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Research Article

Promising Parental Cowpea Genotypes With Resistance to Aphid (*Aphis craccivora* Koch) Biotypes in Uganda

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Cowpea aphids remain a major production constraint affecting productivity on smallholder farms in Uganda. This study aimed to identify cowpea genotypes with resistance to aphid biotypes in Uganda for developing improved cowpea varieties. Forty-eight cowpea genotypes were initially screened using aphids collected at Makerere University Agricultural Research Institute Kabanyolo (MUARIK), and 10 tolerant genotypes were further screened using three aphid biotypes collected from the three experimental stations, namely, MUARIK, NgettaZARDI, and NaSARRI, representing the major cowpea production regions. All experiments were laid out in a completely randomized design (CRD) with three replications in the screen house at MUARIK under free-choice conditions in the screen house at MUARIK (25°C–28°C, 65%–80% relative humidity) and a natural 12:12 h light–dark regime. Significant differences were observed among the cowpea genotypes for aphid infestation and damage (aphid counts, colony scores, and leaf damage) and growth response (days to 50% flowering). There were no significant differences in the response of genotypes to aphids collected from the three locations representing Uganda's diverse agroecologies. Sanzi, TVNu 1158 (wild relative), and NE 51 showed high levels of resistance to the aphid biotypes and can be used as parents for developing aphid-resistant cowpea varieties in Uganda. However, genotype Tvu 310, the resistant check from IITA, was found to be susceptible, while IT97K-556-6 was moderately resistant to aphid biotypes from Uganda. The results from this study provide an understanding of resistance to aphid biotypes, and resistant cowpea genotypes can be used as a source for resistance to aphids in Uganda.

Keywords: aphids; biotypes; resistant varieties

1. Introduction

Cowpea (*Vigna unguiculata* L. Walp.) (Fabaceae) is a vital legume crop cultivated by many subsistence smallholder farmers in sub-Saharan Africa, Asia, and South America [1]. Cowpea is consumed both as a vegetable and grain and serves as an inexpensive source of protein in the diet. The protein content in cowpea varieties ranges between 17% and 32% on a dry-weight basis [2]. Besides its protein content, cowpea provides excellent fodder and can be used as green manure, as it can improve the soil through nitrogen fixation [3]. Cowpea is the fourth most important food legume crop in Uganda, after common beans (*Phaseolus vulgaris* L.), groundnuts (*Arachis hypogea* L.), and soybeans (*Glycine max*), and it is the main legume crop in the drier parts of Uganda that lie in the northern and eastern parts of the country [4].

Despite the importance of cowpea, its productivity in sub-Saharan Africa is very low, at less than 600 kg/ha under smallholder farmer fields compared with a potential grain yield of over 2000 kg/ha [5]. This is partly due to the use of unimproved varieties, limited use of inputs, and poor agronomic practices during crop production. Furthermore, cowpea production is constrained by many biotic and abiotic factors, including low soil fertility and a wide range of factors, such as insects, diseases, and parasitic weeds. Insect pests are the most important yield-reducing biotic factors [6]. Cowpea aphids (*Aphis craccivora* Koch) are one of the most important pests of cowpea and many other crop species worldwide that causes significant losses directly through feeding on plants and indirectly as a viral vector, reduces the leafy quality for consumption, grain yield, and quality [5]. Aphids can cause significant economic damage indirectly through transmission and spread of at least 14 disease-causing viruses in legumes, such as cowpea aphid-borne mosaic virus, even at low population densities [7] and have the most harmful effect on the plant [8]. Most importantly, the black aphid, *A. craccivora*, is an important sap-sucking insect pest of cowpea in most tropical areas where cowpea is grown, causing significant losses in cowpea production [9]. The sap-sucking behavior weakens the aerial parts, resulting in stunted growth, distortion and necrosis of leaves, premature defoliation, and death of seedlings [10]. Additionally, the honeydew crystals released by aphids accumulate on the leaf surface and act as a light-converging lens, leading to the burning of plant tissues during sunny days [11]. The honeydew also encourages the growth of saprophytic fungi, causing a black layer covering the plant's leaves that impairs photosynthesis and blocks the stomata, consequently restricting respiration and leading to defoliation [11].

In Uganda, aphids are among the most damaging pests of cowpea, causing yield reductions of up to 50%–70% under severe infestations [12, 13]. This results in significant economic losses to smallholder farmers, who rely on cowpea as both a food and income source. Management of pests through cultural practices or biological control has proved ineffective, and using insecticides is not economical or environmentally friendly [14]. The use of host plant resistance is the most economical long-term measure for the pest [2]. Several resistant cowpea lines have been identified globally, with significant research conducted at the International Institute of Tropical Agriculture (IITA) in Nigeria [2, 5, 14]. These lines have been evaluated for their resistance to aphids across multiple locations, including Ghana [15], Burkina Faso [16], and California in the United States [7]. However, new aphid biotypes have also evolved that have been reported to overcome resistance in several plant–aphid systems [5]. The resistance to aphids in some cowpea varieties has been reported to be environment-specific [16], as observed in variety IT97K-499-35, which was found to be resistant in Nigeria but was susceptible in the Ghana environment [15]. There is a need to continuously evaluate diverse germplasm in search of new resistant sources. A collection of local and introduced cowpea germplasm is available at the cowpea breeding program of Makerere University Regional Center for Crop Improvement (MaRCCI). However, these have not been screened for resistance to the cowpea aphid. Therefore, this study aimed to determine the response of diverse cowpea germplasm to aphid biotypes in Uganda that can be used to develop improved varieties with resistance to the pest.

