HILGARDIA

A Journal of Agricultural Science Published by the California Agricultural Experiment Station

VOLUME 16 | JUNE, 1945 | NUMBER 12

CONTENTS

CALIFORNIA ASTER YELLOWS ON VEGETABLE AND SEED CROPS

HENRY H. P. SEVERIN and NORMAN W. FRAZIER

ADDITIONAL ORNAMENTAL FLOWERING PLANTS NATURALLY INFECTED WITH CALIFORNIA ASTER YELLOWS

HENRY H. P. SEVERIN and JULIUS H. FREITAG

WEED-HOST RANGE OF CALIFORNIA ASTER YELLOWS

NORMAN W. FRAZIER and HENRY H. P. SEVERIN

This Issue Completes Volume 16

UNIVERSITY OF CALIFORNIA · BERKELEY, CALIFORNIA

WEED-HOST RANGE OF CALIFORNIA ASTER YELLOWS

NORMAN W. FRAZIER AND HENRY H. P. SEVERIN

WEED-HOST RANGE OF CALIFORNIA ASTER YELLOWS[1]

NORMAN W. FRAZIER[2] AND HENRY H. P. SEVERIN[3]

INTRODUCTION

KUNKEL (1926, 1931)[4] recorded for the virus of New York aster yellows an extensive host range of 184 species of plants in 151 genera belonging to 38 families. He found 12 species of naturally infected weeds in 4 families, as follows:

Compositae, composite family:
- Horseweed, *Erigeron canadensis* L.
- *Erigeron speciosus* (Lindl.) DC.
- Galinsoga, *Galinsoga parviflora* Cav.
- *Helenium autumnale* L.
- *Helenium nudiflorum* Nutt.
- Fall dandelion, *Leontodon autumnalis* L.
- Black-eyed Susan, *Rudbeckia hirta* L.
- Perennial sow thistle, *Sonchus arvensis* L.
- Common sow thistle, *Sonchus oleraceus* L.

Plantaginaceae, plantago family:
- Common plantain, *Plantago major* L.

Rosaceae, rose family:
- Rough cinquefoil, *Potentilla monspeliensis* L.

Umbelliferae, parsley family:
- Wild carrot, *Daucus Carota* L.

Ogilvie (1927*a*, 1927*b*) reported aster yellows (strain not specified) to be common in the Bermuda Islands and observed that several wild plants were affected, the commonest being common sow thistle, *Sonchus oleraceus*.

Severin (1929, 1938) determined the following 2 species to be hosts of the California aster-yellows virus:

Plantaginaceae, plantago family:
- Common plantain, *Plantago major* L.

Umbelliferae, parsley family:
- Poison hemlock, *Conium maculatum* L.

Thompson (1944) tested 16 species of wild *Lactuca* and 6 additional strains for their susceptibility to New York aster yellows under field conditions. He reported that the following 13 species showed symptoms: *Lactuca altaica* Fisch. and Mey., *L. canadensis* L., *L. floridana* (L.) Gaertn., *L. graminifolia*

[1] Received for publication May 19, 1944.

[2] Junior Entomologist in the Experiment Station.

[3] Entomologist in the Experiment Station.

[4] See "Literature Cited" at the end of this paper for complete data on citations, referred to in the text by author and date of publication.

Michx., *L. indica* L., *L. muralis* (L.) Fresen, *L. perennis* L., *L. raddeana* Maxim., *L. saligna* L., *L. serriola* L., *L. spicata* (Lam.) Hitchc., *L. Squarrosa* (Thunb.) Miq., and *L. virosa* L. Three species, *L. Bourgaei* (Boiss.) Irish and Taylor, *L. Marschalli* Stebbins, and *L. tatarica* (L.) C. A. Mey., failed to develop symptoms, and Thompson concluded that they seemed to be immune to the virus.

In two companion papers the symptoms of the disease on vegetable and seed crops, and ornamental flower plants have been described (Severin and Frazier, 1945; Severin and Freitag, 1945).

Field investigations were conducted from 1928 to 1944 to determine additional weed-host plants of this virus. Attempts were made to recover the virus from naturally infected weeds. Experiments were also conducted in the greenhouse to ascertain what weeds were susceptible to the virus, and attempts were made to recover the virus. The longevity of the last living male of 4 vectors was ascertained on the inoculated weeds, and a record was kept of all plants on which the vectors completed their life cycle. A study of the symptoms of the disease was undertaken on both naturally infected and experimentally infected weeds.

MATERIALS AND METHODS

Weeds.—Weed seedlings were collected in the field or grown from seeds; and 10 or more plants of each species were planted in 6-inch clay pots, 8 plants to be inoculated and the remaining 2 or more to serve as controls. These controls were used to test the possibility of encountering plants that were infected in the field before being collected, and also of subsequent accidental infection in the greenhouse. They were used also in comparisons of the symptoms that appeared on the infected plants of the same species. The seedlings chosen were apparently free from all diseases. Since the plants were allowed enough time after potting—usually 3 weeks or more—to develop size and vigor for withstanding insects confined on them, there was very slight possibility of using any plant previously infected. Not a single case of aster yellows developed on weed seedlings collected in the field unless they had subsequently been placed in a cage with infective leafhoppers.

All plants were kept in one greenhouse except during the time that insects were confined on them in a second greenhouse about 120 feet away. Accidental infection of any plant with aster yellows has never been observed in the first greenhouse. The insects were maintained in the second greenhouse, and all operations involving their transfer were carried on in a headhouse separate from both greenhouses. Inoculated plants were kept under observation either until after flowering or until they died. Most plants developing symptoms were observed until their death in order to obtain a complete picture of the disease at all stages. Often this period exceeded 8 months, one yellowed plant being under observation for more than 16 months.

Vectors.—Parallel inoculation tests were made with 4 leafhopper vectors of proved ability to transmit the virus of California aster yellows. Infective populations of the mountain leafhopper, *Colladonus montanus* (V.D.) = (*Thamnotettix montanus* V.D.), and the geminate leafhopper, *Idiodonus geminatus* (V.D.) = (*T. geminatus* V.D.), were maintained on either naturally or experimentally infected celery plants, on which both species readily reproduced. Infected asters were used to perpetuate infective populations of both the short-winged leafhopper, *Macrosteles divisus* (Uhl.), and the long-winged aster leafhopper, a race of the same species (Severin, 1940).

Experimental Infection.—Infective insects were used in experiments to determine the ability of the 4 leafhoppers to complete their life cycle on all the weed species tested, as well as in experiments to determine the longevity of the males under those same conditions. Separate lots of 20 male and 20 female leafhoppers of each of the 4 vectors were confined to a single plant of each weed species, making a total of 8 plants that were subjected to experimental infections by all 4 vectors.

Recovery of Virus from Experimentally Infected Weeds.—Populations of noninfective short-winged and long-winged aster leafhoppers were maintained on Sacramento barley, a plant immune to aster yellows (Severin, 1929). Both vectors were used to recover the virus from experimentally infected weeds and transfer it to healthy asters. Twenty-five previously noninfective males, confined on each infected weed, were allowed to feed for 1 to 7 days, the time depending upon their ability to survive on different weed species. They were then removed from the weed and confined on a healthy aster plant for 30 days, to allow ample time for completion of the so-called "incubation period" of the virus in the insect. The leafhoppers were then removed, and the aster was placed in an insectproof cage, where it was observed until it was past the flowering stage or until it had shown reliable symptoms of aster yellows. Male leafhoppers were used in order to avoid egg deposition in the asters; otherwise nymphs hatched from eggs would have provided a source of accidental infection in insectproof cages where such asters were kept after removal of the insects.

Repeated attempts were often made to recover the virus from one or more plants of each species of weed, but one successful transfer of the virus to aster from any weed species was considered proof of the susceptibility of that species.

Recovery of Virus from Naturally Infected Weeds.—The procedure to recover the virus from plants naturally infected with aster yellows was almost the same as the method described above for recovering the virus from plants experimentally infected. There was, however, one difference: the naturally diseased plants, or portions therefrom, were placed in jars of water to keep them fresh. In order to confine previously noninfective insects on such plants, the stems or roots were pulled through a hole cut in the center of a piece of cardboard. The cardboard, placed on the top of a jar of water, acted as a platform upon which the insect cage was placed; and the hole, meanwhile, allowed the roots or stems of the plants to extend into the water. This is the technique described by Severin and Freitag (1934).

LIFE CYCLE AND LONGEVITY OF FOUR VECTORS

Completion of Life Cycle.—Experiments were conducted to determine whether each of the 4 vectors could complete its egg and nymphal stages on each weed species. Lots of 20 infective females of each vector oviposited in healthy weeds for 3 to 5 days, depending upon the size of the plant and upon the season. Egg deposition, on the average, is greater in summer than in winter. As a rule, the shorter period of confinement was used during the summer to avoid producing undesirably high populations of nymphs. After removal of the cage containing the females, an empty cage was placed over the plant. Daily observations were made on the emergence and longevity of the nymphs, and on their completion or noncompletion of the nymphal stages. Immediately after one or two nymphs had become adults, all insects were removed from the plant to prevent egg deposition. The plant, fumigated with "Nico-fume" tobacco-paper insecticide, was then returned to the first greenhouse, where daily observations were continued with respect to infection.

Table 1 shows the plants on which leafhoppers attained the adult stage. The leafhoppers would probably have been able to reach maturity on additional weed species if further trials had been made. In several instances tests were incomplete owing to the premature death of the plant while nymphs were still alive and sometimes in the last nymphal stage. Furthermore, weeds at the time of being caged with the insects varied in size and vigor; and an occasional plant suffered from populations of red spider, which multiplied rapidly on certain species of weeds under cage conditions. Any one of these factors could conceivably influence the results of the test and may constitute a source of error which, because single trials were made, cannot be reduced or evaluated. For these reasons, though the positive results contained in table 1 are valid, the negative results cannot be regarded as reliably significant; additional trials might yield different results with some species.

