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Title: Differential Transmission of Strawberry Mottle Virus by Chaetosiphon thomasi Hille Ris Lambers and Chaetosiphon fragaefolii (Cockerell)

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Richard G. Clarke

The transmission of strawberry mottle virus (SMV) to Fragaria vesca L. by Chaetosiphon thomasi and C. fragaefolii was studied to determine differences between the two species. Acquisition, inoculation, and retention phases of transmission were described. In all phases, C. fragaefolii was found to be the more efficient vector.

Mean transmission rates for both species increased with increasing length of acquisition access period (AAP) reaching a plateau at 12 h. Maximum acquisition efficiency by C. thomasi was achieved after 3-h AAP, and after a 4-h AAP by C. fragaefolii. Transmission rates by C. fragaefolii were signficantly higher than corresponding rates by C. thomasi for most of the AAPs tested. Observed acquisition thresholds were 15 min for C. fragaefolii and 30 min for C. thomasi. Theoretical acquisition thresholds calculated from least squares regression models were 5 min for C. fragaefolii and 9 min for C. thomasi.

Mean transmission rates for both species increased with increasing length of the inoculation access period (IAP) while C. thomasi plateaued after the 15-min IAP. Maximum inoculation efficiency by C. thomasi was

achieved during a 15-min IAP, and during a 60-min IAP by C. fragaefolii. Transmission rates by C. fragaefolii were significantly higher for all IAPs tested. Observed inoculation thresholds were 7 min for both species. Theoretical inoculation thresholds calculated from least squares regression models were approximately the same for both species, 4 min.

Mean transmission rates for both species decreased during successive hourly feeds. Chaetosiphon thomasi transmitted only during the 1st hourly feed, while C. fragaefolii transmitted during 3 successive hourly feeds. Theoretical retention of inoculativity, calculated from a least squares regression model was 4 h for C. fragaefolii.

Differences in transmission rates were thought to be related to behavioral and physiological characteristics of each species. While C. thomasi tended to be a restless petiole feeder, C. fragaefolii was a sedentary leaf blade feeder. Test results also indicated that some individuals in the C. fragaefolii population may acquire and inoculate SMV more rapidly than others.

Even though C. fragaefolii is a more efficient vector, it is believed that both species should be considered a collective threat to the Pacific Northwest strawberry industry.

Differential Transmission of Strawberry Mottle Virus by *Chaetosiphon thomas* Hille Ris Lambers and *Chaetosiphon fragaefolii* (Cockerell)

by

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INTRODUCTION

The strawberry, Fragaria x ananassa Duchesne, is grown commercially in the Pacific Northwest on about 7,000 to 9,000 acres annually. These strawberry plantings are typically infected with a complex of one or more aphid-borne viruses: mottle, vein-banding, mild yellow-edge, or crinkle. Strawberry mottle virus (SMV), a frequently encountered member of the complex, causes symptoms ranging from an almost undetectable mottling to severe stunting on Frageria vesca var. semperflorens 'Alpine'. Leaflets of the plant become mottled, crinkled, cupped, or otherwise distorted depending on the strain of SMV (Mellor and Fitzpatrick, 1961).

Although several aphid species occur on commercial strawberries in western Oregon, Chaetosiphon thomasi Hille Ris Lambers and Chaetosiphon fragaefolii (Cockerell) are the most common and economically important because they transmit strawberry mottle as well as mild yellow-edge, crinkle, and vein-banding viruses (Shanks, 1965). C. thomasi and C. fragaefolii are very fragile in appearance, and vary in color from white, to yellow, to pale green depending on age and host plant condition. C. thomasi typically possess four pairs of submarginal setae on abdominal segments I-IV. These submarginal setae are missing in C. fragaefolii (Schaefers and Allen, 1962).

Until recently, only C. fragaefolii was collected from strawberry in western Oregon and Washington. In surveys conducted during 1977-

1979, Clarke and Eulensen (unpublished) found both species throughout western Oregon on strawberry, with C. thomasi occurring in higher numbers. Subsequent examination of weekly strawberry aphid collections made by Dr. R. H. Converse, USDA-SEA Research plant pathologist, between April 1973 and March 1978, from a Corvallis strawberry field revealed that C. thomasi was the most common species collected.

The discovery that C. thomasi was the most commonly encountered species in western Oregon raised questions as to its role in the transmission of strawberry mottle virus, a limiting factor in strawberry production in the Pacific Northwest (Shanks, 1965). Only limited research has been done on the transmission of SMV by C. thomasi with none in the Pacific Northwest. Therefore, it was important to obtain a more thorough knowledge of the transmission of SMV by C. thomasi as compared to C. fragaefolii.

I chose for this thesis research to conduct a comparative study of transmission of a Willamette Valley SMV isolate by these two species. Acquisition, inoculation, and retention phases of transmission were studied to discern possible differences. As a result of this research, new insights into the biological relationship of SMV and these two species were obtained. It is hoped that this information will ultimately lead to the establishment of better SMV management in commercial strawberry cultivars in the Pacific Northwest.

REVIEW OF LITERATURE

Aphids were first implicated in the transmission of strawberry viruses when Plakidas (1927) demonstrated the transmission of xanthosis by C. fragaefolii. Until Whitehead and Wood (1941) demonstrated transmission by Chaetosiphon tetrarhodus Walk., C. fragaefolii was the only reported vector of strawberry viruses. Frazier (1951) reported strawberry virus transmission by Amphorophora rubi (Kalt.), Myzus ornatus (Laing), Macrosiphum perlargonii (Kalt.), Myzaphis rosarum (Walk.), and Myzus porosus Sanderson. None of these transmitted as efficiently as C. fragaefolii. Other reported vectors of strawberry viruses include: Chaetosiphon minor (Forbes)(Demaree and Marcus, 1951), Acyrthosiphon malvae (Theob.) and Myzus ascalonicus Doncaster (Posnette, 1952), and Aphis gossypii Glover (Duffus, 1956; Frazier and Posnette, 1958). Chaetosiphon jacobi Hille Ris Lambers and C. thomasi were demonstrated to be vectors of SMV by Frazier and Posnette (1958). Mellor and Forbes (1960) found C. fragaefolii and C. thomasi to be the most efficient vectors of strawberry viruses, but they did not test C. jacobi. Because of individual and clone characteristics, C. jacobi has been the preferred species in California for strawberry virus transmission experiments to the near exclusion of other aphids (Frazier and Posnette, 1958).

