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HENRY H. P. SEVERIN

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TRANSMISSION OF TOMATO YELLOWS, OR CURLY TOP OF THE SUGAR BEET, BY EUTETTIX TENELLUS (BAKER)

HENRY H. P. SEVERIN¹

(Contribution from the Division of Entomology and Parasitology, College of Agriculture, University of California, cooperating with the United States Department of Agriculture, Bureau of Plant Industry).

INTRODUCTION

According to the literature, the cause of tomato yellows (western yellow blight) has remained a mystery since 1906. It was not until 1927 that the beet leafhopper, *Eutettix tenellus* (Baker), which transmits curly top to sugar beets, was associated as a carrier of the same disease to tomatoes.

Carsner and Stahl (1924)² reported tomato as susceptible to curly top, but from a study of the symptoms in the greenhouse, they state that "this disease has not been found in commercial plantings."

McKay and Dykstra (1927) came to the conclusion, on circumstantial evidence, that tomato yellows is caused by the virus of sugar-beet curly top.

Shapovalov (1927a) proved conclusively that curly-top virus, when introduced into the tomato plant by means of infective beet leafhoppers, produced typical symptoms of yellows with tomatoes grown out-of-doors.

During 1927, experiments conducted on the University Farm at Davis, in cooperation with J. T. Rosa and M. Shapovalov, demonstrated

¹ Assistant Entomologist in Experiment Station.

² Complete data on papers cited will be found in "Literature Cited," pages 270-271, arranged by author and date.

beyond doubt that when infective beet leafhoppers, *Eutettix tenellus* (Baker) were transferred from curly-top beets to healthy tomato plants, typical symptoms of tomato yellows developed.

All of the foregoing conclusions were based on a comparison of the symptoms of tomatoes inoculated with curly top by the beet leafhopper in the greenhouse or out-of-doors, with symptoms of plants naturally infected with tomato yellows. The transfer of curly top from tomatoes experimentally inoculated by infective beet leafhoppers in the field and showing typical symptoms, and from naturally infected tomatoes, back to beets has not been demonstrated. The chief object of the experiments reported in this paper is the demonstration of this transfer.

Other aspects of this subject discussed in the paper are the injury to tomatoes by this disease in natural and migratory breeding areas of the beet leafhopper, the varieties naturally and experimentally infected with curly top, the symptoms in the greenhouse and field, the longevity of the insects on tomato plants, the infection of a tomato plant with two virus diseases, and the relation of the spring migrations of the pest to the time of transplanting tomatoes.

NAMES OF THE DISEASE

The name of this disease first appeared in the literature as 'summer blight' by Smith (1906), Smith and Smith (1911), Rogers (1916), Rosa (1923); then 'yellow blight' by Huntley (1902), Henderson (1905), and Humphrey (1914); next 'western blight' by Thornberg (1912), Eastham (1920), Yaw (1924); and finally 'western yellow blight' by McKay (1921), McKay and Dykstra (1927), Heald (1922), Hungerford (1923), Shapovalov (1925, 1925*a* and 1927), Lesley (1926), Rosa (1927), and Severin (1927). The word 'tomato' has been omitted in some of the above names of this disease, or the list would be longer.

Shapovalov (1925*a*) suggested "that the name 'western yellow tomato blight' be changed to 'tomato yellows'," and this change was approved by the Pacific Division of the American Phytopathological Society (Shapovalov, 1927), but has not been acted upon by the committee on nomenclature. For the present purposes, and to avoid confusion in the Experiment Station literature, that name has been used for the disease in this paper, although it has been most commonly known as western yellow tomato blight.³

³ The name 'tomato curly top' has been proposed to the Committee on Nomenclature of the American Phytopathological Society, but no action has been taken as yet.

INJURY IN NATURAL AND MIGRATORY BREEDING AREAS OF BEET
LEAFHOPPER

It has been known in California for a long time that outbreaks of curly top of sugar beets and tomato yellows show some correlation. During 1905 a disastrous outbreak of beet curly top occurred, and tomato yellows, according to Smith (1906), was more general than ever before, completely ruining many fields in southern California and almost all in the San Joaquin Valley. During 1919 and 1925, curly top destroyed most of the late plantings of sugar beets and seriously reduced the tonnage of early plantings in the San Joaquin and Sacramento valleys and the interior regions of the Salinas Valley; in the same years tomato yellows destroyed most of the tomato crop in these valleys. The disease of these two crops is subject to regional variations, being more severe in or near the natural breeding areas of the beet leafhopper in the San Joaquin and Salinas valleys than in the coastal or other migratory districts.

In years between outbreaks of the pest, the severity of the disease varies according to the number of leafhoppers which invade the cultivated regions in different parts of a natural breeding area. The plains and foothills of most of Kern County, in the southern part of the San Joaquin Valley, are natural breeding grounds, except the Sierra Nevada foothills near the northern end of the county. With this enormous breeding area, even with a relatively low population of the insects, a profitable crop of tomatoes can rarely be grown in Kern County. The foothill breeding regions of the northern San Joaquin Valley are not as favorable as the middle and southern portions of the valley, and yellows is less prevalent, especially in tomato fields planted after the spring dispersal of leafhoppers ceases.

The direction of the wind at the time that the large flights occur is also a factor controlling the amount of tomato yellows in migratory regions of this insect. During 1927 large numbers of beet leafhoppers migrated from the San Joaquin Valley into the fog belt, and about five per cent of the tomatoes were blighted in the districts east of the region between San Francisco and Monterey Bay, as compared with less than one per cent in the Sacramento Valley, where fewer leafhoppers migrated. At the time that the maximum flights occurred in the middle San Joaquin Valley on May 4, the spring brood adults flew with an easterly wind over the Coast Range into the fog belt. Migratory flights into the Sacramento Valley are probably associated with south or southeasterly winds blowing from the San Joaquin Valley and calm spells in the vicinity of Suisun Bay.

