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WEED HOST RANGE AND OVERWINTERING OF  
CURLY-TOP VIRUS

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# WEED HOST RANGE AND OVERWINTERING OF CURLY-TOP VIRUS<sup>1</sup>

HENRY H. P. SEVERIN<sup>2</sup>

(Contribution from the Division of Entomology and Parasitology, California Agricultural Experiment Station, cooperating with the United States Department of Agriculture, Bureau of Entomology.)

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## INTRODUCTION

IT IS IMPORTANT TO KNOW what plants growing in the cultivated areas and on the uncultivated plains and foothills are reservoirs of the curly-top virus. After sugar beets and other economic host plants of the beet leafhopper, *Eutettix tenellus* (Baker), are harvested, the adults of the overwintering generation feed on weeds and perennials during their flights from the cultivated areas to the uncultivated plains and foothills. After the pasture vegetation becomes green, the adults of the overwintering generation leave the perennials and feed on the pasture vegetation. After the pasture vegetation becomes dry on the plains and foothills, the adults of the spring generation fly into the cultivated areas and are often abundant on favorable weeds. Some of these food plants of the beet leafhoppers serve as host plants of the curly-top virus.

A number of papers have appeared on the experimental infection of weeds with curly top, but the contributions on naturally infected weeds are limited. A review of the literature on this subject follows:

Bonequet and Stahl<sup>(1)</sup> experimentally infected dwarf mallow (*Malva rotundifolia* L.) with curly top and demonstrated that this weed growing in the vicinity of beets in the Salinas Valley was naturally infected with the disease.

Severin<sup>(5, 7)</sup> and Severin and Henderson<sup>(11)</sup> reported that 26 species of weeds and shrubs in 10 genera belonging to 6 families were experimentally infected with curly top, and 25 species of wild plants in 11 genera of 8 families were demonstrated to be naturally infected with curly top.

Carsner<sup>(2)</sup> found 11 species of wild plants and 3 species of economic plants belonging to 11 families susceptible to curly top and recovered the virus from 12 species. He reported 24 species of uncultivated and economic plants as nonsusceptible to curly top. In a later paper<sup>(3)</sup> he reported that the virus of curly top became attenuated when passed through certain weeds such as *Chenopodium murale* L., *Rumex crispus* L., and *Suaeda moquini* Greene.

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<sup>1</sup> Received for publication March 24, 1934.

<sup>2</sup> Associate Entomologist in the Experiment Station.

TABLE 1  
LIST OF PLANTS EXPERIMENTALLY INFECTED WITH CURLY TOP

| Family          | Common name  | Scientific name   | Seasons duration   | Source of plants          |
|-----------------|--|---|--------------------|---------------------------|
| Urticaceae      | Small nettle   | <i>Urtica urens</i> L.                                    | Annual             | Seeds                     |
| Polygonaceae    | Water smartweed  | <i>Polygonum amphibium hartwrightii</i> Bissel            | Perennial          | Sacramento Valley         |
|                 | Swamp smartweed  | <i>Polygonum muhlenbergii</i> Wats.                       | Perennial          | Sacramento Valley         |
|                 | Common knotweed  | <i>Polygonum lapathifolium</i> L.                         | Annual             | San Joaquin Valley        |
|                 | Lady's thumb   | <i>Polygonum persicaria</i> L.                            | Annual             | San Joaquin Valley        |
|                 | Wire grass   | <i>Polygonum aviculare</i> L.                             | Annual             | San Joaquin Valley        |
|                 | Curly dock   | <i>Rumex crispus</i> L. <sup>(7)*</sup>                   | Perennial          | Seeds                     |
| Chenopodiaceae  | Arrowscale   | <i>Atriplex phyllostegia</i> Wats. <sup>(11)</sup>        | Annual             | Seeds                     |
|                 | Bractscale   | <i>Atriplex bracteosa</i> Wats. <sup>(11)</sup>           | Annual             | Seeds                     |
|                 | Brittlescale   | <i>Atriplex parishii</i> Wats. <sup>(11)</sup>            | Annual             | Seeds                     |
|                 | Crownscale   | <i>Atriplex coronata</i> Wats. <sup>(11)</sup>            | Annual             | Seeds                     |
|                 | Fogweed (silverscale)  | <i>Atriplex argentea expansa</i> (Wats.) <sup>(11)</sup>  | Annual             | Seeds                     |
|                 |  | <i>Atriplex argentea hillmanii</i> Jones                  | Annual             | Sierra Nevada             |
|                 | Garden orache (garden scale)                                 | <i>Atriplex hortensis rubra</i> L.                        | Annual             | Seeds, Idaho              |
|                 | Heartscale   | <i>Atriplex cordulata</i> Jepson <sup>(11)</sup>          | Annual             | Seeds                     |
|                 | Spear orache (spear scale)                                   | <i>Atriplex patula hastata</i> L. <sup>(11)</sup>         | Annual             | Seeds                     |
|                 |  | <i>Atriplex tularensis</i> Coville <sup>(11)</sup>        | Annual             | Seeds                     |
|                 | Red orache (red scale)                                       | <i>Atriplex rosea</i> L. <sup>(11)</sup>                  | Annual             | Seeds                     |
|                 | Australian saltbush (flesh scale)                            | <i>Atriplex semibaccata</i> R.Br. <sup>(11)</sup>         | Perennial          | Seeds                     |
|                 | Ballscale  | <i>Atriplex fruticulosa</i> Jepson <sup>(11)</sup>        | Perennial          | San Joaquin Valley, seeds |
|                 | Quailbrush (lenscale)  | <i>Atriplex lentiformis</i> (Torr.) Wats. <sup>(11)</sup> | Perennial          | San Joaquin Valley        |
|                 |  | <i>Chenopodium leptophyllum</i> Wats. <sup>(11)</sup>     | Annual             | Seeds                     |
|                 | Lamb's quarters (white pigweed)                              | <i>Chenopodium album</i> L. <sup>(11)</sup>               | Annual             | Seeds                     |
|                 | Sowbane (nettleleaf goosefoot)                               | <i>Chenopodium murale</i> L. <sup>(11)</sup>              | Annual             | Seeds                     |
| Mexican tea     | <i>Chenopodium ambrosioides</i> L. <sup>(11)</sup>           | Perennial   | San Joaquin Valley |                           |
| Soap plant      | <i>Chenopodium californicum</i> Wats. <sup>(11)</sup>        | Perennial   | Root               |                           |
| Russian thistle | <i>Salsola kali tenuifolia</i> G. F. W. Mey. <sup>(11)</sup> | Annual  | San Joaquin Valley |                           |
| Amaranthaceae   | Rough pigweed  | <i>Amaranthus retroflexus</i> L.                          | Annual             | San Joaquin Valley        |
|                 | Tumbleweed   | <i>Amaranthus graecizans</i> L.                           | Annual             | San Joaquin Valley        |
|                 |  | <i>Amaranthus deflexus</i> L.                             | Annual             | San Joaquin Valley        |
| Portulacaceae   | Common purslane  | <i>Portulaca oleracea</i> L.                              | Annual             | Berkeley                  |
| Caryophyllaceae | Common chickweed   | <i>Stellaria media</i> (L.) Cyr.                          | Annual             | Berkeley                  |

