RESISTANCE TO *APHIS CRACCIVORA* (HOMOPTERA:APHIDIDAE) IN SELECTED VARIETIES OF COWPEA

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(Accepted for publication July 3, 1985)

ABSTRACT

Nearly 200 varieties of cowpea, *Vigna unguiculata* (L.) Walp, were screened for resistance to the cowpea aphid, *Aphis craccivora* Koch. Three varieties known to be resistant in West Africa were highly susceptible to an aphid population from the southern United States. Four other varieties, however, inhibited growth of the southern United States population both in the laboratory and in the field. Life-table comparisons using a resistant and a susceptible variety revealed a three-fold difference in the intrinsic rate of increase and a more than twenty-fold difference in the net reproductive rate. High nymphal mortality and low fecundity on resistant plants were largely responsible for these differences.

Key Words: *Aphis craccivora*, cowpeas, host-plant resistance, life-table, *Vigna unguiculata*.

J. Entomol. Sci. 20(2): 263-269 (April 1985)

INTRODUCTION

Cowpea, *Vigna unguiculata* (L.) Walp, is a major grain legume in many developing countries, and is grown as a vegetable in the southern United States. The cowpea aphid, *Aphis craccivora* Koch, has recently become an important pest of cowpeas in the Sahelian zone of west Africa (Singh 1980). Aphids attack primarily the seedling and podding stages and transmit cowpea aphid-borne mosaic virus (Atiri et al. 1984). Efforts to control *A. craccivora* have centered on the development of resistant cowpea cultivars (MacFoy and Dabrowski 1984). As a preliminary step to determining the mechanism of plant resistance, we conducted screening trials and population studies to identify resistant varieties.

Several lines of cowpeas resistant to *A. craccivora* have been developed at the International Institute of Tropical Agriculture in Ibadan, Nigeria (IITA 1984). We examined the generality of this resistance by exposing certain lines to an aphid population collected on cowpeas in south Georgia. We also evaluated nearly 200 additional lines that were preselected for possible resistance to aphids. Where resistance was found, life-table analysis was used to determine which demographic traits were most responsible for reduced population growth.

MATERIALS AND METHODS

A laboratory population of *A. craccivora* was established in mid-November 1983 from aphids collected on cowpea pods near Tifton, Georgia. We maintained the aphid colony and conducted all indoor experiments in a laboratory at 28 ± 2°C (light) and 23 ± 2°C (dark) with a 16-h photophase provided by fluorescent lights. Relative humidity was 35 - 50% (light) and 55 - 70% (dark). The colony was

provided fresh cowpea seedlings of the "California black-eye" variety every two or three days.

Cowpea lines from two sources were used in the experiments. Three resistant varieties (Tvu 3000, IT81D-1007, and IT81D-1020) and two susceptible ones (Vita 6 and Vita 7) were obtained from IITA. Tvu 3000 is a prime original source of resistance used in plant breeding programs, whereas IT81D-1007 and IT81D-1020 are high-yielding advanced lines that are also resistant to bruchids (IITA 1984). One hundred and ninety-three varieties preselected for possible resistance to aphids were supplied by the Regional Plant Introduction Station in Experiment, Georgia (a complete list of PI numbers is available on request). Plants used in laboratory experiments were grown in a greenhouse at ca. 28°C (light) and 23°C (dark) with a 16-h photophase provided by supplemental lighting. Plants were grown singly in 25-cm diameter pots containing Cornell Mix A soil.

Preliminary screening for resistance was accomplished by placing five, 6-day-old, apterous *A. craccivora* females onto cowpea seedlings that had one fully expanded trifoliate and one partially developed trifoliate. Each seedling was covered with a cellulose acetate cylinder (43 cm tall, 17 cm diameter) that had cloth-covered openings to allow adequate ventilation. Growth of aphid populations on two to five plants of a test variety was scored visually (as low, moderate, or high) after seven days and compared with populations on the black-eye variety. Of the 193 varieties screened in this manner, four appeared sufficiently resistant to warrant further testing. These varieties along with those developed at IITA were used in the following population experiments.

Varietal resistance was measured in the laboratory by comparing population growth on the test variety with population growth on Vita 6 or Vita 7. (An earlier experiment confirmed that there was no difference in the susceptibility of the latter two varieties.) Each of 10 plants per variety received a single 6-day-old apterous female. Plants again had one fully expanded trifoliate and one partially developed trifoliate and were covered with the cylindrical cages. After six days the plants were bagged and frozen. We later counted the number of nymphs, apterae and alatae per plant.

