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NEW SOURCES AND STABILITY OF RESISTANCE TO APHIDS IN COWPEA GERMPLASM ACROSS LOCATIONS IN UGANDA

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ABSTRACT

The cowpea aphid (*Aphis craccivora* Koch) is an economically important pest, whose feeding effects cause stunting, delayed flower initiation and yield reduction in cowpea (*Vigna unguiculata* L. Walp). Host plant resistance offers an alternative for controlling aphids; while simultaneously reducing reliance on chemical pesticides. The objective of this study was to evaluate a multi-parent advanced generation inter-cross (MAGIC) population of cowpea against aphids, across cowpea growing regions in Uganda. The study was arranged in alpha lattice design, with two replicates in three locations over two seasons (2018B and 2019A). Results revealed significant effects ($P < 0.001$) for the main treatment effects, genotype x location and location x season interaction for both infestation and damage. The genotype x season interaction was significant ($P < 0.01$) for both aphid infestation and damage; while the three-way interaction was only significant ($P < 0.001$) for aphid infestation, but not for damage. The study identified five new resistant and stable genotypes from the MAGIC panel, including MAGIC131, MAGIC-132, MAGIC149, MAGIC170 and MAGIC280; and one resistant parent, SUVITA-2. The study further revealed MAGIC-125, MAGIC-171, MAGIC153, MAGIC-333, MAGIC177, MAGIC-292, MAGIC282, MAGIC249, MAGIC162, SEC 4W * SEC 5T, NAROCOWPEA 4, MAGIC-204, MAGIC-039, MAGIC060, MAGIC-097, NAROCOWPEA 3, MAGIC-233, MAGIC090 and MU 9 to be moderately resistant and high yielding genotypes. The above genotypes are recommended for use in the cowpea breeding programme, to develop improved resistant lines against aphids in Uganda.

Key Words: *Aphis craccivora*, MAGIC population, *Vigna unguiculata*

RÉSUMÉ

Le puceron du niébé (*Aphis craccivora* Koch) est un ravageur économiquement important, dont les effets alimentaires provoquent un retard de croissance, un retard de floraison et une réduction du rendement du niébé (*Vigna unguiculata* L. Walp). La résistance des plantes hôtes offre une alternative pour lutter contre les ravageurs destructeurs, y compris les pucerons; tout en réduisant simultanément la dépendance aux pesticides chimiques. L'objectif de cette étude était d'évaluer une population multiparentale inter-croisée de génération avancée (MAGIC) de niébé contre les pucerons, dans les régions de culture du niébé en Ouganda afin d'identifier de nouvelles sources de résistance contre le ravageur. L'étude a été organisée en conception de réseau alpha, avec deux répliques à trois endroits sur deux saisons (2018B et 2019A). Les résultats ont révélé des effets significatifs ($P < 0,001$) pour les principaux effets du traitement, le génotype x emplacement et l'interaction emplacement x saison pour l'infestation et les dommages. L'interaction génotype x saison était significative ($P < 0,01$) à la fois pour l'infestation et les dommages causés par les pucerons; tandis que l'interaction à trois facteurs n'était significative ($P < 0,001$) que pour l'infestation de pucerons, mais pas pour les dommages. L'étude a identifié cinq nouveaux génotypes résistants et stables du panel MAGIC, notamment MAGIC131, MAGIC-132, MAGIC149, MAGIC170 et MAGIC280; et un parent résistant, SUVITA-2. L'étude a en outre révélé MAGIC-125, MAGIC-171, MAGIC153, MAGIC-333, MAGIC177, MAGIC-292, MAGIC282, MAGIC249, MAGIC162, SEC 4W * SEC 5T, NAROCOWPEA 4, MAGIC-204, MAGIC-039, MAGIC060, MAGIC -097, NAROCOWPEA 3, MAGIC-233, MAGIC090 et MU 9 pour être des génotypes modérément résistants et à haut rendement. Les génotypes ci-dessus sont recommandés pour une utilisation dans le programme de sélection du niébé pour développer des lignées améliorées résistantes aux pucerons en Ouganda.

Mots Clés: *Aphis craccivora*, population MAGIC, *Vigna unguiculata*

INTRODUCTION

Cowpea (*Vigna unguiculata* L. Walp) is one of the most important food grain legumes grown and widely used in the tropics, especially in the semi-arid regions in Africa (Nualsri *et al.*, 2011). It is the fourth most important grain legume in Uganda (Agbahoungba *et al.*, 2017), after beans (*Phaseolus vulgaris* L.), groundnuts (*Arachis hypogaea*) and soybean (*Glycine max*) (Ronner *et al.*, 2012). In Uganda, the crop is mostly grown in the drier eastern and northern parts of the country because of its tolerance to drought and adaptation to warm weather (Dungu *et al.*, 2015). It is also capable of producing reasonable yields, where other grain legumes and cereals fail.

The high contents of carbohydrates (63%) and proteins (25%) in cowpea grain make it a very important food for human and livestock nutrition (Xiong *et al.*, 2016; Togola *et al.*,

2020). Despite its importance, cowpea productivity levels are generally low among farmers, ranging between 300 and 500 kg ha⁻¹ (Avosa *et al.*, 2020), compared to its yield potential in the range of 1500 and 3000 kg ha⁻¹ (Gbaye and Holloway, 2011). The crop is heavily infested by cowpea aphid (*Aphis craccivora* Koch) pest, inflicting damage through direct feeding, and injecting toxic saliva into phloem, leading to stunted growth and sometimes death of the plant during severe infestation (Huynh *et al.*, 2015). Aphid infestation results in reduced photosynthesis (Huynh *et al.*, 2015), delayed initiation of flowering (Souleymane *et al.*, 2013), stunting of plants (Alabi *et al.*, 2012) and yield reduction (Annan *et al.*, 1995). Besides, aphids are the vectors of the two important cowpea diseases in Africa, namely Blackeye Cowpea Mosaic Virus (BCMV) and Cowpea Aphid Borne Mosaic Virus (CABMV) (Boa, 2014).

