Comparison of Efficiency and Propensity as Measures of Vector Importance in Zucchini Yellow Mosaic Potyvirus Transmission by *Aphis gossypii* and *A. craccivora*

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ABSTRACT

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A comparison of efficiency and propensity as measures of vector importance in zucchini yellow mosaic potyvirus (ZYMV) transmission by *Aphis gossypii* and *A. craccivora* was made. Efficiency was measured in the laboratory with single aphids exposed in sequence to an infected plant and then four noninfected zucchini test plants. Individual *A. craccivora*, a species that does not colonize zucchini, had a significantly higher ZYMV transmission efficiency than did *A. gossypii*, a species that colonizes zucchini. Similar assays for ZYMV transmission efficiency with groups of aphids resulted in significantly higher incidence of infection for both aphid species. Propensity was measured by arena tests in which aphids could move between plants and feed without interference. *A. craccivora* had a significantly higher propensity to transmit ZYMV (52.77%) than *A.* gossypii (11.73%). Thus, both tests of efficiency and propensity showed that *A. craccivora* is responsible for more infections per aphid than *A. gossypii*. No significant variation in propensity was found between several *A. gossypii* populations from different Hawaiian islands. Duration of virus retention did not vary significantly between aphid species; however, the duration of time required for initiation of the first probe was significantly shorter for *A. craccivora* than for *A. gossypii*. In addition, *A. craccivora* dispersed to significantly more plants than *A. gossypii*. These characteristics may contribute to *A. craccivora*'s higher transmission efficiency and propensity. In contrast, the increased time required for *A. gossypii* to initiate the first probe and the reduced dispersal to surrounding plants may relate to its lower transmission efficiency and propensity. These findings highlight the potential importance of noncolonizing, transient vector species in the epidemiology of nonpersistently transmitted viruses and suggest that measures of propensity are most accurate in determining the importance of various vector species in epidemics.

Zucchini yellow mosaic potyvirus (ZYMV) is a major limiting factor to successful cultivation of cucurbit vegetables in the Hawaiian islands and elsewhere (1,3,28). ZYMV is the predominant virus found on the Hawaiian island of Maui and was detected in 100 percent of virus-infected samples collected from zucchini crops on Molokai (3). ZYMV was first reported in Italy in 1981 (17) and rapidly spread to most areas in the world where cucurbits are grown (3,4,10,12,20,23,28). Within the United States, ZYMV infects cucurbit crops in more than 11 states (21,25,28,33).

ZYMV is mainly transmitted in nature by aphids in a nonpersistent manner (25). At least 10 species of aphids have been reported as potential vectors of ZYMV, including the cotton or melon aphid, *Aphis gossypii* Glover (2,5,17,18); the cowpea aphid, *A. craccivora* Koch (5); the spirea aphid, *A. spireacola* (18,26); the erigeron root aphid, *A. middletonii* (5,26); the blue alfalfa aphid, *Acyrthosiphon kondoi* (26); the pea aphid, *Acyrthosiphon pisum* (2,5); the turnip aphid, *Lipaphis erysimi* (5); the potato aphid, *Macrosiphum euphorbiae* (18); the green peach aphid, *Myzus persicae* (2,16,27); and *Uroleucon* sp. (26). In Hawaii, only *A. gossypii* colonizes zucchini plants; surveys of aphid distribution, however, show that all the vector species listed above, plus many others, frequently land on zucchini plants (5).

Aphids transmit ZYMV nonpersistently: a mode of transmission characterized by a short acquisition time in which an aphid can acquire a virus in as little as 15 s (26), no latent period, and an equally short inoculation time. Hence, aphids may acquire and transmit ZYMV during short probes that occur during plant sampling as part of host-selection behavior. Although nonpersistently transmitted viruses are not retained for long periods by their vectors, a single aphid moving between plants in a crop can infect several plants after one acquisition event (35). Aphicides generally are ineffective in reducing the spread of ZYMV in the field because transmission generally occurs before the aphids obtain a lethal dose of aphicide (26).