Often, on unfavorable host plants, nymphs emerged from eggs but soon died. On some plants only a very few of those hatching reached the adult stage. On more favorable host plants higher percentages survived and became adults. Nymphs were hatched from eggs of at least 1 of the 4 vectors on all weed species except *Eremocarpus setigerus,* and attained the adult stage on 50 of the 67 weeds.

Under greenhouse conditions, each of the 4 vectors can complete its nymphal stages on a rather wide range of weeds. In this respect the short-winged aster leafhopper is perhaps more restricted than the other 3 vectors. *Colladonus montanus* and *Idiodonus geminatus* seem slightly more adapted to weeds than the 2 aster-leafhopper vectors. In only 1 weed family was there any marked difference in the host-plant relations between the genera of leafhoppers. In the family Chenopodiaceae, *C. montanus* and *I. geminatus* completed their nymphal stages on 4 of the 6 species tested, but neither the short-winged nor the long-winged aster leafhopper was able to attain the adult stage on any of them.

Longevity of Males.—A comparison was made of the ability of each of the 4 vectors to survive on the 67 species of weeds tested. Lots of 20 infective males of each vector, confined in cages on healthy plants, were allowed to remain until the last insect of each lot had died, as determined by daily examinations. Then, after the cages had been removed, the plants were fumigated and returned to the first greenhouse for continued observation in regard to symptoms. Table 1 gives results of this experiment.

As in the experiments on life cycle, only single tests were made with each vector on each species of weed. Several tests may be regarded as incomplete

TABLE 1

LONGEVITY OF MALES AND COMPLETION OF LIFE CYCLE ON WEEDS*

Family, scientific, and common name of plant	Short-winged aster leafhopper		Long-winged aster leafhopper		*Colladonus montanus*		*Idiodonus geminatus*	
	Longevity	Life cycle	Longevity	Life cycle	Longevity	Life cycle	Longevity	Life cycle
	days		*days*		*days*		*days*	
Amaranthaceae								
Amaranthus retroflexus L., rough pigweed	7	C	10	—	25	C	33	—
Boraginaceae								
Heliotropium curassavicum L., alkali heliotrope	10	—	16	—	57	—	28	C
Caryophyllaceae								
Stellaria media (L.) Cyr., common chickweed	15	—	17	—	38	—	46	—
Spergula arvensis L., corn spurry	37	—	20	—	48	C	53	C
Chenopodiaceae								
Chenopodium album L., lamb's-quarters	8	—	18	—	29	C	20	C
Chenopodium murale L., nettle-leaf goosefoot	12	—	12	—	15	C	3	—
Chenopodium ambrosioides L., Mexican tea	8	—	11	—	36	C	20	C
Atriplex patula L., spear orache	10	—	10	—	29	C	75	C
Atriplex rosea L., redscale	10	—	7	—	7	—	11	C
Salsola Kali L. var. *tenuifolia* G.F.W. Mey, Russian thistle	10	—	7	—	7	—	14	—
Compositae								
Hypochoeris radicata L., hairy cat's-ear	11	—	9	—	4	C	12	—
Lactuca Scariola L. var. *integrata* Gren. & Godr., prickly lettuce	22	—	10	—	6	—	x	—
Sonchus oleraceus L., common sow thistle	50	—	15	—	6	C	8	—
Erigeron linifolius Willd., flax-leaved fleabane	70	C	110	C	12	—	72	C
Taraxacum vulgare (Lam.) Schrank., common dandelion	14	—	57	C	6	—	15	C
Grindelia camporum Greene, gum plant	11	—	56	—	5	C	7	C
Heterotheca grandiflora Nutt., telegraph plant	13	—	8	—	5	C	7	C
Aster chilensis Nees, common aster	45	C	7	C	x	—	x	C
Gnaphalium decurrens Ives var. *californicum* Gray, California everlasting	59	—	7	—	35	C	7	—
Helianthus californicus DC., California sunflower	x	—	x	—	x	—	x	C
Madia sativa Molina, Chilean tarweed	9	C	71	—	59	—	45	—
Xanthium spinosum L., spiny clotbur	28	C	65	C	15	C	10	C
Anthemis Cotula L., mayweed	20	C	10	—	30	—	45	C
Achillea millefolium L. var. *lanulosa* Piper, milfoil	51	—	48	—	72	—	80	—
Matricaria suaveolens (Pursh) Buch., pineapple weed	62	C	40	C	78	C	78	C
Cotula australis Hook., Australian brass buttons	55	—	39	—	39	—	55	—
Centaurea melitensis L., Napa thistle	24	C	22	—	14	—	24	—
Centaurea Cyanus L., cornflower	36	—	35	—	72	—	28	—
Convolvulaceae								
Convolvulus arvensis L., wild morning-glory	16	—	11	C	5	—	7	—
Cruciferae								
Brassica campestris L., common yellow mustard	18	—	41	C	67	—	35	—
Lepidium Draba L., hoary cress	9	—	9	—	14	—	21	—
Dipsaceae								
Dipsacus fullonum L., fuller's teasel	13	—	8	C	28	C	13	C
Euphorbiaceae								
Eremocarpus setigerus Benth., turkey-mullein	3	—	2	—	3	—	3	—
Euphorbia Peplus L., petty spurge	23	—	34	—	96	—	137	C
Geraniaceae								
Geranium dissectum L., cut-leaved geranium	37	C	29	C	49	C	35	C
Erodium moschatum L'Her., whitestem filaree	60	C	60	C	49	C	35	C
Hypericaceae								
Hypericum perforatum L., Klamath weed	9	—	11	—	8	—	12	—

* Explanation of symbols given at end of table on next page.

TABLE 1—*Continued**

Family, scientific, and common name of plant	Short-winged aster leafhopper		Long-winged aster leafhopper		*Colladonus montanus*		*Idiodonus geminatus*	
	Longevity	Life cycle	Longevity	Life cycle	Longevity	Life cycle	Longevity	Life cycle
	days		*days*		*days*		*days*	
Labiatae								
Marrubium vulgare L., horehound	12	—	10	—	—	—	12	—
Stachys bullata Benth.	7	—	x	—	x	—	13	x
Lamium amplexicaule L., dead nettle	7	—	40	—	46	—	25	—
Leguminosae								
Melilotus alba Desr., white sweetclover	16	—	9	C	—	C	—	C
Lotus salsuginosus Greene	14	C	9	—	133	C	35	C
Malvaceae								
Malva nicaeensis All., bull mallow	92	C	85	C	38	C	44	—
Sida hederacea (Dougl.) Torr., alkali mallow	12	—	10	—	7	—	69	—
Onagraceae								
Epilobium californicum Hausskn., willow herb	60	C	9	—	16	—	9	—
Epilobium paniculatum Nutt., panicled willow herb	124	C	22	C	122	C	113	C
Oxalidaceae								
Oxalis rubra A. St. Hill	7	—	11	C	12	—	31	—
Plantaginaceae								
Plantago lanceolata L., buckhorn plantain	61	C	71	C	74	—	97	—
Polygonaceae								
Rumex crispus L., curly dock	34	C	37	C	48	C	93	C
Rumex salicifolius Wienm., willow dock	60	—	31	—	85	C	68	C
Rumex Acetosella L., sheep sorrel	8	—	11	C	22	—	15	—
Polygonum Persicaria L., lady's thumb	8	—	12	C	8	—	34	—
Polygonum aviculare L., knotweed	11	—	18	C	7	—	15	—
Portulacaceae								
Portulaca oleracea L., purslane	12	—	8	—	6	—	12	—
Primulaceae								
Anagallis arvensis L., red pimpernel	81	—	81	C	81	C	31	—
Ranunculaceae								
Ranunculus repens L., creeping buttercup	9	—	34	C	26	—	81	—
Rosaceae								
Fragaria californica C. & S., wood strawberry	8	—	14	—	14	—	21	—
Scrophulariaceae								
Linaria repens Mill.	8	—	8	—	5	—	4	—
Scrophularia californica Cham., figwort	9	—	4	—	16	—	12	—
Diplacus aurantiacus (Curtis) Jepson, bush monkey-flower	15	—	12	—	7	—	7	—
Veronica Buxbaumii Tenore, Byzantine speedwell	26	C	23	C	15	—	34	—
Solanaceae								
Datura Stramonium L., Jimsonweed	10	C	11	C	7	C	14	C
Solanum nigrum L., black nightshade	12	—	11	—	45	C	46	C
Umbelliferae								
Conium maculatum L., poison hemlock	9	—	9	C	37	—	26	—
Foeniculum vulgare, fennel	10	—	49	—	47	C	35	C
Oenanthe sarmentosa Presl., water parsley	31	—	31	—	95	C	94	C
Urticaceae								
Parietaria officinalis L.	5	—	12	—	20	—	25	—
Urtica californica Greene, coast nettle	55	C	16	C	5	—	12	—
Total number of plant species in which life cycle was completed	..	19	..	25	..	27	..	28

* Explanation of symbols: C = Life cycle completed; — = Life cycle not completed; x = no test made.

because occasionally the longevity of the leafhopper was greater than that of the plant, or a plant died prematurely. The same sources of error are applicable in these tests as in those for the life cycle, and a longer adult life might be obtained on any weed with additional trials.

WEEDS EXPERIMENTALLY AND NATURALLY INFECTED

Weeds Experimentally Infected.—As shown in table 2, the virus was recovered from 25 species of weeds in 24 genera belonging to 14 families of plants after experimental infection by means of 1 to 4 vectors. One or more plants of six species of weeds indicated in this table showed characteristic aster-yellows symptoms after exposure to infective leafhoppers; but since the virus was not recovered from them, proof of infection is incomplete. Efforts were made to recover the virus from each of the 67 species of weeds inoculated, even if symptoms were not visible. In no case, however, was it recovered from a symptomless plant.

As may be seen by a comparison of tables 1 and 2, the plants showed no consistent connection in their host range to the virus and to the 4 vectors. Weeds susceptible to the virus were not always favorable food and breeding plants for the leafhoppers. Conversely, plants that proved to be favorable food and breeding plants were not always susceptible to infection.