VARIETIES OF TOMATOES NATURALLY AND EXPERIMENTALLY INFECTED WITH CURLY TOP

All canning and shipping varieties of tomatoes grown in California are naturally infected with tomato yellows. The following varieties have been experimentally infected with the disease: Alameda Trophy, Earliana, First Early, Globe, King of the Earlies, San Jose Canner, Santa Clara Canner, Special Early, Stone, and Wild Mexican. Lesley (1926) reports that varieties of the dwarf type, Red Pear, and certain selected lines of the Canner type, possess a moderate degree of resistance.

SYMPTOMATOLOGY

In the Field.—The principal symptoms of tomato yellows which develop in the field are an inward rolling of the leaflets along the mid-rib (fig. 2); the petiole and mid-rib frequently curve downward (fig. 1), giving the leaf a drooping but not wilting appearance; and the leaves become somewhat thickened and crisp. Later the leaves assume a yellow color with purple veins. The purpling of the veins cannot be considered a reliable symptom of blight, since healthy plants may show purple venation, especially during late summer and autumn. The stems become hollow through the drying of the pith. With the first appearance of these foliage symptoms, the plant stops growing and assumes an erect or rigid habit. Rosa (1927) states that the foliage symptoms are probably due to the abnormal accumulation of carbohydrates in the affected plants, which in turn results from the stoppage of vegetative growth. If small fruits have been formed, they ripen prematurely and the seeds are abortive. A decay of the roots occurs, usually beginning at the tips of the smaller roots. The plant finally dies, the leaves and stems turning brown (fig. 1).

All the field symptoms of yellows develop in the fog belt, but the incubation period of the disease may be longer than in the interior regions.

Tomato seedlings grown and transplanted on the University Farm at Davis were inoculated with curly top of beets at different stages of growth by means of infective leafhoppers, and a study of the symptoms was made during the season. Tomatoes inoculated with the disease two days before transplanting in the spring either developed mild symptoms of yellows or turned yellow and died. Non-infective beet leafhoppers, however, after feeding on the plants that were yellow but had no other symptoms, were transferred to sugar beets,

and symptoms of curly top developed (table 2). Tomatoes infected with curly top three days after transplanting in the field developed typical symptoms of yellows (fig. 1). All tomatoes infected before or shortly after transplanting died before reaching the flowering stage.



Fig. 1. Left, tomato naturally infected with tomato yellows shortly after transplanting, showing stunted plant with downward bending petioles and leaves and decayed root. Right, dried tomato plant which died as a result of tomato yellows.

Old plants inoculated with curly top, with few exceptions, seemed to withstand the disease. Tomatoes transplanted on May 14 were inoculated with curly top by about 100 infective nymphs to a plant on August 15, or about three months after transplanting; they continued normal growth, but some developed a striking sulphur-yellow discoloration of the foliage (fig. 3) on the terminal shoots, with no

other symptoms, by October 19. An examination of these plants on November 11 showed that nine of seventeen plants developed the rolled leaves, a deep purpling of the whole leaf surface as well as the veins, in addition to the conspicuous yellowing of the terminal shoots. The leaflets on some of the plants were dwarfed (fig. 4) near the tips. These late-inoculated plants produced fruit approaching normal in size.

In walking between the rows of tomatoes, diseased plants are easily recognized from a short distance by a lag in growth. The disease may come on gradually or rather suddenly in the field, and affected plants are not uniformly distributed. Later in the season tomato fields often appear spotted with dead brown or missing plants.

In the Greenhouse.—After the curly-top virus was introduced into tomato plants by means of infective beet leafhoppers, a study was undertaken of the symptoms which developed in the greenhouse. In the first experiment the tomatoes were grown in ten-inch pots in the greenhouse and each plant was enclosed in a large cage covered with lawn. The first reliable symptom of curly top to appear in the common California commercial varieties of tomatoes in the greenhouse is transparent venation. An inward curl of some of the leaflets occurs (fig. 5), especially in older plants. Purple venation often does not develop with infected tomatoes enclosed in cages. White excrescences (pl. 1, fig. 1) sometimes appear on the veins resembling somewhat the wart-like protuberances on curly top beets. A yellowing often develops between the veins, while the veins remain green (pl. 1, fig. 2). A marked stunting of young tomato plants occurs (fig. 6). Later the entire plant turns yellow and dies.

In previous years these same symptoms developed in cages and the tomato was considered to be susceptible to curly top. Plant pathologists who examined these infected tomatoes came to the conclusion that these symptoms were not those of tomato yellows as it develops in the field.

In view of the fact that tomatoes enclosed in cages under high temperatures in the greenhouse assume a spindling habit, another experiment was undertaken. Tomatoes grown out-doors were transplanted into soil in the floor of the greenhouse. The lower and upper vents and large windows in the front end of the greenhouse were kept open day and night to allow circulation of air. The tomatoes were inoculated by infective nymphs which were dropped on each plant with a pipette. The symptoms of yellows taken individually appeared in mild form, but the totality or complex of field symptoms such as occur in the hot interior regions of California failed to develop.

