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Influence of okra (*Abelmoschus* spp.) accessions on colonization by *Aphis gossypii* (Hemiptera: Aphididae) and their effects on aphid biological parameters

Albert Fomumbod Abang^{1,2,3,*}, Ramasamy Srinivasan¹, Sévilor Kekeunou², Rachid Hanna³, Regine Kamga⁴, and Charles-Felix Bilong Bilong²

Abstract

Aphis gossypii Glover (Hemiptera: Aphididae) is one of the major pests of okra. Damage severity and high levels of infestation have led to widespread use of chemical insecticides. Okra is ranked fourth in Cameroon among vegetable crops on which chemical insecticides are applied. The objectives of this study were to evaluate resistant okra accessions identified in previous studies, to identify their categories of resistance, and to assess their effects on the non-preference, development, and reproduction of *A. gossypii*. Results showed that VI041210 was resistant to aphid infestation during the first season, and VI057245 and Gombo caféier were resistant during the second season. Kirikou and VI060794 had the highest yields during the first season, although Kirikou was moderately susceptible to aphid infestation. VI041210 was susceptible to aphid infestation during the second season but produced the highest yield. These results indicate that tolerance occurred in some of the accessions. Aphids did not discriminate between resistant and susceptible accessions, indicating that antixenosis (non-preference) was not a category of resistance found in these accessions. VI041210, VI057245, and Gombo caféier were the most resistant due to lower infestation levels, probably due to their antibiotic properties. Considering constitutive resistance, aphid development was poor, with the longest molting and generation time ($T_0 = 15.9$) on VI057245 at the vegetative plant growth stage, leading to poor reproduction (lowest intrinsic and finite rates of natural increases: 0.25 and 1.3 aphids, respectively). Considering induced resistance, observed only in VI041210, nymphal development time was longest (14.2 d) leading to one of the lowest net reproductive rates at the vegetative and reproductive plant growth stages, 27.1 and 27.8, respectively. Thus, tolerance and antibiosis were categories of resistance found in these accessions, but antixenosis was not documented.

Key Words: Host plant resistance; antibiosis; antixenosis; tolerance to aphids; development of *Aphis gossypii*; reproductive performance of *Aphis gossypii*

Resumen

Aphis gossypii Glover (Hemiptera: Aphididae) es una de las principales plagas de okra. La severidad de los daños y los altos niveles de infestación han llevado al uso generalizado de insecticidas químicos. La okra ocupa el cuarto lugar en Camerún entre los cultivos de hortalizas en los que se aplican insecticidas químicos. Los objetivos de este estudio fueron evaluar las muestras resistentes de okra identificadas en estudios anteriores, identificar sus categorías de resistencia y evaluar sus efectos sobre la no preferencia, el desarrollo y la reproducción de *A. gossypii*. Los resultados mostraron que VI041210 fue resistente a la infestación de áfidos durante la primera temporada y VI057245 y Gombo caféier fueron resistentes durante la segunda temporada. Kirikou y VI060794 tuvieron los rendimientos más altos durante la primera temporada, aunque Kirikou fue moderadamente susceptible a la infestación de áfidos. VI041210 fue susceptible a la infestación de áfidos durante la segunda temporada, pero produjo el rendimiento más alto. Estos resultados indican que se produjo tolerancia en algunas de las muestras. Los áfidos no discriminaron entre muestras resistentes y susceptibles, lo que indica que la antixenosis (no preferencia) no era una categoría de resistencia encontrada en estas muestras. VI041210, VI057245 y Gombo caféier fueron los más resistentes debido a niveles de infestación más bajos, probablemente debido a sus propiedades antibióticas. Considerando la resistencia constitutiva, el desarrollo de áfidos fue pobre, con el tiempo de muda y generación más largo ($T_0 = 15.9$) en VI057245 durante la etapa de crecimiento vegetativo de la planta, lo que resultó en una reproducción baja (tasas intrínsecas y finitas naturales más bajas: 0.25 y 1.3 áfidos respectivamente). Considerando la resistencia inducida, observada solo en VI041210, el tiempo de desarrollo de la ninfa fue mayor (14.2 días) y resultó en

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una de las tasas reproductivas netas más bajas en las etapas de crecimiento vegetativo y reproductivo de la plantas, 27.1 y 27.8, respectivamente. Por lo tanto, la tolerancia y la antibiosis fueron categorías de resistencia encontradas en estas muestras, pero la antixenosis no fue documentada.

Palabras Clave: Planta anfitriona resistencia; antibiosis; antixenosis; tolerancia a los áfidos; desarrollo de *Aphis gossypii*; desempeño reproductivo de *Aphis gossypii*

Okra (*Abelmoschus* spp.; Malvaceae) is cultivated mainly for immature pods, which are consumed fresh or dried, and are added to soup, depending on where it is cultivated. The pods contribute viscous fibers to the diet (Kendall & Jenkins 2004) and the viscosity eases consumption of food (Schippers 2000). Okra's mucilage serves as a plasma replacement or blood volume expander, and can reduce cholesterol levels (Markose & Peter 1990; Benchasri 2012). The mucilage also can be used to glaze paper. Roasted seeds are added to coffee or as a coffee substitute (Markose & Peter 1990). Increasing okra production can diversify vegetable production and improve diets (Hughes 2009).

World production of okra is estimated at 8.69 million tons (metric tons) annually at a yield of 7,868 tons per ha. Africa produces 1.84 million tons annually, with a yield of 3,606 tons per ha. Production in Cameroon stands at 72,661 tons per year with a yield of 3,027 tons per ha, below the average yields in both Africa and the world (FAO-STAT 2015). Mohammad and Tasveer (2008) identified a range of factors that negatively affect okra productivity, among which are insect pests. In Cameroon, *Aphis gossypii* Glover (Hemiptera: Aphididae) is one of the major pests of okra, and occupies the top position among pests of vegetables (Kekeunou et al. 2006; Abang et al. 2014a). *Aphis gossypii* damages either directly by feeding, which results in curling and deformation of young leaves and twigs, or indirectly by contaminating the fruits and leaves with honeydew. Honeydew may allow the growth of black sooty mold, which inhibits photosynthesis, and reduces yield (Jacobson & Croft 1998; Andrews et al. 2004; Capinera 2005). Heavily infested okra plants show distorted and stunted leaves and also reduced fruit set (Wanja et al. 2001). Yield losses can be up to 57% (Shannag et al. 2007) when aphid infestation is higher (> 1,000 aphids per plant) (Mohamed-Ahmed 2000; Nderitu et al. 2008) or 100% (Doumbia & Seif 2008) if the attack is at the seedling stage. The severity of aphid infestation has led to widespread use of chemical pesticides for control. Pests including aphids are becoming resistant to pesticides and *A. gossypii* has developed resistance to carbamates, organophosphates, pyrethroids, and neonicotinoids (Denholm et al. 2002; Wang et al. 2002; Andrew et al. 2006; Tabacian et al. 2011).

