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TRANSMISSION OF CALIFORNIA ASTER AND CELERY-YELLOWS VIRUS BY THREE SPECIES OF LEAFHOPPERS[1]

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INTRODUCTION

IT HAS BEEN SUGGESTED that possibly an obligate relation exists between a specific insect vector and the aster-yellows virus, and that developmental changes and multiplication of the virus take place during the incubation period in the insect.(8) It has been assumed in the past that the aster-yellows virus could be disseminated only by the leafhopper, *Cicadula divisa* Uhl., which is widely distributed in America.

Ogilvie(10) reported yellows of China aster (*Callistephus chinensis*) in Bermuda, where *Cicadula sexnotata* (Fall.), responsible for the transmission of the virus there, has been known to occur since 1924. The disease also occurs on cos lettuce, cabbage lettuce, eight species of ornamental flowering plants, and several wild plants in Bermuda.

Fukuski(5) reported that aster yellows occurs in Japan. Kunkel(8) reported that *Cicadula sexnotata* occurs in Japan and probably throughout the Orient.

Dobroscky[3] reported that aster yellows was found in the gardens of the Budapest Experiment Station, and in the vicinity of Lake Balaton Biological Laboratory, Hungary. *Cicadula sexnotata* is widespread and common in Europe.(8)

In California three species of leafhoppers transmit the aster-yellows virus. *Cicadula divisa* transmits the virus with greater efficiency than the mountain leafhopper, *Thamnotettix montanus* Van D. or the geminate leafhopper, *T. geminatus* Van D. Experiments with the leafhoppers *Agallia californicum* (Baker), *A. cinera* (O. & B.), and *Empoasca abrupta* De L. bred on celery failed to transmit the yellows virus.(13)

An investigation was undertaken to determine whether or not California aster and celery yellows are caused by two viruses or a single

[1] Received for publication March 15, 1934.

[2] Associate Entomologist in the Experiment Station.

[3] I. D. Dobroscky, in a personal interview with the author.

virus, and whether the viruses could be separated by the three vectors. Transmission experiments with yellows by the three species of leafhoppers were conducted with the virus obtained from naturally infected asters, celery, and carrots, and from these same host plants experimentally infected by the different species of leafhoppers. Attempts were made to recover the virus from these experimentally infected host plants with the three species of previously noninfective leafhoppers. The host range of the disease among economic plants and weeds was also investigated. The characteristics, distribution, and food plants of two newly discovered vectors of California yellows are discussed in this paper.

METHODS

One method used in the separation of a mixture of viruses in the living plant is by the selective transmission of one virus by the insect vector. Hoggan[7] has shown that the peach aphid, *Myzus persicae* Sulz., transmits only the cucumber mosaic virus from a combination of cucumber and tobacco mosaic viruses, although the tobacco virus was present in the leaves upon which the aphids had fed. Bennett[3] demonstrated that *Aphis rubiphila* Patch transmitted only the curl virus of raspberries and *Amphorophora rubi* Kalt transmitted only the yellow mosaic virus and a medium type of mosaic from a raspberry infected with the three diseases. Smith[16] utilized the peach aphid, *Myzus persicae,* in the separation of potato viruses.

The method adopted to determine whether California aster yellows and celery yellows are caused by two viruses or a single virus was to conduct transmission experiments with yellows by the three species of leafhoppers from naturally and experimentally infected asters, celery, and carrots to healthy plants grown from seeds. It was found that *Cicadula divisa* occurred on all of these host plants in the field. *Thamnotettix montanus* was rare on asters, abundant on celery, and common on carrots. *T. geminatus* was often collected on asters, rarely on celery, and commonly on carrots. These three host plants were transplanted in pots in the greenhouse and healthy plants grown from seeds were used as checks or controls.

Production of Noninfective Leafhoppers.—The production of noninfective *Cicadula divisa* on Sacramento barley immune to the yellows disease has been described in a previous paper.[13] The production of noninfective *Thamnotettix montanus* and *T. geminatus* on barley failed because these species of leafhoppers did not complete their life cycles on that plant. The method adopted was similar to that used with the beet leafhopper, *Eutettix tenellus* (Baker), described in a previous paper.[12]

Several hundred females of each species oviposited in large celery plants for a period of one week and were then removed. Nymphs were transferred after emergence from the egg, before they had an opportunity to feed, from diseased to healthy celery plants, with a fine camel's-hair brush moistened at the tip. The leafhoppers reared to the adult stage on healthy celery, as well as later generations so bred, failed to produce the disease.

DETERMINATION OF THE SPECIES

Thamnotettix Montanus.—The mountain leafhopper, *Thamnotettix montanus*, is 4.5 to 6.0 mm long, with white or yellowish face, a transverse brownish band between the eyes, a conspicuous yellow transverse band on the pronotum, and the scutellum brown (pl. 1, *C, D, E, F*). The summer adults collected in the northern San Joaquin, southern Sacramento, Santa Clara, and Salinas valleys were dark brown (pl. 1, *C, D*) while the specimens taken during the autumn were usually black (pl. 1, *E, F*), with intermediates between the two color patterns.

Thamnotettix montanus has been recorded from British Columbia,[19] Washington,[22,23] Oregon,[22] California, [20,22] Nevada,[4] Idaho,[4] and Colorado[6,19] and probably occurs in most of the western states.

Essig[4] reported that *Thamnotettix montanus* is common on grasses, weeds, carrot, larkspur, goldenrod, apple, and prune.

This leafhopper has a wide range of food plants in California. Adults were collected abundantly on celery growing in the Sacramento Valley, but not so abundantly in the fog belt of the Santa Clara and Salinas valleys. Adults were commonly taken and an occasional nymph on White Icicle radish and Purple Top White Globe turnip in the delta districts near Stockton, in the San Joaquin Valley. The leafhopper was rarely taken on asters in the Salinas Valley. The insects were occasionally captured on the following economic plants in the Sacramento and San Joaquin valleys:

Chenopodiaceae: sugar beets, garden, red, or table beets.
Leguminosae: alfalfa and beans.
Cucurbitaceae: squash, pumpkin, and cucumbers.
Solanaceae: potatoes.
Cruciferae: Chinese cabbage.
Umbelliferae: carrots.
Compositae: lettuce.

Weeds as food and breeding plants of *Thamnotettix montanus* have received little attention up to the present time. The adults were taken

[4] Several shipments of *Thamnotettix montanus* were received from Twin Falls, Idaho, collected by C. F. Henderson.

in small numbers on tumbleweed (*Amaranthus graecizans*). Nymphs hatched from eggs deposited in curly dock (*Rumex crispus*) under natural conditions and were reared to the adult stage on this host plant.