The 4 vectors differed markedly in their ability to transmit the virus to healthy weeds. The number and percentages of weeds infected by each species of leafhopper, using 2 plants of each of the 25 susceptible species of weeds, were as follows: short-winged aster leafhopper 40, or 80 per cent; long-winged aster leafhopper 32, or 64 per cent; *Colladonus montanus* 16, or 32 per cent; and *Idiodonus geminatus* 12, or 24 per cent.

Table 2 shows the range and average period from inoculation by the vectors until the first symptoms developed in the weeds. There was a considerable range between the maximum, 68 days, and the minimum, 5 days. The incubation period of the disease in the plants was usually longer in winter than in summer, and was not the same for all species of weeds nor for all plants of a species.

Weeds Naturally Infected.—Forty-one species of weeds were demonstrated to be hosts of the virus under natural conditions and are listed below with their common names, their season's duration, and the locality in which they were collected.

Amaranthaceae:

Amaranthus retroflexus L., rough pigweed; annual; Montara.

Caryophyllaceae:

Stellaria media (L.) Cyr., common chickweed; annual; Milpitas.
Spergula arvensis L., corn spurry; annual; Montara.

Compositae:

Picris echioides L., bristly oxtongue; biennial; Montara.
Lactuca scariola L. var *integrata* Gren. & Godr., prickly lettuce; annual; West Sacramento.
Sonchus asper L., prickly sow thistle; annual; San Jose.
Sonchus oleraceus L., common sow thistle; annual; Irvington.
Erigeron canadensis L., horseweed; annual or biennial; Irvington.
Erigeron linifolius Willd., flax-leaved fleabane; annual or biennial; Woodlake.
Gnaphalium decurrens Ives var. *californicum* Gray, California everlasting; biennial; Montara.
Gnaphalium ramosissimum Nutt., pink everlasting; biennial; Montara.
Bidens frondosa L., beggar-ticks; annual; Half Moon Bay.

TABLE 2

WEEDS EXPERIMENTALLY INFECTED WITH VIRUS OF CALIFORNIA ASTER YELLOWS

Family and scientific name of plant	Season's duration	Number of plants showing symptoms of 2 inoculated by each of 4 vectors				Virus transferred to aster*	Incubation period of disease	
		Short-winged aster leafhopper	Long-winged aster leafhopper	*Colladonus montanus*	*Idiodonus geminatus*		Range days	Average days
Caryophyllaceae:								
Stellaria media L. (Cyr.)†	Annual	2	2	1	0	+	5–18	15
Spergula arvensis L.†	Annual	2	2	0	1	+	12–46	24
Compositae:								
Lactuca scariola L. var. *integrata* Gren. & Godr.†	Annual	2	0	0	0	+	19–20	20
Aster chilensis Nees	Perennial	0	1	1	0	–	11–22	18
Gnaphalium decurrens Ives var. *californicum* Gray†	Biennial	2	2	0	0	+	10–24	16
Madia sativa Molina	Annual	1	1	1	0	+	14–27	18
Anthemis Cotula L.†	Annual	2	1	1	2	+	5–24	13
Matricaria suaveolens (Pursh) Buch.†	Annual	2	1	2	0	+	8–33	20
Cotula australis Hook	Annual	2	2	2	0	+	18–22	20
Centaurea melitensis L.	Annual	1	1	0	0	+	13–23	18
Centaurea Cyanus L.	Annual	1	1	0	0	–	18–18	18
Cruciferae:								
Brassica campestris L.†	Annual	1	2	1	1	+	25–32	29
Dipsaceae:								
Dipsacus fullonum L.†	Biennial	2	1	0	0	+	15–29	22
Geraniaceae:								
Geranium dissectum L.	Annual	2	2	2	1	+	8–22	16
Erodium moschatum L'Her.†	Annual	2	2	1	2	+	14–20	17
Labiatae:								
Lamium amplexicaule L.†	Annual	1	1	0	0	+	26–33	30
Leguminosae:								
Melilotus alba Desr.	Annual	0	1	1	1	+	10–30	19
Lotus salsuginosus Greene	Annual	2	0	0	0	+	12–46	29
Malvaceae:								
Malva nicaeensis All.	Annual	2	2	2	1	+	12–21	18
Onagraceae:								
Epilobium californicum Hausskn.†	Annual	2	0	0	0	+	9–28	19
Epilobium paniculatum Nutt.†	Annual	2	0	0	1	+	23–36	28
Polygonaceae:								
Polygonum aviculare L.	Annual	0	1	0	0	+	39–39	39
Portulacaceae:								
Portulaca oleracea L.	Annual	1	2	1	1	+	23–53	36
Primulaceae:								
Anagallis arvensis L.†	Annual	2	2	1	0	+	15–68	26
Rosaceae:								
Fragaria californica C. & S.	Perennial	1	0	0	0	–	.....	..
Scrophulariaceae:								
Scrophularia californica Cham.	Perennial	2	2	2	1	–	.....	..
Diplacus aurantiacus Jepson	Perennial	1	0	0	0	+	11–11	11
Veronica Buxbaumii Tenore†	Annual	2	2	0	0	+	13–58	35
Solanaceae:								
Datura Stramonium L.	Annual	2	2	1	0	–	.....	..
Solanum nigrum L.†	Annual	2	2	0	1	+	12–22	16
Urticaceae:								
Urtica californica Greene	Annual	2	1	0	0	–	.....	..
Total		48	39	20	13	25		

* The plus sign (+) indicates that the virus was transferred to aster, and the minus sign (–) shows that the virus was not recovered.

† Species of weeds demonstrated to be both naturally and experimentally infected with the virus.

Compositae (*Continued*):

Bidens pilosa L., hairy bur marigold; annual; Half Moon Bay.
Hemizonia corymbosa (DC.) T. & G., coast tarweed; annual; Half Moon Bay.
Helenium puberulum DC., rosilla; perennial; San Jose.
Anthemis Cotula L., mayweed; annual; Montara.
Matricaria suaveolens (Pursh) Buch., pineapple weed; annual; Montara.
Senecio vulgaris L., common groundsel; annual; Irvington.

Cruciferae:

Raphanus sativus L., wild radish; annual or biennial; Centerville.
Brassica campestris L., common yellow mustard; annual; Niles.
Roripa curvisiliqua (Hook.) Greene, western yellow cress; annual; Geyserville.
Capsella Bursa-pastoris (L.) Medic., shepherd's purse; annual; Irvington.

Dipsaceae:

Dipsacus fullonum L., fuller's teasel; biennial; Santa Clara.

Geraniaceae:

Erodium moschatum L'Her., whitestem filaree; annual; Irvington.
Erodium cicutarium L'Her., redstem filaree; annual; Montara.

Labiatae:

Lamium amplexicaule L., dead nettle; annual; Salinas.

Leguminosae:

Medicago hispida Gaertn., bur-clover; annual; Irvington.

Malvaceae:

Malva rotundifolia L., dwarf mallow; annual; Berryessa.
Malva parviflora L., cheese-weed; annual or biennial; Irvington.

Onagraceae:

Epilobium californicum Hausskn., willow herb; perennial; Montara.
Epilobium paniculatum Nutt., panicled willow herb; annual; Montara.

Polygonaceae:

Rumex Acetosella L., sheep sorrel; perennial; Montara.
Polygonum Convolvulus L., black bindweed; annual; Montara.

Primulaceae:

Anagallis arvensis L., red pimpernel; annual; Alviso.

Scrophulariaceae:

Linaria canadensis Dum., toad flax; annual; Woodlake.
Mimulus guttatus DC., common monkey-flower; annual or biennial; Half Moon Bay.
Ilysanthes dubia Barnh.; annual; Woodlake.
Veronica americana Schwein., American speedwell; annual; Half Moon Bay.
Veronica Buxbaumii Tenore, Byzantine speedwell; annual; Montara.

Solanaceae:

Solanum nigrum L., black nightshade; annual; Montara.

As table 2 shows, 15 of the naturally infected species were included in the tests on experimental host range and were proved to be hosts under greenhouse conditions also.

Five weed species were found with typical symptoms of aster yellows, but the infection could not be demonstrated by recovery of the virus:

Compositae:

Xanthium canadense Mill., cocklebur; annual; Woodlake.

Geraniaceae:

Erodium botrys Bertol., broadleaf filaree; annual; Woodlake.

Polygonaceae:

Polygonum Persicaria L., lady's thumb; annual; Woodlake.

Solanaceae:

Datura Stramonium L., Jimsonweed; annual; Visalia.

Umbelliferae:

Ammi majus L., bishop's weed; biennial; Napa.

The virus may overwinter in certain annuals that germinate during the autumn; in biennials and perennials; and in the vectors.

SYMPTOMS ON INFECTED WEEDS

Several publications have described the symptoms of aster yellows on many plant species. The symptoms on aster have been described by Smith (1902); those on aster and other host plants by Kunkel (1927*a*, 1927*b*) and Severin (1929). No additional symptoms were observed on plants included in the weed-host range reported in this paper.

Symptoms produced on experimentally infected plants were not always identical in their degree of expression with those on weeds infected naturally in the field. There were several reasons: Plants grown under greenhouse conditions, especially when enclosed in cages, tend to become spindling and pale. Plants subjected to populations of insects often become weakened and stunted. Plants infected while young may fail to produce flowers, so that often the flower symptoms could not be ascertained. The effect of the disease on plant longevity was not uniform. Plants of some species died prematurely; the lives of others were apparently lengthened. Symptoms, though never entirely masked, were sometimes very mild. A few weed species partially recovered from severe symptom expression, such plants showing nearly normal shoots and flowers. Opportunity was not available to study the different stages of aster yellows on most naturally infected weeds, as was possible on experimentally infected plants. Symptoms on naturally infected weeds are therefore usually described from one stage only. In some instances, the infection was recent; in others, advanced. Several weeds had no flowers, so that floral symptoms could not be described for them.