Seventy-eight percent of vegetable farmers continue to produce traditional varieties that are susceptible to pests in Cameroon (Abang et al. 2014a). Host-plant resistance has long been established as the hub of a sustainable pest management system (Panda & Khush 1995; Wiseman 1999), and it has potential to reduce insecticide use and reduce economic and environmental costs in okra production systems (Wiseman 1999). Some reports have confirmed the availability of aphid-resistant okra genotypes (Sumathi 2005; Anitha & Nandihalli 2009). However, most of these reports were based on a few local genotypes, and could explain why sources of aphid-resistant okra varieties are still limited (Dogimont et al. 2010). World Veg's GenBank, the world's largest public vegetable germplasm collection, conserves more than 900 accessions of *Abelmoschus* spp. that need to be exploited. In addition, none of the earlier studies involving local genotypes had elucidated the mechanisms of resistance. The mechanisms have long been categorized into 3 types: antixenosis, antibiosis, and tolerance (Painter 1951). The term "mechanisms" of resistance was replaced by Kogan & Ortman (1978) with the term "categories" of resistance. Horber (1980) called the 3 "functional categories," whereas Smith (1989) termed them "functional modalities

of resistance." Studies in such areas have been conducted for other pest species attacking okra and for *A. gossypii* on other crops (Garzo et al. 2004; Hesler & Dashiell 2011; Satar et al. 2012; Moghadam et al. 2013; Mota et al. 2013). Smith (2005) reported that 2 or more mechanisms may be evident within the same host variety or plant, and in some cases, it may be difficult to differentiate between antibiosis and antixenosis as they both adversely affect arthropod populations. In several cases, the reduction in the aphid biotic potential (antibiosis) results from a modification of the aphid feeding behavior (antixenosis). However, this difficulty can be resolved by conducting separate experiments to detect antibiosis by no-choice tests and antixenosis via choice tests (Horber 1980; Webster & Inayatullah 1988; Webster 1991). In several studies, variation in the levels of antibiosis and antixenosis to aphids in resistant varieties has been documented (Schotzko & Bosque-Perez 2000; Lage et al. 2003; Jyoti & Michaud 2005). These variations need to be studied in more detail because based on present knowledge, host incompatibility may be a common phenomenon in *A. gossypii*.

The use of tolerant or resistant varieties is meaningful because they are compatible with other control methods with minimal or no adverse side effects on the environment. Even with the importance of *A. gossypii* as an agricultural pest, information on relationships between aphids and available okra varieties has not been sufficiently studied. Yet knowledge of the ways by which varieties may influence pest biology and behaviors is desirable to appraise the impact of the pest and to create methods to mitigate its effects on yield.

Materials and Methods

CONFIRMATORY FIELD SCREENING

Nine okra accessions were selected as aphid-resistant from World Veg's GenBank and evaluated in a confirmatory screening trial in Cameroon. These accessions were selected as resistant in 3 separate advanced screening trials on arrival of each set of accessions from World Veg Taiwan (Abang et al. 2014b). Three (VI051114, VI036213, and VI033805) out of 19 accessions were selected in the first trial during Mar to Jun 2012, 1 (VI033824) out of 15 accessions in the second trial from Oct 2012 to Mar 2013, and 5 (VI060818, VI060794, VI060688, VI041210, and VI039614) out of 7 accessions in the third trial from Mar to Jul 2013 (Abang et al. 2014b). One farmer's variety (Kirikou) and 1 commercial variety (Gombo caféier) from Cameroon were included as local checks. Accession VI057245 was included because it was initially identified as a susceptible check in Taiwan in 2012 (Abang et al. 2014b). Seeds of Gombo caféier were purchased from a seed store, whereas Kirikou seeds were obtained from local farmers.

The trial was conducted at the World Veg station in Nkolbisson, Yaoundé, Cameroon, during 2 seasons (Mar to Jul 2014 and Sep to Dec 2014) in a randomized complete block design with 3 replicates. Nkolbisson has an agroecology characterized by a warm, humid forest with bimodal rainfall. The rainfall pattern showed 2 peaks during the yr of study (Fig. 1) with 2 dry mo during the experimental period; Jul during the first season and Dec during the second (Precipitation < 2Temperature) (Fig. 1). The trials were maintained using customary cultural practices without pesticide application to control aphids or other insects.

