

Effects of Host Plants on Biology and Life Table Parameters of *Aphis spiraecola* (Homoptera: Aphididae)

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ABSTRACT The development, survivorship, longevity, reproduction, and life table parameters of the spirea aphid, *Aphis spiraecola* Patch, were evaluated at 25°C on seven commonly grown plants (*Polyscias crispata* (Bull) Merrill cultivar chicken-gizzard aralia, *P. scutellaria* (Burman) Fosberg, *Viburnum suspensum* Lindley, grapefruit (*Citrus paradisi* Macfadyen), rough lemon (*C. jambhiri* Lushington), pineapple orange [*C. sinensis* (L.) Osbeck variety pineapple orange], orange jessamine [*Murraya paniculata* (L.) Jack]) in the laboratory. Spirea aphid failed to survive on orange jessamine. The developmental times for the immature stages ranged from 7.9 d on *P. scutellaria* to 9.9 d on grapefruit or pineapple orange. The immature survival varied from 92.7% on *P. scutellaria* to 78.8% on pineapple orange. The average number of nymphs reproduced per female were 42.7, 35.7, 28.7, 22.3, 18.0, and 11.7 on *P. crispata*, *P. scutellaria*, *V. suspensum*, grapefruit, rough lemon, and pineapple orange, respectively. Female adults lived an average of 14.1, 15.3, 12.2, 11.0, 12.0, and 9.3 d on these same hosts. The intrinsic rate of increase (r_m) for spirea aphid on *P. crispata* was highest. Jackknife estimates of r_m varied from 0.308 on *P. crispata* to 0.177 on pineapple orange. The mean population generation time on these hosts ranged from 11.6 to 13.2 d. It was concluded that the ability of spirea aphid to feed and develop on a wide range of host plants increases its chance to infest citrus and thereby spreading the citrus tristeza virus.

KEY WORDS spirea aphid, host suitability, life history

THE SPIREA APHID, *Aphis spiraecola* Patch, is a polyphagous species with a worldwide distribution and is a pest of citrus (Cole 1925, Miller 1929, Yokomi and Tang 1995), apples (Pfeiffer et al. 1989), and ornamentals, and transmits a number of plant viruses (Blackman and Eastop 1984). Spirea aphid is one of the most abundant aphids on citrus in the United States (Yokomi and Tang 1995) and is a vector of citrus tristeza virus (CTV) (Yokomi and Garnsey 1987). Citrus tristeza is found in most citrus-producing areas of the world and is the most economically important viral disease of citrus (Rocha-Pena et al. 1995). CTV is known primarily to cause decline and death of citrus trees grafted on sour orange, *Citrus aurantium* L., rootstock; but some CTV isolates can cause stem pitting regardless of rootstock (Bar-Joseph et al. 1989) and can result in long-term debilitation that reduce yields of sweet orange and grapefruit from 5 to 45% (Yokomi and Tang 1995). In addition, young citrus shoots fed upon by this aphid often result in foliage distortion, and the honeydew excreted by aphids not only promotes growth of sooty mold (Cole 1925, Miller 1929) but also attracts ants, which fend off natural enemies of aphids resulting in additional pest damage (Yokomi and Tang 1995).

The spirea aphid is thought to be of Far Eastern origin (Blackman and Eastop 1984). In the last 10 yr, studies on citrus aphids have mainly concentrated on brown citrus aphid, *Toxoptera citricida* (Kirkaldy). Only a few studies dealing with biocontrol of spirea aphid were reported (Tang and Yokomi 1995, 1996; Yokomi and Tang 1995). Little is known of the biology of spirea aphid. A thorough understanding of pest biology on overwintering hosts is essential for development of effective management strategies. The following experiments were conducted to examine the effect of six host plants on the biology and life table parameters of spirea aphid.

Materials and Methods

Aphid Source. A stock culture of spirea aphid originated from a citrus tree collected in the campus of Fort Lauderdale Research and Education Center, University of Florida, Broward County, FL. The aphids were maintained on potted aralia [*Polyscias crispata* (Bull) Merrill cultivar chicken-gizzard aralia] (40–50 cm tall), in an insect-rearing room at 25 ± 1°C, 80 ± 5% RH, and a photoperiod of 14:10 (L:D) h. After a 4-mo rearing period, the ensuing colonies were used for the test. The identity of spirea aphid was confirmed by S. E. Halbert at the Division of Plant Industry (DPI), Florida Department of Agriculture and Consumer Services (FDACS), Gainesville, FL. Voucher specimens were deposited at the collection of the DPI, FDACS.