The transmission of SMV by strawberry aphids has been intensively studied. Transmission parameters tested include acquisition threshold and efficiency, inoculation threshold and efficiency, and retention of inoculativity. The mechanism of transmission is not known. It has been

postulated to involve accumulation and egestion of virions reversibly adsorbed to the anterior portion of the alimentary canal (Harris, 1977; Sylvester, 1969; Watson and Plumb, 1972).

Acquisition threshold values by strawberry aphids for SMV have been determined to be at least 1 h when using different numbers of aphids per test plant. Using 2 C. fragaefolii per test plant, Prentice and Harris (1946) transmitted virus 1 (SMV) after an acquisition feeding period of 60 min. When using 5 aphids per plant, C. fragaefolii transmitted SMV after a 3-h AAP (Mellor and Fitzpatrick, 1951). The acquisition threshold of C. fragaefolii for SMV when using 20 aphids per plant was found to be 60 min (Duffus, 1956). Miller (1951), using 3 aphids per plant, found that the minimum acquisition feeding was 60 min by C. fragaefolii for strawberry yellows (SMV). In comparative studies of strawberry mottle virus isolates from East Malling Research Station, England and Berkeley, California, the acquisition thresholds were found to be nearly identical (Frazier and Posnette, 1958). Three of 4 Berkeley isolates were acquired in 50 min while the other was acquired in 60 min. The shortest acquisition period that resulted in transmission of the East Malling isolates was 60 min. Using three C. jacobi per plant, the theoretical acquisition curves for two Berkeley isolates were similar, and had acquisition threshold times of approximately 30 min. The acquisition threshold by C. jacobi for SMV was found to be 90 min when using single aphids (Frazier, 1968b).

In addition to determining acquisition threshold, acquisition efficiency rates have also been determined when using different numbers of strawbery aphids per test plant. In general, it has been found that

transmission increases with increasing acquisition access periods. The maximum acquisition efficiency rates by C. fragaefolii (3 aphids per plant) was 93% after a 3-h AAP (Miller, 1951). When using 20 aphids per plant, Duffus (1956) found that maximum acquisition efficiency (90%) was achieved following a 12-h AAP. When using 3 aphids per plant, C. jacobi required an 8-h AAP in order to achieve maximum acquisition efficiency (Frazier and Posnette, 1958).

Although only limited research has been conducted to determine inoculation threshold and efficiency by strawberry aphids for SMV, it has been found that C. fragaefolii (20 aphids per plant) can transmit SMV during inoculation feedings of 5 min. Under these conditions, the inoculation efficiency at 1 h increased to a maximum of 80% (Duffus, 1956). The inoculation threshold of C. fragaefolii for virus 1 (SMV), when using 2 aphids per plant, was found to be a little longer, 10 min (Prentice and Harris, 1946). When using 5 aphids per plant, C. fragaefolii seldom transmitted SMV during inoculation feedings of less than 90 min (Mellor and Fitzpatrick, 1951).

Published data of all workers agree that the inoculativity of SMV is retained by strawberry aphid vectors for less than 6 h following their removal from a virus source, provided the aphids are allowed to feed during the test interval. Retention may be considerably longer if vectors are fasting at low temperatures following acquisition of virus. Using serial transfers of viruliferous aphids (20 per plant), C. fragaefolii was found to retain SMV for 3 h (Duffus, 1956). When using 3 aphids per plant, SMV was retained for up to 6 h by C. fragaefolii and

C. jacobi, although retention varied according to aphid species and virus isolate (Frazier and Posnette, 1958). Single C. jacobi were reported to retain SMV inoculativity for 4 h (Frazier, 1968b). Under post-acquisition fasting conditions, retention of SMV inoculativity by C. fragaefolii (3 aphids per plant) was found to be less than 6 h (Mellor and Fitzpatrick, 1951). Post-acquisition fasting is thought to measure the rate of virus inactivation in the vector. A decrease in the retention of inoculativity of SMV was reported for C. thomasi, C. fragaefolii, and C. jacobi with increasing time of post-acquisition fasting (Frazier and Sylvester, 1960). They concluded that the rate of virus inactivation during fasting was an intrinsic property of the virus isolate and was independent of vector species or vector efficiency. Duffus (1956) reported that during post-acquisition fasting C. fragaefolii retained SMV for 48 h at 6°C. Retention was temperature related and decreased to 12 h at 28°C.

DEFINITIONS

Inoculativity: ability of an aphid to inoculate a plant as measured by symptom expression by the inoculated plant.

Transmission rate: a rating (%) based upon the number of insects transmitting virus divided by the number of insects tested.

Acquisition threshold: the minimum feeding time required for an aphid to become inoculative.

Inoculation threshold: the minimum feeding time required for an aphid to inoculate a plant.

Retention of inoculativity: a measure of how long an aphid remains inoculative, expressed in units of time.

Acquisition efficiency: a comparative rating (%) of the ability of a group of aphids to become inoculative as measured by their transmission rates.

Inoculation efficiency: a comparative rating (%) of the ability of a group of aphids to inoculate a plant as measured by their transmission rate.

MATERIALS AND METHODS

Plant material

Commercial varieties of strawberry do not produce diagnostic symptoms of strawberry viruses (Mellor and Fitzpatrick, 1961). Therefore, the virus indicator plant Fragaria vesca var. semperflorens 'Alpine' was used. Alpine also has the advantage of being propagated by seed rather than runners (Frazier, 1968a). Seed was germinated in water-filled petri dishes, planted in Vitagro® and allowed development of 2-leaf stage seedlings. Seedlings were transplanted into 2-in diameter plastic pots. Only plants of approximately the same height, age, and condition were used as transmission test plants. Test plants were single crowned and approximately 5 cm tall. Test plants were kept in a greenhouse at 20-25°C with supplemental lighting producing a 16-h photophase.

Aphid vectors

C. thomasi and C. fragaefolii collected from Willamette Valley strawberry fields during 1977 were used as vectors during all tests. Species identification was confirmed by Dr. Victor Eastop, British Museum, London. Individual aphids were verified as to species prior to use in each transmission experiment. Aphids were reared on Alpine in rectangular whole cages as described by Adams and van Emden (1972) and kept in the greenhouse at 20-25°C with supplemental lighting producing a 16-h photophase. Aphids were removed and transferred weekly to new Alpine plants to maintain vigorous colonies. Aphids used for virus transmission were 1-5 day old viviparae approximately the same size, obtained by rearing groups of 1st and 2nd instar nymphs to adults.