The following is a brief description of the symptoms that appeared on experimentally and naturally infected weeds, from which the virus was recovered and transferred to healthy asters by previously noninfective short-winged or long-winged aster leafhoppers.

AMARANTHACEAE, AMARANTH FAMILY

A single young naturally infected plant of rough pigweed (*Amaranthus retroflexus*) was collected, which showed vein clearing on several of the younger leaves.

CARYOPHYLLACEAE, PINK FAMILY

Common chickweed (*Stellaria media*) both naturally and experimentally infected is extremely dwarfed, with stunted shoots rising from the leaf axils, often along the entire length of the stem. The stems are often twisted and curved, and the stunted tips of shoots are bent downward. The leaves are reduced in size, often rolled outward toward the petiole (plate 1, *A*), sometimes forming a small ball. The shoot tips become rosetted through shortening of internodes and production of many stunted axillary shoots. The flowers are abnormal, with some or all parts of the perianth and gynoecium green, enlarged, and leaflike. Diseased plants sometimes live longer than healthy ones; and some severely infected show a tendency toward partial recovery, producing normal shoots and flowers from rosetted parts.

The early symptoms on experimentally infected corn spurry (*Spergula arvensis*) are elongation of the internodes of floral shoots, and chlorosis of leaves and stems; the stems become angled at the nodes and sometimes slightly twisted. Stunted, chlorotic axillary shoots are formed later, which, with the main shoots and leaves, tend to assume a vertical position. The flowers are abnormal and yellowish green, and often appear vegetative. The naturally infected plants examined displayed the following symptoms: They were stunted; all diseased parts were dwarfed; the stems and (less often) the leaves were chlorotic. The stems were spindling and showed curving and twisting. The flowers often were extremely dwarfed, almost vestigial. The sepals were enlarged, linear, and thick; their tips curved tightly inward over the remainder of the floral parts, which remained undersized; the number and size of their glandular hairs were strikingly reduced. The petals were green, especially over their basal two thirds, and smaller than normal. The stamens were dwarfed and usually lacked pollen. The gynoecium was reduced in size and often chlorotic.

COMPOSITAE, SUNFLOWER FAMILY

Affected parts of naturally infected bristly oxtongue (*Picris echioides*) are spindling, chlorotic, with upright habit of growth, tending to become stunted, their parts reduced in size. The stems, especially the apical portions and young shoots, are often curved and twisted. The leaves commonly exhibit cleared venation; they are pale chlorotic green, narrowed, becoming linear and elongate, with reduction in size of the leaf spines. The upper apical leaves are often outwardly curled toward the petiole. The flowers are chlorotic and reduced in size, the involucre being much less affected than the remaining floral parts. In some plants the involucre may be only slightly reduced, its flowers chlorotic green; but when more severely affected, it may be extremely dwarfed, widely opened, almost scarious, with undeveloped flowers.

Cleared veinlets (plate 2, *A*) appear on the youngest leaves of both naturally and experimentally infected prickly lettuce (*Lactuca scariola* var. integrata), which become dwarfed. Stunted, chlorotic axillary shoots are produced, especially from the apical parts of the stem, bearing many chlorotic flower buds (plate 2, *B*). These buds generally become dry before expanding or, if they open, are yellowish green and wither quickly. The tips of such stems become rosetted because of shortened internodes with profuse production of axillary shoots.

The most conspicuous symptom on naturally infected common sow thistle (*Sonchus oleraceus*) is the bushy appearance of the infected plants, owing to the stunted, chlorotic axillary and apical shoots.

Prickly sow thistle (*Sonchus asper*) naturally infected with aster yellows shows numerous chlorotic shoots with curved petioles and upright outer leaves (fig. 1). Infected tall plants are conspicuous in the field because of the stunted axillary shoots with dwarfed, yellow leaves.

The symptoms on naturally infected horseweed (*Erigeron canadensis*) are as follows: axillary shoots arising from the axils of the leaves on the main stem; stunted floral shoots bearing dwarfed, yellowish green flower heads, loosely expanded, with the corollas elongated.

Naturally infected flax-leaved fleabane (*Erigeron linifolius*) is stunted, with an enormous number of chlorotic axillary shoots bearing recurved linear leaves (fig. 2). The younger leaves on the main stem and often on the axillary shoots show cleared veinlets. The leaves are stiff and brittle. A purplish discoloration occurs on the upper part of the main stem and axillary shoot, including the leaves.

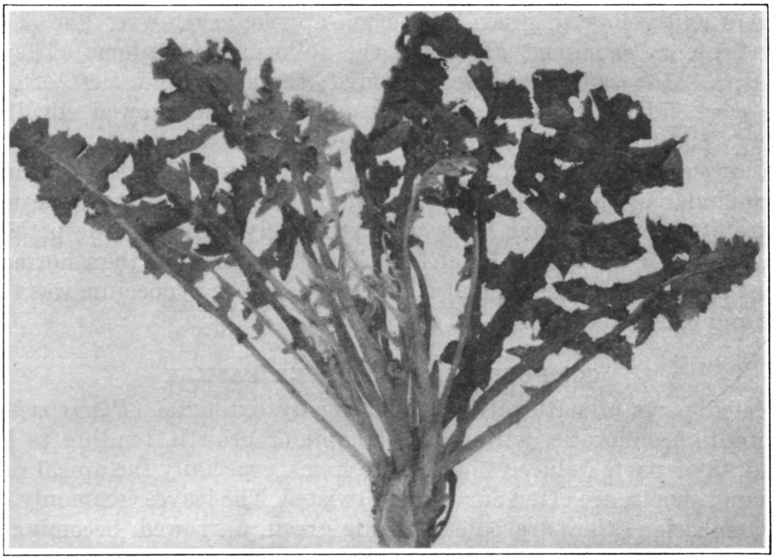

Fig. 1.—Naturally infected prickly sow thistle (*Sonchus asper*): longitudinal section of infected plant, showing chlorotic axillary shoots with curved petioles and upright outer leaves. (Santa Cruz, October 20, 1936.)

The first symptom on experimentally infected California everlasting (*Gnaphalium decurrens* var. *californicum*) is a clearing of the veinlets on the younger leaves, often only on half the blade, the midrib then usually becoming curved. The plants soon appear dwarfed, the younger leaves being chlorotic, curled outward and downward. Stunted axillary shoots develop. The flowers are dwarfed, yellowish green, almost scarious, with loose involucres. The naturally infected plants observed did not show any marked stunting. Other symptoms were essentially those that appeared on experimentally infected plants.

Symptoms found on naturally infected pink everlasting (*Gnaphalium ramosissimum*) were rather obscure and were confined to the flower heads. The latter were but slightly chlorotic green; they were inconspicuously larger than normal heads, owing to a slight elongation of the florets and to a more loosely expanded condition of the head instead of a compact arrangement as in the healthy head. The parts tend to be slightly more scarious than normal.

On beggar-ticks (*Bidens frondosa*) naturally infected with aster yellows, the younger apical leaves are dwarfed; and many of the older leaves are chlorotic, with vein clearing. The plants are dwarfed and develop stunted

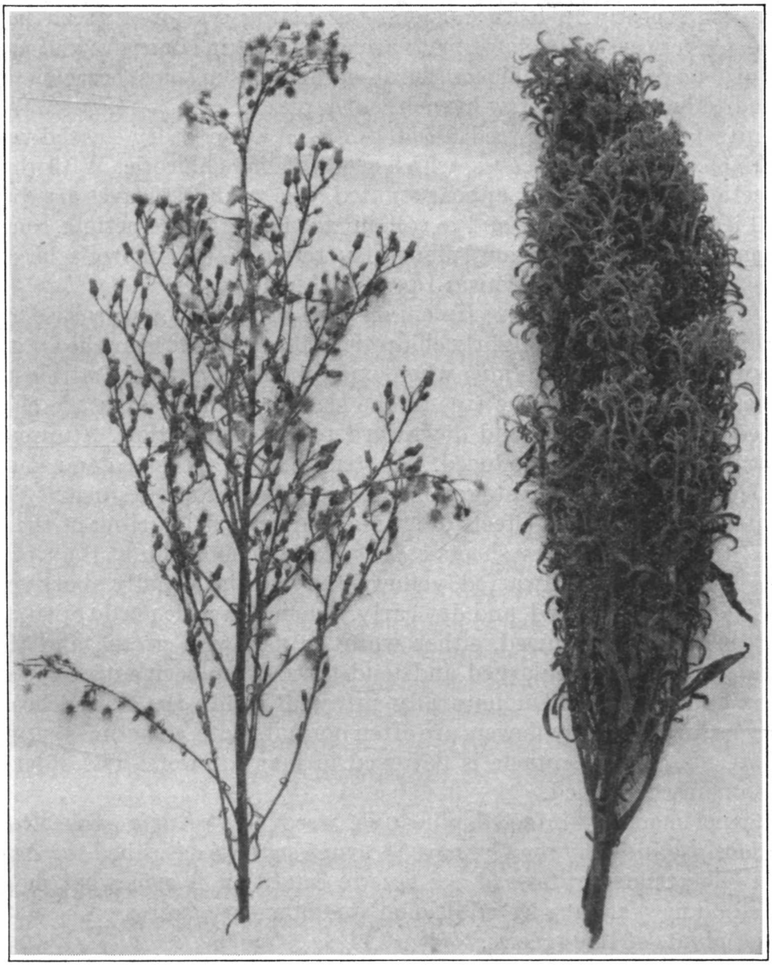

Fig. 2.—Flax-leaved fleabane (*Erigeron linifolius*): left, main apical branch from a healthy plant; right, main apical branch from a naturally infected plant, showing an enormous number of axillary shoots bearing recurved, linear leaves. (King City, September 11, 1928.)

axillary shoots. The flower heads and the flowers themselves are usually very dwarfed and yellowish green. The bracts of the receptacle and flowers often are enlarged and spreading, so that the head is loosely open rather than compact.