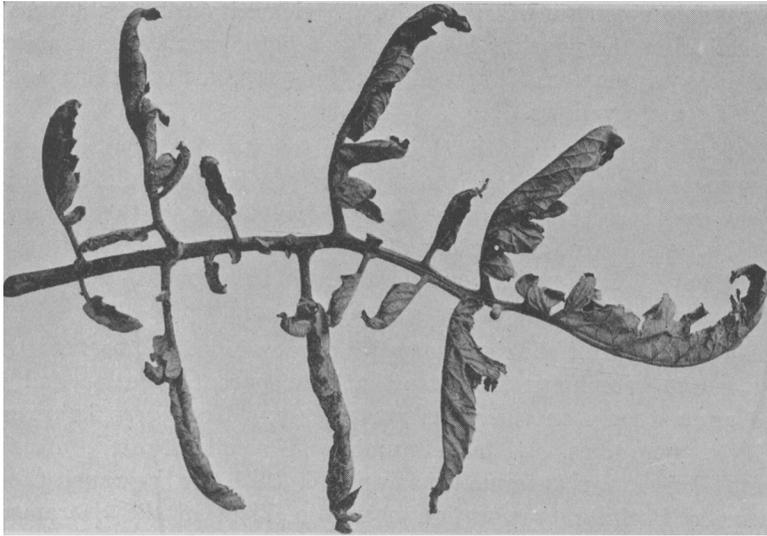


Fig. 2. Leaf from tomato plant naturally infected with tomato yellows, showing inward-rolled leaflets.



Fig. 3. Leaf from tomato plant infected with curly top on August 15, showing white leaflets which were sulfur yellow in October and November.

The reliable symptom of curly top, the cleared veinlets, were again discernible on the younger leaves. Plant pathologists who examined these diseased tomatoes all agreed that the symptoms resembled a mild form of tomato yellows.

McKay and Dykstra (1927) infected tomato plants with the beet leafhoppers and "typical symptoms of western yellow blight developed in the greenhouse. These were general yellowing of the foliage, a rolling of the leaves, a purpling of the veins, and a marked stunting of the plant." McKay and Dykstra failed to mention the development of transparent venation under greenhouse conditions.

A comparison of the symptoms which developed in the field with those in the greenhouse indicates that transparent venation and the white excrescences on the veins must be considered greenhouse and not field symptoms. A large number of small, stunted, diseased tomato plants were examined on June 16, 1925, on the ranch of the California Packing Corporation near Rio Vista in the Sacramento Valley, but transparent venation was absent. This reliable symptom of curly top has not been found in older diseased tomato plants in the San Joaquin and Salinas valleys during 1926. Tomato plants infected with curly top by the beet leafhopper in different stages of growth on the University Farm at Davis during 1927 did not show the cleared veinlets.

Incubation Period.—The incubation period varies from 2 weeks to 4 weeks. In 1927 an unusually cool spring prevailed, no very high temperatures occurring until June 15. From June 13 to June 15, the maximum temperatures were 96°, 99°, and 103° Fahrenheit. Tomatoes inoculated May 14–16 showed symptoms of yellows on June 10, an incubation period of 24 to 26 days. Plants inoculated May 30 developed symptoms of yellows on June 15, an incubation period of 16 days. These experiments indicate that although tomato yellows may develop before the first 'hot spell,' high temperatures and perhaps other factors materially shorten the incubation period.

LONGEVITY AND LIFE HISTORY OF BEET LEAFHOPPERS ON TOMATO PLANTS

Experiments were made to determine the longevity of the last living male and female beet leafhoppers of the spring, summer, and winter broods, when these were confined on tomato plants. These experiments were often repeated with different lots of adults. The results are shown in table 1.

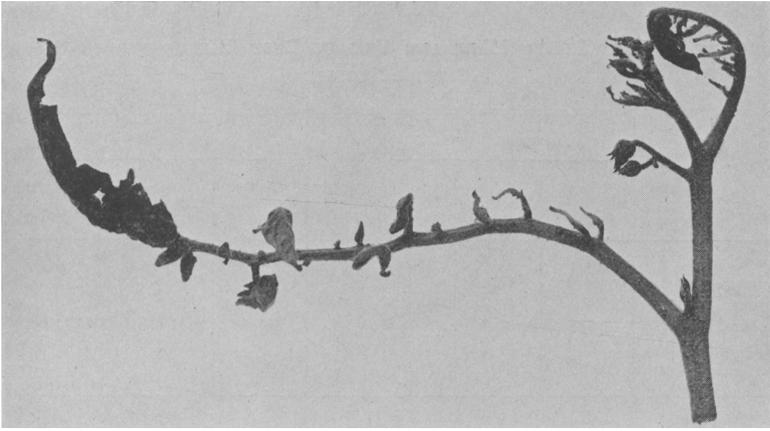


Fig. 4. Terminal shoot of tomato affected with curly top, showing dwarfed leaflets.



Fig. 5. Leaves showing inward curl of leaflets from a plant infected with curly top in the greenhouse.

TABLE 1
LONGEVITY OF LAST LIVING MALE AND FEMALE BEET LEAFHOPPER ON SAN JOSE
CANNER TOMATO

Brood	Longevity of males <i>days</i>	Temperatures			Longevity of females <i>days</i>	Temperatures			Height of tomato plants <i>inches</i>
		Mean maximum °F	Mean minimum °F	Mean °F		Mean maximum °F	Mean minimum °F	Mean °F	
Spring.....	3-4	111.7	60.2	85.9	4-9	111.5	60.0	86.6	6-8
Spring.....	7-8	91.0	66.2	77.8	16-19	92.8	66.0	79.4	14-24
Summer.....	6	107.8	66.7	87.2	13	109.6	64.8	87.2	6-8
Summer.....	14-23	102.8	61.2	82.0	28	101.5	61.5	81.5	18-24
Winter.....	7	82.0	62.2	72.1	22	81.2	63.4	72.3	6-8, 6-19
Winter.....	5-9	78.9	61.2	70.0	23	75.2	56.6	65.9	8-19, 19-25

It is evident from table 1 that the males live for a shorter period than the females when confined on a tomato diet. The adult life of the spring and summer broods on tomatoes at transplanting size (6 to 8 inches) is shorter than on older tomatoes (14 to 24 inches). The males of the winter brood die during the winter and many of the specimens tested for longevity may have been near the end of their natural life. The experiments made on the overwintering females show very little difference in the adult life on transplanted and older tomatoes.

