# Population Parameters and Probing Behavior of Cowpea Aphid (Homoptera: Aphididae), on Preferred and Non-Preferred Host Cover Crops[1]

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**ABSTRACT** Developmental time, fecundity, nymphal mortality, generation time, intrinsic and finite rates of increase, and time for population to double were compared for cowpea aphid, *Aphis craccivora* Koch, reared on cover crop seedlings of sesbania, *Sesbania exaltata* (Rafinesque-Schmaltz) Cory; cowpea, *Vigna unguiculata* [L.] Walpers; hairy indigo, *Indigofera hirsuta* L.; hairy vetch, *Vicia villosa* Roth; crimson clover, *Trifolium incarnatum* L.; and cereal rye, *Secale cereale* L. The study was conducted under near-ambient temperatures in a greenhouse from late January to mid-April. Developmental, pre-reproductive, and generation times of *A. craccivora* were the shortest on *V. unguiculata,* followed by *S. exaltata* and *I hirsuta.* However, mean total fecundity, fecundity rate, and intrinsic and finite rates of increase were higher on *V. unguiculata* and *I. hirsuta* than on the other species. No differences in life parameters were detected when *A. craccivora* developed on the same plant species at different evaluation periods. Probing behavior of individual *A. craccivora* differed on various cover crops. Mean probe duration was longer on *V. unguiculata* and *I. hirsuta,* but time to start the first probe, number of probes per access period, and non-probing duration were shorter than on other plant species evaluated.

**KEY WORDS** Insecta, *Aphis craccivora*, cover crop, probing behavior, intrinsic rate, cowpea, sesbania, indigo, cowpea aphid.

The cowpea aphid, *Aphis craccivora* Koch, is cosmopolitan and has a host range extending to crop and noncrop species (Eastop 1966, Wightman and Amin 1988). It causes plant damage by sucking the phloem sap and by transmitting aphid-borne virus diseases (Gutierrez et al. 1971, Singh and Van Emden 1979, Macfoy and Dabrowski 1984, Atiri et al. 1984, Wightman and Amin 1988, Padgham et al. 1990).

Cover crops can be manipulated in pecan orchards to maintain a high population density of *A. craccivora* as alternate prey for generalist predators of the pecan aphid complex (Bugg et al. 1991). However, a high rate of increase of *A. craccivora* on cover crops is also essential for maintenance of dense predator populations. Maintenance of alternate hosts on cover crops for the entire summer is potentially important in maintaining natural enemies at high densities (Bugg and Dutcher 1989) and thus, for successful biological control of pecan aphids in the pecan orchard-cover crop system.

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The general objective of this study was to gain insight into variation in the rate of increase of *A. craccivora*. The two specific objectives were: (1) to compare population parameters (developmental time, reproduction, intrinsic and finite rates of increase, generation time, and time for population to double) of *A. craccivora* on certain preferred and non-preferred host cover crops, and (2) to observe the probing behavior of *A. craccivora* on the cover crops to determine if the number and duration of feeding probes are correlated with the rate of aphid increase.

## Materials and Methods

Apterous, parthenogenetic aphids used for these studies came from colonies reared on 4-6 wk-old naturally-infested cowpea plants, *Vigna unguiculata* [L.] Walp. cultivar 'Pinkeye Purple Hull', grown in the greenhouse at the University of Georgia, Coastal Plain Experiment Station, Tifton, GA. The greenhouse was equipped with a water cooling unit that maintained air temperature at near-ambient and 60 ± 10% RH. Experiments were performed over four separate time periods in 1991: 28 January-15 February, 17 February-7 March, 9-27 March, and 29 March-16 April. The mean daily temperature of the greenhouse for each time period was calculated by averaging all hourly readings of the day obtained from a Hygrothermograph Chart Model H311 (Weather Measure Corp., Sacramento, Calif.).

