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CONTENTS

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H I L G A R D I A

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EXPERIMENTS WITH THE ASTER-YELLOWS VIRUS FROM SEVERAL STATES[1]

HENRY H. P. SEVERIN[2]

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

INTRODUCTION

IN 1929 THE AUTHOR[10] reported that *Cicadula divisa* Uhl. [*C. sexnotata* (Fall.)] transmitted yellows from naturally and experimentally infected varieties of celery to asters and from asters to celery in California. Kunkel[5] failed to infect 9 varieties of celery with the aster-yellows virus from New York by means of *Cicadula divisa.* In later papers the author[11,13] reported the transmission of yellows from naturally and experimentally infected varieties of carrot, parsley, and parsnip in California, but Kunkel[5] questions whether this disease is identical with aster yellows in New York, since the California aster-yellows virus is readily transmitted to celery and to *Zinnia elegans,* plants that are highly resistant if not immune to New York aster yellows.

Dorst,[1] who has made a study of the genus *Cicadula,* found that *Cicadula sexnotata* (Fall.) is a European species and that the American species is *Cicadula divisa* Uhl. Specimens of *Cicadula* were sent to Dorst by Kunkel from New York and by the writer from California, and all were determined as *Cicadula divisa.*

A review of the literature indicates that the celery yellows found in California probably occurs in other states. According to Linford,[7] aster and celery yellows first made its appearance in Utah during 1927.

Folsom[2] states that apparently the same disease as described by the author[10] was seen in southwestern Maine on an experimental farm,

[1] Received for publication February 7, 1934.

[2] Associate Entomologist in the Experiment Station.

where by systematic sweepings, the vector *Cicadula divisa* was caught for the first time in three years in which the work was carried on.

According to Vaughan and Foster,[19] aster yellows was found on celery in Wisconsin, but there was more infection in carrots than in celery or lettuce, when all three were growing adjacent to an experimental aster-yellows plot. Foster[3] planted about an acre of celery with asters between the rows at Madison, Wisconsin. He reports, "There were 3 celery plants in the entire field that developed symptoms that could be called typical aster yellows, without the twisting of the petioles.... In the same field I had a dozen large cages over celery plants in which colonies of *Cicadula divisa* were transferred early. This colony was collected from cages containing yellowed aster plants. Aster plants with yellows were also transplanted to the cages containing celery. These plants remained under the cages until late fall, and the hopper was present in large numbers at all times. None of the celery plants showed any of the yellows symptoms at any time."

Kunkel[6] experienced no difficulty in transmitting yellows to healthy aster and celery by means of *Cicadula divisa* from asters, celery, and carrots infected with California aster yellows, but failed to transmit the disease to zinnia. Yellows was also transferred from celery experimentally infected with California aster yellows, to healthy asters. California yellows on asters could not be distinguished by symptoms from the yellows disease prevalent on aster in New York. Kunkel came to the conclusion that celery yellows of California is not identical with aster yellows of New York.

Transmission experiments were performed, using *Cicadula divisa* occurring in California, with the aster-yellows virus obtained from New York, Indiana, and Wisconsin, carrot-yellows virus from Maine and Idaho, and celery-yellows virus from Utah, to determine whether healthy asters and celery could be experimentally infected with the disease. Tests were made to determine whether there are host-range differences between yellows viruses obtained from various states. Attempts were made to recover the virus from the experimentally infected plants. Experiments were also conducted to determine whether *Thamnotettix montanus* Van D., a newly discovered vector of California yellows, could transmit yellows from asters infected with the disease in New York and Wisconsin to healthy asters and celery. Attempts were also made to transmit yellows by feeding previously noninfective *Cicadula* on feeding solutions containing crushed infective leafhoppers which had fed on yellows-infected plants from New York and Wisconsin.

[3] Foster, A. C., letter to author dated February 18, 1931.

ASTER-YELLOWS VIRUS FROM NEW YORK

Through the courtesy of L. O. Kunkel, Rockefeller Institute for Medical Research, Princeton, New Jersey, three shipments of asters and salsify infected with yellows were received in good condition from New York.

TABLE 1

TRANSMISSION OF NEW YORK ASTER YELLOWS TO HEALTHY ASTERS AND CELERY BY *Cicadula divisa**

Experiment 1			Experiment 2		Experiment 3	
Insects transferred from New York aster yellows to healthy celery	Same insects transferred from celery to healthy asters	Same insects transferred from infected asters to healthy celery	Insects transferred from experimentally infected asters to healthy asters	Insects transferred from experimentally infected asters to healthy celery	Insects transferred from experimentally infected asters to healthy asters	Insects transferred from experimentally infected asters to healthy celery
Infections resulting						
−	+	−	−	3−	−	5−
−	+	−	+	1+ 4−	−	5−
−	+	−	−	5−	−	5−
−	+	−	+	1+ 4−	−	5−
−	−	....	....	....	....	....
−	+	−	+	1+ 4−	−	5−
−	+	−	+	5−	−	5−
−	+	−	+	1−	+	1+ 4−
−	+	−	+	1−	−	5−
−	+	+	−	1−	+	5−
−	−	....	....	....	....	....
−	+	....	....	....	−	5−
−	+	....	....	....	+	5−
−	−	....	....	....	....	....
−	+	....	....	....	+	1+ 4−
−	−	....	....	....	....	....
−	+	....	....	....	−	5−
——	——	——	——	——	——	——
	13+	1+	6+	3+	4+	2+
17−	4−	8−	3−	28−	9−	63−

* The plus sign (+) indicates the production of the disease, and the minus sign (−) shows that no disease resulted.