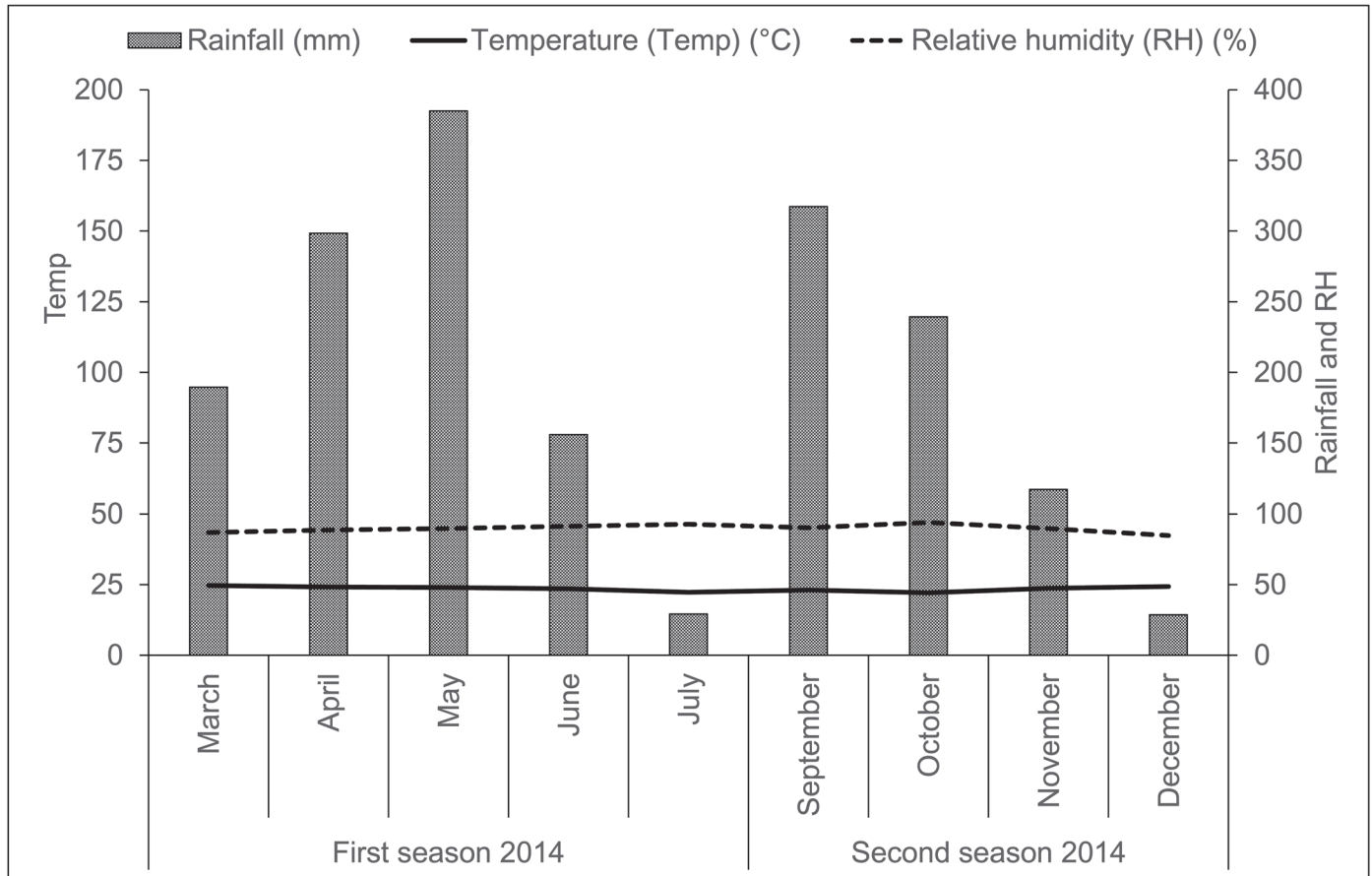


Fig. 1. Pattern of climatic factors for the bimodal warm, humid forest of Yaoundé.

Hibiscus plants were planted around the screening plot to increase pest pressure, and a row of okra plants of each accession was sown around the borders of each accession plot, and were exempted from sampling to minimize the border effects. The trials were exposed to the natural infestation of aphids, and the aphid population was directly scored at weekly intervals, starting from 4 wk after sowing in the field. Five plants of each accession were randomly selected, and on each plant 3 leaves were randomly selected, 1 each from the bottom, middle, and top strata of each plant, to record the number of aphids and other insects present. Aphids were scored using the following rating scale: 0 = no aphids present; 1 = 1 to 10 aphids per leaf; 2 = 11 to 100 aphids per leaf; 3 = 101 to 1,000 aphids per leaf; and 4 = > 1,000 aphids per leaf.

TOLERANCE

The yield performance was evaluated by recording the number of pods per plant (daily harvest). The plant parameter recorded for vigor was leaf area (average of 5 plants estimated at the seedling, vegetative, and reproductive stages) estimated by measuring with a ruler and multiplying the maximum values of leaf width by leaf length according to Mack et al. (2017).

ANTIXENOSIS

The plants for studies of antibiosis were sown in plastic trays, and 1 plant was transplanted at the first true leaf stage in plastic pots (25 cm ht × 20 cm diam) containing substrate made of 50% dark top soil from the region + 25% sand + 25% fowl manure. Aphids used for the study were harvested from a neighboring okra field at the International

Institute of Tropical Agriculture, and a pure colony of *A. gossypii* was maintained on okra variety Gombo paysan for 2 wk.

For no-choice conditions, 2 potted plants per accession were placed individually using a completely randomized design in 2 rows spaced at 1 m between rows and within rows. The experiment was replicated 3 times. Because the screenhouses were small and each could not accommodate all 3 replicates, 3 screen houses were used with each representing a replicate. The settling behavior or antixenosis of aphids on different okra accessions was determined by assessing aphid permanence for feeding and oviposition on the plants. The second fully expanded leaf from the apex of okra plants at 2 wk after transplant was infested with 10 adult apterous aphids previously starved for 2 h. After 72 h, all aphids were counted to evaluate their permanence on the infested leaf.

Under choice conditions, the test was conducted according to Moghadam et al. (2013). The bottom of a Petri dish (145 mm diam) was covered with moist cotton wool and the surface of the cotton covered with 125 mm Whatman No. 1 filter paper. At the edge of the paper, leaf-pieces (2 × 1 cm) from the second fully expanded leaf of each accession at 2 wk after transplant were placed alternately. Then, 100 adult aphids after 2 h starvation were placed at the center of each Petri dish, equidistant from each leaf piece. The dishes were then transferred to a growth chamber at 25 ± 1 °C, 70 ± 10% RH, and 12:12 h (L:D) photoperiod. Five Petri dishes (replicates) were used with 2 leaf pieces of each okra accession used per replicate (24 leaf pieces per Petri dish). The number of aphids located on each leaf piece was counted after 48 h to determine the relative preference among the 12 accessions tested.

ANTIBIOSIS

Plants were sown and aphids harvested, reared, and prepared in a manner similar to that described for studies on antixenosis. The experiment using plants at the vegetative growth stage started 2 wk after transplant, whereas the experiment with plants at the reproductive growth stage started at 10 wk after transplant. The potted plants were placed individually in mesh cages (1 m height, 50 cm length, and 50 cm width) and the mesh cages were then placed in a screen house. Each plant was inoculated with 5 adult aphids on the second fully expanded leaf from the top of plants at 2 wk after transplant to give birth. Twenty-four hours later, all adults and nymphs, except 1 nymph, were removed per plant and monitored for life traits. The method was a modified version of the Harris (1980) cohort test. These modifications include leaving the leaves attached to the plants and observing only 1 aphid nymph because mechanical injury due to the use of excised leaves might induce changes in plant chemistry (Cipollini 1997).

To investigate whether the effect of antibiosis is systemic or localized to the aphid feeding zone, other potted plants were prepared in a similar manner but were previously infested with 25 to 35 aphids per plant at the vegetative growth stage (2 wk after transplant), and 100 to 200 aphids per plant at the reproductive stage (10 wk after transplant). The aphids were then removed from the plant 5 d later by spraying a soap solution (3.55 mL of liquid detergent in 1 L water) onto the okra leaves. The plants were rinsed with water and used for the experiment 24 h later. The plants of the 2 experiments (plants previously infested and plants not previously infested) were arranged in a completely randomized design, with 10 plants per accession replicated 3 times (3 screen houses). Greenhouse temperatures and relative humidity fluctuated in a daily cycle between 21.3 to 28 °C and 79.1 to 100%, respectively, during the first experiment with plants not previously inoculated, and 22.2 to 29 °C and 68.6 to 89.5%, respectively, during the second experiment with plants previously inoculated with aphids.