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Host Source. Seven host plants commonly found in South Florida were used for this study. These included the following: *P. crispata* (Bull) Merrill cultivar chicken-gizzard aralia, *P. scutellaria* (Burman) Fosberg, *Viburnum suspensum* Lindley, grapefruit (*Citrus paradisi* Macfadyen), rough lemon (*C. jambhiri* Lushington), pineapple orange [*C. sinensis* (L.) Osbeck variety pineapple], and orange jessamine [*Murraya paniculata* (L.) Jack]. All tested plants were maintained in a greenhouse using Pine Bark Mix as growing media (50% pine bark, 40% Florida sedge peat, and 10% sand). The plants were fertilized with a controlled release fertilizer (Osmocote, 14:14:14 [N:P:K], Scotts, Marysville, OH) and watered as required.

Development and Survivorship of Nymphs. For each experiment, ≈ 50 young apterous adult females of the same age from the stock colonies (maintained on each host plant for at least two generations) were transferred to each of the seven host plants at 30–40 cm tall for nymph production at 25°C. Sixty to 90 first instars collected within 4 h of birth were used for each host plant experiment. Each nymph was transferred individually to a host plant seedlings grown in a vial and caged with a plastic cage (7 by 4.5 cm diameter with a nylon cloth top) using a camel's-hair brush. The test plants were placed in growth chambers (Percival, Boone, IA) at $25 \pm 1^\circ\text{C}$, 70–80% RH, and a photoperiod of 14:10 (L:D) h (Wang and Tsai 2000). Individual insects were checked twice daily for ecdysis and survivorship. The exuviae were used to determine molting.

Adult Longevity and Reproductive Capacity. After the fourth molt and the initiation of reproduction, adult mortality and fecundity were recorded daily and offspring were removed from each caged plant until the death of the adult. All test plants were changed every 3–4 d throughout the study.

Data Analysis. We estimated the following life history parameters: developmental time and survivorship of each nymphal stage and combined nymphal stages, adult longevity, and fecundity. Selection of statistical methods for analyzing the data followed that of Ballou et al. (1986), as well as Michels and Behle (1988). All parameters were analyzed among treatments of host plants using the general linear model (GLM) procedure of SAS; means were separated by the Fisher protected least significant difference (LSD) test after a significant *F*-test at $P = 0.05$ (SAS Institute 1988). The survival data were transformed to arcsine square-root before statistical test.

Variations in natality (average nymphs per day per adult) over time for a specific host plant were analyzed as a fourth-order polynomial regression with natality as the dependent variable, and host plants and age as discrete, independent variables. Host plants effects were analyzed by using least-square means to adjust for the polynomial age effects. These means of natality were then compared among host plants, and means were separated with option of Fisher protected LSD test in the GLM.

Mortality data were analyzed as a multiple regression, with the percentage of surviving adult as the

dependent variable and age and host plants as independent variables. An age-by-host plant interaction term was also included in the GLM procedure.

Life table statistics were calculated for the populations on different hosts as described by Hulting et al. (1990). The differences in r_m values among populations were also analyzed using Student-Newman-Keul sequential tests (Sokal and Rohlf 1969) based on jackknife estimates of variance for r_m (Meyer et al. 1986). For any difference between two r_m s from the sequence, in which the r_m s were arrayed in order of magnitude, to be significant at the α level, it must be equal to or greater than

$$LSR = Q_{\alpha[K,V]} \sqrt{S_{av}^2 \frac{n_i + n_j}{2n_i n_j}},$$

where K is the number of r_m in the set whose range is tested. The degrees of freedom equal V . The n_i and n_j were sample sizes of the two r_m s; and $Q_{\alpha[K,V]}$ is a value from the table of the studentized range. S_{av}^2 is the weighted average variance of r_m and it is calculated as follows:

$$S_{av}^2 = \frac{\sum_{i=1}^a (n_i - 1) S_i^2}{\sum_{i=1}^a (n_i - 1)},$$

where α equals the number of r_m to be tested, the sample size of i th r_m is n_i . S_{av}^2 is the jackknife estimate of the variance for the i th r_m .

