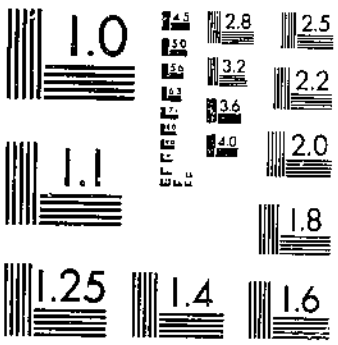
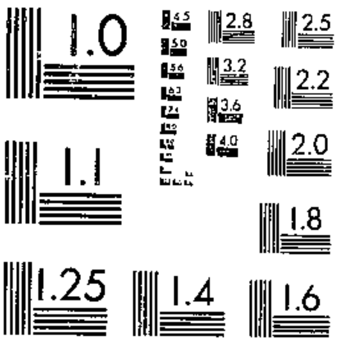
TB 624 (1938) USDA TECHNICAL BULLETINS UPDATA
STUDIES ON THE EPIDEMIOLOGY OF CURLY TOP IN SOUTHERN IDAHO, WITH SPECIAL
WALLACE, J. M. MURPHY, A. M. 1 OF 1

START



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



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

Technical Bulletin No. 624 September 1938

STUDIES ON THE EPIDEMIOLOGY OF CURLY TOP IN SOUTHERN IDAHO, WITH SPECIAL REFERENCE TO SUGAR BEETS AND WEED HOSTS OF THE VECTOR EUTETTIX TENELLUS

By

JAMES M. WALLACE
Associate Pathologist

and

ALBERT M. MURPHY
Junior Pathologist
Division of Sugar Plant Investigations
Bureau of Plant Industry

United States Department of Agriculture, Washington, D. C.

For sale by the Superintendent of Documents, Washington, D. C. - - - - - - - - - - Price 10 cents

TECHNICAL BULLETIN No. 624 — SEPTEMBER 1938

UNITED STATES DEPARTMENT OF AGRICULTURE
WASHINGTON, D. C.

STUDIES ON THE EPIDEMIOLOGY OF CURLY TOP IN SOUTHERN IDAHO, WITH SPECIAL REFERENCE TO SUGAR BEETS AND WEED HOSTS OF THE VECTOR EUTETTIX TENELLUS[1]

By JAMES M. WALLACE, *associate pathologist*, and ALBERT M. MURPHY, *junior pathologist, Division of Sugar Plant Investigations, Bureau of Plant Industry*[2]

CONTENTS

INTRODUCTION

Curly top is a virus disease of sugar beets (*Beta vulgaris* L.) and other plants. In areas where it occurs as an epidemic it is the most destructive of all beet diseases and also causes great losses in other crops, especially beans and tomatoes. The geographic distribution of the disease corresponds with the distribution of the beet leafhopper, *Eutettix tenellus* (Baker), the only known agent of transmission. The studies reported in this bulletin were conducted in southern Idaho, where curly top has been regularly important in limiting the production of sugar beets, beans, and certain garden crops.

Since Ball (*2*)[3] announced the discovery of a causal relation between the feeding of the beet leafhopper and "curly leaf" or "blight" of

[1] Received for publication Jan. 12, 1938.

[2] The writers acknowledge the many helpful suggestions of Eubanks Carsner, senior pathologist, Division of Sugar Plant Investigations. Thanks are due P. N. Annand, special research assistant, formerly in charge of beet leafhopper investigations, and J. C. Chamberlin, associate entomologist, Bureau of Entomology and Plant Quarantine, for their cooperation and for facilities offered at the Twin Falls (Idaho) station. Thanks are also due R. L. Piemeisel, physiologist, Division of Sugar Plant Investigations, for information on desert host plants.

[3] Italic numbers in parentheses refer to Literature Cited, p. 45.

59244—38——1

sugar beets, both the disease and the insect vector have been studied extensively by many investigators.

Haegele (*12*, *13*) studied the distribution of the beet leafhopper and its plant hosts in Idaho. Carter (*10*) made extensive ecological studies on the beet leafhopper in southern Idaho and reported on the plant host sequence and the spring movements of the leafhopper from its desert breeding grounds to the cultivated areas. The above-named studies showed that in southern Idaho the beet leafhopper breeds in desert areas, where it completes its early summer brood or broods on the spring-maturing annuals. The three important spring weed hosts are tumble mustard (*Norta altissima* (L.) Britton),[4] flixweed (*Sophia parviflora* (Lam.) Standl.),[5] and green tansymustard (*S. longipedicellata* (Fourn.) Howell).[6] The important summer host in the desert areas is Russian-thistle (*Salsola pestifer* A. Nels.).

From the standpoint of the habits of the beet leafhopper in southern Idaho, the knowledge of the facts pertinent to the epidemiological studies reported in this bulletin has been well summarized by Annand et al. (*1*), who state as follows:

> These annuals [mustards] mature and disappear early in the season, and the leafhoppers fly to places where green hosts are available, including irrigated sections where certain cultivated crops serve as summer hosts. These flights may carry the insects many miles from their breeding grounds. In some breeding areas a portion of the insects remain in the desert on summer annuals. This is true in southern Idaho, where Russian-thistle (*Salsola pestifer* A. Nels.) maintains large populations in the desert during the summer after the mustards, chiefly *Norta altissima* (L.) Britton and *Sophia parviflora* (Lam.) Standl., have matured and dried.

Although none of the past studies has dealt specifically with epidemiology of curly top, various authors have pointed out certain facts that are of an epidemiological nature. Such information has resulted chiefly from investigations made in California.

Boncquet and Hartung (*5*) reported that beet leafhoppers taken from *Artemisia* and *Atriplex* did not produce curly top on beets, but that after feeding on diseased beets they were then capable of producing infection. Smith and Boncquet (*22*) corroborated Boncquet and Hartung regarding the inability of leafhoppers from desert weed hosts to produce infection.

Boncquet and Stahl (*6*) first demonstrated that wild vegetation may serve as a source of the causal agent of curly top. By means of nonviruliferous leafhoppers they proved that a disease on common mallow (*Malva parviflora* L.) was the same as curly top on beets.

Stahl and Carsner (*23*) demonstrated that leafhopper nymphs were "nonvirulent" upon emergence from the eggs, but became able to produce infection after feeding on diseased plants.

Severin (*16*) discovered that some of the leafhoppers from desert vegetation were capable of producing infection on beets. He listed 10 plant species from which leafhoppers acquired the curly top virus and transmitted it to beets.

Carsner and Stahl (*9*) observed fields in Utah where leafhoppers had been present a sufficient time to allow for the emergence of a high population of nymphs (50 to 75 per plant), yet less than 0.5 percent of the plants in the field were diseased. They concluded that evidently

[4] Also called Jim Hill mustard. *Sisymbrium altissimum* L. is a synonym.
[5] Synonyms: *Sophia sophia* (L.) Britton; *Sisymbrium sophia* L.
[6] Synonyms: *Sophia filipes* (A. Gray) Heller; *Sisymbrium incisum filipes* A. Gray.

most of the leafhoppers that flew into these fields in the spring were nonviruliferous.

The work of Severin and his coworkers [7] (*16, 17, 19, 20, 21*) greatly extended the list of plant species susceptible to curly top. Many species, in a wide range of plant families, were found naturally infected and a great many others were shown to be susceptible by experimental inoculations. Included in this list were a number of food crops as well as a large number of flowering ornamentals.

Severin (*19*) reported briefly on the overwintering of the virus in perennial plants. He also gave consideration to overwintering of the virus in the leafhoppers and concluded that overwintering leafhoppers do not retain their power to infect during all of their adult life unless they acquire additional virus at some time.

OBJECT OF INVESTIGATIONS

The object of these investigations has been to discover the factors that appear to be important in the epidemiology of the curly top disease in southern Idaho and to study their resultant interaction. The reaction of the important desert host plants of the beet leafhopper to infection with the curly top virus has been determined. The question of overwintering of the virus, both in the leafhopper and in host plants, has been investigated. The possible importance of leafhoppers that overwinter in the cultivated areas has been considered. General studies have been made of the percentages of leafhoppers found to be viruliferous, and of the types of virus (attenuated or virulent) present in the leafhopper populations in the desert breeding areas during the spring, summer, and fall seasons and in beet fields during spring and summer. These latter studies have included 6 successive years and have given results varying widely from year to year. An attempt has been made to explain these yearly variations and finally to correlate some of the results with the amount of curly top occurring in cultivated crops for the respective years.

REACTION OF DESERT HOST PLANTS TO CURLY TOP VIRUS

The areas of desert host plants of the beet leafhopper are, of course, constantly changing, but their relative extent in southern Idaho in 1934 is shown by Piemeisel and Chamberlin (*15*). A survey of close to 12,000,000 acres of desert lands in the Snake River plains showed approximately 2,000,000 acres classified as "primary" weed areas. Nearly one-fourth of this was covered by Russian-thistle. As the survey was made in the fall, figures for the acreages of the mustard species could not be obtained, but it is believed that usually the mustards cover an acreage about equal to that of Russian-thistle. About 9,000,000 acres of overgrazed sagebrush lands were classified as "secondary" areas. Although irregular in its occurrence, green tansymustard appears abundantly in favorable seasons throughout a considerable part of this sagebrush area. This is particularly true in the fringes of sagebrush lands bordering the more permanent weed areas. In such situations green tansymustard is important as an overwintering and spring host of the leafhopper.

[7] SEVERIN, H. H. P., and FREITAG, J. H. LIST OF ORNAMENTAL FLOWERING PLANTS NATURALLY INFECTED WITH CURLY TOP OR YELLOWS DISEASES IN CALIFORNIA. U. S. Bur. Plant Indus. Plant Disease Reptr. 17: 1-5. 1933. [Mimeographed.]

Since the three mustard species are of such importance in the development of the spring brood leafhoppers that move into the cultivated lands, it was obviously important that their reaction to curly top be determined. Likewise, since Russian-thistle is the principal summer host in the desert, maintaining both the leafhopper and the virus until the mustards are again available, it was of interest to determine its reaction to and its effect on the virus.

TUMBLEMUSTARD

In the early studies of the reaction of tumblemustard to infection with curly top virus, it became apparent that this species bore a peculiar relationship to the virus. Because of this, tests on tumblemustard were more extensive and the results are reported in more detail than is the case with other weed hosts.

NATURAL INFECTION

Tumblemustard frequently supports large leafhopper populations in the desert areas, but comparatively few plants develop symptoms from natural infection. In the spring of 1931 occasional tumblemustard plants in desert stands showed symptoms that were suspected to be those of curly top. Some of the plants were yellowed and dwarfed and remained in the rosette stage. Others developed flowering stalks to varying degrees, but these were abnormal. The central stem and petioles were twisted and sometimes enlarged, and the leaves were narrow, thickened, and curled. If seed pods were formed at all, they were dwarfed and produced only a few shriveled seeds. One of these plants is shown in figure 1 in contrast to a normal plant.

Twenty of the apparently naturally infected plants were tested separately for the presence of curly top virus. Nonviruliferous leafhoppers were caged on each mustard plant, and after several days they were transferred to seedling beets. Usually two insects, but sometimes as many as five, were caged on each beet. In a total of 80 beets exposed to leafhoppers from the 20 mustard plants there were 9 cases of disease, 1 each from 4 different mustard plants and 5 from a fifth plant. The mild symptoms on the infected beets indicated that the virus from the mustard plants was decidedly low in virulence.

In 1935 a trace of diseased tumblemustard plants was again noticeable in desert stands. Ten of these plants were tested for curly top, but only two afforded successful transfers of the virus. In a total of 80 leafhoppers transferred singly from the mustards to seedling beets, only 3 produced infection—1 from plant No. 4 and 2 from plant No. 10. Symptoms on the infected beets were very mild.

In addition to these tests, attempts were made to obtain virus from naturally infected plants by the alcoholic precipitation method used by Bennett (*3*). In one test, 120 leafhoppers were allowed to feed for 6 hours on a sugar solution containing the precipitate from green plants. The leafhoppers were then caged singly on beet seedlings for 1 week. One beet seedling developed curly top. In another test, precipitations were made from each of the 10 plants mentioned in the preceding paragraph on which tests had been made by direct feeding of leafhoppers. The plants had been dried at room temperature and stored for 4 months. After each plant had been ground separately in a food chopper, the 10 lots of ground material were moistened with distilled water and allowed to stand overnight. The liquid expressed from each of the 10 samples was precipitated

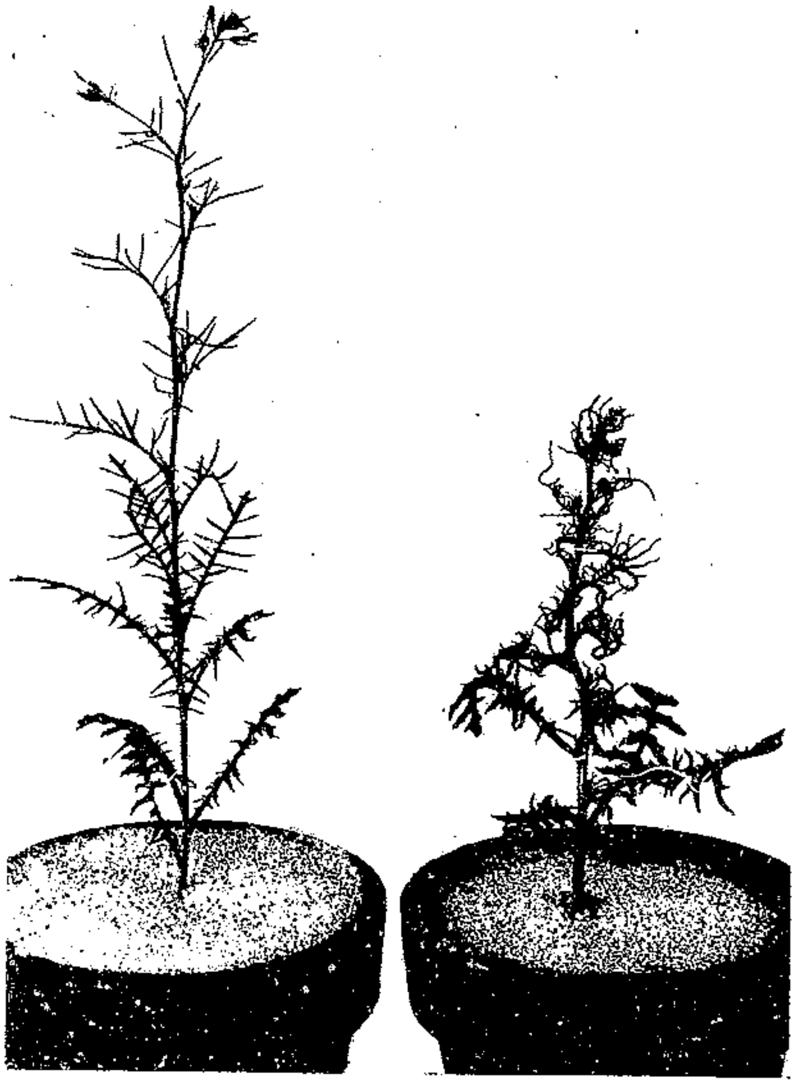


FIGURE 1.—*A*, Healthy tumblemustard plant in flowering stage; *B*, diseased tumblemustard plant of the type occasionally found in the desert.

with alcohol, and 40 nonviruliferous leafhoppers were fed for 6 hours on the sugar solutions containing the precipitates. They were then transferred singly to beet seedlings, where they remained for 7 days. The results showed that no virus was obtained from solutions prepared from plants No. 4 and No. 10, from which leafhoppers had acquired a limited supply by direct feeding when the plants were first collected. However, virus was obtained from the solutions prepared from plants Nos. 6, 7, and 8. Of a total of 120 leafhoppers fed on the solutions from these three plants, only 4 produced infection on the beets to which they were transferred.