Two field experiments were conducted in 1984 to determine whether the level of resistance seen in the laboratory would persist when plants were grown outdoors. The first experiment compared aphid performance on Vita 6, Tvu 3000 and IT81D-1020. Seeds were germinated in the greenhouse, and on June 27, the newly germinated seedlings (12 per variety) were transferred to a field plot in Ithaca, NY, where they were replanted in three rows, with 1-m spacing between and within rows. The three varieties were completely interspersed in a systematic arrangement (ABC, BCA, CAB, etc.). On July 12, by which time the plants had produced two expanded trifoliates, two 6-day-old apterous females were added to each plant. Plants were covered with organdy cloth-covered cages ($40 \times 25 \times 25$ cm). Plants and aphids were bagged and frozen on July 20. A second similar experiment compared aphid performance on six varieties. Newly germinated seedlings (10 per variety) were transferred to the field on August 3. The varieties were interspersed in a randomized complete block design (6 plants per block), again with 1-m spacing between and within rows. Three 6-day-old apterous females were added to each plant on August 16, when the plants bore one expanded trifoliate. Plants and aphids were bagged and frozen on August 29.

Two varieties, Vita 7 and PI 367860, were used in a life-table study. A single 6-day-old female was added to each of 21 seedlings (one expanded trifoliate) of Vita 7 and 25 seedlings of PI 367860. After 4 h, by which time each female had produced one to three nymphs, females and excess nymphs were removed so as to leave a single 0 to 4 h-old nymph per plant. For each nymph we recorded daily survivorship, time to reach adulthood and age at first reproduction. As the new adult females began to reproduce, we counted and removed the second-generation nymphs daily. From the survivorship (l_x) and age-specific fecundity (m_x) data we calculated the intrinsic rate of increase (r_m), the net reproductive rate (R_o) and the mean generation time (T) using standard formulae (Birch 1948).

RESULTS AND DISCUSSION

The design and short duration of our laboratory experiments provided a conservative estimate of differences in resistance to aphids among varieties. Each 6-day-old founding female had been reared on a high-quality host (California black-eye variety) and had already begun to reproduce before transfer to test varieties (under our conditions, age at first reproduction is usually five days on a good host). When the experiment was terminated six days after the females were introduced, aphid populations typically consisted of many nymphs plus small numbers of apterae (Table 1). Nymphal populations thus included progeny of the original female plus second-generation nymphs from apterae that had just begun to reproduce. Production of alatae was rare on all varieties; mean densities ranged from 0 to 1.1 per plant.

The three varieties resistant to *A. craccivora* in West Africa, Tvu 3000, IT81D-1007, and IT81D-1020, were as suitable for aphid population growth as were the two susceptible varieties, Vita 6 and Vita 7 (Table 1). Comparison of means after ANOVA (Tukey-Kramer test, Sokal and Rohlf 1981) indicated that the mean population size on Tvu 3000 in Expt. 6 was not significantly different from that on Vita 7 ($P > 0.10$). In contrast, the four Plant Introduction varieties, PI205139, 339572, 339596 and 367860, all supported significantly fewer nymphs and apterae, with total populations one-fourth to one-half as large as those on the susceptible control (Table 1).

Field experiments were performed to validate the laboratory results. The duration of these experiments (8 days in Expt. 1 and 13 days in Expt. 2) again led to the mingling of at least two generations of nymphs. Because of the greater heterogeneity of the field data, a non-parametric analysis of variance, the Kruskal-Wallis test, was used (Sokal and Rohlf 1981). No differences in population growth were found among the three IITA varieties tested in Expt. 1 (Table 2). In Expt. 2 there was a nearly six-fold difference in the total number of aphids on the most and least resistant varieties, PI 367860 and Vita 7, respectively. These two varieties were therefore chosen for the life-table study described below. Population sizes on the other four varieties in Expt. 2 were also in accord with predictions based on the laboratory experiments, i.e., Tvu 3000 was susceptible while PI 205139, 339572 and 339596 were resistant (Table 2). Only densities of alatae did not vary significantly among varieties, but these were relatively low and highly variable among plants within a variety. For none of the varieties was the ratio of apterae to alatae correlated with the total number of aphids per plant, i.e., with the level of crowding ($P > 0.10$). Nor was there any effect of host variety on

Table 1. Growth of *A. craccivora* populations on cowpea for 6 days in the laboratory. Each of 10 plants initially received a single 6-day-old apterous female.

