HILGARDIA

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

VOLUME 19 APRIL, 1949 NUMBER 6

CHARACTERS, DISTRIBUTION, AND FOOD PLANTS OF LEAFHOPPER VECTORS OF VIRUS CAUSING PIERCE'S DISEASE OF GRAPEVINES

DWIGHT M. DELONG and HENRY H. P. SEVERIN

LIFE HISTORY OF THE BLUE-GREEN SHARPSHOOTER, NEOKOLLA CIRCELLATA

HENRY H. P. SEVERIN

TRANSMISSION OF THE VIRUS OF PIERCE'S DISEASE OF GRAPEVINES BY LEAFHOPPERS

HENRY H. P. SEVERIN

UNIVERSITY OF CALIFORNIA · BERKELEY, CALIFORNIA

PAPERS IN THIS ISSUE

TRANSMISSION OF THE VIRUS OF PIERCE'S DISEASE OF GRAPEVINES BY LEAFHOPPERS[1]

HENRY H. P. SEVERIN[2]

INTRODUCTION

FOURTEEN SPECIES of leafhoppers in the subfamily Tettigoniellinae have been reported to transmit the virus of Pierce's disease of grapevines. These species are listed and a number of reports on the virus and its vectors summarized in the first paper of this issue (DeLong and Severin, 1949).[3]

The report (Hewitt, Houston, Frazier, and Freitag, 1946) that the virus causing Pierce's disease of grapevines was identical with that causing alfalfa dwarf stimulated further tests on intertransmission. Frazier and Freitag (1946) reported that ten vectors transmitted virus both from grapevines infected with Pierce's disease to healthy vines and alfalfa, and from alfalfa plants infected with dwarf to healthy vines and alfalfa. These tests, like all others previously reported, were made with multiple lots of vectors, and hence do not furnish data on comparative efficiency. For this purpose, single-insect tests must be used.

In order to find out which vectors were most important, single-insect tests were undertaken in 1942. Efficiency was determined not only for transmission from diseased to healthy grapevines and from diseased to healthy alfalfa plants, but also for intertransmission between grapevines and alfalfa; not all of these tests were made on every vector, however. The present paper reports results with nine of the vectors described in the first paper of this issue (DeLong and Severin, 1949). With two species that proved to be inefficient vectors, multiple-lot tests for transmission were made. Unsuccessful transmission tests with a number of other leafhoppers and a few fulgorids and cicadas are also reported.

Longevity records were kept on three species, and are reported here.

In planning control experiments, it is important to know how soon after acquiring the virus a vector can transmit it to a healthy plant, and how long the vector can continue to transmit the virus after becoming infective. Accordingly, tests were made on the latent period in three important leafhopper vectors of Pierce's-disease virus, and on retention of the virus in the blue-green sharpshooter, *Neokolla circellata* (Baker). Results are reported in this paper. Previous reports on these aspects in the leafhopper vectors of other viruses are summarized for comparison with results on vectors of Pierce's disease.

METHODS

The method of obtaining noninfective green sharpshooters, *Draeculacephala minerva* Ball, was one first used by J. H. Freitag. Large populations of this leafhopper were collected in the field, and 100 or more adults were allowed to deposit eggs in the leaves of mildew-resistant Sacramento barley,

[1] Received for publication May 17, 1948.

[2] Entomologist in the Experiment Station.

[3] See "Literature Cited" for citations, referred to in the text by author and date.

Hordeum vulgare. A few days before hatching, the packets of eggs were dissected from the leaves, and placed on a strip of moist filter paper, one end extending out of the mouth of a phial and the other end submerged in water. The bottom of the phial was embedded in soil in a 6-inch flower pot in contact with barley plants. The nymphs upon hatching crawled on the barley plants, and some completed the nymphal stages, but only a low population of adults was reared.

The method of obtaining noninfective blue-green sharpshooters, *Neokolla circellata,* was similar to that first described by Stahl and Carsner (1918) for the beet leafhopper, and later illustrated by Severin (1921).

Other species of leafhoppers collected in the field were transferred in lots of 20 adults to healthy grapevines or alfalfa plants, to test natural infectivity before using them in vector-efficiency tests in virus transmission. The vines and alfalfa plants served as control plants. The insects were rarely naturally infective. This confirms the results of Hewitt, Houston, Frazier, and Freitag (1946) with *Carneocephala fulgida* and *Helochara delta.*

The grapevines used were the varieties Emperor, Ribier, Palomino, and Thompson Seedless (*Vitis vinifera*) propagated from indexed cuttings, and wild grapevine (*V. californica*) grown from seeds. Vines grown from cuttings were used in all tests with multiple lots and also in all single-lot tests except in 1943 and 1944, when seedlings were used. The alfalfa was in all cases the California Common variety of *Medicago sativa.*

Details of methods used for specific aspects of transmission tests are given in appropriate sections.

EFFICIENCY

In the efficiency tests, each species of leafhopper was fed on infected grapevines, and some species also on diseasd alfalfa, for 2 days. *Friscanus friscanus* survived only 2 to 6 days on grapevines and 3 to 12 days on alfalfa plants (table 3, page 193), and hence this species was sometimes kept on diseased grapevines for 1 day only. After the feeding period on diseased plants, the insects were transferred singly and kept on healthy plants during adult life.