\* Superscript number in parentheses refers to paper number in Literature Cited.

TABLE 1—(Concluded)

| Family         | Common name                       | Scientific name  | Seasons duration      | Source of plants   |
|----------------|-----------------------------------|--|-----------------------|--------------------|
| Cruciferae     | Wild radish.....                  | <i>Raphanus sativus</i> L.....                                       | Annual                | Seeds              |
|                | Charlock.....                     | <i>Brassica arvensis</i> (L.) B.S.P.....                             | Annual                | Seeds              |
|                | Shepherd's purse.....             | <i>Capsella bursa-pastoris</i> (L.)<br>Moench. <sup>(7)*</sup> ..... | Annual                | Seeds              |
| Leguminosae    | Bur clover.....                   | <i>Medicago hispida</i> Gaertn. <sup>(11)</sup>                      | Annual                | Seeds              |
| Oxalidaceae    | Yellow sorrel.....                | <i>Oxalis corniculata</i> L.....                                     | Perennial             | Berkeley           |
|                | .....                             | <i>Oxalis corniculata atropur-<br/>purea</i> Planch.....             | Perennial             | Berkeley           |
| Geraniaceae    | .....                             | <i>Erodium botrys</i> Bertol.....                                    | Annual                | San Joaquin Valley |
|                | White-stem filaree.....           | <i>Erodium moschatum</i> L'Her. <sup>(6)</sup>                       | Annual                | Berkeley           |
|                | Red-stem filaree.....             | <i>Erodium cicutarium</i> L'Her.....                                 | Annual                | Seeds              |
| Euphorbiaceae  | Petty spurge.....                 | <i>Euphorbia peplus</i> L.....                                       | Annual                | Berkeley           |
| Malvaceae      | Dwarf mallow.....                 | <i>Malva rotundifolia</i> L. <sup>(7)</sup> .....                    | Annual or<br>biennial | Seeds              |
|                | Cheeseweed.....                   | <i>Malva parviflora</i> L. <sup>(7)</sup> .....                      | Annual or<br>biennial | Seeds              |
| Primulaceae    | Poor man's weather-<br>glass..... | <i>Anagallis arvensis</i> L.....                                     | Annual                | Berkeley           |
| Solanaceae     | Tree tobacco.....                 | <i>Nicotiana glauca</i> Graham.....                                  | Perennial             | San Joaquin        |
|                | .....                             | <i>Solanum douglasii</i> Dunal. <sup>(7)</sup>                       | Perennial             | Seeds              |
|                | .....                             | <i>Physalis wrightii</i> Gray.....                                   | Annual                | Seeds              |
|                | Stramonium.....                   | <i>Datura stramonium</i> L. <sup>(7)</sup> .....                     | Annual                | Seeds              |
| Plantaginaceae | Common plantain.....              | <i>Plantago major</i> L.....   | Perennial             | San Jose           |
|                | .....                             | <i>Plantago erecta</i> Morris.....                                   | Annual                | San Joaquin Valley |
| Compositae     | Common sow-<br>thistle.....       | <i>Sonchus oleraceus</i> L.....                                      | Annual                | Berkeley           |
|                | Prickly sow-<br>thistle.....      | <i>Sonchus asper</i> L.....  | Annual                | San Joaquin Valley |
|                | Cotton-batting<br>plant.....      | <i>Gnaphalium chilense</i> Spreng.                                   | Annual or<br>biennial | Sacramento Valley  |
|                | Spiny clotbur.....                | <i>Xanthium spinosum</i> L.....                                      | Annual                | Seeds              |
|                | Common groundsel.....             | <i>Senecio vulgaris</i> L.....                                       | Annual                | Berkeley           |
|                | Mayweed.....                      | <i>Anthemis cotula</i> L.....  | Annual                | Berkeley           |

\* Superscript number in parentheses refers to paper number in Literature Cited.