SMV isolate

A strawberry mottle virus isolate (SM3E) obtained in 1977 from a strawberry field near Hillsboro, Oregon was used as the test isolate. This isolate produced moderate mottling, stunting, and leaf distortion. Five to 6 wk infected Alpine plants were used as virus source plants for virus acquisition. Virus infected plants were maintained in a separate greenhouse from other plant material at 20-25°C with supplemental lighting producing a 16-h photophase.

Acquisition efficiency

Aphids of both speices were placed on SM3E infected Alpine and provided acquisition access periods (AAP) of 5, 15, 30, 45, and 60 min, and 2, 3, 4, 6, 9, 12, and 24 h. After completion of each AAP, 20 aphids were transferred via camel hair brush to the terminal growing point of Alpine test plants (1 aphid/plant). After a 48-h inoculation access period (IAP), the test plants were fumigated with Vapona® insecticide and maintained in a greenhouse to allow SMV symptom development. Results were recorded 3 to 4 wk after completion of the IAPs. This experiment consisted of 24 treatment combinations (2 aphid species X 12 AAPs) with 20 test plants/ treatment combination and was replicated 4 times.

Inoculation efficiency

Aphids of both species were given a 24-h AAP on SM3E infected Alpine. Aphids were then transferred via camel hair brush to the terminal growing point of Alpine (1 aphid/plant) for designated IAPs of 5, 7, 10, 15, 30, 45, and 60 min. After completion of the designated

IAPs, the test plants were fumigated with Vapona® insecticide and maintained in a greenhouse to allow SMV symptom development. Results were recorded 3 to 4 wk after completion of the IAPs. This experiment consisted of 14 treatment combinations (2 aphid species X 7 IAPs) with 20 test plants/treatment combination and was replicated 4 times.

Retention of inoculativity

Aphids of both species were given a 24-h AAP on SM3E infected Alpine. The aphids were then transferred via camel hair brush to the terminal growing point of Alpine for 6 successive 1-h IAPs on a series of 6 test plants. Aphids remained on the last test plant of the series for a 24-h IAP. After completion of the IAPs, the test plants were fumigated with Vapona® insecticide, and maintained in a greenhouse to allow symptom development. Results were recorded 3 to 4 wk after completion of the IAPs. This experiment consisted of 3 treatments with 10 test plants per treatment and was replicated 5 times.

Analysis

The transmission rates (%) were transformed by arc sin and treatment effects were determined by analysis of variance (two-way classification). Multiple comparisons of treatment means were made using the Newman-Keul's test (Cochran and Cox, 1957). Relationships of transmission rate (%) to acquisition access period, inoculation access period and to the retention of inoculativity for each aphid species were determined by stepwise least squares regression analysis.

RESULTS

Acquisition efficiency

Mean transmission rates by C. thomasi and C. fragaefolii for SMV increased with increasing length of acquisition access periods (AAP) reaching a plateau at 12 h (Figure 1). Neither aphid species transmitted following the 5-min AAP. C. fragaefolii transmitted (5.0%) following a 15-min AAP, while C. thomasi first transmitted (3.0%) after a 30-min AAP. Both species transmitted at different rates for all AAPs of 30 min or longer. Transmission rates following the 24-h AAP test interval were 21.3% for C. thomasi and 56.3% for C. fragaefolii. Nevertheless, there was no significant difference in transmission rates by C. thomasi following AAPs greater than 2 h (Table 1). Transmission rates by C. fragaefolii were also not significantly different following AAPs greater than 3 h. Transmission rates by C. fragaefolii were significantly higher than corresponding rates by C. thomasi for all AAPs of 1 h or longer (Table 1). The mathematical relationship of transmission rate to AAP was best described, using a stepwise regression, by a linear function (r^2=.706) for C. thomasi and by a cubic function (r^2=.822) for C. fragaefolii (Figure 2). The acquisition threshold for each species calculated using these functions was 9 min for C. thomasi and 5 min for C. fragaefolii.