In order to control aphids, most farmers in Africa use chemical pesticides (Onyishi *et al.*, 2013). Foliar applications with various insecticides has been reported to be effective against *A. craccivora* (Nualsri *et al.*, 2011); however, rapid development of aphid resistance to pesticides renders chemical treatments ineffective (Karunamoorthi and Sabesan, 2012). Besides, use of chemicals has attracted a lot of public health concerns; apart from contributing to high costs of production (Nicolopoulou-Stamati *et al.*, 2016).

Host plant resistance (HPR) can provide a safe and reliable avenue for aphid pest management, being an environmentally safe and cost-effective pest management technique (Flint *et al.*, 2003). Its potential is generally high because of the availability and access to plant germplasm collections containing genes of resistance; and because of the recent developments in plant science technologies (Ehrhardt, 2014), where plant resistance has been embraced as an important component of integrated pest management.

The most common approaches for evaluating the resistance of cowpea to aphids involve seedling damage, aphid infestation (Omoigui *et al.*, 2017), pod infestation and yield reduction (Zheng *et al.*, 2017). Cowpea germplasm has not been extensively evaluated in Uganda for aphid resistance and this has hindered exploitation of this trait to improve cowpea production in the country. Recently, a multi-parent advanced generation intercross (MAGIC) population was introduced in Uganda, with a view of providing a plant population resource for aphid resistance breeding among other traits.

A MAGIC population typically comprises of 4, 8 or 16 founder parents, selected for various desirable traits, such as disease resistance, plant height, flowering time, yield (Riaz *et al.*, 2020) and/or pest resistance. The founder parents are subjected to several generations of intercrossing, followed by multiple generations of selfing to create recombinant inbred lines (RILs), each of

which carry a mosaic of the founder haplotypes (Rakshit *et al.*, 2012). Several MAGIC populations have been developed for numerous plant species, including arabidopsis (Kover *et al.*, 2009), wheat (Huang *et al.*, 2012), rice (Bandillo *et al.*, 2013), barley (Sannemann *et al.*, 2015), tomato (Pascual *et al.*, 2015), maize (Jiménez-Galindo *et al.*, 2019) and cowpea (Huynh *et al.*, 2018).

For cowpea, the MAGIC population was created by Huynh *et al.* (2018), by inter-mating eight parents, using a strategy described in Cavanagh *et al.* (2008), to produce 315 F8 recombinant inbred lines of the MAGIC core set. The founder parents used were collected from the Institute of Agricultural Research, Burkina Faso (SUVITA 2); University of California – Riverside, United States (CB27); and; International Institute of Tropical Agriculture, IITA Nigeria (IT93K-503-1, IT89KD-288, IT84S-2049, IT82E-18, IT00K-1263 and IT84S-2246). The agronomic and resistance/tolerance characteristics of these parents are described in Huynh *et al.* (2018). A desirable genotype for improving pest resistance is one which is stable across environments (locations and seasons) (Oliveira *et al.*, 2014). The objective of this study was to identify new sources of resistance to aphids in cowpea collections, through field evaluation across growing locations of cowpea in Uganda.

MATERIALS AND METHODS

Experimental sites. The study was conducted in three locations in Uganda; namely at (i) Makerere University Agricultural Research Institute, Kabanyolo (MUARIK), located at 0°16'24"N, 32°53'37"E, at 1217 meters above sea level (m.a.s.l), with soil being mostly sandy clay loam; (ii) National Semi-Arid Resources Research Institute (NaSARRI) in Serere district at 1°35'N, 33°35'E, at 1140 m.a.s.l with black clay soils; and (iii) Ngetta Zonal Agricultural Research and development institute (Ngetta ZARDI) in Lira at 02°17'N,

32°56'E, at 1180 m.a.s.l, with sandy loam soils (Otim *et al.*, 2015; Agbahoungba *et al.*, 2017). The experiment was planted in two consecutive rainy seasons in 2018B (August - November 2018) and 2019A (March - June 2019).

Treatments and design. Materials used in the study were obtained from the cowpea gene bank maintained at MUARIK, and contained 279 genotypes including 253 MAGIC lines, 7 founder parents, 4 land races and 15 breeding lines from Uganda. At each of the three experimental sites, the study was established in an alpha lattice design in 14 blocks, each block containing 20 plots (14 blocks x 20 genotypes per block), with two replicates. Each genotype was planted in a two row plot of 8 plants within a row, at a seed rate of two per hill; and later thinned to one plant per hill. The blocks were separated by 1.5 m alleys with 1 m between plots. Plant spacing was 75 cm between and 25 cm within rows. No pesticides were used and the experiments were planted in isolated fields to avoid effects of pesticide drift from other experimental fields.

Data collection. Six plants were selected from the centre of each row (12 plants selected per plot) for scoring aphid infestation and damage, days to 50% flowering, days to 50% physiological maturity (when pod colour was brown/light brown as described in Cruz *et al.* (2019)), number of pods per plant, number of grains per pod, 100 grain weight and grain weight per plant per genotype. Aphid infestation and damage symptoms in experimental plots were scored at 30, 60 and 80 days after planting (DAP), as recommended by Huynh *et al.* (2015). Aphid infestation and damage on each of the plants were assessed using a scale of 1 to 5 (Omoigui *et al.*, 2017), as shown in Table 1. Resistance was assessed by scoring for aphid infestation and damage, separately on individual plants.