According to Lackey<sup>(4)</sup> the attenuated curly-top virus was restored to its original virulence by passing it through common chickweed, *Stellaria media* (L.) Cyr. (plate 1 A, B, C).

Starrett<sup>(13)</sup> experimentally infected *Oxalis stricta* L. with curly top by means of infective beet leafhoppers and transferred the virus from the infected plants to sugar beets through the agency of previously noninfective beet leafhoppers.

In this paper new wild host plants of curly top are listed and also those previously recorded in the literature.<sup>(5, 7, 11)</sup> Field investigations

to determine the weeds which are naturally infected with curly top in the cultivated areas and on the uncultivated plains and foothills have been conducted over a period of sixteen years. Investigations to ascertain the weeds which could be experimentally infected with the disease were also made. Further investigations were conducted on the overwintering of the curly-top virus in host plants growing on the uncultivated plains and foothills, in perennial plants growing in the cultivated areas, and in the overwintering generation of beet leafhoppers.

### METHODS

The methods used in determining whether weeds, economic plants, and ornamental flowering plants were naturally infected with curly top, have been described in previous papers.<sup>(5, 11, 12)</sup> The methods of experimentally infecting plants have also been described in a previous paper.<sup>(11)</sup>

### PLANTS EXPERIMENTALLY INFECTED WITH CURLY TOP

A list of plants experimentally infected with curly top is given in table 1. These plants occur in the cultivated areas and were either grown from seeds or transplanted from the field.

As indicated in table 1, the weeds experimentally infected with curly top include 41 species of annuals, 3 species of annuals or biennials, and 13 species of perennials—a total of 57 species or varieties of weeds in 28 genera belonging to 16 families. The virus was recovered from each species of infected plant by previously noninfective beet leafhoppers and transferred to sugar beets.

### PLANTS NATURALLY INFECTED WITH CURLY TOP

Table 2 lists the weeds and other wild plants which were demonstrated to be naturally infected with curly top. The list includes plants which were growing on the uncultivated plains and foothills and in the cultivated areas.

The plants growing on the uncultivated plains and foothills demonstrated to be naturally infected with curly top include, as shown in table 2, 11 species of annuals and 3 species of perennials—a total of 14 species in 13 genera belonging to 8 families.

In the cultivated areas 19 species of annuals, 3 species of annuals or biennials, and 4 species of perennials—a total of 26 species in 15 genera belonging to 9 families—were proved to be naturally infected with the disease.

Many plants in which the beet leafhopper has not been bred from eggs deposited under natural conditions up to the present time were experi-

TABLE 2  
LIST OF PLANTS NATURALLY INFECTED WITH CURLY TOP

| Family                            | Common name                         | Scientific name   | Seasons duration | Valley in which plants were obtained |
|-----------------------------------|-------------------------------------|---|------------------|--------------------------------------|
| Uncultivated plains and foothills |                                     |   |                  |                                      |
| Chenopodiaceae                    | Patata.....                         | <i>Monolepsis nuttalliana</i> (R. & S.) Wats.....                   | Annual           | San Joaquin                          |
|                                   | Ballscale.....                      | <i>Atriplex fruticulosa</i> Jepson <sup>(5)*</sup> .....            | Perennial        | San Joaquin                          |
| Cruciferae                        | .....                               | <i>Thelypodium lasiophyllum</i> (H. & A.) Greene.....               | Annual           | San Joaquin                          |
|                                   | Common pepper-grass.....            | <i>Lepidium nitidum</i> Nutt.....                                   | Annual           | San Joaquin                          |
|                                   | Shepherd's purse.....               | <i>Capsella bursa-pastoris</i> (L.) Moench.....                     | Annual           | San Joaquin                          |
| Geraniaceae                       | .....                               | <i>Erodium macrophyllum</i> H. & A.....                             | Annual           | San Joaquin                          |
|                                   | Red-stem filaree.....               | <i>Erodium cicutarium</i> L'Her. <sup>(5,6)</sup> .....             | Annual           | San Joaquin, Salinas                 |
| Leguminosae                       | Bur clover.....                     | <i>Medicago hispida</i> Gaertn. <sup>(5)</sup> .....                | Annual           | Bitterwater                          |
|                                   | .....                               | <i>Lotus strigosus</i> (Nutt.) Greene.....                          | Annual           | San Joaquin                          |
| Malvaceae                         | .....                               | <i>Modiola caroliniana</i> Don.....                                 | Perennial        | San Joaquin                          |
| Hydrophyllaceae                   | .....                               | <i>Phacelia ramosissima</i> Dougl.....                              | Perennial        | San Joaquin                          |
| Plantaginaceae                    | .....                               | <i>Plantago erecta</i> Morris.....                                  | Annual           | San Joaquin                          |
| Compositae                        | .....                               | <i>Microseris douglasii</i> Gray.....                               | Annual           | San Joaquin                          |
|                                   | .....                               | <i>Baeria uliginosa</i> (Nutt.) Gray.....                           | Annual           | San Joaquin                          |
| Cultivated areas                  |                                     |   |                  |                                      |
| Polygonaceae                      | Water smartweed.....                | <i>Polygonum amphibium hartwrightii</i> Bissel <sup>(7)</sup> ..... | Perennial        | Sacramento                           |
|                                   | Swamp smartweed.....                | <i>Polygonum muhlenbergii</i> Wats. <sup>(7)</sup> .....            | Perennial        | Sacramento                           |
|                                   | Common knotweed.....                | <i>Polygonum lapathifolium</i> L. <sup>(7)</sup> .....              | Annual           | San Joaquin                          |
|                                   | Lady's thumb.....                   | <i>Polygonum persicaria</i> L. <sup>(7)</sup> .....                 | Annual           | San Joaquin                          |
|                                   | Wire grass.....                     | <i>Polygonum aviculare</i> L. <sup>(7)</sup> .....                  | Annual           | San Joaquin, Sacramento              |
| Chenopodiaceae                    | Bractscale.....                     | <i>Atriplex bracteosa</i> Wats. <sup>(5,11)</sup> .....             | Annual           | San Joaquin                          |
|                                   | Fogweed (silverscale).....          | <i>Atriplex argentea expansa</i> (Wats.) <sup>(5,11)</sup> .....    | Annual           | San Joaquin                          |
|                                   | Spear orache (spearscale).....      | <i>Atriplex patula hastata</i> L. <sup>(11)</sup> .....             | Annual           | Sacramento                           |
|                                   | Red orache (redscale).....          | <i>Atriplex rosea</i> L. <sup>(5,11)</sup> .....                    | Annual           | San Joaquin, Salinas                 |
|                                   | .....                               | <i>Chenopodium leptophyllum</i> Wats. <sup>(11)</sup> .....         | Annual           | San Joaquin                          |
|                                   | Sowbane (nettleleaf goosefoot)..... | <i>Chenopodium murale</i> L. <sup>(11)</sup> .....                  | Annual           | San Joaquin, Salinas                 |
|                                   | Mexican tea.....                    | <i>Chenopodium ambrosioides</i> L. <sup>(11)</sup> .....            | Perennial        | San Joaquin                          |
|                                   | Russian thistle.....                | <i>Salso kali tenuifolia</i> G. F. W. Mey. <sup>(5,11)</sup> .....  | Annual           | San Joaquin, Salinas                 |