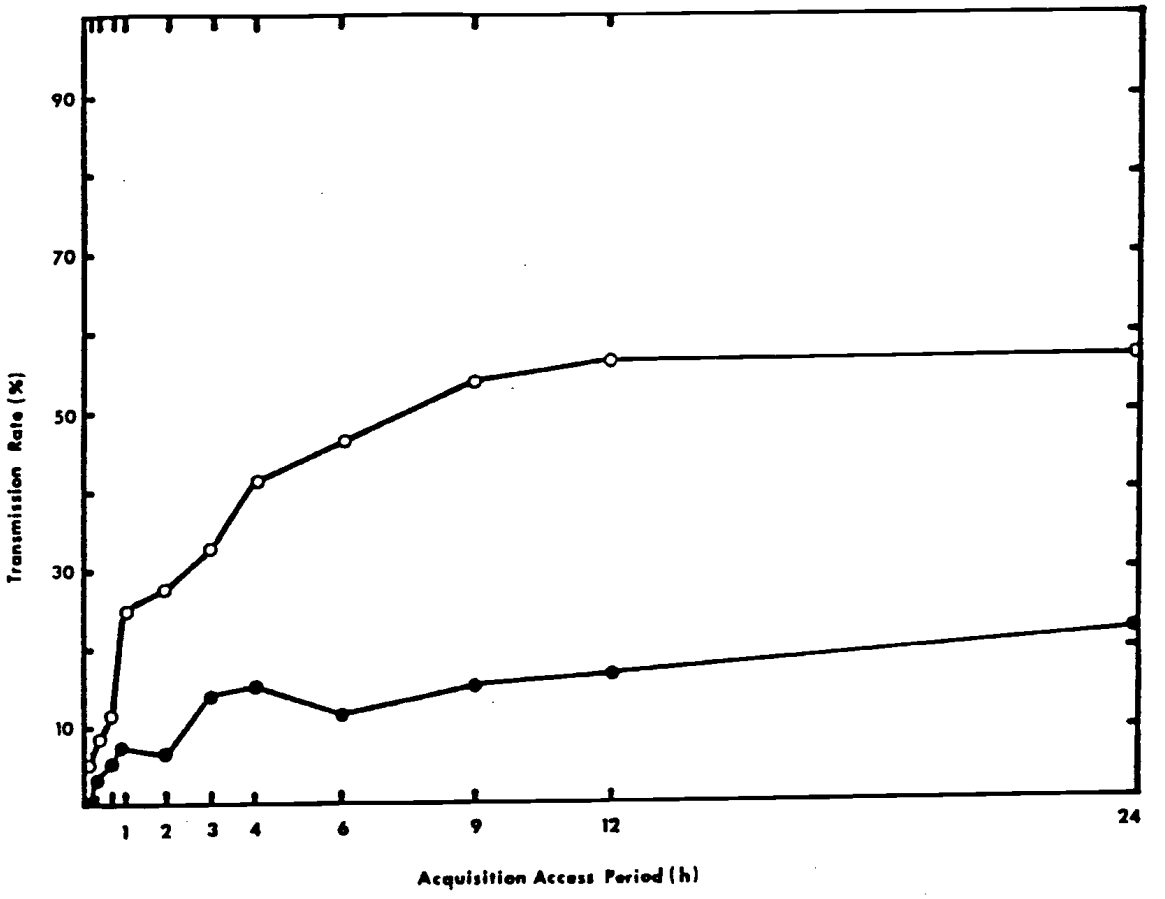

Figure 1. Relationship of transmission rate of strawberry mottle virus (SMV) by Chaetosiphon thomasi (●——●) and C. fragaefolii (○——○) and the length of the acquisition access period (AAP). Means from 4 replications of 20 aphids per species are plotted. Aphids were given a 48-h inoculation access period (IAP) on Alpine following the indicated AAP.

Table 1. Mean percent transmission rate of strawberry mottle virus (SMV) to Alpine indicators by Chaetosiphon thomasi and C. fragaefolii following varied acquisition access periods (AAP).

Acquisition Access Period (AAP)	Aphid species[a]			
	C. thomasi[b]		C. fragaefolii[b,c]	
5 min	0.0	a	0.0	a
15 min	0.0	a	5.0	b
30 min	3.8	b	8.8	b
45 min	5.0	b	11.3	b
60 min	7.5	b	25.0	c*
2 h	6.3	b	27.5	cd*
3 h	13.8	bc	32.5	cde*
4 h	15.0	bc	41.3	def*
6 h	11.3	bc	46.3	ef*
9 h	15.0	bc	53.8	f*
12 h	16.3	bc	56.3	f*
24 h	21.3	c	56.3	f*

a Mean percent transmission in 4 replicates of 20 aphids per species.

b Means followed by the same letter are not significantly different (P = 0.05) using Newman-Keul's multiple comparison test.

c *indicates significantly higher transmission rate by C. fragaefolii than corresponding AAP of C. thomasi (P = 0.05) using Newman-Keul's multiple comparison test.

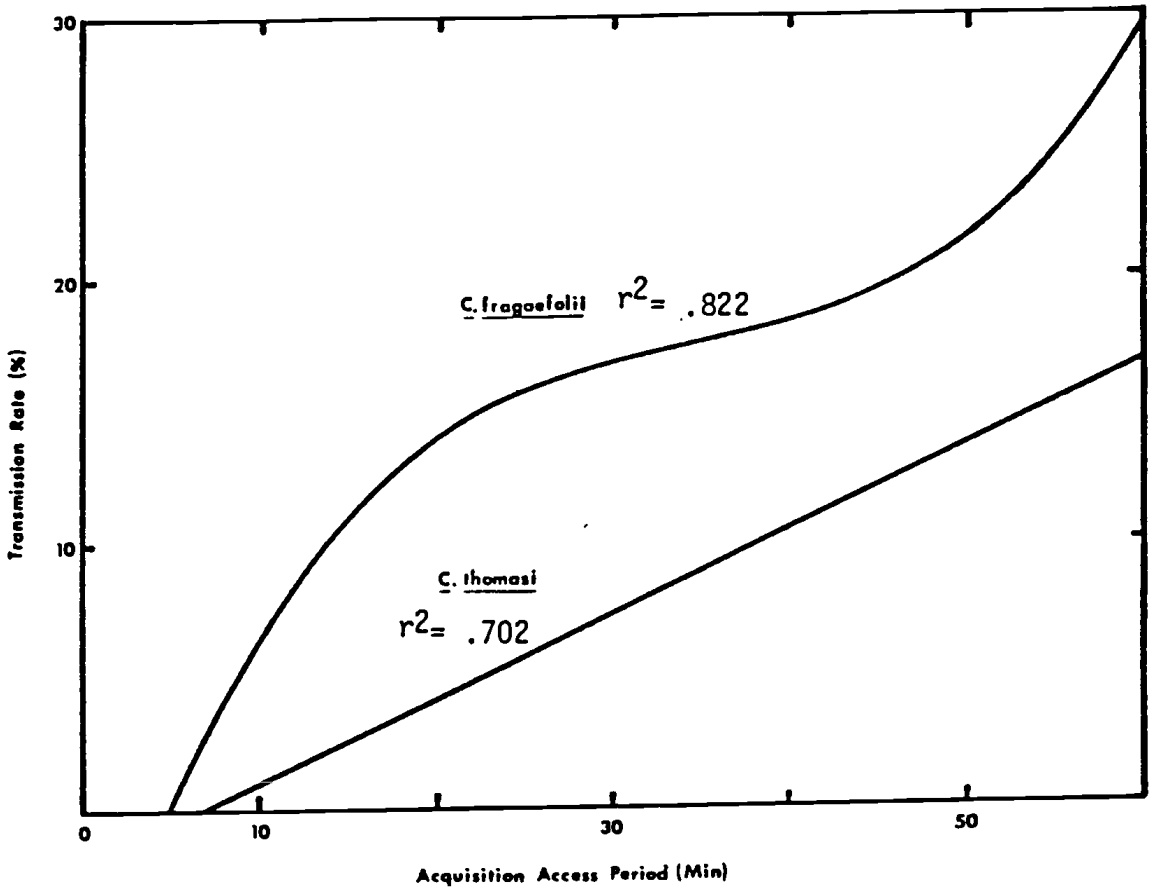

Figure 2. Least squares regression models of the relationship of transmission rate of strawberry mottle virus (SMV) by Chaetosiphon thomasi and C. fragaefolii to the length of the acquisition access period (AAP).

Inoculation efficiency

Mean transmission rates by C. thomasi and C. fragaefolii for SMV increased with increasing length of the inoculation access period (IAP) (Figure 3). Neither species transmitted during the 5-min IAP, while both transmitted during a 7-min IAP. Both species transmitted at different rates for all IAPs of 7 min or longer. Transmission rates during the 60-min IAP were 20.0% for C. thomasi and 58.8% for C. fragaefolii. There was no significant difference in transmission rates by C. thomasi during IAPs of 15 min or longer (Table 2). The transmission rate by C. fragaefolii during the 60-min IAP was significantly higher than the other shorter IAPs tested. Transmission rates by C. fragaefolii were significantly higher than corresponding rates by C. thomasi for all IAPs of 15 min or longer (Table 2). The mathematical relationship of transmission rate to IAP for C. thomasi was best described, using a stepwise regression, by a cubic function (r^2=.718) and by a quartic function (r^2=.909) for C. fragaefolii (Figure 4). The inoculation threshold for both species calculated using these functions was approximately 4 min.

