agriculture

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Identifying Cassava Genotypes Resistant to the African Cassava Whitefly, *Bemisia tabaci* (Gennadius)

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Abstract: The whitefly, *Bemisia tabaci*, is a major pest of cassava in Africa. Developing whitefly-resistant cassava can control both whiteflies and viral diseases. The main aim of this study was to identify cassava genotypes resistant to four *B. tabaci* populations, sub-Saharan Africa 1—subgroups 1, 2, and 3 (SSA1-SG1, SSA1-SG2, and SSA1-SG3) and sub-Saharan Africa 2 (SSA2) that colonize cassava, as well as understand the mechanisms of resistance. Utilizing the antixenosis and antibiosis techniques in the choice and no-choice tests, respectively, to screen for whitefly resistance, we tested 46 cassava genotypes. Of these, 11 (Njule Red, Nase 3, Nase 1, Kibandameno, Sagonja, Aladu, Kiroba, Magana, 72-TME-14, Sauti, and PER 415) exhibited antixenosis, as they were least preferred for oviposition by all four whiteflies population in choice tests. Ten genotypes exhibited antibiosis (nymph mortality) against SSA1-SG1 and SSA1-SG3 in no-choice tests, and these were, Pwani, Nase 14, Kalawe, Eyope, NGA11, CoI2246, Mkumbozi, KBH2002/0066, Yizaso, and PER 608. Eight genotypes—Tongolo, Mbundumali, Colicanana, Orera, Ofumbachai, Nam 130, Tajirika, and MECU72—exhibited both antixenosis and antibiosis mechanisms against SSA1-SG1 and SSA1-SG3. And these can be considered the best sources of resistance for the potential development of whitefly-resistant cassava varieties in African countries.

Keywords: African whitefly; *Manihot esculenta Crantz*; whitefly resistance; whitefly populations; choice and no-choice test

Citation: Atim, J.; Kalyebi, A.; Bohorquez-Chaux, A.; Lopez-Lavalle, L.A.B.; Omongo, C.A.; Colvin, J.; Maruthi, M.N. Identifying Cassava Genotypes Resistant to the African Cassava Whitefly, *Bemisia tabaci* (Gennadius). *Agriculture* **2024**, *14*, 1016. https://doi.org/10.3390/agriculture14071016

Academic Editor: Ana Isabel López-Sesé

Received: 8 May 2024
Revised: 20 June 2024
Accepted: 21 June 2024
Published: 27 June 2024

1. Introduction

The whitefly *Bemisia tabaci* (Gennadius) *sensu lato* causes direct damage to cassava (*Manihot esculenta Crantz*) by feeding on the phloem sap of the leaves [1]. This causes symptoms such as chlorosis and stunting in plants. Feeding by high numbers of whiteflies can result in the development of sooty mold on lower leaves due to excessive deposition of honeydew, thereby reducing the plant's photosynthetic capacity [1], which can result in 60% root and stem yield loss [2,3]. However, the most important damage caused by *B. tabaci* to cassava is the transmission of plant viruses [4,5]. *B. tabaci* vectors over 200 virus species, including cassava brown streak ipomoviruses (CBSIs) and cassava mosaic begomoviruses (CMBs), which cause cassava brown streak disease (CBSD) and cassava mosaic disease (CMD), respectively [6–8]. CMD and CBSD are the two devastating viral diseases of cassava in Africa [9,10]. The viral diseases and the high populations of *B. tabaci* reported on cassava are the most important threats to cassava production in Africa [8,9]. The main whitefly

(*Bemisia tabaci*) populations that infest cassava are sub-Saharan Africa 1 (SSA1) and sub-Saharan Africa 2 (SSA2). SSA1 has been divided into separate species/subgroups (Subgroup 1-SG1/Subgroup 2-SG2 and Subgroup 3-SG3); SG1 and SG2 are a single biological species since they interbreed [11–16].

The development of whitefly-resistant cassava varieties is arguably the best means of controlling whiteflies and the viruses they transmit [8,17]. The need to combine whitefly and virus resistance with other farmer-preferred qualities of cassava has accelerated efforts to identify resistance [17].

The International Centre for Tropical Agriculture (CIAT) in Colombia has evaluated more than 5000 cassava clones for resistance to *Aleurotrachelus socialis*, another predominant whitefly species attacking cassava in the Latin American countries of Venezuela, Panama, Ecuador, and Colombia [18,19]. Several of these cassava cultivars, including MECU72, were identified with high levels of resistance to *A. socialis* [18,20,21], which experienced higher nymphal mortality rates, less oviposition, longer developmental time, and reduced nymph size [20]. The MECU72 and some Ugandan cassava landraces, such as Ofumbachai, Nabwire 1, and Mercury, have also shown good levels of resistance to the African cassava whitefly *B. tabaci* [17]. However, the mechanism of resistance to the whiteflies in cassava is not well understood.