Several experiments were conducted to determine whether asters, celery, carrots, and parsley could be experimentally infected with the aster-yellows virus from New York. In the first experiment previously non-infective male *Cicadula divisa* were fed on yellows-infected asters from New York for a period of 2 or 3 days and then 20 insects were transferred to each of 17 healthy celery plants. After feeding on the celery plants for a period varying from 19 to 27 days, each lot of leafhoppers was

transferred to a healthy aster plant. Ten of the 17 lots of leafhoppers, some of which had died, were again transferred from the inoculated asters to a second set of healthy celery plants for a period of 25 days. Table 1, experiment 1, shows that the first lot of celery plants remained healthy, 13 of the 17 asters inoculated became diseased, and 1 of the 9 celery plants in the second lot developed typical symptoms of yellows as described in a previous paper.[10] Celery plants used as a check or control remained healthy.

In the second experiment noninfective nymphs were exposed to 9 asters which had been experimentally infected with yellows in experiment 1. After the nymphs acquired the winged stage, lots of 5 to 35 males were transferred from each diseased aster to healthy asters and celery plants. Table 1 shows that in experiment 2, 6 of the 9 asters, and 3 of the 31 celery plants inoculated, showed typical symptoms of celery yellows.

In the third experiment 13 lots of leafhoppers after being exposed for a period of 8–28 days to 13 diseased asters from experiment 1, were transferred in groups of 5, to 13 healthy asters and 65 celery plants. Table 1, experiment 3, shows that 4 of the 13 asters and 2 of the 65 celery plants inoculated developed symptoms of yellows.

In the three experiments a total of 122 celery plants were inoculated with the New York aster-yellows virus, and 6 showed symptoms of celery yellows. The central leaves were chlorotic with a slight twisting of the petioles. Previously noninfective leafhoppers were exposed to the 6 celery-yellows plants and were then transferred to healthy asters and celery. The virus was repeatedly recovered by 3 lots of previously noninfective leafhoppers from only one celery-yellows plant, and typical symptoms of yellows developed with 3 asters. Previously noninfective leafhoppers, after feeding on the 3 diseased asters, failed to transmit yellows to 12 healthy celery plants.

It was decided to use larger numbers of leafhoppers with the salisfy infected with the aster-yellows virus from New York. Lots of 50 to 100 previously noninfective leafhoppers, after feeding on salsify infected with yellows for a period of 4 to 6 days, were transferred to successive healthy celery plants for periods of 2 weeks until all of the insects were dead. Eighty-five healthy celery plants were inoculated and 2 plants developed typical symptoms of yellows in the cages. Previously noninfective leafhoppers after feeding on the infected celery plants failed to transmit yellows to healthy asters and celery.

Carrots (*Daucus carota sativa*) showing symptoms of yellows have been reported by Whetzel,[20] Newhall,[8] and Kunkel[5] in New York, by Folsom[2] in Maine, by Zundel[21] in Pennsylvania, by Vaughan and Foster[19] in Wisconsin, and by the author[11,13] in California.

An experiment was conducted to determine whether varieties of carrots could be experimentally infected with the yellows virus from asters infected in New York by means of *Cicadula divisa*. Previously noninfec-

TABLE 2

INCUBATION PERIOD OF NEW YORK ASTER YELLOWS IN EXPERIMENTALLY INFECTED CARROTS AND RECOVERY OF VIRUS BY *Cicadula divisa*

Variety of carrot	Number of plants inoculated	Number of leafhoppers on each plant	Number of plants infected	Number of plants healthy	Incubation period in plant, days	Yellows transferred	
						From carrot to aster	From carrot to celery
Short White	1	20♂	1	0	15	−	−
	1	20♀	1	0	40	+	−
White Mastodon	1	20♂	1	0	40	−	−
	1	20♀	1	0	37	+	−
White Belgian	1	20♂	1	0	28	+	−
	1	30♀	1	0	18	+	−
Yellow Belgian	1	20♂	1	0	39	−	−
	1	30♀	1	0	53	−	−
Chantenay	1	20♂	1	0	24	−	−
	1	30♀	0	1	....	−	−
Danvers Half Long	1	20♂	1	0	39	+	−
	1	20♀	1	0	22	−	−
Early Scarlet Horn	1	20♂	1	0	21	−	−
	1	20♀	1	0	21	−	−
French Forcing	1	20♂	1	0	24	−	−
	1	30♀	1	0	42	−	−
Long Orange	1	10♀	1	0	16	−	−
	1	10♀	0	1	....	−	−
Nantes	1	20♂	1	0	39	+	−
	1	30♀	1	0	37	−	−
Oxheart or Guerande	1	20♂	1	0	28	−	−
	1	20♀	1	0	35	−	−
Total	22	.....	20	2	.....	6	0
Average	....	.....	....	....	30.9	....	....

tive leafhoppers, varying in number from 10 to 30 males or females, were exposed to aster-yellowed plants and then transferred to 3 white, 1 yellow, and 7 orange varieties of carrots, as indicated in table 2.