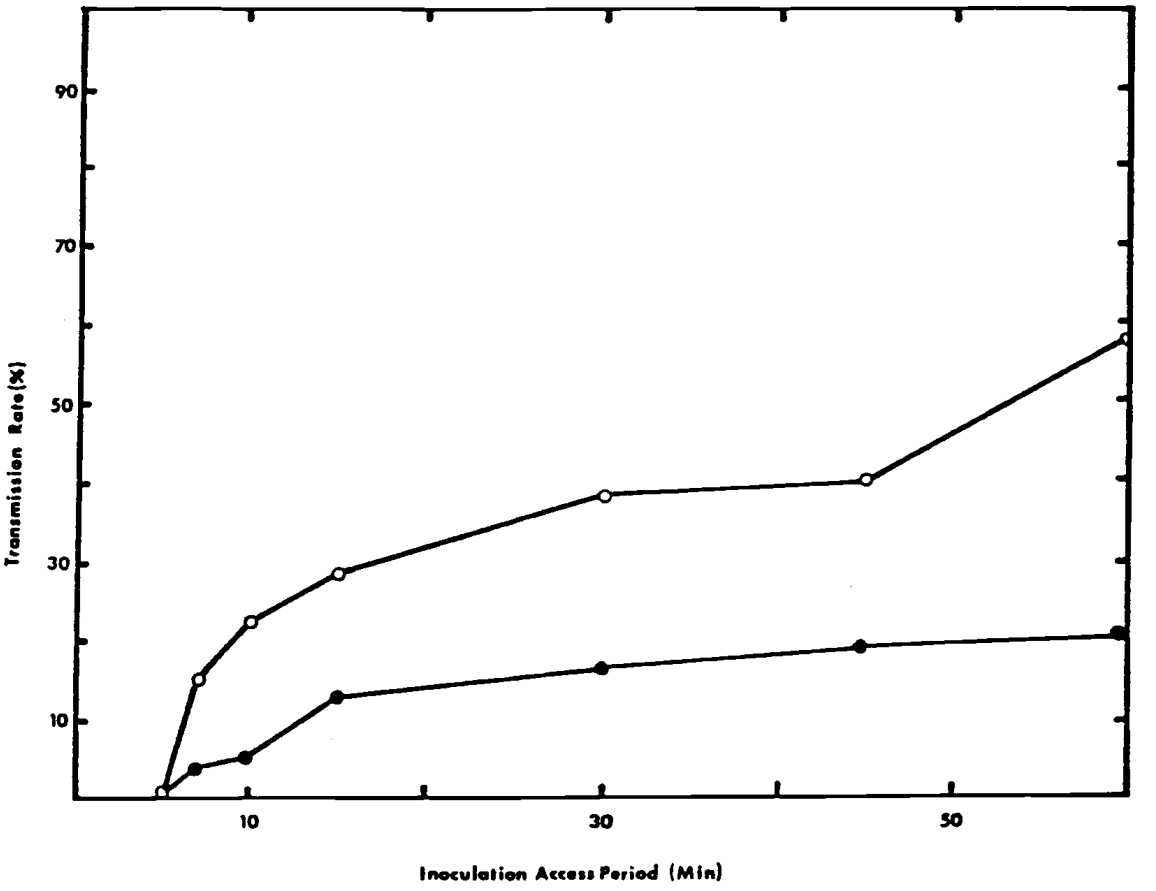

Figure 3. Relationship of transmission rate of strawberry mottle virus (SMV) by Chaetosiphon thomasi (●——●) and C. fragaefolii (○——○) and the length of the inoculation access period (IAP). Aphids were given a standard 24-h acquisition access period (AAP) on SMV-infected Alpine prior to beginning the indicated IAPs. Means from 4 replications of 20 aphids per species are plotted.

Table 2. Mean percent transmission rates of strawberry mottle virus (SMV) to Alpine indicators by *Chaetosiphon thomasi* and *C. fragaefolii* following varied inoculation access periods (IAP).

Inoculation Access Period (IAP)	Aphid Species [a]			
	C. thomasi [b]		*C. fragaefolii* [b,c]	
5 min	0.0	a	0.0	a
7 min	3.8	b	12.0	b*
10 min	5.0	b	22.5	bc*
15 min	12.5	c	28.8	cd*
30 min	16.3	c	38.8	d*
45 min	18.8	c	40.0	d*
60 min	20.0	c	58.8	e*

a Mean percent transmission in 4 replicates of 20 aphids per species.

b Means followed by the same letter are not significantly different (P = 0.05) using Newman-Keul's multiple comparison test.

c *indicates significantly higher transmission rate by *C. fragaefolii* than corresponding IAP of *C. thomasi* (P = 0.05) using Newman-Keul's multiple comparison test.