Naturally infected *Bidens pilosa* exhibits symptoms essentially the same as those on beggar-ticks (*B. frondosa*). The proliferation of dwarfed, stunted axillary shoots from nodes, especially on the apical parts of stems, is more profuse and striking than on the beggar-ticks.

Plants of naturally infected coast tarweed (*Hemizonia corymbosa*) are stunted; the internodes of the affected parts of the plants are greatly shortened. The most striking symptoms consist of abnormal flowers, from which are proliferated stunted, dwarfed, entirely vegetative, green, leafy shoots. The shoots occur mostly in loose clusters, resembling scattered green balls. In some less severe cases the floral parts are green, but in structure and arrangement are more recognizable as floral organs. Symptoms occasionally are confined to only one or a few branches of a plant.

On infected Chilean tarweed (*Madia sativa*), a transitory cleared venation appears on the younger leaves, which soon become chlorotic. With the onset of infection, plants quickly appear stunted. The youngest leaves are dwarfed, and all leaves tend to twist and to roll outward toward the petiole, sometimes to a marked degree. A young plant may resemble an umbrella because of severe stunting and the downward position of the leaves.

Naturally infected rosilla (*Helenium puberulum*) shows profuse axillary branching, with stunted, slightly chlorotic axillary shoots near the apex.

Mayweed (*Anthemis Cotula*) when experimentally infected with aster yellows becomes stunted at the tips of the shoots. Young leaves are chlorotic, dwarfed, curled outward and downward toward the petiole. Stunted, chlorotic axillary shoots are produced. The stems often are twisted and sometimes curved; and, during early stages of infection, the internodes usually become elongated. The combined effects of stunting, downward curling of the leaves, and production of axillary shoots cause a rosette condition at the tips of the shoots. The flowers are dwarfed, yellowish green, and usually abortive; their heads often fail to expand, and dry early. When flower heads do open, the ray flowers are greatly reduced, either white or yellowish green; and the disk flowers are somewhat enlarged and tend toward replacement of their parts by leaflike structures. On naturally infected plants the flower heads are usually reduced; the ray flowers are often normal white, sometimes suppressed and scarious. The receptacle is flattened in many flowers. The older leaves are commonly reddened.

On experimentally infected pineapple weed (*Matricaria suaveolens*) the symptoms produced by the virus are the same as those described for *Anthemis Cotula*. The tendency toward the rosette condition is somewhat more pronounced on most plants. No additional symptoms are expressed by naturally infected plants of this species.

On *Cotula australis*, experimental infection causes chlorosis and stunting of the tips of the stems. In early stages of the disease the internodes and petioles of young leaves sometimes become elongated. Later all growth is retarded, the internodes are greatly shortened, and the leaves are dwarfed, curling outward and downward toward the petiole. Chlorotic, stunted axillary shoots are produced, and the tips of the stems form rosettes. The flowers are much reduced in size, with pedicels shortened and all parts chlorotic. The longevity of some plants is increased. Partial recovery was observed in one: the chlorosis disappeared, new growth developed, and apparently normal flowers were produced.

The symptoms on naturally infected common groundsel (*Senecio vulgaris*) are as follows: spindling, chlorotic stems with the apical part crooked and often twisted; internodes somewhat lengthened; peduncles chlorotic, greatly elongated, and spindling; involucre reduced and loose; flowers yellowish green, with the gynoecium and corolla elongated; disk flowers in extreme cases transformed into abnormal flower heads subtended by elongated spindling pedicels (plate 3, *A*, *B*). The pappus is sometimes absent.

Napa thistle (*Centaurea melitensis*) experimentally infected with aster yellows becomes stunted and spindling. The leaves are dwarfed and mildly chlorotic, assuming an upright position. Seven months after the first symptoms appeared, one plant developed flowers that were reduced in size but were apparently normal.

CRUCIFERAE, MUSTARD FAMILY

Wild radish (*Raphanus sativus*) naturally infected with aster yellows shows a clearing of the veins, and a slight chlorosis is evident on the younger leaves. A curvature of the midrib, a slight twisting of the petioles, and twisting and curvature of the stem occur. Flowers are green and often proliferated, with enlarged, thickened, green sepals; the petals reduced and colorless; the stamens enlarged, yellowish green, trilobed, leaflike; and the two carpels separate, dark green, and leafy.

Common yellow mustard (*Brassica campestris*), both naturally and experimentally infected with aster yellows, produces chlorotic axillary shoots and abnormal, green flowers on elongate, chlorotic peduncles. The pods on these peduncles are often greatly enlarged, curved, and flattened (plate 1, *C*) or sometimes become modified into 2 dwarfed floral shoots, which develop additional, abnormal flowers. The stems are often twisted and crooked. The floral shoots at first show accelerated growth; but later all floral and axillary shoots, flowers, and leaves become dwarfed. After periods of severe symptoms, occasional plants produce normal-appearing flowers.

Naturally infected western yellow cress (*Roripa curvisiliqua*) is stunted and dwarfed; leaves, especially the younger, are chlorotic; petioles are often curved or twisted; and pinnules show varying degrees of outward cupping. The older leaves tend to become flattened on the ground.

Shepherd's purse (*Capsella Bursa-pastoris*) naturally infected with aster yellows is stunted, with stems and peduncles of flowers thin and spindling. The flowers are often abnormal and dwarfed, with little chlorosis. They are usually normal in color, but develop dwarfed, compounded, floral shoots from the gynoecium (plate 2, *C*, *D*).

DIPSACEAE, TEASEL FAMILY

The first symptoms of the disease on experimentally infected fuller's teasel (*Dipsacus fullonum*) was clearing of the veinlets and chlorosis of young leaves, sometimes only in localized areas on one side or near the base of a leaf. Growth occasionally was temporarily accelerated after the onset of the disease, the petioles of some leaves becoming slightly twisted. Later, plants were somewhat stunted, the leaves remaining faintly chlorotic and assuming an upright habit of growth. No flowers were produced. Individual flowers of the affected floral heads of naturally infected plants are yellowish green and leaflike. The stem may continue growth through the terminal flower head, so that often more than one floral head is borne on a single stalk. The bracts are reduced and softened.

GERANIACEAE, GERANIUM FAMILY

Cut-leaved geranium (*Geranium dissectum*), experimentally infected with aster yellows, develops leaves with divisions reduced in number from 5 to 3, with entire margins. The younger and older leaves become cupped outward toward the petiole. In the first stages of the disease the petioles and primary shoots become elongated and chlorotic. Subsequent growth is retarded, spindling, and chlorotic; the internodes are shortened, and the leaves dwarfed (plate 1, *B*). Stunted axillary shoots appear, and the plants assume an upright habit of growth. The flowers are dwarfed and abnormal; the perianth and gynoecium often become leaflike and yellowish green. Plants are often rosetted through production of stunted axillary shoots from the crown.

Naturally and experimentally infected whitestem filaree (*Erodium moschatum*) develop dwarfed, chlorotic leaves with leaflets inwardly rolled along the margins. Stunted, chlorotic axillary shoots are produced from the crown or nodes of the stems. Often shoots continue to grow without reduction in length of the internodes, producing dwarfed axillary shoots that form rosettes at the nodes (plate 4, *A*). The tips of stems are chlorotic and often stunted. Abnormal flowers are formed, with all parts usually yellowish green, the sepals enlarged and crinkly (plate 4, *B*, *D*), the petals reduced and generally greenish but often normal in color, and the gynoecium shortened and enlarged. Often the replacement of the flower parts by vegetativelike structures is extreme, with the sepals and especially the carpels remarkably leaflike (plate 4, *C*, *D*). Affected leaves commonly become reddened during later stages of infection. Partial recovery is not uncommon among plants that have shown severe symptoms.

Symptoms of aster yellows on naturally infected redstem filaree (*Erodium cicutarium*) include general slight chlorosis of the entire plant, often with reddening of the outer, older leaves. The plants are stunted. Younger, inner leaves of crowns and shoot tips and apical leaves appear chlorotic and dwarfed. Petals and stems are often moderately twisted. Dwarfed, chlorotic axillary crowns are produced.

LABIATAE, MINT FAMILY

The apical part of the stem of experimentally infected dead nettle, or giraffe head (*Lamium amplexicaule*) becomes chlorotic and stunted, with mild chlorosis of the young leaves on the dwarfed plants. Stunted, chlorotic axillary shoots are produced. The flowers are abnormal and green, sometimes of usual size. Often, however, the calyx tube is elongated, and there is broadening of the tips of the sepals and petals, usually accompanied by an elongation of the pistil, which develops leaflike parts. Plants naturally infected are more severely stunted; and the gynoecia of abnormal flowers usually are transformed, each into a dwarfed shoot. The closely appressed, dwarfed, chlorotic, abnormal flowers form capitate heads at the tips of affected shoots.

LEGUMINOSAE, PEA FAMILY

Bur-clover (*Medicago hispida*) infected in nature is stunted, showing twisted stems angled at nodes, with shortened internodes, stunted axillary shoots. Leaves are dwarfed, mildly chlorotic (fig. 3), with faint vein clearing.