\* Superscript number in parentheses refers to paper number in Literature Cited.

TABLE 2—(Concluded)

| Family                       | Common name               | Scientific name  | Seasons duration   | Valley in which plants were obtained |
|------------------------------|---------------------------|--|--------------------|--------------------------------------|
| Cultivated areas—(Continued) |                           |  |                    |                                      |
| Amaranthaceae                | Rough pigweed.....        | <i>Amaranthus retroflexus</i> L. <sup>(5)*</sup> .....           | Annual             | San Joaquin, Sacramento              |
|                              | Tumbleweed.....           | <i>Amaranthus graecizans</i> L. <sup>(5)</sup> .....             | Annual             | San Joaquin                          |
|                              |                           | <i>Amaranthus deflexus</i> L. <sup>(5)</sup> .....               | Annual             | San Joaquin                          |
| Cruciferae                   | Charlock.....             | <i>Brassica arvensis</i> (L.) B.S.P. <sup>(5,7)</sup> .....      | Annual             | Sacramento                           |
|                              | Shepherd's purse.....     | <i>Capsella bursa-pastoris</i> (L.) Moench. <sup>(7)</sup> ..... | Annual             | Salinas                              |
| Leguminosae                  | Spanish clover.....       | <i>Lotus americanus</i> (Nutt.) Bisch.....                       | Annual             | San Joaquin                          |
| Geraniaceae                  |                           | <i>Erodium botrys</i> Bertol.....                                | Annual             | San Joaquin                          |
| Malvaceae                    | Dwarf mallow.....         | <i>Malva rotundifolia</i> L. <sup>(7)</sup> .....                | Annual or biennial | Salinas                              |
|                              | Cheeseweed.....           | <i>Malva parviflora</i> L. <sup>(7)</sup> .....                  | Annual or biennial | San Joaquin, Sacramento              |
| Solanaceae                   |                           | <i>Solanum douglasii</i> Dunal. <sup>(5,7)</sup> .....           | Perennial          | San Joaquin, Salinas                 |
|                              |                           | <i>Physalis wrightii</i> Gray <sup>(7)</sup> .....               | Annual             | San Joaquin                          |
| Compositae                   | Prickly sow-thistle.....  | <i>Sonchus asper</i> L.....                                      | Annual             | San Joaquin                          |
|                              | Cotton-batting plant..... | <i>Gnaphalium chilense</i> Spreng.....                           | Annual or biennial | Sacramento                           |
|                              | Spiny clotbur.....        | <i>Xanthium spinosum</i> L.....                                  | Annual             | Salinas                              |

\* Superscript number in parentheses refers to paper number in Literature Cited.

mentally infected with curly top. The beet leafhopper was bred from eggs deposited under natural conditions from 8 species of plants growing on the uncultivated plains and foothills and from 38 species growing in the cultivated areas, as reported in a previous paper.<sup>(9)</sup>

### SYMPTOMS OF CURLY TOP

The symptoms of curly top on the sugar beet, economic, and ornamental flowering plants have been described in four previous papers.<sup>(7, 8, 11, 12)</sup> A general description of the symptoms of the disease on weeds is given, with illustrations of a few typical examples, rather than a detailed description of the symptoms on each weed. Weeds infected with curly top show a variation in symptoms, but the following symptoms are characteristic of many diseased plants: stunting (figs. 1, 6A); abnormal development of secondary shoots (fig. 6C) with dwarfed leaves arising from the axils of the leaves (fig. 3); shortening of the internodes; dwarf-



Fig. 1. *Erodium botrys*: left and upper, stunted plants naturally infected with curly top showing curled leaves; right, healthy plant. Niles Garden, March 6, 1934.