It is evident from table 2 that 20 of the 22 carrots inoculated were experimentally infected with the New York aster-yellows virus. The virus was recovered by means of previously noninfective leafhoppers

from 6 experimentally infected carrots and transferred to 6 healthy asters. The virus was not transferred by previously noninfective leafhoppers from infected carrots to any of the 22 healthy celery plants inoculated. The incubation period of the disease in the plant varied from 15 to 53 days, with an average of 30.9 days.

Three Single or Plain parsley plants (*Petroselinum hortense*) were experimentally infected with the yellows virus from asters infected in New York. The infected parsley plants showed typical symptoms of yellows as described in a previous paper,[13] but the virus was not transferred by leafhoppers from the infected parsley plants to 8 healthy asters and 6 celery plants. The incubation periods of the disease in the plants were 30, 45, and 48 days, respectively, averaging 41 days.

Four Hamburg or Turnip-rooted parsley plants (*Petroselinum hortense radicosum*) were inoculated with the aster yellows virus from New York by means of *Cicadula divisa*, but only 2 plants developed the symptoms of yellows described in a previous paper.[13] The incubation periods of the disease were 40 and 44 days, respectively, averaging 42 days. Previously noninfective leafhoppers, after feeding on the inoculated plants, failed to transmit the disease to 8 healthy asters and 6 celery plants.

An attempt was made to retain the aster yellows virus through the winter in a perennial plant. Infective leafhoppers were transferred from asters infected with yellows from New York to common plantain or ribgrass (*Plantago major*). Large numbers of insects were reared on common plantain; when one lot of plants became unfavorable as food, the insects were transferred to healthy plants. Common plantain was experimentally infected with yellows and showed typical symptoms of the disease, but the virus was not recovered by previously noninfective leafhoppers during the following spring.

Thamnotettix montanus Van D., a newly discovered vector of California aster and celery yellows, failed to transmit yellows from asters infected in New York to any of 71 healthy asters and 10 celery plants. Previously noninfective *Cicadula divisa* after feeding on the 10 celery plants and some of the asters exposed to *Thamnotettix montanus* failed to transmit yellows to healthy asters and celery.

California aster and celery yellows has been transmitted on rare occasions from a feeding solution containing crushed infective *Cicadula divisa* bred on diseased plantain or ribgrass (*Plantago major*). The feeding solution containing the crushed infective leafhoppers was centrifuged at 3,500 r.p.m. for 1 hour and a portion was fed directly to previously noninfective leafhoppers, while the remainder was filtered through coarse and fine Berkefeld candles and the filtrate was fed to previously

noninfective leafhoppers. The methods of feeding the insects were the same as those used with the beet leafhopper and described in previous papers.[12, 16, 17]

Similar experiments were performed with feeding solutions containing crushed infective *Cicadula divisa* which had fed on yellows-infected asters from New York and Wisconsin. Previously noninfective leafhoppers were fed on the centrifuged feeding solutions containing the crushed infective leafhoppers and also on the filtrates. The feeding solutions contained autoclaved filtered root juice from celery, celeriac, carrot, or parsnip plants, or a combination of petiole and root juice from these plants, various proportions of a 2 per cent solution of maltose, and sometimes a 2 per cent solution of soluble starch solution. The same percentage of maltose, or soluble starch, or a combination of both without the plant extract, was also used. The infective leafhoppers were also crushed in sterile distilled water. All efforts to transmit yellows to 130 healthy asters by feeding previously noninfective leafhoppers on centrifuged feeding solutions or on the filtrates failed.

CARROT-YELLOWS VIRUS FROM MAINE

D. Folsom, of the Maine Agricultural Experiment Station, sent ornamental flowering plants, plantain, and carrots naturally infected with yellows, but only the carrots and a species of *Calendula* arrived in good condition.

Experiments were conducted to determine whether the virus could be transmitted by *Cicadula divisa* from carrots infected with yellows in Maine to healthy asters and celery. Previously noninfective leafhoppers after being exposed to carrots naturally infected with yellows obtained from Maine were transferred to 17 healthy asters and 17 healthy celery plants. One typical case of aster yellows developed and one celery plant showed symptoms of yellows, both being transmitted from the same diseased carrot plant. Previously noninfective leafhoppers failed to transmit yellows from the infected celery to several healthy celery plants.

Previously noninfective leafhoppers, after being exposed to yellows-infected carrot plants received from Maine, transmitted yellows to 3 white, 1 yellow, and 7 orange varieties of carrots. Yellows was not transferred by leafhoppers from the experimentally infected carrots to 11 healthy asters and 11 celery plants, as shown in table 3. The incubation period of the disease in the plants varied from 19 to 81 days, with an average of 48.7 days, as indicated in table 3.

Hollow Crown parsnip (*Pastinaca sativa*) was experimentally infected with yellows by previously noninfective leafhoppers which had

been exposed to naturally infected carrots obtained from Maine. The virus was not recovered from infected parsnips by leafhoppers, for they failed to transmit yellows to healthy asters and celery.