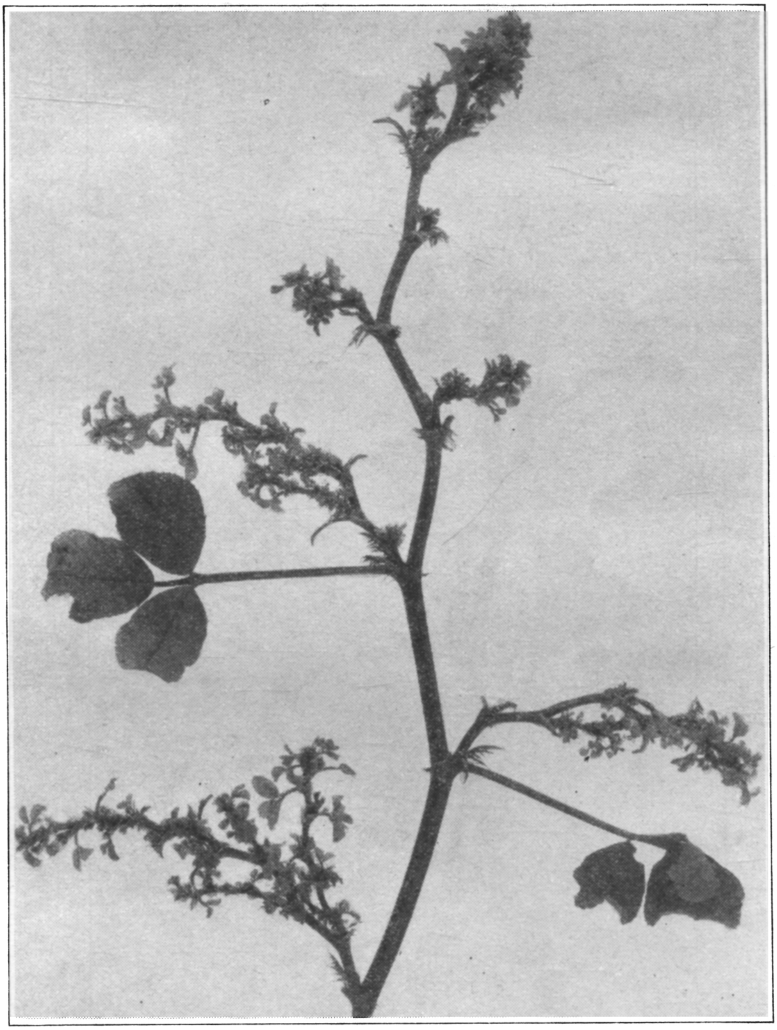

Fig. 3.—Tip of a main branch of bur-clover (*Medicago hispida*) from a plant naturally infected with aster yellows, showing stunting, twisting, and angling of the stem at the nodes; shortened internodes; and stunted axillary shoots with dwarfed, mildly chlorotic leaves. (Irvington, January 11, 1939.)

Experimentally infected white sweetclover (*Melilotus alba*) develops numerous stunted axillary shoots on the dwarfed plants. The flower heads are dwarfed and chlorotic; the buds often become dry before expanding. Infected plants die prematurely.

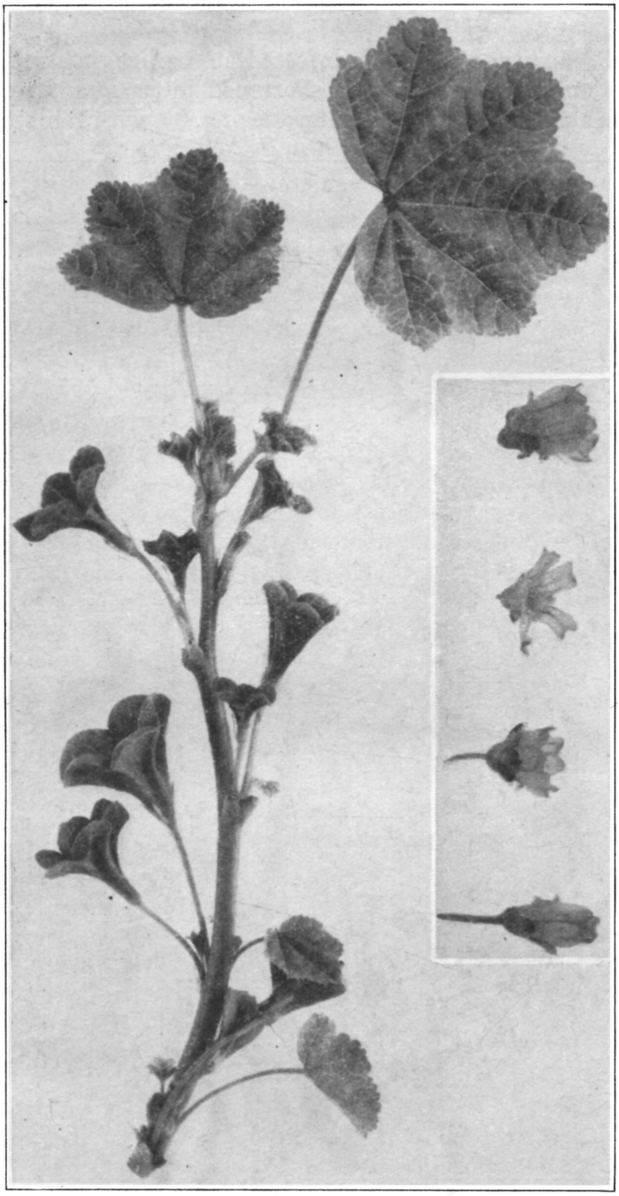

Fig. 4.—Dwarf mallow (*Malva rotundifolia*) naturally infected with aster yellows, showing apical portion of shoot with cleared veinlets on the larger leaves and with dwarfed axillary shoots bearing outwardly rolled dwarfed leaves. A striking symptom is the enlarged green corolla. (Berryessa, September 26, 1934.)

Lotus salsuginosus, experimentally infected, is dwarfed. The stunted axillary shoots bear small, brittle, slightly chlorotic leaves, which later assume a reddish discoloration. The stems become angular at nodes. No flowers are produced.

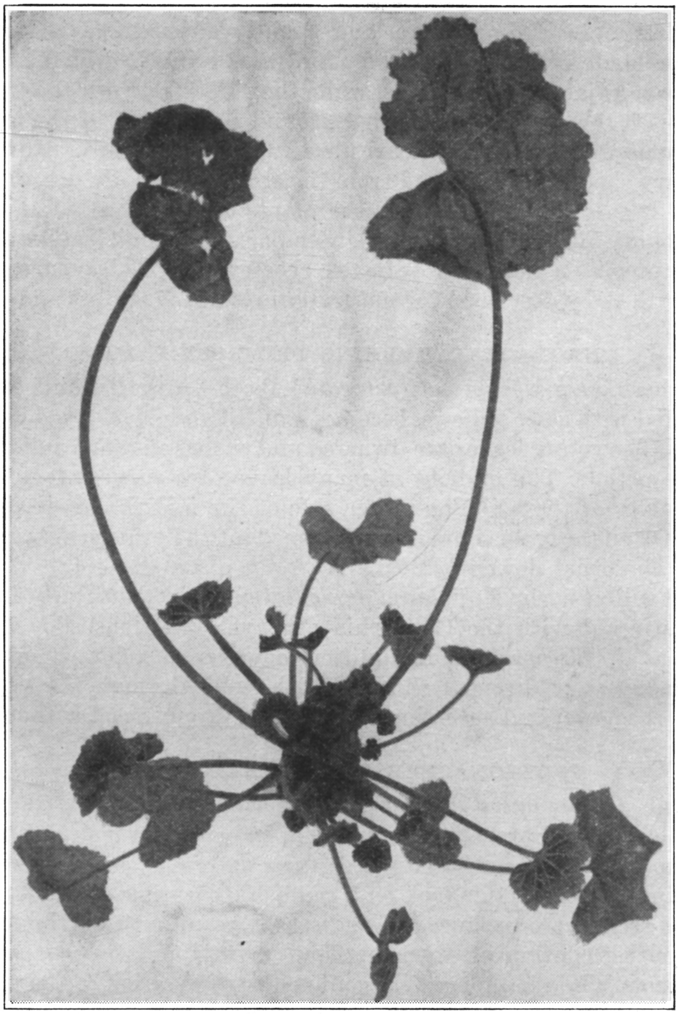

Fig. 5.—Bull mallow (*Malva nicaeensis*) experimentally infected with aster yellows, showing outward-cupped older and younger leaves; and stunted axillary shoots forming a rosette at crown of plant.

MALVACEAE, MALLOW FAMILY

Dwarf mallow (*Malva rotundifolia*) naturally infected with aster yellows shows cleared veinlets on the younger leaves, with yellow veinbanding on the older leaves. Small axillary shoots are developed that bear dwarfed, outwardly rolled leaves (fig. 4). A striking symptom is the enlarged green corolla (fig. 4). Plants infected when young present, in an advanced stage of the disease, a dwarfed appearance, are bunched close to the surface of the ground, and have several large older leaves with greatly elongated petioles.

During early stages of experimental infection of bull mallow (*Malva nicaeensis*), the young leaves develop cleared veinlets and elongated petioles. Later the young leaves are dwarfed and display a unique condition in being upright in habit, stiff in texture, and slightly cupped inward toward the petiole. The blade is fluted, with the main veins lying in troughs, which are usually green adjacent to the veins, while the ridges between the troughs are chlorotic, with the chlorosis extending around the margin of the leaf. Sometimes older as well as younger leaves are cupped outwardly. Stunted, chlorotic axillary shoots are produced from the crown; these are upright in habit of growth. If infected while young, the plants become rosetted at the crown (fig. 5). Abnormal flowers are formed, with parts becoming leaflike and green.

The symptoms on naturally infected cheeseweed (*Malva parviflora*) are identical with those described for naturally infected *M. rotundifolia.*

ONAGRACEAE, EVENING PRIMROSE FAMILY

Willow herb (*Epilobium californicum*), both naturally and experimentally infected with aster yellows, becomes stunted and develops chlorotic axillary shoots. The young leaves are dwarfed and curled outward and downward toward the petiole. The midribs of many leaves are curved, forming asymmetrical halves of the blade on either side of the midrib. Green flowers are produced. Often the gynoecium is transformed into a floral shoot that develops additional abnormal flowers.

Panicled willow herb (*Epilobium paniculatum*), both naturally and experimentally infected with the California aster-yellows virus shows the same symptoms as *E. californicum;* in addition, however, the elongate ovary often develops many very dwarfed shoots, which grow through the sides of the receptacle, the flower bud becoming abortive and dropping off without opening (fig. 6).