Aborted seed pods were collected from diseased tumblemustard and precipitations were made of the material 4 months after collection. Curly top virus was obtained from the precipitates but in no higher concentration than was obtained from leaf and stem tissues. Bennett and Esau (*4*) showed a higher concentration of virus in the seeds and adjacent tissues of beets.

EXPERIMENTAL INOCULATIONS

In studying the reaction of tumblemustard to curly top, many different series of plants were experimentally inoculated and then tested by means of nonviruliferous leafhoppers to determine whether the plants were infected. Tests were conducted at different times of the year and included plants in various stages of development. Only certain representative experiments are included in the following discussion.

In one inoculation series, 15 viruliferous leafhoppers were caged on each of 40 small tumblemustard plants. In some instances the leafhoppers remained on the mustard plants 30 days. The viruliferous leafhoppers were replaced by nonviruliferous leafhoppers. The latter were allowed to remain on the inoculated mustard plants 6 days and were then transferred singly or in groups to seedling beets. A total of 841 beet plants were exposed to leafhoppers from the mustard plants; of this group only 5 beets became diseased. Symptoms were mild on the beets, indicating that the virus from the mustard plants was low in virulence even though it was highly virulent in the leafhoppers used for inoculation of the mustard plants. None of the mustard plants developed visible symptoms. The low percentage of leafhoppers that acquired virus from the inoculated mustard plants was evidence that there was very little increase of virus in these plants even though some of them were infected.

In a summer seeding of tumblemustard under field conditions, 18 plants were inoculated and tested for infection, but no virus was obtained from them. These plants survived the following winter, and in the spring two of them showed symptoms resembling curly top. Swollen veins and pronounced papillae on the leaves were typical of curly top. Thirty nonviruliferous leafhoppers fed on each of these plants for 11 days and were then transferred to seedling beets. None of the beets became diseased. It seemed almost certain that the symptoms on these mustard plants were due to infection with curly top. The failure of leafhoppers to acquire sufficient virus from these plants to infect susceptible seedling beets indicated that the virus, if present at all, was in such low concentration that the leafhoppers could not acquire it, or else that it was restricted to tissues on which the leafhoppers did not feed.

Infection tests were made on large numbers of tumblemustard plants during the winter of 1931–32. By planting the mustard outside in the fall, so that the seedlings were exposed to frost and low temperatures, the plants could be induced to flower when transferred to the greenhouse. Inoculations of plants in various stages of growth and with large numbers of leafhoppers resulted occasionally in the infection of a tumblemustard plant. However, in all positive cases a very low percentage of infection resulted in the transfers from the mustards. In all cases, too, the virus from the mustards produced mild symptoms on beets. Less than 2 percent of the inoculated mustard plants developed disease symptoms. Extensive tests of three plants showing symptoms resembling those of curly top gave negative results.

It is concluded that tumblemustard is highly resistant to the virus of curly top. Even though some plants developed pronounced abnormalities that from all appearances were symptoms of curly top, nonviruliferous leafhoppers only occasionally acquired virus when they fed on such plants. Not only was it difficult to infect the plants, but it seems that the virus did not increase to any great extent in plants that became infected. Furthermore, there was evidence that virulent curly top virus was usually attenuated on passage through tumblemustard plants. The results of the study of tumblemustard warrant the conclusion that this species, even though very important as a host for the beet leafhopper, is relatively unimportant in supplying leafhoppers with curly top virus.

FLIXWEED

Results of early inoculation studies of flixweed suggested that plants of this species became infected without showing symptoms. Leafhoppers obtained virus from symptomless plants, and even though virulent virus was used to inoculate the flixweed plants, it was rather uniformly attenuated on passage through this host. However, later tests did not give such consistent results.

During the winter of 1931–32 the senior author, while stationed at Riverside, Calif., conducted tests on the reaction of flixweed to the curly top virus. Most of the inoculations were made by caging viruliferous leafhoppers on one or two leaflets of the plant, with the remainder of the plant uncovered throughout the experiment. No symptoms developed on any of the plants, although the results showed that this species was susceptible. Under the conditions of these tests there seemed to be a rather consistent and uniform attenuation of the virus upon passage through flixweed. C. F. Henderson, associate entomologist, Bureau of Entomology and Plant Quarantine, called the writers' attention to the fact that in some inoculations he had made of this species, plants exposed to small groups of viruliferous leafhoppers and covered with a Pyralin cage throughout the experiment under relatively high greenhouse temperatures commonly developed severe symptoms. Through Mr. Henderson's cooperation, the writers examined some of the plants showing advanced symptoms of curly top, and tests on this material, as well as on other material furnished them, substantiated his results.

Inoculated plants covered continuously with Pyralin cages and grown under high temperatures in the greenhouse frequently developed pronounced symptoms. It seemed evident that the increased temperature induced by covering the plants with cages influenced the expression of symptoms. Figure 2 shows the difference in expression of symptoms between an inoculated plant covered continuously by a Pyralin cage and a plant inoculated by means of a small leaf cage. The fact that virus was transferred from both of these plants proved that both were infected.

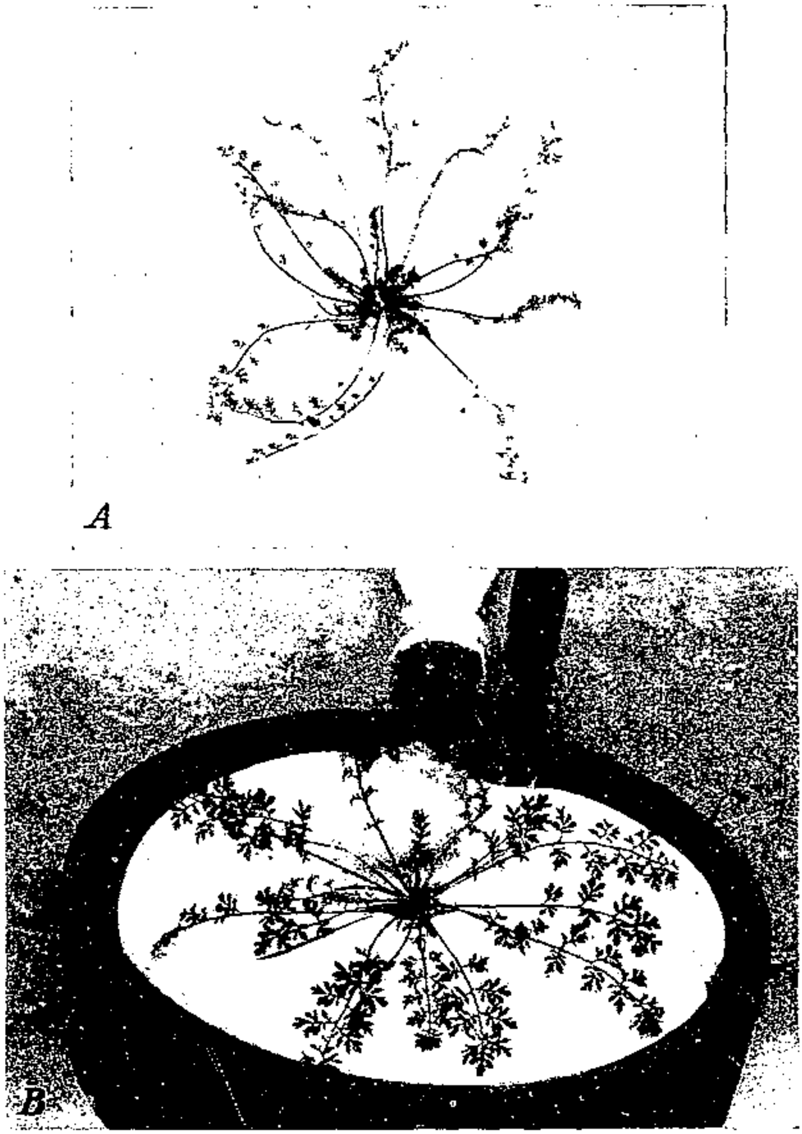


FIGURE 2.—*A*, Flixweed plant showing severe curly top symptoms. Plant exposed to five viruliferous leafhoppers for 10 days and grown continuously under a Pyralin cage in greenhouse. *B*, Flixweed plant exposed to eight viruliferous leafhoppers for 9 days by means of a small leaf cage and grown in open in greenhouse. No curly top symptoms when photographed 26 days after beginning of inoculation.

Flixweed plants inoculated and grown under such conditions did not always attenuate the virus. Sometimes both attenuated and virulent virus was obtained from the same plant. Carsner (*7*) reported the attenuation of curly top virus on passage through *Chenopodium murale* L. and other hosts. The fact that some of the beets inoculated with virus from *C. murale* recovered completely from symptoms while others retained definite symptoms suggests a range in the degree of attenuation. Lackey (*14*) found that complete restoration of the virulence of curly top virus was not always obtained by passing attenuated virus from *Chenopodium* through chickweed (*Stellaria media* (L.) Cyr.). The mechanics of attenuation of virus is not understood, but the results with flixweed suggest that in plants developing pronounced symptoms the virus increases to such an extent or at such a rate that the plants do not have the power to attenuate all the virus.

Conspicuous symptoms did not develop on flixweed growing under natural conditions. Curly top virus was obtained from naturally infected plants taken from the desert stands even though no symptoms other than yellowing of leaves and a slight stunting of the plants were evident. Only attenuated virus was obtained from such plants.

Experimental studies showed that under certain environmental conditions a virulent strain of virus, on passage through flixweed, is unchanged in virulence or is attenuated in varying degrees. Flixweed is believed to be of considerable importance as a source of virus in the breeding areas of the leafhopper in southern Idaho. It is believed, however, that leafhoppers, for the most part, acquire attenuated virus from this species.

GREEN TANSYMUSTARD

Green tansymustard does not occur as regularly from year to year as the other mustard species. In 1931 it was so scarce that there was difficulty in collecting sufficient seed for experimental purposes. In 1932 there was a dense growth over most of the area, and early in the season it formed a green mat over the ground in a large part of the sagebrush area. In 1933, again it was relatively scarce, but in both 1934 and 1935 it was abundant and was generally distributed over the vast acreage of sagebrush lands. A point of special interest in connection with this species is that it is indigenous to the southern Idaho breeding areas of the beet leafhopper.

Green tansymustard plants inoculated in the greenhouse as well as under natural conditions developed severe symptoms of curly top and died without flowering. Under greenhouse conditions there appeared to be little difference in the reaction of this species to virulent and attenuated strains of virus. Attenuated virus from flixweed, which produced mild symptoms on seedling beets, produced severe symptoms on green tansymustard. There was no evidence that this attenuated virus was increased in virulence on passage through green tansymustard.

Figure 3 shows a green tansymustard plant at the time of inoculation, and the same plant 7 days later showing severe curly top symptoms.

When any sizeable populations of leafhoppers were found on stands of green tansymustard in the desert in the spring, it was not difficult to find diseased plants. Because of the dense stands the percentage of diseased plants was, of course, very low, but it was evident that this species is easily infected under natural conditions. It is obvious that

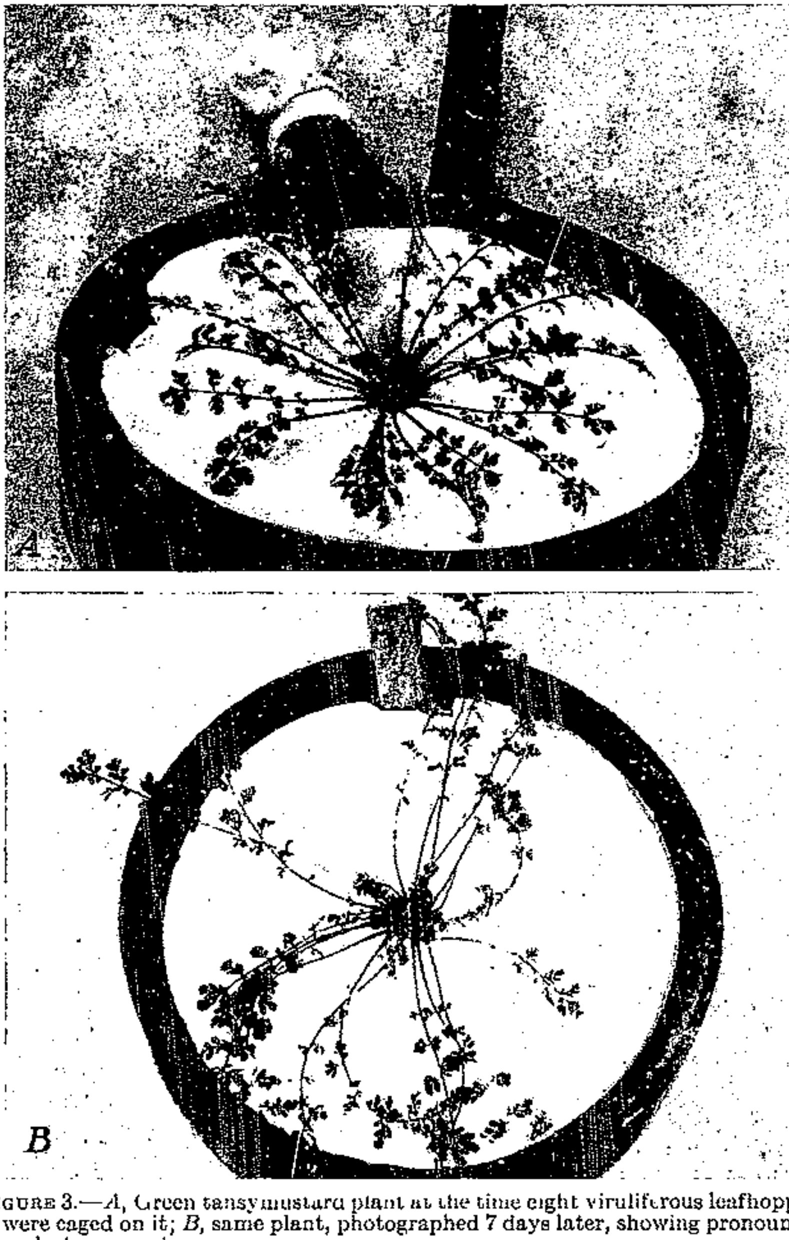


FIGURE 3.—*A*, Green tansymustard plant at the time eight viruliferous leafhoppers were caged on it; *B*, same plant, photographed 7 days later, showing pronounced curly top symptoms.

in some years this extremely susceptible species is important in the development of a supply of virus for the leafhoppers in the desert areas.

RUSSIAN-THISTLE

As a host of the beet leafhopper, Russian-thistle is of extreme importance in the maintenance of populations in the desert breeding areas throughout the summer. Since it is the principal summer weed host for the desert leafhopper populations during the interval between the early summer maturity and fall germination of mustards, the role of Russian-thistle as a host of curly top virus is also very important.

Seedlings of Russian-thistle were infected in greenhouse inoculation tests. No definite symptoms developed on the infected plants, but tests with nonviruliferous leafhoppers showed that the virus was present in the plants. There was evidence that virulent virus was sometimes attenuated on passage through Russian-thistle, but often virus recovered from inoculated plants of this species showed no change in virulence.

Russian-thistle plants growing along a roadside were inoculated in June, and virus was obtained from them in September. The plants made a luxuriant growth and at no time showed any disease symptoms. Plants taken in September from a desert area where large populations of leafhoppers were present throughout the summer were tested with nonviruliferous leafhoppers. Virus was obtained from a low percentage of these plants. Even though some of the leafhoppers acquired virus by feeding on certain plants, thus proving that the plants were infected, most of the leafhoppers failed to become viruliferous even after feeding on the diseased plants for 2 weeks. The dry, hardened condition of the plants probably made it difficult for the leafhoppers to feed in tissues containing virus.