The beet leafhopper failed to complete its life cycle on California canning and shipping tomatoes listed under experimentally infected varieties.

CURLY-TOP INOCULATION OF TOMATOES IN THE FIELD

Tomatoes grown on the University Farm at Davis were inoculated with the curly-top virus by means of infective beet leafhoppers. In a series of seven experiments, inoculations were made in tomatoes at different stages of growth during a period of three months. In order to carry on these experiments, four rows of tomatoes were transplanted on May 14 to 17, each row containing from 35 to 40 plants (fig. 7). The variety used was a selection of San Jose Canner. The soil was kept free from host plants of the beet leafhopper and weeds susceptible to curly top.

Experiment 1.—In the first experiment 40 healthy tomato plants were inoculated with curly top in the greenhouse, using 10 infective male beet leafhoppers for a period of two days on each plant. Males were used rather than females, to prevent oviposition. These tomatoes

were transplanted on the University Farm on May 17. The 40 infected plants either developed symptoms of tomato yellows or turned yellow and died (table 2).



Fig. 6. Comparison of growth of two tomatoes planted on the same date: left, inoculated with curly top by infective beet leafhoppers; right, check or control plant on which non-infective males fed.

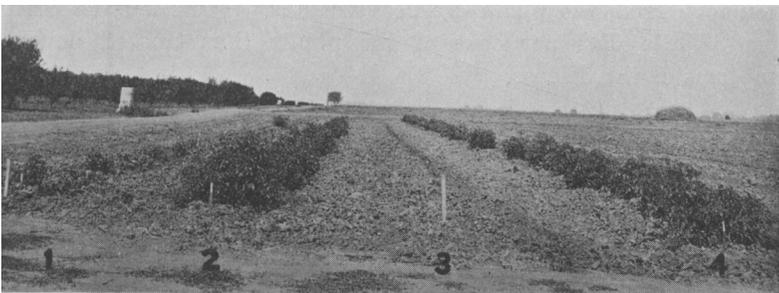


Fig. 7. Plot used in experiments 1 to 7. Row 1 was used in experiments 2 and 3, and shows the badly diseased plants in the foreground. One plant shown in the background remained healthy, all others died. Rows 2 and 4 were used as a check at the time that this photograph was taken, but later the tomato plants were infected in experiments 4 to 7. Row 3 in experiment 1, the tomato seedlings were infected with curly top before transplanting and all of the plants died.

Experiment 2.—In the second experiment, repeated eight times, a curly-top beet was planted near a healthy tomato plant, and both were covered with a cylindrical cage in which 25 infective males were liberated. The beet leafhoppers did not all congregate on the beets—a few were actually seen feeding on the tomato plants. The cages were removed 13 days later and a few males were still alive in each cage. The eight tomato plants developed typical symptoms of yellows, as indicated in table 2.

Experiment 3.—In the third experiment 20 healthy tomato plants were enclosed in 20 cages in each of which 10 infective males were set free. The cages were removed at the end of one week. Table 2 shows that all but one tomato plant developed symptoms of yellows. Terminal shoots were repeatedly removed from this plant during the season, but non-infective males which had fed on them failed to transmit curly top to sugar beets. It is evident that 10 infective beet leafhoppers confined in a cage for a week did not infect this tomato plant. The number of bugs required for 100-per-cent infection should be taken into consideration in the development of a tomato resistant to curly top.

Experiments 4 to 6.—In the next three experiments 10 or 20 infective nymphs or males were confined in small leaf-cages (fig. 8), but in fastening the cages to the leaves some of the hoppers escaped. Two of 140 tomato plants to be inoculated during the season were either naturally infected or were inoculated with the disease by bugs which escaped while attaching the leaf-cages. A high mortality of the insects occurs in leaf-cages during hot weather. These cages were often torn from the plants by heavy winds. Table 2 indicates that from 33.3 to 61.5 per cent of the plants thus treated developed symptoms of the disease.

TABLE 2
CURLY-TOP INOCULATION OF TOMATO PLANTS AT VARIOUS STAGES OF GROWTH
UNDER FIELD CONDITIONS

Experiment No.	Dates plants were inoculated	Type of cage	Number of beet leafhoppers on each plant	Date cages were removed	Number of plants inoculated	Number of diseased plants	Percentage of diseased plants
1	May 14-16.....	Cylindrical.....	10 males.....	May 17.....	40	40	100.0
2	May 17-30.....	Cylindrical.....	25 males.....	May 30.....	8	8	100.0
3	May 30-June 6..	Cylindrical.....	10 males.....	June 6.....	20	19	95.0
4	June 6-27.....	1 leaf-cage.....	10 nymphs....	June 27.....	26	16	61.5
5	June 27-July 25	1 leaf-cage.....	10 males.....	July 25.....	12	6	50.0
6	July 25-Aug. 15	2 leaf-cages....	20 males.....	Aug. 15.....	15	5	33.3
7	Aug. 15.....	No cage.....	100 nymphs....	17	9	52.9
					138	103	74.6

Experiment 7.—In the last experiment 100 infective nymphs were dropped on the inner leaves of 17 large tomato plants on August 15. The last examination of these plants on November 11 showed that nine plants had developed symptoms of yellows and eight were *apparently* healthy, as indicated in table 2.

