet leafhopper (*Circulifer tenellus* (Baker)) is a desert insect that breeds on wild annual plants. It suddenly appears in cultivated areas carrying curly top, a serious virus disease that affects many plants. From three to five broods per year are produced in different parts of the West, depending on temperature and availability of host plants.

About 35 economically important host plants belonging to 7 plant families are discussed, and their relative importance is estimated. Most of these are annuals, and many of them are introduced weeds.

Breeding areas extending over the Western States from Washington south into Mexico are roughly outlined and the principal features discussed. Migrations of the leafhopper from its desert breeding areas into cultivated fields are described.

Detailed studies of the life history, host plants, and migrations are presented, and the constantly shifting leafhopper-host plant relationship is described.

LITERATURE CITED

(1) ANNAND, P. N., CHAMBERLAIN, J. C., HENDERSON, C. F., and WATERS, H. A.
1932. MOVEMENTS OF THE BEET LEAFHOPPER IN 1930 IN SOUTHERN IDAHO. U.S. Dept. Agr. Cir. 244, 24 pp., illus.

(2) ARMITAGE, H. M.
1952. CONTROLLING CURLY TOP VIRUS IN AGRICULTURAL CROPS BY REDUCING POPULATIONS OF OVERWINTERING BEET LEAFHOPPERS. Jour. Econ. Ent. 45: 432–435.

(3) BALL, E. D.
1906. THE BEET LEAFHOPPER (EUTETTIX TENELLA). Utah Agr. Expt. Sta. Ann. Rpt. 16 (1904–5): XVI.

(4) ———
1917. THE BEET LEAFHOPPER AND THE CURLY-LEAF DISEASE THAT IT TRANSMITS. Utah Agr. Expt. Sta. Bul. 155, 56 pp., illus.

(5) ———
1934. THE NUMBER OF GENERATIONS OF THE BEET LEAFHOPPER UNDER NATURAL CONDITIONS. Jour. Econ. Ent. 27: 945–959.

(6) CARTER, WALTER.
1930. ECOLOGICAL STUDIES OF THE BEET LEAFHOPPER. U.S. Dept. Agr. Tech. Bul. 206, 114 pp., illus.

(7) COOK, W. C.
1933. SPRAYING FOR THE CONTROL OF THE BEET LEAFHOPPER IN CENTRAL CALIFORNIA IN 1931. Calif. State Dept. Agr. Bul. 22 (2–3): 138–141.

(8) ———
1938. A SUGGESTED METHOD FOR THE DETERMINATION OF THE ETHER-EXTRACTIVES CONTENT OF SMALL INSECTS. U.S. Dept. Agr. Bur. Ent. and Plant Quar. ET–136, 4 pp., illus. [Processed.]

(9) ———
1941. THE BEET LEAFHOPPER. U.S. Dept. Agr. Farmers' Bul. 1886, 21 pp., illus.

(10) ———
1943. EVALUATION OF A FIELD-CONTROL PROGRAM AGAINST THE BEET LEAFHOPPER. Jour. Econ. Ent. 36: 382–385.

(11) ———
1944. STUDIES OF THE VITALITY OF THE BEET LEAFHOPPER DURING THE FALL AND WINTER IN CALIFORNIA AS RELATED TO THE FAT CONTENT OF THE INSECTS. Ecology 25: 327–340, illus.

(12) COOK, W. C.
1945. THE RELATION OF SPRING MOVEMENTS OF THE BEET LEAFHOPPER (EUTETTIX TENELLUS BAKER) IN CENTRAL CALIFORNIA TO TEMPERATURE ACCUMULATIONS. (HOMOPTERA). Ent. Soc. Amer. Ann. 38: 149–162, illus.

(13) ———
1946. THE ABILITY OF THE BEET LEAFHOPPER TO REGAIN LOST VITALITY WHEN TRANSFERRED FROM UNFAVORABLE TO FAVORABLE HOST PLANTS. Ecology 27: 37–46, illus.

(14) DAVIS, E. W.
1927. NOTES ON COLLECTIONS OF THE SUGARBEET LEAFHOPPER SHOWING THE EXTENSION OF ITS KNOWN RANGE INTO BRITISH COLUMBIA AND TO THE COAST OF WASHINGTON AND OREGON. Jour. Econ. Ent. 20: 581–586, illus.

(15) DORST, H. E.
1938. MODIFICATIONS OF SQUARE-FOOT SAMPLER. U.S. Dept. Agr. Bur. Ent. and Plant Quar. ET–126, 3 pp., illus. [Processed.]

(16) ——— and DAVIS, E. W.
1937. TRACING LONG-DISTANCE MOVEMENTS OF BEET LEAFHOPPER IN THE DESERT. Jour. Econ. Ent. 30: 948–954, illus.

(17) DOUGLASS, J. R.
1954. OUTBREAKS OF BEET LEAFHOPPERS NORTH AND EAST OF THE PERMANENT BREEDING AREAS. Amer. Soc. Sugarbeet Technol. Proc. 8: 185–193, illus.