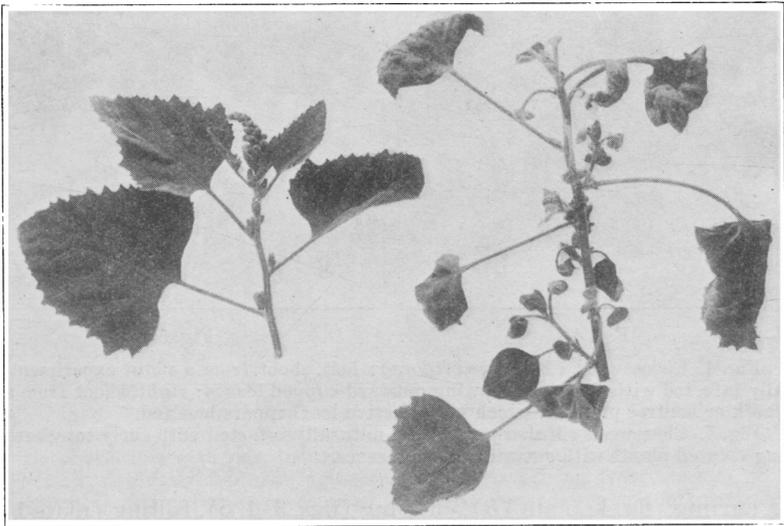


Fig. 2. Garden orache or gardenscale (*Atriplex hortensis rubra*): left, shoot from check or control plant on which noninfective beet leafhoppers had fed; right, shoot from a plant experimentally infected with curly top showing secondary shoots arising from the axil of the leaves bearing dwarfed, balled leaves.



Fig. 3. Rough pigweed (*Amaranthus retroflexus*) experimentally infected with curly top showing outward-cupped leaves and axillary shoots.

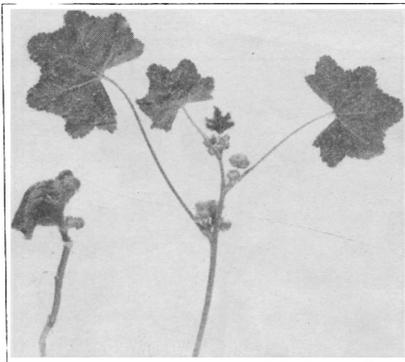


Fig. 4



Fig. 5

Fig. 4. Cheeseweed (*Malva parviflora*): left, shoot from a plant experimentally infected with curly top showing outward-cupped leaves; right, shoot from a check or control plant on which noninfective leafhoppers had fed.

Fig. 5. Cheeseweed (*Malva parviflora*) naturally infected with curly top showing stunted plants with outward-cupped leaves.

ing, curling (fig. 1; plate 1*B*), cupping (figs. 3, 4, 5), rolling (plate 1*A*, *E*), balling (fig. 2), twisting (fig. 6*A*), puckering, mottling, and chlorosis of the leaves; cleared or transparent veinlets (plate 2*A*); vein distortions (fig. 6, *B*, *D*); and protuberances (plate 1*D*; plate 2*B*) on the lower surface of the leaves.