Management strategies need to be targeted at appropriate aphid species; hence, it is important to know which aphid species are most important in virus spread. Irwin and Ruesink (14) proposed two measures for determining vector importance: efficiency and propensity. Efficiency has been defined as the probability of obtaining infection with a virus isolate with a vector species biotype under a set of environmental conditions (32). This measure of importance is generally relevant in the laboratory to determine the competence or genetic capacity of a species as a virus vector (8). Because aphid behavior is largely controlled by the researcher when measuring efficiency, this measure may not approximate vector importance in field epidemics. Propensity has been defined as a measure of vector importance quantifying the natural ability of a species to inoculate a plant with a virus (14). Propensity is measured in the field or under conditions that allow aphids to move and feed freely. Irwin and Ruesink (14) suggested that propensity may better approximate the importance of an aphid species under field conditions. To our knowledge, there have been no studies that have directly compared efficiency and propensity of aphid vectors of nonpersistent viruses.

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The aim of this study was to compare the efficiency and propensity of two species of aphids that commonly land in zucchini fields in Hawaii that are thought to be important in ZYMV spread: *A. gossypii* and *A. craccivora* (5,33). In addition, aspects of probing behavior, virus retention, and dispersal activity were studied to investigate potential mechanisms underlying differences in transmission efficiency and propensity between these species. The possibility that interisland variation in aphid populations may impact propensity also was studied by comparing the populations of aphids from several Hawaiian islands. The relative importance of *A. gossypii* and *A. craccivora* to the epidemiology of ZYMV in zucchini is discussed.

MATERIALS AND METHODS

Virus source plants. An isolate of ZYMV was collected from zucchini on the Hawaiian island of Maui. This isolate was further passaged through three local-lesion transfers on *Chenopodium amaranticolor* Coste & A. Reynier and *C. quinoa* Willd. followed by propagation in zucchini (*Cucurbita pepo* L.) plants. Further confirmation that the isolate was ZYMV was obtained by double-antibody sandwich enzyme-linked immunosorbent assay (DAS-ELISA) by previously described methods (9,34). The isolate was maintained by aphid transmission with the cotton or melon aphid (*A. gossypii*) in zucchini. Inoculated plants were grown in an aphid-free greenhouse. The youngest leaves on infected plants showing virus symptoms were used as virus sources in all transmission experiments.

Confirmation of ZYMV infection with DAS-ELISA. Each DAS-ELISA test included six to eight zucchini leaves infected with each of the viruses assessed as positive controls and the same number of noninfected zucchini leaves and buffer wells as negative controls. Polyclonal antibodies for ZYMV, cucumber mosaic cucumovirus, papaya ringspot potyvirus watermelon strain, and watermelon mosaic potyvirus 2 were provided by D. Gonsalves, Cornell University, Ithaca, NY. Two ELISA plate readers (Bio-Tek EL307B, Winooski, VT, and Bio-Rad model 450, Richmond, CA) were used to quantify ELISA results depending on availability. Samples were considered positive if absorbance at 405 nm was greater than 3 SD around the mean of the healthy controls.

Test plants. Zucchini (cv. Ambassador) seeds were obtained from Petoseed Co. (Saticoy, CA) and sown in 15-cm-diameter plastic pots. All plants were grown in an aphid-free greenhouse separate from virus sources. Seedlings with one pair of true leaves were used as inoculation test plants in all transmission experiments.

Virus vectors. *A. gossypii* colonies initiated from a single female collected from zucchini plants on the Hawaiian island of Maui were reared on zucchini. These colonies had been maintained for 4 years prior to the beginning of these experiments. *A. craccivora* was initiated from a single female collected on the Hawaiian island of Oahu from yard-long bean (*Vigna unguiculata* var. *sesquipedalis*) and reared on yard-long bean. This aphid species was collected less than 1 month prior to the beginning of these experiments. Both colonies were maintained in nylon-meshed cages inside a growth chamber (25°C ± 2, 16-h photoperiod). All transmission experiments were conducted with alate aphids selected from colonies in the following manner: late instar aphid nymphs with wing buds were selected and placed in a plastic pot with a healthy seedling leaf for 24 h. At the end of 24 h, those emerging as alate adults were used for transmission experiments. Newly emerged alate aphids were used to eliminate variation due to physiological state or age and because these aphids are highly motivated to disperse and are most important in virus epidemiology (13).