Data analysis. Data were subjected to analysis of variance (ANOVA), using the Linear Model, with restricted maximum likelihood

TABLE 1. Aphid colony (infestation) and visual plant damage scores

Score	Infestation description	Damage description used in this study	Resistance status
1	No/Few individual aphids	No symptom of attack	Resistant
2	Few small individual colonies	plant showing little symptoms (plant slightly stunted)	Moderately resistant
3	Several small colonies	Plant showing symptoms of attack (plant slightly stunted with slight yellowing of older leaves); no plant damage	Moderately resistant
4	Large individual colonies	Plant showing weak stem, leaves and seedling damage (plant moderately stunted with yellowing of older leaves and curling of young leaves)	Susceptible
5	Large continuous colonies	Severely stunted plant with severely curled and yellow leaves, stem and leaves covered with sooty mould or dead plant	Highly susceptible

Source: Omoigui *et al.*, 2017

(ReML) statistical procedures in Genstat version 18.0, following the model across locations and seasons as described by Smith *et al.* (2005) to minimise the sums of squares for the error. The statistical model for ANOVA was:

$$y_{ijklm} = \mu + \rho_i + l_j + s_k + r_l + b_{m(l)} + ls_{kj} + \rho s_{ki} + \rho l_{ji} + \rho ls_{ijk} + \varepsilon_{ijklm}$$

Where:

- y_{ijklm} is the observed value for the i^{th} genotype from j^{th} location, k^{th} season m^{th} block nested within the l^{th} replication;
- μ is the overall mean;
- ρ_i is the i^{th} genotype effect (considered as fixed effect);
- l_j is the j^{th} location effect (considered as fixed effect);
- s_k is the k^{th} season effect (considered as random effect);
- r_l is the l^{th} replication effect (considered as random effect);
- $b_{m(l)}$ is the effect of m^{th} block nested within the l^{th} replication (considered as random);
- ls_{kj} is the k^{th} season and j^{th} location interaction effect considered as random;
- ρs_{ki} is the interaction effect of k^{th} season and i^{th} genotype (considered as random);
- ρl_{ji} is the interaction effect of j^{th} location and i^{th} genotype (considered as random);
- ρls_{ijk} is the effect of the three-way interaction between k^{th} season, j^{th} location and i^{th} genotype (considered as random); and

ε_{ijklm} is the experimental error considered as random.

Comparative analysis for aphid infestation and damage among genotypes was based on scores captured at 60 DAP, when distinct phenotypic differentiation would be expected among genotypes for the biotic stress factors. Separation of means was done using the Scott-Knott test at 5% level of significance, to allow for the formation of homogeneous groups of treatments and avoid ambiguity in the interpretation of results (Silva, 2007).

Genotype plus genotype by environment (GGE) biplot analysis was performed on resistance (inverse infestation), to explore the genotype plus genotype x environment interaction. Resistance stability among genotypes was assessed using GGE biplots and Additive Main effects and Multiplicative Interaction (AMMI) scores of the genotypes across environments.

RESULTS

The results of the combined analysis of variance (ANOVA) for 230 genotypes were used based on completeness of data for aphid infestation, damage and grain yield per plant (Table 2). There were highly significant effects ($P < 0.001$) for the main treatment effects, genotype by location, and location by season interaction for aphid infestation, damage and grain yield per plant. The genotype by season, and location by season interactions were significant ($P < 0.001$) for both aphid infestation and damage, but not for grain yield per plant. The three-way interaction was only significant ($P < 0.001$) for aphid infestation, but not for damage; nor for grain yield per plant (Table 2). For aphid damage, highly significant effects were observed for all possible interactions, except for the three-way interaction. Grain yield per plant differed significantly ($P < 0.001$) among genotypes, locations and seasons. The interaction between

TABLE 2. Mean squares for aphid infestation, damage and cowpea grain yield per plant in three locations over two seasons

Source of variation	Degrees of freedom	Mean squares		
		Aphid infestation	Aphid damage score	Grain weight (g) per plant
Rep*(Location*Season)	6	0.75423 ^{ns}	3.005 ^{ns}	276 ^{ns}
Block*(Rep)(Location*Season)	156	0.23935 ^{ns}	0.20124 ^{ns}	120.1 ^{ns}
Genotype	229	3.42964 ^{***}	0.84515 ^{***}	1136.5 ^{***}
Location	2	471.496 ^{***}	523.701 ^{***}	56898 ^{***}
Season	1	146.848 ^{***}	1093.55 ^{***}	15804 ^{***}
Genotype*Location	458	0.44943 ^{***}	0.53037 ^{***}	782.6 ^{***}
Genotype*Season	229	0.46906 ^{***}	0.34433 ^{***}	251.7 ^{ns}
Location*Season	2	293.238 ^{***}	8.53395 ^{***}	2.7 ^{ns}
Genotype*Location*Season	458	0.33297 ^{***}	0.0018 ^{ns}	6.9 ^{ns}
Residual	1218	0.34671	0.21266	232.5
Total	2759	1.25542	1.08	408.68
S.E.D		0.59	0.66	27.08
C.V		25.54	23.8	37.23

Note: *, ** and *** = significant at $P < 0.05$, $P < 0.01$, $P < 0.001$, respectively; ns = non-significant

genotype and location was also significant ($P < 0.01$) for grain yield per plant.

Relationships between aphid infestation and cowpea yield traits.

The correlation coefficients among the captured resistance to aphids and yield-related traits are shown in Table 3. Aphid infestation and damage were positively correlated ($r = 0.245$, $P < 0.001$); while days to 50% flowering and 50% maturity correlated positively with aphid damage ($r = 0.486$ and $r = 0.573$, respectively). Aphid infestation negatively correlated with number of grains per pod, and there was a highly positive correlation ($r = 0.856$, $P < 0.001$) between days to 50% flowering and days to 50% maturity. Number of pods per plant also correlated positively with grain weight per plant ($r = 0.928$).

Based on aphid infestation levels, 6 genotypes were found to be resistant (Mean score = 1), 219 moderately resistant (score = 2-3), 4 susceptible (score = 4) and 1 highly

susceptible (score = 5) from evaluations across the three locations (Table 4).

According to infestation scores, genotypes MAGIC131, MAGIC-132, MAGIC280, MAGIC149, MAGIC170 and SUVITA-2 were recorded as resistant (Table 5). Accessions MAGIC301, SECOW 1T, MAGIC-194 and IT93K-503-1 were susceptible; while accession IT82E-18 was the most susceptible (highly susceptible). The rest of the accessions were moderately resistant. None of the local materials evaluated was resistant; while 14 of them were moderately resistant. The best 20 and worst 20 genotypes for aphid resistance based on average aphid infestation scores are presented in Table 5.

Resistance stability of genotypes across locations.