(18) ——— and COOK, W. C.
1953. THE BEET LEAFHOPPER. U.S. Dept. Agr. Ybk. 1952: 544–550.

(19) ——— and COOK, W. C.
1954. THE BEET LEAFHOPPER. U.S. Dept. Agr. Cir. 942, rev., 21 pp., illus.

(20) ——— DORST, H. E., and PEAY, W. E.
1942. BEET LEAFHOPPER POPULATIONS IN SOUTHERN IDAHO AND NORTHERN UTAH DURING THE SEASONS OF 1940 AND 1941. Amer. Soc. Sugarbeet Technol. Ann. 1942: 1–14, illus.

(21) ——— and HALLOCK, H. C.
1957. RELATIVE IMPORTANCE OF VARIOUS HOST PLANTS OF THE BEET LEAFHOPPER IN SOUTHERN IDAHO. U.S. Dept. Agr. Tech. Bul. 1155, 11 pp., illus.

(22) ——— and HALLOCK, H. C.
1958. RUSSIAN-THISTLE DISTRIBUTION IN SOUTHERN IDAHO AND EASTERN OREGON IN RELATION TO BEET LEAFHOPPER POPULATIONS. U.S. Dept. Agr. Prod. Res. Rpt. 18, 20 pp., illus.

(23) ——— HALLOCK, H. C., and PEAY, W. E.
1944. A NEW WEED HOST OF THE BEET LEAFHOPPER. Jour. Econ. Ent. 37: 714–715, illus.

(24) ——— ROMNEY, V. E., and HALLOCK, H. C.
1950. SURVIVAL OF THE BEET LEAFHOPPER IN SOUTHERN IDAHO DURING THE SEVERE WINTER OF 1948–49. Amer. Soc. Sugarbeet Technol. Proc. 1950: 494–498, illus.

(25) ——— ROMNEY, V. E., and JONES, E. W.
1955. BEET LEAFHOPPER CONTROL IN WEED-HOST AREAS OF IDAHO TO PROTECT SNAPBEAN SEED FROM CURLY TOP. U.S. Dept. Agr. Cir. 960, 12 pp., illus.

(26) FOX, D. E.
1938. OCCURRENCE OF THE BEET LEAFHOPPER AND ASSOCIATED INSECTS ON SECONDARY PLANT SUCCESSIONS IN SOUTHERN IDAHO. U.S. Dept. Agr. Tech. Bul. 607, 43 pp., illus.

(27) FULTON, R. A.
1937. DETERMINATION OF CHLOROFORM EXTRACT OF BEET LEAFHOPPER, A MICROMETHOD. Indus. and Engin. Chem. Analyt. Ed. 9: 437–438, illus.

(28) ——— and CHAMBERLIN, J. C.
1931. A NEW AUTOMATIC INSECT TRAP FOR THE STUDY OF INSECT DISPERSION AND FLIGHT ASSOCIATIONS. Jour. Econ. Ent. 24: 757–761, illus.

(29) ——— and ROMNEY, V. E.
1940. THE CHLOROFORM-SOLUBLE COMPONENTS OF BEET LEAFHOPPERS AS AN INDICATION OF THE DISTANCE THEY MOVE IN THE SPRING. Jour. Agr. Res. 61: 737–743, illus.

(30) HAEGELE, R. W.
1927. THE BEET LEAFHOPPER (EUTETTIX TENELLA BAKER). A SURVEY IN IDAHO. Idaho Agr. Expt. Sta. Bul. 156, 28 pp.

(31) HALLOCK, H. C., and DOUGLASS, J. R.
1956. STUDIES OF FOUR SUMMER HOSTS OF THE BEET LEAFHOPPER. Jour. Econ. Ent. 49: 388–391, illus.

(32) HARRIES, F. H.
1943. SOME EFFECTS OF ALTERNATING TEMPERATURES AND EXPOSURE TO COLD ON EMBRYONIC DEVELOPMENT OF THE BEET LEAFHOPPER. Jour. Econ. Ent. 36: 505–509, illus.

(33) ———
1944. DIFFERENTIAL EFFECTS OF TEMPERATURE ON THE DEVELOPMENT OF THE BEET LEAFHOPPER. Jour. Agr. Res. 69: 127–136.

(34) ——— and DOUGLASS, J. R.
1948. BIONOMIC STUDIES ON THE BEET LEAFHOPPER. Ecol. Monog. 18: 45–79, illus.

(35) HENDERSON, C. F.
1955. OVERWINTERING, SPRING EMERGENCE AND HOST SYNCHRONIZATION OF TWO EGG PARASITES OF THE BEET LEAFHOPPER IN SOUTHERN IDAHO. U.S. Dept. Agr. Cir. 967, 16 pp., illus.

(36) ———
1955. PARASITIZATION OF THE BEET LEAFHOPPER IN RELATION TO ITS DISSEMINATION IN SOUTHERN IDAHO. U.S. Dept. Agr. Cir. 968, 16 pp., illus.