POLYGONACEAE, BUCKWHEAT FAMILY

Knotweed (*Polygonum aviculare*), experimentally infected, produced slightly chlorotic axillary shoots near the apical end of a main branch. These axillary shoots were somewhat stunted; their dwarfed leaves showed faintly cleared veinlets, which later took on a reddish coloration. Normal-appearing flowers and seeds were produced. The diseased plant outlived the controls by several months, continuing to make slow growth and to produce stunted axillary shoots. The symptoms were confined to one section of the plant only, and this was the last to die.

The only signs of aster yellows discernible on two plants of naturally infected black bindweed (*Polygonum Convolvulus*) were the abnormal, chlorotic, green proliferated flowers.

The most striking symptoms displayed by naturally infected sheep sorrel (*Rumex Acetosella*) were stunting and yellowing. The older leaves were generally tinged with red, the petioles often curved, and secondary crowns produced. Since no flowers were present on the plants observed, the floral symptoms could not be ascertained.

PORTULACACEAE, PURSLANE FAMILY

Experimentally infected common purslane (*Portulaca oleracea*) shows a spindling upright growth, with internodes somewhat elongated, and with the stems and leaves paler than normal. The apical leaves are dwarfed and chlorotic, and the younger leaves are usually bent downward from the base of the petioles. The stems are often twisted and slightly curved. The leaves drop early, and the plants die prematurely.

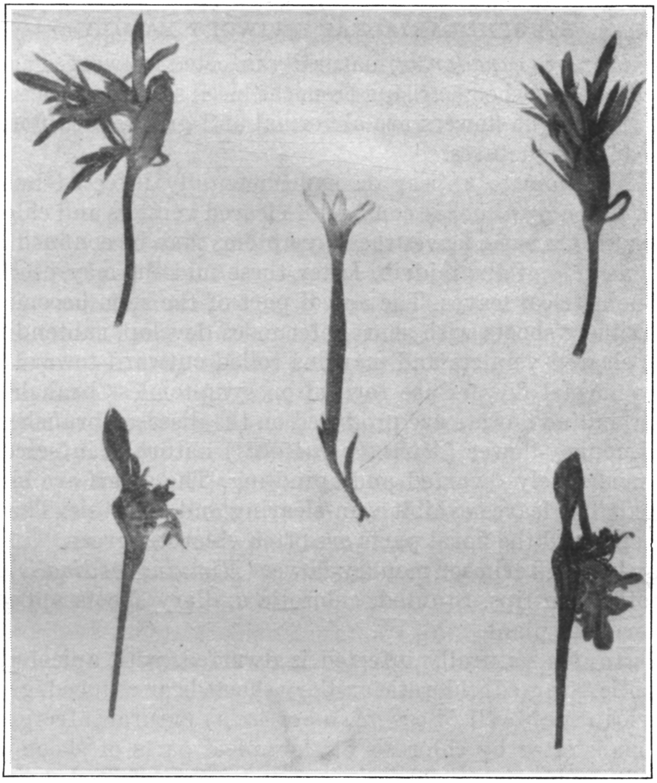

Fig. 6.—Panicled willow herb (*Epilobium paniculatum*): center, healthy flower from check or control plant, surrounded by four abnormal flowers from plant experimentally infected with aster yellows, showing stages in the development from the gynoecium of many dwarfed shoots, which grew through the sides of the receptacle. The abortive flower buds are still present on the two lower flowers.

PRIMULACEAE, PRIMROSE FAMILY

The growth of affected stems of experimentally infected red pimpernel (*Anagallis arvensis*) is accelerated during the early stages of infection. The stems are spindling, chlorotic, and often twisted, with elongated internodes. Young leaves near the tips of affected stems are cupped upward and slightly chlorotic. The flowers are subtended on elongated, spindling, chlorotic peduncles; the floral parts are yellowish green and sometimes greatly reduced.

Or, more often, the calyx is enlarged, the corolla is reduced, and the gynoecium develops into an abnormal shoot, with the carpels separated and leaflike. Naturally infected plants are dwarfed, with the stems twisted and slightly curved. The flowers are abnormal, with pedicels shortened; the calyx is enlarged and flatly expanded; the petals are reduced and are dark green, edged with magenta, or entirely magenta in color, cupped inwardly, or vestigial and yellowish. The gynoecium usually is reduced and flattened, sometimes on a peduncle; often the carpels are separated and leaflike.

SCROPHULARIACEAE, FIGWORT FAMILY

Toad flax (*Linaria canadensis*) naturally infected is dwarfed and chlorotic, with stunted axillary shoots arising from the basal section of the stems. Stems are often twisted. The flowers are abnormal and green, with floral parts replaced by leaflike structures.

The first symptom to appear on experimentally infected bush monkey-flower (*Diplacus aurantiacus*) consists of cleared veinlets and chlorosis of the youngest leaves. On some leaves these symptoms may be confined to the basal section on one side of the midrib. Later these midribs may become curved, causing asymmetrical leaves. The apical part of the stem becomes chlorotic. Chlorotic axillary shoots with short internodes develop, subtending reduced leaves with cleared veinlets and margins rolled outward toward the petiole. Apparently normal flowers are formed on symptomless branches of an infected plant, but no flowers are produced on the diseased branches.

Common monkey-flower (*Mimulus guttatus*) naturally infected with aster yellows is moderately dwarfed and spindling. The stems are chlorotic and often twisted. The leaves exhibit vein clearing and chlorosis. The flowers are reduced in size, and the floral parts are often chlorotic green.

Naturally infected crimson monkey-flower (*Mimulus cardinalis*) is dwarfed, with chlorotic stem tips. Stunted, chlorotic axillary shoots appear near the basal section of the plant.

Ilysanthes dubia naturally infected is dwarfed, with apical parts of the stems chlorotic. Stunted, chlorotic axillary shoots bear reduced, green flowers.

On American speedwell (*Veronica americana*) natural infection with aster yellows is manifested by chlorosis of the apical parts of shoots and leaves. Cleared venation is often visible on younger leaves. Affected shoots are somewhat spindling and tend to adopt an upright habit of growth. Stunted, chlorotic axillary shoots are sometimes produced at the nodes. The floral parts often are chlorotic green; and proliferated, chlorotic green, abnormal flowers are sometimes produced.

The leaves of naturally and experimentally infected Byzantine speedwell (*Veronica Buxbaumii*) develop faint, cleared veinlets; become reduced in size, broader, shorter, and more rounded; and are curled outward toward the petioles on the dwarfed plants. The apical parts of the stems are chlorotic and often twisted. Stunted, chlorotic axillary shoots are produced. The flowers are abnormal and yellowish green, and are subtended on elongated spindling peduncles that wither early. Some plants partially recover later. Similar symptoms are expressed on plants naturally infected, chlorosis and green flowers being the most striking of those exhibited.

SOLANACEAE, NIGHTSHADE FAMILY

During early stages of both natural and experimental infection in black nightshade (*Solanum nigrum*), interveinal chlorosis often appears on the young leaves of the dwarfed plants, the main veins being banded with green. Cleared veinlets are present on some leaves. The leaves are sometimes cupped inward or outward; occasionally the margins are rolled inward toward the midrib. Often the midribs are curved, and the leaf margins indented. Many leaves are bent downward from the base of the petiole. New leaves are very dwarfed, chlorotic, and usually deformed. Stunted, chlorotic axillary shoots are produced from the buds in the axil of the leaves. In severe infections growth is greatly inhibited; the entire plant becomes yellowish green and rigid, and dies prematurely. No recovery takes place.

HOST-RANGE DIFFERENCES BETWEEN CALIFORNIA AND NEW YORK ASTER YELLOWS

Kunkel (1926) was unable to infect plants belonging to the family Leguminosae with the virus of New York aster yellows. He states: "Yellows was not transmitted to any leguminous plant although many species and varieties were exposed under favorable conditions for infection."

Two species of weeds, white sweetclover (*Melilotus alba*) and *Lotus salsuginosus* in the family Leguminosae, proved susceptible to the virus of California aster yellows under greenhouse conditions (table 1); and one species in the same family, bur clover (*Medicago hispida*), was proved to be infected under natural conditions. It is not known whether any of these three species in the Leguminosae were included among those species tested by Kunkel. Conceivably, however, the susceptibility of these Leguminosae may constitute another difference between the strains of California and New York aster yellows.

Overlapping host ranges of the viruses of California and New York aster yellows include the following 3 species of weeds: *Plantago major* (Severin, 1929), *Erigeron canadensis,* and *Sonchus oleraceus,* belonging to two families.

SUMMARY

Leafhopper vectors of California aster yellows completed their life cycles on various weed species as follows: short-winged aster leafhopper (*Macrosteles divisus*), 19 species; long-winged aster leafhopper (*M. divisus*), 25 species; mountain leafhopper (*Colladonus montanus*), 27 species; and geminate leafhopper (*Idiodonus geminatus*), 28 species.

The longevity of adult males of the 4 vectors on 67 weed species was compared.

Experimentally, 25 species of weeds in 24 genera belonging to 14 families were infected with the aster-yellows virus by means of 1 to 4 vectors, including 22 annuals, 2 biennials, and 1 perennial. The virus, recovered by previously noninfective short-winged or long-winged aster leafhoppers from the infected weeds, was transferred to asters. Six species of inoculated weeds developed symptoms of aster yellows, but the virus was not recovered from them. Partial disappearance of symptoms occurred in some of the species.

In all, 41 species of weeds in 31 genera belonging to 14 families were demonstrated to be naturally infected with the aster-yellows virus, including 28 annuals, 5 annuals or biennials, 4 biennials, and 4 perennials. The virus was recovered by previously noninfective short-winged or long-winged aster leafhoppers from the infected weeds and transferred to asters. Although 5 additional weed species showed typical symptoms of aster yellows under natural conditions, all efforts to recover the virus from them were unsuccessful. The virus overwinters in annual, biennial, and perennial weeds and in its leafhopper vectors.