The presence of exuviae was used to determine molting time and number of instars; the nymphs were observed daily for molting. Evaluation of oviposition started after the fourth molt, and neonates were removed after counting. The following attributes of development and reproduction were studied: development time, nymphal mortality, molting, instar development, reproductive time, and duration of the life (biological) cycle. Other parameters of reproduction were obtained by conducting age-specific fertility life tables. To construct the age-specific fertility life table, age specific survival rate (l_x) and average aphid progeny in x age class (m_x) were obtained. Based on these data, the intrinsic rate of natural increase (r_m), was calculated by iteratively solving the equation (Birch 1948):

$$\sum l_x m_x e^{r_m x} = 1$$

Where x is the age of the aphid in days, r_m is the intrinsic rate of natural increase, l_x is the age-specific survival, and m_x is the age-specific number of female offspring. Other parameters computed were the net reproductive rate ($R_0 = \sum l_x m_x$), generation time ($T_0 = (\ln R_0) / r_m$), population doubling time ($(\ln 2) / r_m$), and the finite rate of increase ($\lambda = e^{r_m}$) (Carey 1993).

STATISTICAL ANALYSIS

The scored data for aphids from the screening experiment were expressed as the area under infestation pressure curve (AUIPC), calculated using the following formula modified from Shaner & Finney (1977):

$$\sum_{i=1}^{n-1} \frac{(y_i + y_{i+1})(t_{i+1} - t_i)}{2}$$

Where n = number of assessment times, and Y = number of insects at time t .

The AUIPC (N) values for aphid population per leaf were subjected to a statistical analysis based on mean (m) and standard deviation (SD) (AVRDC 1979) as follows:

$N < (m-2SD)$ = Highly Resistant (HR), $(m-2SD) < N < (m-SD)$ = Resistant (R), $(m-SD) < N < (m)$ = Moderately Resistant (MR), $(m) < N < (m+SD)$ = Moderately Susceptible (MS), $(m+SD) < N < (m+2SD)$ = Susceptible (S), $N > (m+2SD)$ = Highly Susceptible (HS).

Yield and plant data from the screening trial and values of the development and reproductive performance of *A. gossypii* were subjected to analysis of variance (ANOVA) with the Proc GLM procedure of SAS, version 9.1 (SAS Institute, Cary, North Carolina, USA). The antixenosis and settling behavior of aphids were analyzed using the Kruskal-Wallis test. Tukey's test was used to separate the means at the 5% significance level of probability.

Results

RESISTANCE STATUS

The farmers' check Kirikou was more susceptible than 8 accessions in the first season and 11 accessions in the second season. Also, VI051114 and VI060818 were susceptible during the first season and VI060794 during the second season. Only VI041210 was resistant during the first season, while 2 accessions (VI057245 and Gombo caféier) were resistant during the second season. Seven accessions were moderately resistant during the first season and 3 during the second season (Table 1).

TOLERANCE

Significant differences occurred in yield among the accessions. In the first season, the farmers' variety Kirikou and 1 of the selected accessions (VI060794) had the highest yields ($F = 8.74$; $df = 11,24$; $P < 0.0001$). Second season yields were generally low; however, VI041210 produced significantly more pods per plant than all other accessions (Table 1; $F = 6.59$; $df = 11,23$; $P < 0.0001$). Accessions also significantly differed in leaf area ($F = 3.20$; $df = 11,24$; $P = 0.008$) during the first season only, with Gombo caféier having the largest leaf area (Table 1). Largest mean leaf area ($P = 0.096$) and pod weight ($P \geq 0.05$) did not statistically differ among accessions in the second season. However, numerically, VI051210 had the largest mean leaf area in the second season, and VI051114 had the greatest pod weight during both seasons.

ANTIXENOSIS

Studies on settling behavior showed that aphids did not discriminate 48 h after release when provided choices between susceptible and resistant okra accessions. There were no significant differences among the accessions for non-preference in the choice test ($\chi^2 = 3.94$; $df = 11,24$; $P = 0.97$) (Table 2). In the no-choice test, no significant differences were found among accessions in terms of aphid retention on leaves ($\chi^2 = 6.30$; $df = 11,24$; $P = 0.85$) (Table 2).

ANTIBIOSIS

Antibiosis with Uninfested Plants

Development of Aphis gossypii at vegetative and reproductive stages of plants previously uninfested. At the vegetative stage of the plants

Table 1. Yield parameters and ratings^a for resistance of okra (*Abelmoschus* spp.) accessions to control *Aphis gossypii* during 2 cropping seasons.

Species	Accession	AUIPC ^b (N)		Yield (Pods/plant) ^c		Leaf area (cm ²) ^c		Pod weight (g)	
		First	Second	First	Second	First	Second	First	Second
<i>Abelmoschus esculentus</i>	VI041210	39.8 R	59.8 MS	1.6 c	7.7 a	254 ab	266.7	9.70	9.4
<i>Abelmoschus esculentus</i>	VI060688	47.5 MR	57.9 MR	7.8 bc	0.6 b	199 abc	59.1	15.8	5.8
<i>Abelmoschus caillei</i>	Gombo caféier	49.2 MR	50.6 R	11.5 b	1.8 b	282 a	110.8	13.2	6.7
<i>Abelmoschus esculentus</i>	VI036213	49.6 MR	57.7 MR	4.2 bc	0.9 b	185 bc	116.8	13.1	5.6
<i>Abelmoschus esculentus</i>	VI033824	49.7 MR	63.8 MS	7.2 bc	1.9 b	179 bc	70.1	18.6	6.5
<i>Abelmoschus caillei</i>	VI060794	50.1 MR	66.5 S	20.5 a	2.1 b	157 c	232.0	14.4	6.9
<i>Abelmoschus esculentus</i>	VI039614	50.9 MR	60.4 MS	9.6 b	1.0 b	139 c	49.0	10.4	3.8
<i>Abelmoschus esculentus</i>	VI057245	52.9 MR	49.7 R	6.6 bc	0.2 b	142 c	30.4	14.6	3.5
<i>Abelmoschus esculentus</i>	Kirikou	55.4 MS	68.0 S	23.7 a	1.5 b	222 abc	108.6	17.5	9.4
<i>Abelmoschus esculentus</i>	VI033805	56.8 MS	62.2 MS	4.1 bc	0.2 b	256 ab	109.2	17.9	6.7
<i>Abelmoschus esculentus</i>	VI051114	68.3 S	59.8 MS	4.0 bc	0.5 b	161 c	62.6	18.8	14.0
<i>Abelmoschus esculentus</i>	VI060818	66.4 S	54.8 MR	10.7 b	0.9 b	196 abc	65.5	17.8	9.8
	Mean	53.0	59.3						
	SD	7.91	5.6						
	<i>P</i> value				< 0.0001	0.008	0.096	0.226	0.055
	<i>F</i> value				6.59	3.2	1.88	1.43	2.39
	Treatment and error df				11,23	11,24	11,23	11,24	11,16

^aResistance status: susceptible (S), moderately susceptible (MS), moderately resistant (MR), resistant (R).

