Leafhopper Vectors of the Peach X-Disease Pathogen and Its Seasonal Transmission from Chokecherry

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ABSTRACT

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The peach X-disease organism (XDO) was transmitted during June, July, and August to peach and chokecherry indicator plants exposed for 5-wk periods beside X-diseased chokecherry (*Prunus virginiana*) in the field. Twenty-six percent of 387 indicator plants exposed in 1974 developed X-disease symptoms compared to 5% of 359 plants exposed in 1975 and 3% of 273 plants exposed in 1976. Transmission to indicator plants could not be directly correlated with the numbers of *Paraphlepsius irroratus*, *Scaphytopius acutus*, and *Colladonus clitellarius* vectors captured on sticky-boards at the exposure sites. *Paraphlepsius irroratus* accounted for 87% of 9,986 specimens of X-disease vector species trapped in orchards during 3 yr and was common from June to November. Thirty-seven percent of 331 *P. irroratus* leafhoppers, but only 26% of 150 *S. acutus* leafhoppers transmitted the XDO from diseased celery to celery test plants in greenhouse transmission tests. Twenty-one *P. irroratus* leafhoppers tested individually transmitted the XDO on 24% of the days (counting from the day of their first transmission) they fed on celery test plants. Four of 15 *Orientus ishidae* (Mat.) and eight of 44 *Scaphoideus*, tentatively identified as *S. carinatus* and as *S. diutius* or *S. melanotus* transmitted the XDO to celery. These new vector species were not abundant in cultivated orchards. *Paraphlepsius irroratus* is considered the most important X-disease vector in Michigan because of its abundance and high transmission efficiency.

Additional key words: mycoplasma, *Prunus persica*, vector populations.

X-disease affects stone fruits in the northeastern and western areas of the United States and probably is caused by a mycoplasma (7, 12, 13). Hildebrand (8) found some differences in symptoms between eastern and western forms of X-disease, but these differences were no greater than differences between the several forms which have been described within each geographic area (5, 20). The term "X-disease" is now used to refer to all of the forms of this highly variable disease (4).

Leafhoppers are the only known vectors of the X-disease organism (XDO) in established orchards. Species capable of transmitting the XDO include *Euscelidius variegatus* Kirsh. (10) and *Scaphytopius delongi* Young (28) in addition to the 10 species listed in a recent review (4). The most important vector species are *Colladonus montanus* (Van D.) in the west (4) and *Scaphytopius acutus* (Say) in New York (6).

In the eastern United States, vectors acquire the XDO primarily from chokecherry (*Prunus virginiana* L.) and are believed to transmit it from about 15 June to 15 July (8, 27). Spread of the XDO from diseased to healthy peach trees has been considered unimportant and eradication of chokecherry within 210 m of orchards has provided satisfactory X-disease control (4, 19). However, the XDO spreads from diseased to healthy peach trees in the western United States (21), and recent studies have suggested that the same thing is now occurring in the eastern United States (11, 22).

The rapid spread of the XDO in Michigan peach orchards during recent years, including orchards where chokecherries were removed (22), stimulated research on the leafhopper vectors and on their relationship to disease spread. The objectives of this study were to determine: (i) when transmission of the XDO occurs in the field, (ii) if the size and the seasonal fluctuation of vector populations are related to transmission in the field, (iii) the transmission efficiencies for the most common vector species in Michigan, and (iv) if other leafhopper species vector the XDO.

MATERIALS AND METHODS

Transmission of the X-disease organism to indicator plants in the field.—Successive groups of peach and chokecherry indicator plants were exposed beside clumps of X-diseased chokecherry bushes. Indicator plants were exposed at two sites near East Lansing and at two sites in southwestern Michigan (Berrien and Van Buren counties) in 1974, 1975, and 1976 except that only one East Lansing

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site was used in 1976. The sites were located in abandoned meadows, near railroad right-of-ways, and along road embankments. Indicator plants were taken to the sites 20 May 1974, 8 May 1975, and 18 May 1976. They were changed on 17 June, 19 July, and 23 August in 1974; on 16 June, 25 July, and 28 August in 1975; and on 21 June, 26 July, and 28 August in 1976. The exposure periods ended 27 September 1974, 30 September 1975, and 2 October 1976.