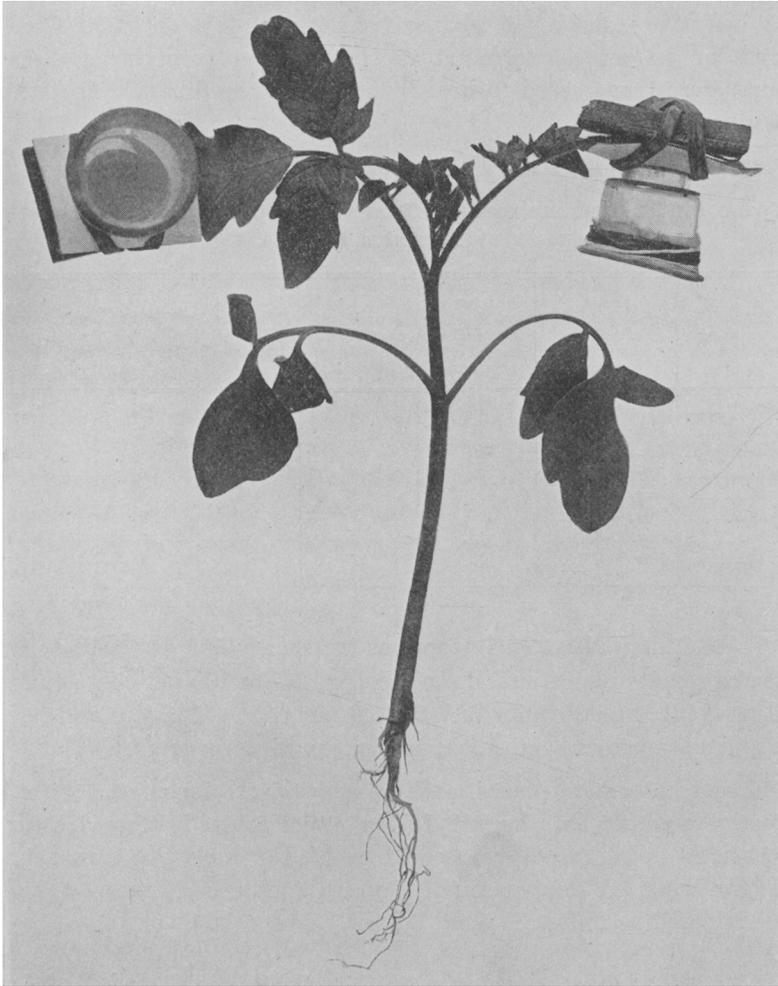


Fig. 8. Leaf-cages attached to tomato leaves.

Check or Control.—Two thousand tomato plants used as a check or control, about 500 feet north of the four rows of inoculated plants mentioned above, showed less than 1 per cent of yellows at the end of the season. These tomatoes were transplanted on May 14 to 16,

and included a selection of San Jose Canner. Sugar beets showing 100 per cent curly top were growing about 50 feet northwest from this tomato field used as a check.

Curly-top Transmission from Inoculated Tomatoes to Sugar Beets. Cross inoculations were made from the tomato plants showing symptoms of yellows in experiments 1 to 7, to healthy sugar beets. Non-infective males after feeding from 2 to 6 days on small diseased plants or on several terminal shoots removed from large diseased plants were transferred to healthy sugar-beet seedlings. The results are given in table 3.

TABLE 3
 CURLY TOP TRANSMITTED TO SUGAR BEETS FROM TOMATOES EXPERIMENTALLY
 INOCULATED BY INFECTIVE BEET LEAFHOPPERS

Date of inoculating tomatoes	Dates non-infective males fed on inoculated tomatoes	Number of non-infective males on each inoculated tomato	Number of inoculated tomatoes tested	Number of beets inoculated	Number of beets infected	Percentage of beets infected with curly top
May 14-16.....	June 30-July 1....	10	16	16	15	93.7
May 17-30.....	June 30-July 1....	25	8	8	8	100.0
May 30-June 6..	June 30-July 1....	10	10	10	10	100.0
June 6.....	Aug. 15-18.....	20	6	6	6	100.0
June 27.....	Aug. 15-18.....	20	6	6	6	100.0
July 25.....	Nov. 12-17.....	15	6	6	5	83.3
Aug. 15.....	Oct. 20-23.....	15	9	9	7	77.7
Aug. 15.....	Nov. 11-17.....	15	11	11	9	81.8

Table 3 shows that curly top was transmitted to sugar beets from infected tomato plants as follows: spring 93.7 to 100 per cent; summer 100 per cent; and autumn 77.7 to 83.3 per cent. The size and age of the spring, summer, and autumn plants are not comparable.

Seventeen tomato plants, each of which were inoculated with 100 infective nymphs on August 15, in experiment 7, were tested on October 20 to 23 and November 11 to 17, for curly-top transmission to sugar beets. A comparison of the results obtained in each test may be illustrated as follows:

Oct. 20-23.	Plant No.....	{	C	C	C	C	C	C	C	?	?	C							
		{	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33
		{	H	H	H			H				H	H					H	H
Nov. 11-17.	Plant No.....	{	H	?	H			H					H		?			H	H
		{	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33
		{				C	C		C	C	C	C	C		C		C		

C indicates that curly top was transmitted to sugar beets from the inoculated plants.
 H indicates that the plant was apparently healthy.

Plant No. 18 was apparently healthy in October; in November this plant showed mild symptoms of yellows, but curly top was not transmitted to sugar beets. Plant No. 26 was apparently healthy in October, but in November the terminal shoots were yellow, with no other symptoms. Curly top was communicated from this plant to beets. Plants 29 and 30 showed a yellowing of leaves on the tips of the stems in October and a mild form of yellows in November. Cross inoculation of curly top from plant No. 29 was made to beets, but negative results were obtained from plant No. 30.