2. Materials and Methods

2.1. Plant Material and Experimental Layout. In this study, forty-eight (48) cowpea genotypes were used, including four resistant and four susceptible checks obtained from the Genetic Resources Unit (GRU) of the International Institute of Tropical Agriculture (IITA) Nigeria, and 40 local and introduced genotypes sourced from the Cowpea Breeding Program at MaRCCI. The description of the cowpea genotypes used in this study is presented in Table 1. The study was conducted in two stages in the screenhouse. The screen house was maintained under natural conditions with temperatures ranging from 25°C to 28°C, relative humidity between 65% and 80%, and a 12:12 h light–dark regime. In the first experiment, 48 cowpea genotypes were screened using aphids collected from the Makerere University Agricultural Research Institute Kabanyolo (MUARIK). The *A. craccivora* were collected from cowpea plants in the field and reared on the susceptible cowpea variety TVX 3236. The second experiment was conducted using 10 selected cowpea genotypes in Table 2 based on their response to aphids from the first experiment and were subjected to aphid biotypes collected on cowpea plants at MUARIK, Ngetta Zonal Agricultural Research and Development Institute (Ngetta-ZARDI), and National Semi-Arid Resources Research Institute (NaSARRI), respectively [4]. MUARIK (central Uganda) is a humid agro-ecology with bimodal rainfall (1200–1500 mm annually). NgettaZARDI (northern Uganda) lies in a drier agro-ecology with unimodal rainfall (800–1000 mm annually), while NaSARRI (Serere, eastern Uganda) represents a semi-arid agro-ecology with low rainfall (700–900 mm annually) and higher temperatures. Including these sites allowed us to capture the variation in cowpea production environments. The *A. craccivora* were collected and transported in clear plastic beakers with perforated lids to allow air into the beakers on cotton soaked in sucrose at the bottom to act as a food source for aphids [17]. At MUARIK, aphids collected from the three sites were reared in the screen house before infestation. To avoid mixing aphid biotypes, experiments for aphids collected from different locations were conducted in different net cages for each site in the screen house. The cages, covered with an insect-proof plastic net, also prevented natural enemies from entering and contained the aphids on the plants. Within the cages, the experiments were treated as a free choice [18], whereby the aphids could move freely

Table 1: List of cowpea genotypes used in the study.

Name	Status	Source
1. TVNu 1158	Resistant	IITA
2. TVu 408	Resistant	IITA
3. TVX3236	Susceptible	IITA
4. IT82E-18	Susceptible	IITA
5. TVu 946	Susceptible	IITA
6. IT97K-556-6	Resistant	IITA
7. TVu 310	Resistant	IITA
8. Tvu 15114	Susceptible	IITA
9. KVU27-1	Unknown	Uganda
10. NE 40	Unknown	Uganda
11. NE 51 × SECOW 4	Unknown	Uganda
12. WC 15	Unknown	Uganda
13. CIS	Unknown	Uganda
14. IT2841Brown	Unknown	Uganda
15. WC 69	Unknown	Uganda
16. 3306	Unknown	Uganda
17. CJO	Unknown	Uganda
18. LUDARA-KK	Unknown	Uganda
19. SANZI	Unknown	Uganda
20. NE 39 × SEC 2W	Unknown	Uganda
21. MU17	Unknown	Uganda
22. ACC 23 × SEC 3B	Unknown	Uganda
23. Secow 5 * NE 51	Unknown	Uganda
24. ACC 12 × SEC 3B	Unknown	Uganda
25. WC 37	Unknown	Uganda
26. NE5	Unknown	Uganda
27. IT84	Unknown	Uganda
28. SEC 1 × Sec 4W	Unknown	Uganda
29. WC 16	Unknown	Uganda
30. SECOW 2W	Unknown	Uganda
31. EBELATE × NE 51	Unknown	Uganda
32. EBELATE × NE 39	Unknown	Uganda
33. Acc 2 × Secaw 2W	Unknown	Uganda
34. 2419	Unknown	Uganda
35. IT 109	Unknown	Uganda
36. C2A	Unknown	Uganda
37. ALEGI × ACC 12	Unknown	Uganda
38. NE 51	Unknown	Uganda
39. 2282	Unknown	Uganda
40. WC 66	Unknown	Uganda
41. WC 63	Unknown	Uganda
42. IT91	Unknown	Uganda
43. WC 35A	Unknown	Uganda
44. WC5	Unknown	Uganda
45. WC 13	Unknown	Uganda
46. NE 20	Unknown	Uganda
47. NE 51 × SEC 3B	Unknown	Uganda
48. IT889	Unknown	Uganda

Table 2: List of genotypes used in the second experiment.

No.	Genotype	Source	Response
1	TVNu 1158	IITA	Highly resistant
2	NE 51	Uganda	Highly resistant
3	Sanzi	Uganda	Highly resistant
4	IT97K-556-6	IITA	Resistant
5	2282	Uganda	Moderately resistant
6	IT82E-18	IITA	Moderately resistant
7	WC 66	Uganda	Moderately resistant
8	Tvu 310	IITA	Susceptible
9	KVU 27-1	Uganda	Susceptible
10	WC 15	Uganda	Highly susceptible

from one plant to another and from one pot to another within the same cage. The experiments were laid out in a completely randomized design (CRD) with three replications.

Eight seeds of each genotype were planted in a 5 L volume bucket filled with a mixture of sterilized lake sand with decomposed farmyard manure. After germination, the plants in each plot represented by a pot/bucket were thinned to four. Each plant was infested with five adult aphids using a camel brush 10 days after planting (7 days after emergence) using the protocol of Souleymane et al. [2]. In the first experiment, one big cage inside the screen house contained all 48 genotypes and their replications simultaneously. An additional modification was made in the second screening, where the experiment was split into three experiments under different net-caged houses, with each cage representing the aphids collected from one site replicated three times each.