The following nine vectors were used in single-insect tests for efficiency in transferring the virus of Pierce's disease of grapevines from infected to healthy grapevines:

Helochara delta Oman (plate 2,*B,C*)
Redheaded sharpshooter, *Carneocephala fulgida* Nottingham (plate 1,*A,B*)
Green sharpshooter, *Draeculacephala minerva* Ball (plate 1,*C,D*)
Blue-green sharpshooter, *Neokolla circellata* (Baker) (plate 1,*E,F;* plate 2,*A;* plate 4)
Neokolla confluens var. *pacifica* DeLong and Severin (plate 3,*A,B*)
Neokolla severini DeLong (plate 2,*D,E,F*)
Pagaronia confusa Oman (plate 3,*C,D*)
Pagaronia triunata Ball (plate 3,*G,H*)
Friscanus friscanus (Ball) (plate 2,*G,H,I*)

Four of these—*Draeculacephala minerva, Neokolla circellata, Pagaronia confusa,* and *P. triunata*—were also tested for transfer of the virus from infected grapevines to healthy alfalfa. The numbers and sex of the insects tested and the results obtained are shown in table 1. The blue-green sharpshooter, *Neokolla circellata,* proved to be the most efficient of those tested;

it infected 65 per cent of the 250 grapevines and 35 per cent of 150 alfalfa plants. The species of *Pagaronia* are inefficient vectors: *P. confusa* infected only 6 per cent of 50 grapevines and *P. triunata* none of 50 vines inoculated, and no transmissions to alfalfa were obtained with either species. One infection of alfalfa was obtained with *Draeculaceplala minerva*, of 100 plants

TABLE 1

TRANSMISSION OF THE VIRUS OF PIERCE'S DISEASE OF GRAPEVINES BY SINGLE LEAFHOPPERS

Vector	Transferred to healthy grapevines					Transferred to healthy alfalfa				
	Males		Females		Per cent infections, both sexes	Males		Females		Per cent infections, both sexes
	Number tested	Infections	Number tested	Infections		Number tested	Infections	Number tested	Infections	
Helochara delta	50	18	50	14	32	..	..	..	..	..
Carneocephala fulgida	50	9	50	24	33	..	..	..	..	..
Draeculacephala minerva	100	27	100	3	15	50	1	50	0	1
Neokolla circellata	150	101	100	62	65	50	11	100	42	35
Neokolla confluens var. *pacifica*	5	0	1	0	0	..	..	..	..	..
Neokolla severini	50	6	50	7	13	..	..	..	..	..
Pagaronia confusa	25	2	25	1	6	25	0	..	..	0
Pagaronia triunata	25	0	25	0	0	..	..	25	0	0
Friscanus friscanus	50	4	50	10	14	..	..	..	..	..

TABLE 2

TRANSMISSION OF THE VIRUS OF ALFALFA DWARF BY SINGLE LEAFHOPPERS

Vector	Transferred to healthy alfalfa					Transferred to healthy grapevines				
	Males		Females		Per cent infections, both sexes	Males		Females		Per cent infections, both sexes
	Number tested	Infections	Number tested	Infections		Number tested	Infections	Number tested	Infections	
Draeculacephala minerva	100	0	100	0	0	..	..	..	..	..
Neokolla circellata	50	0	50	0	0	..	..	..	..	..
Pagaronia confusa	25	0	..	..	0	25	0	..	..	0
Pagaronia triunata	20	0	25	0	0	..	..	..	..	..
Friscanus friscanus	3	0	7	0	0	..	..	..	..	..

inoculated. Because of the scarcity of *Neokolla confluens* var. *pacifica*, only 6 insects were tested, and all were negative. Further tests are needed to establish the efficiency of this leafhopper.

Single-insect tests of transmission of alfalfa dwarf to healthy alfalfa were made with five vectors, and one of these—*Pagaronia confusa*—was also tested for transmission of the virus from infected alfalfa plants to healthy grapevines. The number of insects tested and their sex are shown in table 2. A total of 380 insects was used. As recorded in the table, all tests were negative.

MULTIPLE-LOT TESTS

Although efficiency can be determined only in single-insect tests, lots of 5 were tested with *Pagaronia triunata* and *Friscanus friscanus,* which proved inefficient in single-insect tests.

Frazier and Freitag (1946), in multiple-lot tests with *Pagaronia triunata,* obtained no transmission of the virus from infected to healthy grapevines, from infected grapevines to healthy alfalfa, or from infected alfalfa to healthy grapevines; but in transfers from infected to healthy alfalfa, 3 of 10 plants were infected. With *Friscanus friscanus,* they transmitted the virus from alfalfa dwarf to 3 of 3 grapevines and 3 of 25 alfalfa plants; no tests of virus from infected grapevines were made with this species.

TABLE 3

LONGEVITY OF THREE LEAFHOPPER SPECIES ON GRAPEVINES AND ALFALFA

Vector	On grapevines		On alfalfa	
	Range	Average	Range	Average
Pagaronia confusa:				
Males	5–14	7.8	3–8	5.2
Females	2–26	12.2	3–7	7.6
Pagaronia triunata:				
Males	4–5	4.2	2–14	5.0
Females	4–9	5.4	4–29	7.8
Friscanus friscanus:				
Males	2–6	3.6	5–6	5.2
Females	2–6	4.1	3–12	7.3

In the present tests with 5-insect lots of *Pagaronia triunata,* 3 infections were obtained with 11 lots transferred from infected to healthy grapevines; and 1 infection in 10 lots transferred from infected alfalfa to healthy vines. No infections were obtained in alfalfa, either from infected alfalfa or from infected grapevines; 10 lots were tested from each host.

With *Friscanus friscanus,* no infections were obtained with 4 lots of 5 adults transferred from infected to healthy alfalfa.

LONGEVITY OF LEAFHOPPERS

Longevity of adults was determined with *Pagaronia confusa, P. triunata, Friscanus friscanus,* and *Neokolla circellata.* In the records for the first three species, given in table 3, results on diseased and on healthy plants are not separated; there seemed to be no significant difference. On both hosts the females average somewhat higher than the males; but the longevity is low for all three species on both hosts—a fact which may partially account for the low percentages of infection obtained with these vectors.

Longevity of *Neokolla circellata* is reported in connection with retention of virus in table 7 (page 200). One male lived for 129 days, one female for 92 days on wild grapevine seedlings in the greenhouse. As noted in the second

paper of this issue (Severin, 1949), under natural conditions at Berkeley, adults of this species live from summer of one year to spring of the next. This species has been collected on wild grapevines (DeLong and Severin, 1949) and is probably better adapted to this host than the other three species, whose natural food plants seem to be grasses and weeds, especially legumes.