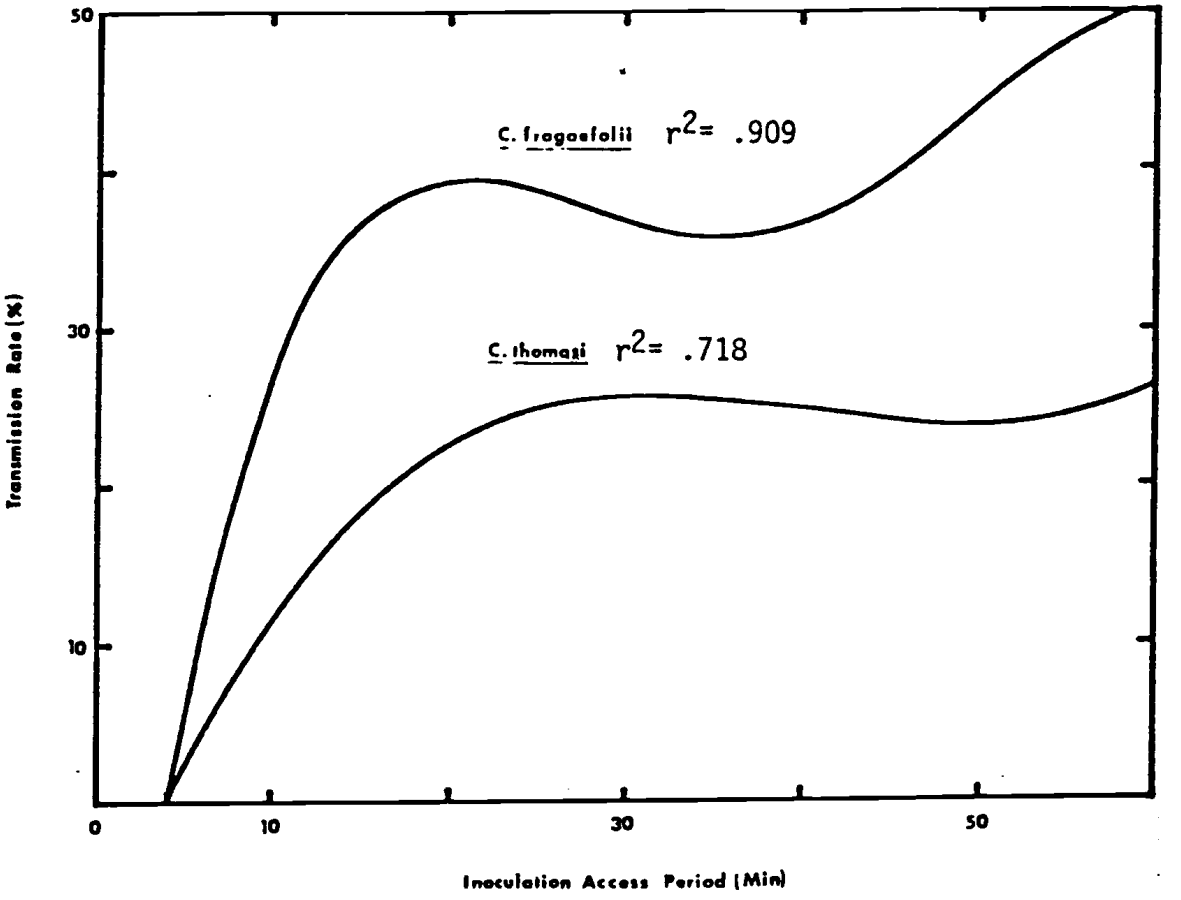

Figure 4. Least squares regression models of the relationship of transmission rate of strawberry mottle virus(SMV) by Chaetosiphon thomasi and C. fragaefolii to the length of the inoculation access period (IAP).

Retention of inoculativity

Mean transmission rate by C. thomasi and C. fragaefolii for SMV decreased during a series of hourly feedings on Alpine (Figure 5). C. thomasi inoculated only during the 1st hourly feeding (28.0%) while C. fragaefolii inoculated for 3 consecutive hourly feedings. The transmission rate during the 1st hourly feeding was 84.0%, declined to 32.0% during the 2nd hourly feeding, which finally declined to 8.0% during the 3rd h. These rates were significantly different for all test intervals (Table 3). The mathematical relationship of transmission rate to the number of hourly feedings for C. fragaefolii, using a stepwise regression, was best described by a quadratic function (r^2=.851) (Figure 6). The endpoint of retention of inoculativity for C. fragaefolii calculated using this function was 4 h. No valid regression model could be determined for C. thomasi.

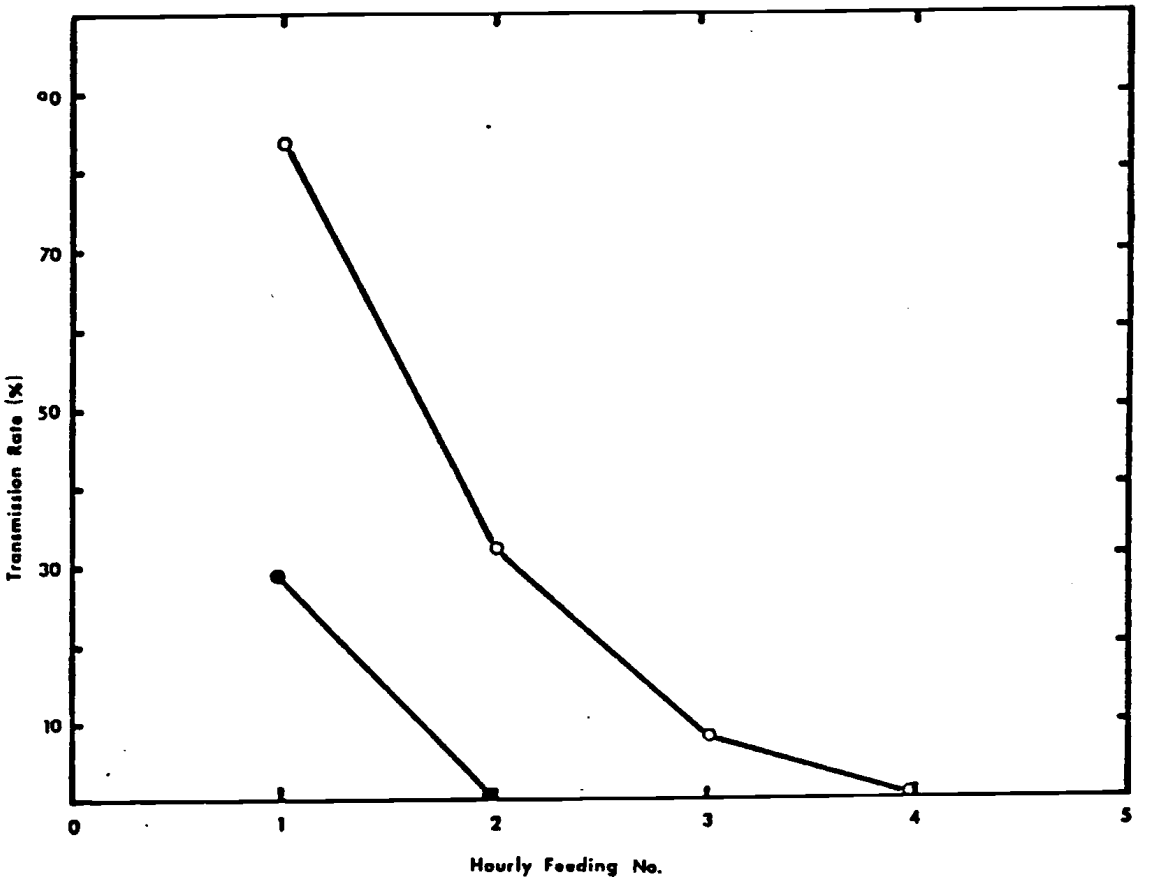

Figure 5. Relationships of transmission rate for strawberry mottle virus (SMV) by Chaetosiphon thomasi (●——●) and C. fragaefolii (○——○) and the number of hourly feedings on healthy Alpine. Aphids were given a 24-h acquisition access period (AAP) on SMV-infected Alpine followed by a series of 1 h feedings on a series of healthy Alpine indicators. Means from 5 replications of 10 aphids per species are plotted.