Under natural conditions in the Idaho desert areas, Russian-thistle does not seem to be a favorable plant for the increase and distribution of the curly top virus. During the period of these investigations, summer and fall collections of leafhoppers from this species have been consistently low in percentage viruliferous. As shown later in this bulletin, the percentage of viruliferous leafhoppers does not increase as rapidly nor rise as high in the population on Russian-thistle in the desert areas as it does in the population in beet fields.

SUPPLY AND VIRULENCE OF VIRUS IN LEAFHOPPER POPULATIONS

A significant factor in the curly top problem in southern Idaho is the supply of virus brought into the fields of cultivated crops by the spring brood leafhoppers that move in from the desert areas. The percentage of leafhoppers with virulent virus is also important. The amount and character of virus carried by the spring brood are influenced by the supply and virulence of virus in the summer and fall populations of the preceding year. Thus a logical starting point for a seasonal study of virus development is with the summer and fall populations. Winter survivors from this group infect spring hosts from which some of the spring brood obtain virus. A "season," as here used, extends from the summer of one year to the summer of the following year.

METHODS AND PROCEDURE

Collections of leafhoppers were made at intervals throughout the respective seasons from the desert breeding areas. The leafhoppers were caged singly on susceptible beet seedlings in the greenhouse. Individual infection records were made for each leafhopper, and the symptoms developing on diseased plants were classed as severe or mild. Plants developing mild symptoms were considered to have been infected by leafhoppers with attenuated virus, while the leafhoppers inoculating the plants that developed severe symptoms were classified as having virulent virus. No doubt many insects with virulent virus also carried attenuated virus, which was masked in the symptoms on the inoculated beets. This was not important, because the aim of the tests was to determine the proportions of the population carrying, respectively, attenuated and virulent virus.

The usual procedure was to select certain points in the desert as collection stations and to make tests of leafhoppers from these points at intervals throughout the season. It was not always possible to obtain sufficient numbers for significant results. In some years this was particularly true of overwintered leafhoppers during the winter or early spring months. Collections were taken in late summer or during the fall months, usually from desert stands of Russian-thistle, and tests were made to determine the percentage of viruliferous leafhoppers and the predominating type of virus. This gave information regarding the virus supply in the population that was to go into the winter. In early spring, when overwintered leafhoppers became active again, and when adults were numerous enough for collection, tests were made of samples of winter survivors. The plant species on which the overwintered leafhoppers were feeding and ovipositing were noted, and successive collections were made to determine whether the virus was being distributed in the host plants and whether the overwintered population was becoming more viruliferous.

Occasionally other plant species besides mustards and Russian-thistle were present at the points of collection. This was true in some of the abandoned farm lands where species of *Amaranthus*, *Solanum*, and *Atriplex* sometimes occurred and served as food plants for the leafhoppers. In other instances, because of the absence or sparseness of the usual host plants, the leafhoppers were concentrated on whatever green plants were available. Tests were made of collections from such temporary or incidental hosts not particularly to show the influence of these species on the supply and virulence of the virus but primarily to provide a more or less continuous picture of the virus supply in the leafhopper populations that were to maintain the virus and pass it on through host plants to the following generations.

RESULTS OF STUDY OF DESERT LEAFHOPPERS

YEARLY VARIATIONS IN SUPPLY OF VIRUS

Studies on the virus supply in leafhoppers in desert breeding areas were begun in the season of 1929–30. Details of this work are reported in table 1. The results from the various calculations made in the period 1929–35 are discussed in general terms, and the computed percentages referred to in round numbers. No tests were made of fall populations in 1929. Overwintered leafhoppers collected in the spring of 1930 averaged 46 percent viruliferous. Limited tests of spring brood taken in the desert showed that 73 percent had acquired virus by the middle of June. Samples of spring brood taken in beet fields after dispersal from desert areas tested 63 percent viruliferous.

TABLE 1.—*Results of leafhopper tests for 6 years, showing seasonal virus development.*

Season	Brood or population	Period of collection	Collections	Leafhoppers tested	Leafhoppers viruliferous			
					Total		Attenuated	Virulent
			Number	*Number*	*Number*	*Percent*	*Percent*	*Percent*
1929–30	Summer and fall		0					
	Overwintered	Mar. 12 to Apr. 11	5	149	68	45.6	43.6	2.0
	Spring brood in desert	June 14 to June 21	2	52	38	73.0	73.0	0
	Spring brood in beet fields	May 27 to June 14	5	143	90	62.9	62.2	.7
1930–31	Summer and fall		0					
	Overwintered	Apr. 9 to Apr. 30	5	212	91	42.9	39.1	3.8
	Spring brood in desert	June 27	2	80	7	8.8	7.5	1.3
	Spring brood in beet fields	May 25 to June 27	5	164	19	11.6	8.5	3.1
1931–32	Summer and fall	Aug. 4 to Nov. 6	14	1,847	84	4.5	4.5	0
	Overwintered	Apr. 14 to Apr. 28	2	171	13	7.6	7.6	0
	Spring brood in desert	May 26 to June 28	3	158	19	12.0	11.4	.6
	Spring brood in beet fields	June 13 to June 23	4	132	16	12.1	9.1	3.0
1932–33	Summer and fall	July 20 to Nov. 15	21	1,430	48	3.4	3.2	.2
	Overwintered	Apr. 28 to May 17	2	46	0	0	0	0
	Spring brood in desert	June 1 to June 6	2	41	0	0	0	0
	Spring brood in beet fields	June 9 to June 26	12	350	15	4.3	3.7	.6
1933–34	Summer and fall	July 28 to Oct. 6	6	773	19	2.5	.9	1.6
	Overwintered	Feb. 2 to Apr. 18	13	1,488	44	3.0	2.5	.5
	Spring brood in desert	May 14 to June 11	7	829	425	51.3	34.5	16.8
	Spring brood in beet fields	Apr. 27 to May 15	12	964	294	30.5	19.0	11.5
1934–35	Summer and fall	July 2 to Oct. 1	45	3,916	464	11.8	11.2	.6
	Overwintered	Jan. 30 to May 13	14	1,556	302	19.4	15.0	4.4
	Spring brood in desert	May 13 to June 10	7	610	314	[1] 51.5	43.0	12.0
	Spring brood in beet fields	June 11 to July 2	23	1,352	761	56.3	34.5	21.8

[1] Total percentage viruliferous not equal to sum of percentage attenuated and percentage virulent; 1 of the collections was not divided on the basis of virulence.

In the spring of 1931, tests of overwintered leafhoppers showed that approximately 43 percent were viruliferous. About 9 percent of the spring brood in the desert were viruliferous. Collections taken in beet fields after the influx of desert leafhoppers averaged nearly 12 percent viruliferous. In this year, even though the overwintered leafhoppers were rather plentifully supplied with virus, it appears that factors were not favorable for the dissemination and increase of the virus in the plants on which the spring brood developed.

Large numbers of leafhoppers in the summer and fall populations in 1931 were tested, and an average of only 4.5 percent of them were viruliferous. All of the virus in these tests was attenuated. The following spring, overwintered leafhoppers averaged about 8 percent viruliferous, and these, too, carried only attenuated virus. Spring brood from the desert tested 12 percent viruliferous, with less than 1 percent of the population carrying virulent virus. Collections taken in beet fields after dispersal averaged 12 percent viruliferous, closely approximating the percentage for those taken in the desert areas. Three percent of the beet-field leafhoppers carried virulent virus.

In the summer and fall of 1932, collections from the desert averaged 3.4 percent viruliferous. The following spring, limited tests of both overwintered and spring brood leafhoppers collected in the desert gave no viruliferous individuals. Four percent of the spring brood that moved into the beet fields were viruliferous. In this season, as in the previous one, the desert leafhopper populations at no time became highly viruliferous.

Tests of summer and fall collections in 1933 showed that 2.5 percent of the population were viruliferous, and in the spring of 1934 overwintered leafhoppers tested 3 percent viruliferous. The summer and fall tests included more than 700 leafhoppers in 6 collections made between July 28 and October 6; in the spring more than 1,400 individuals were tested from 13 collections of overwintered leafhoppers made between February 2 and April 18. Because of the extremely early movement of spring brood leafhoppers, collections of this brood from desert areas were not made until after there had been a general dispersal over the desert and into the cultivated areas. The influx into beet fields began on April 27, and collections made from the fields between that date and May 15 showed that an average of about 31 percent of the incoming leafhoppers were viruliferous. Collections from desert areas from May 14 to June 11 showed that about 51 percent of the population there had become viruliferous by that time. This season, from an apparently small supply of virus in the overwintered leafhoppers, there was a rapid increase and distribution of virus throughout the host plants, so that the spring brood became rather highly viruliferous.

Summer and fall collections in 1934 gave tests on approximately 4,000 leafhoppers. An average of 12 percent of these were viruliferous. In the spring of 1935, collections of overwintered leafhoppers averaged 19 percent viruliferous. These collections were made between January 30 and May 13. Collections made prior to April 2 averaged about 12 percent viruliferous, but as the season progressed more of the overwintered leafhoppers acquired the virus. The spring brood in the desert in 1935 averaged about 52 percent viruliferous. That this percentage was representative of the desert spring brood is substantiated by tests of leafhoppers that moved into beet fields. Collections from beet fields after dispersal from breeding areas averaged 56 percent viruliferous.

Pertinent data from these tests have been assembled in table 1 to show the sequence of virus development in the leafhopper populations for each respective year. No tests were made of fall populations in either 1929 or 1930. In other instances, because of the small number of individuals tested, the data are limited. Included in table 1 are the results of tests of spring brood leafhoppers collected in beet fields after dispersal from the breeding areas had commenced. Since most of the leafhoppers in this latter group were originally from the desert areas, tests of these increased the total numbers of spring brood on which data were obtained.

It is clear from these studies that the supply of virus in leafhoppers varies appreciably from year to year. Furthermore, they show that there must be certain environmental factors which influence the development of the virus in the leafhopper populations. If it is assumed that the supply of virus in the spring-brood leafhoppers results from that brought through the winter by the overwintering population, there may be the following combinations or developments in regard to the amount of virus in the overwintered and spring-brood leafhoppers: (1) Overwintered leafhoppers highly viruliferous, followed by a highly viruliferous spring brood; (2) overwintered leafhoppers highly viruliferous, followed by a spring brood with a low percentage viruliferous; (3) low percentage of overwintered population viruliferous, followed by a highly viruliferous spring brood; and (4) verwintered leafhoppers with a low percentage viruliferous, followed by a spring brood with a low percentage viruliferous.

During the 6 years of this study, each of the above-named conditions occurred at least once. In 2 years the combination of a low viruliferous percentage of overwintered leafhoppers followed by a low viruliferous percentage of spring brood occurred, and in 2 years a high percentage of the spring brood leafhoppers became viruliferous even though a relatively small proportion of the overwintered population carried virus when they first became active in the spring.

SEASONAL DEVELOPMENT OF VIRUS

The supply of virus, as measured by the percentage of viruliferous leafhoppers in a given brood or population in one season, often differed in varying degrees from the supply in the corresponding brood or population in other seasons. This was particularly true of the spring brood, which in some years included a low percentage of viruliferous individuals and in other years a high percentage. In order to study the development of virus supply in desert leafhoppers, tests were begun with collections of the summer and fall populations. These were followed by tests of overwintered leafhoppers as soon as they became active the following spring. Tests of spring brood gave a measure of the development of virus in this population, and later tests showed to what extent the virus was being maintained in the summer and fall populations. Regardless of whether a high or low percentage of the spring brood became viruliferous, the summer and fall populations were low in percentage viruliferous in all years.

As an illustration of the changes in the virus supply in desert leafhopper populations, data on collections from three desert stations during 1933–34 are given in detail in table 2. These data show that a low percentage of the leafhoppers were viruliferous in the fall (Castleford and Hubbs Butte) and that a low percentage of the overwintered leafhoppers at these stations were viruliferous the following spring.

TABLE 2.—*Results of tests of leafhopper collections from three desert stations in Idaho throughout 1933–34*

Station and collection No.	Date of collection	Brood or population	Host plants	Leafhoppers tested	Viruliferous leafhoppers		
					Attenuated	Virulent	Total
				Number	*Percent*	*Percent*	*Percent*
Castleford:							
1	Sept. 21, 1933	Fall	*Salsola pestifer*	24	0	4.2	4.2
2	Mar. 12, 1934	Overwintered	*S. pestifer, Sophia parviflora.*	170	0	.6	.6
3	Mar. 26, 1934	do	*S. pestifer, S. parviflora, Norta altissima.*	175	4.0	3.0	7.0
4	Apr. 9, 1934	do	*S. pestifer, S. parviflora, N. altissima,* and *S. longipedicellata.*	48	2.0	0	2.0
5	May 14, 1934	Spring	*S. pestifer, S. parviflora, N. altissima,* and *S. longipedicellata.*	200	23.0	10.0	33.0
6	July 2, 1934	do	*S. parviflora, S. pestifer*	106	53.0	0	53.0
7	July 22, 1934	Spring and summer.	*S. pestifer*	85	15.0	0	15.0
8	Aug. 20, 1934	Summer	*S. pestifer*	45	2.0	0	2.0
Hubbs Butte:							
1	Sept. 5, 1933	Fall	*S. pestifer*	394	.3	0	.3
2	Sept. 19, 1933	do	*S. pestifer*	50	0	0	0
3	Feb. 2, 1934	Overwintered	*Artemisia tridentata*	13	0	0	0
4	Apr. 5, 1934	do	*N. altissima, S. pestifer, S. longipedicellata.*	97	4.0	1.0	5.0
5	May 31, 1934	Spring	*N. altissima, S. pestifer, S. longipedicellata,* and *S. parviflora.*	107	23.0	19.0	42.0
6	July 31, 1934	Spring and summer.	*S. pestifer*	95	9.0	0	9.0
7	Aug. 10, 1934	Summer	*S. pestifer*	67	1.0	0	1.0
Wendell:							
1	Mar. 12, 1934	Overwintered	*S. parviflora, S. longipedicellata, N. altissima.*	140	0	0	0
2	Mar. 19, 1934	do	*S. parviflora, S. longipedicellata, N. altissima.*	100	5.0	0	5.0
3	May 14, 1934	Spring	*S. parviflora, S. longipedicellata, N. altissima,* and *S. pestifer.*	114	61.0	33.0	94.0
4	July 2, 1934	Summer	*S. pestifer*	44	2.0	0	2.0
5	July 23, 1934	do	*S. pestifer*	87	2.0	1.0	3.0
6	Aug. 20, 1934	do	*S. pestifer*	50	4.0	0	4.0

The spring season of 1934 was decidedly early. Warm weather in March and April was favorable for both the development of spring-brood leafhoppers and the distribution and increase of virus in plants. The maturity of the spring brood was so hastened that a movement of leafhoppers began on April 27, almost a month earlier than any recorded date of movement in previous years. Within a short time high populations were generally distributed over the desert and cultivated areas.

No collections of spring-brood leafhoppers were obtained from desert stations until after the dispersal began. Therefore, there was no assurance that spring-brood leafhoppers taken from a given station had actually developed there.

The general distribution of the susceptible green tansymustard is believed to have aided materially in building up an abundant supply of virus in the desert spring-brood leafhoppers in 1934. At one station, not included in table 2, where this mustard was the only host, tests showed that 22 percent of the overwintered leafhoppers were viruliferous on April 9. Collections taken at about this same time from other stations where tansymustard was absent or scarce averaged from 0 to 5 percent of viruliferous leafhoppers. A collection of spring brood taken on May 21 from the above-mentioned station, where green tansymustard was the exclusive host, showed that 91 percent of the population were viruliferous. All collections of spring brood leafhoppers taken in May and June averaged 51 percent viruliferous (table 1).