Measurement of vector efficiency. *Single aphid inoculation.* Newly emerged, alate adult *A. gossypii* and *A. craccivora*, obtained as described above, were used individually in transmission experiments. Individual aphids were placed on a virus source leaf and

observed with a dissecting microscope (30 to 45×) for probing behavior. When an aphid pressed its labium to the plant surface and placed its antennae back across its dorsum, it was considered to be probing. This was the criterion for probing in all our experiments. The acquisition access period was considered to begin with the first probe, after which the aphids were allowed to remain on the leaf for 5 min. After the acquisition access period, the aphid was removed from the virus source leaf with a camel-hair brush and placed on the first of four plants for inoculation.

On each test plant, the time required for the initiation of the first probe (the time elapsed after the aphid was placed on the test plant to the time the aphid began probing) was recorded. As described for acquisition, inoculation access was considered to begin with the first probe, after which aphids were left on the leaf for 5 min. After the inoculation access period, the aphid was removed and placed on the second test plant for an inoculation access period. This process was repeated until four plants had been subjected to sequential inoculation by each aphid. This experiment was replicated 40 times for *A. gossypii* and 60 times for *A. craccivora*. Test plants were dipped in Safer soap (Safer, Eden Prairie, MN) or M-Pede soap (M. Mycogen Co., Eden Prairie, MN) to kill the aphids and were placed in an aphid-free greenhouse for symptom development. After 20 days, symptoms were recorded, and leaves were taken from each plant for DAS-ELISA confirmation of ZYMV infection.

Group aphid inoculations. Groups of *A. gossypii* and *A. craccivora* treated in the same manner as single aphids were used to inoculate four plants sequentially, as described earlier. There were four aphids in each group, and a total of 108 groups of *A. gossypii* and 40 groups of *A. craccivora* were used in the transmission tests. The modification from single aphid inoculations was that acquisition and inoculation access periods began when the first aphid began probing, because it was not possible to observe the behavior of every individual in the group of aphids.

Measurement of vector propensity. An arena test modified from one described by Irwin and Ruesink (14) was used to measure vector propensity in a greenhouse under ambient conditions. Each arena test consisted of eight pots, each containing two plants, for a total of 16 test plants per arena. The test seedlings, which were at the first true leaf stage, were all set in a circular pattern along the edge of the cage. The uppermost fully expanded leaf with symptoms was cut from a ZYMV source plant and placed into a test tube containing water. The stem was sealed to the mouth of the tube by a strip of Parafilm, and the tube was inserted into the center of a soil-filled plastic pot that was placed at the center of the arena. Ten newly emerged alate aphids (selected as described previously) were placed on the source leaf, and the cage was closed for 24 h. Aphids could probe, feed, and move freely from plant to plant. After 24 h, aphids were removed, and test plants were treated with Safer (Safer) or M-Pede soap (M. Mycogen) and placed in the greenhouse and observed for symptom development. Infection was confirmed by DAS-ELISA as described earlier. This test was replicated nine times for *A. craccivora* and for the Maui colony of *A. gossypii*. The arena test was used to measure the propensity of *A. gossypii* colonies collected from the islands of Hawaii (two colonies: one from zucchini in Waimea and one from greenhouse cucumber in Waimea, south Kohalo District, seven replications per colony) and Oahu (colony from Waimanalo, eight replications). The propensities of these colonies to transmit ZYMV were compared with the *A. gossypii*-Maui colony.