SPECIES THAT FAILED TO TRANSMIT THE VIRUS

Leafhoppers, Subfamily Anthysaninae. Four species of leafhoppers of the subfamily Anthysaninae that had not previously been reported upon were tested for transmission of the virus causing Pierce's disease and alfalfa dwarf. The species tested and the number of lots used were as follows:

	Lots tested in transfers from: Infected to healthy grapevines	Infected to healthy alfalfa
Beet leafhopper, *Eutettix tenellus* (Baker)	6	6
Short-winged aster leafhopper, *Macrosteles divisus* (Uhler)	12	12
Long-winged aster leafhopper, *Macrosteles divisus* (Uhler)	12	12
Xerophloea vanduzee Lawson	15	15

In addition, *Xerophloea vanduzee* was tested for transmission of the virus from infected grapevines to healthy alfalfa (5 lots) and from infected alfalfa to healthy grapevines (5 lots). In all tests, 20 adult males were used in each lot.

All results were negative. Including tests previously reported, the species in this subfamily that have failed to transmit the virus are:

Texananus lathropi Baker (Severin, 1945)
Texananus latipex DeLong (Severin, 1945)
Texananus spatulatus (Van Duzee) (Severin, 1945)
Acinopterus angulatus Lawson (Severin, 1947*a*)
Cloanthanus irroratus (Van Duzee) (Severin, 1947*b*)
Euscelis maculipenis DeLong and Davidson (Severin, 1947*b*)
Geminate leafhopper, *Colladonus geminatus* (Van Duzee) (Severin, 1948)
Mountain leafhopper, *Colladonus montanus* (Van Duzee) (Severin, 1948)
Beet leafhopper, *Eutettix tenellus* (Baker)
Short-winged aster leafhopper, *Macrosteles divisus* (Uhler)
Long-winged aster leafhopper, *Macrosteles divisus* (Uhler)
Xerophloea vanduzee Lawson

A large number of other undetermined species of leafhoppers belonging to the subfamily Anthysaninae were tested but none transmitted the virus causing Pierce's disease of grapevines and alfalfa dwarf.

Fulgorids, or Lantern Flies, Family Issidae. Since the adults and egg masses of *Hysteropterum severini* (Caldwell and DeLong, 1948) (plate 3, *I, J*) were occasionally taken on grapevines, an attempt was made to transmit the virus causing Pierce's disease of grapevines and alfalfa dwarf by means of this species of fulgorid. Fifty males and 50 females were kept on diseased grapevines for one day and then each adult was fed on a healthy vine until it died. All attempts to transmit the virus to 100 healthy vines were failures. Negative results were obtained with 20 lots of 5 adults kept on infected grapevines for one day and then transferred to healthy vines and alfalfa plants. The virus was not transmitted by 10 lots of 5 adults fed on infected alfalfa and trans-

ferred to healthy grapevines; or by 20 lots of 10 adults transferred from diseased to healthy alfalfa plants.

This species of fulgorid also failed to transmit the California aster yellows virus from infected celery to healthy celery plants.

The adults of *Hysteropterum severini* were collected on July 2, 1946 on California mugwort, *Artemisia vulgaris,* and on *Brickellia californica,* growing along the banks of the Russian River, near Geyserville, Sonoma County. The adults were commonly taken on olive trees, on coyote brush, or chaparral broom, *Baccharis pilularis,* and occasionally on grapevines on July 2, 17, and 25 near Cloverdale, Sonoma County.

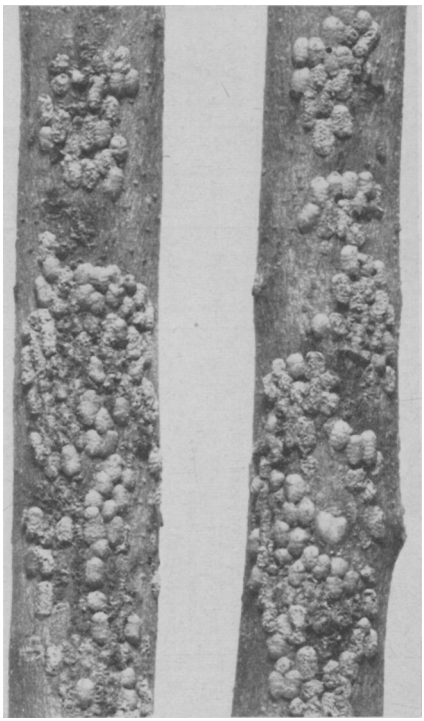

Fig. 1. Egg masses of *Hysteropterum severini* Caldwell and DeLong, deposited on branches of olive trees.

Egg masses were abundant on the trunks and branches of olive trees (fig. 1), occasionally on apple, plum, Oregon oak trees (*Quercus garryana*), poison oak (*Rhus diversiloba*), grapevines, and on fence posts.

Another species of fulgorid, *Neathus maculatus* Melichar, was commonly collected on Parry manzanita, *Arctostaphylos manzanita,* in grape-growing districts of Sonoma County. The transmission of the virus was not accomplished with 50 males and 50 females kept on diseased grapevines for 1 or 2 days and then transferred singly to healthy vines. Twenty lots of 5 adults failed to transmit the virus from Pierce's disease of grapevines to 10 healthy vines and 10 healthy alfalfa plants. The virus was not transmitted by 20 lots of 5 adults fed on infected alfalfa for 2 days and then transferred to 10 healthy vines and 10 healthy alfalfa plants. This species of fulgorid also failed to transmit the curly-top virus.

Some undetermined species of fulgorids failed to transmit the virus causing Pierce's disease of grapevines and alfalfa dwarf.

Cicadas, or Harvest Flies. R. Flock carried on extensive tests with undetermined nymphs of cicadas or harvest flies, which survived on the roots of diseased and healthy grapevines for months. No infections were obtained.

LATENT PERIOD

Since *Neokolla circellata, Carneocephala fulgida,* and *Draeculacephala minerva* proved to be three of the most important vectors of Pierce's-disease virus, they were used in determinations of the latent ("incubation") period. *Helochara delta,* another vector, was also used in some tests.