It is shown further, in table 2, that as the season progressed the summer and fall populations in 1934 did not maintain the supply of virus at its earlier high level. This was true in each of the 4 years that tests were made of fall collections from Russian-thistle. In 1933, 2 small collections of spring brood taken from the desert and totaling only 41 leafhoppers showed 0 percent viruliferous. More extensive collections taken from beet fields during the influx from the desert tested 4.3 percent viruliferous. It is therefore assumed that between 4 and 5 percent of the spring brood desert population was viruliferous in 1933. Fall populations in the desert that year averaged only 2.5 percent viruliferous. The failure of desert fall populations to maintain the supply of virus carried by spring populations is more striking in other years when the spring broods were more highly viruliferous.

Special studies on the maintenance of virus in desert leafhopper populations on Russian-thistle were made in 1932. Square-rod plots of a susceptible variety of beets were planted at two places in the desert. Water was hauled to these plots throughout the summer. The beets remained alive until late fall but did not have sufficient water for good growth. These plots were surrounded by Russian-thistle, and both the beets and Russian-thistle had the same natural exposure to leafhoppers. Collections were made at intervals from the beets and from Russian-thistle nearby, and tests were made to determine the percentage of viruliferous leafhoppers. The results of these tests are presented in table 3 and show clearly that a much higher percentage of the populations on the beets became viruliferous.

TABLE 3.—*Comparison of leafhoppers from sugar beets grown in the desert and from Russian-thistle growing adjacent to the beets, 1932*

Station and collection No.	Date of collection	Host plants	Leafhoppers tested	Viruliferous leafhoppers	
			Number	*Number*	*Percent*
Tuttle:					
1	Sept. 6	*Beta vulgaris*	20	9	45
		Salsola pestifer	50	1	2
2	Sept. 22	*B. vulgaris*	15	5	33
		S. pestifer	50	3	6
3	Oct. 19	*B. vulgaris*	50	9	18
		S. pestifer	21	0	0
Castleford:					
1	Aug. 30	*B. vulgaris*	50	5	10
		S. pestifer	100	0	0
2	Sept. 7	*B. vulgaris*	50	10	20
		S. pestifer	50	1	2
3	Sept. 23	*B. vulgaris*	50	16	32
		S. pestifer	50	0	0
4	Oct. 21	*B. vulgaris*	100	25	25
5	Nov. 28	*B. vulgaris*	94	51	54
Total or average		*B. vulgaris*	429	130	30.3
		S. pestifer	321	5	1.5

The decrease shown (table 3) in the viruliferous percentage between September 6 and October 19 on the Tuttle beets is accounted for by the heavy movement of nonviruliferous leafhoppers to beets from adjacent Russian-thistle because of the early drying of this plant. The increase in the population was quite noticeable on the beet plot. At Castleford, Russian-thistle matured later and the leafhoppers were not forced to the beets until after September 23. On October 24 there was a concentration of leafhoppers on the beets, while the Russian-thistle had dried and very few leafhoppers could be found on it. Tests of 100 leafhoppers taken from beets on this date showed that 25 percent were viruliferous. This was a decrease of 7 percent from the percentage viruliferous in the collection of September 23. A collection made on this beet plot on November 28 showed that 54 percent of the population had become viruliferous by that time. No collections were obtained from Russian-thistle on these last two dates.

All curly top produced on greenhouse plants by leafhoppers, both from beets and Russian-thistle at Tuttle, was of a mild type. In some of the early collections from beets at Castleford an occasional leafhopper carried virulent virus. During September, October, and November there was an increase in both percentage of viruliferous leafhoppers and degree of virulence of virus. The collection from beets on November 28 showed that more than half of the leafhoppers had acquired virulent virus by that date. All infection produced by leafhoppers taken from Russian-thistle at this station throughout the season was of a mild type.

Throughout the 6 years of this study virulent virus was relatively rare in leafhoppers taken from Russian-thistle in summer and fall. However, a large majority of the leafhoppers collected in the summer from beet fields were well supplied with virulent virus. Figure 4 shows beets inoculated by leafhoppers taken from desert stands of Russian-thistle in midsummer, in comparison with beets inoculated by beet-field leafhoppers taken at the same time. The severity of symptoms on the plants inoculated by beet-field leafhoppers is apparent, but symptoms are not obvious in the group inoculated by leafhoppers from Russian-thistle, even though some of the plants were actually infected.

DEVELOPMENT OF VIRUS IN LEAFHOPPER POPULATIONS IN BEET FIELDS

As a result of infection and spread of curly top in beets, the spring-brood leafhoppers that moved into the fields from the desert breeding areas became more highly viruliferous as the season progressed. By the time the summer field brood matured, a high percentage of the field population was viruliferous. In studies of beet-field populations it was found that, even though the incoming leafhoppers carried a limited supply of virulent virus, practically all of the leafhoppers in the late summer population in the fields were supplied with the virulent type.

Table 4 gives the results of tests on collections taken from beet fields in 1932. Leafhoppers from desert breeding areas began to reach the fields on June 13. Collections from four fields taken between June 13 and June 23 averaged 12 percent viruliferous.

FIGURE 4.—*A*, Beets inoculated by leafhoppers collected in midsummer from beet field; *B*, beets inoculated by leafhoppers taken at the same time as in *A* from desert stands of Russian-thistle.

Three-fourths of the leafhoppers viruliferous at this time carried attenuated virus. Disease counts taken in the fields at the times of collections showed that the increase in percentage of viruliferous leafhoppers was proportional to the increase of disease.

TABLE 4.—*Tests of spring and summer collections of leafhoppers from beet fields in 1932*

Beet field	Approximate location	Date of collection	Collection No.	Curly top incidence in field	Leafhoppers tested	Viruliferous leafhoppers		
						Attenuated	Virulent	Total
				Percent	*Number*	*Percent*	*Percent*	*Percent*
Beckley	Twin Falls (2 miles north, 1 mile west).	June 13	1	0	33	6	3	9
		June 25	2	(1)	85	13	5	18
		Aug. 6	3	63	55	24	45	69
		Aug. 10	4	79	97	6	78	84
Sackett	Filer (1 mile north, 1 mile west).	June 13	1	0	30	17	3	20
		June 28	2	4	60	23	5	28
		July 15	3	42	100	23	26	49
		July 25	4	76	90	13	47	60
		Sept. 12	5	52	100	3	64	67
Johnson	Castleford (3 miles east, 1 mile north).	June 16	1	0	59	9	3	12
		June 20	2	2	141	21	9	30
		June 28	3	15	180	24	6	30
		July 6	4	34	100	26	26	52
		Aug. 2	5	91	104	3	87	90
		Aug. 15	6	98	100	3	92	95
Factory	Twin Falls (1 mile east, 1 mile south).	July 14	1	30	30	27	10	37
Boone	Twin Falls (1 mile west)	June 23	1	(1)	10	0	0	0
		July 15	2	32	66	27	14	41

[1] Trace.

Figure 5 shows graphically the change in the viruliferous condition of the population in the Johnson beet field near Castleford in 1932. On June 16, 3 days after the movement into the fields began, 12 percent of the leafhoppers were viruliferous and only a fourth of these, or 3 percent of the total population, carried virulent virus. It can be seen in figure 5 that the incubation period, or time required for symptoms to develop, was much longer in the first collections, and that this period became shorter as a larger proportion of the population acquired virulent virus.

The results of tests of beet-field leafhoppers in 1933 are shown in table 5. These data show again that even though a relatively small proportion of the incoming leafhoppers were viruliferous when the insects reached the fields, there was a gradual increase of virus in the populations as the season progressed. The extent to which the population becomes viruliferous is, of course, dependent on the amount of curly top and the rate of its development. If high populations move into a field of young, susceptible beets, there may be a rapid distribution of disease over the entire field. Obviously with a high percentage of the plants diseased, more of the leafhoppers acquire virus. The variations in the rate of development of disease and rate of increase in viruliferous leafhoppers between different fields are no doubt due largely to differences in the degree of infestation in the respective fields and to differences in the age of plants at the time of infestation.

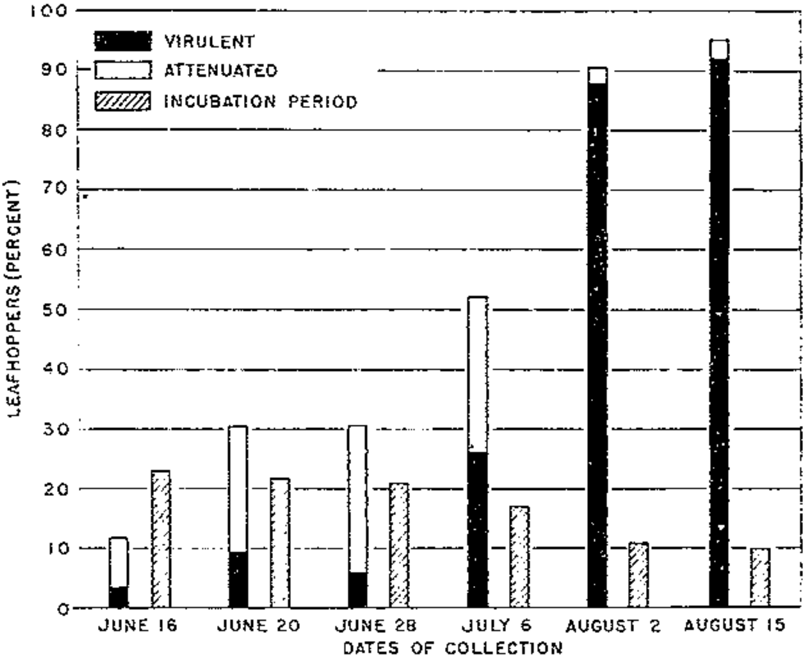


FIGURE 5.—Percentages of leafhoppers with virulent and attenuated virus, total percentage viruliferous, and average incubation period of all infections produced in greenhouse tests of collections made at intervals from the Johnson beet field near Castleford, Idaho, during 1932.

TABLE 5.—*Tests of spring and summer collections of leafhoppers from beet fields in 1933*

Beet field	Approximate location	Date of collection	Collection No.	Curly top incidence in field	Leafhoppers tested	Viruliferous leafhoppers: Attenuated	Viruliferous leafhoppers: Virulent	Viruliferous leafhoppers: Total
				Percent	*Number*	*Percent*	*Percent*	*Percent*
Tenchinck	Twin Falls (1 mile west)	June 22	1	0	5	0	0	0
J. Thomas	Castleford (3 miles south, 1 mile west).	June 29	1	5	52	10	2	12
G. Thomas	Castleford (2 miles south, 2 miles west).	June 12	1	(¹)	36	2	2	4
		July 25	2		52	17	33	50
		Aug. 22	3	30	108	6	56	62
Machacek	Buhl (2 miles east, 1 mile north).	June 9	1	0	6	0	0	0
		June 19	2	0	14	0	0	0
Roubinek	Buhl (3 miles north, 2 miles east).	June 9	1	0	50	4	0	4
		June 14	2	0	60	1	1	2
		June 19	3	0	78	3	0	3
		July 5	4	10	69	28	12	40
		July 17	5	32	49	12	31	43
		Aug. 2	6	68	97	3	89	92
Sackett	Filer (1 mile north, 1 mile west).	June 19	1	0	18	6	0	6
		June 26	2	0	19	5	0	5
Zweigle	do	June 26	1	(¹)	34	7	2	9
		July 7	2	1	61	0	3	3
		Aug. 4	3	4	117	11	10	21
		Aug. 23	4		200	6	23	29
		Sept. 27	5	20	159	3	62	65
Tickner	Twin Falls (2 miles north)	June 24	1	(¹)	7	0	0	0
		July 24	2	5	156	3	6	9
		Aug. 12	3	17	85	5	15	20
		Sept. 26	4	32	204	4	47	51
Waite	do	July 15	1	(¹)	23	0	0	0
		July 21	2	(¹)	186	2	1	3
		Aug. 11	3	3	78	5	1	6
		Sept. 30	4	18	100	7	26	33

¹ Trace.

Tests of beet-field collections in 1934 are shown in table 6. With one exception, this table shows that in 1934 all of the early collections of incoming leafhoppers agreed quite closely in the percentage viruliferous. The fields from which collections were made were in some instances widely separated. In the collections made during the first 12 days after the leafhoppers began to reach the fields, the different collections ranged from 26 to 45 percent viruliferous. The low percentage of viruliferous leafhoppers in the collection from the Thomas field on April 27 may probably be explained by the location of this field and the date of collection. The field was on a farm immediately adjacent to the desert. On April 27 there was a sizeable infestation of leafhoppers in the field, while the fields farther into the cultivated tract showed only an occasional leafhopper. Within a few days, however, there was a general infestation over most of the sugar-beet area. It appeared that the leafhoppers first infesting the Thomas field came from some nearby weed area, and that the leafhoppers developing at that source had not acquired as much virus as those coming in later from other areas.

In 1934 most of the beets were unthinned at the time the leafhoppers began to reach the fields. Curly top developed slowly in the unthinned beets. For 2 weeks after the infestation began there was only a trace of disease in many unthinned fields as compared with from 40 to 50 percent of plants with well-advanced disease in some of the thinned fields. Since most of the collections shown in table 6 were taken from unthinned beets, it is believed that very little increase in the percentage of viruliferous leafhoppers took place in the populations in the unthinned beets up to May 15.

TABLE 6.—*Results of tests of leafhoppers collected in beet fields in 1934*

Beet field	Approximate location	Thinned or unthinned fields	Date of collection	Collection No.	Leafhoppers tested	Viruliferous leafhoppers		
						Attenuated	Virulent	Total
					Number	*Percent*	*Percent*	*Percent*
J. Thomas	Castleford (3 miles south, 1 mile west).	Unthinned	Apr. 27	1	98	2	2	4
		do	May 10	2	102	25	6	31
		Thinned	May 24	3	95	19	24	43
Reubinek	Buhl (3 miles north, 2 miles east).	Unthinned	May 4	1	160	23	7	30
		Thinned	June 8	2	94	6	80	86
Britt	Kimberly (3 miles south, 2 miles east).	do	May 9	1	27	15	11	26
		do	June 6	2	197	5	74	79
Marhneck	Buhl (2 miles east, 1 mile north).	Unthinned	May 4	1	83	23	17	40
Zweigle	Filer (1 mile north, 1 mile west).	do	do	1	133	29	3	32
Laboratory	Twin Falls (1 mile north).	Thinned	May 7	1	56	14	20	34
McClain	Twin Falls (2 miles southeast).	Unthinned	May 9	1	60	22	13	35
Steen	Twin Falls (2 miles north).	do	do	1	112	21	21	42
Factory	Twin Falls (1 mile east, 1 mile south).	do	May 7	1	18	28	17	45
Sprague	Hansen (4 miles south)	do	May 9	1	36	0	31	31
Putzier	Twin Falls (4 miles east)	Thinned	May 15	1	79	10	19	29
Skinner	Buhl (2 miles east, 2 miles north).	do	May 17	1	60	23	27	50
Wilson	Murtaugh (4 miles south, 2 miles east).	Unthinned	June 6	1	95	5	24	29

OVERWINTERING OF CURLY TOP VIRUS UNDER NATURAL CONDITIONS

OVERWINTERING OF VIRUS IN LIVING PLANTS

WILD HOSTS

Severin (*19*) lists 14 species of plants, belonging to 11 families, in which curly top virus overwinters in the uncultivated plains and foothills of California. The same author records 16 perennial species susceptible to curly top, and plants of 3 of these species were found infected naturally.

In the leafhopper breeding areas of southern Idaho, there is, so far as known, aside from sagebrush, no perennial plant species of importance in the life history of the beet leafhopper. Normally, the overwintering leafhoppers are inactive for periods during the winter, and in winters of steady low temperatures there may be little or no feeding over a period of several weeks. Under such conditions the curly top virus must survive the winter either in the body of the leafhoppers or in fall-germinating annual plants that are infected before the leafhoppers become inactive.

In southern Idaho, germination of the mustard species frequently occurs in the fall, and often there is a considerable period for the leafhoppers to feed on these plants before cold weather brings on inactivity or dormancy of the insects. This has suggested that the mustard hosts germinating in the fall in the desert areas might be infected in the fall and act as reservoirs for the virus throughout the winter in the leafhopper breeding areas.