Results

Development and Survivorship of Nymphs. Spirea aphid failed to survive on orange jessamine. For this reason, this plant was excluded from analysis. Developmental time of immature stages on the other six host plants is presented in Table 1. There were significant differences in developmental time of immature stages among the populations on different hosts (Table 1; $F = 29.36$; $df = 5, 238$; $P < 0.0001$). Individuals fed on *P. scutellaria* developed significantly faster than those on any other host plants did during the immature stages ($P < 0.0001$). On the contrary, the nymphs reared on grapefruit and pineapple orange had a significantly longer combined developmental time (≈ 9.9 d) than those reared on *V. suspensum*, rough lemon, or *P. crispata* (≈ 8.9 d).

The percentage of survival of the combined immature stages showed significant difference within the group of six host plants tested (Table 2; $F = 23.30$; $df = 5, 12$; $P < 0.0001$) although the difference for each instar was not always significant. Spirea aphid fed on *P. scutellaria* had the highest percentage of survival from the first through fourth stadia (92.7%), whereas the populations fed on grapefruit, rough lemon or pineapple orange had significantly lower survivorship (83.8, 82.3, and 78.8%, respectively). The highest nymphal mortality occurred in the first instar stage (Table 2).

Table 1. Mean ± SE developmental periods (d) of immature stages of *A. spiraeicola* on six host plants at 25°C

Host	n	1st instar	2nd instar	3rd instar	4th instar	Combined nymphs
<i>P. crispata</i>	31	1.9 ± 0.12b	2.1 ± 0.09cd	2.2 ± 0.07b	2.6 ± 0.11b	8.9 ± 0.20b
<i>P. scutellaria</i>	42	1.8 ± 0.07b	1.8 ± 0.07d	1.9 ± 0.06c	2.3 ± 0.08b	7.9 ± 0.10c
<i>V. suspensum</i>	40	2.0 ± 0.08b	2.3 ± 0.07ab	2.1 ± 0.04b	2.6 ± 0.09b	8.9 ± 0.13b
Grapefruit	40	2.3 ± 0.09a	2.5 ± 0.09a	2.4 ± 0.09a	2.7 ± 0.10ab	9.9 ± 0.13a
Rough Lemon	45	2.0 ± 0.07b	2.2 ± 0.07bc	2.1 ± 0.05b	2.6 ± 0.09b	8.9 ± 0.16b
Pineapple orange	46	2.5 ± 0.09a	2.4 ± 0.07ab	2.1 ± 0.05b	3.0 ± 0.11a	9.9 ± 0.12a
F		8.30	5.92	7.04	5.41	29.36
df		5, 238	5, 238	5, 238	5, 238	5, 238
P		0.0001	0.0001	0.0001	0.0001	0.0001

Means within a column followed by the same letters are not significantly different ($P > 0.05$; GLM) in ANOVA (Fisher protected LSD).

Adult longevity and reproductive capacity. Adult longevity of spirea aphid was affected significantly by host plants (Fig. 1A; $F = 23.83$; $df = 5, 211$; $P < 0.0001$). Analysis of covariance (ANCOVA) for the adult survival data also showed the significant main effects of host plants ($F = 4.07$; $df = 5, 104$; $P = 0.0020$) and aphid age ($F = 682.12$; $df = 1, 104$; $P < 0.0001$). However, the effect of age by host plants interaction was not significant ($F = 1.39$; $df = 5, 104$; $P = 0.2356$). Adult females lived significantly longer on *P. scutellaria* or *P. crispata* (15.3 and 14.1 d, respectively) than on *V. suspensum* plant (12.2 d), rough lemon (12.0 d), grapefruit (11.0 d), or pineapple orange (9.3 d) (Fig. 1A; $P < 0.05$). The observed and simulated age-specific (in d) survivals of spirea aphid on six host plants are shown in Fig. 2. No mortality occurred until 5–7 d after emergence of adult on all hosts tested. The longest individual female longevity on *P. scutellaria*, *P. crispata*, *V. suspensum*, rough lemon, grapefruit, and pineapple orange were recorded at 24, 24, 18, 17, 15, and 14 d, respectively. The median longevity on the above host plants were 13.8, 15.6, 12.5, 11.4, 12.6, and 9.5 d, respectively (Fig. 2).