2.2. Data Collection.

The following variables were collected in each experiment to assess the cowpea genotypes for resistance and susceptibility:

a. Aphid counts: In the first experiment, the number of aphids per plant was counted and recorded at 6, 12, and 17 days after infestation (DAI), which is a modification to the method of [2] due to a large number of genotypes used. In experiment 2, the same data were collected at 5, 9, 13, and 17 DAI [2] to observe the multiplication and survival rate of the aphids on the plants.

b. Aphid distribution (colonies): the distribution of aphid population on each plant was assessed using a 0 to 5 rating scale (0 = *no aphids*, 1 = *a few individual aphids*, 2 = *a few small individual colonies*, 3 = *several small colonies*, 4 = *large individual colonies*, 5 = *large continuous colonies*) [2]. The colony scores were taken at the same intervals as the aphid count.

c. Aphid damage: the damage on the plant leaves caused by aphid infestation was scored based on a scale of 1–5 by Alabi et al. [18], as shown in Table 3 at 17 days after aphid infestation. This is the stage when aphid damage causes distinct phenotypic variation among cowpea plants based on leaf damage, and the extent of aphid occurrence multiplies to more than 60% of plants in each plot [16].

d. Number of days to 50% flowering: this is the number of days to 50% flowering collected when at least half of the plot has flowered.

2.3. Data Analysis.

The aphid count data collected were transformed using logarithm transformation $[\log(x+1)]$ [18] and subjected to analysis of variance using the general linear model statistical procedures with Genstat 18th edition software [21]: the linear model fitted was $Y_{ijk} = Y + G_i + B_j + e_{ijk}$, Where Y = Grand mean, $G_i = i$th

Table 3: Scale for leaf damage.

Damage index	Response	Damage characteristics
1	HR	No visible damage
2	R	Slight yellowing of older leaves
3	MR	Plants appear slightly stunted with the yellowing of older leaves
4	S	Plants appear moderately stunted with yellowing of older leaves and slight curling of young leaves.
5	HS	Plants appear severely stunted with severely curled and yellow leaves, and most of the stems and leaf surfaces are covered with sooty mold, resulting in the death of the plant.

Note: Source: [18]. R, resistant; S, susceptible.
Abbreviations: HR, highly resistant; HS, highly susceptible; MR, moderately resistant.

genotype mean effect, $R_j = j$th replication mean effect, and e_{ijk} = experimental error. Treatment means separation was carried out using the Fisher's protected least significant difference (LSD) test at a 5% significance level. Pairwise Pearson correlations were performed between all the traits collected [2].

3. Results

3.1. Response of Cowpea Genotypes to Aphids. The results of the analysis of variance on aphid counts, aphid colony scores, and damage scores are presented in Table 4. There were significant differences among genotypes for aphid counts ($p < 0.01$) at 6 and 12 DAI and ($p < 0.001$) at 17 DAI. Aphid distribution (colony) varied significantly ($p < 0.01$) among genotypes at 12 and 17 DAI but not at 6 DAI. The evaluated genotypes were also significantly ($p < 0.01$) differently damaged by aphids. The means for aphid counts, colony scores, aphid damage scores, and response to aphid attacks according to the damage scores for 48 genotypes are presented in Table 5. The results showed that at 6 DAI, four genotypes, namely NE 51, NE 5, TVNu 1158, and WC 37, recorded no aphids on the plants, while Tvu 310 had the highest mean aphid count of 19 per plant. At 12 DAI, three genotypes, namely NE 51, NE 5, and Alegi × Acc12, had no aphid mean counts, while Tvu 310 still recorded the highest mean counts of 88 aphids per plant. At 17 DAI, genotype NE 51 had the lowest aphid mean count of 7 aphids per plant, making it the only genotype that stood out consistently with low aphid counts at all three-time points, while WC 15 recorded the highest mean counts of 876 aphids per plant.

The colony scores were shown to be dependent on the aphid population, whereby the lower aphid population showed lower colony scores. At 6 DAI, seven genotypes, namely NE 5, NE 39 × Sec 2W, WC 16, 2282, Sec 2W, TVX 3236, and NE 51 × Sec 4W, had no visible aphid colonies formed on the plants, while genotypes MU 17 and WC 13 had a high aphid buildup, averaging at 0.4 colony score. At 12 DAI, four genotypes, namely NE 5, Alegi × Acc12, NE 51, and TVNu 1158, had no colony buildups on the plants, while Tvu 310 had the highest buildup of colonies with a score of 1.4. Two genotypes, Alegi × Acc12 and NE 51, had the lowest average aphid buildup colony score of 0.17 at 17 DAI, while WC 69 had the highest average aphid buildup of 3.6 scores (Table 5).

Additionally, the results revealed that genotype TVNu 1158 was the most resistant to aphid damage, followed by six other genotypes, namely NE 51, Alegi × Acc12, Sanzi, NE 5, Ludara, and 3306, which were all classified as highly resistant as evidenced by the minimal levels of damage inflicted by aphids on the plants with damage scores of 1 and lower than 2. Eighteen genotypes were resistant, while 11 were moderately resistant according to their damage scores. Nine genotypes were susceptible to aphid damage, whereas three genotypes, namely WC 15, KVU27-1, and Tvu 310, were highly susceptible, with the highest aphid damage score of 5 (Table 5).