**Cover crops.** Six cover crop species were grown in the greenhouse from seeds planted in commercial soil mixture in plastic containers (20 cm high by 15 cm diameter). Plants were watered when the surface of the soil was dry to the touch. Sesbania, *Sesbania exaltata* [Rafinesque-Schmaltz] Cory; hairy indigo, *Indigofera hirsuta* L.; and V. *unguiculata* are warm-season cover crops and preferred host plants for *A. craccivora* (Bugg and Dutcher 1989). Hairy vetch, *Vicia villosa* Roth; crimson clover, *Trifolium incarnatum* L.; and cereal rye, *Secale cereale* L., are cool-season cover crops (non-preferred host plants for *A. craccivora*), and they sustain high densities of pea aphid, *Acyrthosiphon pisum* (Harris) and low densities of bird cherry-oat aphid, *Rhopalosiphum padi* L., and blue alfalfa aphid, *Acyrthosiphon kondoi* Shinji (Bugg et al. 1991). All the cover crops tested, except cereal rye, are legumes. Detailed descriptions of the morphology and biology of the cover crops have been presented by Duke (1981). One seedling from each cover crop was replanted in a plastic container (8.0 cm high by 4.5 cm diameter, with holes on the bottom for drainage) two days before the test was conducted. Seedlings at the beginning of the experiment were 9-11 cm tall and 3-4 wk old. Each container was placed inside a glass globe (7 cm lower diameter, 10 cm middle diameter, 5.5 cm upper diameter by 22 cm high) to prevent the escape of aphids. The top of the globe was covered with a fine mesh screen for ventilation. Six replicate blocks of containers with one container per cover crop per block were used each time period.

**Aphid Development.** One female aphid was transferred with a fine, camel's-hair brush to the upperside of a terminal leaf of each test plant and left to produce nymphs. The female and all but one nymph per individual plant were removed after 24 h. The remaining nymph was observed each day to determine the number of days taken to reach the adult stage (developmental

time) and the number of days from birth to first reproduction (pre-reproductive time). No attempt was made to determine the developmental time of instars. If a new adult female died during a period equal in duration to its pre-reproductive time, no data from that female were included in the analyses.

**Fecundity and Morality.** The number of offspring produced was recorded daily for a period equal to the pre-reproductive time. Fecundity rate (number of progeny produced per female per day) was estimated by dividing the total fecundity by the pre-reproductive time period. All nymphs (dead or live) were recorded and removed after each count.

**Intrinsic and Finite Rates of Increase.** The intrinsic rate of increase ($r_m$ = female progeny per female per day) was estimated separately for each time period, using the method of Wyatt and White (1977): $r_m = 0.74 (\log_e M_d) /d$ where d = the pre-reproductive time, $M_d$, the number of progeny produced in a time equal to the pre-reproductive time, and 0.74 is a constant. Finite rate of increase (the number of individuals added to the population per female per day) was estimated using the equation $\lambda = \text{antilog}_e r_m$ (DeLoach 1974).

**Generation Time and Population Doubling Time.** Generation time of *A. craccivora* ($T_d$) was estimated using $T_d = 4d/3$ (Wyatt and White 1977), and time for population to double (DT) was estimated using $DT = [\log_e (2)]/r_m$ (DeLoach 1974). These were estimated separately for each time period on all cover crops.

**Probing Behavior.** Leaf and stem surfaces of cover crop seedlings were examined under a binocular microscope (50×) to determine morphological differences of trichomes between plant parts. Leaves and stems, excised from greenhouse-grown cover crop seedlings, were used for observations on probing behavior of *A. craccivora*. Aphids were starved for 40-60 min before the test was conducted. One apterous, adult female was placed on the upper surface of a leaf attached to 2-3 cm of stem held by hand; this arrangement enabled the aphid to move freely between the leaf and the stem. It also allowed the plant to be rotated in all directions to facilitate microscopic viewing of the aphids. A new aphid and piece of plant tissue (leaf and stem) were used for each observation period, which were of 6 min duration. Fiber-Lite High Intensity Illuminator Model 180 (Dolan-Jenner Industries, Inc., Woburn, MA.) provided a cool light source. The following observations were recorded for each individual aphid: time for the aphid to begin the first probe, duration of each probe (defined as stylet penetrating the tissue surface with labium extended vertical to the body plane and its tip touching the stem or leaf tissue), and probing site (leaf or stem). Probes starting 20 s before the end of the timed period and lasting beyond that period were counted and recorded as 20 s in duration. Duration of non-probing was defined as including time for the aphid to begin the first probe and non-probing times between separate probes, or 360 s minus total probing duration. Fifteen aphids were observed on each plant species at room temperature of 23 ± 2°C and 50 ± 10% RH.