CURLY-TOP TRANSMISSION FROM TOMATOES NATURALLY INFECTED WITH YELLOWS TO SUGAR BEETS

In 1925 and 1926 it was demonstrated that during the autumn non-infective beet leafhoppers do not always transmit curly top from tomatoes naturally infected with yellows to sugar beets. During 1927 three shipments of tomato plants naturally infected with yellows, grown on the grounds of the United States Cotton Field Station at Shafter in the southern San Joaquin Valley, were received from M. Shapovalov and F. S. Beecher. Non-infective males were fed on the diseased plants for a period of two days and were then transferred to healthy beet seedlings. Table 4 shows the number and percentage of beets which developed curly top.

TABLE 4

CURLY TOP TRANSMITTED FROM TOMATOES NATURALLY INFECTED WITH YELLOWS TO SUGAR BEETS

Number of tomatoes naturally infected with yellows	Dates non-infective males fed on diseased tomatoes	Number of non-infective males on each diseased tomato	Number of beets inoculated	Number of beets infected with curly top	Percentage of beets infected with curly top
12	May 28-30.....	15	12	12	100.0
15	June 28-30.....	15	15	14	93.3
49	Aug. 24-26.....	15	49	35	71.4

It is evident from table 4 that the beet leafhoppers transmitted curly top from 100 per cent of the tomato plants naturally infected with yellows to sugar beets during the spring. During the summer, curly-top transmission from diseased tomatoes to sugar beets varied from 71.4 to 93.3 per cent. The summer plants were larger and older than those used in the spring.

TOMATO PLANTS NATURALLY INFECTED WITH BOTH TOMATO YELLOWS
AND MOSAIC

During 1926, 100 acres of tomatoes growing on the Spreckels ranch near King City in the Salinas Valley were destroyed by yellows, mosaic, and possibly other diseases. Eighty acres of sugar beets affected with curly top had been plowed under on this ranch, causing a dissemination of the beet leafhoppers to other cultivated plants and weeds. The terminal shoots from many tomato plants showing only symptoms of mosaic were removed, and the cut ends were placed in tumblers filled with water while the tips projected into cages. Non-infective males after feeding on the shoots affected with mosaic transmitted curly top to sugar beets. This transmission to beets demonstrated that the mosaic tomatoes were also naturally infected with the virus of curly top, but the symptoms of the latter had not developed. An infection of mosaic and curly top in the same beet is common in the beet fields of California, but the leaves always show symptoms of both diseases.

An experiment was conducted in the greenhouse to determine whether symptoms of curly top and mosaic develop with tomatoes infected with the virus of the two diseases. Tomatoes were inoculated with mosaic on May 20 by crushing and rubbing the diseased leaves on healthy ones. Ten infective beet leafhoppers were fed on each plant inoculated with mosaic on May 20 to 22. The tomatoes inoculated with the two diseases were removed from the cages and transplanted into soil in the floor of the greenhouse. The cleared veinlets of curly top developed in all of the inoculated plants but were difficult to distinguish from normal venation in mosaic leaves. In some cases the leaflets nearest the terminal end of the leaf showed pronounced transparent venation while the basal leaflets or those nearest the petiole showed mosaic symptoms (pl. 2, fig. 1). In addition to the cleared veinlets of curly top, other symptoms developed on these plants as follows:

1. Mosaic, no yellows (pl. 2, fig. 2).
2. Mosaic on the leaves of the terminal shoots and a mild form of yellows on the leaves of the lower portion of the plant.
3. Mosaic on the younger leaves and a mild form of yellows affecting the entire plant.

Non-infective beet leafhoppers were fed July 2 to 4 on the tomatoes infected with the two diseases, with symptoms described above (1, 2, 3), and then were transferred to healthy sugar beets, which developed curly top. This experiment should be repeated under field conditions.

RELATION OF SPRING MIGRATIONS TO TIME OF TRANSPLANTING
TOMATOES

Flights.—According to E. A. Schwing, a small flight of the beet leafhoppers into the beet fields of Sacramento Valley occurred on April 24, 1927. The maximum flights occurred on May 4, in the Delta regions, and on May 12, in the Sutter Basin and Marysville districts. No further increase of the leafhoppers took place in the beet fields after May 12.

After a large flight occurs the adults are generally distributed on all green vegetation. The first stimulus after a flight is apparently a food stimulus, and the insects are often found on unsuitable food plants on which they cannot survive. Later, however, the hoppers congregate on their most favorable food and breeding plants.

Occurrence of Beet Leafhoppers on Tomatoes.—During the spring and summer of 1927, an effort was made to find the beet leafhopper on the 2,000 tomato plants used as a check or control at Davis. The plants were shaken and insects were captured on the soil beneath with a pipette. During the season not a single specimen of *Eutettix tenellus* was taken on tomatoes. The first examination was made on May 17, and not immediately after the large flight on May 4. In a nearby beet field the pest was generally abundant. The percentage of curly top which appeared in the beet field early in the season was as follows: May 17, 20 per cent; May 30, 27 per cent, at which time no yellows had appeared in the tomato field.

In years between outbreaks, the beet leafhoppers feed on tomatoes after their migratory flights but probably find the food unsuitable, and a dispersal to other host plants occurs. During the serious 1919 and 1925 outbreaks of the pest, however, the leafhoppers were taken on tomatoes during the spring and summer. During terrific hot spells, favorable weeds of this insect often wilt and become sun-scorched—a condition which stimulates a movement to unfavorable host plants such as tomatoes, other cultivated plants, and weeds.

During 1927 other species of leafhoppers such as *Agallia californicum* Bak. and a green leafhopper, *Empoasca* sp.?, were commonly captured on tomatoes. *E.* sp.? was able to complete its life cycle on tomatoes.