Flats of tumblemustard, green tansymustard, and flixweed were placed outside in October 1933 and covered with cloth cages. Fifty viruliferous male leafhoppers were caged for 3 weeks on each flat. All surviving leafhoppers were removed on November 7. The flats were brought into the greenhouse on February 10, and the plants were carefully examined for symptoms of curly top. No evidence of disease could be found on tumblemustard or flixweed. In the flat of green tansymustard, 90 percent of the plants showed curly top symptoms. Nonviruliferous leafhoppers were caged for 7 days on groups of plants of the three species and were then transferred to healthy beet seedlings. Most of the leafhoppers from the green tansymustard plants infected the beets. An occasional leafhopper from the symptomless flixweed plants infected the beets, but no virus was obtained from the leafhoppers from tumblemustard.

After 3 weeks at greenhouse temperatures, about 2 percent of the flixweed plants developed curly top symptoms. The virus was recovered from some of these plants and transferred to beet seedlings. No symptoms developed on any of the tumblemustard plants. All of the green tansymustard plants that developed symptoms eventually died, while those plants that apparently escaped infection produced normal flower stalks and seed pods.

These studies prove that under experimental conditions, two of the common desert weed hosts of the beet leafhopper can serve as reservoirs for the virus throughout mild winters in southern Idaho. The extent to which this occurs under natural conditions is not known.

SUGAR BEETS

The writers have obtained curly top virus from sugar beets left in the field at harvesttime and exposed to subzero temperatures at

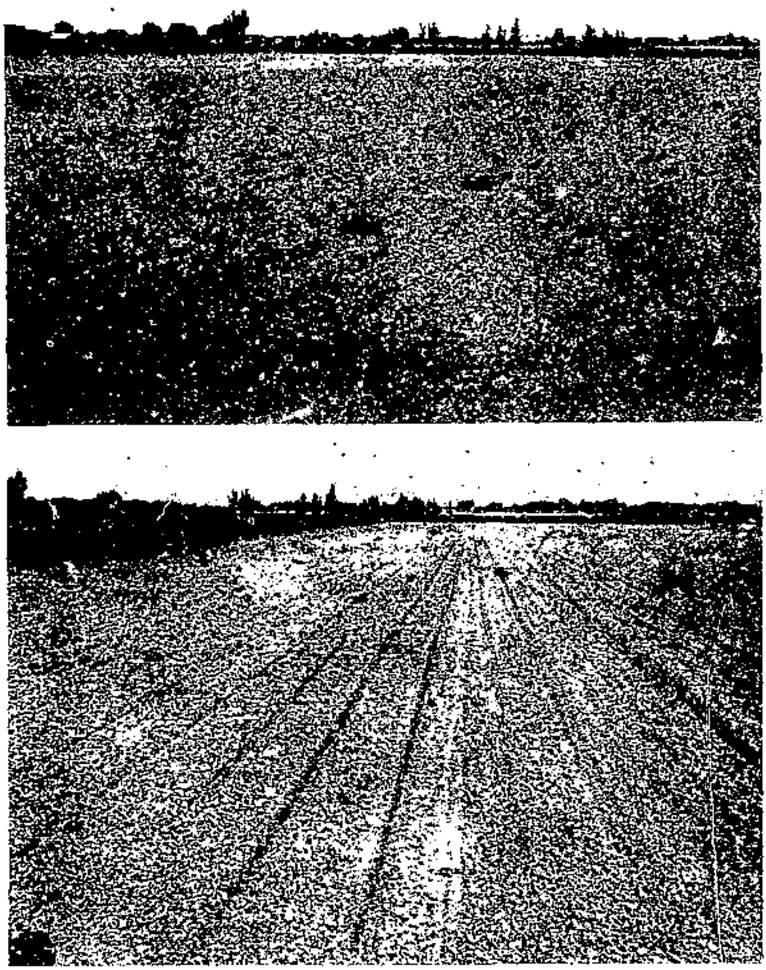


FIGURE 6.—Two views of the same field, showing overwintered beets remaining in the field after emergence of seedling beets, Twin Falls, Idaho, 1934.

times during the winter. Some of these beets were brought into the greenhouse early in March, and the new growth developing on them showed curly top symptoms. Beet seedlings infected by leafhoppers that were nonviruliferous when caged on the overwintered beets developed severe curly top symptoms. Since there had been no chance of reinfection of these field beets, it was certain that the virus had remained in them throughout the winter.

In the spring of 1934, after a mild winter, many fields showed that most of the beets left in the fields at harvest in 1933 had survived the winter. Overwintered roots developed new growth in the spring, and many of them showed curly top symptoms. Figure 6 gives two views of a field in which new plants from overwintered roots are scattered conspicuously throughout the rows of spring-planted beets. Leafhoppers taken from the old plants averaged much higher in percentage viruliferous than those taken from weeds in the cultivated area. This was additional proof that the virus had passed the winter in these plants.

OVERWINTERING OF VIRUS IN BEET LEAFHOPPERS

On the basis of general observations it has been commonly assumed that the curly top virus overwinters in the beet leafhopper, but heretofore no experiments have been conducted to confirm this belief. Severin (*19*) found that the average period of infectivity during the adult life of 10 female beet leafhoppers, which completed the nymphal stages on diseased beets, was 83.9 days, followed by an average period of 50.1 days between the last infection and the death of the insect. Severin concluded that the infective power is not retained during the adult life of the overwintering female leafhoppers unless they acquire a new supply of virus during the winter. Whether or not the character of the virus carried by the leafhopper changed during the winter period was not known. Carter (*10*) suggested the possibility of such a change in virus.

During the winters of 1932–33 and 1933–34, the writers conducted some experiments to determine whether the virus remains active throughout the winter within the body of the leafhopper and whether any change in virulence takes place. Tumblemustard, flixweed, and green tansymustard were used as hosts for the leafhoppers in these experiments, since these are the principal overwintering hosts under natural conditions in this area.

WINTER OF 1932-33

Studies were made of groups of leafhoppers carrying a virulent strain of virus as well as of groups carrying an attenuated strain. For a supply of leafhoppers with virulent virus, collections were made from a beet field on October 29 and caged on a severely diseased beet for 20 days before being placed outside in hibernation cages for overwintering.

Since there was not an available supply of nonviruliferous leafhoppers for building up a colony carrying attenuated virus, collections were made from a Russian-thistle area in the desert. Collections from this point throughout the season had shown that a very low percentage of the population was viruliferous and that very few of these carried virulent virus. These leafhoppers were collected on October 29 and were caged for 20 days on a beet that was known to have been infected with an attenuated strain of virus.

On November 18, another collection was made from the Russian-thistle area, and these leafhoppers were transferred directly to the hibernation cages. Tumblemustard, flixweed, and green tansy-mustard, both as pure stands and as a combined stand, were used as food plants in the cages. The mustards had been previously planted in wooden flats fitted with a square cloth cage of the type used by the Bureau of Entomology and Plant Quarantine in the study of winter mortality of the beet leafhopper.

At the time the leafhoppers were placed outside for overwintering, on November 18, samples from each of the three groups were tested on beet seedlings, one leafhopper to each seedling for 6 days, to determine the viruliferous percentages of the respective groups of leafhoppers and the virulence of the virus carried by them. The infections resulting from the feedings were graded into five classes ranging from extremely mild to extremely severe, and assigned numerical values of 1 to 5, inclusive. This method of grading is essentially the same as that described by Giddings (*11*). At the completion of a test, a numerical average severity was calculated, and the average severity obtained in this manner was used as a measure of the average virulence of the virus carried by the leafhoppers being tested.

For about 2 weeks after the cages were placed outside, day temperatures were high enough to permit considerable activity of the insects. No doubt some of the susceptible plants became infected. Early in December there was a rather sharp drop in temperature, and for 8 days the minimum daily temperature was below zero. It is quite certain that the leafhoppers were inactive throughout the last 3 weeks of this month. In January, day temperatures sometimes were sufficiently high to suggest that the leafhoppers might have been active during a part of the month, but it is not known to what extent feeding occurred. While the cages were out in February the temperatures were quite low, many daily minima being below zero. There was certainly little, if any, feeding during that time.

The surviving leafhoppers were removed from the cages on February 20 and tested on beets to determine whether any change had occurred in their ability to produce infection or in the virulence of the virus. Table 7 shows the host plants on which the leafhoppers overwintered, the percentages of infection produced by samples of each group, and the virulence of the virus carried by the respective groups before and after overwintering. These data show that the virus brought through the winter by the leafhoppers in this experiment was apparently unchanged in virulence. There is an indication that some of the leafhoppers that were viruliferous in November may have actually become nonviruliferous during the 94 days of winter environment. It should be pointed out that in the tests of November 18, each leafhopper was caged for 6 days on only one plant. It is now known that such a test may not give the actual percentage of viruliferous leafhoppers in the group being tested. Even though a leafhopper may be viruliferous, it does not always infect the plants on which it feeds. Repeated transfers of a group of leafhoppers often show that a much higher percentage of the group is viruliferous than is shown by the infections resulting from a single feeding of each individual. This is particularly true in groups of leafhoppers carrying attenuated virus.

TABLE 7.—*Tests on overwintering of curly top virus in the beet leafhopper, fall and winter of 1932–33*

Group number, source, and treatment of leafhoppers before being placed in hibernation cages	Host plants on which leafhoppers overwintered	Infection produced by samples of leafhoppers and average virulence of virus before overwintering, Nov. 18, 1932		Infection produced by surviving leafhoppers and average virulence of virus after overwintering, Feb. 20, 1933	
		Plants infected[1]	Average virulence[2]	Plants infected[3]	Average virulence[2]
		Percent		*Percent*	
Group 1; collected in desert and caged on a mildly diseased beet for 20 days.	*Norta altissima*	26	1.1	32	1.1
	Sophia longipedicellata			42	1.2
	S. parviflora			24	1.3
	Combined stand of above-named species.			33	1.1
Group 2; collected in beet field and caged on a severely diseased beet for 20 days.	*N. altissima*	88	4.3	48	4.3
	S. longipedicellata			64	4.6
	S. parviflora			73	4.0
	Combined stand of above-named species.			69	4.3
Group 3; collected in desert and transferred directly to hibernation cages.	*N. altissima*	10	1.0	10	1.1
	S. longipedicellata			3	1.0
	S. parviflora			6	1.0
	Combined stand of above-named species.			5	1.0

[1] In the November tests each leafhopper fed on only 1 beet plant, hence the resulting infection percentages were probably somewhat lower than the actual viruliferous percentages, particularly in groups 1 and 3.

[2] Severity of symptoms in test plants was graded numerically 1 to 5, inclusive. Thus a numerical average severity was obtained, which is here used as a measure of the average virulence of the virus carried by the respective groups of leafhoppers.

[3] Each surviving leafhopper fed on 4 plants. The infection percentages therefore gave a close index of the actual viruliferous percentages.

Each of the surviving leafhoppers taken from the cages in February was transferred successively to four beet seedlings. It is believed these tests showed closely the actual percentage of viruliferous leafhoppers in the respective groups after overwintering.

Leafhoppers in group 2 supplied with virulent virus tested 88 percent viruliferous in November. Repeated tests of this group could not have increased this total more than 12 percent. Thus it seems safe to make a study of the differences in the viruliferous percentages of this group at the beginning and at the end of the experiment. There is evidence that there was a decrease in the supply of virus in these leafhoppers during the winter, regardless of the host on which they were caged. At least 88 percent of them were viruliferous when they were placed in the cages on November 18. On February 20, the surviving leafhoppers from the four cages in this group averaged from 15 to 40 percent lower in percentage viruliferous. The greatest decrease, 40 percent, was in the cage that contained the highly resistant species, *Norta altissima*. In spite of this apparent decrease in supply of virus, the virulence of the virus in the different groups on February 20 was not significantly different from that of the same groups in November.

WINTER OF 1933–34

Additional tests on the overwintering of the virus in the body of the leafhopper were made during the winter of 1933–34. These tests were similar to those made the previous year, except that only two groups of leafhoppers were used and, further, that all of the leafhoppers came originally from the same source.

These leafhoppers were collected from Russian-thistle in the breeding area early in October. In order to determine the percentage carrying virus at the time of collection, 156 leafhoppers were tested on beet plants. Five plants developed faint symptoms of curly top, but all of them lost all signs of infection within 5 days after the vein clearings appeared. It was evident that there was little virus in these leafhoppers and, further, that the virus present was extremely attenuated. Two groups of these leafhoppers were caged on diseased beets for 2 weeks before being placed in the hibernation cages. Group 1 was caged on a beet known to be infected with an attenuated virus, and group 2 was caged on a severely diseased beet infected with a virulent virus.

On October 20, the leafhoppers were placed in the hibernation cages on pure stands of tumblemustard, flixweed, and green tansymustard, and on a combined stand of these species. At this time, tests were made on samples of leafhoppers from each group to determine the percentage viruliferous and the virulence of the virus carried by the respective groups. In these tests, each leafhopper was caged successively for 3 days on each of three seedling beets. If a leafhopper infected one or more of the plants it fed on, that insect was classed as viruliferous. Those that failed to infect at least one plant were classed as nonviruliferous. Similar tests of the surviving leafhoppers were made when they were removed from the cages, except that each one was caged for 7 days on each of three seedling beets.

The winter was very mild as compared with that of the previous year. The lowest temperature during the time the cages were outside was 8° F. Numerous examinations of the cages during the winter showed that the leafhoppers were active. When the cages were brought in on February 15, the leafhoppers could be captured immediately without any warming-up period. In the cages having pure stands of green tansymustard, many of the plants showed curly top symptoms when the cages were brought in, and other plants developed symptoms after a few days at greenhouse temperatures.

The detailed results of the tests on the overwintering of the virus in the leafhoppers in 1933–34 are shown in table 8. A random sample of the leafhoppers with attenuated virus (group 1) tested 55 percent viruliferous when the hibernation cages were set up in October. When they were brought in on February 15, separate tests were made of samples from each cage of separate or of combined host plants. In the attenuated group, leafhoppers from the highly resistant tumblemustard tested 19 percent lower after overwintering. Those on flixweed, which is at least partially resistant to curly top, tested 20 percent less in February than in October. The survivors on the extremely susceptible host, green tansymustard, showed an increase of 41 percent in virulence. It was expected that the leafhoppers from green tansymustard would test quite high, as many of the plants in that cage showed curly top symptoms when the leafhoppers were removed in February. The weather had been sufficiently warm to permit infection of these plants and thereby provide a source of virus for those leafhoppers that were nonviruliferous when they were caged.

TABLE 8.—*Tests on overwintering of curly top virus in the beet leafhopper, fall and winter of 1933–34*

Leafhopper group	Virus carried	Host plants on which leafhoppers overwintered	Leafhoppers before overwintering, Oct. 20, 1933		Leafhoppers after overwintering, Feb. 15, 1934	
			Viruliferous	Average virulence[1]	Viruliferous	Average virulence[1]
			Percent		*Percent*	
1	Attenuated	*Norta altissima*	55	1.5	36	1.0
		Sophia longipedicellata			96	1.6
		S. parviflora			35	1.3
		Combined stand of above-named species			50	1.6
2	Virulent	*N. altissima*	98	4.4	93	4.3
		S. longipedicellata			94	4.0
		S. parviflora			93	4.7
		Combined stand of above-named species			93	4.6

[1] Severity of symptoms in the test plants was graded numerically 1 to 5, inclusive. Thus a numerical average severity was obtained, which is here used as a measure of the average virulence of the virus carried by the respective groups of leafhoppers.

These results suggest that some of the leafhoppers originally carrying attenuated virus became nonviruliferous while overwintering on curly-top-resistant plants. It seems evident, however, that during such mild winters as 1933–34, the viruliferous percentage of leafhopper populations on green tansymustard may be increased simply by infection and spread of the virus throughout the plants on which the leafhoppers overwinter. Results on average virulence confirm these views.