Genotype plus genotype by environment (GGE) biplot (Fig. 1) performed on aphid resistance (based on "inverse infestation") explained 90.48% of the total G+GE and revealed that the first principal

TABLE 3. Correlation coefficients (r) of resistance traits evaluated for the cowpea genotypes

	Infestation	Damage	100 seed weight (g)	Days to 50% flowering	Days to 50% maturity	No. of grains per pod	Grain weight/plant (g)
Infestation							
Damage	0.245***						
100 seed weight	-0.069	0.098*					
Days to 50% flowering	-0.091*	0.486***	-0.016				
Days to 50% maturity	-0.114*	0.573***	0.053	0.856***			
Grains per pod	-0.034	-0.052	-0.139**	-0.028	-0.082		
Grain weight per plant	0.033	0.088	0.107*	0.048	-0.001	0.71***	
Pods per plant	0.043*	0.092*	-0.071	0.064	0.006	0.548**	0.928***

Spearman's rank correlation coefficients adjusted for ties. *** = $P < 0.001$, ** = $P < 0.01$, * = $P < 0.05$, Correlation is significant at the 0.05 and 0.01 level (2-tailed), respectively

component (PC1) accounted for 67.38%; while the second principal component (PC2) was responsible for 23.10% of the variation in resistance to aphids. The which-won-where pattern visualisation in the GGE biplot, revealed that a polygon was formed by genotype connectors that were furthest away from the origin (Fig. 1). A polygon view of GGE biplot was formed by connecting the vertex genotypes with straight lines and the rest of the genotypes were placed within the polygon. The vertex genotypes, MAGIC-292, MAGIC006, MAGIC-279 and MAGIC-175, having the longest distances from the origin were more responsive to environmental changes and highly variable in resistance to aphids. The perpendicular lines to the sides of the polygon separated mega-environments. Figure 1 further reveals that the GGE biplot formed three mega-environments, including MUARIK, NaSARRI and Ngetta ZARDI.

Since the analysis contained a large number of genotypes which could not be clearly visualised on the biplots, further analysis was done to explore best genotypes in different locations, using the Additive Main effects and Multiplicative Interaction (AMMI) analysis, and the genotypes ranked according to AMMI resistance stability estimates. In this case, a desirable genotype is one with a high stability estimate, which is associated with resistance performance. Accordingly, the best genotypes for resistance to aphids across all locations based on AMMI averages were MAGIC131, MAGIC-132, MAGIC280, MAGIC149, MAGIC170, MAGIC101, MAGIC-287, MAGIC-139 and SUVITA-2. The best 20 resistant and stable genotypes in each location and across all locations are summarised in Table 6.

Results of the AMMI biplot analysis for genotypes across environments are presented in Figure 2. The biplot showed that the three tested environments were scattered without definite grouping, being consistent with the observation of mega environments in the GGE biplot in Figure 1. Most of the genotypes were clustered close to the midpoint. AMMI biplot

TABLE 4. Distribution of cowpea genotypes for resistance against cowpea aphids in the study locations in Uganda

Description of infestation	Aphid infestation score	Location			
		Overall	MUARIK	NaSARRI	Ngetta ZARDI
Resistant	1	6	102	6	140
Moderately resistant	2 - 3	219	123	158	87
Susceptible	4	4	4	60	2
Highly susceptible	5	1	1	6	1
Total		230	230	230	230

MUARIK = Makerere University Agricultural Research Institute, Kabanyolo, NaSARRI = National Semi-Arid Resources Research Institute

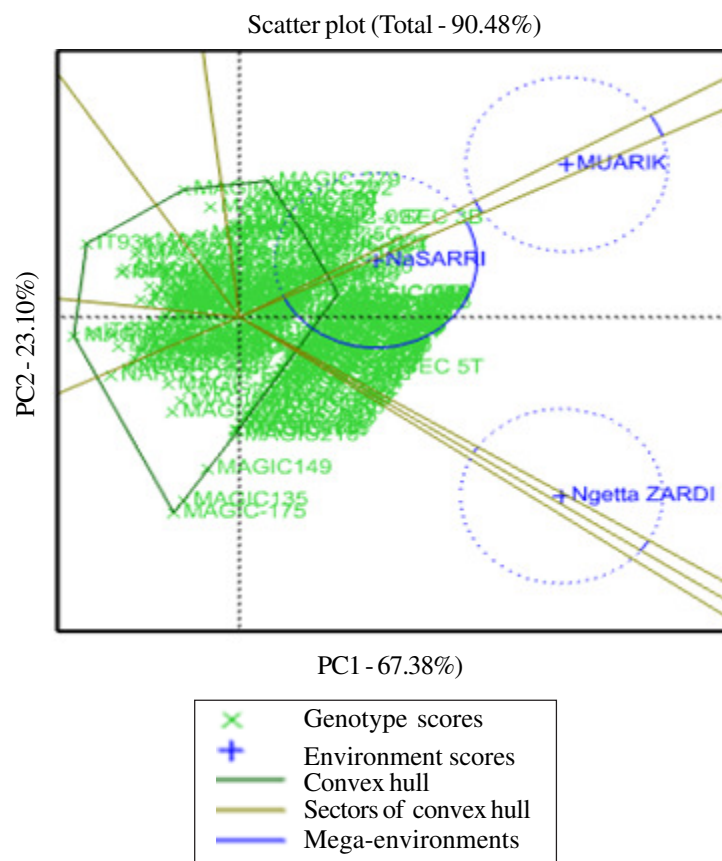


Figure 1. GGE biplot analysis for resistance to aphids among cowpea genotypes across three environments in Uganda.