Expt.	Cowpea variety	No. ($\bar{x} \pm$ SE) aphids/plant		
		Nymphs	Apterae	Total*
1	Vita 6	63.3 ± 6.2	8.1 ± 1.0	71.4 ± 6.7
	IT81D-1007	75.6 ± 10.4	7.6 ± 1.2	83.2 ± 11.5
	P (ANOVA)	> 0.10	> 0.10	> 0.10
2	Vita 6	95.6 ± 12.6	11.6 ± 1.6	107.2 ± 17.2
	IT81D-1020	110.2 ± 11.0	12.7 ± 0.9	122.9 ± 11.7
	P	> 0.10	> 0.10	> 0.10
3†	Vita 7	94.1 ± 14.5	8.8 ± 1.6	103.9 ± 15.9
	PI 205139	34.6 ± 5.1	3.4 ± 1.1	38.2 ± 6.1
	P	< 0.001	< 0.01	< 0.001
4	Vita 7	115.8 ± 12.3	11.0 ± 1.2	127.9 ± 13.1
	PI 367860	29.2 ± 3.2	4.2 ± 0.9	33.4 ± 6.1
	P	< 0.001	< 0.001	< 0.001
5	Vita 7	146.2 ± 16.5	15.9 ± 1.5	162.1 ± 17.6
	PI 339596	71.0 ± 7.8	8.9 ± 1.5	79.9 ± 9.0
	P	< 0.001	< 0.01	< 0.001
6	Vita 7	99.4 ± 19.4	12.8 ± 1.8	112.2 ± 21.1
	Tvu 3000	71.9 ± 7.6	9.0 ± 0.9	81.0 ± 6.2
	PI 339572	28.8 ± 4.5	3.0 ± 0.8	31.8 ± 5.1
	P	< 0.01	< 0.001	< 0.001

* Includes small numbers of alatae.
† No. plants = 12.

Table 2. Growth of *A. craccivora* populations on cowpea in the field. Each of 10 plants initially received 2 (Expt. 1) or 3 (Expt. 2) apterous 6-day-old females.

Expt.	Cowpea variety	No. ($\bar{x} \pm$ SE) aphids/plant		
		Nymphs	Apterae	Alatae
1	Vita 6*	190.0 ± 50.5	14.7 ± 3.7	0
	Tvu 3000	225.5 ± 49.8	19.5 ± 4.9	0.3 ± 0.2
	IT81D-1020†	187.2 ± 36.9	21.8 ± 6.2	0.1 ± 0.1
	P‡	> 0.10	> 0.10	> 0.10
2	Vita 7	1131.6 ± 234.8	59.4 ± 12.5	8.3 ± 2.6
	Tvu 3000	948.0 ± 169.4	33.8 ± 7.6	16.4 ± 6.9
	PI 205139	280.5 ± 59.3	14.6 ± 2.9	5.3 ± 1.9
	PI 367860	198.0 ± 40.8	13.5 ± 3.6	3.1 ± 1.0
	PI 339572	299.7 ± 44.9	14.1 ± 2.1	7.3 ± 1.9
	PI 339596	329.5 ± 62.3	15.0 ± 3.5	5.6 ± 2.5
	P‡	< 0.001	< 0.001	> 0.10

* No. plants = 12.
† No. plants = 11.
‡ Kruskal-Wallis test.

morph ratios; the mean percentage of adults that were alate ranged from 10 on Vita 7 to 30 on Tvu 3000 ($P = 0.50$, ANOVA after arcsine-transformation of percentages). A high proportion of alatae might have been expected on the resistant varieties, since low food quality stimulates alate production in *A. craccivora* (Johnson 1966).

The life-table study provided a more accurate estimate of varietal differences in resistance because there was no contribution to population growth by a founding female transferred from a high-quality host. As explained below, virtually all aspects of aphid performance were adversely affected when aphids were restricted to feeding on PI 367860. The population reared on Vita 7 consequently exhibited a much greater intrinsic rate of increase (r_m) and net reproductive rate (R_o) (Table 3). The generation time (T), which indicates the mean period of time elapsing between the birth of a female and the birth of her offspring, was actually longer on Vita 7, but this was caused by the sharply abbreviated period of reproduction on PI 367860 (Fig. 1). Only 9 of 25 nymphs reached adulthood on PI 367860, whereas no nymphal mortality occurred on Vita 7. All adults were apterous. Nymphs also took longer to develop into adults on PI 367860, which led to a higher age at first reproduction (Table 3). Females that were able to reproduce on PI 367860 had a lower daily output of progeny plus a short life expectancy (Fig. 1). Thus even when only successful reproducers are considered, there was a nearly ten-fold difference in mean lifetime fecundity on Vita 7 and PI 367860 (96.8 ± 6.9 vs. 12.5 ± 3.3, $P < 0.001$, Mann-Whitney U-test). Note that nearly a third of the females on Vita 7 were still alive at the end of the experiment. Because they were post-reproductive, however, these females no longer contributed to the above life-table statistics.

Table 3. Life-table statistics for cohorts of *A. craccivora* developing on Vita 7 (n = 21) or PI 367860 (n = 25).