Duration of ZYMV retention. To determine the duration of virus retention, aphids were given an acquisition access period, as described earlier, on ZYMV-infected zucchini plants. After this acquisition access period, aphids were sequestered in a plastic petri dish for 5 min, 1 h, 4 h, or 24 h. Individual aphids from each of the four groups were allowed an inoculation access period, as described earlier, on healthy zucchini plants. Two controls were included: healthy zucchini plants not treated (to verify absence of

contamination in the greenhouse) and sap-inoculated plants (to verify infectivity of virus source plants). After all inoculations were done, the plants were dipped in Safer or M-Pede soap, placed in the aphid-free greenhouse, and observed for symptom development. Symptoms were recorded after 15 days, and leaf samples were taken for confirmation of ZYMV infection with DAS-ELISA. These tests were performed with *A. gossypii* (treatment = retention time; treatment 1: 8 aphids per replication; and treatments 2 to 4: 5 aphids per replication, five replications per treatment) and *A. craccivora* (treatment 1: 10 aphids per replication, three replications; treatment 2: replication 1: 11 aphids; replication 2: 10 aphids; replication 3: 8 aphids; and treatments 3 and 4: 10 aphids per replication, three replications per treatment).

Possible role of aphid behavior in vector transmission. *Aphid probing behavior.* During vector efficiency experiments, the time from placement of an aphid on a plant to the first probe was recorded for each aphid on each plant in each sequential inoculation series.

Aphid dispersal behavior. Arenas, as described earlier, were used to measure the dispersal behavior of *A. gossypii* (Maui colony) and *A. craccivora*. The only modification was that rather than seedlings, 16 single zucchini leaves were used. As in the previous measurement of propensity, 10 newly emerged alate aphids were placed on an infected leaf in the center of the arena, and the cage was closed. After 24 h, the location of each aphid was recorded. This test was replicated six times.

Data analysis. The Minitab program (24) was used for statistical analysis. Duration of time required for initiation of the first probe was compared within aphid species on each plant in an inoculation series and between aphid species by a t test. Percents were arcsine-transformed and submitted to a t test to compare vector propensities and dispersal activity of the aphid species (19). Incidence of infection among sequentially inoculated plants for both species and ZYMV retention by the two aphid species in each treatment were compared by chi-square. Similarly, chi-square was used to compare single and group aphid transmissions. The propensities of *A. gossypii* colonies collected from the islands of Hawaii, Maui, and Oahu were analyzed by analysis of variance. In all cases, $P \le 0.05$ was considered significant.

RESULTS

Measurement of vector efficiency. *Single aphid inoculations.* After a single acquisition access period, individuals of both aphid species were able to transmit ZYMV to at least four plants. When the efficiency of ZYMV transmission to each plant in the inoculation series by the two aphid species was compared, individual *A. craccivora* were more efficient in ZYMV transmission than individual *A. gossypii* across all four plants in the inoculation series (Table 1). With both aphid species, transmission efficiency decreased as the number of plants in the sequence increased (Table 1), decreasing more quickly in *A. gossypii* than in *A. craccivora*. There were no significant differences between the first and second plants in the sequence for *A. gossypii* ($\chi^2 = 2.81$, $P > 0.05$), whereas the incidence of virus infection decreased significantly at the third ($\chi^2 = 5.54$, $P \le 0.05$) and fourth plants ($\chi^2 = 7.44$, $P \le 0.01$). In contrast, for *A. craccivora* there were no significant differences in incidence of virus infection until the fourth plant in the inoculation series (A and B [$\chi^2 = 0.86$, $P > 0.05$], B and C [$\chi^2 = 0.95$, $P > 0.05$], C and D [$\chi^2 = 1.68$, $P > 0.05$], A and C [$\chi^2 = 3.59$, $P > 0.05$], and A and D [$\chi^2 = 9.86$, $P \le 0.01$]).