Two mechanisms of resistance against insect pests are identified: antixenosis and antibiosis. Whereas antixenosis refers to the lack of preference by insects to feed, oviposit, or shelter on a specific host, antibiosis refers to the adverse biological consequences of feeding on resistant host plants during the life stages of the pest [22–25]. To understand these mechanisms of resistance, two types of assessments are used: choice and no-choice tests [20,26,27]. In the choice tests, whiteflies are given the opportunity to choose between two or more different host varieties/genotypes, while in the no-choice tests, only one host is accessible to the whiteflies, and failure to successfully feed on it would lead to slow growth or death of the whitefly. Choice tests reveal genotypes with both antixenosis and antibiosis resistance mechanisms, and no-choice tests focus only on antibiosis [28]. The broader objective of our study was to identify cassava genotypes resistant to African cassava whitefly *B. tabaci* and to characterize the mechanisms of whitefly resistance. Resistant genotypeswhen identified, can be incorporated into breeding programs as parents to transfer the whitefly resistance to farmer-preferred cassava varieties.

2. Materials and Methods

2.1. Cassava Genotypes

Screening of cassava genotypes for resistance to *B. tabaci* was conducted in the quarantine insectary laboratories of the Natural Resources Institute (NRI), UK, in 2016–2017 under controlled conditions of 27–30 °C, 60% relative humidity, and a 14L:10D photoperiod. A total of 46 cassava genotypes were selected for evaluation in this study based on (i) previous records of resistance to the Latin American whitefly, *A. socialis*, and African cassava whitefly, *B. tabaci*, and (ii) resistance/tolerance to CMD and CBSD, the two major diseases of cassava (Table 1). Twelve of these genotypes were from Latin America, LA (resistant to *A. socialis*), seven were landraces from Uganda (resistant to *B. tabaci*), and 32 were improved cassava cultivars assembled under the project "5CP". 5CP refers to the cassava genotypes derived from submissions of the best virus-resistant varieties evaluated in five African countries: Uganda, Malawi, Mozambique, Kenya, and Tanzania [29]. The test plants were raised from virus-indexed, tissue-cultured plantlets and planted in insect-proof glasshouses, maintained as stock plants [29,30]. Cassava stems (10–15 cm long) were cut and dipped in rooting hormones (Strike, Bayer Garden, Cambridge, UK) before planting in 50:50 soil and compost (John Innes No. 2, UK) in 5 cm × 5 cm × 8 cm disposable plastic pots. They were grown in incubation trays covered with transparent lids to retain moisture. The lid was removed after 14 days when the plants had 2–3 leaves after which the plants were grown for a further 6–8 weeks before their use in the experiments.

Table 1. List of genotypes screened for *Bemisia tabaci* resistance at NRI insectary, 2016–2017.