Thamnotettix Reductus.—Van Duzee[5] determined the species from California and Idaho as *Thamnotettix reductus,* and "considers *reductus* as a species distinct from *montanus,* although it was described as a variety."[22] De Long[6] could find no genital character which is constant and distinctive on the adults from California and Idaho, but in certain groups it is very difficult to find characters on the genitalia. He states, "I do not feel, however, that *reductus* is a distinct species."

Since *Thamnotettix montanus* and *T. reductus* are considered distinct species on the basis of color pattern only and since there is a difference of opinion among systematists as to the species, the name used in this paper is *montanus.* The description of *T. montanus reductus* by Van Duzee[22] follows:

> This form seems to be purely a color variety in which the yellow saddle is reduced to a small mark on the apex of the claval nervures, often on the outer nervures only, or in a few dark males it may be entirely wanting. The brown band on the base of the vertex is also reduced, sometimes to a mere shade, but there may be a dark line next the eye and a geminate spot on the basal middle. Both forms are found together throughout their range, but the present form is much more abundant toward the south, while those from Oregon and Washington are almost entirely typical *montanus.*

Specimens of *Thamnotettix* received from C. F. Henderson, Twin Falls, Idaho, were determined as *T. reductus* by Van Duzee and as *T. montanus* by De Long. The leafhoppers from Idaho transmitted yellows to healthy celery but not to asters. The virus was recovered and transferred by previously noninfective *Cicadula divisa* from the celery infected with yellows by the *Thamnotettix* from Idaho to healthy asters and celery.

Thamnotettix Geminatus.—The geminate leafhopper, *Thamnotettix geminatus,* is 5 to 6 mm long, greenish yellow or brown, with a pair of black spots on the anterior border of the head, a black spot on each side of the eye, an arched band near the front border of the pronotum, and black spots on the scutellum (pl. 1, *G, H*). A more detailed description of the species is given by Van Duzee.[19]

Thamnotettix geminatus has been recorded from Colorado,[6,18] Idaho,[7] California,[20,22,23] Washington,[11] and Alaska.[1] It has been recorded under the name *Cicadula laeta* from Alaska and Shumagin and

[5] Van Duzee, E. P., letter to author dated November 25, 1930.

[6] DeLong, D. W., letter to author dated August 15, 1932.

[7] Several shipments of *Thamnotettix geminatus* were received from Twin Falls, Idaho, collected by C. F. Henderson.

Popof islands by Ashmead.[1] One specimen under the same name also is in the United States National Museum from Unga Island.[1]

Osborn[11] reported that *Thamnotettix geminatus* occurred in such numbers upon clover, alfalfa, and timothy in the state of Washington, especially at Pullman, as to threaten to become destructive. Additional food plants recorded by Essig[4] include grasses, grains, and apple. Van Duzee[20] found the leafhopper common on *Malvastrum* in San Diego County, California

No intensive study has been made of the food and breeding plants of *Thamnotettix geminatus* in California. The adults were commonly taken on carrots in the Sacramento and Salinas valleys, but rarely on celery, and often on asters in the Salinas Valley.

TRANSMISSION OF YELLOWS BY THAMNOTETTIX MONTANUS TO HEALTHY ASTERS AND CELERY

Collected on Celery Under Natural Conditions.—During 1931 a serious outbreak of celery yellows occurred in the Sacramento and Santa Clara valleys, and celery in many fields was plowed under. *Thamnotettix montanus* was very abundant in the celery fields near Sacramento. Adults captured in the celery fields transmitted yellows to 2 of 12 healthy celery plants but not to asters, as shown in table 3 (p. 348). These results demonstrate that this insect is a vector of celery yellows under natural conditions.

Fed on Naturally Infected Asters and Celery.—A comparison was made of the transmission of yellows by previously noninfective *Cicadula divisa* and *Thamnotettix montanus* from 10 asters naturally infected with the disease to healthy asters and celery. Ten lots, each consisting of 10 *C. divisa* or 10 *T. montanus* were fed for a period of 2 days on 10 diseased asters, one lot to a plant, and then each lot was fed for a period of 21 days on a healthy aster or celery plant; *T. montanus* was used only on celery. Each lot was then transferred to successive healthy aster or celery plants and was kept on each plant for a period of 10 days. In the recovery of the virus from celery experimentally infected by *T. montanus* with the virus from naturally infected asters, the feeding period on the infected celery plants varied from 4 to 33 days. The results obtained are indicated in table 1.

The results in table 1 show that previously noninfective *Cicadula divisa* after feeding 2 days on asters naturally infected with yellows transferred the virus to 45 per cent of the healthy asters and to 48.3 per cent of the healthy celery plants. Previously noninfective *Thamnotettix mon-*

tanus after feeding 2 days on asters naturally infected with yellows transferred the virus to 20 per cent of the healthy celery plants as shown in table 3, and recovered the virus from 3 of the 4 celery plants which they had infected (table 1), or 75 per cent.

Tests were made on the transmission of yellows by *Thamnotettix montanus* from naturally infected celery. Seventeen lots of 10 or 20 *T. montanus* each were fed for a period of 3 weeks on diseased celery plants. Each lot was then transferred at weekly intervals to 3 successive healthy celery plants and to 1 aster. A comparison was also made of the recovery of the virus by previously noninfective *T. montanus* and *Cicadula divisa* from celery experimentally infected with yellows by *T. montanus*. The same procedure was used in the recovery of the virus from experimentally infected celery with the two insects except that with *T. montanus* 2 successive healthy celery and 1 aster plants were used, and with *C. divisa* 1 healthy celery and 1 aster. Table 2 indicates the results obtained.