Host-range differences included 3 species of weeds, in the family Leguminosae, apparently reacting differently to the California and New York strains of the aster-yellows virus, although it is not known whether these species were subjected to experimental infection by Kunkel. Overlapping host ranges of the two strains of viruses include 3 weed species.

The symptoms are described for each weed species proved to be either experimentally or naturally infected with the virus.

ACKNOWLEDGMENT

The species and varieties of weeds were identified by Dr. H. L. Mason and the late Miss Ethel Crum, Department of Botany, University of California.

LITERATURE CITED

KUNKEL, L. O.

1926. Studies on aster yellows. Amer. Jour. Bot. 13:646–705. *Also in:* Boyce Thompson Inst. Contrib. 1:181–240.

1931. Studies on aster yellows in some new host plants. Boyce Thompson Inst. Contrib. 3:85–123.

OGILVIE, L.

1927*a*. Aster yellows. Bermuda Dept. Agr. Bul. 6(5):7–8.

1927*b*. Aster yellows. Bermuda Dept. Agr. Bul. 6(8):3.

SEVERIN, H. H. P.

1929. Yellows disease of celery, lettuce, and other plants, transmitted by *Cicadula sexnotata* (Fall.). Hilgardia 3(18):543–83.

1940. Potato naturally infected with California aster yellows. Phytopathology 30(12): 1049–51.

SEVERIN, H. H. P., and J. H. FREITAG.

1934. Ornamental flowering plants naturally infected with curly top and aster-yellows viruses. Hilgardia 8(8):233–60.

1938. Western celery mosaic. Hilgardia 11(9):459–558.

SEVERIN, H. H. P. and N. W. FRAZIER.

1945. California aster yellows on vegetable and seed crops. Hilgardia 16(12):573–96.

SEVERIN, H. H. P. and J. H. FREITAG.

1945. Additional ornamental flowering plants naturally infected with California aster yellows. Hilgardia 16(12):599–618.

SMITH, R. E.

1902. Growing China aster. Hatch Exp. Sta., Massachusetts Agr. Col. Bul. 79:1–26.

THOMPSON, ROSS C.

1944. Reactions of *Lactuca* species to the aster yellows virus under field conditions. Jour. Agr. Res. 69(3):119–25.

PLATES

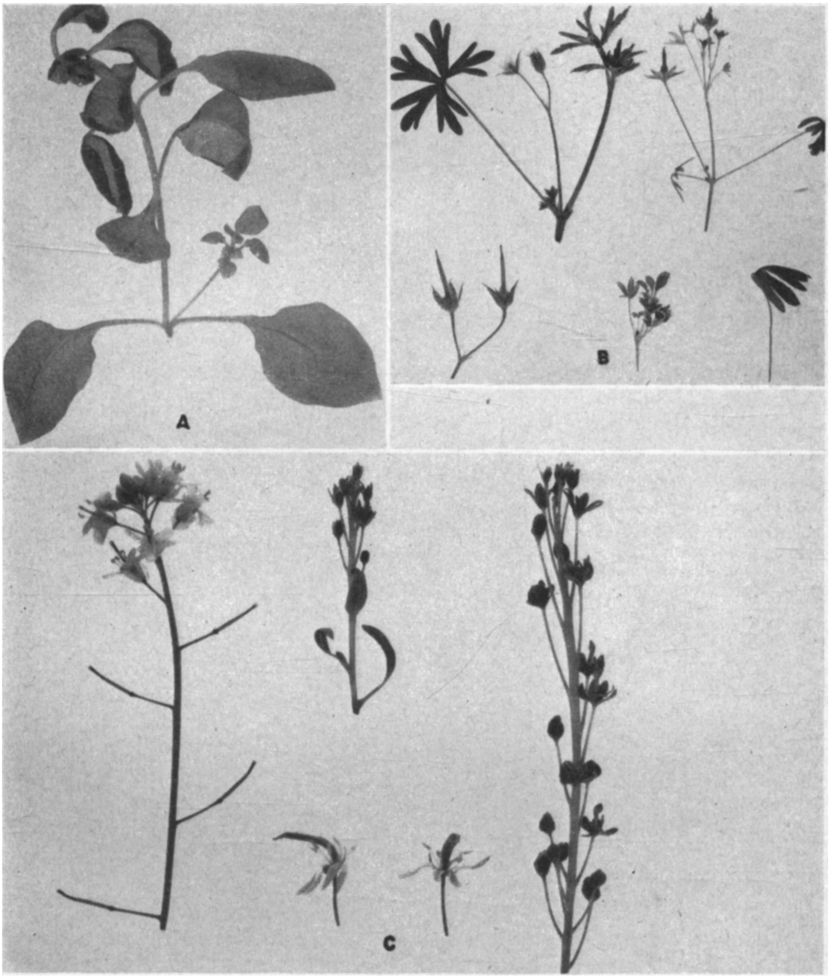

Plate 1.—*A*, Common chickweed (*Stellaria media*) experimentally infected with aster yellows, showing outward rolling of the leaves toward the petioles. *B*, Cut-leaved geranium (*Geranium dissectum*): upper left, apical end of stem from healthy check or control plant; upper right, tip of stem from an experimentally infected plant, showing retarded, chlorotic, and spindling growth with dwarfed leaves; lower left, gynoecium from normal plant; lower center, dwarfed floral shoot with small, abnormal, yellowish-green flowers; lower right, leaf from an experimentally infected plant, showing outward cupping toward the petiole. *C*, Common yellow mustard (*Brassica campestris*): left, tip of floral shoot from healthy plant used as a check or control, showing normal flowers and pods; upper center and right, tips of floral shoots from plants experimentally infected with aster yellows, showing abnormal green flowers on elongated, chlorotic peduncles; lower center, diseased flowers with enlarged, curved, and flattened pods.

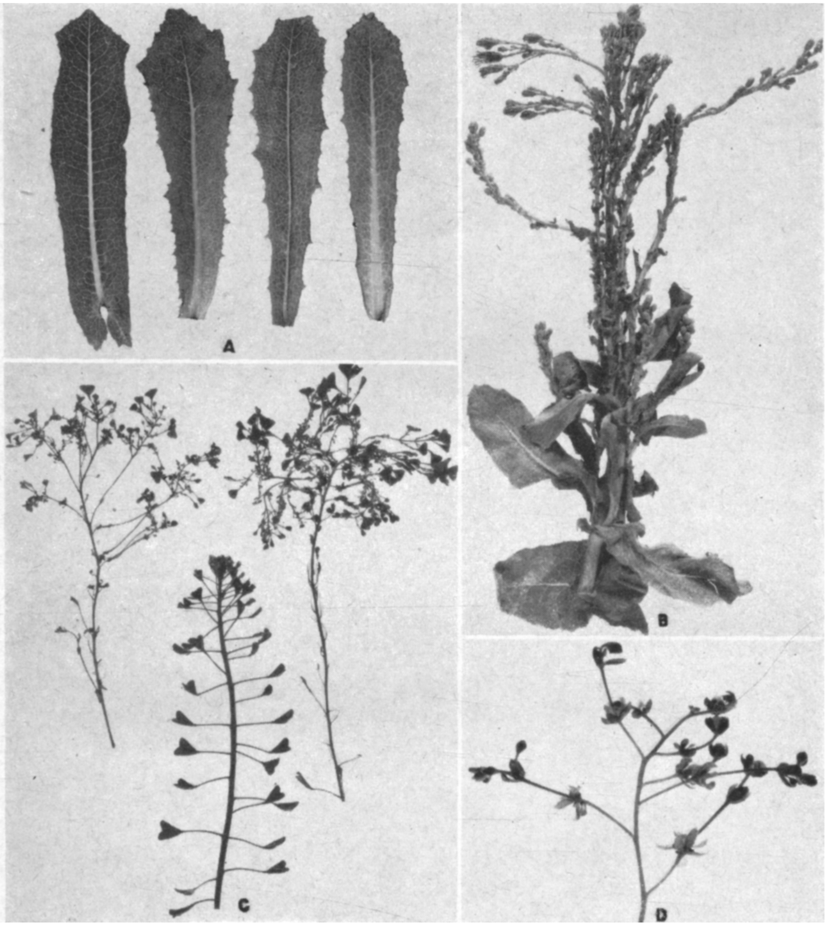

Plate 2.—*A*, *B*, Prickly lettuce (*Lactuca scariola* var. *integrata*): *A*, Left, leaf from healthy plant; right, three leaves showing cleared venation. *B*, Apical part of main branch, showing axillary shoots and numerous yellowish-green flower buds. (West Sacramento, October 9, 1931.) *C*, *D*, Shepherd's purse (*Capsella Bursa-pastoris*) naturally infected with aster yellows. *C*, Center, tip of floral shoot from healthy plant; left and right, apical end of floral shoots from diseased plants naturally infected with aster yellows, showing thin, spindling stems and peduncles; abnormal, dwarfed flowers; and dwarfed, compounded floral shoots developing from the gynoecium. *D*, Compound floral shoot originating from the gynoecium of a single abnormal flower. (Irvington, January 13, 1939.)

Plate 3.—Common groundsel (*Senecio vulgaris*): *A*, Center, flower head from a healthy plant, surrounded by four abnormal flower heads from plants naturally infected with aster yellows, showing chlorotic, elongated, and spindling peduncles; reduced, loose involucre; and yellowish-green disk flowers subtended by elongated, spindling pedicels. *B*, Single abnormal flower head from a plant infected with aster yellows under natural conditions, showing abnormal, chlorotic disk flowers subtended on elongated, spindling pedicels. (*A* and *B* were collected at Irvington, January 13, 1939.)

Plate 4.—Whitestem filaree (*Erodium moschatum*), from plants naturally infected with aster yellows: *A*, part of stem showing rosette formation at node by dwarfed axillary shoots; *B*, floral cluster at apical end of shoot, showing stunting, chlorosis, and several stages of phyllody; *C*, *D*, single abnormal flowers greatly enlarged, showing two stages of phyllody.

4500-7,'45(3082)