^bAUIPC = area under infestation pressure curve, a measure of population size.

^cMeans with the same letter(s) in a column are not significantly different at $P < 0.05$.

Table 2. Settling behavior due to antixenosis of *Aphis gossypii* on okra accessions.

Accession	Choice test (aphids per leaf)	No-choice test (aphids per plant)
VI051114	4.4	22.2
VI036213	4.2	44.4
VI033805	3.7	55.6
VI057245	5.6	22.2
VI060794	3.7	55.6
VI039614	3.1	55.6
VI041210	4.0	33.3
VI033824	4.5	33.3
VI060688	3.3	22.2
VI060818	2.4	33.3
Gombo caféier	3.3	33.3
Kirikou	3.2	33.3
<i>P</i> value	0.97	0.85
χ^2	3.94	6.30

that were not previously infested with aphids, differences among accessions were not significant during the first and second selections, except for development time (nymphal period) ($F = 4.56$; $df = 5,12$; $P = 0.015$) (Table 3). Accession VI033805, one of the most susceptible accessions, had a significantly shorter nymphal period at 2 wk after transplant.

In the third selection significant differences among accessions were found in the number of molts per aphid at 2 wk after transplant ($F = 3.38$; $df = 7,16$; $P = 0.02$) and at 10 wk after transplant ($F = 5.08$; $df = 7,16$; $P = 0.003$); duration per molt at 2 wk after transplant ($F = 2.96$; $df = 7,16$; $P = 0.03$) and at 10 wk after transplant ($F = 7.28$; $df = 7,16$; $P = 0.0005$); and generation time (T_g) only at 2 wk after transplant ($F = 3.27$; $df = 7,16$; $P = 0.02$). Two of the 3 most resistant accessions (VI057245 and VI041210) had the fewest molts (2.7 at 2 wk after transplant and 2.4 at 10 wk after transplant, respectively). The number of molts was 4.3 and 4.1 at 2 wk after transplant and 10 wk after transplant, respec-

tively, with VI060818, one of the most susceptible accessions. The duration per molt and generation time were also longest with VI057245 and shortest with susceptible Kirikou at 2 wk after transplant. Accession VI060818 and Kirikou, which were among the susceptible accessions, had the shortest duration per molt compared to Gombo caféier, one of the most resistant ones (Table 3).

Reproduction of Aphis gossypii during vegetative and reproductive stage of plants previously uninfested. In the first and second selections, all reproductive attributes except net reproduction rate showed significant differences among accessions at 2 wk after transplant (Table 4). However, resistant and susceptible accessions did not statistically differ. Accession VI033824 had significantly higher reproductive time ($F = 4.13$; $df = 5,12$; $P = 0.021$), population doubling time ($F = 3.2$; $df = 5,12$; $P = 0.046$), lower finite rate of increase ($F = 3.4$; $df = 5,12$; $P = 0.038$), intrinsic rate of natural increase ($F = 4.19$; $df = 5,12$; $P = 0.019$), and longer life cycle ($F = 4.67$; $df = 5,12$; $P = 0.013$). At 10 wk after transplant, there were no significant differences among accessions.

The third selection results showed significant differences among accessions in intrinsic rate of increase ($F = 3.72$; $df = 5,12$; $P = 0.014$) at 2 wk after transplant, ($F = 2.83$; $df = 5,12$; $P = 0.04$) at 10 wk after transplant; finite rate of increase ($F = 3.46$; $df = 5,12$; $P = 0.019$) at 2 weeks after transplant, ($F = 2.81$; $df = 5,12$; $P = 0.041$) at 10 wk after transplant; net reproductive rate ($F = 4.3$; $df = 5,12$; $P = 0.007$), and population doubling time ($F = 4.12$; $df = 5,12$; $P = 0.009$) at 10 wk after transplant (Table 4). Resistant VI057245 had the lowest intrinsic rate of increase and finite rate of increase, and longest population doubling time compared to the susceptible Kirikou, all at 2 wk after transplant (Table 4). At 10 wk after transplant there were also significant differences among accessions in net reproduction rate, and the intrinsic and finite rates of natural increases, but no significance among the susceptible and resistant accessions.

Antibiosis on Previously Infested Plants

Development of Aphis gossypii during vegetative and reproductive stage of plants previously infested. For plants previously infested with

Table 3. Development of *Aphis gossypii* at vegetative and reproductive stages of okra plants that were previously uninfested.