The indicators were planted in 15.4-cm-diameter tins, were fertilized periodically to maintain growth until early September, and were held in a lath house before and after exposure. They were at least 35 cm tall at the time of exposure. Groups of about 25 indicator plants per exposure period were placed at each site. In 1974, each group included 10 "Baby Gold" peach trees, seven Halford peach seedlings, and eight chokecherry seedlings, except that three Halford seedlings were substituted for three chokecherry seedlings during the fourth exposure period. Each group included 15 Halford and 10 chokecherry seedlings in 1975, and 13 Halford and 13 chokecherry seedlings in 1976.

To prevent the indicator plants from drying out during the exposure periods, the plants were placed in shallow trenches lined with plastic, mulched with sawdust and woodchips, and watered weekly. Weeds and grass near the plants were controlled with a contact herbicide. In 1975 and 1976, yellow ribbon was placed over each group of plants to attract leafhoppers.

Exposed plants were sprayed with insecticide when returned to the lath house to eliminate resident insects. One hundred indicator plants were maintained in the lath house each year to check for possible transmission in the house. All indicator plants were placed in a cooler at 3 C from October until January and then moved to the greenhouse and observed for symptom development.

Leafhopper trapping.—Sticky-board traps (29) were used from 1974 through 1976 to monitor leafhopper populations at the sites where indicator plants were exposed and in two tart cherry and in three peach orchards (two in 1976) in southwestern Michigan. From descriptions provided by Bierne (2) and DeLong (3) and from experience gained during a previous project (29), we were able to identify and count specimens of *S. acutus*, *Paraphlepsius irroratus* (Say), *Colladonus clitellarius* (Say), *Norvellina seminuda* (Say), *Norvellina chenopodii* (Osb.), *Orientus ishidae* (Matsumura), and *Fieberiella florii* (Stål.): J. P. Kramer, Smithsonian Institute, Washington, D.C.; D. E. Barnett, Department of Entomology, University of Kentucky; and O. Taboada, Department of Natural Science, Michigan State University, assisted us with identification of other species counted on traps and used in transmission tests.

Transmission tests with Paraphlepsius irroratus and Scaphytopius acutus.—*Paraphlepsius irroratus* and *S. acutus* were tested under controlled conditions to determine their capabilities as vectors of the XDO. Our colony of *S. acutus*, which originated from insects collected in Nebraska and sent to us by Carol Musgrave in 1973, was maintained on red and ladino clovers under a 16-hr photoperiod. The *P. irroratus* were field-captured adults. Initially, they were collected with a sweepnet, but later an aspirator was used to collect adults attracted to yellow 60-W lights on warm calm evenings.

The acquisition access period (AAP) varied from 5 hr to 20 days. Groups of 10 to 50 leafhoppers were caged together during the AAP and incubation period. Leafhoppers were tested individually starting about 20 days after their initial exposure to X-diseased plants and were moved to new test plants at regular intervals.

Periwinkle (*Vinca rosea* L.), celery (*Apium graveolens* 'Utah 52-70'), chokecherry seedlings, and Halford peach seedlings were used as acquisition host plants and as test plants. Celery was used extensively because it was the most suitable host for the insects being tested, it has been shown to develop high titers of mycoplasmalike bodies in its phloem cells (9, 13), and it shows distinctive symptoms of X-disease 4-8 wk after inoculation.

Transmission studies were conducted in controlled environment chambers at 22-24 C with a 16-hr/day photoperiod except for a few experiments in which diseased peach or chokecherry plants growing in the field were the acquisition hosts. In the latter cases, insects were held in flexible screen cages tied over branches on diseased plants.

Following the inoculation access period, celery and periwinkle plants were held at 20-25 C in a greenhouse for 8 and 15 wk, respectively, and were observed regularly for X-disease symptoms. After inoculated peach and chokecherry seedlings had stopped growing, they were stored in a cooler for about 4 mo and were observed for

TABLE 1. Incidence of X-disease in peach and chokecherry indicator plants exposed beside naturally infected chokecherry bushes during 1974, 1975, and 1976

Year	Indicator plant	Exposure period[a] 1	2	3	4	Yearly total
1974	Peach	31/65[b]	17/65	20/68	12/73	80/271
		48%[c]	26%	30%	17%	30%
	Chokecherry	1/32	4/32	14/32	2/20	21/116
		3%	13%	44%	10%	18%
1975	Peach	0/37	2/61	5/58	2/58	9/210
		0%	3%	9%	3%	4%
	Chokecherry	0/36	0/34	4/39	6/36	10/145
		0%	0%	10%	17%	7%
1976	Peach	0/28	4/31	4/31	0/39	8/129
		0%	13%	13%	0%	6%
	Chokecherry	0/37	0/39	1/34	0/31	1/144
		0%	0%	3%	0%	0.7%

[a]Exposure periods one to four began, respectively: 20 May, 17 June, 19 July, and 23 August in 1974; 8 May, 16 June, 25 July, and 28 August in 1975; and 18 May, 21 June, 26 July, and 28 August in 1976. The first three exposure periods ended with the beginning of the subsequent periods. Period 4 ended 24 September 1974, 30 September 1975, and 2 October 1976.