Yellows was transmitted by previously noninfective leafhoppers from naturally infected *Calendula sp.* from Maine to healthy asters but not to celery.

TABLE 3

INCUBATION PERIOD OF MAINE CARROT YELLOWS IN EXPERIMENTALLY INFECTED CARROTS AND RECOVERY OF VIRUS BY *Cicadula divisa*

Variety of carrot	Number of plants inoculated	Number of leafhoppers on each plant	Number of plants infected	Number of plants healthy	Incubation period in plant, days	Yellows transferred	
						From carrot to aster	From carrot to celery
Short White	1	55	1	0	54	—	—
White Mastodon	1	50	1	0	54	—	—
White Belgian	1	50	1	0	81	—	—
Yellow Belgian	1	50	1	0	52	—	—
Chantenay	1	50	1	0	45	—	—
Danvers Half Long	1	30	1	0	19	—	—
Early Scarlet Horn	1	50	1	0	54	—	—
French Forcing	1	50	1	0	52	—	—
Long Orange	1	30	1	0	44	—	—
Nantes	1	30	1	0	37	—	—
Oxheart or Guerande	1	30	1	0	44	—	—
Total	11	....	11	0	....	11—	11—
Average	....	43	....	....	48.7	.....	.....

ASTER-YELLOWS VIRUS FROM INDIANA

Asters infected with yellows were sent by R. W. Samson, of the Purdue University Agricultural Experiment Station, La Fayette, Indiana.

Transmission experiments were conducted with *Cicadula divisa* to determine whether asters, celery, and parsnips could be infected with yellows from diseased asters received from Indiana. Previously noninfective leafhoppers were exposed for a period of 1 or 2 days on asters infected with yellows from Indiana and were then transferred in lots of 10 or 20 to healthy asters and celery. Ten asters were inoculated with yellows and 5 typical cases of aster yellows developed, while 5 plants failed to show symptoms of the disease. Previously noninfective leafhoppers exposed to the 5 infected asters failed to transmit yellows to 5 healthy celery plants. Ten celery plants exposed to infective leafhoppers failed to develop symptoms of celery yellows.

Hollow Crown parsnip was experimentally infected with aster yellows

from Indiana and showed typical symptoms of the disease as described in a previous paper.[13] The virus was not transferred by leafhoppers from infected parsnips to healthy asters and celery.

Common plantain or ribgrass (*Plantago major*) was experimentally infected with yellows during the autumn and showed typical symptoms of the disease, but the virus was not recovered by previously noninfective leafhoppers during the following spring.

ASTER-YELLOWS VIRUS FROM WISCONSIN

Asters naturally infected with yellows were received from A. J. Riker, of the Wisconsin Agricultural Experiment Station, Madison, Wisconsin.

Asters, celery, and parsnip were inoculated by means of *Cicadula divisa* with the virus of aster yellows obtained from Wisconsin. Twenty-six healthy asters were inoculated, and 18 plants developed typical symptoms of aster yellows. Six of the 82 celery plants inoculated showed symptoms of celery yellows. The virus was transferred by previously noninfective leafhoppers from 2 of the 6 celery-yellows plants to asters.

Hollow Crown parsnip was experimentally infected with aster yellows from Wisconsin, but the virus was not transferred by previously noninfective leafhoppers from infected parsnips to healthy asters and celery.

Three white, 1 yellow, and 7 orange varieties of carrots were experimentally infected with yellows from asters naturally infected in Wisconsin. Nineteen of the 22 inoculated carrots showed typical symptoms of carrot yellows as indicated in table 4. Previously noninfective leafhoppers exposed to the inoculated carrots failed to transmit yellows to healthy asters and celery, as shown in table 4. The incubation period of the disease varied from 14 to 44 days, with an average of 29.8 days (table 4).

Male *Thamnotettix montanus* exposed to yellows-infected aster plants from Wisconsin failed to transmit yellows to 18 healthy asters.

CARROT YELLOWS FROM IDAHO

C. F. Henderson,[4] of the United States Department of Agriculture Bureau of Entomology, reported that carrots infected with yellows occurred in Twin Falls, Jerome, and Cassia counties, Idaho, during 1930. He found 17 per cent of the carrots infected with yellows in one field near Twin Falls that year, but during the season of 1932 carrot yellows

[4] Henderson, C. F., letter to author dated November 29, 1932.

was rarely observed in the vicinity of Twin Falls. Henderson sent several shipments of carrots naturally infected with yellows collected near Twin Falls, and the foliage symptoms were identical with carrot yellows in California.