Table 3. Retention of inoculativity for strawberry mottle virus (SMV) by *Chaetosiphon thomasi* and *C. fragaefolii* during a series of 1 h feeding on Alpine indicators following a 24 h acquisition access period (AAP).

Number of Hourly Feedings	Aphid species [a]			
	C. thomasi [b]		*C. fragaefolii* [b]	
1	28.0	a	84.0	a
2	0.0	b	32.0	b
3	0.0	b	8.0	c
4	0.0	b	0.0	d
5	0.0	b	0.0	d
6	0.0	b	0.0	d

a Mean percent transmission in 5 replicates of 10 aphids per species.

b Means followed by the same letter are not significantly different (P = 0.05) using Newman-Keul's multiple comparison test.

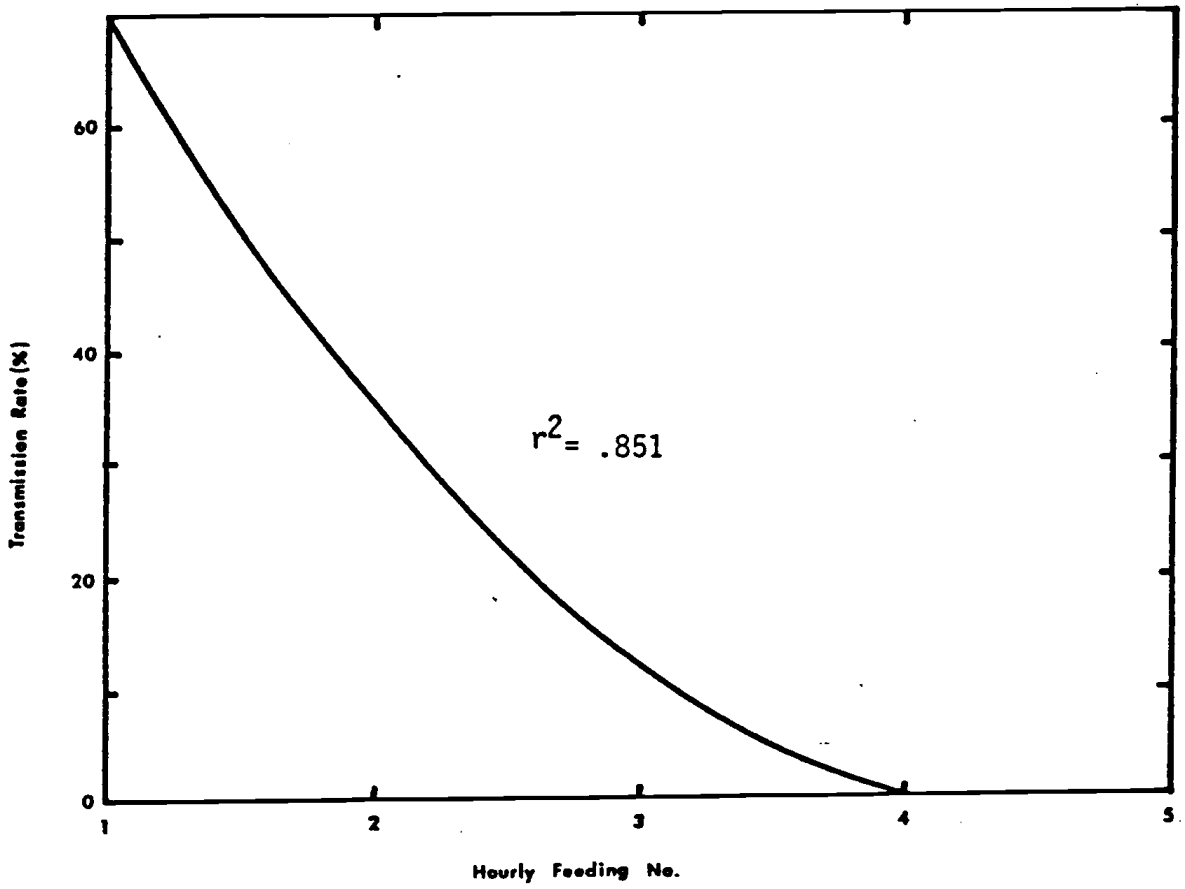

Figure 6. Least squares regression model of the relationship of the transmission rate for strawberry mottle virus (SMV) by Chaetosiphon fragaefolii to the number of hourly feedings on healthy Alpine indicators.

DISCUSSION

This study demonstrated significant differences between C. thomasi and C. fragaefolii for SMV transmission by direct comparisons of virus acquisition, inoculation, and retention. Previous research describing SMV transmission by strawberry aphids involved the use of 2 or more aphids per indicator plant. However, current tests were conducted using 1 aphid per indicator plant. The single-insect approach resulted in a more precise delineation of the vector relationships of SMV than currently occur in the literature.

Comparisons between C. thomasi and C. fragaefolii showed the latter to be superior in acquiring SMV. Chaetosiphon fragaefolii was capable of acquiring an infective charge of virus during a shorter AAP and transmitted at significantly higher rates than C. thomasi. Maximum acquisition efficiency was achieved after a 3-h AAP by C. thomasi and after a 4-h AAP by C. fragaefolii. Although actual transmission rates were higher for the longer AAPs, there was no significant difference between these transmission rates and the rates following a 3-h and 4-h AAP by C. thomasi and C. fragaefolii, respectively. Miller (1951) found the maximum acquisition efficiency by C. fragaefolii for SMV to occur at 3 h, when using 3 aphids per indicator plant (F. vesca). Duffus (1956) when using 20 aphids per plant (F. vesca), reported that C. fragaefolii attained maximum acquisition efficiency following a 12-h AAP. Neither worker tested his results statistically.

The 2 aphid species differed in both their observed and theoretical acquisition threshold values. This is the first report of calculated

thresholds for SMV acquisition for these vector species. Chaetosiphon fragaefolii was reported to have an observed acquisiton threshold for SMV of 60 min (Prentice and Harris, 1946; Miller, 1951; Mellor and Fitzpatrick, 1951; Duffus, 1956). The acquisition threshold of SMV by C. thomasi had not been previously reported.