The percentage of transmission of yellows by *Thamnotettix montanus* to successive healthy celery and aster plants and the recovery of the virus by the same species of leafhopper and by *Cicadula divisa* from experi-

TABLE 1

COMPARISON OF TRANSMISSION OF YELLOWS BY PREVIOUSLY NONINFECTIVE CICADULA DIVISA AND THAMNOTETTIX MONTANUS FROM NATURALLY INFECTED ASTERS TO SUCCESSIVE HEALTHY ASTERS AND CELERY, AND RECOVERY OF VIRUS BY T. MONTANUS*

Source of inoculation: aster-yellows plant no.	Successive aster and celery plants inoculated							Virus recovered from celery infected by *T. montanus* and transferred by this leafhopper to celery	
	By *C. divisa*					By *T. montanus*			
	Asters		Celery			Celery			
	First set	Second set	First set	Second set	Third set	First set	Second set	First set	Second set
1	+	+	+	+	+	−	−	....	....
2	+	+	+	+	....	−	+	+	−
3	−	−	−	−	−	−	−	....	....
4	−	−	−	−	−	−	−	....	....
5	−	+	+	+	−	−	+	−	+
6	−	−	−	−	−	−	−	....	....
7	−	−	−	−	−	−	−	....	....
8	+	+	+	−	−	−	+	−	−
9	+	+	+	+	+	−	+	−	+
10	−	−	+	+	+	−	−	....	....
Total +	4+	5+	6+	5+	3+	0+	4+	1+	2+
Total −	6−	5−	4−	5−	6−	10−	6−	3−	2−

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

mentally infected celery to healthy celery and asters is given in table 2 and summarized in table 3. With 3 successive sets of celery plants, 9 of the 51 inoculated, or 17.6 per cent, and with 1 set of asters 2 of the 17 plants inoculated, or 11.8 per cent, were infected with yellows by *T. mon-*

TABLE 2

TRANSMISSION OF YELLOWS BY THAMNOTETTIX MONTANUS FROM NATURALLY INFECTED CELERY TO SUCCESSIVE HEALTHY CELERY AND ASTERS AND RECOVERY OF VIRUS FROM EXPERIMENTALLY INFECTED PLANTS BY T. MONTANUS AND CICADULA DIVISA*

Number of *T. montanus* transferred from infected celery	Successive celery and aster plants inoculated by *T. montanus*				Virus recovered from experimentally infected celery and transferred				
					By *T. montanus*			By *C. divisa*	
	Celery			Aster	To celery		To aster		
	First set	Second set	Third set		First set	Second set		To celery	To aster
10	−	+	+	−	++	++	−−	++	++
10	−	+	−	−	−	−	−	+	+
20	+	−	−	−	+	+	−	+	+
20	+	−	−	+	−	−	−	+	+
20	+	−	−	+	+	−	−	+	+
20	−	+	−	−	+	−	−	+	+
20	−	+	−	−	−	−	−	+	+
20	−	−	+	−	−	−	−	+	+
20	−	−	−	−	....	....	....	....	....
20	−	−	−	−	....	....	....	....	....
20	−	−	−	−	....	....	....	....	....
20	−	−	−	−	....	....	....	....	....
20	−	−	−	−	....	....	....	....	....
20	−	−	−	−	....	....	....	....	....
20	−	−	−	−	....	....	....	....	....
20	−	−	−	−	....	....	....	....	....
20	−	−	−	−	....	....	....	....	....
Total +	3+	4+	2+	2+	5+	3+	0+	9+	9+
Total −	14−	13−	15−	15−	4−	6−	8−	0−	0−
Percentage	*17.6*	*23.5*	*11.8*	*11.8*	*55.5*	*33.3*	*0.0*	*100*	*100*

* The plus sign (+) indicates the production of the disease, and the minus sign (−) shows that no disease resulted. ++ = Virus recovered from 2 sets of experimentally infected celery. −− = Failure to recover virus from 2 sets of plants tested.

tanus that had fed on naturally infected celery plants (table 3). From experimentally infected plants, the virus was recovered by *T. montanus* and transferred to celery from 5 of the 9 infected celery plants, or 44.4 per cent, but was not transferred to any of 9 asters inoculated; it was recovered by *C. divisa* from all of the 9 infected celery plants and transferred to all of the 9 celery and 9 aster plants inoculated, or 100 per cent (table 2).

In another experiment to test transmission by *Thamnotettix montanus* to asters, each lot of 5 or 10 adults of *T. montanus,* after feeding for a period of 3 weeks on celery naturally infected with yellows, was transferred to healthy asters. Four of 15 aster plants inoculated, or 26.6 per cent, were infected with yellows, as shown in table 3. The virus was not recovered from the 4 experimentally infected asters by *T. montanus,* but was recovered by *Cicadula divisa* and transferred to healthy asters and celery.

Bred on Naturally Infected Asters and Celery.—Aster was an unfavorable food plant for the adults of *Thamnotettix montanus,* but the nymphs often acquired the winged stage on large aster plants. Lots of 10, 20, or 25 adults bred on asters naturally infected with yellows were transferred to one or more healthy celery plants and then to healthy asters. Thirty-two celery plants were thus inoculated, and 8, or 25 per cent, became diseased as indicated in table 3. Twenty-two asters were inoculated by the same lots of leafhoppers, but not a single case of aster yellows developed (table 3).

Fifty lots of 20 *Thamnotettix montanus* which had completed the nymphal stages on celery naturally infected with yellows were transferred to healthy celery, one lot to each plant. Fifteen of 50 celery plants thus inoculated, or 30 per cent, developed the disease (table 3).

Fed on Asters and Celery Experimentally Infected by Thamnotettix Montanus.—Nymphs were fed on asters experimentally infected with yellows by *Thamnotettix montanus* and after they acquired the winged stage, each of 25 lots of 5 adults were transferred to a healthy aster, but again all of the plants remained healthy (table 3).

An attempt was made to transfer the virus from asters experimentally infected with yellows by *Thamnotettix montanus* to healthy celery by lots of 50 or 100 males. Each lot of leafhoppers was fed on diseased asters and healthy celery, alternating daily, until all of the insects were dead. With this method the leafhoppers lived from 21 to 42 days. All of the four celery plants inoculated by this method failed to develop the disease (table 3).

Fifteen lots of *Thamnotettix montanus* were fed for a period of 3 weeks or longer on celery experimentally infected by this leafhopper and then each lot was transferred to a healthy aster. One of the 15 asters inoculated, or 6.6 per cent, developed the disease (table 3).

Males of *Thamnotettix montanus* were fed for a period of 3 weeks or longer on 18 celery plants experimentally infected with yellows by *T. montanus* and then each lot of 20 males was transferred to 1 or 2 healthy celery plants. Thirty-four of 70 lots transmitted yellows to 34 of 96 cel-

ery plants inoculated, or 35.4 per cent (table 3). The virus was transferred by *Cicadula divisa* from the original celery plants infected with yellows by *Thamnotettix montanus,* to 14 of the 18 healthy asters inoculated, or 77.7 per cent.

Fed on Asters and Celery Experimentally Infected by Cicadula Divisa.—Thamnotettix montanus, after feeding on asters experimentally infected with yellows by *Cicadula divisa,* were transferred to 104 healthy asters, but only 2 asters, or 1.9 per cent, became diseased (table 3). A high mortality of the leafhoppers occurred on small asters, and in all probability the incubation period of the virus in many of the insects was not completed.