3.2. Genotype Response to Aphid Biotypes Collected From Different Environments. The results of the analysis of variance for aphid counts, aphid colony scores, damage scores, and days to 50% flowering for the 10 genotypes evaluated for their response to aphids collected from three locations at 6, 9, 13, and 17 DAI are presented in Table 6. The interaction between genotype and aphid biotypes was insignificant for all the traits measured. This indicates that the aphids did not show differential feeding preference for plants based on their origins (environment). The genotypes responded significantly differently to the three aphid biotypes in aphid damage ($p < 0.01$) as well as in aphid counts at 5 DAI ($p < 0.05$), 9 DAI ($p < 0.01$), 13 DAI ($p < 0.01$), and 17 DAI ($p < 0.05$). The biotypes displayed no significant differences in colony scores and days to 50% flowering. Significant variations among genotypes were also observed in aphid counts at 5 ($p < 0.05$), 13 ($p < 0.05$), 9($p < 0.01$), and 17 DAI ($p < 0.01$). Also, colony scores were significantly different at 9 ($p < 0.05$), 13 ($p < 0.01$), and 17 ($p < 0.01$) DAI among genotypes. Furthermore, aphid damage on the leaves and days to 50% flowering were significantly ($p < 0.001$) different among genotypes.

The means for aphid counts, aphid colony scores for 9 and 17 DAI, which were highly significant, and aphid damage scores at 17 DAI for the 10 genotypes measured on aphids collected from the three locations at all four intervals are presented in Figure 1. The results showed that the aphid biotypes from NgettaZARDI were highest at 9 DAI for most of the genotypes except WC 66. In contrast, aphid biotypes from NaSARRI showed low counts without a definite trend. At 17 DAI, the number of aphids from MUARIK and NgettaZARDI began to drop, with the genotypes Sanzi,

Table 4: Analysis of variance for aphid counts, aphid colony scores, and leaf damage.

SOV	df	AC (DAI)			ACS (DAI)			Plant damage
		6	12	17	6	12	17	
Rep	2	$0.09^{\dagger\text{ns}}$	$0.13^{\dagger\text{ns}}$	$0.53^{\dagger\text{ns}}$	$0.01^{\dagger\text{ns}}$	$0.21^{\dagger\text{ns}}$	$1.23^{\dagger\text{ns}}$	$1.97^{\dagger\text{ns}}$
Genotype	47	0.36^{**}	0.66^{**}	0.86^{***}	0.04^{ns}	0.40^{**}	2.91^{**}	2.92^{**}
Residual	94	0.19	0.36	0.4	0.06	0.23	1.5	1.47
CV (%)		74	68.7	31	158.7	108.6	65.3	38.6

Note: Rep, replication.

Abbreviations: AC, aphid Counts; ACS, aphid colony score; CV, coefficient of variation (%); DAI, days after infestation; df, degrees of freedom; SOV, source of variation.

$^{\dagger\text{ns}}$, not significant.

*Significant at the 0.05 probability level.

**Significant at the 0.01 probability level.

***Significant at the 0.001 probability level.

TVNu 1158, and NE 51 recording the lowest average mean aphid counts, while KVU27-1, IT97K-556-6, WC 15, and WC 66 recorded the highest average mean counts across aphid biotypes from the three locations at all time points. Similar observations were recorded on aphid colonies.

High damage scores were observed in aphid collections from MURAIK, followed by aphids collected from NgettaZARDI, and the aphids from NaSARRI with the lowest leaf damage. Five genotypes, 2282, IT82E-18, KVU 27-1, Tvu 310, and WC 15, recorded the highest scores (3.7) of damages inflicted by the aphid from MURAIK, while TVNu 1158 recorded the lowest score from these aphids. KVU 27-1 showed the highest score (4) of damage from the aphid collected from NgettaZARDI, while Sanzi and TVNu 1158 showed no damage (score = 1) by the same aphids. Aphids collected from NaSARRI caused the highest damage to Tvu 310 and WC 15 (score = 1.7), while they did not inflict damage (score = 1) to 2282, NE 51, Sanzi, and TVNu 1158 (Figure 1).

Comparisons of the growth and multiplication trends among the three aphid populations using the sum of aphid counts per location at 5, 9, 13, and 17 DAI are shown in Figure 2. MUARIK aphids scored the highest population at 5 and 13 DAI, NgettaZARDI aphids were higher at 9 and 17 DAI, and NaSARRI aphids had the lowest population at all four time points. Aphids from MUARIK and NgettaZARDI showed the highest survival rate compared to the ones from NaSARRI.

The correlations of aphid counts, colony score, and leaf damage at 17 DAI, days to 50% flowering, for MUARIK (lower diagonal) and NgettaZARDI (upper diagonal) aphid collections are shown in Table 7. Leaf damage due to aphid scores was positively correlated ($p < 0.001$) with aphid counts for the two aphid biotypes and with the aphid colonies for NgettaZARDI aphid collections. The leaf damage scores were also positively associated ($p < 0.01$) with aphid colonies for the MUARIK collection. Aphid counts were positively correlated to aphid colony scores ($p < 0.001$) for all the two aphid collections. No relationship was observed between the number of days to 50% flowering and the aphid counts, colony scores, and aphid damage for the two biotypes. Supporting Table S1 presents the mean aphid counts, colony scores, and damage scores of genotypes across the three aphid biotypes. This additional information supports the graphical trends shown in Figures 1 and 2 and provides detailed genotype-level data.

4. Discussion

Plants respond to pest attacks through different defense mechanisms: resistance or tolerance. Resistance is when the plant has traits that enable insect–pest resistance by preventing or reducing herbivore damage through the expression of traits that prevent pests from settling, attaching to surfaces, feeding, and oviposition or that reduce their preference [20]. At the same time, plant tolerance of insect pests comprises the expression of traits that minimize and limit the damage effects caused by the pest on productivity and yield [20].