TABLE 4

LATENT PERIOD OF VIRUSES IN PHLOEM-FEEDING LEAFHOPPERS

Virus and leafhopper species	Authority	Temperature, °F	Adults per lot	Latent period		
				Minimum	Maximum	Mean
Curly top, by beet leafhopper, *Eutettix tenellus* (Baker)	Smith and Boncquet (1921)	....	....	24–48 hrs.	.....	.....
	Severin (1921)	103–120	25–50	4–6 hrs.	.....	.....
	Carsner and Stahl (1924)	.....	1	21¾ hrs.	.....	.....
	Severin (1931)	106–115.6	40	20 min.	.....	.....
	Severin (1931)	94	1	7 hrs.	.....	.....
	Bennett and Wallace (1938)	....	1	4 hrs.	.....	.....
	Freitag (1936)	....	1	1 day	44 days	9.6 days
New York aster yellows, by aster leafhopper, *Macrosteles divisus* (Uhler)	Kunkel (1926)	70	30–100	10 days	19 days	.....
Eastern aster yellows:						
By aster leafhopper, *Macrosteles divisus*	Black (1941)	....	1	11 days	45 days	.....
California aster yellows:						
By aster leafhopper, *Macrosteles divisus*	Kunkel (1932)	70	30–125	17 days	26 days	23 days
By *Texananus lathropi* Baker	Severin (1945)	....	80	7 days	33 days	13.7 days
By *Texananus latipex* DeLong	Severin (1945)	....	80	8 days	37 days	22.5 days
By *Texananus spatulatus* (Van Duzee)	Severin (1945)	....	40	6 days	35 days	20.0 days
By *Gyponana hasta* DeLong	Severin (1946)	....	40	19 days	35 days	26.2 days
By *Acinopterus angulatus* Lawson	Severin (1947*a*)	....	40	11 days	26 days	18.4 days
By geminate leafhopper, *Colladonus geminatus* (Van Duzee)	Severin (1948)	....	1	31 days	.....	31 days
			100	18 days	36 days	28 days
By mountain leafhopper, *Colladonus montanus* (Van Duzee)	Severin (1948)	....	1	23 days	31 days	27.0 days
			100	8 days	40 days	23.6 days
Streak of corn (maize), by maize leafhopper, *Cicadulina mbila* Naude	Storey (1928)	86	.....	6 hours	63 hours	.....
		77	.....	.....	84 hours	.....
		60.8	.....	.....	84 hours	.....
Peach-yellows, by plum leafhopper, *Macropsis trimaculata* Fitch	Hartzell (1936)	....	4–20	7 days	26 days	.....
Potato yellow dwarf, by clover leafhopper, *Aceratagallia sanguinolenta* (Provancher)	Black (1936)	....	....	.....	.....	9 days
	Black (1943)	....	Many	6 days	10 days	.....
Dwarf or stunt disease of rice, by rice leafhopper, *Nephotettix apicalis* Motsch. var. *cincticeps* Uhler	Fukushi (1940)	....	....	10–25 days	60–73 days	30–45 days
Pierce's disease of grapevines, by *Draeculacephala minerva* Ball	Hewitt, Houston, Frazier, and Freitag (1946)	....	....	4 days	.....	.....

These species are xylem-feeding insects (Houston, Esau, and Hewitt, 1947). Like all xylem-feeding species, they excrete large quantities of excrement while feeding. When the blue-green sharpshooter, *Neokolla circellata,* was abundant on shrubs and trees in a Berkeley garden, the feces dropping from nymphs and adults resembled a fog.

Until the work on vectors of Pierce's-disease virus began, there had been no reports of xylem-feeding vectors, and no studies on latent period or re-

TABLE 5

LATENT PERIOD OF VIRUS CAUSING PIERCE'S DISEASE OF GRAPEVINES IN ADULTS OF THREE SPECIES OF LEAFHOPPERS WITH GRAPEVINE CUTTING AS A HOST PLANT

Lot no.	Adults in each lot	Hours on infected grapevine	Successive plants inoculated	Plants infected	Hours on which successive infections occurred including period on infected plant	Latent period, days	Adults alive at end of 7 hours
				Carneocephala fulgida			
1	20	1	6	4	2, 4, 6, 7	2	20
2	20	1	6	1	3	3	20
3	20	1	6	4	4, 5, 6, 7	4	20
4	20	1	6	1	5	5	20
5	20	1	6	1	5	5	20
6	20	1	6	1	7	7	20
7	20	1	6	1	7	7	20
				Draeculacephala minerva			
8	20	3	11	4	7, 8, 9, 13	7	20
9	20	1	13	2	10, 12	10	18
10	20	4	10	1	10	10	19
11	16	2	12	1	24	24	..
				Neokolla circellata			
12	5	1	7	4	2, 3, 4, 6	2	5
13	5	1	7	3	2, 3, 4	2	4
14	5	1	7	4	2, 5, 6, 8	2	4
15	5	1	7	2	5, 6	5	4
16	5	1	7	1	7	7	5

tention of the virus in such insects. However, the length of the latent or "incubation" period of viruses in phloem-feeding species of leafhoppers may be of interest for comparison with that in the three xylem-feeding leafhoppers included in this investigation. These periods, as reported in the literature, are summarized in table 4.

Hewitt, Houston, Frazier, and Freitag (1946) reported that the incubation period of the virus causing Pierce's disease of grapevines in *Draeculacephala minerva,* "if such exists," was less than 4 days.

Tests on Grapevines. Lots of from 5 to 20 males were fasted from 1 to 2 hours, and then were kept on diseased grapevines for 1 hour (with a few lots,

2 to 4 hours—see table 5). Hourly transfers were made to successive healthy grapevines for a period of 2 to 13 hours. A total of 16 lots of three species was tested.

As shown in table 5, the minimum latent period of the virus in *Carneocephala fulgida* and in *Neokolla circellata* was 2 hours, maximum 7 hours; in *Draeculacephala minerva* minimum 7 hours, maximum 24 hours.

Future experiments may demonstrate that the minimum latent period in the three species of leafhoppers may be shorter than 2 hours.