Group aphid inoculation. In all cases, except the third plant in the sequential inoculation series for *A. craccivora*, the transmission efficiency of both aphid species was significantly increased when groups of four aphids were used rather than single aphids (Table 1). In contrast to single aphid inoculations, there were no significant differences between the two aphid species with regard to transmission efficiency when groups of aphids were used for inoculation (Table 1). Within each species, incidence of virus infection decreased significantly after two sequential inoculations (*A. gossypii*: plants A and B [$\chi^2 = 1.60$, $P > 0.05$], A and C [$\chi^2 = 5.52$, $P \le 0.05$], and A and D [$\chi^2 = 11.70$, $P \le 0.01$]; *A. craccivora*: plants A and B [$\chi^2 = 1.73$, $P > 0.05$], A and C [$\chi^2 = 15.22$, $P \le 0.01$], and A and D [$\chi^2 = 13.65$, $P \le 0.01$]) and was still very high (more than 40%) on the fourth plant in the sequential inoculation series (Table 1).

Measurement of vector propensity. The propensity of *A. craccivora* to transmit ZYMV (52.7%) was significantly higher than that of *A. gossypii* (11.73%) ($t = 4.82$, $P \le 0.01$). There were no significant differences with regard to propensity among *A. gossypii* colonies collected from different islands ($F = 1.17$, $P = 0.039$) (Fig. 1).

ZYMV retention by *A. gossypii* and *A. craccivora*. In the absence of plant material to probe, both aphid species retained ZYMV up to, but not beyond, a 1-h sequestration period. Furthermore, both species transmitted ZYMV to a greater number of plants after a 5-min sequestration period (*A. gossypii*: 17.5%; *A. craccivora*: 20%) than after 1 h (*A. gossypii*: 8%; *A. craccivora*: 3.4%). The difference between these two sequestration periods was significant for *A. craccivora* ($\chi^2 = 3.86$, $P \le 0.05$) but not for *A. gossypii* ($\chi^2 = 1.16$, $P > 0.05$). There were no significant differences in transmission efficiency between the species in the same sequestration period (5-min sequestration: $\chi^2 = 0.071$, $P > 0.05$; 1-h sequestration: $\chi^2 = 0.53$, $P > 0.05$).

Time required for initiation of the first probe. Time required for initiation of the first probe by *A. craccivora* was significantly shorter than for *A. gossypii* on each of the four plants in the se-

TABLE 1. Results of sequential inoculation of zucchini plants with zucchini yellow mosaic virus (ZYMV) with *Aphis gossypii* and *A. craccivora*

| Plant sequence | Mean % ZYMV infection[w] | | | | | | χ^{2z} | |
| | *A. gossypii* | | | *A. craccivora* | | | | |
	Single ($n = 40$)	Group[x] ($n = 108$)	χ^{2y}	Single ($n = 60$)	Group ($n = 40$)	χ^{2y}	Single	Group
A	27.5 a	66.7 a	18.18 ($P \le 0.01$)	45.0 a	82.5 a	14.06 ($P \le 0.01$)	3.12 ($P > 0.05$)	3.55 ($P > 0.05$)
B	12.5 ab	58.3 ab	24.69 ($P \le 0.01$)	36.7 a	70.0 a	10.67 ($P \le 0.01$)	7.11 ($P \le 0.01$)	1.68 ($P > 0.05$)
C	7.5 b	50.9 bc	23.10 ($P \le 0.01$)	28.3 ab	40.0 b	1.48 ($P > 0.05$)	6.51 ($P \le 0.05$)	1.40 ($P > 0.05$)
D	5.0 b	43.5 c	19.56 ($P \le 0.01$)	18.3 b	42.5 b	6.95 ($P \le 0.01$)	3.78 ($P \le 0.05$)	0.01 ($P > 0.05$)

[w] n = number of replications per inoculation sequence. Values followed by different letters in a column indicate significant differences between plants in the sequential inoculation series at $P < 0.05$ according to χ^2 test.
[x] Each group contains four alate aphids.
[y] χ^2 values and probabilities for within-species comparison of single and group aphid transmission of ZYMV in each inoculation sequence.
[z] χ^2 values and probabilities for between-species comparison of ZYMV transmission.