TABLE 5. Top 20 most resistant and the 20 most susceptible cowpea genotypes across three environments (locations) based on mean aphid infestation in Uganda

Overall			MUARIK			NaSARRI			Ngetta ZARDI		
Genotype	Infestation (x =2.3, s.e=1.19)	Resistance status	Genotype	Infestation (x =1.9, s.e=0.92)	Resistance status	Genotype	Infestation (x =3.2, s.e=1.25)	Resistance status	Genotype	Infestation (x =1.8, s.e=0.80)	Resistance status
MAGIC280	1.1	R	MAGIC280	1.0	R	MAGIC131	1.3	R	MAGIC009	1.3	R
MAGIC131	1.1	R	MAGIC131	1.0	R	MAGIC-132	1.3	R	MAGIC020	1.3	R
MAGIC-132	1.1	R	MAGIC-132	1.0	R	MAGIC135	1.3	R	MAGIC033	1.3	R
MAGIC149	1.3	R	MAGIC216	1.3	R	MAGIC149	1.3	R	MAGIC099	1.3	R
MAGIC170	1.3	R	MAGIC006	1.3	R	MAGIC170	1.3	R	MAGIC101	1.3	R
SUVITA-2	1.5	R	MAGIC030	1.3	R	MAGIC280	1.3	R	MAGIC113	1.3	R
MAGIC101	1.6	MR	MAGIC-035	1.3	R	MAGIC-078	2.0	MR	MAGIC-122	1.3	R
MAGIC-139	1.6	MR	MAGIC045	1.3	R	SUVITA-2	2.0	MR	MAGIC-126	1.3	R
MAGIC-287	1.6	MR	MAGIC-046	1.3	R	MAGIC-287	2.2	MR	MAGIC-139	1.3	R
MAGIC216	1.6	MR	MAGIC-073	1.3	R	MAGIC-083	2.2	MR	MAGIC157	1.3	R
MAGIC-126	1.7	MR	MAGIC101	1.3	R	MAGIC101	2.2	MR	MAGIC-171	1.3	R
MAGIC-211	1.7	MR	MAGIC-155	1.3	R	MAGIC-139	2.2	MR	MAGIC-195	1.3	R
WC 35C	1.7	MR	MAGIC-174	1.3	R	MAGIC-224	2.2	MR	MAGIC-202	1.3	R
MAGIC138	1.7	MR	MAGIC184	1.3	R	MAGIC276	2.2	MR	MAGIC-211	1.3	R
MAGIC270	1.7	MR	MAGIC-209	1.3	R	MAGIC-296	2.2	MR	MAGIC242	1.3	R
MAGIC-315	1.7	MR	MAGIC-287	1.3	R	MAGIC216	2.3	MR	MAGIC-271	1.3	R
MAGIC030	1.7	MR	MAGIC302	1.3	R	MAGIC-195	2.5	MR	MAGIC280	1.3	R
MAGIC112	1.7	MR	MAGIC-315	1.3	R	WC 35C	2.6	MR	ITOOK-1263	1.3	R
MAGIC-019	1.7	MR	ITOOK-1263	1.3	R	MAGIC270	2.6	MR	MAGIC-005	1.3	R
MAGIC029	1.7	MR	MAGIC009	1.3	R	MAGIC112	2.6	MR	MAGIC008	1.3	R
MAGIC-081	3.2	MR	MAGIC300	2.9	MR	MAGIC232	4.1	S	MAGIC-129	2.6	MR
MAGIC243	3.3	MR	MAGIC-081	3.0	MR	MAGIC-257	4.1	S	MAGIC225	2.6	MR
MAGIC176	3.3	MR	MAGIC177	3.0	MR	MAGIC336	4.1	S	MAGIC-292	2.6	MR
MAGIC182	3.3	MR	IT93K-503-1	3.2	MR	MAGIC-238	4.2	S	MAGIC176	2.8	MR
MAGIC-117	3.3	MR	MAGIC095	3.2	MR	MAGIC297	4.2	S	MAGIC-117	2.9	MR
MAGIC-104	3.3	MR	MAGIC-129	3.2	MR	MU 9	4.2	S	MAGIC090	3.3	MR
MAGIC-238	3.3	MR	MAGIC-324	3.2	MR	SECOW 1T	4.2	S	MAGIC-104	3.3	MR
MAGIC177	3.4	MR	MAGIC-117	3.3	MR	MAGIC130	4.3	S	MAGIC-107	3.3	MR

Sources and stability of resistance to aphids in cowpea germplasm

TABLE 5. Contd.

Overall			MUARIK			NaSARRI			Ngetta ZARDI		
Genotype	Infestation (x =2.3, s.e=1.19)	Resistance status	Genotype	Infestation (x =1.9, s.e=0.92)	Resistance status	Genotype	Infestation (x =3.2, s.e=1.25)	Resistance status	Genotype	Infestation (x =1.8, s.e=0.80)	Resistance status
MAGIC-116	3.4	MR	MAGIC166	3.3	MR	MAGIC-303	4.3	S	MAGIC130	3.3	MR
MAGIC-292	3.4	MR	MAGIC-238	3.3	MR	MAGIC146	4.5	S	MAGIC-181	3.3	MR
MAGIC-233	3.4	MR	MAGIC-273	3.3	MR	MAGIC176	4.5	S	MAGIC182	3.3	MR
SECOW 2W	3.4	MR	MAGIC-194	3.4	MR	MAGIC177	4.5	S	MAGIC-257	3.3	MR
MAGIC-107	3.4	MR	MAGIC240	3.4	MR	NAROCOWPEA 2	4.5	S	MAGIC-282	3.3	MR
MAGIC-257	3.4	MR	MAGIC-323	3.4	MR	SECOW 5T	4.5	S	MAGIC301	3.3	MR
MAGIC130	3.5	MR	SECOW 1T	3.5	MR	MAGIC243	4.6	HS	NAROCOWPEA	13.3	MR
MAGIC301	3.6	S	SECOW 2W	3.8	S	MAGIC-292	5.0	HS	SECOW 1T	3.3	MR
SECOW 1T	3.7	S	MAGIC301	3.8	S	IT82E-18	5.0	HS	MAGIC-194	3.4	MR
MAGIC-194	3.9	S	MAGIC135	3.8	S	IT93K-503-1	5.0	HS	MAGIC-233	3.9	S
IT93K-503-1	4.4	S	MAGIC-175	3.8	S	MAGIC-116	5.0	HS	IT82E-18	4.5	S
IT82E-18	4.8	HS	IT82E-18	5.0	HS	MAGIC-194	5.0	HS	IT93K-503-1	4.9	HS