	Cowpea variety				
Statistic*	Vita 7	N	PI 367860	N	P†
r_m (days^{-1})	0.576	–	0.198	–	–
R_o	96.62	–	4.00	–	–
T	9.92	–	7.17	–	–
Development time ($\bar{x} \pm$ SE in days)	5.00 ± 0.00	21	5.89 ± 0.26	9	< 0.01
Age 1st reproduction ($\bar{x} \pm$ SE in days)	5.19 ± 0.09	21	6.50 ± 0.46	8	< 0.01

* r_m, intrinsic rate of increase; R_o, net reproductive rate; T, mean generation time in days.
† Mann Whitney U-test.

The lack of resistance in the IITA varieties could be explained by geographic variation in the aphid populations (i.e., biotype differences), variation in plant growing conditions, or both. Of greater interest is the resistance found in the four PI varieties, which suppressed aphid populations under the fairly different conditions of the laboratory and field. At present there is little reason to suppose that the mechanism of resistance is similar in all four varieties, or that the demographic results using PI 367860 apply to the other three varieties. Two of the resistant varieties originated in southern Africa (PI 339572 from Botswana, 339596 from

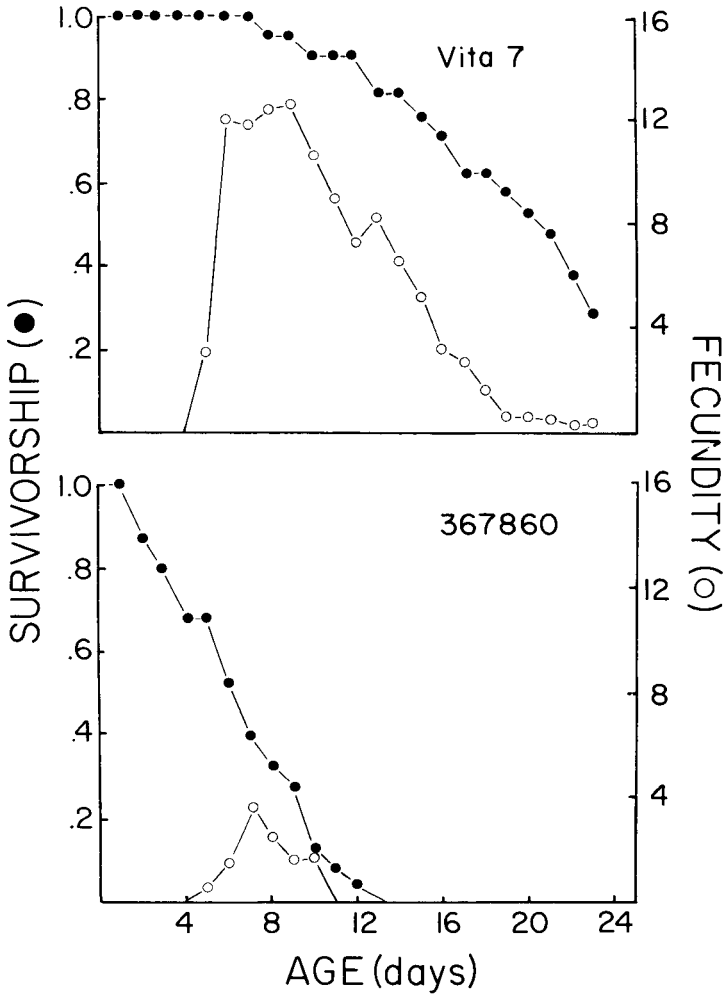

Fig. 1. Survivorship (l_x) and age-specific fecundity (m_x) of cohorts of *A. craccivora* developing on Vita 7 (n = 21) or PI 367860 (n = 25).

South Africa), and two were introduced from India. PI 205139 is the only variety of the 193 tested to be classified in the subspecies *cylindrica* (L.) Verdcourt, which is a fodder and seed type from India (Wien and Summerfield 1984). This variety is thus genetically distinct from the others, which all belong to the subspecies *unguiculata*.

Our experiments did not permit distinction between antibiosis and non-preference as the principal mechanism of resistance in PI 367860. Antibiosis seems most likely, however, because of the detrimental effects on fecundity. Although aphids were observed feeding most of the time on PI 367860, they appeared to change feeding sites more frequently compared to aphids on Vita 7. On a few occasions,

adults were seen wandering over the PI 367860 plants. MacFoy and Dabrowski (1984) noted that compared to cowpea aphid females on susceptible plants, females on two resistant varieties probed more frequently and fed for shorter intervals. They further suggested that concentrations of phenols and flavonoids (but not those of sugars and amino acids) were correlated with level of resistance. Elucidation of chemical differences among resistant and susceptible lines used in this study would be useful.

ACKNOWLEDGMENTS

We thank R. B. Chalfant for collecting the aphids, and G. R. Lovell for supplying cowpea varieties. Research was supported in part by grant AID/DSAN/XII/0216 Bean/Cowpea CRSP-Cameroon to the University of Georgia.

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