[b]The numerator is the number of indicator plants with X-disease; the denominator is the total number observed for symptom development. The results are totals for exposures at four sites.

[c]The percentage of indicator plants with X-disease.

symptom development during their next growth cycle in the greenhouse.

Transmission tests with other leafhopper species.—Selected leafhopper species collected from around yellow lights were caged for 4-14 days on X-diseased chokecherry or celery plants and then were tested individually on celery test plants. White silica sand was spread over the soil under the test plants so that dead insects could be recovered for identification.

RESULTS

Occurrence of X-disease on field-exposed Prunus seedlings.—Twenty-six percent of 387 peach and chokecherry indicator plants exposed in 1974, 5% of 355 exposed in 1975, and 3% of 273 exposed in 1976 developed X-disease symptoms (Table 1). For each exposure period, the proportions of infected peach and chokecherry indicators were compared using the χ^2 test applied to results arranged in a 2×2 contingency table. The only significant difference in infection between the two plant species occurred during the first exposure period in 1974 when 48% of the peach indicators, but only 3% of the chokecherry indicators, developed X-disease.

Thirty-seven percent of the total transmission to indicator plants during the 3 yr occurred during the third exposure period in July and August, 21% occurred during the second period, and 17% occurred during the fourth period. Nearly half of the peach indicators exposed during the first period in 1974 developed X-disease, but none of the peach or chokecherry indicators exposed from 8 May to 19 June 1975 or from 18 May to 21 June 1976 developed X-disease (Table 1).

X-disease symptoms never developed on any of the control plants kept in the lath house each summer. Plants which did not develop symptoms the first year following field exposure in 1974 remained healthy when observed for a second season. Five peach seedlings from the first exposure period in 1974 developed X-disease symptoms in 1974, but none of the plants exposed during subsequent years developed symptoms during that same year.

Vectors trapped in orchards and in chokecherries.—Of the leafhopper species surveyed, only *P. irroratus*, *S. acutus*, and *C. clitellarius* were common in peach and cherry orchards: 8,662, 803, and 402 specimens of the respective species, were trapped in orchards during 3 yr (Table 2). Only 19 *N. seminuda* and 21 *N. chenopodii* were captured in orchards, although 107 and 242 specimens of the respective species were trapped in chokecherries in southwestern Michigan. Seventy-nine *O. ishidae* were trapped in orchards during 1975 and 1976.

All vector species were more common in orchards in late summer and autumn than in spring and early summer. Of the total of each species trapped in orchards during 3 yr, 74% of the *P. irroratus*, 88% of the *S. acutus*, and 49% of the *C. clitellarius* were captured after 25 August.

Three traps were placed in chokecherry bushes at each of two East Lansing sites from 1974 to 1976. The vector populations at these sites were similar in size and species distribution to the populations in chokecherry in southwestern Michigan except that *O. ishidae* was unusually abundant at a chokecherry site in East Lansing where 407 individuals were captured during 1976. Populations of adult *O. ishidae* first appeared in early July, peaked in mid-July, and slowly declined in August and early September.

Seasonal population trends of Paraphlepsius irroratus.—Leafhopper trapping data from 1974-1976 were used to establish seasonal population trends for *P. irroratus* in peach and tart cherry orchards sprayed with insecticides and in nonsprayed chokecherry sites. To compensate for varying trap exposure periods and for varying numbers of traps between sites, the data are

TABLE 2. Numbers of the three most common X-disease vector species captured on yellow sticky-board traps in peach and tart cherry orchards and in nonsprayed chokecherry bushes in southwestern Michigan from 1974 to 1976

Leafhopper species	Year	Total number of insects captured in: Tart cherry[a]	Peach[b]	Choke-cherry[c]
Paraphlepsius irroratus	1974	3,358[d]	1,564	477
	1975	1,171	859	319
	1976	1,134	576	399
Scaphytopius acutus	1974	52	126	426
	1975	87	94	275
	1976	353	91	140
Colladonus clitellarius	1974	122	54	84
	1975	59	19	60
	1976	124	24	99

[a]Leafhoppers were trapped in two tart cherry orchards on a total of 10 traps in 1974 and 1975 and five traps in 1976.