TABLE 4

INCUBATION PERIOD OF WISCONSIN ASTER YELLOWS IN EXPERIMENTALLY INFECTED CARROTS AND RECOVERY OF VIRUS BY *Cicadula divisa*

Variety of carrot	Number of plants inoculated	Number of leafhoppers on each plant	Number of plants infected	Number of plants healthy	Incubation period in plant, days	Yellows transferred	
						From carrot to aster	From carrot to celery
Short White	1	20♂	1	0	29	—	—
	1	20♀	0	1	....	—	—
White Mastodon	1	20♂	1	0	31	—	—
	1	20♀	0	1	....	—	—
White Belgian	1	20♂	1	0	42	—	—
	1	20♀	1	0	23	—	—
Yellow Belgian	1	20♂	1	0	42	—	—
	1	20♀	1	0	28	—	—
Chantenay	1	20♂	1	0	14	—	—
	1	20♀	1	0	28	—	—
Danvers Half Long	1	20♂	1	0	42	—	—
	1	20♀	1	0	28	—	—
Early Scarlet Horn	1	20♂	1	0	22	—	—
	1	20♀	1	0	23	—	—
French Forcing	1	20♂	1	0	18	—	—
	1	20♀	1	0	23	—	—
Long Orange	1	10♂	1	0	30	—	—
	1	10♀	1	0	26	—	—
Nantes	1	20♂	1	0	29	—	—
	1	20♀	1	0	44	—	—
Oxheart or Guerande	1	20♂	1	0	44	—	—
	1	20♀	0	1	....	—	—
Total	22	.....	19	3	....	22—	22—
Average	....	.....	....	....	29.8	.....	.....

Transmission of yellows by previously noninfective *Cicadula divisa* from naturally infected carrots obtained from Idaho to healthy carrots was accomplished with 3 white, 1 yellow, and 5 orange varieties, as shown in table 5. Previously noninfective leafhoppers exposed to the experimentally infected varieties of carrots failed to transmit yellows to

healthy asters and celery. The incubation period of the disease in the plants varied from 24 to 48 days, with an average of 34.2 days, as indicated in table 5.

In another experiment previously noninfective males reared on barley, which is immune to aster yellows, were exposed to carrots naturally

TABLE 5

INCUBATION PERIOD OF IDAHO ASTER YELLOWS IN EXPERIMENTALLY INFECTED CARROTS AND RECOVERY OF VIRUS BY *Cicadula divisa*

Variety of carrot	Number of plants inoculated	Number of leafhoppers on each plant	Number of plants infected	Number of plants healthy	Incubation period in plant, days	Yellows transferred	
						From carrot to aster	From carrot to celery
Short White	1	25 ♀	1	0	24	—	—
White Mastodon	1	10 ♀	1	0	45	—	—
	1	30 ♀	1	0	48	—	—
White Belgian	1	25 ♀	0	1	....	—	—
	1	10 ♀	1	0	41	—	—
Yellow Belgian	1	25 ♀	1	0	31	—	—
Chantenay	1	25 ♀	1	0	27	—	—
French Forcing	1	10 ♀	1	0	43	—	—
	1	20 ♀	1	0	29	—	—
Long Orange	1	25 ♀	0	1	....	—	—
	1	20 ♀	1	0	31	—	—
	1	20 ♀	1	0	29	—	—
	1	20 ♀	1	0	33	—	—
Nantes	1	25 ♀	1	0	32	—	—
Oxheart or Guerande	1	25 ♀	1	0	31	—	—
Total	15	.....	13	2	....	15—	15—
Average	...	.....	....	....	34.2	....	.....

infected with yellows from Idaho and then transferred to healthy asters and celery. In other tests previously noninfective females deposited eggs in the foliage of the diseased carrots, and after nymphs hatched and acquired the winged stage, the males were transferred to healthy asters and celery. Twenty-seven inoculated asters failed to show symptoms of yellows. Sixty-one celery plants were inoculated and 3 of them showed a chlorotic condition of the central leaves with a marked twisting of the petioles. The virus was not recovered from the 3 celery plants showing symptoms of yellows.

CELERY YELLOWS FROM UTAH

In 1927 Linford[7] reported a yellows disease on celery in Salt Lake and Weber counties, Utah. He first observed aster yellows on September 9, 1927, in four localities in Salt Lake and Davis counties, Utah, with a maximum severity of 3 per cent.

Kunkel[6] states, however, that there is no convincing evidence that celery yellows reported in Utah is California yellows.

H. L. Blood, United States Department of Agriculture Bureau of Plant Industry, stationed at the Utah Agricultural Experiment Station, sent 3 small celery-yellows plants from Salt Lake City. Previously noninfective *Cicadula divisa*, after feeding on the celery-yellows plants, transmitted yellows from 2 of the 3 plants to 2 healthy celery plants and 1 aster plant. Unfortunately one of the inoculated aster plants died before symptoms of aster yellows developed. The virus was transferred by previously noninfective *Cicadula divisa* from the 2 experimentally infected celery plants to 2 healthy celery plants. Celery yellows of Utah is probably identical with California aster yellows.

YELLOWS AND CURLY TOP OF ZINNIA

Severin[10] reported that a circular bed of zinnias (*Zinnia elegans*) showing 100 per cent California yellows was found in the center of a lawn in front of the Spreckels Agricultural Experiment Station. *Cicadula divisa* was abundant on the zinnias and on the grass. The plants were stunted, chlorotic, and with abnormal flowers. Noninfective leafhoppers after feeding on the diseased zinnias transmitted yellows to asters and celery.

Kunkel[6] failed to infect *Zinnia elegans* with California yellows experimentally. He was able to infect *Zinnia multiflora* L. with the New York aster-yellows virus, but this species is not grown for seed production in California.