TABLE 6

RETENTION OF VIRUSES BY SPECIES OF PHLOEM-FEEDING LEAFHOPPERS

(As reported in the literature)

Virus and leafhopper species	Authority	Retention of virus, days
Curly top of sugar beets by beet leafhopper, *Eutettix tenellus* (Baker)	Boncquet and Stahl (1917)	15–35
	Carsner (1919)	58–111*
	Severin (1924)	97–104
	Freitag (1936)	1–167
	Wallace and Murphy (1938)	92–121*
New York aster yellows by aster leafhopper, *Macrosteles divisus* (Uhler)	Kunkel (1926)	33–75*
California aster yellows:		
By *Texananus lathropi* Baker	Severin (1945)	10–77
By *Texananus latipex* DeLong	Severin (1945)	1–42
By *Texananus spatulatus* (Van Duzee)	Severin (1945)	27–99
By *Gyponana hasta* DeLong	Severin (1946)	11–46
By *Acinopterus angulatus* Lawson	Severin (1947*a*)	51
By *Cloanthanus irroratus* (Van Duzee)	Severin (1947*b*)	15
By *Cloanthanus dubius* (Van Duzee)	Severin (1947*b*)	1–29
By *Euscelis maculipenis* DeLong and Davidson	Severin (1947*b*)	2–59
By *Idiodonus heidemani* (Ball)	Severin (1948)	11
By *Colladonus commissus* (Van Duzee)	Severin (1948)	6–27
Streak of corn (maize) by maize leafhopper, *Cicadulina mbila* Naude	Storey (1925)	84–150
Potato yellow dwarf by clover leafhopper, *Aceratagallia sanguinolenta* (Provancher)	Black (1936, 1937, 1943)	44, 52*, 167†
Dwarf or stunt disease of rice, by rice leafhopper, *Nephotettix apicalis* Motsch. var. *cincticeps* Uhler	Fukushi (1940)	53–97

* Highly resistant or nonsusceptible host plants.
† Hibernating without access to plants.

Tests on Alfalfa. Five lots of 20 adult *Carneocephala fulgida* were kept on alfalfa dwarf plants 1 day and then each lot was transferred daily to six successive healthy alfalfa plants. One lot caused 2 infections during the sixth and seventh days, another lot 1 infection during the seventh day, and three lots failed to transmit the virus to any of the inoculated plants.

In a similar test, 3 lots of 20 adults of *Draeculacephala minerva* failed to transmit the virus from alfalfa dwarf to healthy alfalfa plants.

In a test of *Helochara delta* conducted in the same manner, 5 lots of 20 adults failed to transmit the virus from alfalfa dwarf to successive healthy alfalfa plants.

One lot of 25 *Neokolla circellata* was kept on alfalfa dwarf for 1 day and was transferred daily to 6 successive healthy alfalfa plants. All plants were

infected. Two other lots of 20 adults failed to transmit the virus to any of the plants. Hourly transfers were not attempted on alfalfa.

Further experiments are necessary to determine the minimum latent periods of the virus causing alfalfa dwarf in the first three species of leafhoppers.

RETENTION OF VIRUS BY THE BLUE-GREEN SHARPSHOOTER

Single adults of the blue-green sharpshooter, *Neokolla circellata,* were tested for retention of the virus from infected grapevines and alfalfa.

As with the latent period, previous reports on retention of viruses concern phloem-feeding leafhoppers. But a summary of these reports (see table 6) may be of interest for comparison with the results with the xylem-feeding blue-green sharpshooter.

Many species of phloem-feeding leafhoppers have been reported to lose their infectivity after varying periods. Ten species of leafhoppers that transmit the California aster-yellows virus lost their infectivity after 1 to 99 days (table 6) (Severin, 1945, 1946, 1947*a,* 1948). Some species retain the virus over winter. Thus Wallace and Murphy (1938) report that the beet leafhopper, *Eutettix tenellus* (Baker), may retain the curly-top virus throughout the winter without apparent change in virulence; they state, however, that under certain environmental conditions, some specimens lose their infectivity when restricted to a nonsusceptible host plant. Black (1936, 1937) reports that the clover leafhopper, *Aceratagallia sanguinolenta* (Provancher), retained the potato-yellow-dwarf virus for 167 days while hibernating without access to food.

Several species retain viruses, at least occasionally, throughout life. This has been reported of the following viruses and vectors:

Curly-top virus by the beet leafhopper, *Eutettix tenellus* (Baker) (Severin, 1924; Freitag, 1936).

New York aster-yellows virus by the aster leafhopper, *Macrosteles divisus* (Uhler) (Kunkel, 1926).

Streak of corn (maize) by the maize leafhopper, *Cicadulina mbila* Naude (Storey, 1925).

Dwarf or stunt of rice by the rice leafhopper, *Nephotettix apicalis* Motsch. var. *cincticeps* Uhler (Fukushi, 1940).

With most of these species, some specimens lost infectivity before death.

Tests on Grapevines. The retention of the virus was determined with single males and females of the blue-green sharpshooter which had completed the nymphal stages on grapevines infected with Pierce's disease. Each adult was transferred daily to successive healthy wild grapevine seedlings until it died. The results are shown in table 7.

The longevity of most of the insects was too short to furnish much evidence on retention. But one male retained the virus 122 days. The male lived 7 days after its last infection; but since the elapsed time between some earlier infections was greater than this, and since infections were as frequent in late adult life as earlier, there is no evidence that this male had lost its infectivity before death. Several females caused infectivity on the last day of adult life, including one female that lived 92 days. Evidently the virus is retained throughout adult life, under greenhouse conditions.