**Statistical Analysis.** A randomized complete-block design was used to test for significant differences in life parameters and probing responses of *A. craccivora* among cover crop seedlings. The data were analyzed separately for each time period among cover crops and among time periods within each cover crop using SAS PROC GLM (SAS Institute 1985). When $F$ values were significant ($P < 0.05$),

means were compared using least significant difference (LSD) for all aspects of this study. Data on life parameters ($X$) were transformed to square root scale of ($X + 0.5$) to stabilize variances before analysis. Means of nontransformed data are presented.

## Results

**Aphid Development.** Mean daily temperatures of the greenhouse for the four periods evaluated were 22.4°C, 21.8°C, 21.1°C, and 22.9°C. However, the temperatures inside the glass globes covering the plants were 1-2°C higher than the greenhouse temperature, depending on the time of the day. Differences in developmental and pre-reproductive times for *A. craccivora* on various cover crops were highly significant ($P < 0.05$) during all four time periods (Table 1). Aphids developed faster on cowpea, followed by sesbania and hairy indigo, than other cover crops. Developmental times ranged from 5.3-5.7 d on cowpea, 5.5-6.0 d on sesbania, 5.3-6.0 d on indigo, 7.5-7.8 d on vetch, 6.8-7.5 d on clover, and 6.3-7.0 d on rye, depending on evaluation period. Adult females took 0.8-1.2 d to reach first reproduction depending on the cover crop. Developmental and pre-reproductive times were not significantly different for the same plant species tested among time periods.

**Fecundity and Mortality.** Significant differences ($P < 0.05$) in reproductive capability of *A. craccivora* on certain plant species were observed during each time period (Table 1). Total fecundity was higher on cowpea than on other cover crops. No significant differences in total fecundity were detected when *A. craccivora* developed on the same plant species at different evaluation periods.

Fecundity rates for *A. craccivora* were significantly different ($P < 0.05$) on various cover crop plants. The fecundity rate on cowpea was significantly ($P < 0.05$) higher at all periods, except for period I, than that produced on other cover crops. The average increase of *A. craccivora* was greater on preferred than on non-preferred host plants. Differences in percentage mortality of immature stages of *A. craccivora* on selected plants were not detected among any of the evaluation periods.

**Intrinsic and Finite Rates of Increase.** Significantly different $r_m$ values ($P < 0.05$) were found for *A. craccivora* on selected cover crops at all evaluation periods (Table 1). Aphids had the lowest intrinsic rates of increase on vetch and clover, and the highest values on cowpea and hairy indigo. The $r_m$ estimates ranged from 0.374-0.394 progeny per female per day on cowpea, 0.344-0.364 on sesbania, 0.333-0.353 on indigo, 0.248-0.265 on vetch, 0.256-0.262 on clover, and 0.267-0.273 on rye. The higher $r_m$ values were generally related to shorter developmental and pre-reproductive times. No differences in $r_m$ values of *A. craccivora* were detected for the same cover crop tested among evaluation periods.

The finite rate of increase for *A. craccivora* ranged from 1.281-1.484 (Table 1), depending on the host plant and period evaluated.