The variations observed among the aphid counts and damage were influenced by the survival and multiplication rate of aphids on genotypes and their preference to stay or move to specific genotypes and not others in the free-choice experiment [16]. The variations in the aphid population could also be an indication of antibiosis, where the aphids fail to survive or undertake effective oviposition on the plants, or antixenosis, resulting in aphids selectively settling on some genotypes and not on others [21]. Several studies have also reported significant differences in the number of aphids on susceptible and resistant varieties [15, 18]. The preference for aphids in the plant depends on many factors, such as the presence of attractants, which leads to susceptibility, secondary metabolites, environmental conditions, and phenotypic and genotypic traits [22]. The genotypes responded differently to aphid infestation and attack, as indicated by the highly significant differences among genotypes for aphid damage. This suggests an opportunity for selection and breeding for aphid resistance in the cowpea population evaluated in the study.

There were no significant differences in the aphid distribution (colony score) at 5 and 6 DAI because the aphids were still adapting to the new host [23]. These results indicated that the genotype with fewer aphid counts also had lower colony scores. As days progressed, colonies were significantly ($p < 0.05$) different at 9 DAI as aphids fed and multiplied on the undersurface of the leaves and young shoots of the susceptible plants, causing damage to the plants as reported by Baidoo and Mochiah [1].

There were no variations observed in the interaction of genotype × biotype interaction for the traits measured, indicating that genotypes responded consistently to the three

Table 5: The means for aphid counts and colony scores for 48 genotypes 6, 12, and 17 days after infestation.

	Days after infestation							
Genotypes	**Aphid counts**			**Colony scores**			**Damage**	**Response**
	6	**12**	**17**	**6**	**12**	**17**		
TVNu 1158	0	1	53	0.0	0.0	0.7	1.0	Highly resistant
Alegi × Acc12	0	0	10	0.2	0.0	0.2	1.3	
NE 51	0	0	7	0.0	0.0	0.2	1.3	
Sanzi	2	8	86	0.1	0.3	0.9	1.3	
3306	1	2	36	0.1	0.1	0.4	1.7	
Ludara	2	3	28	0.1	0.1	0.6	1.7	
NE 5	0	0	56	0.0	0.0	0.6	1.7	
Acc 2 × Sec 2W	4	7	13	0.3	0.2	0.3	2.0	Resistant
IT109	2	13	150	0.2	0.3	1.2	2.3	
NE 40	1	2	68	0.1	0.1	0.9	2.3	
IT84	5	10	78	0.1	0.5	1.3	2.7	
IT889	5	12	297	0.1	0.4	1.9	2.7	
IT97K-556-6	4	6	80	0.2	0.2	1.0	2.7	
NE 20	0	10	122	0.3	0.3	1.2	2.7	
Tvu 408	3	8	109	0.3	0.1	1.3	2.7	
Tvu 946	4	4	66	0.1	0.1	1.1	2.7	
TVX 3236	5	9	140	0.0	0.3	1.4	2.7	
2419	6	19	296	0.3	0.6	1.9	3.0	Moderately resistant
Acc 12 × Sec 3B	13	24	301	0.2	0.6	2.2	3.0	
IT Brown	11	21	466	0.2	0.5	3.0	3.0	
Sec 1 × Sec 4W	3	3	151	0.3	0.1	1.5	3.0	
WC 13	5	10	121	0.4	0.3	1.3	3.0	
WC 35A	1	4	109	0.2	0.2	1.3	3.0	
WC 37	0	7	218	0.3	0.2	1.5	3.0	
WC 5	4	12	226	0.2	0.3	2.1	3.0	
2282	3	6	201	0.0	0.2	1.7	3.3	
ACC23 × Sec 3B	4	8	252	0.1	0.3	2.2	3.3	
Ebelate × NE39	2	9	138	0.2	0.2	1.7	3.3	
IT82E-18	5	15	192	0.2	0.3	2.0	3.3	
NE 51 × Sec 3B	11	25	342	0.2	0.7	2.8	3.3	
CIS	5	20	378	0.2	0.6	2.6	3.7	
CJO	9	17	274	0.1	0.5	2.3	3.7	
MU 17	9	24	376	0.4	0.8	3.0	3.7	
NE 51 × Sec 4W	10	15	247	0.0	0.3	1.8	3.7	
WC 16	10	23	354	0.0	0.4	2.4	3.7	
WC 66	4	13	215	0.2	0.3	2.0	3.7	
Ebelate × NE51	5	32	375	0.3	0.8	2.9	4.0	Susceptible
IT91	11	65	477	0.1	1.0	3.3	4.0	
NE 39 × Sec 2W	6	32	334	0.0	0.8	2.5	4.0	
Sec 2W	8	16	226	0.0	0.5	2.4	4.0	
Tvu 15114	14	35	711	0.2	0.6	3.5	4.0	
WC63	10	67	561	0.3	1.1	3.3	4.0	
C2A	14	22	399	0.1	0.8	3.1	4.3	
Sec 5 × NE51	15	78	295	0.2	1.3	2.3	4.3	
WC69	9	33	486	0.2	0.7	3.6	4.3	
KVU 27-1	14	31	812	0.1	1.0	3.4	4.7	Highly susceptible
Tvu 310	19	88	799	0.3	1.4	3.4	4.7	
WC 15	13	51	876	0.3	1.2	3.4	5.0	
LSD$_{0.05}$	11	47	492	0.4	0.8	2.0	4.1	

Note: LSD ($\alpha \leq 0.05$): least significant difference.

aphid populations in such a way that a genotype that showed resistance to the biotype from MUARIK was also resistant to the other two biotypes from NaSARRI and NgettaZARDI, respectively. This implied that the three aphid collections could be of the same biotype or genetically related. However, variations were observed among the biotypes whereby aphids collected from MUARIK and NgettaZARDI recorded more significant damage with a high aphid multiplication rate, which was measured by the trends for aphid population as compared to the aphids collected from NaSARRI. This could be attributed to the change in environment and adaptability of the aphids from NaSARRI in the MUARIK

Table 6: Mean squares for aphid counts, colony, and leaf damage scores collected from three locations in Uganda.