TABLE 7

RETENTION OF VIRUS BY SINGLE ADULTS OF BLUE-GREEN SHARPSHOOTER, *NEOKOLLA CIRCELLATA*, WITH WILD GRAPE SEEDLINGS AS A HOST PLANT

Sex and insect no.	Plants inoculated	Plants infected		Days on which successive infections occurred	Longest period between two infections, days	Adult age when last infection was produced, days	Period between last infection and death of adult, days	Longevity of adults, days
		Number	Per cent					
Males:								
1	129	27	20.9	15, 22, 23, 39, 49, 59, 61, 64, 65, 66, 67, 71, 76, 78, 84, 85, 86, 87, 91, 94, 103, 106, 114, 117, 118, 120, 122	16	122	7	129
2	50	9	18.0	4, 6, 8, 9, 11, 13, 14, 20, 40	20	40	10	50
3	36	3	8.4	3, 6, 34	28	34	2	36
4	31	7	22.6	3, 6, 7, 11, 15, 16, 17	4	17	14	31
5	32	3	9.4	5, 9, 12	4	12	20	32
Av.	*55.6*	*9.8*	*15.9*		*14.4*	*45.0*	*10.6*	*55.6*
Females:								
6	92	23	25.0	3, 6, 11, 13, 19, 25, 48, 49, 51, 56, 59, 61, 64, 69, 76, 78, 79, 83, 84, 86, 89, 91, 92	23	92	0	92
7	50	11	22.0	1, 3, 7, 8, 13, 16, 17, 20, 25, 49, 50	..	50	0	50
8	37	8	21.6	8, 11, 13, 15, 17, 29, 32, 36	12	36	1	37
9	23	5	17.4	14, 15, 17, 20, 23	..	23	0	23
10	15	10	66.7	1, 2, 4, 7, 8, 9, 10, 11, 12, 15	3	15	0	15
11	11	5	45.5	4, 6, 7, 8, 10	2	10	1	11
12	14	3	....	1, 6, 10	4	10	4	14
13	9	7	77.8	2, 3, 4, 5, 6, 7, 8	0	8	1	9
14	9	3	....	1, 5, 7	2	7	2	9
15	9	5	55.6	1, 2, 3, 5, 6	2	6	3	9
16	9	5	55.6	1, 2, 3, 4, 5	0	5	4	9
17	7	4	55.6	2, 3, 4, 5	0	5	2	7
Av.	*23.7*	*8.0*	*37.9*		*4.8*	*22.6*	*1.5*	*23.7*

Under natural conditions the adults overwinter, and the virus may not be retained during the entire adult life. The investigation furnished no evidence on this point.

Tests on Alfalfa. All attempts to determine the retention of the virus by 5 *Neokolla circellata* tested singly in transfers from alfalfa dwarf to healthy alfalfa plants were failures; none of the specimens transmitted the virus.

ACKNOWLEDGMENTS

I am indebted to J. H. Freitag and N. W. Frazier, who made the final determination of alfalfa dwarf (from root cuttings) reported in this paper.

LITERATURE CITED

BENNETT, C. W., and H. E. WALLACE.
1938. Relation of the curly top virus to the vector, *Eutettix tenellus*. Jour. Agr. Res. **56**:31–52.

BLACK, L. M.
1936. Some insect and host relationships of the potato yellow dwarf virus. Phytopathology **26**:87.
1937. A study of potato yellow-dwarf in New York. Cornell Univ. Agr. Exp. Sta. Mem. **209**:1–23.
1941. Further evidence for multiplication of the aster-yellows virus in the aster leaf hopper. Phytopathology **31**:120–35.
1943. Some relationships between potato yellow-dwarf virus and the clover leafhopper. Phytopathology **33**:363–71.

BONCQUET, P. A., and C. F. STAHL.
1917. Wild vegetation as a source of curly-top infection of sugar beets. Jour. Econ. Ent. **10**:392–97.

CALDWELL, J. S., and D. M. DELONG.
1948. A new species of Issidae from California (Homoptera: Fulgoridae). Ohio Jour. Sci. **48**(5):176–77.

CARSNER, E.
1919. Susceptibility of various plants to curly top of sugar beet. Phytopathology **9**(8): 413–21.

CARSNER, E., and C. F. STAHL.
1924. Studies on curly-top disease of the sugar beet. Jour. Agr. Res. **28**:297–319.

DELONG, D. M., and H. H. P. SEVERIN.
1949. Characters, distribution, and food plants of leafhopper vectors of virus causing Pierce's disease of grapevines. Hilgardia **19**(6):171–86.

FRAZIER, N. W.
1944. Phylogenetic relationship of the nine leafhopper vectors of Pierce's disease of grape. (Abstract.) Phytopathology **34**:1000–1.

FRAZIER, N. W., and J. H. FREITAG.
1946. Ten additional leafhopper vectors of the virus causing Pierce's disease of grapes. Phytopathology **36**:634–37.

FREITAG, J. H.
1936. Negative evidence on multiplication of curly-top virus in the beet leafhopper, *Eutettix tenellus*. Hilgardia **10**:305–42.

FUKUSHI, T.
1940. Further studies on the dwarf disease of rice plant. Jour. Facul. Agr. Hokkaido Imper. Univ., Sapparo, **47**(3):83–154.

HARTZELL, A.
1936. Incubation period of peach yellows in its insect vector. Boyce Thompson Inst. Contrib. **8**:113–20.