[b]Leafhoppers were trapped in three peach orchards on a total of 15 traps in 1974 and 1975 and on five traps deployed in two peach orchards in 1976.

[c]Two traps per site were used at two sites in 1974 and 1976 and at three sites in 1975.

[d]The totals represent the numbers of insects counted on traps and have not been adjusted to compensate for the smaller numbers of traps used in 1976.

presented as the number of *P. irroratus* captured per trap per day. The average number of insects captured per trap was divided by the number of days traps were exposed. The resulting daily values were averaged with values for the preceding 3 days and the following 3 days to produce a rolling average which was plotted against time (Fig. 1, 2).

The timing of seasonal fluctuations in populations of *P. irroratus* in orchards and in chokecherry was similar to that reported for 1972-1973 (29). Each year, early- and late-season populations peaked at about the same levels in chokecherries (Fig. 2), but in orchards, the number of insects captured per trap after 1 August was about four times the number captured before August (Fig. 1). Populations of adult *P. irroratus* began to increase earlier in tart cherry orchards than in peach orchards, probably because cherry orchards were sprayed with insecticides until early July whereas peach orchards were sprayed through mid-August. The numbers of *P. irroratus* captured per trap were higher in 1974 and 1976 than 1975.

Transmission of the X-disease organism by Paraphlepsius irroratus and Scaphytopius acutus.—Over 50% of the leafhoppers present at the start of transmission tests died during the AAP and incubation period, so only results from leafhoppers surviving more than 20 days from the beginning of each experiment are reported. Both *P. irroratus* and *S. acutus* transmitted the XDO from celery to celery and from chokecherry to celery (Table 3), but only *S. acutus* transmitted from periwinkle to celery. None of 53 *P. irroratus* and 94 *S. acutus* transmitted the XDO after feeding for 7-14 days on X-diseased peach trees. In one experiment, a group of eight *S. acutus* transmitted the XDO from celery to chokecherry seedlings, and two of 15 *S. acutus* transmitted from celery to small peach seedlings.

Thirty-seven percent of 331 *P. irroratus* and 26% of 150 *S. acutus* transmitted the XDO after feeding on X-diseased celery (Table 3), and this difference in the proportions of transmitting insects was significant ($P < 0.05$) when tested against the χ^2 distribution. Only 24% of the *P. irroratus* and 9% of the *S. acutus* transmitted after acquisition feedings on X-diseased chokecherry, but *S. acutus* survived poorly during AAP's on chokecherry. The ability of *S. acutus* to acquire the XDO from chokecherry was calculated from two experiments in which 1 of 19 and 3 of 27 insects transmitted after AAP's of 1 and 4 days.

Thirty-eight percent of the *P. irroratus* and 27% of the *S. acutus* transmitted the XDO after AAP's of 4-8 days compared to 34% and 22% for the respective species after AAP's of 9-20 days. The difference in transmission after the shorter AAP compared to transmission after longer AAP's was not significant ($P > 0.05$) for either species when tested against the χ^2 distribution. In two additional trials, one of nine and three of 31 *S. acutus* transmitted after AAP's of 5 and 26 hr, respectively.

Male and female *P. irroratus* were equally effective as vectors. In a group of 83 adults, 39% of the males and 40.5% of the females transmitted the XDO from diseased to healthy celery.

Field-captured *S. acutus* were tested to determine if the Michigan population of *S. acutus* was similar to the Nebraska strain in its ability to transmit the XDO. Three of 32 adults transmitted the XDO (Table 6), but 14 of the insects died 20-25 days after beginning the AAP and may not have survived long enough to transmit. Eighteen percent of the insects surviving beyond 25 days transmitted the XDO, and this proportion did not differ significantly ($P > 0.05$) from the proportion of the Nebraska strain which transmitted.

Symptoms of X-disease never developed in control plants exposed regularly in the greenhouse, in growth chambers, or to groups of *S. acutus* taken directly from the colony.