Most females began to reproduce nymphs within 24 h of emergence. The mean total number of nymphal reproduction was affected by host plants significantly (Fig. 1B; $F = 128.7$; $df = 5, 211$; $P < 0.0001$). The females reared on *P. crispata* produced significantly more nymphs (42.7) than those on *P. scutellaria* (35.7), *V. suspensum* (28.7), grapefruit (22.3), rough lemon (18.0), and pineapple orange (11.7) (Fig. 1B). The natality patterns observed over life span of the aphids were best described by polynomial regression and were not a linear function of age, and formed a

skewed-right pattern (Fig. 2). The regression analysis (Table 3) showed a very strong effect of host plants on natality, even after variation due to age was removed ($F = 18.46$; $df = 5, 101$; $P < 0.0001$). The highest numbers were recorded from four to 8 d after emergence, with values of 6.0, 5.3, 4.9, 4.1, 3.5, and 2.7 per day on *P. crispata*, *P. scutellaria*, *V. suspensum*, grapefruit, rough lemon, and pineapple orange, respectively. Overall, the number of nymphs per female per day on *P. crispata* and *P. scutellaria* was higher than that of nymphs on the other four hosts. In most cases, the reproduction periods lasted as long as adult longevity.

The intrinsic rate of increase (r_m), net reproductive rate (R_o), mean generation time (MT), and population doubling time (t) were calculated for the populations on six host plants (Table 4). There were significant differences in r_m values among the populations on six host plants ($P < 0.05$). Spirea aphid reared on *P. crispata* and *P. scutellaria* had significantly higher r_m values (0.308 and 0.301) (jackknife estimate of r_m) compared with the females reared on other hosts ($P < 0.05$). The population reared on *P. scutellaria* had a much lower R_o value (33.1) than that on *P. crispata* (38.8). However, the r_m values on both host plants were essentially same due to the population reared on *P. scutellaria* plants had the shorter immature development (7.9 d), higher nymphal survival (93.0%), and shorter mean generation time (11.6 d). The lowest r_m and R_o values (0.177 and 9.3) were all obtained when individuals fed upon pineapple orange. MT ranged from 11.6 to 13.2 d. Doubling times for spirea aphid populations varied from 2.3 d on *P. crispata* and *P. scutellaria* to 3.9 d on pineapple orange.

Table 2. Survivorship of immature stages of *A. spiraeicola* on six host plants at 25°C

Host	1st instar	2nd instar	3rd instar	4th instar	Combined nymphs
<i>P. crispata</i>	95.10	98.28	98.00	98.89	90.56ab
<i>P. scutellaria</i>	96.30	97.41	99.26	99.56	92.66a
<i>V. suspensum</i>	95.74	96.67	96.67	98.89	88.45b
Grapefruit	92.26	95.65	96.13	98.82	83.80c
Rough Lemon	90.41	95.90	97.77	97.19	82.34cd
Pineapple orange	91.08	94.07	96.18	95.57	78.75d

There were three replicates for each host plant and the initial number of first instar nymph ranged from 30 to 45. Means of the combined nymphs followed by different letters are significantly different ($F = 23.30$, $df = 5, 12$; $P < 0.0001$) in ANOVA (Fisher protected LSD). Data were transformed arcsine square-root before ANOVA; untransformed data are presented.