Thamnotettix montanus, after feeding on asters infected with yellows by *Cicadula divisa,* were transferred in lots of 20 specimens to 1 or 2 healthy celery plants. Seven of the 39 celery plants inoculated, or 17.9 per cent, became diseased (table 3).

Since a high mortality of the adults occurred on asters, it was decided to feed the leafhoppers for periods varying from 3 to 5 weeks on celery experimentally infected with yellows by *Cicadula divisa.* In one experiment each lot of 5 adults was transferred to 1 or 2 healthy asters and they remained on the plants until all were dead. With twenty-nine lots of 5 insects each, 49 asters were inoculated, but no yellows developed (table 3). In a second experiment lots of 20 leafhoppers were used to inoculate 124 asters, and 3 plants, or 2.4 per cent, developed symptoms of yellows (table 3). Previously noninfective *C. divisa* transferred the virus from the 3 infected asters to healthy asters and celery, but *Thamnotettix montanus* failed to recover the virus. In a third experiment 4 lots of 100 *T. montanus,* after feeding for a period of 27 days on celery experimentally infected with yellows by *C. divisa,* failed to transmit the virus to 4 healthy asters (table 3). In a fourth experiment repeated inoculations of each of 6 healthy aster plants were made by lots of 20 male *Thamnotettix montanus* which had fed for periods varying from 26 to 57 days on celery experimentally infected with yellows by *Cicadula divisa;* when one lot of 20 leafhoppers died on an aster another lot of 20 specimens was put in the cage enclosing the plant, and so on until 5 successive lots of 20 insects were used on each plant. Three lots of 20 males were dead at the end of 1 day on small asters while 1 specimen of another lot lived 18 days. The average longevity of the last living male with 30 lots of 20 leafhoppers was 5 days on small asters. The six asters inoculated by this method remained healthy (table 3).

Lots of 20 *Thamnotettix montanus* were fed for a period of 3 weeks or longer on celery infected by *Cicadula divisa* and then each lot was trans-

ferred to 1 or 2 healthy celery plants. Thirty-six of the 134 celery plants inoculated, or 26.9 per cent, developed symptoms of yellows (table 3).

Fed on Celery Experimentally Infected by Thamnotettix Geminatus.—*Thamnotettix montanus* transmitted yellows from celery experimentally infected by *T. geminatus* to 6 of 26 healthy celery plants inoculated,

TABLE 3

SUMMARY OF RESULTS ON TRANSMISSION OF YELLOWS BY THAMNOTETTIX MONTANUS TO HEALTHY ASTERS AND CELERY

Source of virus	Asters inoculated	Asters infected	Asters healthy	Per cent infected
Collected on celery under natural conditions	12	0	12	0.0
Fed on naturally infected celery	17	2	15	11.8
Fed on naturally infected celery	15	4	11	26.6
Bred on naturally infected asters	22	0	22	0.0
Fed on asters experimentally infected by *T. montanus*	25	0	25	0.0
Fed on celery experimentally infected by *T. montanus*	15	1	14	6.6
Fed on asters experimentally infected by *Cicadula divisa*	104	2	102	1.9
Fed on celery experimentally infected by *C. divisa*	49	0	49	0.0
	124	3	121	2.4
	4	0	4	0.0
	6	0	6	0.0
Fed on celery experimentally infected by *T. geminatus*	19	0	19	0.0
Total	412	12	400	.....
Percentage	.....	....	.....	*2.9*

Source of virus	Celery inoculated	Celery infected	Celery healthy	Per cent infected
Collected on celery under natural conditions	12	2	10	16.7
Fed on naturally infected asters	20	4	16	20.0
Fed on naturally infected celery	51	9	42	17.6
Bred on naturally infected asters	32	8	24	25.0
Bred on naturally infected celery	50	15	35	30.0
Fed on asters experimentally infected by *T. montanus*	4	0	4	0.0
Fed on celery experimentally infected by *T. montanus*	96	34	62	35.4
Fed on asters experimentally infected by *C. divisa*	39	7	32	17.9
Fed on celery experimentally infected by *C. divisa*	134	36	98	26.9
Fed on celery experimentally infected by *T. geminatus*	26	6	20	23.1
Total	464	121	343	.....
Percentage	.....	.....	.....	*26.1*

or 23.1 per cent, but failed to transmit the virus to any of 19 healthy asters inoculated (table 3). The virus was not recovered from the 6 celery plants by *T. montanus* but was recovered by previously noninfective *Cicadula divisa* and transferred to healthy aster and celery.

The transmission of yellows from all sources by *T. montanus* to asters average 2.9 per cent and to celery 26.1 per cent as summarized in table 3.

TRANSMISSION EXPERIMENTS WITH SUGAR-BEET CURLY TOP

Since the beet leafhopper, *Eutettix tenellus* (Baker), the vector of sugar-beet curly top in North America, is closely related to the genus, *Thamnotettix,* (it was originally placed in the latter genus [2, 6]) tests were made on whether or not *T. montanus* could transmit sugar-beet curly top. Previously noninfective nymphs or adults, after feeding on curly-top beets, were transferred to 24 healthy beet seedlings, but no curly top developed. Since a high mortality of the leafhoppers occurred on sugar beets, 5 lots of 100 males were fed alternating daily on curly-top beets and healthy celery for a period varying from 1 to 2 weeks, and then each lot of leafhoppers was kept on a healthy beet until the last specimen died. The five beets remained healthy.

ADDITIONAL HOST PLANTS EXPERIMENTALLY INFECTED WITH YELLOWS BY THAMNOTETTIX MONTANUS

Carrot Yellows.—Thamnotettix montanus was collected on carrots (*Daucus carota* var. *sativa*) in the Salinas, San Juan, and Sacramento valleys. Previously noninfective leafhoppers, after feeding on 5 carrots naturally infected with yellows, were transferred to 10 healthy celery plants, and 4 of these developed symptoms of yellows. The virus was transferred by previously noninfective *T. montanus* from 2 of these 4 experimentally infected celery plants to healthy celery plants, but attempts to transfer it to asters and carrots were unsuccessful.