**Generation Time and Population Doubling Time.** Significant differences in mean generation times of *A. craccivora* were observed on the various cover crops for each evaluation period. Because of the method of estimation of generations, differences are the same as those observed for the pre-reproductive time (Table 1). Generation times ranged from 8.4-8.8 d on cowpea, 8.8-9.3 d on

**Table 1. Developmental and reproductive characteristics of *A. craccivora* reared on cover crops under near-ambient air temperatures in a greenhouse.**

| Variable | Cover crop | | | | | | (SEM, *F*) |
|---|---|---|---|---|---|---|---|
| | cowpea | hairy indigo | sesbania | hairy vetch | crimson clover | cereal rye | |
| **28 January - 15 February, I** | | | | | | | |
| Days to reach adult stage | 5.5 c | 5.7 bc | 5.5 c | 7.7 a | 7.5 a | 6.3 b | (0.28, 12.3) |
| Pre-reproductive time, d | 6.5 c | 6.5 c | 6.5 c | 8.7 a | 8.3 a | 7.5 b | (0.27, 13.9) |
| Mean total fecundity | 26.7 a | 24.5 ab | 21.2 bc | 20.0 c | 19.5 bc | 15.8 d | (1.43, 7.19) |
| Fecundity rate | 4.1 a | 3.8 a | 3.3 b | 2.3 c | 2.3 c | 2.1 c | (0.12, 53.4) |
| Intrinsic rate of increase | 0.374 a | 0.364 ab | 0.348 b | 0.255 d | 0.262 cd | 0.273 c | (0.006, 77.3) |
| Finite rate of increase | 1.454 | 1.439 | 1.416 | 1.290 | 1.300 | 1.314 | |
| Mean generation time, d | 8.8 c | 8.8 c | 8.8 c | 11.7 a | 11.3 a | 10.2 b | (0.36, 13.9) |
| Days for population to double | 1.86 d | 1.91 cd | 2.00 c | 2.72 a | 2.65 ab | 2.55 b | (0.04, 86.9) |
| **17 January - 7 March, II** | | | | | | | |
| Days to reach adult stage | 5.3 b | 6.0 b | 5.8 b | 7.5 a | 7.5 a | 7.0 a | (0.25, 13.9) |
| Pre-reproductive time, d | 6.2 c | 6.8 b | 6.7 bc | 8.7 a | 8.2 a | 8.0 a | (0.23, 19.4) |
| Mean total fecundity | 26.5 a | 24.0 a | 19.8 b | 18.2 b | 17.2 b | 17.7 b | (1.10, 12.0) |
| Fecundity rate | 4.3 a | 3.5 b | 3.0 c | 2.1 d | 2.1 d | 2.2 d | (0.16, 33.9) |
| Intrinsic rate of increase | 0.394 a | 0.344 b | 0.333 b | 0.248 c | 0.257 c | 0.267 c | (0.010, 38.1) |
| Finite rate of increase | 1.483 | 1.411 | 1.395 | 1.281 | 1.293 | 1.306 | |
| Mean generation time, d | 8.4 c | 9.3 b | 9.0 bc | 11.7 a | 11.1 a | 10.8 a | (0.31, 19.4) |
| Days for population to double | 1.8 c | 2.0 b | 2.1 b | 2.8 a | 2.7 a | 2.6 a | (0.07, 36.0) |
| **9 - 27 March, III** | | | | | | | |
| Days to reach adult stage | 5.7 d | 6.0 cd | 5.3 d | 7.8 a | 6.8 b | 6.7 bc | (0.28, 10.9) |
| Pre-reproductive time, d | 6.3 c | 6.8 c | 6.3 c | 9.0 a | 8.0 b | 7.7 b | (0.29, 13.5) |
| Mean total fecundity | 27.7 a | 26.5 ab | 20.5 c | 23.0 bc | 16.8 d | 16.3 d | (1.35, 12.6) |
| Fecundity rate | 4.4 a | 3.9 b | 3.2 c | 2.6 d | 2.1 e | 2.1 e | (0.11, 75.3) |
| Intrinsic rate of increase | 0.389 a | 0.355 b | 0.353 b | 0.257 c | 0.259 c | 0.271 c | (0.008, 55.4) |