S/No	Variety	Country of Origin	Characteristics *
1	BRA 327	Brazil	Whitefly-susceptible (*Aleurotracheus socialis*)
2	ECU 64	Ecuador	Whitefly-resistant (*Aleurotracheus socialis*)
3	Col2246	Colombia	Whitefly-susceptible (*Aleurotracheus socialis*)
4	MECU72 (ECU72)	Ecuador	Whitefly-resistant (*Aleurotracheus socialis*)
5	PER 273	Peru	Whitefly-resistant (*Aleurotracheus socialis*)
6	PER 330	Peru	Whitefly-resistant (*Aleurotracheus socialis*)
7	PER 334	Peru	Whitefly-resistant (*Aleurotracheus socialis*)
8	PER 317	Peru	Whitefly-resistant (*Aleurotracheus socialis*)
9	PER 335	Peru	Whitefly-resistant (*Aleurotracheus socialis*)
10	PER 368	Peru	Whitefly-resistant (*Aleurotracheus socialis*)
11	PER 415	Peru	Whitefly-resistant (*Aleurotracheus socialis*)
12	PER 608	Peru	Whitefly-resistant (*Aleurotracheus socialis*)
13	Aladu (Alado alado)	Uganda (Landraces)	Whitefly-resistant (*Bemisia tabaci*)
14	Magana	Uganda (Landrace)	Whitefly-resistant (*Bemisia tabaci*)
15	Nam 130 (NaroCass1/UG3/Tz30)	Uganda (cultivar)	Whitefly-resistant (*Bemisia tabaci*)
16	Njule Red	Uganda (cultivar)	Whitefly-resistant (*Bemisia tabaci*)
17	Ofumbachai	Uganda (Landrace)	Whitefly-resistant (*Bemisia tabaci*)
18	Tongolo	Uganda (Landrace)	Whitefly-resistant (*Bemisia tabaci*)
19	LM1/2008/363	Kenya	Moderate resistance to CMD and CBSD
20	F19-NL	Kenya	Moderate resistance to CMD and CBSD
21	Tajirika	Kenya	Moderate resistance to CMD and CBSD
22	Shibe	Kenya	Moderate resistance to CMD and CBSD
23	F10-30-R2	Kenya	Moderate resistance to CMD and CBSD
24	Kibandameno	Kenya	Susceptible to CMD and CBSD
25	Mkumbozi	Tanzania	Moderate resistance to CMD and CBSD
26	Kaleso	Kenya	Resistant to CBSD and susceptible to CMD
27	Yizaso	Malawi	Moderate resistance to CMD and CBSD
28	Mbundumali	Malawi	Susceptible to CMD and CBSD
29	Sauti	Malawi	Moderate resistance to CMD and CBSD
30	CHO 5/203	Malawi	Moderate resistance to CMD and CBSD
31	Sagonja	Malawi	Moderate resistance to CMD and CBSD
32	Kalawe	Malawi	Moderate resistance to CMD and CBSD
33	Oekhumelela	Mozambique	Moderate resistance to CMD and CBSD
34	Eyope	Mozambique	Moderate resistance to CMD and CBSD
35	Nziva	Mozambique	Susceptible to CMD, moderate to CBSD
36	Colicanana	Mozambique	Susceptible to CMD, moderate to CBSD
37	Orera	Mozambique	Susceptible to CMD, moderate to CBSD
38	KBH 2002/066	Tanzania	Moderate resistance to CMD and CBSD
39	Pwani	Tanzania	Moderate resistance to CMD, strong to CBSD
40	Mkumba	Tanzania	Moderate resistance to CMD, strong to CBSD
41	Kizimbani	Tanzania	Moderate resistance to CMD and CBSD
42	KBH 2006/26	Tanzania	Moderate resistance to CMD and CBSD
43	Albert	Tanzania	Susceptible to CMD and CBSD
44	Kiroba	Tanzania	Moderate resistance to CMD and CBSD
45	Nase 3 (Migyera)	Uganda	Moderate resistance to CMD and CBSD
46	TME 204	Uganda	Strong resistance to CMD, susceptible CBSD
47	Tz 130 (NaroCass1)	Tanzania	Strong resistance to CMD, moderate CBSD
48	Nase 18	Uganda	Strong resistance to CMD, moderate CBSD
49	72-TME 14	Uganda	Strong resistance to CMD, moderate CBSD
50	Nase 14	Uganda	Strong resistance to CMD, moderate CBSD
51	Nase 1	Uganda	Strong resistance to CMD, moderate CBSD

* CMD—cassava mosaic disease, CBSD—cassava brown streak disease.

2.2. Whitefly Colonies

Colonies of *B. tabaci* sub-Saharan Africa 1—subgroups 1–3 (SSA1-SG1/SG2 and SSA1-SG3) and *B. tabaci* sub-Saharan Africa 2 (SSA2) collected initially from Uganda and Tanzania were used [31]. The colonies were maintained on egg plants in the NRI insectary at 27–30 °C, 60% relative humidity, and a 14L:10D photoperiod. The species and subgroups were confirmed using PCR-RFLP analysis of the mtCO1 amplicons [14,15]. The analysis confirmed the presence of four whitefly cryptic species: SSA1-SG1, SSA1-SG2, SSA1-SG3, and SSA2. Since SSA1-SG1 and SSA1-SG2 interbred, they are considered one species/populations [16]. Therefore, in this study, for simplicity, the four whitefly groups are referred to as populations instead of species.

2.3. Choice Tests

A choice test was carried out on all 46 cassava genotypes in the insectary. Six-week-old plants (five per genotype) of the 46 genotypes were randomly placed in eight BugDorm cages (Mega View Science Co. Ltd., Taichung City, Taiwan) measuring 32.5 cm × 32.5 cm × 77.0 cm (width × diameter × height). A susceptible control genotype (Col2246) was included. The cages were laid out in a completely randomized design (CRD) in five replications. About 2000 whitefly adults of the SSA1-SG1 populations reared on eggplants were released into each cage containing at least 27 cassava plants. Three days after whiteflies were released into the cages, the first three expanded leaves of each test plant were labeled using a marking tape, and eggs laid on them were counted with the aid of a magnifying glass and a tally counter. Total numbers of nymphs were observed and recorded on each test plant when 90% of adults emerged from the susceptible control. The same experiments were conducted for SSA1-SG2, SSA1-SG3, and SSA2. All experiments were terminated 30 days after infestation except for SSA1-SG3, which went on for 37 days, which is when about 90% of the nymphs emerged on Col2246. To assess the numbers of third and fourth instar nymphs and empty pupal cases (EPC: Figure 1), the leaves from each cassava genotype were collected in zip-lock plastic bags (to prevent moisture loss), and pictures of leaves with nymphs on the abaxial side were taken using a camera and photo box. With the aid of a tally counter, the numbers of eggs laid, nymphs developed, and adults that emerged were counted, as well as the empty pupal cases on each genotype, and recorded.