Selection	Accession and resistance status	Nymphal mortality (%)		Number of molts		Nymphal period (d)		Duration per molt (d)		T ₀	
		2WAT	10WAT	2WAT	10WAT	2WAT	10WAT	2WAT	10WAT	2WAT	10WAT
1st and 2nd selection	Gombo caféier ^{MR,R}	11.1	0.00	3.8	2.7	6.3 ab	9.3	1.7	4.1	6.3	7.3
	VI036213 ^{MR,MR}	0.0	0.00	3.6	2.9	6.3 ab	6.5	1.8	2.5	3.0	11.5
	VI033824 ^{MR,MS}	0.0	11.1	3.2	2.3	6.5 ab	6.7	2.1	3.0	9.9	7.4
	VI033805 ^{MS,MS}	0.0	16.7	3.5	3.0	5.7 c	6.3	1.6	2.2	7.6	6.9
	VI051114 ^{S,MS}	0.0	08.3	3.9	2.3	6.1 bc	6.0	1.6	2.7	7.5	8.4
	Kirikou ^{MS,S}	0.0	16.7	4.0	3.0	6.8 a	6.7	1.8	2.4	7.8	8.4
	F _{5,12} value	1.00	0.46	0.66	0.3	4.56	1.4	1.16	1.1	2.59	0.93
	P value	0.46	0.8	0.66	0.9	0.015	0.29	0.38	0.41	0.08	0.50
3rd selection	Gombo caféier ^{MR,R}	0.00	6.7	3.4 ab	3.0 ab	8.0	7.4	2.4 abcd	2.5 ab	8.3 b	9.5
	VI057245 ^{MR,R}	19.4	0.0	2.7 b	3.5 ab	8.8	7.2	3.2 a	2.0 bc	15.9 a	6.4
	VI041210 ^{R,MS}	41.7	0.0	4.0 ab	2.4 b	8.1	5.6	2.0 bcd	2.4 abc	7.8 b	6.4
	VI060688 ^{MR,MR}	0.00	0.0	3.0 ab	3.8 a	8.3	7.4	3.0 ab	2.0 bc	9.3 ab	7.8
	VI039614 ^{MR,MS}	11.1	0.0	3.2 ab	3.3 ab	8.8	7.8	2.8 abc	2.4 abc	9.9 ab	5.9
	VI060794 ^{MR,S}	11.1	0.0	3.3 ab	2.8 ab	8.8	7.8	2.7 abcd	2.8 a	9.0 ab	6.6
	VI060818 ^{S,MR}	16.7	5.6	4.3 a	4.1 a	7.0	7.2	1.6 d	1.8 c	9.6 ab	8.7
	Kirikou ^{MS,S}	28.3	0.0	3.9 ab	3.9 a	6.8	7.6	1.8 cd	1.9 bc	6.7 b	5.6
	F _{7,16} value	1.68	0.86	3.38	5.08	0.75	2.08	2.96	7.28	3.27	1.86
	P value	0.18	0.56	0.02	0.003	0.63	0.11	0.03	0.0005	0.02	0.14

Means with the same letter(s) in a column are not significantly different at $P < 0.05$.

Resistance status: susceptible (S); moderately susceptible (MS); moderately resistant (MR); resistant (R); WAT (weeks after transplant).

aphids, significant differences were found among accessions in development time ($F = 5.55$; $df = 11,24$; $P = 0.0002$) and mortality of nymphs ($F = 2.44$; $df = 11,24$; $P = 0.033$) at 2 wk after transplant, and in generation time ($F = 3.18$; $df = 11,24$; $P = 0.009$) at 10 wk after transplant. However, there were no significant differences between susceptible and resistant accessions in these parameters except the development

time (nymphal period) that was significantly the longer on one of the resistant accessions (VI041210) (Table 5).

Reproduction of Aphis gossypii at vegetative stage of plants previously infested with aphids. During the vegetative stage of the plants previously infested with aphids, the differences among accessions were not significant for all *A. gossypii* reproduction parameters (Table

Table 4. Reproduction of *Aphis gossypii* at vegetative and reproductive stages of okra plants that were previously uninfested.

Selection	Accession and resistance status	Reproductive time (RT)		Net reproductive rate (R ₀)		Intrinsic rate of natural increase (r)		Finite rate of increase (λ)		Population doubling time (DT)		Life cycle	
		2WAT	10WAT	2WAT	10WAT	2WAT	10WAT	2WAT	10WAT	2WAT	10WAT	2WAT	10WAT
1st and 2nd selection	Gombo caféier ^{MR,R}	12.3 ab	13.5	43.4	16.7	0.6 ab	0.4	1.9 ab	1.5	1.2 ab	2.0	18.7 ac	22.8
	VI036213 ^{MR,MR}	5.9 b	21.7	21.8	47.4	1.1 a	0.4	3.0 a	1.4	0.7 b	2.1	12.2 c	28.2
	VI033824 ^{MR,MS}	20.0 a	15.1	78.6	44.0	0.4 b	0.5	1.5 b	1.7	1.6 a	1.4	26.5 a	21.8
	VI033805 ^{MS,MS}	13.3 ab	13.7	40.8	49.9	0.5 b	0.6	1.7 ab	1.8	1.4 ab	1.3	19.0 bc	20.0
	VI051114 ^{S,MS}	16.3 ab	17.1	55.4	43.5	0.6 ab	0.5	1.8 ab	1.6	1.3 ab	1.6	22.4 ab	23.1
	Kirikou ^{MS,S}	15.7 ab	15.5	50.6	36.0	0.5 b	0.4	1.7 ab	1.5	1.4 ab	1.6	22.5 ab	22.8
	F _{5,12} value	4.13	1.22	1.38	2.34	4.19	2.0	3.4	2.03	3.20	1.52	4.67	1.33
	P value	0.021	0.36	0.30	0.11	0.019	0.15	0.038	0.15	0.046	0.26	0.013	0.32
3rd selection	Gombo caféier ^{MR,R}	19.0	20.7	40.0	56.9 a	0.46 ab	0.4 ab	1.6 ab	1.5 abc	1.6 b	1.7	26.9	28.0
	VI057245 ^{MR,R}	25.4	13.7	44.0	22.0 b	0.25 b	0.5 ab	1.3 b	1.6 abc	2.9 a	1.5	34.3	20.9
	VI041210 ^{R,MS}	16.7	14.8	40.4	31.7 ab	0.47 ab	0.5 a	1.6 ab	1.7 ab	1.5 b	1.3	24.8	20.4
	VI060688 ^{MR,MR}	16.8	15.7	25.9	21.0 b	0.37 ab	0.4 ab	1.5 ab	1.5 bc	2.0 ab	1.8	25.2	23.0
	VI039614 ^{MR,MS}	20.3	11.4	34.0	23.4 b	0.34 ab	0.5 a	1.4 ab	1.7 ab	2.1 ab	1.4	29.2	19.2
	VI060794 ^{MR,S}	18.2	12.6	37.3	38.7 ab	0.36 ab	0.6 a	1.4 ab	1.8 a	2.0 ab	1.3	27.0	20.4
	VI060818 ^{S,MR}	23.0	17.4	48.7	22.5 b	0.39 ab	0.35 b	1.5 ab	1.4 c	1.7 ab	2.1	30.0	24.6
	Kirikou ^{MS,S}	12.3	12.7	36.1	20.1 b	0.54 a	0.5 a	1.7 a	1.7 ab	1.3 b	1.3	10.1	20.3
	F _{5,12} value	1.54	1.77	0.43	4.3	3.72	2.83	3.46	2.81	4.12	2.32	1.71	1.71
	P value	0.23	0.16	0.87	0.007	0.014	0.040	0.019	0.041	0.009	0.077	0.18	0.18

Means with the same letter(s) in a column are not significantly different at $P < 0.05$.

Resistance status: susceptible (S); moderately susceptible (MS); moderately resistant (MR); resistant (R). WAT (weeks after transplant).