SOV	df	Aphid counts				Aphid colony scores				Aphid damage	50% DF
DAI		5	9	13	17	5	9	13	17		
B	2	1.4^{*}	3.8^{**}	16.4^{**}	9.9^{*}	$1.1^{\dagger\text{ns}}$	$5.9^{\dagger\text{ns}}$	$9.6^{\dagger\text{ns}}$	$4.4^{\dagger\text{ns}}$	24.9^{**}	$0.3^{\dagger\text{ns}}$
Rep/Biotype	6	0.3^{*}	$0.3^{\dagger\text{ns}}$	1.0^{**}	1.8^{***}	$0.2^{\dagger\text{ns}}$	1.2^{**}	2.1^{***}	2.1^{***}	2.2^{**}	$0.7^{\dagger\text{ns}}$
G	9	0.3^{*}	0.5^{**}	0.7^{*}	0.8^{**}	$0.2^{\dagger\text{ns}}$	0.9^{*}	0.9^{**}	0.6^{**}	4.4^{***}	289^{***}
G × B	18	$0.1^{\dagger\text{ns}}$	$0.1^{\dagger\text{ns}}$	$0.2^{\dagger\text{ns}}$	$0.2^{\dagger\text{ns}}$	$0.1^{\dagger\text{ns}}$	$0.3^{\dagger\text{ns}}$	$0.3^{\dagger\text{ns}}$	$0.3^{\dagger\text{ns}}$	$0.7^{\dagger\text{ns}}$	$2.1^{\dagger\text{ns}}$
Pooled error	54	0.1	0.2	0.3	0.3	0.1	0.4	0.3	0.2	0.6	1.1
CV (%)		25.4	31.6	47.2	51.9	50.3	67.5	67.6	71.6	33.4	1.9

Note: B, biotype; G, genotype; GxB, genotype × biotype.

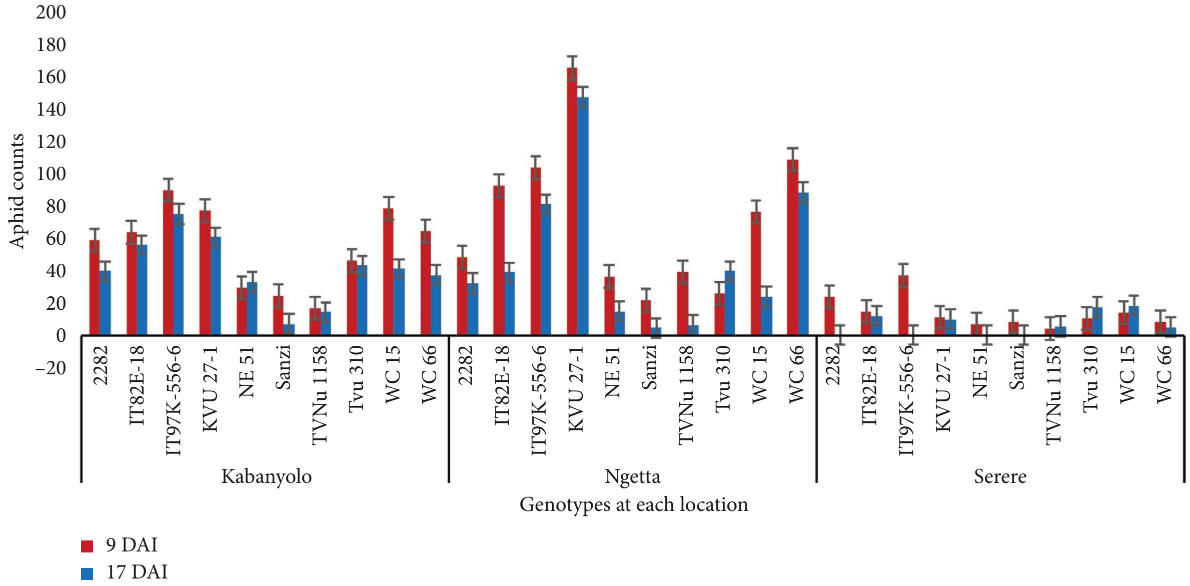
Abbreviations: CV, coefficient of variation (%); DAP, days after infestation; df, degrees of freedom; SOV, source of variation.

$^{\dagger\text{ns}}$not significant.

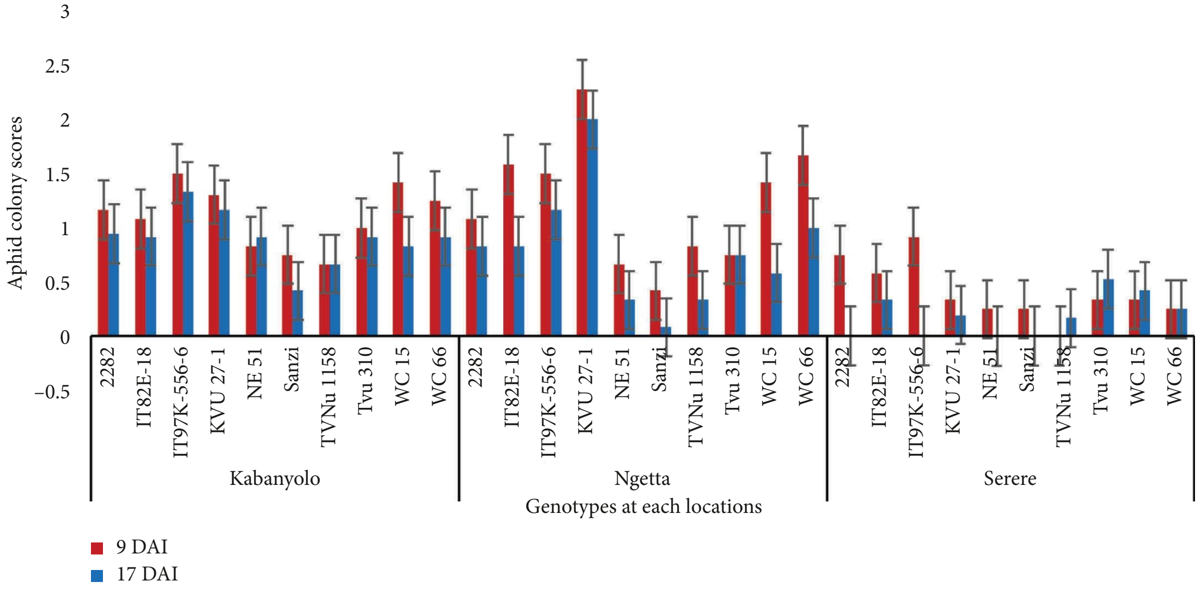
*Significant at the 0.05 probability level.