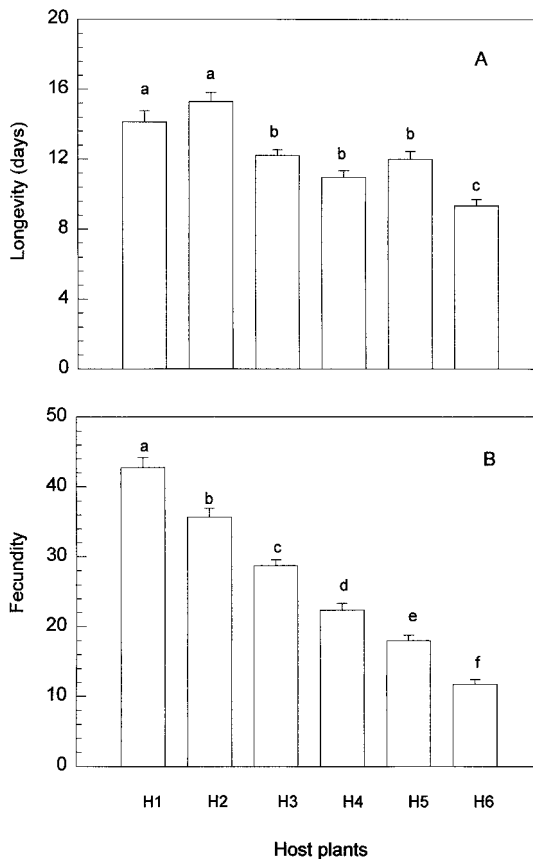


Fig. 1. (A) Longevity (mean \pm SE) of spirea aphid females reared on *Polyscias crispata* (H1), *Polyscias scutellaria* (H2), *Viburnum suspensum* (H3), grapefruit (H4), rough lemon (H5), and pineapple orange (H6). (B) Fecundity (mean \pm SE) per each female of spirea aphid reared on six host plants listed above. Bars followed with same letter means no significant difference at $P > 0.05$ (Fisher protected LSD).

Discussion

Plant species differ greatly in terms of their suitability as hosts for specific insects when measured in terms of insect mortality and reproductive rates. van Lenteren and Noldus (1990) stated that shorter development times and greater total reproduction on a host reflect the suitability of the plant. Although developmental rates and reproduction provide important clues concerning the ability of the host to support a complete insect life cycle, these data should be linked to other parameters such as mortality before definitive conclusions can be drawn concerning host suitability for reproductive purpose. Recent study on brown citrus aphid also demonstrated that the development, survivorship and reproduction varied significantly with plant hosts (Tsai 1998). Spirea aphid generally has a wide range of host plants. However, no host suitability study has been done to support the claims. It is well known that maternal effects are very marked in aphids (Dixon et al. 1982) due to the telescoping of generations (Kindlmann and Dixon 1989).

However, we overcome this effect by rearing spirea aphids for at least two generations on each host plant before being tested.

Our results showed that the developmental time of combined immature stages was longer, and the variation in development rates on different hosts (Table 1) was greater than those reported for brown citrus aphid (Tsai 1998). Generally, spirea aphid fed on citrus hosts (grapefruit, rough lemon, and pineapple orange) had longer developmental times and lower survivorship compared with other *P. crispata*, *P. scutellaria*, and *V. suspensum*. Early mortality could be attributed to the longer times required for first instar crawlers to settle down on citrus hosts than on other three hosts that we observed throughout this study (J.H.T. and J.-J.W., unpublished data). Tang and Yokomi (1995) also stated that the leaves of red tip photinia, *Photinia \times fraserii* (Rosaceae), support the black citrus aphid, *Toxoptera aurantii* (Boyer de Fonscolombe) longer than citrus.

We have demonstrated that host plants had a significant effect on both the longevity and reproduction of spirea aphid. However, no direct correlation was observed between the nymphal production and survival rate or development time. For example, among those hosts tested, *P. scutellaria* had the shortest development time (7.9 d) and highest survival rate (92.7%) (Tables 1 and 2), but the nymphal production was significantly lower than that of *P. crispata* ($P < 0.05$; Table 3; Fig. 1). The similar results were also observed between grapefruit and rough lemon. This suggests that before reproduction, spirea aphid females may not be able to evaluate, or respond to, the potential quality of a host plant, with respect to optimum survival rate and development times of immature stages. This study showed that the total life span (i.e., from birth to death) (21.1 d) of spirea aphid reared on *V. suspensum* was longer than 19.6 d reared on sweet viburnum, *V. odoratissimum* Awabuki (Caprifoliaceae) reported by Tang and Yokomi (1996), whereas the fecundity (28.7 nymphs per female) in this study was much lower than 39.7 in their study. The longevity of spirea aphid on the six tested plants (9.3–15.3 d) were much shorter than those of brown citrus aphid (14.6–22.8 d) on eight different host plants reported by Tsai (1998). Accordingly, the fecundity of spirea aphid on the six tested plants (11.7–42.8 nymphs per female) were much lower than those of brown citrus aphid (17.7–58.8 nymphs per female) on eight different host plants.