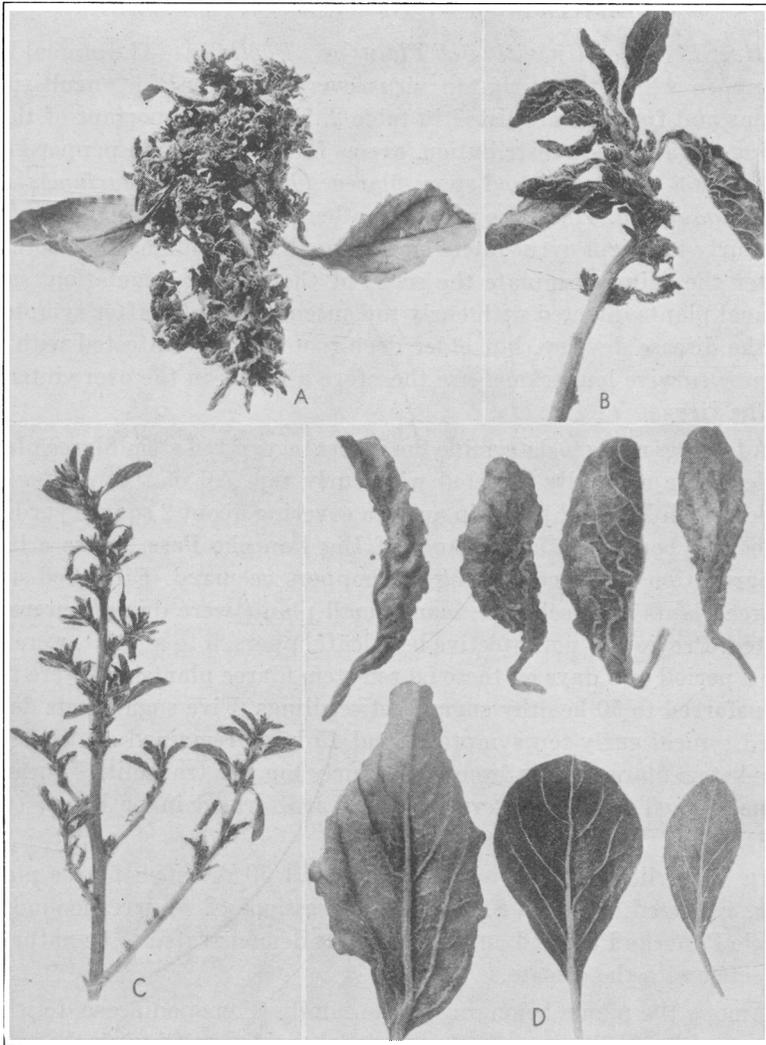


Fig. 6. Tumbleweed (*Amaranthus graecizans*): *A*, Plant naturally infected with curly top showing stunting and compact mass of twisted leaves. *B*, Branch showing leaves with vein distortions. *C*, Branch from a plant experimentally infected with curly top showing secondary shoots arising from the axil of the leaves. *D*, upper row, leaves showing vein distortions; lower row, left, leaf showing protuberances on the lower surface; center and right, leaves from the same plant showing no vein distortions and protuberances.

## OVERWINTERING OF CURLY-TOP VIRUS

*In Host Plants on Uncultivated Plains and Foothills.*—The annual host plants in which the curly-top virus overwinters on the uncultivated plains and foothills are listed in table 2. The most important of these, owing to their wide distribution, are as follows: common pepper-grass (*Lepidium nitidum*), red-stem filaree (*Erodium cicutarium*), and *Plantago erecta*. There are probably other important annuals in which the curly-top virus overwinters on the uncultivated plains and foothills. After the rains germinate the seeds of the pasture vegetation, small annual plants infected with curly top succumb rapidly after symptoms of the disease develop, but older deep-rooted plants infected with the disease survive longer, and are therefore a factor in the overwintering of the virus.

A test was made to determine the percentage of red-stem-filaree plants which were naturally infected with curly top. All of the plants were collected on March 2, 1926, in an area covering about 2 square yards on a foothill bounding the entrance of Big Panoche Pass, where a large congregation of overwintering leafhoppers occurred. Fifty red-stem-filaree plants were selected; many small plants were dry and were rejected. Previously noninfective beet leafhoppers, 5 to a plant, were fed for a period of 3 days on these 50 red-stem filaree plants and were then transferred to 50 healthy sugar-beet seedlings. Five sugar beets developed typical curly-top symptoms and 45 beets remained healthy. The 5 red-stem filaree plants from which curly top was transmitted to sugar beets showed reddish outer leaves and malformed inner leaves (figs. 7, 8).

In an earlier test previously reported,<sup>(6)</sup> 50 red-stem filaree plants were collected on April 8, 1924, in depressions of squirrel mounds in Little Panoche Pass and only 1 plant was demonstrated to be naturally infected with the disease.

Among the plants belonging to the family Chenopodiaceae, to which the sugar beet belongs, a single perennial species growing on the uncultivated plains and foothills has been demonstrated to be naturally infected with curly top; ballscale (*Atriplex fruticulosa*), a small spreading saltbush often grazed down by cattle and sheep to a mat-like form, and commonly found on the plains and foothills of the San Joaquin Valley, has been proved to be naturally infected with the disease. Four plants transplanted from the uncultivated plains were experimentally infected with curly top, and the virus was repeatedly recovered by previously noninfective beet leafhoppers and transferred to beets during



Fig. 7. Red-stem filaree (*Erodium cicutarium*) naturally infected with curly top showing twisted petioles and inward-curved leaflets.



Fig. 8. Red-stem filaree (*Erodium cicutarium*) naturally infected with curly top with outer leaves removed, showing curled petioles and leaves; lower right, drooping flower.

a period of six months from May to October inclusive, when the tests were discontinued.

Two other perennial species growing on the plains and foothills in the San Joaquin Valley were demonstrated to be naturally infected with curly top as follows: (1) *Modiola caroliniana* belonging to the family Malvaceae, introduced from the southeastern part of the United States into California; and (2) *Phacelia ramosissima*, belonging to the family Hydrophyllaceae, and occurring on the foothills and mountain slopes at an elevation of 200 to 9,000 feet almost throughout California, north to Washington, and south to Lower California.

*In Host Plants in Cultivated Areas.*—Four perennials growing in the cultivated areas and demonstrated to be naturally infected with curly top are listed in table 2. Since the annuals become dry during the autumn, they play no role in the overwintering of the virus.

Repeated tests were made to recover the curly-top virus from Mexican tea (*Chenopodium ambrosioides*), a perennial weed demonstrated to be naturally infected with the disease in the San Joaquin Valley. The virus was transferred from 4 naturally infected plants by different lots of previously noninfective beet leafhoppers to sugar beets during a period of 1 year, after which no further tests were made.<sup>(11)</sup>

Among economic plants, Hairy Peruvian alfalfa (*Medicago sativa*) and horse-radish (*Amoracia rusticana*), both perennials; Single or Plain parsley (*Petroselinum hortense*), a biennial or short-lived perennial; and potato (*Solanum tuberosum*), a herbaceous plant, were demonstrated to be naturally infected with curly top.<sup>(7, 11)</sup> The virus was rarely recovered from naturally infected horse-radish plants during the summer, and not at all during the autumn. The virus was not recovered from cuttings grown from naturally infected horse-radish roots.<sup>(7)</sup> No experiments have been conducted up to the present time to prove potato-tuber transmission of the disease, nor to test whether the virus could be recovered during the autumn and winter from alfalfa and parsley.