HEWITT, W. B., N. W. FRAZIER, and B. R. HOUSTON.
1942. Transmission of Pierce's disease of grapevines with a leafhopper. (Abstract.) Phytopathology **32**(1):8.
HEWITT, W. B., N. W. FRAZIER, H. E. JACOB, and J. H. FREITAG.
1942. Pierce's disease of grapevines. California Agr. Exp. Sta. Cir. **353**:1–32.
HEWITT, W. B., B. R. HOUSTON, N. W. FRAZIER, and J. H. FREITAG.
1946. Leafhopper transmission of the virus causing Pierce's disease of grape and dwarf of alfalfa. Phytopathology **36**:117–28.
HOUSTON, B. R., K. ESAU, and W. B. HEWITT.
1947. The mode of vector feeding and the tissues involved in the transmission of Pierce's disease virus in grape and alfalfa. Phytopathology **37**:247–53.
HOUSTON, B. R., N. W. FRAZIER, and W. B. HEWITT.
1942. Leafhopper transmission of alfalfa-dwarf virus. (Abstract.) Phytopathology **32**(1):10.
KUNKEL, L. O.
1926. Studies on aster yellows (Reprinted from: Amer. Jour. Bot. **13**:646–705, 1926.) Boyce Thompson Inst. Contrib. **1**:181–240.
1932. Celery yellows of California not identical with the aster yellows of New York. Boyce Thompson Inst. Contrib. **4**:405–14.
SEVERIN, H. H. P.
1921. Minimum incubation periods of causative agent of curly leaf in beet leafhopper and sugar beet. Phytopathology **11**:424–29.
1924. Curly-leaf transmission experiments. Phytopathology **14**(2):80–93.
1931. Modes of curly-top transmission by the beet leafhopper, *Eutettix tenellus* (Baker). Hilgardia **6**:253–76.
1945. Evidences of nonspecific transmission of California aster-yellows virus by leafhoppers. Hilgardia **17**(1):22–59.
1946. Transmission of California aster-yellows virus by the first reported vector in Gyponinae. Hilgardia **17**(3):141–53.
1947*a*. *Acinopterus angulatus*, a newly discovered leafhopper vector of California aster-yellows virus. Hilgardia **17**(5):197–210.
1947*b*. Newly discovered leafhopper vectors of California aster-yellows virus. Hilgardia **17**(16):511-24.
1948. Transmission of California aster-yellows virus by leafhopper species in *Thamnotettix* group. Hilgardia **18**(4):201-18.
1949. Life history of the blue-green sharpshooter, *Neokolla circellata*. Hilgardia **19**(6): 187–89.
SMITH, R. E., and P. A. BONCQUET.
1915. Connection of a bacterial organism with curly leaf of the sugar beet. Phytopathology **5**:335–42.
STAHL, C. F., and E. CARSNER.
1918. Obtaining beet leafhoppers nonvirulent as to curly-top. Jour. Agr. Res. **14**:393–94.
STOREY, H. H.
1925. The transmission of streak disease of maize by the leafhopper *Balcultha mbila* Naude. Ann. Appl. Biol. **12**(4):422–39.
1928. Transmission studies of maize streak disease. Ann. Appl. Biol. **15**(1):1–25.
WALLACE, J. M., and A. M. MURPHY.
1938. Studies on the epidemiology of curly top in southern Idaho, with special reference to sugar beets and weed hosts of the vector *Eutettix tenellus*. U. S. Dept. Agr. Tech. Bul. **624**:1–46.
WEIMER, J. L.
1931. Alfalfa dwarf, a hitherto unreported disease. Phytopathology **21**:71–75.
1933. Effect of environmental and cultural factors on dwarf disease of alfalfa. Jour. Agr. Res. **47**:351–68.
1936. Alfalfa dwarf, a virus disease transmissible by grafting. Jour. Agr. Res. **53**:333–47.
1937. The possibility of insect transmission of alfalfa dwarf. Phytopathology **27**:697–702.

5*m*-4.'49(B2207) 141

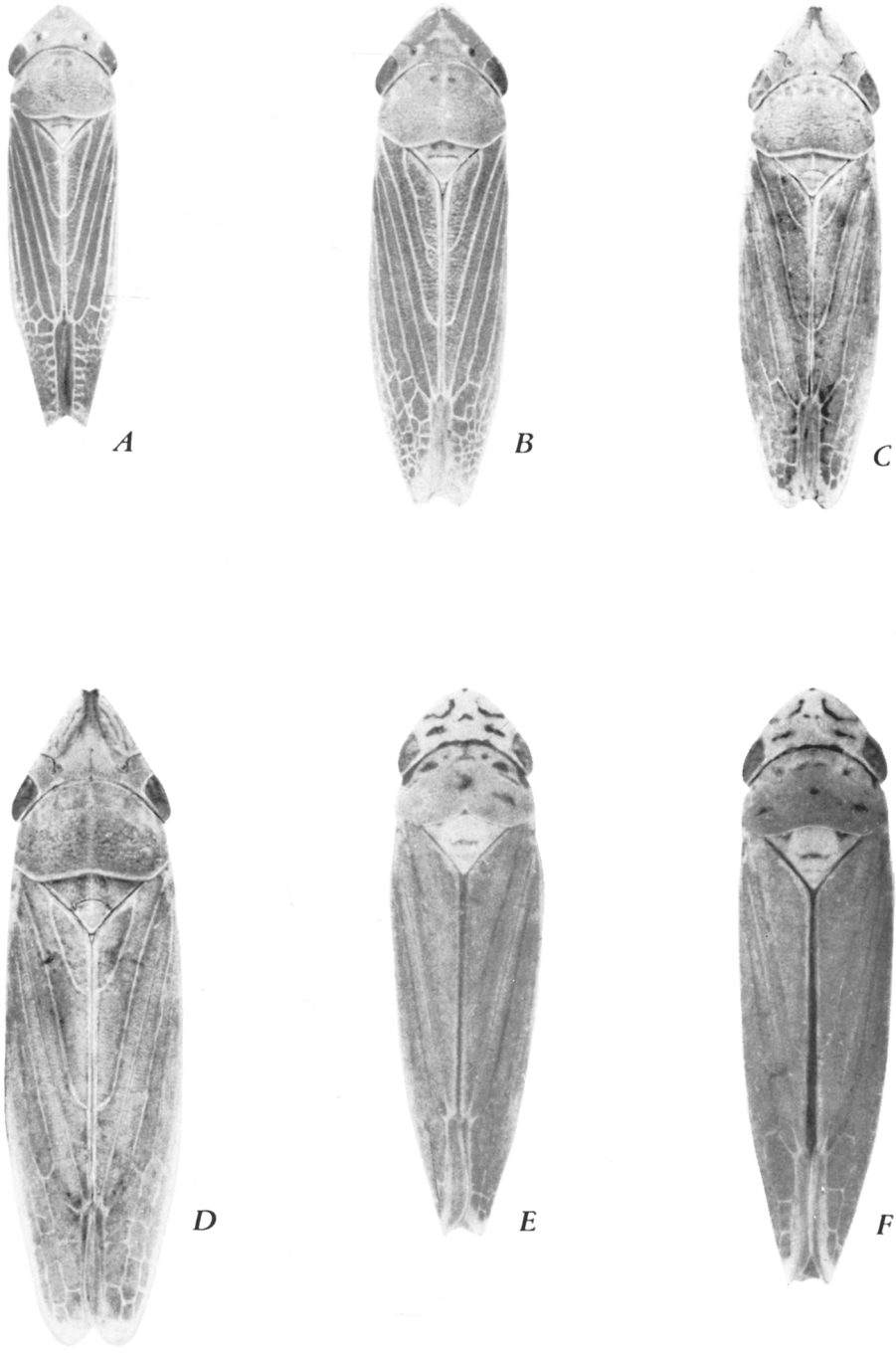

Plate 1. Three of the most important leafhopper vectors of the virus causing Pierce's disease of grapevines and alfalfa dwarf: *A*, male, *B*, female redheaded sharpshooter, *Carneocephala fulgida* Nottingham; *C*, male, *D*, female green sharpshooter, *Draeculacephala minerva* Ball; *E*, male, *F*, female blue-green sharpshooter, *Neokolla circellata* (Baker).