Frequency of daily transmission by Paraphlepsius irroratus.—To determine the consistency of transmission by infective *P. irroratus*, 76 adults were transferred to new

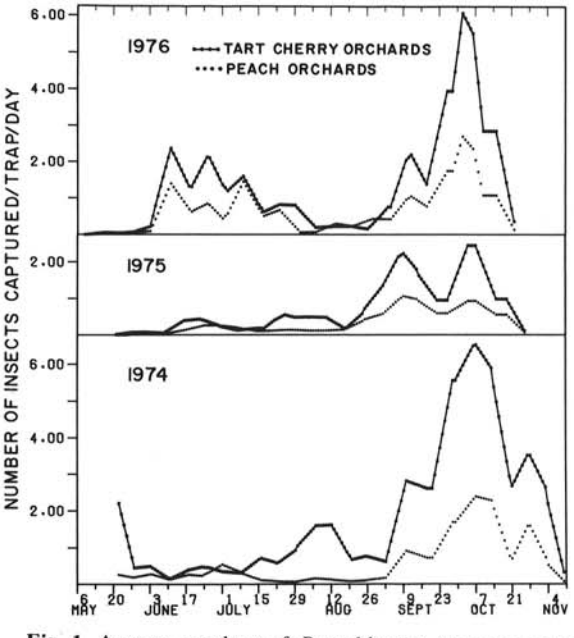

Fig. 1. Average numbers of *Paraphlepsius irroratus* adults captured per day trap per day in peach and tart cherry orchards in southwestern Michigan during 3 yr.

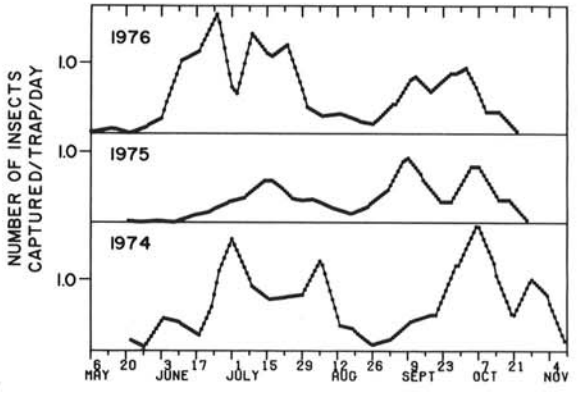

Fig. 2. Average numbers of *Paraphlepsius irroratus* adults captured per trap per day in chokecherry in southwestern Michigan during 3 yr.

celery test plants at 1-4 day intervals starting 20-30 days after the beginning of a 7-day AAP on diseased celery. Twenty-one insects transmitted at least once during the test period (Table 4). Transmission skips of 4-5 days were not uncommon, and one insect failed to transmit for 14 days between its last two transmissions.

Results of 1-, 2-, 3-, and 4-day exposures were totaled for 20 infective insects (insect #21, Table 4, produced no usable data). Counting from the day each insect first transmitted the XDO, the 20 insects were on test plants a total of 173 days. The expected numbers of daily transmissions for the 2-, 3-, and 4-day exposures were calculated using the probability equation $P_1 = 1-(1-P_n)^{1/n}$ where P_1 is the expected proportion of diseased plants from 1-day exposures and P_n is the proportion of diseased plants observed after exposures of n days (30). These calculations showed that transmission probably occurred on 42 days, or on 24% of the total exposure days (Table 5).

Transmission trials with other leafhopper species.—At least two species not previously reported as X-disease vectors transmitted the XDO in our trials (Table 6). Four of 15 *O. ishidae* transmitted to celery test plants following a 7-day AAP on diseased celery. Seven of 43 *Scaphoideus* transmitted the XDO to celery test plants following AAP's of 7-13 days on X-diseased celery, and one *Scaphoideus* transmitted to celery after a 9-day AAP on diseased chokecherry. The transmitting *Scaphoideus* were females and the species could not be identified with certainty because identification of *Scaphoideus* species is based on characteristics of the male genitalia (2, 3). One of the two males in the group of 43 specimens was identified as *S. diutius* DeL. M. and the other as *S. melanotus* Osb. The female which transmitted X-disease from chokecherry was larger than those transmitting from celery, and may be *S. carinatus* Osb.