quential inoculation series (Table 2). For *A. gossypii*, time required for initiation of the first probe was significantly longer on the first two plants in an inoculation series than on the last two plants in the sequence (plants A and B [$t = 0.23$, $P = 0.82$], A and C [$t = 2.16$, $P = 0.034$], A and D [$t = 2.09$, $P = 0.041$], B and C [$t = 2.23$, $P = 0.029$], B and D [$t = 2.16$, $P = 0.034$], and C and D [$t = 0.15$, $P = 0.88$]). In contrast, the time required for the initial probe by *A. craccivora* did not change significantly on any plant in the sequential inoculation (plants A and B [$t = 0.80$, $P = 0.43$], B and C [$t = 0.46$, $P = 0.65$], C and D [$t = 0.45$, $P = 0.65$], A and C [$t = 1.23$, $P = 0.22$], A and D [$t = 0.54$, $P = 0.59$], and B and D [$t = 0.11$, $P = 0.91$]) (Table 2). When the time required for initiation of the first probe on inoculated and noninoculated plants was compared for each species, no significant differences were found (*A. gossypii*: plant A [$t = 1.38$, $P = 0.18$], B [$t = 0.27$, $P = 0.80$], C [$t = 1.58$, $P = 0.26$], and D [$t = 1.74$, $P = 0.18$]; *A. craccivora*: plant A [$t = 1.33$, $P = 0.19$], B [$t = 0.09$, $P = 0.93$], C [$t = 1.94$, $P = 0.058$], and D [$t = 2.0$, $P = 0.051$]).

Aphid dispersal activity. Results from arena tests indicated that significantly more *A. craccivora* dispersed from the infected source leaf to surrounding plants than *A. gossypii* ($t = 5.35$, $P \leq 0.01$). Twenty-four hours after placement on the infected source leaf in the arena, 78% of the *A. craccivora* aphids were found on surrounding plants compared to only 12.5% of the *A. gossypii* aphids.

Confirmation of ZYMV infection with DAS-ELISA. None of the leaves sampled from negative control plants or from test plants without symptoms were positive by DAS-ELISA nor did they differ significantly from buffer controls. With the Bio-Tek ELISA reader, mean absorbance of the negative control plants at 405 nm = 0.171 ± 0.013, buffer absorbance = 0.170. With the Bio-Rad ELISA reader, mean absorbance of the negative control plants at 405 nm = 0.03 ± 0.003, buffer absorbance = 0.002. ELISA absorbance values for ZYMV-infected plants ranged from 0.25 to 2.46.

DISCUSSION

Our results show that *A. craccivora*, an aphid species that does not colonize zucchini (6), transmits ZYMV more efficiently and has a greater propensity to transmit ZYMV than *A. gossypii*, a species that commonly colonizes zucchini (6,26). This is consistent with earlier findings in which noncolonizing aphid species played an important role in epidemics of nonpersistently transmitted viruses (11,29,31). Data from efficiency tests of single aphids show that both species we investigated can potentially transmit virus to at least four plants (Table 1). The species differed in that *A. crac-*

civora's efficiency did not begin to decline significantly until the fourth plant in a series, whereas *A. gossypii*'s efficiency began to decrease earlier. In the inoculation sequence, significantly more individual *A. craccivora* (18.3%) were able to transmit ZYMV to the fourth plant than did individual *A. gossypii* (5.0%). Although we did not exceed four plants in our sequential inoculations, these data suggest that after ZYMV acquisition by a single aphid, *A. craccivora* would be more likely to transmit the virus to several plants beyond the fourth plant than would *A. gossypii*. When the number of aphids was increased from one to four per inoculation, there were no significant differences in the efficiency of the two species on any plant in the sequential inoculation series. Furthermore, for both aphid species, groups of aphids were significantly more efficient than individual aphids (Table 1). The possibility that this occurred due to an increased number of probes is well supported by previous research relating numbers of probes to greater virus incidence (22,35). A very large number of the last (fourth) plants in the sequential inoculation series were infected by groups of each aphid species (more than 40%), which may help to explain why ZYMV epidemics in Hawaii develop so rapidly (34). Both aphid species occur frequently in landing-trap catches in zucchini fields in Hawaii (5,34), where aphid movement is continuous throughout the year.