The average virulence of the attenuated virus was 1.5 in October. Leafhoppers from tumblemustard produced infections that averaged 1.0 in severity in February. The infections produced by the survivals from flixweed averaged 1.3 in severity, while those produced by the survivals from a pure stand of green tansymustard and those from the mixture of the three species each averaged 1.6. The differences are suggestive of some host influence, but further study would be necessary before any definite conclusion could be made.

In the tests of leafhoppers with virulent virus during the mild winter of 1933–34, there was apparently no influence of host plants on the number of leafhoppers carrying the virus, or on the virulence of the virus itself, as is indicated in table 8.

Studies in the winter of 1932–33 showed that in the leafhoppers with virulent virus caged on *Norta altissima* (group 2), the viruliferous percentage decreased 40 percent. The following year a similar group showed no significant decrease. No satisfactory explanation of this variation has been experimentally established. The apparent loss of virus by some of the leafhoppers in the winter of 1932–33 and the retention of virus by nearly all of the leafhoppers the following year may have been due to the difference in the severity of the winter in the respective years through an effect on the activity of the leafhoppers. During the first winter it is certain that the leafhoppers fed very little, if any, between December 1 and February 20. With the existing cold weather, the leafhoppers were dormant during this period with the exception of possibly a few days in January. The following year, winter temperatures were such that leafhoppers were active during the warm part of most of the days. Whether leafhoppers feeding more or less continuously on an immune plant lose less virus than those dormant or inactive is still to be determined.

From these investigations on the overwintering of curly top virus in the beet leafhopper, the writers conclude that the virus may remain in the leafhoppers throughout the winter without apparent change in virulence. There is evidence that, if viruliferous leafhoppers are restricted for a period to highly resistant or immune plant species, under certain environmental conditions, some of them may become nonviruliferous.

EARLY INFECTIONS IN BEET FIELDS BY OVERWINTERED LEAFHOPPERS

It has been demonstrated by Carter (*10*) that the type of winter is directly correlated with the percentage of hibernating leafhoppers surviving the winter. Carter's conclusions are based on hibernation cage tests as well as on field studies of the populations going into hibernation in desert areas and the populations of overwintered forms the following spring. Carsner and Stahl (*9*) point out that beets infected by leafhoppers overwintering in or near beet fields may serve as sources of inoculum for spring-brood leafhoppers in the field. Severin (*18*) reported that before the spring flights occurred in 1919 in the Salinas Valley of California 55 percent of the sugar beets were infected by overwintered adults that had remained in the cultivated areas. Carter (*10*) reported the occurrence of "dark forms" in beet fields as early as the first week of May in 1926, but the influx of spring-brood leafhoppers had already occurred and Carter inferred that these dark-colored leafhoppers had come in from the desert and that they were from the overwintered population. Severin (*18*) cites numerous instances of autumn dispersals of beet leafhoppers from cultivated areas to uncultivated plains and foothills in California.

The writers have obtained evidence that leafhoppers may also overwinter in the cultivated lands in southern Idaho, and a study was made of the importance of locally overwintering leafhoppers in the epidemiology of the curly top disease. It is well known that at harvesttime there are large numbers of leafhoppers in beet fields, many of which probably go into hibernation along the borders of the fields or in nearby weed areas. There is as yet no direct evidence in the Twin Falls area that leafhoppers from beet fields return to the desert breeding grounds when the beets are removed. It is granted that there may be some return movement, but so far it has not been detected experimentally. In 1932, leafhoppers were found in beet fields feeding on the remains of leaves and petioles 10 days after the beets had been topped and removed from the field. A few days later, as the food in the field disappeared, leafhoppers were found rather abundantly on grass and weeds in a pasture adjacent to one of the beet fields. Whether any of the leafhoppers moved to more distant points was not determined.

It is quite possible that sometimes there may be an early movement of overwintered leafhoppers from the desert areas to the cultivated lands in the spring, but it is not believed that such a movement is common in this section of Idaho. The extremely sparse populations of overwintered leafhoppers found in beet fields, the irregularity of early infections over the cultivated area as a whole, and the striking predominance of these early cases of disease along the outer margins of the fields argue against a general movement of overwintered leafhoppers from the desert to the cultivated areas.

Observations in beet fields in 1930 and 1931 before any detectable movement of spring-brood leafhoppers occurred, showed that in most fields there could usually be found at least a trace of disease and in some instances from 5 to 15 percent. Most of the diseased plants showed severe symptoms, and it was evident that they had been infected at an early stage. The infected plants were localized, and sometimes as many as five consecutive plants in a row or else several plants within a radius of 3 or 4 feet were diseased. This indicated that probably all of the diseased plants within one of the local spots had been infected by the same leafhopper.

In 1931, collections of overwintered leafhoppers were made in beet fields or from weeds bordering the fields, and these leafhoppers were tested in comparison with samples of the overwintered population in the desert areas. The number of such leafhoppers in beet fields is usually very low, and much time and effort are required to collect desired numbers. The leafhoppers were caged singly on seedling beets, and the resulting infections were classified as mild or severe, thus giving the numbers of leafhoppers with attenuated or virulent virus. The details of the tests of these collections are presented in table 9, along with comparative tests of overwintered desert leafhoppers collected over approximately the same period. It will be observed that in this year the total percentage of viruliferous leafhoppers was higher in the desert collections than in those from beet fields. However, the quality of virus seemed to be significantly different. In the desert areas, 43 percent of the leafhoppers were viruliferous, but only 4 percent of them carried virulent virus; in the beet-field collections, only 32 percent were viruliferous, but 18 percent carried virulent virus. Such a difference in the virulence of the virus found in leafhoppers from the two sources, i. e., beet fields and desert areas, strongly suggests that at least some of those collected in the beet fields had moved off of beets the preceding fall and had overwintered near the fields.

TABLE 9.—*Tests of overwintered leafhoppers collected in desert areas and in or near beet fields in the spring of 1931*

Source	Collection No.	Date of collection	Host plants	Leafhoppers tested	Viruliferous leafhoppers		
					Attenuated	Virulent	Total
				Number	*Percent*	*Percent*	*Percent*
Desert	1	Apr. 9	*Norta altissima, Sophia parviflora, S. longipedicellata.*	25	45	9	54
	2	Apr. 30	do	110	39	0	39
	3	Apr. 16	do	38	28	8	36
	4	Apr. 28	do	19	53	11	64
	5	Apr. 30	do	20	44	2	40
Beet field	1	Apr. 10	*Salsola pestifer, Chenopodium album* L., *Lactuca scariola integrata* Gren. and Godr.	10	0	60	60
	2	Apr. 17	do	20	10	25	35
	3	Apr. 28	do	22	32	9	41
	4	May 1	Seedling beets	10	0	10	10
	5	May 6	do	17	12	0	12
Total leafhoppers from desert areas				212	39	4	43
Total leafhoppers from beet fields				79	14	18	32

It was obvious in 1932 that overwintered leafhoppers in beet fields were negligible, and correlated with their scarcity was the almost total absence of the "early" infections such as were commonly observed in 1930 and 1931. Many fields were examined closely, but only two plants showing symptoms were found before the dispersal of desert spring-brood leafhoppers began on June 13.

In 1933, early examinations of field beets and weeds adjacent to fields revealed only an occasional overwintered leafhopper. Because of the severe winter this area had experienced, the writers concluded that there would be little evidence of overwintered leafhoppers in the beet fields this season. Later developments, however, showed that there had been enough overwintered leafhoppers in some of the fields to produce a noticeable amount of curly top. At the time the spring brood adults were moving into the fields, many beet plants could be found with well-advanced symptoms of curly top. These cases of early infection were most frequently encountered along the outside edges of the fields and were definitely localized. Of still more interest was the fact that no curly top could be found at this time in the late-planted fields. With the natural mortality that occurs in the overwintered population in the spring, it seems evident that late-planted fields may partially, or sometimes totally, escape exposure to overwintered leafhoppers.

In the spring of 1934 a total of 590 overwintered adults taken from the cultivated area averaged 20 percent viruliferous. Of those viruliferous, 83 percent carried virulent virus. A total of 1,488 overwintered leafhoppers from desert weed areas averaged 3 percent viruliferous. Of those viruliferous in this group, only 18 percent carried virulent virus.

SPREAD OF CURLY TOP FROM EARLY INFECTION CENTERS

In 1933, some field studies were made of the spread of curly top from infections produced by overwintered leafhoppers. Tests showed that only 4 percent of the incoming spring-brood leafhoppers were viruliferous, and the movement into the beet fields did not begin until June 6. Under such conditions it was easy to follow the development of disease in the fields and to trace the spread of curly top from the early infection centers.

Two fields near Twin Falls gave a very satisfactory set-up for this study. These are recorded as the Tickner and Waite fields. The Tickner field was planted on March 31 and had been in beets the year before. The Waite field was planted on May 2 and had not grown beets the previous year. These fields were about a quarter of a mile apart and were separated by a highway and some farm buildings. They were first visited on June 20, and on this date numerous cases of severely diseased beets were found around the margins of the Tickner (early-planted) field. A careful search through the Waite field revealed no diseased plants. A light influx of spring brood leafhoppers had already taken place, and both fields were infested to about the same degree. Beets in the Tickner field were well advanced, having from 8 to 12 large leaves. In the Waite field the plants were quite small, and thinning was just being completed. The absence of disease in the late-planted field indicated that there had been no infection by overwintered leafhoppers and, furthermore, that plants infected by spring-brood leafhoppers had not had sufficient time to develop symptoms. It was obvious that the disease in the Tickner field on June 20 had resulted from infections by overwintered leafhoppers. If this disease had been produced by spring-brood leafhoppers, the younger and more susceptible plants in the Waite field should have shown even more disease than the older plants in the Tickner field.

In July, August, and September disease counts were made in these fields, and collections of leafhoppers were made for tests. These data are summarized in table 10. It can be seen from this table that in the Tickner field of early planting, more curly top developed, a higher percentage of the leafhopper population acquired the virus, and there was proportionately more virulent virus in the leafhopper population than was shown in similar studies of the later planted Waite field.

The infection centers when first discovered usually consisted of from one to eight diseased plants. As the season progressed, more of the surrounding plants became diseased. Even late in the season it was sometimes possible to trace back to the plants infected early in the season by the overwintered leafhoppers. In the Tickner field on June 20, one of the diseased plants was well separated from others, and the spread of disease from it was followed throughout the season. On August 15, in a square rod surrounding this plant, 16 percent of the plants were diseased as compared with an average of 3.5 percent of diseased plants in four nearby square-rod check plots. It should be stated that in years of heavier infestation, and with a higher percentage of the incoming leafhoppers viruliferous, such a contrast between early- and late-planted beet fields is not maintained. Instead, curly top spreads more rapidly and the leafhopper population becomes more highly viruliferous in the late-planted beets. Under such conditions, the disease may become so general, even in the early-planted fields, that centers of infection caused by overwintered leafhoppers may be masked quite early in the season.

TABLE 10.—*Rate at which curly top developed and leafhopper populations became viruliferous in early- and late-planted beets near Twin Falls, Idaho, 1933*

Beet field	Date of planting	Date of collection	Curly top incidence in field	Leafhoppers tested	Viruliferous leafhoppers		
					Attenuated	Virulent	Total
			Percent	*Number*	*Percent*	*Percent*	*Percent*
Tickner	Mar. 31	July 21	5	186	3	7	10
Waite	May 2	do	(1)	186	2	1	3
Tickner	Mar. 31	Aug. 12	17	95	6	14	20
Waite	May 2	Aug. 11	3	78	5	1	6
Tickner	Mar. 31	Sept. 30	32	204	4	46	50
Waite	May 2	do	18	100	7	26	33

1 Trace.

In another early-planted field west of Twin Falls, numerous cases of severely diseased plants were found around the margins on June 26. At one point there were 10 severely diseased plants within a radius of 5 feet. A square rod was marked off surrounding these plants, and disease counts were made. Seventeen additional diseased plants were found out of a total of 211 plants. Symptoms were just beginning to appear on these later-infected plants. On July 25, August 29, and September 27 there were 32, 81, and 92 percent of diseased plants, respectively, in this plot. In other parts of this field not showing infection centers an average of about 15 percent of diseased plants were obvious on September 27.

Leafhopper populations in most fields remained quite low during the 1933 season.. Even the late-planted fields produced good yields in most instances. In one late field, planted May 12, counts showed 50 leafhoppers per 100 feet of row on June 23. On August 4 there were only 4 percent of diseased plants in this field and only 20 percent on September 27. On June 26, tests showed that 9 percent of the leafhoppers in the field were viruliferous but less than 2 percent carried a virulent strain of virus. It seems that in this particular field all injury from curly top had to result from a gradual increase and spread of the virus brought in by spring-brood leafhoppers.

It is obvious that the damage to field beets is greatest when a high percentage of the leafhoppers carry virulent virus while the plants are small and very susceptible. If the leafhoppers from the desert areas do not bring in an abundant supply of virulent virus, they must gradually build it up from the seemingly limited amount that is brought in, or else they must acquire it after they reach the beet fields. The writers believe that, in some years at least, the initial infections produced in field beets by overwintered leafhoppers are important sources of inoculum for spring-brood leafhoppers moving into the beet fields from their natural breeding grounds. However, in years, such as 1934, when the fields become infested with high populations of spring-brood leafhoppers while the beets are small and extremely susceptible, the infections produced by overwintered leafhoppers are probably of little significance.

In addition to the infections produced in beet fields by overwintered leafhoppers, it may be that the nymphal progeny of the overwintered leafhoppers is also important in curly top development. No data were obtained regarding the amount of disease produced by nymphs from eggs laid by overwintered leafhoppers in the beet fields. However, observations in 1932 showed that there were noticeable numbers of nymphs in some fields before any spring brood adults could be found. It was evident that these were the progeny of the overwintered adults that had been in the fields earlier in the season.

SEASONAL EPIDEMIOLOGY OF CURLY TOP

Although each of the six seasons studied presented interesting developments in the epidemiology of curly top, only the seasons of 1933–34 and 1934–35 are discussed in detail in this bulletin. In both of these years, the harvested acreage of beets consisted almost entirely of resistant varieties, yet the average yield in 1934 was 4.79 tons per acre as contrasted with 15.3 tons per acre in 1935. With such extreme differences in yields, it is of particular interest to study the operation of the various epidemiological factors in these years.[8]

SEASON OF 1933–34

FALL AND WINTER CONDITIONS

The extreme drought during the summer of 1933 caused a reduction in the stands of desert annuals, and there was a corresponding reduction in the fall population of leafhoppers. Early maturity of Russian-thistle and the absence of fall-germinated mustards forced the leaf-

[8] During these studies, data obtained by the Twin Falls (Idaho) laboratory, Division of Truck Crop and Garden Insects, Bureau of Entomology and Plant Quarantine, as to movement of beet leafhoppers into the cultivated area have been made available to the writers.

hoppers to sagebrush quite early in the fall. This precluded any carry-over of virus in fall-infested breeding hosts, and, further, it meant that the surviving overwintered leafhoppers would be distributed throughout the sagebrush area when the mustards germinated and would not be concentrated in the usual weed areas. The following winter was decidedly mild, and this favored a high survival of the leafhopper population.

Germination of mustards occurred to some extent in the Glenns Ferry area late in November, but did not begin in the breeding areas nearer Twin Falls until the latter part of January. Both temperature and precipitation were above normal in February, and the mustards developed abundantly over the sagebrush lands, thus providing a host for the leafhoppers that had moved to the sagebrush in the fall.

Overwintered leafhoppers were active on the desert near Twin Falls early in February. Although the population was considered to be low, leafhoppers were rather uniformly distributed over wide areas. Higher populations were present in the breeding areas around Glenns Ferry.