**Table 1. Continued.**

| Variable | Cover crop: cowpea | hairy indigo | sesbania | hairy vetch | crimson clover | cereal rye | (SEM, *F*) |
|---|---|---|---|---|---|---|---|
| | | | 9 - 27 March, III | | | | |
| Finite rate of increase | 1.476 | 1.426 | 1.423 | 1.293 | 1.296 | 1.311 | |
| Mean generation time, d | 8.6 c | 9.3 c | 8.6 c | 12.2 a | 10.8 b | 10.4 b | (0.39, 13.5) |
| Days for population to double | 1.8 c | 2.0 b | 2.0 b | 2.7 a | 2.7 a | 2.6 a | (0.06, 52.2) |
| | | | 29 March - 16 April, IV | | | | |
| Days to reach adult stage | 5.7 c | 5.5 c | 6.0 c | 7.5 a | 7.3 ab | 6.7 b | (0.22, 14.6) |
| Pre-reproductive time, d | 6.3 e | 6.7 de | 7.0 cd | 8.8 a | 8.3 ab | 7.7 bc | (0.24, 17.0) |
| Mean total fecundity | 29.0 a | 23.2 b | 21.7 b | 23.3 b | 17.8 c | 16.2 c | (1.03, 19.7) |
| Fecundity rate | 4.6 a | 3.5 b | 3.1 c | 2.6 d | 2.1 e | 2.1 e | (0.09, 99.8) |
| Intrinsic rate of increase | 0.395 a | 0.349 b | 0.327 c | 0.265 d | 0.256 d | 0.268 d | (0.008, 52.7) |
| Finite rate of increase | 1.484 | 1.417 | 1.387 | 1.303 | 1.292 | 1.300 | |
| Mean generation time, d | 8.6 e | 9.0 de | 9.5 cd | 12.0 a | 11.3 ab | 10.4 bc | (0.32, 17.0) |
| Days for population to double | 1.8 c | 2.0 b | 2.1 b | 2.6 a | 2.7 a | 2.6 a | (0.06, 49.0) |

Means within rows followed by the same letter are not significantly different ($P < 0.05$) by Fisher LSD test (SAS Institute 1985). I - IV represent four time periods when tests were conducted. $N = 6$ aphids and df = 5, 25 for each time period.

indigo, 8.6-9.5 d on sesbania, 11.7-12.2 d on vetch, 10.8-11.3 d on clover, and 10.2-10.8 d on rye. Aphid populations had the capacity to double with a range of 1.8-2.8 d on various plant species.

**Probing Behavior.** Aphids completed nymphal development on all cover crops even though the leaf and stem surface of indigo and clover were pubescent. Factors other than pubescence may contribute to aphid preference for a given plant.

Aphids moved randomly in all directions for a period of 30-60 s after placement on the upper leaf surface before starting the first probe on either the leaf or stem surfaces (Table 2). The time required for aphids to start the first probe differed significantly between plant species and was shortest on cowpea. Duration of probing was significantly longer on cowpea and hairy indigo than on other cover crops. The number of feeding probes was less and nonprobing duration was shorter on cowpea and indigo than on other plants. *A. craccivora* preferred to probe on stems of sesbania and indigo (53% of total probes), and on the lower leaf surface of other plants (60% for clover, 67% for cowpea and vetch, 100% on rye).

## Discussion

Developmental, pre-reproductive times, and total mean fecundity of *A. craccivora* for each evaluation period obtained in this study are similar to those reported previously on cowpea (Macfoy and Dabrowski 1984, Ansari and van Emden 1989), broad bean (Mansour et al. 1982), groundnut (Padgham et al. 1990), and pasture legumes (Gutierrez et al. 1971). Fecundity varies among aphid species and even between individuals within the same species (Kennedy and Stroyan 1959). Feeding by aphids on host or nonhost plants may result in different fecundity rates (McLean and Kinsey 1968). Aphids usually have shorter developmental periods and higher reproductive rates on susceptible host plants than on resistant hosts (Kindler and Staples 1969, Kennedy and Kishaba 1976, Mansour et al. 1982, Macfoy and Dabrowski 1984).