Previous studies indicated that nonpersistently transmitted viruses were not retained for long periods by their aphid vectors at room temperature (7,35). Our data show this also to be true of the relationship between ZYMV and the two vector species we studied (Table 2). Because retention of ZYMV is brief for both species, we hypothesized that one factor contributing to the difference in efficiency and propensity between the two species could be duration of time required to initiate the first probe on inoculation test plants. Our data support this hypothesis, because *A. craccivora*, the more efficient transmitter of ZYMV, made its first probe in significantly less time than did *A. gossypii* (Table 2). Previous research comparing *A. craccivora* probing on several plant species (15) showed that *A. craccivora* made its first probe in less than 1 min regardless of host. Rapid initiation of a first probe is apparently part of *A. craccivora*'s normal behavior and may contribute to the significant differences in efficiency and propensity we recorded between *A. craccivora* and *A. gossypii*. Whereas efficiency of transmission by a single aphid was significantly different between the two species, retention periods between them were not. Thus, these two species would be able to inoculate plants for similar periods, but *A. craccivora* is likely to transmit ZYMV more efficiently than *A. gossypii* as it encounters uninfected hosts.

Surveys of aphids landing in zucchini plantings on the Hawaiian island of Maui suggest that *A. gossypii* is the most common species landing in zucchini crops, followed closely by *A. craccivora*, *Myzus persicae*, and *Brevicoryne brassicae* (3). The latter three species are all aphids that do not colonize the crop. Growers
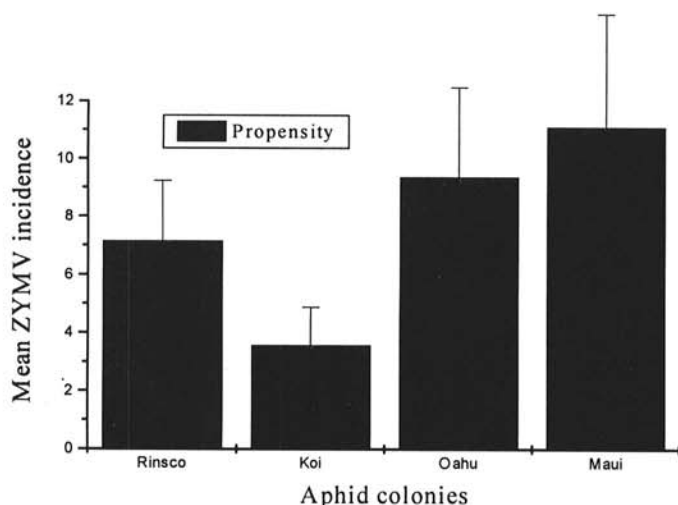
Fig. 1. Comparison of the propensity of four populations of *Aphis gossypii* to transmit zucchini yellow mosaic virus (ZYMV): Maui (nine replications), Oahu (eight replications), and Hawaii (two populations: Rinsco and Koi, seven replications each). Vertical bars represent the standard error of the mean.

TABLE 2. Time required for initiation of first probe by *Aphis gossypii* and *A. craccivora* given inoculation access to four plants sequentially in single aphid inoculation tests

Plant sequence	Mean time required for initiation of first probe (min)[x]		*t* test[y] ($P \leq 0.01$)
	A. gossypii ($n = 40$)	*A. craccivora* ($n = 60$)	
A	8.55 (±0.77) a[z]	2.98 (±0.31) a	6.70
B	8.32 (±0.61) a	2.67 (±0.25) a	8.58
C	6.57 (±0.49) b	2.52 (±0.22) a	7.57
D	6.68 (±0.46) b	2.72 (±0.39) a	6.60

[x] Time from placement of an aphid on a plant to first probe. n = number of replications per inoculation sequence.

[y] *t* value and probabilities for between-species comparison of mean time required for initiation of first probe.