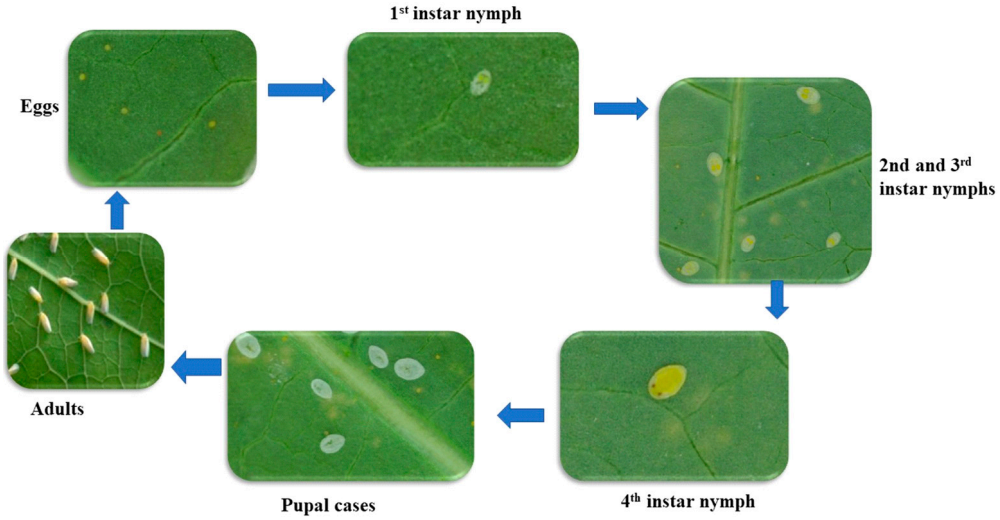

Figure 1. Life cycle stages of the whitefly, *B. tabaci*, showing distinct features taken from the abaxial side of the leaf [32] recorded during data collection.

2.4. No-Choice Tests

Forty-five genotypes were screened in no-choice tests, including one resistant cassava genotype (MECU72) and two susceptible controls (to *A. socialis*) (Col2246 and NGA11) for two populations (SSA1-SG1 or SSA1-SG3). About 50 whiteflies of mixed sex were

introduced onto three plants of each genotype (six weeks old) in individual BugDorm cages with dimensions of 60 cm × 60 cm × 120 cm for width, diameter, and height, respectively. The adults were left to oviposit for 72 h, then removed, and the number of eggs laid on the top 3 leaves was recorded. The numbers of nymphs developed were recorded at 3, 7, 14, 21, 28, and 35 days post infestation to determine the fecundity, oviposition preference, whitefly development time, and behavior of both SSA1-SG1 and SSA1-SG3 on different cassava genotypes.

2.5. Data Analysis

An analysis of variance was conducted to compare cassava genotypes on the basis of the numbers of eggs, nymphs, and EPCs, and the means were compared at the $p = 0.05$ level in R (R Core Team, R version 3.3.2, a language and environment for statistical computing). R Foundation for Statistical Computing, Vienna, Austria. URL https://www.R-project.org/ (accessed on 30 March 2022). Analyses of count data for eggs, nymphs, and EPCs used generalized linear models (GLMs), with data distribution specified as negative binomial. Model residual deviance was checked against residual degrees of freedom to confirm that this was an appropriate distribution choice. Post hoc comparisons between means used a Holm-corrected least significant difference test (R: agricolae package), with standard errors estimated by the negative binomial GLM model [33]. Total nymphs were calculated as the sum of the third and fourth instars as well as the adults (empty pupal cases, EPC) on the three leaves. In both choice and no-choice tests, the average mean from all four or two whitefly populations was calculated, respectively. The whitefly life stage data was pooled due to the presence of numerous genotypes with limited replicates and the substantial penalty associated with multiple comparisons. To address this, we ensured and assumed the absence of repeated counts. Aggregating the data increased the overall sample size, thereby enhancing the statistical power to detect effects or differences that might otherwise remain undetectable in smaller individual samples. An overview of the resistance was assessed by principal component analysis (PCA). The PCA was calculated with the R prcomp function, which uses the singular value decomposition of a centered and scaled data matrix.