Plate 2. Leafhopper vectors of the virus causing Pierce's disease of grapevines: *A*, blue-green sharpshooter, *Neokolla circellata* (Baker); *B*, male, *C*, female *Helochara delta* Oman; *D*, male, *E*, *F*, female *Neokolla severini* DeLong; *G*, *H*, male, *I*, female *Fricanus friscanus* (Ball).

Plate 3. Leafhopper vectors of the virus of Pierce's disease of grapevines: *A*, male, *B*, female *Neokolla confluens* var. *pacifica* DeLong and Severin; *C*, male, *D*, female *Pagaronia confusa* Oman; *E*, male, *F*, female *P. 13-punctata* Ball; *G*, male, *H*, female *P. triunata* Ball; *I*, male, *J*, female *Hysteropterum severini* Caldwell and DeLong.

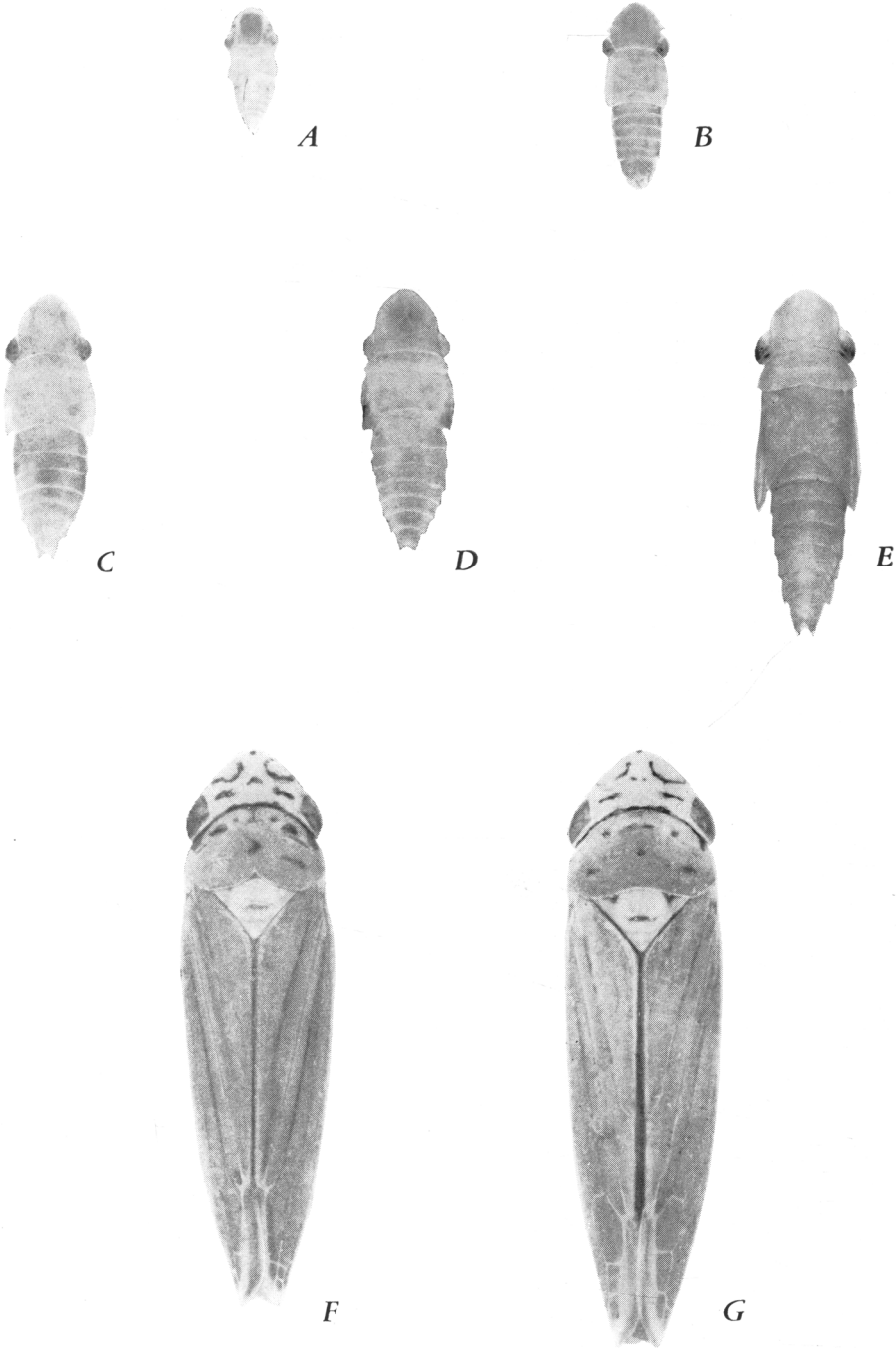

Plate 4. Nymphal instars and adults of blue-green sharpshooter, *Neokolla circellata* (Baker): *A*, *B*, *C*, *D*, *E*, first to fifth nymphal instars respectively; *F*, adult male, and *G*, adult female.

The journal *Hilgardia* is published at irregular intervals, in volumes of about 600 pages. The number of issues per volume varies.

Subscriptions are not sold. The periodical is sent as published only to libraries, or to institutions in foreign countries having publications to offer in exchange.

You may obtain a single copy of any issue free, as long as the supply lasts; please request by volume and issue number from:

Publications Office
College of Agriculture
Berkeley 4, California

The limit to nonresidents of California is 10 separate issues on a single order. A list of the issues still available will be sent on request.