[z] Number in parentheses = standard error. Values followed by different letters in a column indicate significant differences in duration of mean time required for initiation of the probe between plants in an inoculation sequence according to *t* test.

frequently attempt to manage ZYMV epidemics by spraying aphicides to control aphid populations, although this seldom results in adequate control and can even contribute to increased ZYMV spread (34). Our data showing the importance of one of the noncolonizing species, *A. craccivora*, in virus spread, suggest that one reason pesticides fail to manage ZYMV spread is that transient, noncolonizing aphid species contribute very significantly to ZYMV epidemics. Furthermore, these species are moving through the crop and not colonizing it, so they are seldom the targets of routine pesticide spraying. These findings strongly support use of measures preventing aphid landing or virus infection such as reflective mulches and row covers (36), cross-protection (16), or methods (20) for control of ZYMV epidemics other than routine pesticide spraying.

Our data support the hypothesis, as proposed by Irwin and Ruesink (14), that very different views of vector importance are provided by measurements of vector efficiency and propensity. Both tests of efficiency and propensity showed that *A. craccivora* transmits ZYMV more often on a per aphid basis than *A. gossypii*. However, in terms of relevance to epidemiology of aphid-transmitted viruses in agroecosystems, our data strongly suggest that propensity is a more appropriate measure of vector importance. For example, highly significant differences were found between vector efficiency and propensity for both species, with the most striking differences occurring in *A. gossypii* (Fig. 2). If our efficiency data were used in simulation models to predict virus spread, the importance of both *A. craccivora* and *A. gossypii* would be grossly overrated. This problem would be most severe in the case of *A. gossypii*, because its efficiency was more than six times higher than its propensity. There also were very significant differences in the propensity of the two species, with *A. craccivora* transmitting ZYMV at a frequency four times that of *A. gossypii*. In other words, after a single virus acquisition, at least four *A. gossypii* are required to inoculate the number of plants that one *A. craccivora* inoculates in the same period. Hence, given an equal number of each species landing in a field, *A. craccivora* would be by far the more important vector species.

One important element of vector propensity is aphid dispersal from infected plants to surrounding plants or plants in other fields (14,30). Our tests of aphid movement from inoculum sources to surrounding plants in arena experiments show that significantly more *A. craccivora* were found on plants surrounding the infected leaf on which they were released within 24 h than were *A. gossypii*. One explanation for this difference in dispersal is that zucchini was a less suitable host for *A. craccivora* (2,6). The higher rate of movement and shorter time required for the initiation for the first probe of *A. craccivora* likely contribute to its high propensity to transmit ZYMV. In contrast, the longer time required
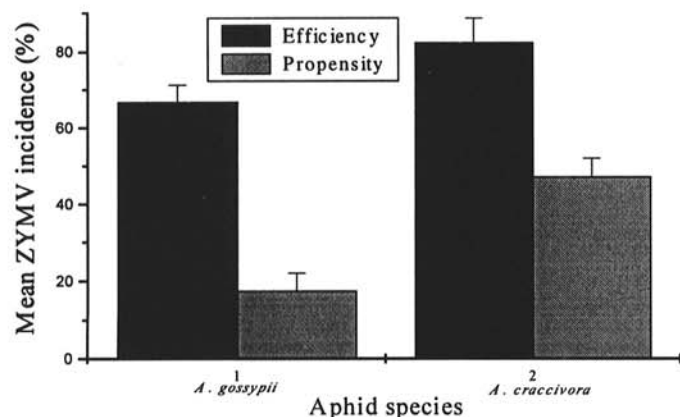
for the initiation of the first probe and lower dispersal activities of *A. gossypii* quite likely contribute to its lower propensity with regard to spread of ZYMV.

Field measurements of vector propensity are difficult, labor-intensive, and expensive. Our findings confirm the suggestion that the "arena method" (14,32) provides an inexpensive and less labor-intensive means of measuring vector propensity. In addition, this method allows for rapid comparison of aphids from different geographic locations, on different plant species, or under varying environments.

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Fig. 2. Comparison of vector efficiency (mean incidence of zucchini yellow mosaic virus [ZYMV] on the first plant in a sequential inoculation by a group of four aphids) and propensity of *Aphis gossypii* and *A. craccivora* in ZYMV transmission. Vertical bars represent the standard error of the mean.

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