**Significant at the 0.01 probability level.

***Significant at the 0.001 probability level.

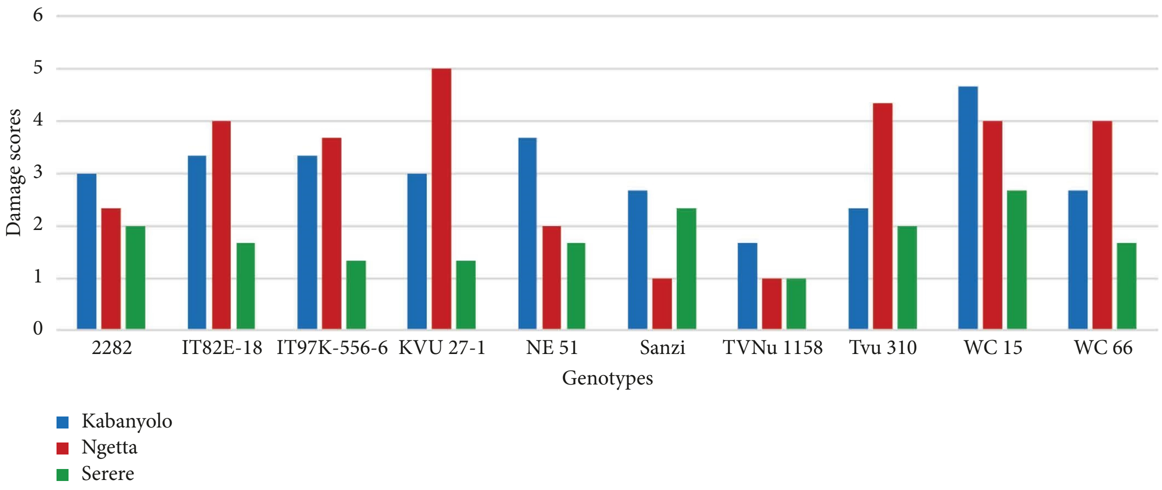


(a)



(b)

Figure 1: Continued.



(c)

Figure 1: The aphid counts (a), aphid colony scores (b), and plant damage scores (c) for the three aphid biotypes from MUARIK, NgettaZARDI, and NaSARRI.

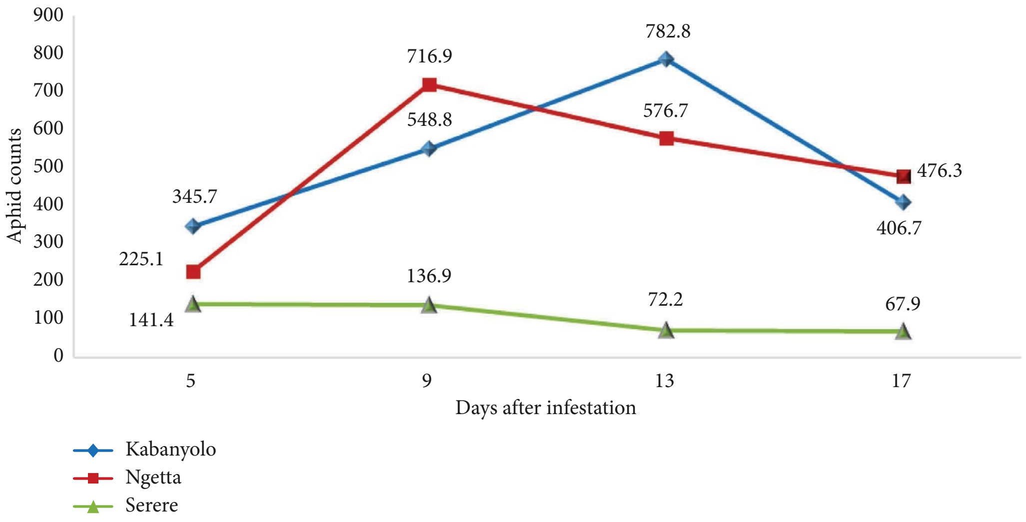


Figure 2: Aphid population trend for the three biotypes at 5, 9, 13, and 19 days after infestation.

Table 7: Correlation coefficients on aphid population and plant parameters among the 10 genotypes for MUARIK (below diagonal) and NgettaZARDI (above diagonal) aphid collections.

MUARIK	NgettaZARDI	Aphid counts	Aphid colonies	Leaf damage	50%_FD
	Aphid counts	—	0.89***	0.80***	−0.09†ns
	Aphid colonies	0.87***	—	0.85***	−0.09†ns
	Leaf damage	0.69***	0.52**	—	−0.31†ns
	50%_FD	−0.08†ns	−0.05†ns	−0.36†ns	—

Note: 50%_FD, days to 50% flowering.