An attempt was made to experimentally infect with yellows from celery by means of *Thamnotettix montanus* 3 white, 1 yellow, and 7 orange varieties of carrots. Two plants of each variety were repeatedly inoculated by different lots of leafhoppers. Oxheart or Guerande, an orange variety of carrot, developed typical symptoms of the disease similar to those on carrots infected by *Cicadula divisa* described in a previous paper.[13] The virus was transferred by previously noninfective *C. divisa* from the carrot experimentally infected with yellows to healthy aster and celery plants, but *T. montanus* failed to recover the virus from the carrot.

White London Mustard Yellows.—White London mustard (*Brassica alba*) is a new host plant of aster yellows. This mustard was experimentally infected with yellows by both *Thamnotettix montanus* (in 1 of 2 tests made) and *Cicadula divisa* from the mustard plants experimentally

infected with yellows to healthy asters and celery, but *T. montanus* failed to recover the virus from mustard.

Plants infected with yellows by the two species of leafhoppers developed similar symptoms. The apical leaves were dwarfed, cupped outward, and yellow. Secondary shoots developed from the axils of the leaves (fig. 1).

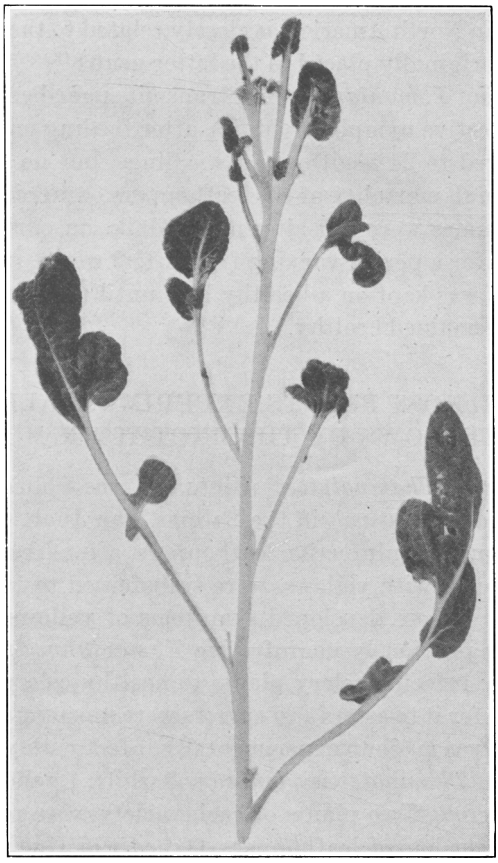

Fig. 1.—White London mustard (*Brassica alba*) experimentally infected with yellows by *Thamnotettix montanus*, showing dwarfed, outward-cupped apical leaves and secondary shoots arising from the axils of the older leaves.

Prickly Winter Spinach Yellows.—Prickly Winter spinach (*Spinacia oleracea*) was experimentally infected with yellows by *Thamnotettix montanus* (in 1 of 10 tests made) and *Cicadula divisa*. The virus was transferred by previously noninfective *T. montanus* from experimen-

tally infected spinach to healthy celery but not to asters, and by *C. divisa* to both celery and asters.

The symptoms of the disease on spinach infected with yellows by the two species of leafhoppers were similar. The petioles of the outer leaves

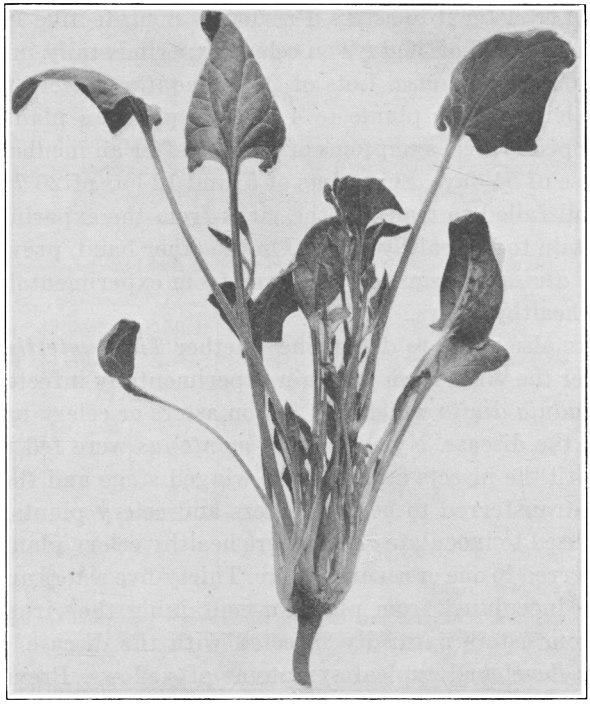

Fig. 2.—Prickly Winter spinach (*Spinacia oleracea*) infected with yellows by *Thamnotettix montanus* showing elongated petioles of the outer leaves and many upright secondary shoots with dwarfed leaves and shortened petioles.

were elongated, and many upright secondary shoots developed with dwarfed leaves and shortened petioles (fig. 2).

Prizehead Lettuce Yellows.—Lettuce (*Lactuca sativa*) of the variety Prizehead was experimentally infected with yellows from celery by *Thamnotettix montanus* (only 1 test was made) and developed symptoms of the disease similar to those on lettuce infected by *Cicadula divisa* as described in a previous paper.[13] The virus was transferred by previously noninfective *C. divisa* from experimentally infected lettuce to asters and celery, but *T. montanus* failed to recover the virus from lettuce.

Plantain or Ribgrass Yellows.—In a previous paper[13] plantain or ribgrass (*Plantago major*) was reported to be naturally infected with yellows. Tests were made to determine whether plantain could be experimentally infected with yellows from celery by *Thamnotettix montanus* and whether the leafhopper could recover the virus from infected plantain and transfer it to asters. Previously noninfective *T. montanus* were fed for a period of 36 days on celery experimentally infected with yellows by *Cicadula divisa*. Lots of 20 *T. montanus* were transferred from the celery-yellows plants to 4 healthy plantain plants, and one plant developed typical symptoms of yellows after an incubation period of the disease of 54 days. Seven lots of 5, and 12 lots of 20 *T. montanus* per plant, all failed to transmit the virus from the experimentally infected plantain to 19 healthy asters. On the other hand, previously noninfective *C. divisa* transmitted the virus from experimentally infected plantain to healthy asters..