MUARIK = Makerere University Agricultural Research Institute, Kabanyolo, NaSARRI = National Semi-Arid Resources Research Institute, R = Resistant, MR = Moderately resistant, S = Susceptible, HS = Highly susceptible

TABLE 6. Top 20 AMMI selections of cowpea genotypes based on resistance stability estimates across environments in Uganda

Overall			MUARIK			NaSARRI			Ngetta ZARDI						
Genotype	AMMI estimate	Infestation (x =2.3, s.e=1.19)	Resistance status	Genotype	AMMI estimate	Infestation (x =1.9, s.e=0.92)	Resistance status	Genotype	AMMI estimate	Infestation (x =3.2, s.e=1.25)	Resistance status	Genotype	AMMI estimate	Infestation (x=1.8, s.e=0.80)	Resistance status
MAGIC131	0.80	1.1	R	MAGIC131	0.88	1.0	R	MAGIC131	0.77	1.3	R	MAGIC009	0.78	1.3	R
MAGIC-132	0.80	1.1	R	MAGIC-132	0.88	1.0	R	MAGIC-132	0.77	1.3	R	MAGIC020	0.78	1.3	R
MAGIC280	0.80	1.1	R	MAGIC280	0.87	1.0	R	MAGIC135	0.75	1.3	R	MAGIC033	0.78	1.3	R
MAGIC149	0.76	1.3	R	MAGIC216	0.78	1.3	R	MAGIC149	0.75	1.3	R	MAGIC099	0.78	1.3	R
MAGIC170	0.76	1.3	R	MAGIC006	0.77	1.3	R	MAGIC170	0.75	1.3	R	MAGIC101	0.78	1.3	R
MAGIC101	0.72	1.6	MR	MAGIC030	0.77	1.3	R	MAGIC280	0.75	1.3	R	MAGIC113	0.78	1.3	R
MAGIC-287	0.71	1.6	MR	MAGIC-035	0.77	1.3	R	MAGIC-287	0.60	2.2	MR	MAGIC-122	0.78	1.3	R
MAGIC-139	0.71	1.6	MR	MAGIC045	0.77	1.3	R	MAGIC-083	0.59	2.2	MR	MAGIC-126	0.78	1.3	R
SUVITA-2	0.70	1.5	R	MAGIC-046	0.77	1.3	R	MAGIC101	0.59	2.2	MR	MAGIC-139	0.78	1.3	R
MAGIC216	0.70	1.6	MR	MAGIC-073	0.77	1.3	R	MAGIC-139	0.59	2.2	MR	MAGIC157	0.78	1.3	R
WC 35C	0.69	1.7	MR	MAGIC101	0.77	1.3	R	MAGIC-224	0.59	2.2	MR	MAGIC-171	0.78	1.3	R
MAGIC270	0.69	1.7	MR	MAGIC-155	0.77	1.3	R	MAGIC276	0.59	2.2	MR	MAGIC-195	0.78	1.3	R
MAGIC-126	0.69	1.7	MR	MAGIC-174	0.77	1.3	R	MAGIC-296	0.59	2.2	MR	MAGIC-202	0.78	1.3	R
MAGIC-211	0.69	1.7	MR	MAGIC184	0.77	1.3	R	MAGIC-195	0.58	2.5	MR	MAGIC-211	0.78	1.3	R
MAGIC030	0.68	1.7	MR	MAGIC-209	0.77	1.3	R	MAGIC-078	0.58	2.0	MR	MAGIC242	0.78	1.3	R
MAGIC-019	0.68	1.7	MR	MAGIC-287	0.77	1.3	R	SUVITA-2	0.58	2.0	MR	MAGIC-271	0.78	1.3	R
MAGIC029	0.68	1.7	MR	MAGIC302	0.77	1.3	R	MAGIC216	0.54	2.3	MR	MAGIC280	0.78	1.3	R
MAGIC-050	0.68	1.7	MR	MAGIC-315	0.77	1.3	R	WC 35C	0.53	2.6	MR	ITOOK-1263	0.77	1.3	R
MAGIC-115	0.68	1.7	MR	ACC12 x SEC 3B	0.77	1.3	R	MAGIC270	0.53	2.6	MR	MAGIC-004	0.77	1.3	R
MAGIC-217	0.68	1.7	MR	ITOOK-1263	0.77	1.3	R	ACC12 x SEC 3B	0.51	2.6	MR	MAGIC-005	0.77	1.3	R

MUARIK = Makerere University Agricultural Research Institute, Kabanyolo, NaSARRI = National Semi-Arid Resources Research Institute

Sources and stability of resistance to aphids in cowpea germplasm

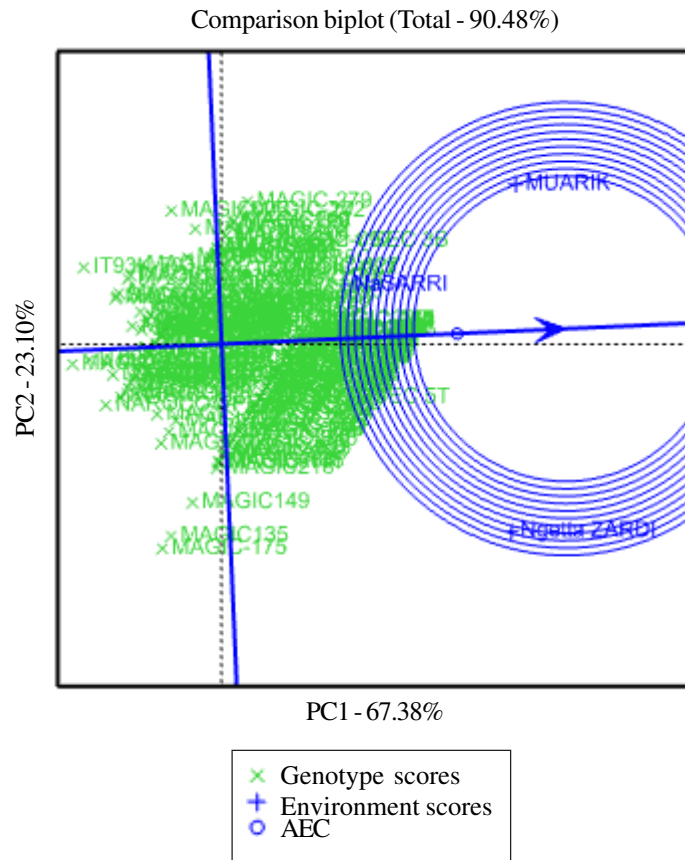


Figure 3. Environment-focused comparison biplot for aphid resistance over two seasons in Uganda.

infestation (Table 2), indicates genetic variability among the cowpea materials evaluated; suggesting the possibility of genetically improving cowpea resistance of the locally available cowpea materials against aphids (Avosa *et al.*, 2020).