Planting Tomatoes after Flights Cease.—Tomato-planting experiments should be conducted after the migratory flights cease in the Sacramento Valley and fog belt. The time of transplanting tomatoes may be benefited by following the late-planting schedule of sugar

beets. When beets are planted after the migratory flights end, better tonnages are obtained in years between severe outbreaks of the beet leafhopper.

When the leafhoppers are at their maximum in numbers, however, planting after the flights cease may not be entirely successful in the Sacramento Valley, since the second brood, which acquires the winged stage in July, may invade the tomato fields. During 1925, however, beets planted in the interval between the two broods made a marketable crop in the Sacramento Valley. According to J. T. Rosa, early-planted tomatoes were destroyed by yellows in 1925 on the University Farm, while late plantings made a crop.

Yaw (1924) states that "it is a common practice where plants show the disease in June to pull them out and replace with new plants in the same hole. Such plants almost never show the disease." His observations and studies as to the prevalence of tomato diseases were made mostly in the San Francisco Bay region, together with frequent trips to the lower Sacramento and San Joaquin valleys and occasional trips to the upper San Joaquin and southern California during the seasons of 1922 and 1923.

The migratory flights into the fog belt rarely occur in June except when a partial second brood develops on the foothills during years with late spring rains. Experiments should also be conducted in the fog belt to determine the time of transplanting tomatoes in relation to the end of the migratory flights of the beet leafhopper. According to Yaw, yellows usually appears in June in those plants which were set in the field in May or earlier. These observations indicate a long incubation period of the disease but do not give a clue as to when tomatoes must be transplanted to escape the beet leafhopper and curly top or yellows that it transmits.

SHADING

Where beets are grown in the shade of trees, a low percentage of curly top usually develops when the beet leafhoppers are not abundant. The leafhopper is a sunshine-loving insect and usually will not enter the shade if its food and breeding plants are favorable. During terrific hot spells favorable weeds often wilt and become sun-scorched, causing a dissemination to other food plants. In the summer of 1925 a dispersal of the adults from badly diseased beets to other host plants occurred in the Sacramento Valley as reported in a previous paper (Severin, 1926). When the food supply is suddenly cut off from the bugs by plowing under diseased beets, the adults will spread to other

food plants. These are some of the factors which stimulate the insects to enter the shade.

Humphrey (1914) noticed "that where a slight degree of shade is afforded by orchard or other trees there are relatively fewer diseased plants than where tomato plants of the same variety are grown in similar soil, but in open situations exposed to the maximum of direct sunlight."

A similar and very striking illustration was observed on the Spreckels ranch near King City in the Salinas Valley during 1926. Tomatoes grown along a fence in the shade of eucalyptus trees were, with few exceptions, healthy, while every plant exposed to sunshine was diseased. Shaded plants which appeared healthy, however, were not tested for curly top.

CLIMATIC FACTORS

Humphrey (1914) discussed the following factors in relation to tomato blight: high soil and atmospheric temperatures, wind movement, rate of evaporation and light intensity.

Shapovalov (1925, 1925a) found that a very striking correlation exists between the rate of evaporation and the prevalence and severity of the disease. He observed that climatic factors which tend to increase the evaporating power of the air, such as sunshine, temperature, humidity, and wind movement, are conducive to the development of the yellows. However, the exact manner in which high rates of evaporation facilitate the progress of the disease at that time was not clear. It is evident now, in the light of recently established etiological relationship of *Eutettix tenellus* to tomato yellows, that weather conditions are secondary factors favoring the development of symptoms and possibly the severity of the disease.

SUMMARY

The data presented in this paper prove that the beet leafhopper, *Eutettix tenellus* (Baker), transmits tomato yellows or curly top to tomatoes. Tomatoes inoculated with the curly-top virus from beets by means of infective leafhoppers developed typical symptoms of yellows under field conditions. Non-infective hoppers after feeding on the infected tomatoes were transferred to healthy sugar beets and typical symptoms of curly top were produced. The disease was also transmitted from tomatoes naturally infected with yellows to sugar beets.

Tomatoes grown in the greenhouse were susceptible to curly top, but typical symptoms of yellows failed to develop when the plants were enclosed in cages. When cages were not used, symptoms of a mild form of yellows appeared in tomatoes inoculated with the disease. The reliable symptom of sugar-beet curly top, the clearing or transparency of the veinlets, appeared in tomatoes infected with the disease in the greenhouse, but this symptom does not occur in plants naturally infected or inoculated with blight in the field.

The incubation period of the disease in the field varied from 16 to 26 days during the spring.

Curly top was also transmitted from tomatoes showing symptoms only of mosaic in a field in which both diseases were present; this transmission to beets demonstrates that the tomatoes were also naturally infected with the causal agent of curly top.

The longevity of the beet leafhoppers on tomatoes varied according to the age of the plant. The adult life of the males was shorter than that of the females on tomatoes.

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PLATE 1

Tomato (*Lycopersicon esculentum*)

Fig. 1. White excrescences on the veins of leaflets from tomatoes infected with curly top in the greenhouse, resembling somewhat the wart-like protuberances on the leaves of diseased sugar beets.

Fig. 2. Leaflets from tomatoes infected with curly top in the greenhouse, showing different stages of yellowing between the veins, the region along the mid-rib and veins remaining green.



Fig. 1.



Fig. 2.

PLATE 2

Tomato (*Lycopersicon esculentum*)

Fig. 1. Leaf showing transparent venation on the terminal leaflets and mottling and puckering of mosaic on the lower leaflets from a plant infected with curly top and mosaic.

Fig. 2. Leaf showing mottling and puckering of mosaic from a plant also infected with curly top but not showing symptoms of tomato yellows.