Tests were also made to determine whether *Thamnotettix montanus* could recover the virus from plantain experimentally infected with yellows by *Cicadula divisa* which had fed on asters or celery naturally infected with the disease. Nymphs of *T. montanus* were fed on diseased plantain until the insects acquired the winged stage and then 10 or 20 males were transferred to healthy asters and celery plants. Often the males were used to inoculate one or more healthy celery plants and then were transferred to one or several asters. Thirty-five asters and 35 celery plants were inoculated from plantain containing the virus originally obtained from asters naturally infected with the disease, but only a single aster developed typical symptoms of yellows. Previously noninfective *T. montanus* recovered the virus from this diseased aster and transferred it to 1 of 4 healthy asters. Twelve asters and 27 celery plants were similarly inoculated from plantain containing the virus originally obtained from celery naturally infected with the disease, but only 1 celery plant developed yellows. The virus was not recovered from the experimentally infected celery plant by *T. montanus,* but was transferred to aster and celery by previously noninfective *C. divisa.*

TRANSMISSION OF YELLOWS BY THAMNOTETTIX GEMINATUS TO HEALTHY ASTERS AND CELERY

Fed on Naturally Infected Asters.—Although *Thamnotettix geminatus* was collected on asters under natural conditions, a high mortality of the adults occurred on small asters in the greenhouse when *T. geminatus* was transferred from large asters in the field. It was found that 6 lots

of 3 leafhoppers fed on 6 healthy asters died within a week, and all of the asters remained healthy as shown in table 6 (p. 356). In all probability the virus incubation period in the insects was not completed.

Bred on Naturally Infected Celery.—Thamnotettix geminatus collected on asters in the San Juan and Salinas valleys deposited eggs in potted celery plants naturally infected with yellows. The nymphs which hatched fed for a period of at least 2 weeks on the celery-yellows plants

TABLE 4

TRANSMISSION OF YELLOWS BY THAMNOTETTIX GEMINATUS TO SUCCESSIVE HEALTHY CELERY AND ASTERS AND RECOVERY OF VIRUS FROM EXPERIMENTALLY INFECTED PLANTS BY CICADULA DIVISA*

Number of *T. geminatus* transferred from infected celery	Successive celery and aster plants inoculated by *T. geminatus*						Virus recovered from experimentally infected plants and transferred by *C. divisa*	
	First set of celery	First set of asters	Second set of celery	Third set of celery	Fourth set of celery	Fifth set of celery	To aster	To celery
3	+	−	−	−	+	−	++	++
3	−	−	−	−	+	−	+	....
3	−	−	−	−	+	....	....	+
3	−	−	−	−	−	....	....	....
3	−	−	−	−	+	....	....	+
3	−	−	−	−	+	....	+	....
Total +	1+	0+	0+	0+	5+	0+	4+	4+
Total −	5−	6−	6−	6−	1−	2−	0−	0−

* The plus sign (+) indicates the production of the disease, and the minus sign (−) shows that no disease resulted; ++ = virus recovered from 2 sets of experimentally infected celery.

and were then transferred in lots of 5 or 10 to 6 healthy celery plants. One of 6 celery plants developed symptoms of yellows. After the nymphs acquired the winged stage, 48 adults were transferred to 1 healthy celery plant, which also became diseased (table 6).

Bred on Asters and Celery Experimentally Infected by Cicadula Divisa.—Nymphs lived longer than adults on aster, and sometimes the nymphs acquired the winged stage on asters. Nymphs which hatched from eggs deposited in healthy celery were transferred to asters experimentally infected with yellows by *Cicadula divisa.* Nymphs and adults reared on diseased asters were transferred singly to 35 healthy asters with negative results. Likewise 2 lots of 5 adults and 2 lots of 20 adults failed to transmit yellows to 4 asters (table 6).

Eleven adults of *Thamnottetix geminatus* bred on celery experimentally infected with yellows by *Cicadula divisa* failed to transmit the virus to 11 healthy asters (table 6).

Adult *Thamnotettix geminatus,* collected on asters in the San Juan

and Salinas valleys, were fed for a period of 3 weeks on a celery plant experimentally infected with yellows by *Cicadula divisa*. Six lots of 3 leafhoppers each were transferred to successive healthy celery and aster plants until all of the insects were dead. The adults were fed on each celery plant for a period of 1 week and on each aster for 1 day. The results obtained are indicated in table 4.

Table 4 shows that from the first transfer (to 6 healthy celery plants) infection occurred in 1 plant which developed typical symptoms of yellows; in the second transfer (to asters) all of the plants remained healthy; in the third and fourth transfers (to celery) no infections occurred; and in the fifth transfer (to celery) 5 plants became diseased. In the fifth transfer 4 of the 5 infections occurred at the end of 8 weeks. The minimum virus incubation period in *Thamnotettix geminatus* is not known; in *Cicadula divisa* it was found to be 13 days.[8] The virus was recovered by previously noninfective *C. divisa* and transferred to healthy asters and celery from each celery infected by *T. geminatus*. The virus was also recovered by previously noninfective *T. geminatus* from 1 of the 6 celery plants infected with the yellows by this leafhopper.

Fed on Naturally Infected Celery and Celery Experimentally Infected by Cicadula Divisa and Thamnotettix Geminatus.—Tests were made on the transmission of yellows by lots of 1, 5, 10, 20, and 25 adults of *Thamnotettix geminatus* which were transferred in succession to one or more healthy celery plants. Some of the leafhoppers were collected on various food plants in the field and were fed for a period of 2 to 4 weeks on celery experimentally infected with yellows by *T. geminatus* or *Cicadula divisa,* or on celery naturally infected with the disease. *T. geminatus* which had been bred on celery experimentally or naturally infected with yellows were also used. The leafhoppers were transferred at the end of every 2 weeks to successive healthy celery plants until all of the insects were dead. Table 5 indicates the results obtained on the transmissions of celery yellows obtained with *T. geminatus* but does not show the number of negative tests. Table 5 also shows the recovery of the virus by *C. divisa* from some of the celery plants experimentally infected with yellows by *T. geminatus,* but all of the infected celery plants were not tested.

It is evident from table 5 that *Thamnotettix geminatus* transmitted yellows at irregular intervals, but infections occurred more often on the first celery plant. However, in one case where 15 leafhoppers were transferred to successive healthy celery plants at intervals of 2 weeks until

[8] Based on unpublished data.