During the summer of 1932, several surveys were made of the yellows and curly-top diseases of ornamental flowering plants grown on seed farms in the San Juan and Salinas valleys. Different varieties and hybrids of *Zinnia elegans* on both seed farms were stunted and showed a yellowing of the apical and secondary shoots. Three varieties of *Zinnia elegans* commonly known as Double Giant Pink, Dahlia Flowered mixed, and Lilliput Scarlet Gem were demonstrated to be naturally infected with yellows. Previously noninfective *Cicadula divisa* after feeding on the 3 varieties of *Zinnia elegans* transmitted yellows to healthy celery.

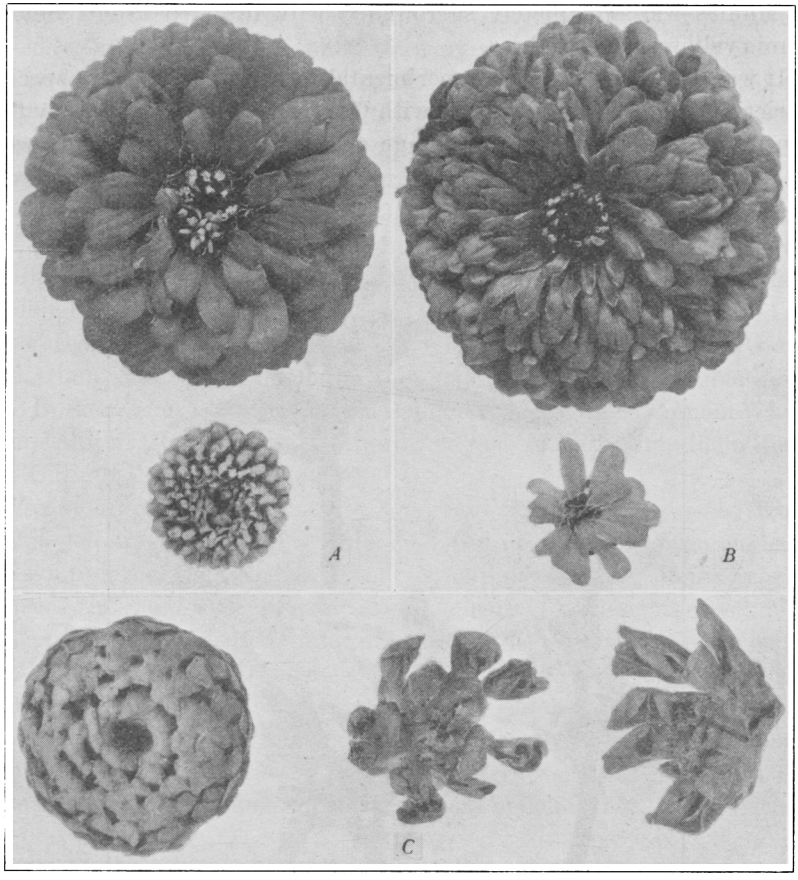

Fig. 1.—*A*, Giant Red zinnia (*Zinnia elegans*): upper, flower from check or control plant; lower, dwarfed flower which was green instead of red in color, from a plant experimentally infected with California aster yellows. *B*, Dahlia Flowered Orange zinnia: upper, flower from check or control plant; lower, dwarfed flower from a plant infected with curly top showing few petals, which were normal in color. *C*, Other abnormal flowers, which were green in color instead of red, from Giant Red zinnia, experimentally infected with California aster yellows.

Previously noninfective beet leafhoppers, *Eutettix tenellus*, after feeding on 9 diseased *Zinnia elegans* transmitted curly top to healthy sugar beets. Four of the 9 zinnias are commonly known as Double Giant type brightness, and were grown adjacent to garden, table, or red beets in the San Juan Valley.

During the summer of 1933 no zinnias infected with yellows or curly top were found on the same seed farms. In the Salinas Valley 40 per cent of the asters were naturally infected with yellows in some plots. Varieties

of zinnias were completely surrounded with diseased asters, but no zinnia yellows was found.

It was decided to attempt experimental infection of different species, varieties, and hybrids of zinnias with California yellows and curly top. Twenty-six Mexican Double Orange zinnias (*Zinnia haageana*) were

Fig. 2.—Giant White zinnia (*Zinnia elegans*) experimentally infected with curly top showing secondary shoots and inward-cupped leaves.

repeatedly inoculated with yellows by lots of 5 or 10 infective *Cicadula divisa*. Three plants developed symptoms of yellows with chlorotic secondary shoots and dwarfed yellow flowers, but the flowers were not abnormal in color. Previously noninfective leafhoppers recovered the virus from the infected plants and transmitted it to healthy asters and celery. No difficulty was experienced in experimentally infecting this species of zinnia with curly top.

Twenty-five varieties or hybrids of *Zinnia elegans* were each inoculated by 2 lots of 10 infective *Cicadula divisa*. Double Pompom White Gem and Giant Red zinnias developed symptoms of yellows, but the virus

was not recovered by previously noninfective leafhoppers. The flowers failed to expand (fig. 1 *A, C*) and were green in color.