†ns indicates nonsignificance.

*Significant at the 0.05 probability level.

**Significant at the 0.01 probability level.

***Significant at the 0.001 probability level.

environment, which cannot be used to conclude that the aphids from NaSARRI differ from the others. In contrast to the results of this study, Adelaïde et al. [16] reported that three biotypes of aphids collected from different agro-ecological zones in Burkina Faso affected genotypes differently, indicating that there existed more than one aphid biotype in Burkina Faso. However, in this study, there were no significant differences in the response of genotypes to aphids collected from the three agro-ecological zones of Uganda, and thus, a genotype that is resistant to aphids from one location was equally resistant to aphids in the other two locations and vice versa. Although Figures 1 and 2 suggest visual crossover trends in aphid population dynamics between MUARIK and NgettaZARDI biotypes, the genotype × biotype interaction was not statistically significant for aphid damage. This indicates that while aphid multiplication trends varied numerically across sites, the overall genotypic responses were consistent across the three biotypes.

Two genotypes, a wild relative, TVNu 1158, and Sanzi, were highly tolerant, as many aphids settled on them and still incurred minimal or no damage [20]. This indicates that under heavy aphid infestation, the two genotypes can accommodate a high aphid population with minimal or no damage to the plant [24]. TVNu 1158 was also highly tolerant to aphid biotypes in Nigeria, where it was the only one with a very high seedling survival 21 DAI [2].

Genotype IT97K-556-6, which is one of the most studied genotypes for aphid resistance [2, 7, 15], was found to exhibit some levels of tolerance in this study, evidenced by its large recorded number of aphids that resulted in low damage, which is an indication of quick recoveries from the attack [2]. However, compared to other genotypes, IT97K-556-6 did not show a high level of resistance that could be used in the development of resistant cowpea lines in Uganda, as was reported by Adelaïde et al. [16], who found a seedling survival rate of up to 93% when subjected to three different aphid biotypes in Burkina Faso. The differential fitness of this genotype might stem from genetic differences between aphid biotypes in Burkina Faso and those in Uganda or variations in environmental and climatic conditions [5]. The same applies to a resistant genotype, Tvu 310 from IITA, which was found to be consistently susceptible to aphid biotypes in Uganda in the two screenings. The implications are that the IITA-sourced genotypes, although proven to be resistant, cannot be used to breed cowpea aphid-resistant genotypes for the Ugandan environment.

The significant positive correlations between the aphid counts, damage, and aphid buildup of colony among genotypes indicated that any of the three traits could be used to determine the response of cowpea genotypes to aphids as a means of reducing phenotyping cost and labor intensity during selection and breeding [25]. The correlation analysis also revealed that aphid damage and aphid attack did not affect the days to flowering, which could be attributed to the recovery of plants after the attack, which enables the plants to fully recover from the aphid damage [5]. These observations are indications that the cowpea genotypes have underlying factors, such as metabolites that are produced at different levels to protect the plant against aphid attack. Therefore, six genotypes have been selected to have metabolites such as tannins, proteins, total phenolics, total flavonoids, alkaloids, and carbohydrates measured to determine their contributions to cowpea resistance to aphid attack.

5. Conclusion

Genotypes reacted differently to aphid attacks and consistently to aphids collected from Uganda's three cowpea-growing environments, showing that aphids from those three environments could be of the same biotype. Sanzi, TVNu 1158, and NE51 were found to be the most aphid-resistant genotypes, while the two genotypes from IITA, IT97K-556-6 and Tvu 310, which are known to be resistant, were found to be moderately resistant and highly susceptible, respectively, to aphid biotypes in Uganda, an indication that there could be genetic differences/variations between aphid biotypes in Uganda and other locations such as Burkina Faso and Nigeria, where they were found to be resistant. This indicated that there are underlying factors in cowpea genotypes that determine their response to aphid attacks. The three resistant genotypes, Sanzi, TVNu 1158, and NE51, can be used in the cowpea breeding program to generate cowpea genotypes resistant to aphid damage in Uganda. However, this study recommends further screening of cowpea germplasms for aphids in the three locations, preferably in the field, to determine the effect of Genotype x Environment on cowpea resistance to aphids. In addition, a modified screening of the no-choice experiment in the screenhouse, whereby each genotype is put in single cages, is also recommended. In addition, while this study employed free-choice screening to simulate natural field infestations, we recognize the need for complementary no-choice screening experiments in which each genotype is evaluated in isolation. Such an approach would eliminate the possibility of pseudo-resistance and further validate the observed resistance.

Data Availability Statement

All relevant data used in this study have been provided in the article, and any additional or supporting data will be available on request from the authors.

Conflicts of Interest

The authors declare no conflicts of interest.

Author Contributions

Selma Ndapewa Nghituwamhata and Ephraim Nuwamanya conceived and designed the research. Selma Ndapewa Nghituwamhata, Faizo Kasule, Chepkoech Evalyne Rono, and Ephraim Nuwamanya conducted data collection for laboratory and field experiments. Selma Ndapewa Nghituwamhata, Arfang Badji, and Isaac Onziga Dramadri performed data analysis. Selma Ndapewa Nghituwamhata, Ephraim Nuwamanya, Faizo Kasule, Chepkoech Evalyne Rono, Richard Edema, Arfang Badji, Albert Chiteka, and Isaac Onziga Dramadri reviewed the manuscript. All authors contributed to the article and approved the submitted version.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section. *(Supporting Information)*

Supporting Table S1: Average scores of 10 cowpea genotypes using aphid biotypes from MUARIK-Kabanyolo, NgettaZARDI-Ngetta, and NaSARRI–Serere at 17 days post-infestation (DAI).

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