Table 5. Development of *Aphis gossypii* at vegetative and reproductive stages of okra plants that were previously infested.

Accession and resistance status	Nymphal mortality (%)		Number of molts		Nymphal period (d)		Duration per molt (d)		T ₀	
	2WAT	10WAT	2WAT	10WAT	2WAT	10WAT	2WAT	10WAT	2WAT	10WAT
Gombo caféier ^{MR, R}	6.7 c	6.7	3.5	2.8	8.4 b	7.1	2.5	2.6	10.3	11.2 ab
VI057245 ^{MR, R}	5.6 c	0.0	2.7	2.1	6.5 b	6.8	2.4	3.4	9.2	8.8 ab
VI041210 ^{R, MS}	11.1 abc	27.8	2.8	1.8	14.2 a	6.0	5.1	3.6	8.2	10.7 ab
VI036213 ^{MR, MR}	18.9 abc	13.3	3.5	2.9	8.1 b	5.9	2.4	2.1	8.7	9.1 ab
VI060688 ^{MR, MR}	11.1 abc	0.0	4.0	2.5	10.7 ab	6.8	2.7	2.7	7.3	7.4 ab
VI033824 ^{MR, MS}	0.0 c	11.1	2.6	2.3	7.3 b	7.7	3.1	3.5	13.6	5.2 b
VI039614 ^{MR, MS}	16.7 abc	0.0	2.8	2.6	8.2 b	8.2	3.1	3.3	6.8	7.4 ab
VI060794 ^{MR, S}	36.1 a	0.0	3.1	3.2	9.2 b	6.4	4.4	2.0	9.8	11.7 ab
VI033805 ^{MS, MS}	0.0 c	4.8	3.2	2.8	6.3 b	8.4	2.2	3.1	9.9	14.7 a
VI060818 ^{S, MR}	33.3 ab	11.1	3.7	3.3	8.5 b	6.7	2.5	2.1	8.7	5.8 b
VI051114 ^{S, MS}	8.3b c	8.3	2.8	3.0	7.9 b	7.0	2.8	2.4	13.0	8.3 ab
Kirikou ^{MS, S}	0.0 c	11.1	3.7	2.9	8.9 b	7.6	2.5	3.1	11.1	11.4 ab
F _{11,24} value	2.44	1.02	0.84	0.98	5.55	1.59	1.15	1.53	1.24	3.18
P value	0.033	0.46	0.60	0.49	0.0002	0.17	0.368	0.19	0.32	0.009

Means with the same letter(s) in a column are not significantly different at $P < 0.05$.

Resistance status: susceptible (S); moderately susceptible (MS); moderately resistant (MR); resistant (R).
WAT (weeks after transplant).

6). In contrast, at 10 wk after transplant of plants previously infested with aphids, all parameters showed significant differences among accessions (Table 6). No significant differences were found between resistant and susceptible accessions except in the case of the net reproductive rate ($F = 3.35$; $df = 11,24$; $P = 0.0065$) for VI033805. The reproductive time of 26.1 d ($F = 2.75$; $df = 11,24$; $P = 0.018$) and life cycle of 34.5 d ($F = 3.25$; $df = 11,24$; $P = 0.008$) were also longer with VI033805 (Table 6).

Discussion

The farmers' check Kirikou was generally more susceptible to aphid infestation than all accessions except VI051114, confirming that *A. gossypii* is an important pest of okra in farmers' fields in Cameroon. Four

of the selected accessions were susceptible in the first season, and 7 in the second season. The first season was a normal cropping season with much rainfall, whereas the second season was from Sep to Dec. Because high rainfall is an important mortality factor of *A. gossypii* in the field (McDonald et al. 2003; Rhinds & Messing 2005), it is possible that more aphids were washed off or destroyed by rains during the first season. This was evident from relatively lower number of aphids in the first season. The second season yields generally were low because it was not the main cropping season. In addition, sowing was done in Sep when the rainfall usually is highest, which affected the plant stand and growth during the seedling stage, suggesting that proper timing for planting is needed. However, VI041210, which produced the lowest yield during the first season, even with well-developed plant parameters, produced the highest yield during the second season. This accession was severely attacked by soft rot disease, *Choanephora*

Table 6. Reproduction of *Aphis gossypii* at vegetative and reproductive stages of okra plants that were previously infested.

Accession and resistance status	Reproductive time (RT)		Net reproductive rate (R ₀)		Intrinsic rate of natural increase (r)		Finite rate of increase (λ)		Population doubling time (DT)		Life cycle	
	2WAT	10WAT	2WAT	10WAT	2WAT	10WAT	2WAT	10WAT	2WAT	10WAT	2WAT	10WAT
Gombo caféier ^{MR, R}	17.6	17.7 ab	59.2	44.3 ab	0.4	0.3 b	1.5	1.4 b	1.8	2.1 ab	25.9	24.7 ab
VI057245 ^{MR, R}	19.1	16.6 ab	50.7	45.1 ab	0.4	0.4 ab	1.5	1.6 ab	1.6	1.6 ab	25.5	23.4 ab
VI041210 ^{R, MS}	17.0	16.5 ab	27.1	27.8 b	0.4	0.3 b	1.5	1.4 b	1.8	2.3 a	31.2	22.5 ab
VI036213 ^{MR, MR}	17.9	14.2 ab	43.5	47.3 ab	0.4	0.4 ab	1.5	1.5 ab	1.6	1.7 ab	26.0	20.1 b
VI060688 ^{MR, MR}	14.2	11.0 b	20.4	19.7 b	0.4	0.4 ab	1.5	1.5 ab	1.7	1.8 ab	24.8	17.9 b
VI033824 ^{MR, MS}	22.2	11.0 b	49.3	28.1 b	0.3	0.6 a	1.3	1.9 a	2.4	1.1 b	29.5	18.7 b
VI039614 ^{MR, MS}	14.2	13.4 ab	24.7	20.5 b	0.4	0.4 ab	1.6	1.5 ab	1.6	1.7 ab	22.3	21.6 ab
VI060794 ^{MR, S}	16.7	19.3 ab	46.6	43.8 ab	0.4	0.3 b	1.5	1.4 b	1.9	2.2 a	25.9	25.8 ab
VI033805 ^{MS, MS}	19.3	26.1 a	47.3	82.1 a	0.4	0.3 b	1.5	1.4 b	1.9	2.3 a	25.7	34.5 a
VI060818 ^{S, MR}	19.3	10.2 b	36.2	14.2 b	0.4	0.6 ab	1.6	1.6 ab	1.7	1.6 ab	27.8	16.8 b
Kirikou ^{MS, S}	24.1	15.6 ab	51.8	30.8 b	0.3	0.4 ab	1.4	1.6 ab	2.3	1.7 ab	32.0	22.6 ab
VI041210 ^{R, MS}	23.3	16.8 ab	44.1	33.5 ab	0.3	0.3 b	1.4	1.4 b	2.1	2.3 a	32.3	23.3 ab
F _{11,24} value	0.90	2.75	1.16	3.35	0.84	3.82	0.79	3.83	1.03	3.49	0.76	3.25
P value	0.552	0.018	0.366	0.0065	0.607	0.0029	0.65	0.0029	0.451	0.0051	0.673	0.008

Means with the same letter(s) in a column are not significantly different at $P < 0.05$.