The following varieties or hybrids of *Zinnia elegans* were experimentally infected with curly top and the virus was recovered by previously noninfective beet leafhoppers and transferred to sugar beets: Dahlia Flowered Lavender, Dahlia Flowered Orange (fig. 1 *B*) Dahlia Flowered Red, Dahlia Flowered Rose, Double Dahlia Flowered Golden Yellow, Double Dahlia Flowered Light Yellow, Double Dahlia Flowered White, Double Elegans Golden Yellow, Double Elegans Bright Scarlet, Double Elegans Salmon Rose, Double Giant Canary Yellow, Double Lilliput (Dwarf Miniature), Giant Orange, Giant Pink, Giant Purple, Giant Red, Giant White (fig. 2), Double Pompom Dark Crimson, Double Pompom Golden Gem, Double Pompom Salmon Rose, Double Pompom White Gem, Lilliput Crimson Gem, Lilliput Golden Gem, Lilliput Salmon Rose, and Lilliput Pompom Scarlet Gem.[5]

The symptoms of zinnia curly top could not be distinguished from zinnia yellows on old plants in the field, but no study has been made of the symptoms of the two diseases on young plants. Young plants experimentally infected with curly top showed cleared or transparent veinlets, but on old plants infected under natural conditions, this symptom could not be distinguished from normal venation. The internodes near the apices of the branches were shortened with chlorotic secondary shoots arising from the axil of the leaves (fig. 2). The leaves frequently were cupped inward along the midrib. The flowers were dwarfed, with the petals reduced in number but not abnormal in color (fig. 1 *B*).

DISCUSSION

Recovery of Virus.—Kunkel experienced difficulty in the recovery of the aster-yellows virus in New York from experimentally infected host plants. In his first paper Kunkel[4] lists 64 species of plants in 23 families that were experimentally infected with aster yellows, but the virus was transferred back to asters from only 32 species. In a later paper Kunkel[5] reported transmitting yellows to 120 species of plants in 30 families, but the virus was recovered from only 12 species. He states, however, in his second paper that ,"while such transmission is necessary in order to bring full proof that the disease observed on any yellowed plant is actually aster yellows, the symptoms are so similar on different hosts that this step was not considered necessary in most cases."

[5] The first seventeen varieties or hybrids were grown from seeds obtained from the Ferry-Morse Seed Co. (1932 catalog) San Francisco, California; the next four from the Germain Seed & Plant Co. (1932 catalog) Los Angeles, California; and the last four from Peter Henderson & Co. (1932 catalog) 35 Cortland St., New York.

The recovery of the aster-yellows virus obtained from other states from host plants showing symptoms of the disease is given in the summary of this paper.

It was sometimes impossible to recover the California aster-yellows virus from naturally infected weeds and experimentally infected economic cultivated plants showing typical symptoms of the disease. Cross inoculations from experimentally infected Double-Curled, Extra-Triple

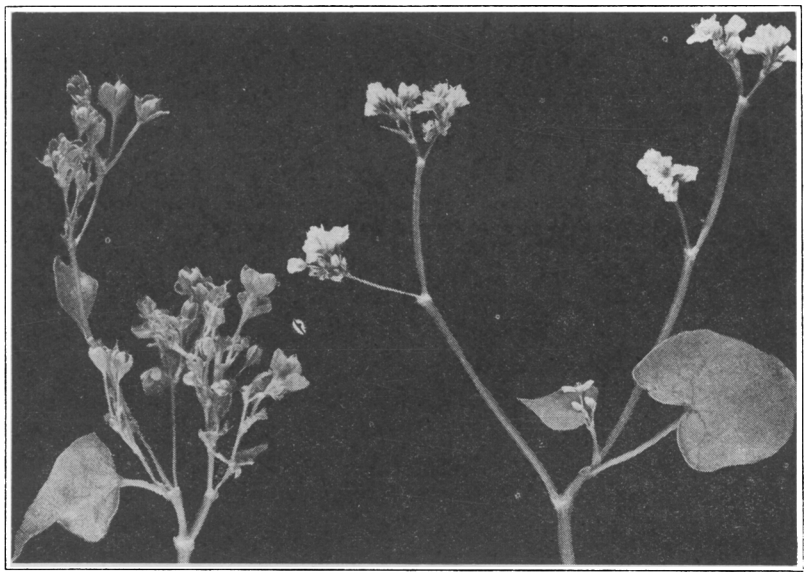

Fig. 3.—Common buckwheat (*Fagopyrum esculentum*): left, shoot from a plant experimentally infected with California yellows showing large number of flowers with petals which were green in color; right, shoot from a healthy plant used as a check or control showing white flowers.

Curled, and Fern-Leaf or Moss-Curled parsley showing symptoms of yellows were failures, as reported in a previous paper.[13]

Host-Range Differences.—There is some evidence to show that host-range differences occur with California and New York aster yellows. Numerous attempts were made by Kunkel[5] to transmit the aster-yellows virus of New York to potatoes by means of the insect vector. The varieties used included Irish Cobbler, Green Mountain, Bliss Triumph, and Spaulding Rose.

During the past five years, California yellows was transmitted to a number of varieties of potatoes including Bliss Triumph.[14] It was impossible, however, to recover the virus from experimentally infected varieties of potatoes showing symptoms of the disease.