The $r_m$ estimates on cowpea were higher than those on other plant species. Rates of increase of *A. craccivora* were the lowest on vetch and clover; due in part to the prolonged developmental time. Differences in $r_m$ values were caused primarily by differences in patterns of fecundity. The $r_m$ values presented in this study are within the range of $r_m$ estimates reported at constant temperatures for *A. craccivora* on legumes (Gutierrez et al. 1971) and cowpea (Givovich et al. 1988), and for other aphid species (Messenger 1964, Frazer 1972, DeLoach 1974, Barlow et al. 1977, Wyatt and Brown 1977).

Our observations of probing response of *A. craccivora* on different cover crops are also within the range reported by others. The mean number of probes and duration per *A. craccivora* per access period was reported on mature leaves of bean, *Phaseolus vulgais* L.; crotalaria, *Crotalaria spectabilis* Roth; and citrus leaves, *Citrus sinensis* (L.) Osbeck (Zettler et al. 1969). Differences in probing behavior of *A. craccivora* on cowpea seedlings have been reported (Atiri et al. 1984, Macfoy and Dabrowski 1984, Givovich et al. 1988) with shorter feeding probes on stems of resistant than susceptible cultivars and the duration of nonfeeding was longer on resistant than susceptible seedlings.

**Table 2. Probing behavior of *A. craccivora* on cover crops.**

| Plant Species | Time to start first probe, s | Mean probe duration, s | No probes per access period | Total duration of non-probing, s |
|---|---|---|---|---|
| Cowpea | 29.3 d | 110.9 a | 2.3 c | 111.8 c |
| Hairy indigo | 32.6 cd | 116.1 a | 2.1 c | 115.0 c |
| Sesbania | 42.0 b | 90.0 b | 2.5 bc | 137.1 bc |
| Hairy vetch | 36.0 c | 63.0 d | 2.8 b | 180.7 a |
| Crimson clover | 51.0 a | 81.0 c | 2.5 bc | 154.9 ab |
| Cereal rye | 41.0 b | 57.0 d | 3.5 a | 161.0 ab |
| SEM | 1.27 | 2.31 | 0.17 | 11.7 |
| *F* | 37.2 | 110.3 | 8.63 | 5.41 |

Means within columns followed by the same letter are not significantly different ($P < 0.01$, df = 5, 84) by Fisher LSD test (SAS Institute 1985). $N = 15$ aphids and df = 5, 84 for each cover crop. SEM = standard error of least square nontransformed means.

A number of factors, some of which were controlled in this study, may contribute to the variation in the population growth rate of *A. craccivora* on cover crops in the pecan orchard. Daylength, light intensity, and soil fertility were similar for all time periods. Population level within an aphid species and reproductive type (sexual or asexual) were controlled by isolating of individual asexual adult females on the seedling inside the globe. The globe also protected aphids from attack by natural enemies. The extent of aphid population increase probably would be less in the field than in the greenhouse because of their exposure to natural enemies, heavy rain, and other extrinsic factors.

Other factors were not controlled in this study. Effects of variations in relative humidity were likely of little importance because aphids were feeding on living leaf tissues. Temperature fluctuations may directly affect the aphid's developmental time, fecundity, and survival (Messenger 1964, Mansour et al. 1982, Padgham et al. 1990), all of which influence the $r_m$ values. Temperatures in this study were near ambient, so the results should not be atypical.

Age and the nutritional value of the host plant can affect aphid numbers (Kennedy and Booth 1951, van Emden and Bashford 1971). Chemical composition and biochemical changes of the plant influence the relationship between plants and aphids (Hsiao 1969). Volatile chemicals emitted by the foliage of the plant, the presence of internal repellents and feeding deterrents, or the lack of suitable probing and feeding stimuli may be factors affecting the development and reproduction of aphids (Mansour et al. 1982).

The results suggest that differences exist among cover crops in suitability for growth and reproduction of *A. craccivora*. Reliable estimates of the aphid density on cover crops in the field are needed to understand factors affecting the rates of increase in the field. Looking at all population parameters, it appears that cowpea and hairy indigo are more superior hosts of *A. craccivora* compared with other cover crops, and these plants deserve attention as pecan orchard cover crops. The ability of these plants to fix nitrogen also makes these cover crops well suited for use in pecan orchards.

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