3. Results

3.1. Performance of Cassava Genotypes in Choice Tests

The averages from the whitefly life stages (eggs, total nymphs, and adults) and four whiteflies population were used to analyze the interaction. There was a highly significant interaction between the cassava genotype and whiteflies population ($p < 0.00001$) (Table 2), and a significant relationship between whitefly life stages and populations.

Table 2. Three-way analysis of deviance showing the relationship between genotypes, pooled counts of eggs, total nymphs, and adults (life stages) for the four *Bemisia tabaci* populations in the choice test.

Interaction	Degree of Freedom	Deviance Chi-Square Units	*p*-Value
genotype	45	560.61	<0.00001
Life stage	2	783.07	<0.00001
Populations	3	928.08	<0.00001
Genotype × life stage	90	103.77	0.15213
Genotype × populations	120	617.86	<0.00001
Life stage × populations	6	116.03	<0.00001
Genotype × life stage × populations	233	172.37	0.99892
Residual	1797	2568.8	

The Chi-square statistic was used to distinguish the interaction between cassava genotypes, the different whitefly stages, and the four populations using a negative binomial generalized linear model.

A three-way analysis of deviance by genotype origin (Latin American or African), whitefly life stages, and whiteflies population also indicated a significant interaction between the origin of the cassava genotype and whiteflies population ($p < 0.01524$) (Table 3). Differential genotype reactions in the *B. tabaci* populations were apparent ($p < 0.00001$). Latin American cassava genotypes recorded significantly fewer numbers of whiteflies (136.5 ± 8.2) as compared to the African genotypes (194.9 ± 5.8) ($p < 0.00001$).

Table 3. Three-way analysis of deviance by genotype origin (Latin America or Africa), pooled counts of eggs, total nymphs, and adults (life stages) for the four *Bemisia tabaci* populations in the choice test.

Interaction	Degree of Freedom	Deviance Chi-Square Units	*p*-Value
Origin	1	37.07	<0.00001
Life stage	2	544.43	<0.00001
Populations	3	670.8	<0.00001
Origin × life stage	2	4.03	0.13332
Origin × populations	3	10.43	0.01524
life stage × populations	6	75.27	<0.00001
Origin × life stage × populations	6	6.27	0.39363
Residual	2273	2674.11	

The Chi-square statistic was used to distinguish the interaction between cassava genotype's origin (Latin America and Africa), the different whitefly stages and four populations using a negative binomial generalized linear model.

The interaction between whitefly life stages and whiteflies population was also highly significant for total averages from eggs, total nymphs, and empty pupal cases ($p < 0.00001$) (Table 3). This was further shown by the mean differences between different whiteflies population (SSA1-SG1/SSA1-SG2, SSA1-SG3, and SSA2) (Table 4). SSA1-SG3 had the highest numbers of whitefly life stages (335.3 ± 16.6 c), followed by SSA1-SG2 and SSA2 (165.3 ± 8.3 b, 170.1 ± 9.2 b, respectively) and the least means were from SSA1-SG1 (69.8 ± 3.3 a).

Table 4. Mean number of life stages (eggs, nymphs, and adults) for the four African whitefly *Bemisia tabaci* populations on cassava genotypes from Latin America and Africa in the choice experiment.

Genotype	Mean ± Standard Error	
NGA11 (Susceptible control)	613.5 ± 120.6	d
Mkumbozi	531.4 ± 100.7	cd
Kaleso	319.2 ± 81.4	cd
Eyope	271.3 ± 52.1	bcd
F10-30-R2	253.2 ± 56.7	bcd
CHO 5/203	251.2 ± 46.6	bcd
KBH 2002/066	243 ± 41.1	bcd
F19-NL	236.5 ± 44.4	abcd
Yizaso	232.3 ± 56.9	abcd
Nziva	231.5 ± 39.1	abcd
Kalawe	229.2 ± 36.7	abcd
Col2246 (Susceptible control)	227.3 ± 29.9	abcd
Pwani	225 ± 37.7	abcd
Oekhumelela	222.9 ± 37.7	abcd
Shibe	208.2 ± 49.1	abcd
Albert	202.3 ± 34.9	abcd
Nase 3	196.3 ± 32.9	abcd
Mkumba	191.7 ± 35.9	abcd
Nase 14	190.2 ± 32.2	abcd
PER 608	188.9 ± 32.6	abcd
Nase 18	186 ± 31.5	abcd
Kibandameno	176.4 ± 27.4	abcd