Among the ornamental flowering plants, grass pink (*Dianthus plumarius*) and fish geranium (*Pelargonium hortorum*), both perennials; common four-o'clock (*Mirabilis jalapa*) and common garden petunia (*Petunia hybrida*), both perennials grown as annuals; and pansy (*Viola tricolor hortensis*), an annual or short-lived perennial, were proved to be naturally infected with curly top.<sup>(12)</sup> Carnation (*Dianthus caryophyllus*), a perennial, and stocks (*Mathiola incana*), a biennial or perennial, showed typical symptoms of curly top under field conditions, but noninfective leafhoppers failed to transmit the virus from these plants to sugar beets.

*In Beet Leafhopper.*—The curly-top virus rarely overwinters in the male beet leafhopper, since most of the males die during the winter.<sup>(10)</sup> The average period of infectivity during the adult life of 10 females 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 death of the insect. When the females lived for a long time, the infective power was lost in most cases. The infective power is not retained during the adult life of the overwintering female beet leafhoppers unless they reinfect themselves during the winter; but in that case the virus does overwinter in the females.

### SUMMARY

The weeds growing on the uncultivated plains and foothills and in the cultivated areas experimentally infected with curly top include 57 species in 28 genera belonging to 16 families.

The wild plants growing on the uncultivated plains and foothills demonstrated to be naturally infected with curly top include 14 species in 13 genera belonging to 8 families.

In the cultivated areas 26 species of weeds in 15 genera belonging to 9 families were found to be naturally infected with the disease in nature.

The curly-top virus overwinters in 11 species of annuals and 3 species of perennial wild plants growing on the uncultivated plains and foothills. Previously noninfective beet leafhoppers repeatedly recovered the virus from a perennial—ballscale (*Atriplex fruticulosa*)—during a period of six months, when the tests were discontinued.

Four species of perennials and 3 species of weeds sometimes annual and sometimes perennial growing in the cultivated areas were demonstrated to be naturally infected with curly top. The virus was repeatedly recovered from a naturally infected perennial—Mexican tea (*Chenopodium ambrosioides*)—during a period of one year, after which no further tests were made. The virus does not overwinter in the annuals growing in the cultivated areas, since these become dry during the autumn.

The following economic plants which may enable the virus to overwinter were demonstrated to be naturally infected with curly top: Hairy Peruvian alfalfa (*Medicago sativa*) and horse-radish (*Amoracia rusticana*) both perennials; Single or Plain parsley (*Petroselinum hortense*), a biennial or short-lived perennial; and potato (*Solanum tuberosum*), a herbaceous plant. The virus was rarely recovered from naturally infected horse-radish during the summer, and not at all dur-

ing the autumn, nor from cuttings grown from naturally infected horse-radish roots.

The following ornamental flowering plants were demonstrated to be infected with curly top under natural conditions: grass pink (*Dianthus plumarius*) and fish geranium (*Pelargonium hortorum*), both perennials; common four-o'clock (*Mirabilis jalapa*) and common garden petunia (*Petunia hybrida*), both perennials grown as annuals; and pansy (*Viola tricolor hortensis*), an annual or short-lived perennial. The virus was not recovered from carnation (*Dianthus caryophyllus*), a perennial, and stocks (*Mathiola incana*), a biennial or perennial, although these showed typical symptoms of curly top under field conditions.

The curly-top virus rarely overwinters in the male beet leafhopper, since most of the males die during the winter. The infective power is not retained during the adult life of the female beet leafhoppers unless they reinfest themselves during the winter, but in that case the virus overwinters in the females.

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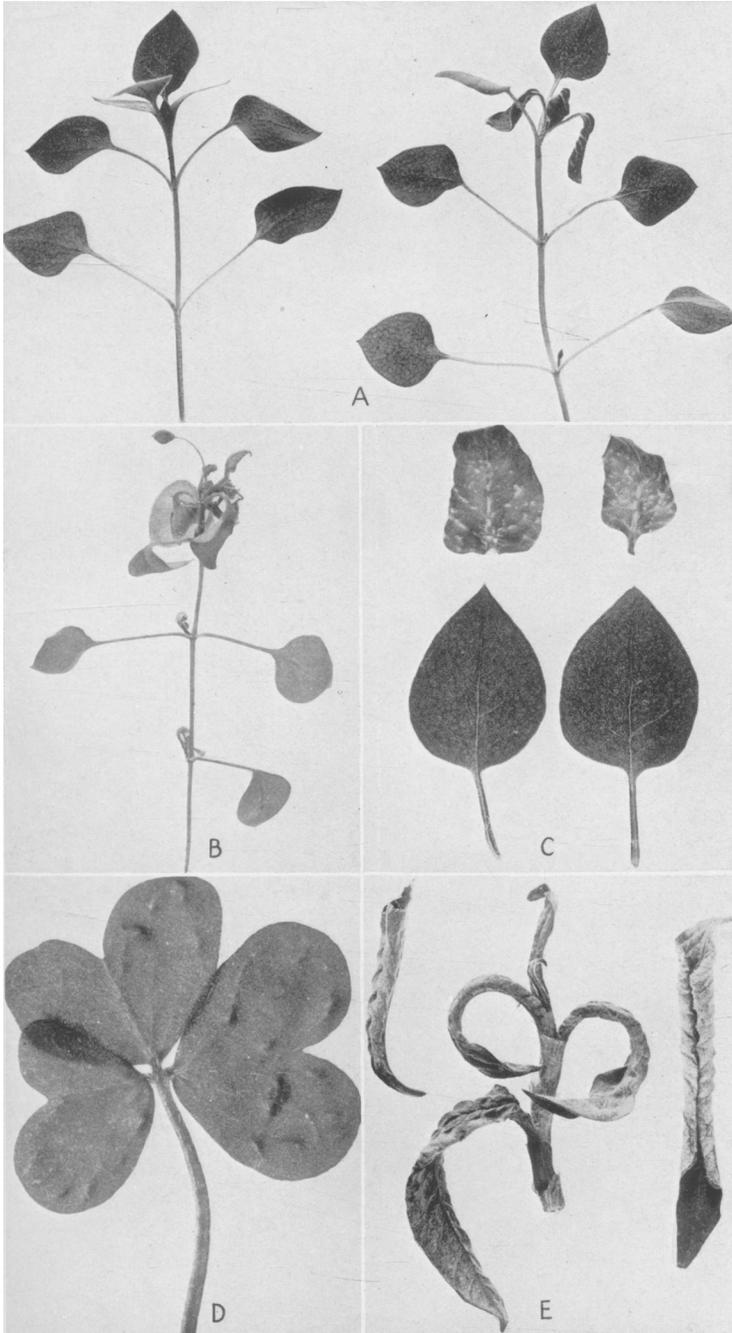