TABLE 5

TRANSMISSION OF CELERY YELLOWS BY THAMNOTETTIX GEMINATUS TO SUCCESSIVE HEALTHY CELERY PLANTS AND RECOVERY OF VIRUS FROM EXPERIMENTALLY INFECTED CELERY BY CICADULA DIVISA*

Number of *T. geminatus* transferred from infected celery	Successive celery plants inoculated by *T. geminatus*								Virus recovered from experimentally infected celery and transferred by *C. divisa*	
	First set	Second set	Third set	Fourth set	Fifth set	Sixth set	Seventh set	Eighth set	To aster	To celery
1	+	....	....	....	....	....	....	....	....	−
1	+	....	....	....	....	....	....	....	....	−
1	+	....	....	....	....	....	....	....	....	−
1	+	−	−	....	....	....	....	....	....	−
1	−	+	−	....	....	....	....	....	....	....
5	+	−	−	−	+	−	−	....	....	−
5	−	+	−	+	−	−	+	....	+¶	++§
5	+	−	−	−	....	....	....	....	+	+
5	−	+	+	−	....	....	....	....	+¶	−¶
5	+	−	−	....	....	....	....	....	....	+
5	+	−	−	....	....	....	....	....	....	+
5	+	−	−	....	....	....	....	....	....	−
5	−	+	−	....	....	....	....	....	+	+
5	+	−	....	....	....	....	....	....	+	+
5	+	−	....	....	....	....	....	....	....	+
5	+	−	....	....	....	....	....	....	+	+
5	−	+	....	....	....	....	....	....	+	+
5	+	−	....	....	....	....	....	....	....	−
5	+	....	....	....	....	....	....	....	....	−
10	−	−	−	−	+	−	−	....	+	....
10	+	+	−	−	−	−	−	....	++	+¶
10	+	−	−	−	−	−	....	....	+	+
10	−	+	−	−	−	−	....	....	....	+
10	+	+	−	−	....	....	....	....	....	−+
10	+	−	−	−	....	....	....	....	....	+
10	+	−	−	−	....	....	....	....	....	+
10	+	+	+	−	....	....	....	....	+++	+++
10	−	+	−	+	....	....	....	....	+¶	+
10	+	−	−	....	....	....	....	....	+	+
10	+	+	−	....	....	....	....	....	....	++
10	−	−	+	....	....	....	....	....	....	+
10	+	−	−	....	....	....	....	....	....	+
10	−	+	....	....	....	....	....	....	....	+
10	+	+	....	....	....	....	....	....	+¶	+
10	+	−	....	....	....	....	....	....	+	....
10	+	+	....	....	....	....	....	....	+¶	+
10	+	....	....	....	....	....	....	....	+	....
10	+	....	....	....	....	....	....	....	....	−
10	+	....	....	....	....	....	....	....	....	−
10	+	....	....	....	....	....	....	....	....	....
10	+	....	....	....	....	....	....	....	....	....
10	+	....	....	....	....	....	....	....	−	−
15	−	−	−	−	−	−	+	+	....	....
15	−	+	....	....	....	....	....	....	+	+
20	+	−	−	−	....	....	....	....	+	+
20	+	−	−	....	....	....	....	....	+	....
20	+	−	−	....	....	....	....	....	....	+
20	+	−	−	....	....	....	....	....	+	....
20	−	+	−	....	....	....	....	....	+	+
20	+	−	−	....	....	....	....	....	....	−
25	+	−	−	....	....	....	....	....	+	+
25	+	....	....	....	....	....	....	....	−	+
25	+	....	....	....	....	....	....	....	....	−
Total +	40+	15+	3+	2+	2+	0+	2+	1+	26+	34+
Total −	13−	25−	28−	13−	5−	7−	3−	0−	2−	15−

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

¶ Only one test made.

§ Only two tests made.

all of the insects were dead, infections were obtained with the seventh and eighth plants but not with the first 6 plants. This means that an infection was obtained at the end of 14 weeks.

One hundred and ten adults of *Thamnotettix geminatus* were transferred singly to 200 celery plants and only 5 plants, or 2.5 per cent, de-

TABLE 6

SUMMARY OF RESULTS ON TRANSMISSION OF YELLOWS BY THAMNOTETTIX GEMINATUS TO HEALTHY ASTERS AND CELERY

Source of virus	Asters inoculated	Asters infected	Asters healthy	Per cent infected
Fed on naturally infected asters	6	0	6	0.0
Bred on asters experimentally infected by *Cicadula divisa*	39	0	39	0.0
Bred on celery experimentally infected by *C. divisa*	11	0	11	0.0
Fed on celery experimentally infected by *C. divisa*	6	0	6	0.0
Total	62	0	62	.....
Percentage	....	....	....	*0.0*

Source of virus	Celery inoculated	Celery infected	Celery healthy	Per cent infected
Fed on naturally infected celery	7	2	5	28.6
Fed on celery experimentally infected by *C. divisa*	26	6	20	23.0
Fed on naturally infected celey and celery experimentally infected by *T. geminatus* and *C. divisa*	527	69	458	11.2
Total	560	77	483	.....
Percentage	.....	....	.....	*13.7*

veloped typical symptoms of yellows. Fifty lots of 5 insects each were transferred to 129 celery plants and 18 positive cases of yellows developed. In the next test 54 lots of 10 leafhoppers each were transferred to 151 celery plants, and yellows was transmitted to 31 plants. A small number of tests were made with larger numbers of leafhoppers as follows: 2 lots of 15 insects each transmitted yellows to 3 of 10 celery plants; 10 lots of 20 insects each to 9 of 32 celery plants; and 3 lots of 25 insects each to 3 of 5 celery plants. A total of 1,205 leafhoppers were tested by transfer to the first set of celery plants. Death of some of the insects occurred in the successive transfers. A total of 527 celery plants were inoculated by means of *T. geminatus* and 69 plants, or 11.2 per cent, developed symptoms of yellows (table 6). The transmission of celery yellows from all sources by *T. geminatus* averaged 13.7 per cent (table 6). The results on the transmission of yellows by *T. geminatus,* as summarized in table 6, show that a total of the 62 asters were inoculated but not a single case of aster yellows developed.

ADDITIONAL HOST PLANTS EXPERIMENTALLY INFECTED WITH YELLOWS BY THAMNOTETTIX GEMINATUS

Carrot Yellows.—Tests were made to determine whether *Thamnotettix geminatus* could recover and transmit the virus more readily from other host plants of yellows. The leafhoppers were commonly taken on carrots in the Salinas and Sacramento valleys. Nymphs and adults after feeding

TABLE 7

TRANSMISSION OF CARROT YELLOWS BY THAMNOTETTIX GEMINATUS AND RECOVERY OF VIRUS FROM INFECTED PLANTS BY CICADULA DIVISA

Variety	Plants inoculated	*T. geminatus* on each plant	Plants infected	Plants healthy	Incubation period in plant, days	Virus recovered and transferred from infected carrots by *C. divisa**	
						To aster	To celery
White varieties:							
Short white	1	5	1	0	33	—	—
	1	15	1	0	30	—	—
	1	20	1	0	36	—	—
	1	25	1	0	37	—	—
	4	1–25	0	4	....	....	....
White Belgian	1	25	1	0	43	—	—
	3	1–25	0	3	....	....	....
Orange varieties:							
Danvers Half Long	5	10–25	0	5	....	....	....
French Forcing	1	10	0	1	....	....	....
Long Orange	9	5–25	0	9	....	....	....
Oxheart or Guerande	7	5–20	0	7	....	....	....
Total	34	....	5	29	.....	5—	5—
Average	....	....	....	....	35.8	....	....