The intrinsic rate of increase (r_m) is the only statistic that adequately summarizes the physiological qualities of an animal relative to its capacity of increase (Andrewartha and Birch 1954). Comparison of r_m values often provides considerable insight beyond that available from independent analyses of several life history parameters (Petitt et al. 1994). Although the component variables of r_m are affected by a large number of factors, there is a close and positive association between the mean relative growth rate and r_m (Guldmond et al. 1998). The mean relative growth rate of an aphid is mainly determined by food quality

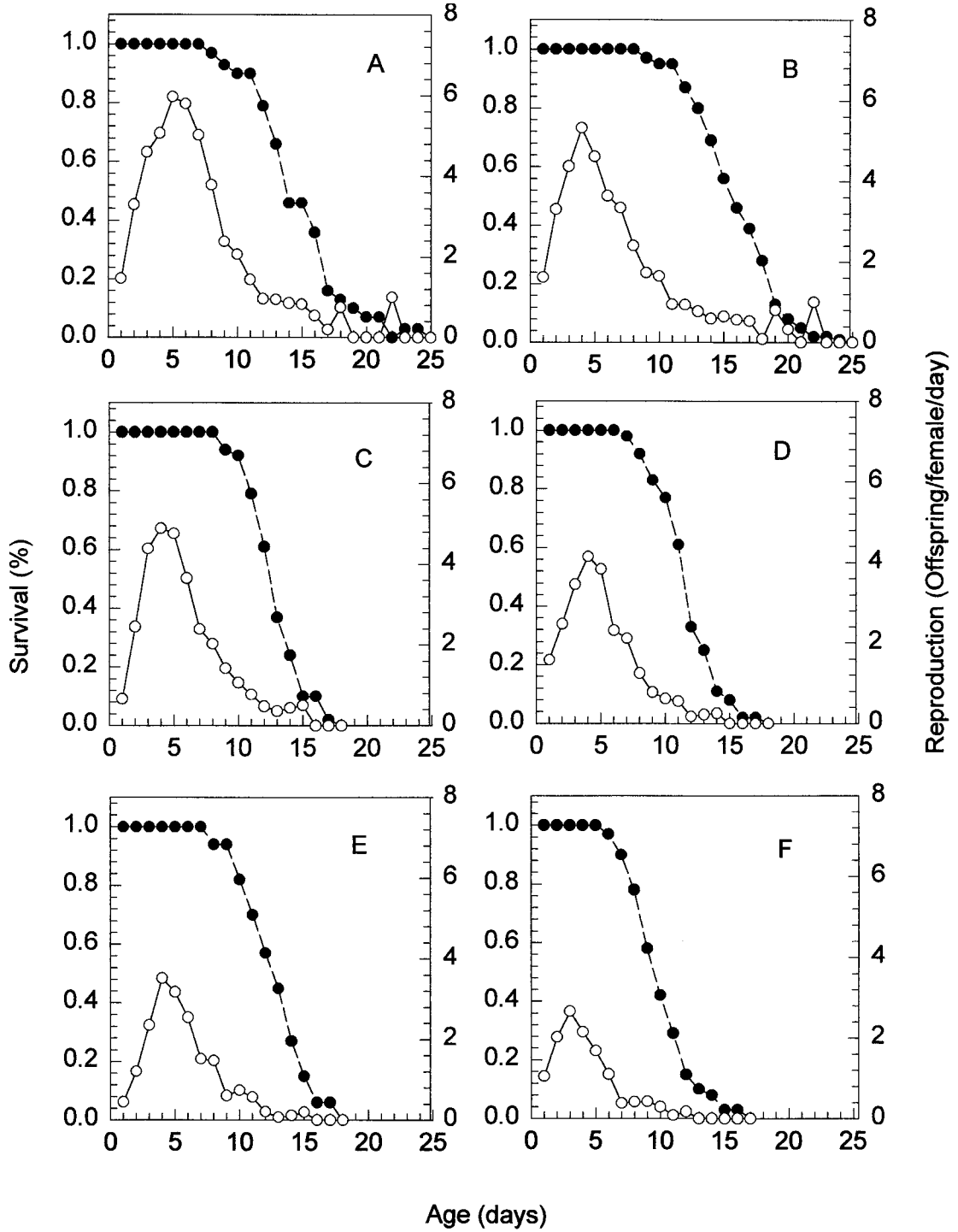


Fig. 2. Observed age-specific reproduction (○—○) and survivorship (●—●) for spirea aphid females reared on *Polyscias crispatum* (A), *Polyscias scutellaria* (B), *Viburnum suspensum* (C), grapefruit (D), rough lemon (E), and pineapple orange (F).

and temperature, whether the aphid is sedentary or active (Dixon 1987). Our study showed that nymphal reproduction of spirea aphid was not a linear function

of adult age but was dependent on host plants (Table 4). Thus, the value of r_m could reflect the suitability of host plant for population increase of spirea aphid. To

Table 3. Polynomial regression analysis of average daily nymphs produced on aphid age and host plant