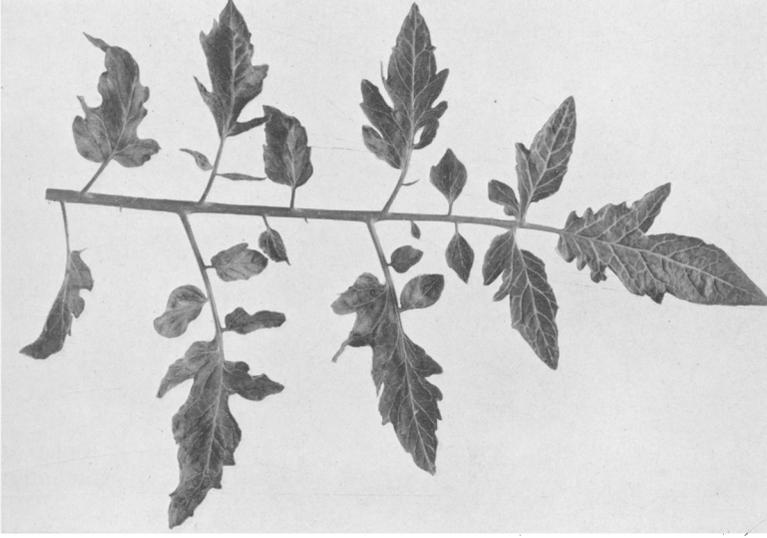


Fig. 1

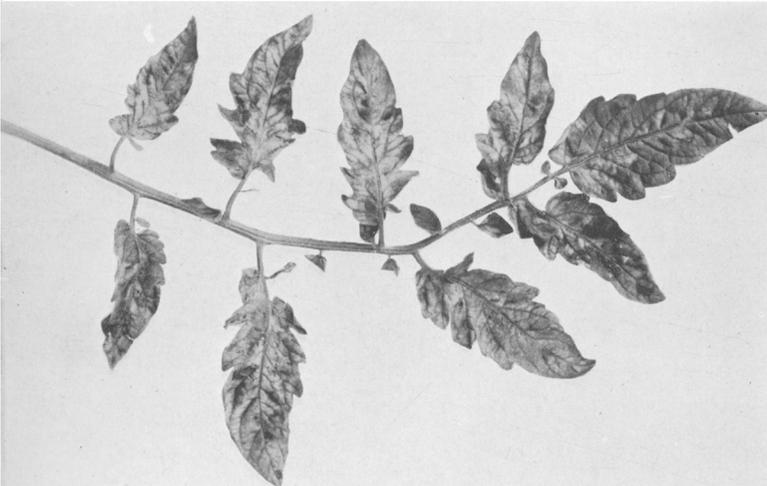


Fig. 2

The titles of the Technical Papers of the California Agricultural Experiment Station, Nos. 1 to 20, which HILGARDIA replaces, and copies of which may be had on application to the Publication Secretary, Agricultural Experiment Station, Berkeley, are as follows:

1. The Removal of Sodium Carbonate from Soils, by Walter P. Kelley and Edward E. Thomas. January, 1923.
3. The Formation of Sodium Carbonate in Soils, by Arthur B. Cummins and Walter P. Kelley. March, 1923.
4. Effect of Sodium Chlorid and Calcium Chlorid upon the Growth and Composition of Young Orange Trees, by H. S. Reed and A. R. O. Haas. April, 1923.
5. Citrus Blast and Black Pit, by H. S. Fawcett, W. T. Horne, and A. F. Camp. May, 1923.
6. A Study of Deciduous Fruit Tree Rootstocks with Special Reference to Their Identification, by Myer J. Heppner. June, 1923.
7. A Study of the Darkening of Apple Tissue, by E. L. Overholser and W. V. Cruess. June, 1923.
8. Effect of Salts on the Intake of Inorganic Elements and on the Buffer System of the Plant, by D. R. Hoagland and J. C. Martin. July, 1923.
9. Experiments on the Reclamation of Alkali Soils by Leaching with Water and Gypsum, by P. L. Hibbard. August, 1923.
10. The Seasonal Variation of the Soil Moisture in a Walnut Grove in Relation to Hygroscopic Coefficient, by L. D. Batchelor and H. S. Reed. September, 1923.
11. Studies on the Effects of Sodium, Potassium, and Calcium on Young Orange Trees, by H. S. Reed and A. R. O. Haas. October, 1923.
12. The Effect of the Plant on the Reaction of the Culture Solution, by D. R. Hoagland. November, 1923.
13. Some Mutual Effects on Soil and Plant Induced by Added Solutes, by John S. Burd and J. C. Martin. December, 1923.
14. The Respiration of Potato Tubers in Relation to the Occurrence of Black-heart, by J. P. Bennett and E. T. Bartholomew. January, 1924.
15. Replaceable Bases in Soils, by Walter P. Kelley and S. Melvin Brown. February, 1924.
16. The Moisture Equivalent as Influenced by the Amount of Soil Used in its Determination, by F. J. Velmeyer, O. W. Israelsen and J. P. Conrad. September, 1924.
17. Nutrient and Toxic Effects of Certain Ions on Citrus and Walnut Trees with Especial Reference to the Concentration and Ph of the Medium, by H. S. Reed and A. R. O. Haas. October, 1924.
18. Factors Influencing the Rate of Germination of Seed of *Asparagus officinalis*, by H. A. Borthwick. March, 1925.
19. The Relation of the Subcutaneous Administration of Living Bacterium abortum to the Immunity and Carrier Problem of Bovine Infectious Abortion, by George H. Hart and Jacob Traum. April, 1925.
20. A Study of the Conductive Tissues in Shoots of the Bartlett Pear and the Relationship of Food Movement to Dominance of the Apical Buds, by Frank E. Gardner. April, 1925.