SPRING CONDITIONS

Unseasonably high temperatures prevailed during March, and by the end of the month the season was approximately 3 weeks in advance of normal for that time of year. April and May temperatures continued warmer than usual with a plus accumulation of 16.16° F. from normal for these 2 months. High populations of overwintered leafhoppers existed in localized parts of the desert, and a low but uniformly distributed population was present on green tansymustard throughout large areas of sagebrush. Conditions were excellent for the development of both leafhoppers and their weed hosts. Spring-brood adults had appeared in some parts of the breeding area by April 15, and the number of spring-brood insects increased rapidly thereafter. In spite of the earliness of the season, beet planting had been delayed from 2 to 3 weeks because of a disagreement between the sugar companies and the beet growers concerning contracts.

DEVELOPMENT OF VIRUS IN LEAFHOPPERS

Tests of six summer and fall collections, totaling 773 leafhoppers, revealed that 2.5 percent were viruliferous. The following spring, 13 collections from desert areas, involving 1,488 overwintered leafhoppers, averaged only 3 percent viruliferous. These data suggested that in general the virus supply was not increasing to any great extent in the areas regarded as usually responsible for infestation of the cultivated lands. The collections were taken mainly from combined stands of the three mustards.

Extensive studies were not made of the overwintered population occurring on the wide expanse of green tansymustard in the sagebrush lands, but limited tests indicated that in such areas the supply of virus increased to a much greater extent than in areas in which tumblemustard and flixweed predominated. At one station where green tansymustard occurred in a pure stand, collections of overwintered leafhoppers taken during April averaged about 20 percent viruliferous. A collection of 118 spring-brood leafhoppers taken there on May 21 was 91 percent viruliferous.

The dispersal of leafhoppers began before any collections of the spring brood were made at desert stations. During the first 19 days after the movement began, April 27 to May 15, collections from 11 widely separated beet fields averaged 31 percent viruliferous. Collections made from seven desert stations between May 14 and June 11 ranged from 14 to 94 percent viruliferous, with an average of 51 percent. It appeared that in certain parts of the breeding area where green tansymustard was prevalent a large proportion of the leafhoppers remaining there until after June 1 acquired virus before moving into the cultivated areas. It was evident that conditions had been favorable for distribution of the virus in the mustards on which the spring brood developed even though not more than 3 percent of the overwintered leafhoppers were viruliferous when they became active in the spring. It is believed that the occurrence of the susceptible green tansymustard over wide expanses of sagebrush lands was mainly responsible for the large increase in the supply of virus.

DAMAGE FROM CURLY TOP

A light movement of desert spring brood was first detected on April 27. The magnitude of the flight increased quite rapidly and within a few days there were high populations of leafhoppers in beet fields over much of the district. Because of delayed planting, most of the beets were then germinating or in the seedling stage. A very few early-planted fields were being thinned. Approximately 21,000 acres had been planted in the Twin Falls-Jerome and the Burley-Paul-Oakley districts. A portion of this acreage consisted of the resistant variety U. S. 1, which had been released commercially this season. Much of the planted acreage was abandoned either before thinning or later in the season. Many of the remaining fields were neglected throughout the season. A total of only 2,619 acres was harvested and the average yield was 4.79 tons per acre. Most of the harvested acreage consisted of U. S. 1. A number of early-planted fields of U. S. 1 that were given good care yielded from 9 to 14 tons per acre, as compared with 2 to 4 tons from European varieties in the same fields.

Leafhoppers that moved into beet fields during the early part of the influx averaged 31 percent viruliferous. About one-third of these carried virulent virus. With later samples from desert areas averaging 51 percent viruliferous while the movement was still continuing, indications were that beet fields were exposed to a population even more highly viruliferous than was shown by the collections taken from the fields during the early part of the movement. Furthermore, curly top developed rapidly in the beet fields that were thinned prior to or during infestation. Collections from two fields on June 6 and June 8 averaged, respectively, 79 and 86 percent viruliferous.

From the standpoint of curly top, it is difficult to conceive of any year in which the sugar-beet crop could be exposed to more drastic conditions. The season demonstrated that under certain environmental conditions a high population of spring-brood leafhoppers, well supplied with virus, could build up from a comparatively low overwintered population having a limited virus supply. It also brought out the fact that even with the use of varieties as resistant as U. S. 1 or probably with varieties much more resistant, exceptional conditions can arise that make the curly top disease still an important factor in sugar-beet production in southern Idaho.

With the early spring season of 1934, bean planting began as early as May 25. In considerable acreage, germination was occurring while the influx of leafhoppers was continuing in June. Curly top caused rather serious losses in both field and garden varieties. Hungerford [9] reported a loss of 10 to 20 percent in Great Northern beans in the Twin Falls area in 1934. Contracting seedsmen estimated a reduction in yields of 60 percent in garden and canning varieties. The plowing out of approximately 17,000 acres of beets in this district at a time when most of the beans were in the seedling stage is believed to have increased the exposure of beans through a further movement of leafhoppers from the beets that were removed.

SEASON OF 1934-35

FALL AND WINTER CONDITIONS

In the fall of 1934, germination of the mustards began during the last of October, and rains in November caused further germination. In general, the mustards were sparsely distributed over the desert areas and were abundant only in low places where moisture had accumulated. High populations of leafhoppers went into the winter. The lowest temperature at Twin Falls in December was 13° F. In January there were two nights with minima of −5° F., but the low temperatures were not of sufficient duration to reduce leafhopper population significantly. Near the end of January leafhoppers were active in the desert during the warm part of the day, and sizeable collections were easily made. Additional host germination occurred in February, and precipitation was sufficient for the production of quite uniform and general stands of annuals, thus providing an abundance of plant hosts for the overwintered leafhoppers.

SPRING CONDITIONS

Conditions in March and April favored the development of the weed hosts. Tumblemustard, flixweed, and green tansymustard were present in the usual areas, and, as in the previous spring, the latter species was generally distributed in dense stands over vast acreages of sagebrush. High populations of overwintered leafhoppers were present in many places in the desert weed areas. The mean temperatures for March, April, and May were very close to the normal, or the average for the past 28 years. Precipitation in April and May totaled 3.9 inches, an excess of 1.9 inches over normal.

The excess of precipitation in April and May and the accompanying cool, cloudy days, greatly retarded the development of leafhoppers in the breeding areas. The beginning of oviposition was delayed to such an extent that by April 15 it seemed highly probable that there would be no appreciable movement of spring brood from local breeding areas before June 1.[10] However, the high population of overwintered leafhoppers and the abundance of weed hosts indicated that there would be large spring populations even though they would be late in maturing.

DEVELOPMENT OF VIRUS IN LEAFHOPPERS

In the summer and fall of 1934, in addition to collections from the usual desert stations, collections of leafhoppers were obtained from the

[9] HUNGERFORD, C. W. CURLY TOP OF VEGETABLES IN IDAHO. U. S. Bur. Plant Indus. Plant Disease Reptr. 18: 173-174. 1934. [Mimeographed.]

[10] Information regarding oviposition of leafhoppers was obtained from F. H. Harries, Bureau of Entomology and Plant Quarantine, Twin Falls, Idaho.

principal Russian-thistle areas of the Snake River Valley between Idaho Falls on the east and the Oregon State line on the west. A total of 3,916 leafhoppers was tested, and an average of 11.8 percent was viruliferous. Only 0.5 percent carried virulent virus.

Tests of fall populations in the 3 years prior to 1934 had never shown more than 5 percent viruliferous. Thus, it appeared that the population in the fall of 1934 went into the winter comparatively well supplied with virus. The winter was generally mild, and collections of leafhoppers were made from some of the desert stations regularly throughout the season. Tests of these showed that the viruliferous percentage of the overwintering leafhoppers in December and January was very close to the average found earlier in the fall population. As the spring season advanced, there was an increase in the percentage viruliferous at the stations where green tansymustard was one of the dominant hosts. At such stations, collections in May showed that nearly one-half of the overwintered population had become viruliferous. Likewise, there had been an increase in the proportion of leafhoppers carrying virulent virus.

The increase in the viruliferous percentage of the overwintered population and the appearance of diseased green tansymustard plants made it obvious that the virus was becoming well distributed in the weed hosts on which the spring brood would develop. It was, therefore, expected that the spring brood would become highly viruliferous. This expectation was borne out by the fact that tests of spring brood taken later from both the desert and beet fields averaged 55 percent viruliferous.

DAMAGE FROM CURLY TOP

All of the commercial acreage of sugar beets in 1935 was planted to resistant varieties. Records of the Amalgamated Sugar Co. show that of a total of 10,542 acres harvested, there were 10,372 acres of U. S. 1 and 170 acres of A–600. Practically all beets were thinned and well established when the spring-brood leafhoppers began to move into the fields on June 4. The movement of leafhoppers continued until early in July, with the peak of the infestation coming June 15 to 25. Beet fields became infested over the entire tract to a degree believed to be equal to the heavy infestation of 1934. A study of time of planting and stage of growth of beets at the time of infestation with leafhoppers in 1935 showed that in this year most of the beets had grown about 40 days longer before becoming infested with leafhoppers than was the case in 1934. With the knowledge that in 1934 many well-cared-for fields of the U. S. 1 variety had yielded from 9 to 14 tons in spite of the extremely early and heavy infestation of leafhoppers, the later infestation of 1935 was not so alarming to the growers as that of 1934. Consequently, no acreage was abandoned.

The summer of 1935 was quite favorable for the growth of beets. In general, the resistant varieties stood up well in spite of the very high populations of leafhoppers. In September, some fields showed average counts of more than 125 leafhoppers per beet. European varieties in experimental plots at Twin Falls yielded 7.8 tons per acre as compared with an average of 21 tons per acre from four resistant varieties. Figures released by the Amalgamated Sugar Co. show that in their territory in south-central Idaho an average yield of 13.7 tons per acre was obtained from a total of 10,542 acres harvested. In the

Twin Falls-Jerome district, an average of 15.3 tons per acre was obtained from a total of 2,953 acres. In this district there were many fields that averaged more than 20 tons per acre.

In the Twin Falls district, serious curly top damage occurred in beans in 1935. Representatives of the seed bean industry estimated that yields of the garden varieties grown for seed were reduced from 40 to 60 percent. Some fields of highly susceptible varieties were total failures. The dry bean varieties, Great Northern and Pinto, were both damaged appreciably.

With the bulk of the leafhoppers moving in between June 15 to 25, practically all of the beans were exposed in the seedling stage. A few observations showed that some of the later-planted fields were damaged less than others. One large field of Great Northern, west of Filer, was planted June 27. There was never more than a trace of curly top in this field, even though extremely high populations of leafhoppers moved into the beet fields in that locality. A number of field observations suggested that a delay in planting of as few as from 5 to 10 days avoided serious damage to beans. The observations in bean fields this season gave additional support to the belief that at least in some years much can be done to avoid curly top damage in bean fields by planting according to the date or period of influx of leafhoppers.

RÉSUMÉ OF EPIDEMIOLOGY STUDIES

For the purpose of summarizing the epidemiological studies, data on the seasonal virus supply in leafhopper populations and some brief notes on other factors for six seasons are presented in table 11. The average yield of beets for each season and a general classification of the damage occurring on beans are also included in this table. Beet yields were good in 3 years and poor in the other 3 years. Likewise, in 3 of the years there was light damage to beans and in 3 of the years severe damage. However, the years of light and of severe damage on beans did not correspond, respectively, to the years of high and of low yields of beets.

The data in table 11 show that the most apparent correlation is between the dates of dispersal of spring-brood leafhoppers and the average yields of beets. This actually means a correlation between the stage of development of beets at time of infestation and average yields at harvest. Furthermore, the same correlation exists between the type of spring season and average yields. This is true because the type of spring governs the time of maturity of the spring brood, which in turn determines the date of dispersal and infestation of beet fields.

Although yield records are available for this district as far back as 1916, no accurate information regarding the time of leafhopper dispersal is available for the years prior to the establishment of the Twin Falls field station of the Bureau of Entomology and Plant Quarantine in 1925. Carter (*10*) reported on the time of movement of leafhoppers in the years 1925–28, and Annand et al. (*1*) recorded this information for 1929 and 1930.

TABLE 11.—*Seasonal factors in curly top epidemiology in southern Idaho and average yields of beets in the Twin Falls-Jerome district, 1929–35*

Epidemiological factors	1929–30	1930–31	1931–32	1932–33	1933–34	1934–35
Fall leafhopper population	High	High	Low	Very low	Low	High.
Type of fall season	Warm and dry	Early, cold	Very cold	Normal, dry	Warm, dry	Warm.
Fall host germination	Very sparse	Early, abundant	Late, sparse	Late	Very sparse	Late, good.
Type of spring season	Very early	Normal, dry	Late, wet	do	Very early	Normal to late.
Date dispersal began, spring brood	May 24	May 24	June 13	June 6	April 27	June 4.
Spring population in beet fields	High	Moderately high	Moderately low	Low	Extremely high	Extremely high.
Viruliferous, fall population ... percent			5	3	3	11.8.
Viruliferous, overwintered population ... do	46	43	8	[1] 0	3	[2] 12.
Viruliferous, spring population [3] ... do	67	11	12	4	40	55.
Average yield of beets per acre ... tons	8.53	7.44	16.43	14.24	4.79	[4] 15.3.
Curly top damage to beans	Severe	Light	Light	Light	Moderately severe	Severe.

[1] Only 46 overwintered leafhoppers tested.
[2] Includes collections taken between Jan. 30 and Apr. 2. Later collections showed that the overwintered population became more highly viruliferous during April and May.
[3] Includes spring-brood leafhoppers taken from desert areas and from beet fields soon after influx from desert areas began.
[4] Entire commercial acreage planted to resistant varieties.

From 1925 to 1935, inclusive, there were 6 years in which the average yields were high and 5 years of low yields. In each year of high yields the movement of leafhoppers into the fields began on or after June 4, while in years of low yields the movement began on or before May 24. In general, yields have been lower in proportion to earliness of leafhopper infestation and higher in years of later infestations. In 9 years when the commercial plantings of beets in this section consisted entirely of susceptible varieties, there were 5 years of high yields and 4 years of low yields. The earliest infestation during the 5 years of high yields was in 1933 when the influx of leafhoppers began on June 6. This was only 13 days later than the date infestation began in both 1930 and 1931, yet the average yield in 1933 was 14.24 tons per acre as compared with averages of 8.53 tons in 1930 and 7.44 tons in 1931. While seedling beets are in the critical cotyledon stage, a delay of only 2 weeks in time of exposure to leafhoppers will not decrease the damage from curly top sufficiently to insure satisfactory yields. However, after the plants have developed true leaves and are ready for thinning, such a delay enables them to reach the post-thinning stage and to acquire more resistance and tolerance to curly top. Furthermore, early dispersals occur in years when the spring seasons are early, and in such seasons the spring brood matures more uniformly and high populations reach the fields quickly. In late spring seasons the maturation of the leafhoppers is uneven; host plants dry more irregularly; and the movement into cultivated areas may be of a slow, dribbling nature, or may consist of a series of light flights. Under the latter conditions more time is required to build up high populations in beet fields, and this gives the beets additional time to develop before becoming heavily infested.

It is clear that the various factors in curly top epidemiology are closely interrelated and that actually all of them are directly dependent on climatic conditions. However, in order to have a more tangible point for discussion, it is concluded that the stage of development of beets at the time of exposure to leafhoppers is the most important factor in epidemiology of curly top in this territory. Theoretically, it might seem that the development of beets should correspond with the rate of development of spring-brood leafhoppers, regardless of whether the spring season is early or late. However, these studies show that such is not the case. In spring seasons that open early the weather may be sufficiently warm during February and March to speed up greatly the development of overwintered female insects so that oviposition begins decidedly early. Even though the spring continues warm and open, the bulk of the beet acreage is not planted until after April 1. Frequently weather conditions, particularly rains, further delay planting so that much of the acreage is not seeded until after April 15. Thus, warm weather in February and March may favor the development of leafhoppers without having any appreciable effect on the beets. In other words, unless exceptional conditions arise, planting occurs over nearly the same calendar period each year, while the period of oviposition of overwintered leafhoppers and subsequent development of the spring brood may vary widely in respective years.