The significant variations observed among genotypes for aphid resistance could be attributed to biochemical factors affecting behavior and metabolic processes of the aphids; or morphological factors influencing the mechanisms of locomotion, feeding, oviposition, ingestion and digestion of the pest (Onyishi *et al.*, 2013). Togola *et al.* (2020) argued that aphid resistance in cowpea is associated with low sucrose and high phenolic aglycones (kaempferol and quercetin) content in host plants. It is possible that a combination of biochemical and morphological factors co-

influence the resistance trait in cowpea against aphids, and these might be controlled by certain genes (Boukar *et al.*, 2016). Van Emden (1991) earlier reported that resistance to aphids in cowpea is governed by a single dominant gene; further studies to confirm this argument will provide useful information in the improvement of the cowpea resistance against aphid in cowpea in Uganda.

Table 5 shows that the MAGIC accessions MAGIC131, MAGIC-132, MAGIC280, MAGIC149 and MAGIC170 were resistant to aphids. This indicates that the multi-parent advanced generation intercross (MAGIC) population contained sources of resistance against cowpea aphid (*Aphis craccivora*), which could be used to introgress aphid resistance into farmers' preferred but susceptible cowpea cultivars in Uganda. Since

TABLE 7. Yield performance of the cowpea genotypes overall and across environments based on AMMI yield values

Genotype	MUARIK			NaSARRI			Ngetta ZARDI				
	Resistance status	Grain weight per plant (\bar{x} =38.46, s.e=29.44)	Genotype	Resistance status	Grain weight per plant (\bar{x} =45.28, s.e=36.0)	Genotype	Resistance status	Grain weight per plant (\bar{x} =25.15, s.e=17.0)	Genotype	Resistance status	Grain weight per plant (\bar{x} =44.95, s.e=27.4)
MAGIC-125	MR	102.39	MAGIC-125	R	209.46	MAGIC-292	HS	65.06	MAGIC153	R	195.63
MAGIC-171	MR	94.57	MAGIC-333	R	188.60	MAGIC-004	MR	59.39	NAROCOWPEA 4	R	119.92
MAGIC153	MR	86.21	MAGIC-282	MR	169.26	NAROCOWPEA 1	S	54.80	MAGIC-094	MR	113.58
MAGIC-333	MR	83.39	MAGIC-171	MR	154.66	MAGIC-323	MR	54.46	MAGIC177	MR	109.67
MAGIC177	MR	79.51	MAGIC060	MR	140.77	MU 9	S	52.15	MAGIC-262	R	107.73
MAGIC-292	MR	78.34	MAGIC-039	R	136.37	MAGIC-279	MR	51.11	MAGIC-195	R	105.08
MAGIC-282	MR	74.12	MAGIC184	R	120.68	MAGIC144	MR	48.75	MAGIC-171	R	101.04
MAGIC249	MR	71.96	MAGIC-238	MR	110.69	ACC12 x SEC 3B	MR	48.11	MAGIC249	R	95.22
MAGIC162	MR	71.75	SEC 4W * SEC 5T	MR	110.15	SECOW 5T	S	47.86	MAGIC265	R	94.20
SECOW 1T	S	70.02	MAGIC-097	R	109.02	MAGIC-183	MR	47.73	MAGIC-040	R	90.10
SEC 4W * SEC 5T	MR	69.34	MAGIC101	R	105.41	MAGIC-046	MR	47.21	MAGIC033	R	87.10
NAROCOWPEA 4	MR	69.15	MAGIC120	R	104.91	MAGIC-234	MR	47.06	SECOW 5T	MR	86.60
MAGIC-204	MR	67.25	MAGIC-204	MR	104.24	MAGIC-181	MR	45.85	MAGIC-129	MR	86.38
MAGIC-039	MR	66.92	MAGIC111	R	103.26	NAROCOWPEA 3	MR	44.99	MAGIC-073	R	86.28
MAGIC060	MR	66.87	SECOW 1T	MR	101.51	MAGIC304	MR	44.72	MAGIC090	MR	85.68
MAGIC-097	MR	66.23	MAGIC162	MR	98.11	MAGIC006	MR	44.68	MAGIC-152	R	85.15
NAROCOWPEA 3	MR	66.12	MAGIC170	R	97.93	MAGIC-081	S	43.76	MAGIC162	MR	84.88
MAGIC-233	MR	66.06	SECOW 4W	R	95.47	MAGIC-027	MR	43.57	MAGIC-292	MR	84.85
MAGIC090	MR	65.26	MAGIC225	MR	95.12	MAGIC320	MR	43.18	MAGIC-104	MR	83.46
MU 9	MR	63.67	MAGIC-087	R	94.02	MAGIC020	MR	42.97	MAGIC-172	R	81.76

R = Resistant, MR = Moderately resistant, S = Susceptible, HS = Highly susceptible

the eight founder parents varied in resistance to aphids, the MAGIC population is likely to segregate for aphid stress resistance traits and could contain lines with unique and novel combinations of resistance genes against aphids. The MAGIC lines generally outperformed the founder parents in their resistance to aphids (Table 6). This could be due to transgressive segregation for the traits in the MAGIC population.

MAGIC populations have great genetic and phenotypic diversity (Huang *et al.*, 2015), providing opportunities for improvement of important traits such as aphid resistance in cowpea, coming from different functional genetic backgrounds. Because of this, the wider phenotypic variations in the MAGIC population could be used to detect quantitative trait loci (QTL) and candidate genes associated with aphid resistance in cowpea.