Table 4. *Cont.*

Genotype	Mean ± Standard Error	
Tongolo	174 ± 33.4	abcd
Mbundumali	166.8 ± 27	abcd
TME 204	162.3 ± 27.2	abcd
KBH 2006/26	157.3 ± 25.7	abcd
Aladu	154.8 ± 25.7	abcd
Kizimbani	152.4 ± 30	abcd
Colicanana	144.9 ± 23.5	abcd
Magana	143.6 ± 29.4	abcd
Nam 130	143.2 ± 23.4	abcd
Tajirika	143.1 ± 23.4	abcd
Sagonja	141.1 ± 25.1	abc
Ofumbachai	140.5 ± 24	abc
Nase 1	133.4 ± 32.7	abc
Orera	132.6 ± 23.8	abc
Kiroba	131.3 ± 24.9	abc
LM1/2008/363	120.1 ± 20.1	abc
MECU72 (Resistant control)	119.1 ± 15.2	abc
72-TME 14	109.2 ± 24.5	abc
PER 317	108.4 ± 18	abc
PER 335	99.4 ± 14.7	abc
PER 415	91.1 ± 16.2	ab
PER 368	76.1 ± 14.1	ab
Njule Red	61.4 ± 11.7	a
Sauti	55.3 ± 10.1	a

Five plants per genotype for each whiteflies population screened. Multiple comparisons between means were from a Holm-corrected least significant difference method, using data from the negative binomial generalized linear model. Means with the same letter code are not significantly different at the $p = 0.05$ level.

Although not significantly different, NGA11 had a slightly higher mean number of whitefly life stages (613.5 ± 120.6) than Mkumbozi (531.4 ± 100.7) and Kaleso (319.2 ± 81.4) when means were combined for the four whiteflies population. The *B. tabaci* populations were few on Sauti, Njule, PER 415, and PER 368, with means of less than 92 total life stages (eggs, nymphs, and adults) per three top leaves for the four-whiteflies population (Table 4). Latin American (LA) genotypes (MECU72, PER 317, PER 335, PER 415, and PER 368) had fewer numbers of whitefly life stages compared to African genotypes, with mean numbers less than 120 for total life stages (eggs, nymphs, and adults) (Table 4). Of the life stages counted on the cassava genotypes, eggs were the highest (mean number 239.0 ± 10.3) but not significantly different from nymphs (236.1 ± 10.3 b) compared to adults (68.3 ± 3.1 a) that had lower means in the choice test.

SSA1-SG1 laid few eggs on Tajirika and PER 415, while fewer numbers of nymphs developed on Sauti, Pwani, PER 415, Njule Red, Nase 3, Mkumba, MECU72, Magana, KBH 2006/26, Kalawe, and F19-NL. The rest of the genotypes did not differ significantly. SSA1-SG1 numbers were relatively higher on NGA 11, Shibe, Kibandameno, and KBH 2002/066 (Figure 2) compared to the other genotypes. SSA1-SG2 laid fewer eggs on Tajirika, PER 415, PER 335, and Kiroba, while more eggs were laid on Nase 14, Mkumbozi, Kalawe, F19-NL, CHO5/203, and Aladu. SSA1-SG3 had fewer eggs or developed nymphs on Tajirika, PER 415, PER 368, PER 317, Ofumbachai, Njule Red, Nase 3, Nase 14, Nam 130, MECU72, Magana, Mkumba, LM1/2008/363, Kibandameno, KBH 2006/26, and Aladu. SSA1-SG3 equally preferred NGA 11, Kaleso, and Kalawe for oviposition (Figure 2).