Regression source	df	Mean square	F	P	R ²
Model	14	17.91	51.96	0.0001	0.815
Age (mean)	1	48.46	140.59	0.0001	
Mean ²	1	53.12	154.10	0.0001	
Mean ³	1	45.38	131.64	0.0001	
Mean ⁴	1	37.62	109.13	0.0001	
Host	5	6.36	18.46	0.0001	
Age × Host	5	1.91	5.55	0.0001	
Error	101	0.34			

Least square means for nymphs

Host	Least-square mean ± SE
<i>P. crispata</i>	2.3 ± 0.13a
<i>P. scutellaria</i>	1.9 ± 0.13b
<i>V. suspensum</i>	1.6 ± 0.14c
Grapefruit	1.3 ± 0.15d
Rough Lemon	1.1 ± 0.15e
Pineapple orange	0.7 ± 0.16f

Least-square means followed by the same letter are not significantly different (Fisher protected LSD, $P > 0.05$).

use r_m value most effectively, levels of confidence must be assigned to observed differences. Without variance estimates it is difficult to interpret the information (Petitt et al. 1994). The use of jackknife techniques to estimate the variance of r_m enables us to test the statistical hypothesis of r_m values. Spirea aphid population reared on *P. crispata* and *P. scutellaria* had the significantly higher r_m value (0.308 and 0.301), whereas the population reared on pineapple orange had the significantly lowest r_m value (0.177). This suggests that *P. crispata* and *P. scutellaria* were presumably the most favorable food source tested, and pineapple orange was the least suitable host for spirea aphid. Tang and Yokomi (1996) reported a higher r_m value (0.31) of spirea aphid reared on sweet viburnum than those of this study. Komazaki (1982) also reported a higher R_o value (30.7) of spirea aphid reared on *C. unshiu* than those of three citrus hosts tested in this study. Compared with other citrus aphids, the r_m values of spirea aphid were lower than those of brown citrus aphid (0.183–0.381) on eight different host plants (Tsai 1998) and of *Aphis gossypii* Glover (0.386) on greenhouse cucumbers (Kocourek et al. 1994). The net reproductive rates of spirea aphid reared on six host plants were also lower than 62.6 reported for brown citrus aphid reared on *citrus unshiu* Mark at 24.9°C (Komazaki 1982). However, the spirea aphid reared on two aralia host plants, *P.*

crispata and *P. scutellaria*, had higher R_o values (38.8 and 33.1) than 23.4 of *A. gossypii* at 24.5°C reared on *C. unshiu* (Komazaki 1982).

The spirea aphid can successfully increase population size on three citrus hosts, grapefruit, rough lemon, and pineapple orange, even though their r_m values were lower than those on the other three host plants tested (Table 4). The exact cause for the differences measured in this study remains unknown and deserves further examination. Although *P. crispata*, *P. scutellaria*, and *V. suspensum* are less economically important than citrus plants, they could play a very important role in increasing natural populations of spirea aphid in the absence of citrus shoot flushes. These plants are widely used in urban areas as landscape ornamental plants in south Florida. It was concluded that the ability of spirea aphid to feed and develop on a wide range of host plants increases its chance to infest citrus groves and thereby spreading the citrus tristeza virus.

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Table 4. Comparison of life table parameters of *A. spiraeicola* on six host plants at 25°C

Host	n	r_m	95% CI	R_o	MT	t
<i>P. crispata</i>	30	0.308a	0.303, 0.314	38.8 ± 1.29	11.9	2.25
<i>P. scutellaria</i>	39	0.301a	0.297, 0.306	33.1 ± 1.15	11.6	2.30
<i>V. suspensum</i>	38	0.257b	0.252, 0.262	25.6 ± 0.73	12.6	2.70
Grapefruit	36	0.223c	0.216, 0.229	18.7 ± 0.80	13.2	3.11
Rough Lemon	33	0.211d	0.204, 0.218	14.8 ± 0.66	12.8	3.28
Pineapple orange	41	0.177e	0.168, 0.187	9.3 ± 0.57	12.6	3.91

n, Number of females included in analysis; r_m , jackknife estimate of the intrinsic rate of increase (per capita rate of population growth); CI, interval estimate for r_m ; R_o , net reproductive rate; MT, mean generation time (in d); t, doubling time (in days) for population. Within column means with the same letters are not significantly different ($P > 0.05$).

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