The founder parent SUVITA-2, which was found to be aphid resistant in this study (Table 5), was also reported to be resistant to Striga, foliar thrips and *Macrophomina* disease; and tolerant to drought (Hyunh *et al.*, 2018); thus could serve as a source of resistance genes against aphids in Uganda. The founder parents, IT84S-2246 and ITOOK-1263, reported to be resistant to aphids by Hyunh *et al.* (2018), were moderately resistant in the present study. In South Africa, Letsoalo (2015) reported the cowpea founder parent ITOOK-1263 to be resistant against aphids in field experiments; while Onyishi *et al.* (2013) earlier reported the genotype IT89KD-288 to be resistant against cowpea aphids in Nigeria. These parents were moderately resistant against aphids in Uganda in the present study, indicating the potential of the genotypes in aphid resistance breeding. This discrepancy in their performance might be due to environmental differences in the countries where the other studies were conducted. This underpins the importance of verification trials for the trait of interest in different locations.

The highly significant genotype by environment interaction (GEI) effects

observed in the present study (Table 2) indicates that variations among genotypes and environments had pronounced effects on the expression of the resistance traits; suggesting that the cowpea genotypes performed differently in different environments on the resistance trait. This result revealed differential resistance among cowpea genotypes across testing environments, due to the presence of GEI. Since both genotype and environment effects were highly significant ($P < 0.001$), both factors are important in governing the expression of the aphid resistance traits (Gedif *et al.*, 2014). The presence of GEI could complicate the selection process of superior genotypes, and might reduce the selection efficiency in aphid resistance breeding (Osei *et al.*, 2017). This justifies the exploration of the stability of the resistance and further evaluation of promising genotypes in various test environments. Therefore, widely adapted cowpea genotypes with dynamic resistance stability are recommended to support cowpea production in aphid-prone areas.

The scatter biplot for mega environments delineation and the environment-focused comparison biplot for aphid resistance against aphids in cowpea identified three mega environments with most of the genotypes close to the origin (Fig. 1). This indicates that the tested environments were unique, with specific resistant genotypes; and emphasised the presence of crossover interaction. The top four AMMI selections in Ngetta ZARDI were MAGIC033, MAGIC-126, MAGIC-171 and MAGIC-195. In MUARIK, the top four were MAGIC-132, MAGIC131, MAGIC280 and MAGIC216; while in NaSARRI, the top four were MAGIC-132, MAGIC131, MAGIC149 and MAGIC135 (Table 6). This means that evaluation and recommendation of genotypes based on any single location would be unreliable because of the differences in genetic response across locations (Mare *et al.*, 2017). Under such a situations, it is recommended that genotype evaluation be based on mean performance and stability (Yan and Kang,

2002). In this case, a desirable genotype is one with a high stability estimate, which is associated with resistance performance (Oliveira *et al.*, 2014).

According to the AMMI stability ranking of genotypes, MAGIC131, MAGIC-132, MAGIC280, MAGIC149, MAGIC170, MAGIC101, MAGIC-287, MAGIC-139 and SUVITA-2 were the most stable in resistance against aphids (Table 6); and are recommended for further investigations. The genotypes appeared to be more resistant in MUARIK than in other test locations (Ngetta ZARDI and NaSARRI). Discriminating and representative test locations are useful for selecting superior genotypes; while eliminating inferior ones (Etnaf *et al.*, 2013). However, since the aphid pressure was highest in NaSARRI; this environment is the best for evaluating promising genotypes for cowpea resistance to aphids.

The positive and significant correlation between aphid infestation and damage indicated linear relationships between these traits (Table 3), suggesting that aphid infestation leads to aphid feeding damage in aphid susceptible genotypes. However, since this correlation coefficient was low, both resistance measures should be considered when screening reaction of cowpea against aphids in field trials. Nevertheless, aphid damage symptoms in field experiments can be confounded by several other factors (such as diseases and other pests) that might be difficult to control leading to misleading results. The positive correlations between days to 50% flowering and 50% maturity with aphid damage ($r = 0.486$ and $r = 0.573$, respectively) indicate that aphid infestation and damage resulted in delayed flowering and late maturity in susceptible genotypes. Accordingly, the resistant and moderately resistant genotypes showed lower aphid infestation and damage scores, reduced number of days to 50% flowering; and 50% maturity and 50% maturity and higher number of pods per plant.

Souleymane *et al.* (2013) also reported delayed initiation of flowering in cowpea due to high aphid infestation at vegetative stage; while Zheng *et al.* (2017) indicated that aphid infestation would result in yield reduction in susceptible cowpea genotypes in the field. This is because aphid infestation reduces the photosynthetic surface due to sooty mould and colony cover, and aphid feeding reduces yield through withdrawing/sucking materials and nutrients that would otherwise be deposited in the sinks for grain filling (Åhman *et al.*, 2019). In the present study, aphid infestation negatively correlated with number of grains per pod, indicating that the infestation caused reduction in number of pods in susceptible genotypes.

CONCLUSION

The study identified new aphid resistant and stable cowpea genotypes, including MAGIC131, MAGIC-132, MAGIC149, MAGIC170 and MAGIC280 from the MAGIC panel; SUVITA-2 from the parental genotypes; and moderately resistant and stable genotypes MAGIC101, MAGIC-139, MAGIC-287. These genotypes are recommended as promising donor sources for cowpea aphid resistance breeding in Uganda. The moderately resistant genotypes, MAGIC-125, MAGIC-171, MAGIC153, MAGIC-333, MAGIC177, MAGIC-292, MAGIC282, MAGIC249, MAGIC162, SEC 4W * SEC 5T, NAROCOWPEA 4, MAGIC-204, MAGIC-039, MAGIC060, MAGIC-097, NAROCOWPEA 3, MAGIC-233, MAGIC090 and MU 9, which are also high yielding are recommended for further testing as promising accessions against aphids in cowpea growing areas. The data generated in this study can be used in genome-wide association studies to identify quantitative trait loci (QTL) and candidate genes associated with aphid resistance in cowpea.

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