During inoculation efficiency testing, C. fragaefolii again, proved its superiority in vectoring SMV but was slower than C. thomasi in reaching its maximum inoculation efficiency. Maximum inoculation efficiency was reached during IAPs of 15 min by C. thomasi and in 60 min by C. fragaefolii. However, the transmission rate of C. fragaefolii during the 15-min IAP was significantly higher than that of C. thomasi, even though it had not reached its maximum inoculation efficiency. In similar experiments, Duffus (1956) found C. fragaefolii to achieve maximum inoculation efficiency during a 1-h IAP.

The observed inoculation threshold for both species was 7 min. This was the minimum time necessary to introduce enough of a virus charge to result in subsequent infection of indicator plants. Theoretical inoculation thresholds (4 min) for both species had not been previously reported. Mellor and Fitzpatrick (1951), even though using 5 aphids per plant, found that C. fragaefolii seldom effected transmission during IAPs of less than 90 min. Duffus (1956), however, reported that C. fragaefolii transmitted SMV during inoculation feeds of 5 min when using 20 aphids per plant. This illustrates the fact that regardless of how many vectors are placed on an indiator plant, a minimum of several min is still necessary for aphids to settle down and feed. The shorter 5 min inoculation threshold reported by Duffus (1956) was probably a

result of a larger virus dose being introduced to the plant in a shorter time because of the high numbers of vectors used. Prentice and Harris (1946) found C. fragaefolii capable of transmitting virus 1 (SMV) during IAPs of 10 min when using 2 aphids per plant.

It was assumed that during a 24-h AAP both aphids acquired a saturated charge of virus. Therefore, the retention of inoculativity would be directly dependent upon the amount of the initial virus charge. Retention of inoculativity was determined by feeding aphids for 1 h on a series of health indicator plants (Frazier, 1968b). Thereby, virus depletion in feeding would be the primary cause of loss of inoculativity. This is different than retention of inoculativity based upon post-acquisition fasting (Frazier and Sylvester, 1960) where virus inactivation within the aphid is measured. Results of the current research showed clearly that virus was depleted more rapidly in C. thomasi than in C. fragaefolii. Retention of inoculativity by C. thomasi was approximately 1 h, versus approximately 3 h for C. fragaefolii. The calculated endpoint of retention was 4 h for C. fragaefolii. No valid endpoint could be determined for C. thomasi. Frazier and Posnette (1958) found that C. fragaefolii and C. jacobi retained SMV inoculativity up to 6 h, however, they used 3 aphids per plant. During studies of SMV retention, Duffus (1956) found that C. fragaefolii retained SMV inoculativity for 12 h using the fasting method. Frazier and Sylvester (1960), while conducting SMV retention studies by C. thomasi, C. fragaefolii, and C. jacobi using the post-acquisition fasting method, found these aphids retained inoculativity for at least 4 h. Transmission rates after a 4-h fast decreased to 10% for both C.

fragaefolii and C. thomasi. They proposed that the decrease in the rate of transmission was independent of vector species and efficiency, and that it was a measure of virus inactivation. This was thought to be an intrinsic property of the virus. Because aphids remain inoculative after a 12-h fast (Duffus, 1956), inactivation must be a slower process than virus depletion by feeding. Current results suggest that SMV is probably depleted primarily through feeding.

The marked differences between C. fragaefolii and C. thomasi regarding their transmission efficiency may be related to physiological differences between 2 vectors. The anterior portion of the alimentary canal has been suggested as a site of virion accumulation by a selective adsorption mechanism for the so called semi-persistent viruses, which are transmitted similarly to SMV (Harris, 1977). Virions are thought to adsorb and resist being quickly dissociated from aphids by egestion or flushing through with virus-free sap from healthy plants (Harris, 1977). SMV may persist in strawberry aphids by selective adsorption to sites in their alimentary canal. The increase in transmission rates by both aphids with increasing length of the AAP suggests that SMV accumulates in the aphids, attaining maximum charge after a 3- or 4-h AAP. If selective adsorption of SMV occurs, then C. fragaefolii may have greater selective adsorption for SMV than C. thomasi and thus may acquire a greater virus concentration. Not only did C. fragaefolii transmit at significantly higher rates than C. thomasi, but its retention of inoculativity was significantly longer. This suggests that depletion of virus probably occurs more slowly in a vector with a higher virus concentration.

The marked differences between C. fragaefolii and C. thomasi regarding their transmitting ability may also be related to behavioral habits of the 2 vectors. The preference of C. thomasi for petioles and C. fragaefolii for leaves of Alpine was noted. When placed on Alpine leaves, C. thomasi nearly always moved to the petioles, at times wandering from the plant. C. fragaefolii, on the other hand, remained on leaves when placed there, and quickly commenced feeding. That C. thomasi is a wandering petiole feeder may account for its lower efficiency of acquisition, inoculation, and retention. Not only is feeding time lost, but virus titer in petioles may lower than that in new leaves. Alternatively, petioles may not be as easily infected as new leaves.

It is evident from the current tests that transmission is effected quite differently by the 2 species. Whereas, C. thomasi demonstrates a steady increase in transmission rate during IAPs of 5-15 min, reaching a plateau between 15-60 min, C. fragaefolii showed a second significant increase between 45-60 min (Table 2). During acquisition, C. fragaefolii also demonstrated a significant increase between 45-60 min. These transmission rate increases by C. fragaefolii may indicate that some individuals in the population acquire and inoculate SMV more rapidly than others.

Surveys by Clarke and Eulensen (unpublished) have indicated that both species of strawberry aphids are present in western Oregon strawberries. Chaetosiphon fragaefolii, once believed to be the premier vector of SMV in this region, has been found in relatively low numbers throughout the Willamette Valley, while C. thomasi has been found in

considerably higher numbers. On the basis of its proven vector ability, even though not very commonly encountered, it is felt that C. fragaefolii may still play an important role in the spread of this disease. Similarly, C. thomasi should be of concern to strawberry growers as an important vector of SMV and other strawberry viruses. Despite its lower vector efficiency, this species is the most prevalent one throughout the Willamette Valley.

Additional study on transmission dynamics of these two species, as well as more detailed information concerning their biologies in relation to the spread of SMV in western Oregon strawberries, should be conducted Until such work is accomplished, it is believed that both species should be considered a collective threat to the strawberry industry.

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