A late spring season retards the development of spring-brood leafhoppers and delays the movement into cultivated areas. Beet planting and seedling growth may proceed under weather conditions that are decidedly unfavorable for ovipositing, hatching of eggs, or nymphal development of leafhoppers. In a late spring, climatic conditions seldom cause the average date of planting to be more than 2 weeks later than in an early spring, while in these two types of season there may be a difference of 6 weeks in time of appearance of the first spring-brood nymphs.

The percentage of viruliferous leafhoppers in the population that moves into beet fields is believed to be of considerable importance, but because of numerous other factors affecting beet yields, it is difficult to measure the importance of the virus supply. In 1930 leafhoppers began to reach the fields on May 24, and fields became infested with high populations averaging 67 percent viruliferous. The following year the infestation began on the same date. High populations reached the fields, but the degree of infestation was somewhat lower than in 1930. Only 11 percent of the incoming leafhoppers were viruliferous, yet the yield was slightly lower than in 1930, when 67 percent of the spring population carried virus. In 1930 planting in general was unusually early. After the fields became so heavily infested with leafhoppers late in May, about half of the acreage was taken out or abandoned. Consequently the average yield of 8.53 tons per acre was obtained from fields that were quite well advanced when they became infested. In 1931 the planting season was later, and the summer was decidedly unfavorable for beets under curly top exposure. These factors were no doubt responsible for the fact that the average yield was 1.1 tons per acre higher in 1930, even though greater numbers of leafhoppers moved into the fields and a much higher percentage of them was viruliferous than in 1931.

In 1932 an average of 12 percent of the spring population was viruliferous. A moderately light infestation that did not begin until June 13 and a summer of excellent growing conditions were no doubt largely responsible for the exceptionally high average yield of 16.43 tons per acre. In 1933 there was a light infestation of leafhoppers that began on June 6. Only 4 percent were viruliferous. Yields averaged 14.24 tons per acre. It is believed that had high percentages of the leafhoppers carried virus when they first reached the fields in 1932 and 1933 there would have been more damage from curly top, but probably not enough to have caused an unsatisfactory average yield unless the infestation had occurred at an earlier date.

In 1934 the extremely early and heavy movement of leafhoppers that began on April 27 was sufficient to drastically reduce yields even if the viruliferous percentage of the incoming population had been very low. The average yield of 4.79 tons per acre was the lowest on record since beet production began in this territory in 1916. Since this low yield was obtained from resistant varieties, it is clear that all factors were decidedly favorable for a serious epidemic. The fact that 40 percent of the incoming leafhoppers were viruliferous was no doubt one of the factors which made the curly top epidemic so severe.

Excellent yields were obtained in 1935 in spite of the fact that 55 percent of the leafhoppers that moved into the fields were viruliferous. The beets were well advanced when they became infested. Thus it appears that with the use of resistant varieties the supply of virus in the leafhoppers reaching the fields is not of great importance except in years when beets are infested during the seedling stage.

The supply of virus in the leafhoppers that infest bean fields is believed to largely determine the extent of damage to beans. In 1930, 1934, and 1935, when the spring populations were highly viruliferous, curly top caused serious damage to beans. Negligible damage resulted in bean fields in 1931, 1932, and 1933, when low percentages of the spring populations were viruliferous. Time and degree of infestation are important factors in the epidemiology of curly top in beans. Beans are not favorable as food plants for beet leafhoppers (*1*, *8*), and since bean fields are exposed chiefly during the flight of leafhoppers into the cultivated lands and not to a continuously high summer population it seems evident that the supply of virus carried by the spring brood at dispersal time is of primary importance.

SUMMARY AND CONCLUSIONS

These investigations included studies on the most important desert host plants of the beet leafhopper in Idaho, with special attention to their reaction to curly top and their role in supplying leafhoppers with curly top virus. The three mustard species, tumblemustard, flixweed, and green tansymustard, are usually considered as spring annuals, although there may be abundant germination in the fall and winter months if there is sufficient moisture and if temperatures are favorable. Russian-thistle is the principal summer and fall breeding host for the desert beet leafhoppers.

Tumblemustard is apparently of little importance as a source of virus. It is extremely difficult to infect, and evidence suggests that even though some individual plants become infected, the virus does not multiply readily in them or else it is inactivated to a great extent. A low percentage of the viruliferous leafhoppers that fed on infected plants produced infection when transferred to beet seedlings.

Flixweed is susceptible to curly top but often requires heavy inoculation under high temperatures before developing pronounced symptoms. Plants are sometimes infected, and the virus can be obtained from them even though no symptoms are evident. As a rule, the virus is attenuated on passage through this species. It is believed that flixweed is responsible for the fact that the virus carried by desert leafhoppers is predominantly of the attenuated type.

Green tansymustard is extremely susceptible to curly top, and under greenhouse inoculations it seems to be as susceptible to attenuated strains of virus as to virulent strains. This species is very important in the development of the supply of virus in the desert-breeding areas of the beet leafhopper.

Inoculation tests on Russian-thistle showed that this species is susceptible to curly top. Virus was recovered from inoculated plants even though no conspicuous symptoms were discernible. The virus was sometimes attenuated by passage through Russian-thistle plants.

Fall leafhopper populations on Russian-thistle in desert areas were consistently low in percentage viruliferous, and the virus carried by such leafhoppers was largely attenuated.

The viruliferous percentage of spring-brood leafhoppers varied appreciably from year to year, with a low of 4 percent in one year and a high of 67 percent in another. Frequently this population carried attenuated virus almost exclusively, while in other years a fairly high proportion of the leafhoppers acquired virulent virus.

Even though spring-brood leafhoppers that moved into beet fields often tested very low in percentage viruliferous, repeated tests of collections taken from the fields during the summer showed that more of the leafhoppers acquired virus as the disease developed in the beets, so that by harvesttime practically 100 percent of the beet-field population carried virulent virus.

Experimental studies showed conclusively that curly top virus can survive the winter in living beet leafhoppers without any apparent change in virulence. Other studies proved that both flixweed and green tansymustard plants, infected in the fall under experimental conditions, may retain the virus during the winter and that the virus can be recovered from such plants in the following spring. No data have been obtained with respect to the extent that such occurs under natural conditions.

Field observations gave evidence that in some years leafhoppers which overwinter in the cultivated areas are important in initiating outbreaks of curly top and that this source of infection may sometimes increase the damage from the disease. The fact that many of the locally overwintered leafhoppers carried virulent virus suggested that some of them had moved off of beet fields the preceding fall.

With respect to desert populations of leafhoppers and their influence on sugar-beet production in Idaho, a point of importance is the proportion of viruliferous leafhoppers in the populations that move into beet fields. The size of the overwintered population, the prevalence and distribution of weed hosts, and the rate of development and size of the spring brood all affect the development of the supply of virus in the weed hosts on which the spring brood develops. However, the type of spring season determines how these factors operate in the development of the virus supply. Generally, the spring brood becomes more highly viruliferous in years when the spring is warm and early. However, even in some years of early spring seasons, the virus supply may be restricted by the scarcity of susceptible weed hosts, low leafhopper populations, or by combinations of various factors.

The magnitude of leafhopper infestations in beet fields is, no doubt, of importance from the standpoint of damage from curly top, but the writers are inclined to believe that in every season, unless resistant varieties are used, sufficiently high populations to produce serious damage reach the beet fields during the dispersal, provided other factors are favorable for an epidemic.

Although many of the various epidemiological factors are directly related, the single factor of most importance in the epidemiology of curly top is believed to be the stage of development of beets at the time they become infested with leafhoppers. Records show that in the past 11 years, there have been 6 years of high yields and 5 years of low yields of sugar beets in the Twin Falls (Idaho) district. In the years of good yields the movement of leafhoppers into the fields began on or after June 4. In years of poor yields the movement began on or before May 24. A delay of relatively few days in time of infestation is decidedly advantageous to beets if the delay comes after the plants have developed beyond the cotyledon stage. The rapid growth of beets after they develop true leaves, and particularly after thinning, increases their resistance or tolerance to curly top. In southern Idaho, beets in general reach this stage during the latter half of May, so that a delay in infestation until after June 1 enables the plants to escape exposure during the critical seedling stage.

The size of beets, or stage of development at time of infestation with leafhoppers, will continue to be an important factor in the curly top problem in southern Idaho, even with the general use of resistant beet varieties. Early plantings usually will result in more or less negligible injury from curly top, while late plantings may be damaged appreciably. Early planting is desirable, and seeding should not be extended over too long a period, as this will automatically place a certain proportion of the acreage in the critical stage of development when leafhoppers move into the fields.

LITERATURE CITED

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

(2) BALL, E. D.
1906. THE BEET LEAF-HOPPER (EUTETTIX TENELLA). Utah Agr. Expt. Sta. Ann. Rept. (1904–05) 16: XVI.

(3) BENNETT, C. W.
1935. STUDIES ON PROPERTIES OF THE CURLY TOP VIRUS. Jour. Agr. Research 50: 211–241, illus.

(4) ——— and ESAU, KATHERINE.
1936. FURTHER STUDIES ON THE RELATION OF THE CURLY TOP VIRUS TO PLANT TISSUES. Jour. Agr. Research 53: 595–620, illus.

(5) BONCQUET, P. A., and HARTUNG, WILLIAM J.
1915. THE COMPARATIVE EFFECT UPON SUGAR BEETS OF EUTETTIX TENELLA BAKER FROM WILD PLANTS AND FROM CURLY TOP BEETS. (Phytopath. Note) Phytopathology 5: 348–349, illus.

(6) ——— and STAHL, C. F.
1917. WILD VEGETATION AS A SOURCE OF CURLY-TOP INFECTION OF SUGAR BEETS. Jour. Econ. Ent. 10: 392–397, illus.

(7) CARSNER, EUBANKS.
1925. ATTENUATION OF THE VIRUS OF SUGAR BEET CURLY-TOP. Phytopathology 15: [745]–757, illus.

(8) ———
1926. SUSCEPTIBILITY OF THE BEAN TO THE VIRUS OF SUGAR-BEET CURLY-TOP. Jour. Agr. Research 33: 345–348, illus.

(9) ——— and STAHL, C. F.
1924. STUDIES ON CURLY-TOP DISEASE OF THE SUGAR BEET. Jour. Agr. Research 28: 297–320, illus.

(10) CARTER, WALTER.
1930. ECOLOGICAL STUDIES OF THE BEET LEAF HOPPER. U. S. Dept. Agr. Tech. Bull. 206, 115 pp., illus.

(11) GIDDINGS, NAHUM J.
1937. A GREENHOUSE METHOD FOR TESTING CURLY TOP RESISTANCE IN SUGAR BEETS. Phytopathology 27: 773–779, illus.

(12) HAEGELE, ROLAND W.
1927. THE BEET LEAF-HOPPER (EUTETTIX TENELLUS BAKER); A SURVEY IN IDAHO. Idaho Agr. Expt. Sta. Bull. 156, 28 pp., illus.

(13) ———
1932. FIELD STUDIES OF THE BEET LEAFHOPPER, EUTETTIX TENELLUS BAKER. Idaho Agr. Expt. Sta. Bull. 182, 51 pp., illus.

(14) LACKEY, C. F.
1932. RESTORATION OF VIRULENCE OF ATTENUATED CURLY TOP VIRUS BY PASSAGE THROUGH STELLARIA MEDIA. Jour. Agr. Research 44: 755–765, illus.

(15) PIEMEISEL, R. L., and CHAMBERLIN, J. C.
1936. LAND-IMPROVEMENT MEASURES IN RELATION TO A POSSIBLE CONTROL OF THE BEET LEAFHOPPER AND CURLY TOP. U. S. Dept. Agr. Cir. 416, 24 pp., illus.

(16) SEVERIN, HENRY H. P.
1927. CROPS NATURALLY INFECTED WITH SUGAR BEET CURLY-TOP. Science 66: 137–138.

(17) ———
1929. ADDITIONAL HOST PLANTS OF CURLY TOP. Hilgardia 3: [595]–636, illus.

(18) ———
1933. FIELD OBSERVATIONS ON THE BEET LEAFHOPPER, EUTETTIX TENELLUS, IN CALIFORNIA. Hilgardia 7: [281]–360, illus.

(19) ———
1934. WEED HOST RANGE AND OVERWINTERING OF CURLY-TOP VIRUS. Hilgardia 8: 263–280, illus.

(20) ——— and FREITAG, JULIUS H.
1934. ORNAMENTAL FLOWERING PLANTS NATURALLY INFECTED WITH CURLY-TOP AND ASTER-YELLOWS VIRUSES. Hilgardia 8: 233–260, illus.

(21) ——— and HENDERSON, CHARLES F.
1928. SOME HOST PLANTS OF CURLY TOP. Hilgardia 3: [339]–392, illus.

(22) SMITH, RALPH E., and BONCQUET, P. A.
1915. CONNECTION OF A BACTERIAL ORGANISM WITH CURLY LEAF OF THE SUGAR BEET. Phytopathology 5: [335]–342, illus.

(23) STAHL, C. F., and CARSNER, EUBANKS.
1918. OBTAINING BEET LEAFHOPPERS NONVIRULENT AS TO CURLY-TOP. [PRELIMINARY PAPER.] Jour. Agr. Research 14: 393–394.

ORGANIZATION OF THE UNITED STATES DEPARTMENT OF AGRICULTURE WHEN THIS PUBLICATION WAS LAST PRINTED

Secretary of Agriculture	HENRY A. WALLACE.
Under Secretary	M. L. WILSON.
Assistant Secretary	HARRY L. BROWN.
Coordinator of Land Use Planning and Director of Information.	M. S. EISENHOWER.
Director of Extension Work	C. W. WARBURTON.
Director of Finance	W. A. JUMP.
Director of Personnel	ROY F. HENDRICKSON.
Director of Research	JAMES T. JARDINE.
Solicitor	MASTIN G. WHITE.
Agricultural Adjustment Administration	H. R. TOLLEY, *Administrator.*
Bureau of Agricultural Economics	A. G. BLACK, *Chief.*
Bureau of Agricultural Engineering	S. H. MCCRORY, *Chief.*
Bureau of Animal Industry	JOHN R. MOHLER, *Chief.*
Bureau of Biological Survey	IRA N. GABRIELSON, *Chief.*
Bureau of Chemistry and Soils	HENRY G. KNIGHT, *Chief.*
Commodity Exchange Administration	J. W. T. DUVEL, *Chief.*
Bureau of Dairy Industry	O. E. REED, *Chief.*
Bureau of Entomology and Plant Quarantine	LEE A. STRONG, *Chief.*
Office of Experiment Stations	JAMES T. JARDINE, *Chief.*
Farm Security Administration	W. W. ALEXANDER, *Administrator.*
Food and Drug Administration	WALTER G. CAMPBELL, *Chief.*
Forest Service	FERDINAND A. SILCOX, *Chief.*
Bureau of Home Economics	LOUISE STANLEY, *Chief.*
Library	CLARIBEL R. BARNETT, *Librarian.*
Bureau of Plant Industry	E. C. AUCHTER, *Chief.*
Bureau of Public Roads	THOMAS H. MACDONALD, *Chief.*
Soil Conservation Service	H. H. BENNETT, *Chief.*
Weather Bureau	WILLIS R. GREGG, *Chief.*

This bulletin is a contribution from

Bureau of Plant Industry	E. C. AUCHTER, *Chief.*
Division of Sugar Plant Investigations	E. W. BRANDES, *Principal Pathologist, in Charge.*

U. S. GOVERNMENT PRINTING OFFICE: 1938

END