* The minus sign (—) shows that no disease resulted.

on carrots experimentally infected with yellows by *Cicadula divisa* or on carrots naturally infected with the disease were transferred to healthy carrots. Table 7 indicates the results obtained.

Table 7 shows that 4 of 8 Short White carrots and 1 of 4 White Belgian carrots were experimentally infected with yellows by *Thamnotettix geminatus.* The leafhoppers failed to infect any of the 4 orange varieties of carrots. The incubation period of the disease in the plant varied from 33 to 43 days, with an average of 35.8 days. The virus was not recovered by *Cicadula divisa* from carrots infected with yellows by *T. geminatus.*

Thamnotettix geminatus failed to transmit yellows to healthy asters

and celery from 5 carrots of an orange variety naturally infected with the disease.

Hollow Crown Parsnip Yellows.—Twelve lots of 3 adult *Thamnotettix geminatus* each, after feeding on Hollow Crown parsnip (*Pastinaca sativa*) infected with yellows by *Cicadula divisa,* failed to transmit the virus to 12 healthy celery plants.

DISCUSSION

If aster and celery yellows are caused by two viruses, then *Cicadula divisa* and *Thamnotettix montanus* failed to separate them, and apparently only one virus is concerned. Host-range differences and overlapping of host ranges have been discussed in a previous paper by the author[15] and by Kunkel[9] and Smith.[17] Among the economic plants infected with California aster yellows by *C. divisa* and by *T. montanus* no host-range differences have been found.

Cicadula divisa transmitted the virus with greater efficiency than *Thamnotettix montanus* or *T. geminatus. C. divisa* transferred the virus from naturally infected asters to 48.3 per cent and *T. montanus* to 20 per cent of the healthy celery plants (table 1). In the recovery of the virus from experimentally infected celery in one experiment, *C. divisa* transferred the virus to 100 per cent of the healthy aster and celery plants while *T. montanus* failed to transmit the virus to healthy asters but transferred the virus to 44.4 per cent of the healthy celery plants (table 2).

SUMMARY

A summary of the results obtained on the transmission of yellows by *Thamnotettix montanus* and *T. geminatus* is given in tables 3 and 6.

It was demonstrated that *Thamnotettix montanus* is a vector of celery yellows under natural conditions.

The transmission of yellows by *Thamnotettix montanus* to asters averaged 2.9 per cent and to celery 26.1 per cent.

Thamnotettix montanus failed to transmit curly top to sugar beets.

The host plants experimentally infected by *Thamnotettix montanus* include, aster, celery, carrots, White London mustard, Prickly Winter spinach, Prizehead lettuce, and plantain or ribgrass (*Plantago major*). White London mustard is a new host plant of California aster yellows.

Thamnotettix geminatus failed to transmit yellows from naturally infected asters, and from asters and celery experimentally infected by *Cicadula divisa,* to healthy asters; but further investigation is being

made on this point. The transmission of yellows from all sources to celery by *T. geminatus* averaged 13.7 per cent.

Thamnotettix geminatus tested singly transmitted yellows to 2.4 per cent of the healthy celery plants.

The host plants experimentally infected with yellows by *Thamnotettix geminatus* were celery and Short White and White Belgian carrots.

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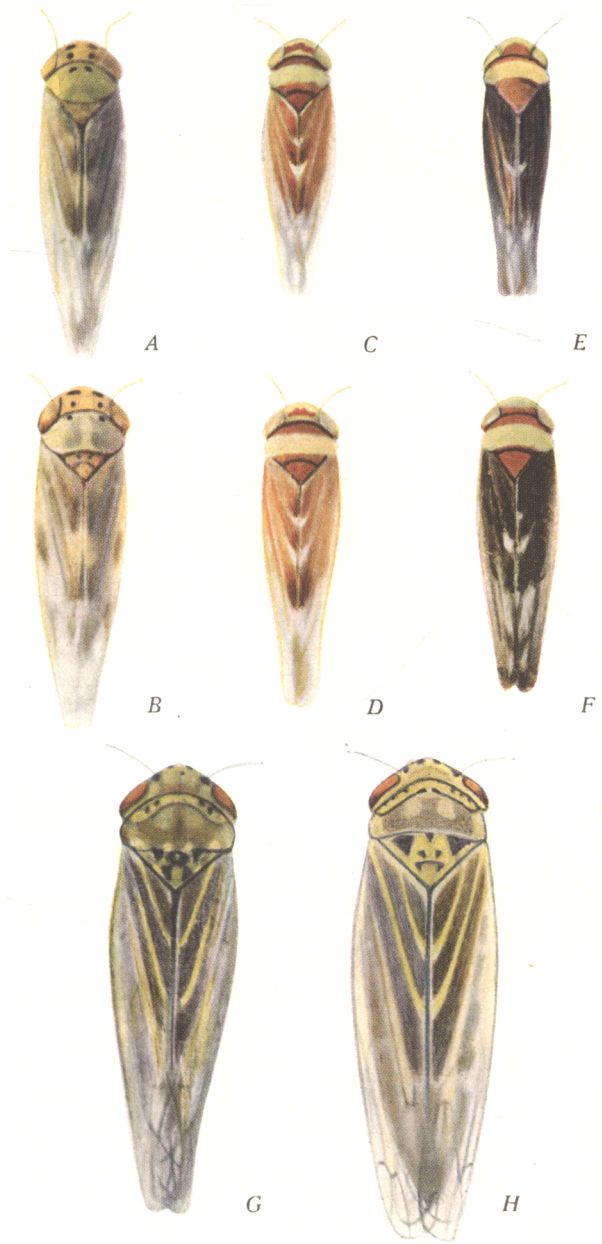

Plate 1.—*A*, *B*, *Cicadula divisa*; *C*, *D*, *Thamnotettix montanus*, adults of summer generation; *E*, *F*, *T. montanus*, adults of autumn generation; *G*, *H*, *T. geminatus*.