Texananus majestus, *Prescottia lobata*, and *Osbornellus auronitens* failed to transmit the XDO (Table 6). *Texananus majestus* occasionally was trapped in orchards and was tested because other *Texananus* species transmit California aster yellows (24). *Prescottia lobata* is rare in Michigan orchards (30) but could not be distinguished from *Scaphoideus* species until the specimens were examined and identified after the transmission tests. *Osbornellus auronitens* was tested because *O. borealis* (DeL. & M.) is a vector of X-disease in the western United States (4). However, *O. borealis* and *O. auronitens* represent two distinctly different groups of *Osbornellus* species (14), and *O. auronitens* feeds primarily on ferns (2, 14).

Norvellina seminuda and *Gyponana lamina* vector X-disease in New York (6) but the *N. seminuda* and *Gyponana* we tested failed to transmit the XDO in limited trials.

TABLE 3. Transmission of the X-disease organism by the leafhopper vectors *Scaphytopius acutus* and *Paraphlepsius irroratus* following acquisition access periods on four species of X-diseased plants[a]

	Acquisition host plants			
Leafhopper vector species	Celery	Choke-cherry	Peach	Periwinkle
Scaphytopius acutus				
Positive/total number of trials[b]	45/62	2/7	0/9	1/5
Total no. of insects surviving 20 days	984	95	94	33
No. of individual insects tested in positive trials	150	46		
Fraction of tested individuals which transmitted	26%	9%		Groups of five and eight insects transmitted
Paraphlepsius irroratus				
Positive/total number of trials	27/33	5/8	0/6	0/3
Total no. of insects surviving 20 days	424	61	53	14
No. of individual insects tested in positive trials	331	45		
Fraction of tested individuals which transmitted	37%	24%		

[a]Transmission tests were conducted in controlled environment chambers at 22-24 C except when diseased peach or chokecherries growing in the field were used as acquisition hosts. Celery was used as the inoculation test plant in all trials. Acquisition access periods were 4-20 days. Tests were conducted from 1973-1975 using *S. acutus* from a colony and field-captured *P. irroratus*.

[b]A trial refers to the process of testing transmission by insects caged together on the same acquisition host plant. In positive trials, at least one insect transmitted the X-disease organism to at least one test plant.

TABLE 4. Transmission[a] of the X-disease organism by individual *Paraphlepsius irroratus* during frequent transfers on celery test plants period on X-diseased celery

Insect number	Sex	Observed time of transmission of peach X-disease organism to celery test plants after the beginning of acquisition access (Day 20, Day 25, Day 30, Day 35, Day 40, Day 45, Day 50, Day 55, Day 60)
1	F[a]	0 - - - - - X 0 0 X - X - X 0 0 0[b]
2	F	X - - - 0 0 0 X 0 -
3	F	0 - - - - - - - X X -
4	F	0 - - 0 0 0 0 0 0 - 0 - X 0
5	F	X - - - - - - - X 0 -
6	F	X - - 0
7	F	0 - - - - - 0 - X - 0 -
8	F	0 - - - - - 0 - - 0 - X - 0 - - -
9	F	0 - - 0 0 0 0 0 0 - X - 0 0 0 X - 0 - 0 0 X 0
10	M	0 - - - - - X 0 0 0 - 0 - 0 0
11	M	0 - - - 0 0 0 0 0 - 0 - 0 0 0 X - 0 - 0 X 0 0
12	M	0 - - - - - X - 0 - 0 - 0 0 - 0 - 0 - 0 -
13	M	0 - - - - - 0 - X - 0 - 0
14	M	0 - - - - - 0 - - 0 - X - 0 - - -
15	M	0 X - 0 - X - 0 X - X - 0 - 0 X - - 0 - - -[c]
16	M	0 0 - X - 0 - 0
17	F	0 0 - 0 - 0 - 0 X -
18	M	0 X - X - 0 - X 0 - 0 - 0 - 0 0 - - 0 - - - X - - X - - 0 - 0 - 0 - - -
19	M	X - - 0 - 0 - 0 - - -
20	M	0 - - 0 - 0 - X - - - X - 0 - - - -
21	F	0 - - 0 - 0 - 0 - - - 0 - - 0 - - - - - - - - - - X - - - - - -

[a]M=male, F=female.

[b]There was a 7-day acquisition access period on X-diseased celery and then the insects were held on healthy celery until the observations were begun. Each column represents 1 day. If an insect remained on a test plant >1 day, the number of additional days is represented by dashes. The symbol X indicates plants that developed X-disease, zero indicates plants that remained healthy. For cases in which an insect remained on a plant for >1 day, the X designating the diseased plant is shown on the first day of exposure, although transmission may have occurred on some other day.