Overlapping Host Ranges.—The overlapping economic host plants of California aster yellows and aster yellows of New York so far investigated are as follows: common buckwheat (*Fagopyrum esculentum*) (fig. 3), spinach (*Spinacia oleracea*), carrot (*Daucus carota* var. *sativa*), dill (*Anethum graveolens*), parsnip (*Pastunaca sativa*), peasant's tobacco (*Nicotiana rustica*) (fig. 4), salsify (*Tragopogon porrifolius*), and lettuce (*Lactuca sativa*). The symptoms of the disease on these over-

Fig. 4.—Peasant's tobacco (*Nicotiana rustica*): *A*, cluster of secondary shoots from a plant experimentally infected with California yellows; *B*, apical shoot from a check or control plant.

lapping host plants infected with the California and New York aster yellows appear to be identical.

It is not to be expected that two different viruses would have identical host ranges. It is not uncommon for two different virus diseases to have overlapping host ranges or to produce similar symptoms.[5] It is difficult to explain, however, why an occasional celery plant developed symptoms of yellows with the aster-yellows virus from other states and the leafhoppers were not able to recover the virus except on very rare occasions. Similar difficulties were encountered with resistant host plants of curly top such as pink beans (*Phaseolus vulgaris*) and Australian saltbush (*Atriplex semibaccata*), as reported in a previous paper.[15]

Smith[18] expressed the opinion that slight differences in the host range do not justify the separation into distinct viruses of entities which are otherwise identical.

Strains of Aster Yellows.—Strains or variants of the aster-yellows viruses transmitted by different species of leafhoppers may occur in the United States, Bermuda Islands,[9] Japan,[8] or Europe.

According to Kunkel,[6] "whether the yellows from California is a strain of aster yellows or is a different disease is a question that cannot be answered at this time." The facts that both are transmitted by the same insect vector, have long incubation periods in the leafhopper, and produce similar symtoms in aster and some other host plants, support the view that they may be related.

According to Smith,[18] "Perhaps the best illustration of two apparently independent strains of a plant virus is afforded by the case of aster yellows and celery yellows. . . . Here then is apparently a case of a virus having 'mutated' or adapted itself to a new host plant in one district and after sojourn in this host [having] acquired the ability to infect it as easily as any other plant in its host range. Such a virus may be regarded merely as a slightly different strain of aster yellows, or it may be regarded as a different entity and be referred to as 'celery yellows.' It is also possible that celery yellows is a stage in the evolution of an entirely new virus."

SUMMARY

Yellows was transmitted by previously noninfective *Cicadula divisa* from asters naturally infected in New York, Indiana, and Wisconsin to asters. Previously noninfective leafhoppers exposed to asters or salsify infected with the disease in New York transmitted yellows to 8 of the 207 celery plants inoculated. The virus was transferred from 1 experimentally infected celery plant to 3 successive healthy asters, but was not transferred from the 3 infected asters back to 12 healthy celery plants. The virus from yellows-infected asters in Wisconsin was transferred to 6 of the 82 celery plants inoculated and from 2 of the 6 experimentally infected celery plants back to asters. Ten celery plants inoculated with the virus of aster yellows from Indiana failed to develop symptoms of the disease.

Yellows was transmitted from celery naturally infected with yellows in Utah to aster and celery plants. The virus was recovered from the experimentally infected celery plants and again transferred to healthy celery plants.

Yellows was readily transmitted to healthy carrots from asters naturally infected with the disease in New York, Maine, and Wisconsin. The transfer of yellows by previously noninfective leafhoppers from experimentally infected carrots to healthy asters was accomplished with 6 of the 22 plants with the aster-yellows virus obtained from New York, but was not performed with 22 healthy celery plants. All efforts to transfer yellows from experimentally infected carrots to healthy asters or celery

with the virus of aster yellows obtained from Maine and Wisconsin failed. No difficulty was experienced in transmitting aster yellows to healthy carrots from carrots naturally infected with the disease in Maine and Idaho. Yellows was transferred from one carrot naturally infected with the disease in Maine to aster and celery, but the virus was not transferred from the infected aster to celery nor from the celery-yellowed plant to any of several healthy celery plants. The transfer of yellows from carrots naturally infected with the disease in Idaho was accomplished with 3 of the 61 celery plants inoculated, but the virus was not recovered from the 3 celery plants showing symptoms of yellows.

Single or Plain parsley, Hamburg or Turnip-rooted parsley, and common plantain or ribgrass (*Plantago major*) were experimentally infected with yellows by previously noninfective leafhoppers which had been exposed to aster yellows obtained from New York, but the virus was not recovered from any of the infected plants. Hollow Crown parsnip was experimentally infected with yellows with the aster-yellows virus from Indiana and Wisconsin and carrot-yellows virus from Maine, but the virus was not recovered from the infected parsnips. The number of tests, however, with all of the species or varieties of plants, was not sufficient to state that the virus could not be recovered on rare occasions.

Thamnotettix montanus Van D., a newly discovered vector of California aster and celery yellows, failed to transmit yellows from asters naturally infected with the disease in New York and Wisconsin to healthy asters and celery.

The results of this investigation show that carrots and asters can be experimentally infected with the aster-yellows virus obtained from New York, Indiana, and Wisconsin, also the carrot-yellows virus from Maine and Idaho, and with the aster-yellows virus from California. Celery was found to be highly resistant to the aster or carrot-yellows virus obtained from all states except California.[10]

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