Resistance status: susceptible (S); moderately susceptible (MS); moderately resistant (MR); resistant (R).
WAT (weeks after transplant).

cucurbitarum (Berk. & Ravenel) Thaxt. (Choanephoraceae), and lost most of its flower buds during the first season, suggesting that it is not adapted to the warm, humid climate of the first season in the bimodal warm, humid forest agroecological part of Cameroon. Although rainfall usually is high in Sep, which is the beginning of the second cropping season in this agroecological zone, generally there is less rain through the season, which enables the VI041210 to express its yield potentials under very limited and erratic rainfall (Siemonsma 1982). As previously demonstrated (Siemonsma & Hamon 2004; Siemonsma & Kouamé 2004), the growth and development of okra can be affected by season. The current study also supported that okra yield varied with seasons.

Apart from the effect of season, the higher aphid populations in the second season contributed in a reduction of yield during that season (Wanja et al. 2001). But within seasons, aphid infestation seemed not to have affected the yield of the susceptible okra accessions because the farmers' variety Kirikou was the most tolerant. It produced the highest yield during the first season when it was moderately susceptible. This suggests that tolerance is a category of resistance of okra against aphids (Painter 1951; Kogan & Ortman 1978). Resistance through tolerance may be achieved through higher plant vigor, because vigorous plants not only harbor more pests but also compensate for insect feeding damage, consequently ensuring good crop yields, and thereby augmenting the crop's tolerance (Chabi-Olaye et al. 2005). The increased leaf area that could harbor huge aphid populations may have contributed to the susceptibility status. Kirikou has a large leaf area, which accommodated more aphids. Large leaf size could be responsible for the moderate susceptibility of VI041210 and the susceptibility of VI060794 during that second season. In addition to VI041210, VI057245, and Gombo caféier, which were most resistant, VI060794 displayed resistance because it was not susceptible during the first season, and it was the second most productive; in the second season it was classified as susceptible but was the second most productive. This could justify the moderate resistance and good yield of VI060794. Gombo caféier, which was also resistant, was the third most productive accession. Gombo caféier and VI060794 were the only *Abelmoschus caillei* (A. Chev.) J.M.C. Stevels (Malvaceae) among the accessions. *Abelmoschus caillei* has gradually replaced *Ab. esculentus* in the tropical-humid regions because of its better adaptation under humid conditions, and tolerance to biotic stresses (Siemonsma 1982). They are vegetatively well-developed, bearing numerous, large leaves, producing larger plants, and they easily survive dry conditions (Siemonsma & Hamon 2004).

Non-preference or antixenosis was not a resistance mechanism displayed by *A. gossypii* when presented with accessions of okra. No reports exist for aphid antixenosis in okra, but reports show aphid antixenosis in cotton (the same botanical family as okra), the primary host of *A. gossypii*, resulting from activation of the natural plant defense elicitor cis-jasmone (Hegde et al. 2012), "Vat" and "Agr" genes (Garzo et al. 2004), and by the presence of leaf pubescence (Moghadam et al. 2013). Although some plants have been reported to cause antixenosis (Kianmatee & Ranamukhaarachchi 2007), the settling behavior study revealed that *A. gossypii* did not discriminate among accessions under choice or no choice conditions. Thus, the existence of aphid antibiosis in okra is yet to be documented. Sarria et al. (2010) likewise did not find aphid antixenosis in cotton; aphids were attracted to settle on all accessions, but the ability to feed and oviposit (Shereen 2007), and to develop and reproduce varied among the accessions. Smith (2005) reported that at times it may be difficult to differentiate between antibiosis and antixenosis as they both adversely affect arthropod populations, and antibiosis

may result from antixenosis. This was not the case in this study, because we conducted both choice and no choice tests to distinguish between antibiosis and antixenosis, as recommended by Horber (1980), Webster (1991), and Webster & Inayatullah (1988).

For 2 of the resistant accessions (VI057245 and Gombo caféier), the ability of okra to resist aphids always seemed present in the plant (constitutive resistance), whereas resistance in VI041210 was induced in response to pest attack and damage (Khatab 2007; Wilson et al. 2011). The antibiotic properties of these 3 accessions led to the fewest aphid molts at 2 wk after transplant in VI057245, and 10 wk after transplant in VI041210. The duration per molt and generation time also were longest with VI057245 at 2 wk after transplant, and longer duration per molt with Gombo caféier at 10 wk after transplant. However, it was only with VI057245 that poor nymphal development led to poor reproduction by aphids, because at 2 wk after transplant, VI057245 had the lowest intrinsic rate of increase and finite rate of increase, and the longest population doubling time. These mechanisms of resistance were constitutive, but those of Gombo caféier remain unidentified. Resistance in VI041210 was induced because when plants were previously infested, the developmental time was the longest on this accession at 2 wk after transplant. However, the effect of this slow development could lead only to poor reproduction of aphids when the plants were 10 wk after transplant, when the net reproductive rate was lower. These variations in the levels of antibiosis in resistant varieties to aphids have been reported by Schotzko & Bosque-Perez (2000) and Lage et al. (2003). Prior infestation induced resistance to aphids in VI041210; thus, secondary infestation is irrelevant in this accession. Primary infestation is irrelevant in VI057245 and Gombo caféier as they display constitutive resistance.

Overall, the farmers' check Kirikou was one of the okra accessions that was most susceptible to aphid infestation, but also was one of the most productive accessions, showing how important it is to consider host plant yields while identifying resistance of okra germplasm. In addition to the high levels of resistance in VI041210, VI057245, and Gombo caféier, VI060794 could be mentioned because it was productive and moderately resistant. Two categories of resistance, tolerance and antibiosis, were evident in VI041210 in addition to induced resistance, whereas VI057245 and Gombo caféier displayed antibiosis and their resistance was largely constitutive.

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