[c]Insects 15-21 were members of groups which transmitted the X-disease organism prior to individual tests shown here.

Minimum incubation periods in the leafhopper vectors.—The shortest period between first access to X-diseased plants and transmission of the XDO was 23 days in *S. acutus*, 22 days in *P. irroratus*, and 20 to 35 days in *O. ishidae* and the *Scaphoideus* sp. No symptoms developed on plants from which *S. acutus* adults were removed before the 23rd day after initial access to diseased plants. A single *P. irroratus* (insect #6, Table 4) transmitted the XDO 22 days after first access to diseased plants. One *O. ishidae* transmitted to a test plant between days 28 and 35, and the earliest transmission with *Scaphoideus* was between days 20 and 27.

With all vector species tested, some infective individuals failed to transmit for more than 30 days after first access to X-diseased plants. The *S. acutus* given AAP's of 5 hr and 26 hr on X-diseased chokecherry did not transmit for at least 32 days, and one *P. irroratus* did not transmit for 41 days after the end of the AAP (insect #21, Table 4).

Natural infectivity in field-captured vectors.—Insects captured at lights about 40 m from three infected chokecherry bushes were tested for field-acquired infectivity in 1975 and 1976. One hundred fifteen *P. irroratus* captured in 1975, and 150 *P. irroratus*, 10 *N. seminuda*, and 7 *C. clitellarius* captured in 1976 were placed (five to nine insects per plant) on celery test plants and were transferred to new test plants at 7- to 14-days intervals. One group of nine *P. irroratus* collected in 1975 transmitted the XDO to celery 38 to 47 days following capture and four remaining insects from this group transmitted to another celery plant 30 days later. None of the control insects tested in 1976 transmitted the XDO up to 30 days after capture.

TABLE 5. Calculated frequency of daily transmission of X-disease by infective *Paraphlepsius irroratus* leafhoppers during 1- to 4-day inoculation access periods on celery test plants

Inoculation access period (days)	Test plants: Exposed (no.)	Test plants: Infected (no.)	Plant exposure (days)	Calculated[b] number of transmission days
1	35	10	35	10.0
2	44	19	88	21.7
3	6	5	18	8.1
4	8	2	32	2.2
		Totals	173	42
Percent of plant-exposure days on which transmission occurred				24.3%

[a]Plant-exposure days are equal to the number of plants exposed multiplied by the length of the inoculation access period.

[b]The calculated number of transmission days were determined from the dequation $P_1 = 1-(1-(_n)^{1/n}$ where P_1 is the expected proportion of diseased plants from 1-day exposures and P_n is the proportion of diseased plants observed after exposures of n days. The proportion P_1 was then multiplied by the number of plant exposure days.

TABLE 6. Results of X-disease transmission tests with nine species of leafhoppers following acquisition access periods of 5-13 days on X-diseased celery or chokecherry plants

Leafhopper species[a]	Acquisition host	Number of insects[b] Tested	Transmitting
Osbornellus auronitens	celery	11	0
Norvelina seminuda	celery	3	0
	chokecherry	7	0
Texananus majestus	celery	16	0
Prescottia lobata	celery	8	0
Scaphytopius acutus	celery	32	3 (9.4%)
Orientus ishidae	celery	15	4 (26.7%)
Gyponana sp.	celery	7	0
Scaphoideus sp.[c]			
(*S. diutius*)	celery	43	7 (16.2%)
(*S. carinatus*)	chokecherry	1	1

[a]All leafhoppers were field-captured adults.

[b]Only results from insects surviving 20 days after their first exposure to X-disease-infected plants are reported.

[c]The transmitting *Scaphoideus* could not be identified as to species with certainty because they were females.

DISCUSSION

Our results support an earlier suggestion (29) that *P. irroratus* is a major vector of the XDO in Michigan, although it is not considered as such in other fruit-growing areas (4). *Paraphlepsius irroratus* accounted for 87% of the vectors we trapped in orchards, was common from June to November, and has been reported to occur in virtual swarms under certain environmental conditions (16, 26). This species could account for long-distance spread of X-disease since adults have been trapped at altitudes of 137.2 m (450 feet) (17) and more than 14.5 km (9 miles) from land (25). Individual *P. irroratus* acquired and transmitted the XDO more efficiently than the other vector species tested.