Plate 1. *A*, Common chickweed (*Stellaria media*): left, healthy plant; right, plant experimentally infected with curly top showing rolled leaves. *B*, Plant in an advanced stage of the disease showing curled apical leaves. *C*, Upper leaves from an infected plant showing protuberances; lower leaves from a healthy plant. *D*, Yellow sorrel (*Oxalis corniculata*); leaf from a plant experimentally infected with curly top showing protuberances. *E*, Swamp smartweed (*Polygonum muhlenbergii*) naturally infected with curly top, showing inward-rolled leaves.

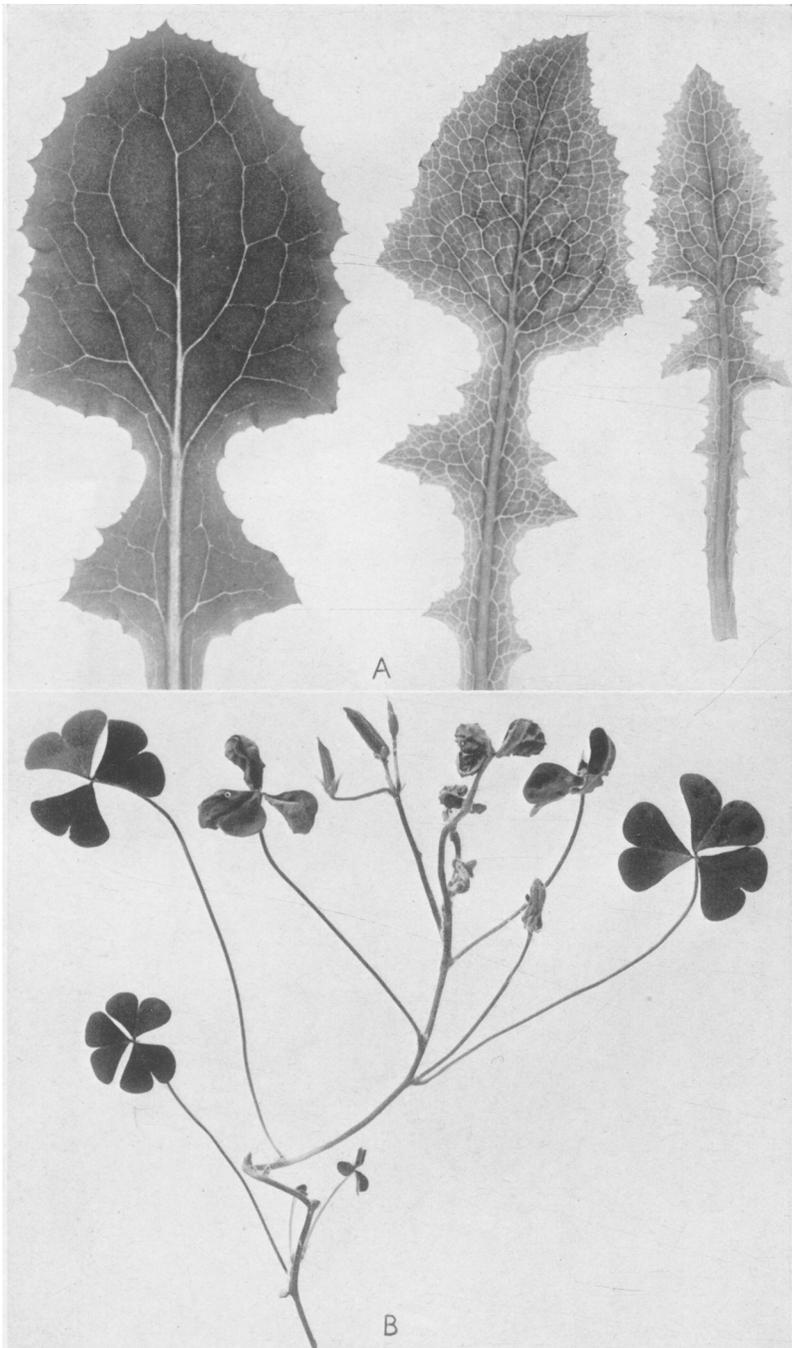


Plate 2. A, Prickly sow-thistle (*Sonchus asper*): left, leaf from a healthy plant; center and right, leaves from a plant experimentally infected with curly top showing cleared or transparent veinlets. B, Yellow sorrel (*Oxalis corniculata*) experimentally infected with curly top showing protuberances on the curled leaves.