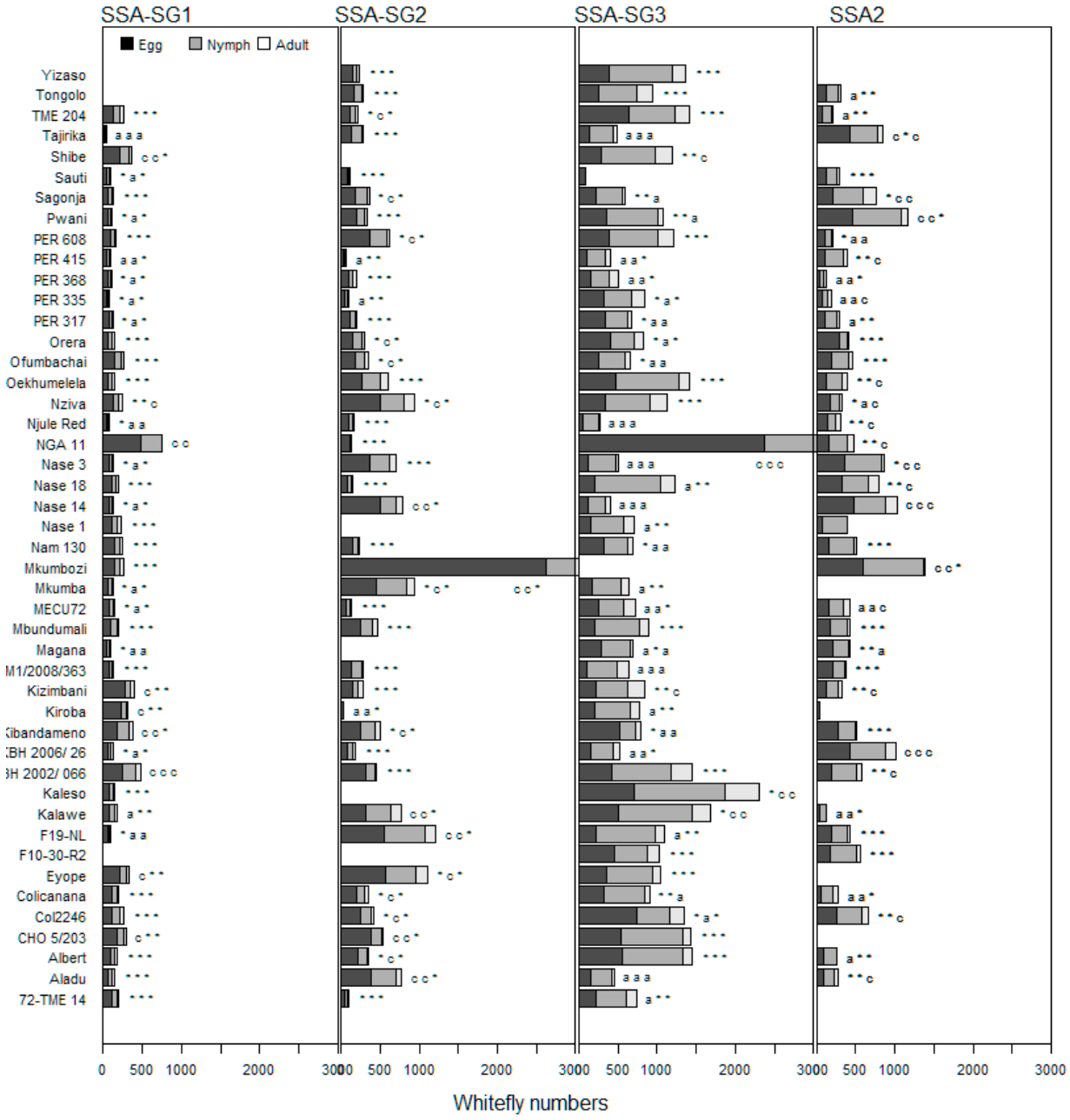

Figure 2. The mean number of eggs, nymphs, and adults of the four whiteflies population (SSA1-SG1, SSA1-SG2, SSA1-SG3, and SSA2) on the cassava genotypes from Latin America and Africa in the choice experiment. Multiple comparisons between means were from the Holm-corrected least significant difference method, using data from the negative binomial generalized linear model. Means with the same letter code are not significantly different at the $p = 0.05$ level. a: (resistant group) significantly different from the most susceptible genotypes. c: (susceptible group) significantly different from the most resistant genotypes. *: Not significantly different from any other genotype, either for eggs, nymphs, or adults.

SSA2 laid few eggs on Tongolo, TME 204, and PER 317, and fewer eggs developed into nymphs on PER 608, PER 368, PER 335, MECU72, Kalawe, and Eyope. Relatively more SSA2 eggs were laid, and nymphs developed on Tajirika, Sagonja, Pwani, Nase 3, Nase 14, Mkumbozi, and Kibandameno. SSA2 egg numbers did not differ significantly from other genotypes (Figure 2).

3.2. Performance of Cassava Genotypes in No-Choice Tests

In no-choice tests, cassava genotypes were screened for antibiosis and antixenosis resistance against two whiteflies population (SSA1-SG1 and SSA1-SG3) that were found most abundant in the field in Uganda. The mean numbers of eggs, nymphs, and adults (EPC) for the genotypes were compared between populations and among genotypes. SSA1-SG1 laid fewer eggs, and nymphs developed on Tongolo, Tarijika, and PER 334 (<20 eggs, Figure 3). The genotypes TME 204, Sauti, PER 415, Njule Red, Nase 3, Nase 18, Mkumba, Mbundamali, Kiroba, Kaleso, F10-30-R2, BRA 327, Albert, Aladu, and 72-TME-14 supported a high number of nymphs (>200 nymphs on the top three leaves) (Figure 3). However, the genotypes did not differ significantly in terms of the numbers of adults that emerged (Figure 3).