Nymphs and adults of *P. irroratus* generally stay hidden in orchard ground cover where they feed at the base of herbaceous plants (Rosenberger and Jones, *unpublished*). Adults appear to feed on woody plants primarily during the evening when they are particularly active. If adults acquire the XDO while feeding in trees, they must survive a 20- to 30-day incubation period before they can transmit the XDO. These factors suggest *P. irroratus* should be less efficient in vectoring the XDO than vector species which feed on woody plants for extended periods as nymphs and adults. In orchards, however, vector species that prefer woody hosts would be exposed directly to insecticide sprays whereas *P. irroratus* is somewhat protected by the ground cover. *Scaphytopius acutus* also feeds and breeds on herbaceous plants (3, 16) and may have survived DDT sprays in perennial ground cover in New York orchards (18).

Only a small proportion of a vector population feeding primarily in the ground cover is likely to acquire the XDO, but the ability of large populations to survive in sprayed orchards could compensate for the low probability of transmission by any given individual. *Paraphlepsius irroratus* and *S. acutus* failed to acquire the XDO from diseased peach trees in our experiments,

but too few insects may have been tested to detect low levels of transmission.

Undetermined factors other than the size of vector populations affected transmission of the XDO to indicator plants exposed beside diseased chokecherries. Similar numbers of vectors were trapped at the chokecherry sites in 1974 and in 1976, but 26% of the indicator plants developed X-disease after 1974 exposures compared to only 3% after 1976 exposures. Furthermore, the number of indicators that developed X-disease during the various exposure periods could not be related to population fluctuations of the vector species we counted except that the large number of diseased peach indicators resulting from the first period exposure in 1974 may have been related to the unusually early appearance of *P. irroratus* in May 1974 (Fig. 1).

Our results from 3 yr of study show that the period of transmission of the XDO varies from season to season but is longer than the 15 June to 15 July period reported by Hildebrand (8) and Stoddard (27). Transmission of the XDO in Michigan occurs from at least early June (the latter part of the first exposure period) through late August (the early part of the last period).

Transmission of the XDO to indicator plants during late August and early September suggests that significant infection may be occurring in orchards during autumn. The incidence of X-disease in indicator plants was not significantly greater in the last exposure period than in earlier periods, but the indicators were exposed near chokecherries where vector populations in autumn were lower than in peach orchards.

Surveys of Michigan peach orchards showed many trees developed X-disease symptoms in 1976 whereas few new infections were noted in 1975 (22). Both the orchard surveys and the indicator plant exposures were made in the same area of Michigan. Because transmission to indicator plants and leafhopper vector populations in peach orchards were greater in 1974 than in 1975, we suspect that the increase in disease incidence noted in peach orchards in 1976 resulted from natural inoculations made in 1974. Thus, mature peach trees naturally inoculated with X-disease may not develop X-disease symptoms for more than 20 mo after inoculation. Based on X-disease development in young, nonbearing orchards, Stoddard (27) suggested that naturally inoculated peach trees develop X-disease symptoms about 1 yr after inoculation. However, the XDO might reach high titers more rapidly in small trees than in larger, mature trees.

Orientus ishidae and the *Scaphoideus* vector species are probably of minor economic importance because they are far less abundant in orchards than *P. irroratus*. Because they feed primarily on woody plants and occur in the same ecological niche as wild chokecherry, they may spread the XDO in chokecherry. Although *Scaphoideus* species previously had not been reported to be a vector of the XDO, *Scaphoideus luteolus* Van D. and *Scaphoideus littoralis* Ball. are known to transmit elm phloem necrosis and flavescence dorée of grape, respectively (1, 23).

Orientus ishidae was introduced from Japan during the early 1900's at about the same time that *F. florii* was introduced from Europe (14). Oman (15) has suggested that X-disease may have evolved with *F. florii* in Europe, but the discovery that *O. ishidae* can vector the XDO introduces the possibility that X-disease originated in Japan.

Results of this study indicate that X-disease control measures should include more effective leafhopper control in orchards in addition to chokecherry eradication. The fact that the XDO is transmitted during late summer indicates that growers should control the large vector populations which develop in orchards during late summer. Because *P. irroratus* apparently benefits from perennial ground cover in orchards, eliminating ground cover or planting orchards to a grass species less acceptable to leafhoppers might increase a grower's ability to control X-disease vectors in peach orchards.

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