(37) HILLS, O. A.
1933. A NEW METHOD FOR COLLECTING SAMPLES OF INSECT POPULATIONS. Jour. Econ. Ent. 26: 906–910, illus.

(38) ———
1937. THE BEET LEAFHOPPER IN THE CENTRAL COLUMBIA RIVER BREEDING AREA. Jour. Agr. Res. 55: 21–31, illus.

(39) ———
1938. A COUNTING CAGE HEATER FOR WINTER STUDIES OF INSECT POPULATION IN THE FIELD. U.S. Dept. Agr. Bur. Ent. and Plant Quar. ET–125, 3 pp., illus. [Processed.]

(40) JEPSON, W. L.
1923–25. A MANUAL OF THE FLOWERING PLANTS OF CALIFORNIA. 1238 pp., illus. Calif. Univ., Assoc. Students Store, Berkeley.

(41) KNOWLTON, G. F.
1932. THE BEET LEAFHOPPER IN NORTHERN UTAH. Utah Agr. Expt. Sta. Bul. 234, 64 pp., illus.

(42) LAWSON, F. R., CHAMBERLIN, J. C., and YORK, G. T.
1951. DISSEMINATION OF THE BEET LEAFHOPPER IN CALIFORNIA. U.S. Dept. Agr. Tech. Bul. 1030, 59 pp., illus.

(43) ——— FOX, D. E., and COOK, W. C.
1941. THREE NEW DEVICES FOR MEASURING INSECT POPULATIONS. U.S. Dept. Agr. Bur. Ent. and Plant Quar. ET–183, 6 pp. [Processed.]

(44) ——— and PIEMEISEL, R. L.
1943. THE ECOLOGY OF THE PRINCIPAL SUMMER WEED HOSTS OF THE BEET LEAFHOPPER IN THE SAN JOAQUIN VALLEY, CALIFORNIA. U.S. Dept. Agr. Tech. Bul. 848, 37 pp., illus.

(45) PIEMEISEL, R. L.
1938. CHANGES IN WEEDY PLANT COVER ON CLEARED SAGEBRUSH LAND AND THEIR PROBABLE CAUSES. U.S. Dept. Agr. Tech. Bul. 654, 44 pp., illus.

(46) ——— and CHAMBERLIN, J. C.
1936. LAND-IMPROVEMENT MEASURES IN RELATION TO POSSIBLE CONTROL OF THE BEET LEAFHOPPER AND CURLY TOP. U.S. Dept. Agr. Cir. 416, 23 pp., illus.

(47) ——— and LAWSON, F. R.
1937. TYPES OF VEGETATION IN THE SAN JOAQUIN VALLEY OF CALIFORNIA AND THEIR RELATION TO THE BEET LEAFHOPPER. U.S. Dept. Agr. Tech. Bul. 557, 28 pp., illus.

(48) ROMNEY, V. E.
1939. BREEDING AREAS AND ECONOMIC DISTRIBUTION OF THE BEET LEAFHOPPER IN NEW MEXICO, SOUTHERN COLORADO AND WESTERN TEXAS. U.S. Dept. Agr. Cir. 518, 14 pp., illus.
(49) ———
1945. THE EFFECT OF PHYSICAL FACTORS UPON CATCH OF THE BEET LEAFHOPPER (EUTETTIX TENELLUS BAKER) BY A CYLINDER AND TWO SWEEP-NET METHODS. Ecology 26: 135–147, illus.
(50) SEVERIN, H. H. P.
1930. LIFE HISTORY OF BEET LEAFHOPPER, EUTETTIX TENELLUS (BAKER) IN CALIFORNIA. Calif. Univ. Pubs., Ent. 5 (4): 87–88, illus.
(51) ———
1933. FIELD OBSERVATIONS ON THE BEET LEAFHOPPER, EUTETTIX TENELLUS, IN CALIFORNIA. Hilgardia 7: 282–360, illus.
(52) SHANTZ, H. L.
1924. THE PHYSICAL BASIS OF AGRICULTURE, SECTION E, NATURAL VEGETATION. U.S. Dept. Agr. Atlas Amer. Agr., pt. 1, 29 pp., illus.
(53) SMITH, G. L., CLARK, J. C., and SCALES, A. L.
1935. A REVOLVING SCREEN TRAP FOR COLLECTING INSECTS. U.S. Dept. Agr. Bur. Ent. and Plant Quar. ET–36, 2 pp., illus. [Processed.]
(54) STAHL, C. F.
1920. STUDIES ON THE LIFE HISTORY AND HABITS OF THE BEET LEAFHOPPER. Jour. Agr. Res. 20: 245–252, illus.
(55) TALBOT, M. W., BISWELL, H. H., and HORMAY, A. L.
1939. FLUCTUATIONS IN THE ANNUAL VEGETATION OF CALIFORNIA. Ecology 20: 394–402, illus.
(56) YORK, G. T.
1944. FOOD STUDIES OF GEOCORIS SPP., PREDATORS OF THE BEET LEAFHOPPER. Jour. Econ. Ent. 37: 25–29, illus.

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