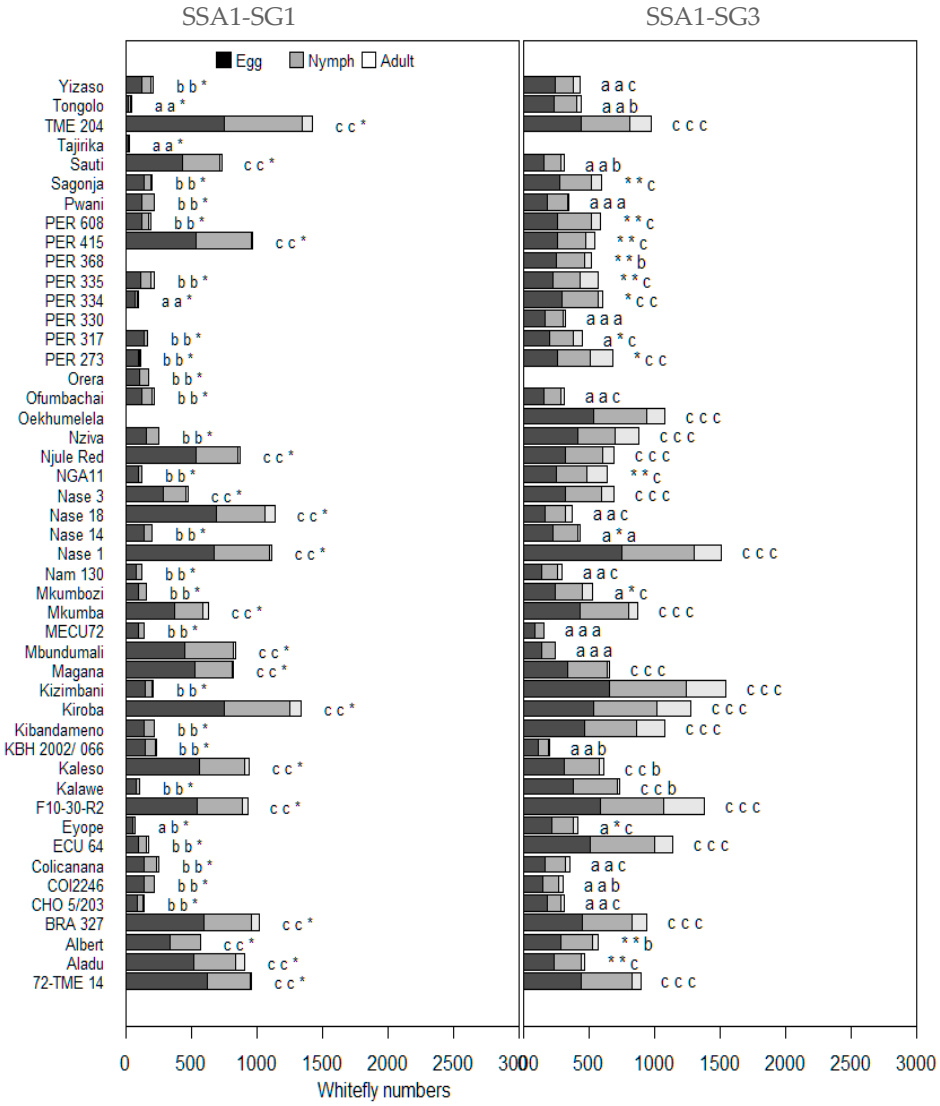

Figure 3. Mean number of eggs, nymphs, and adults of two whiteflies population (SSA1-SG1 and SSA1-SG3) on the cassava genotypes from Latin America and Africa in the no-choice experiment. Multiple comparisons between means were from a Holm-corrected least significant difference method, using data from the negative binomial generalized linear model. Means with the same letter code are not significantly different at the $p = 0.05$ level. a: (resistant group) significantly different from the most susceptible genotypes. b: (intermediate group) significantly different from both the most susceptible and the most resistant genotypes. c: (susceptible group) significantly different from the most resistant genotypes. *: Not significantly different from any other genotype, either for eggs, nymphs, or adults.

SSA1-SG3 laid fewer eggs, fewer nymphs developed, and a few adults emerged on Pwani, PER 330, Nase 14, MECU72, and Mbundamali (Figure 3). Also, fewer eggs were laid, and nymphs developed on Tongolo, Sauti, KBH2002/066, and Col2246 (Figure 3). Most Latin American cassava genotypes (PER 608, PER 415, PER 335, PER 334, PER 317, PER 273, ECU 64) and some African genotypes (TME 204, Sagonja, Oekhumelela, Nziva, Njule Red, NGA 11, Nase 3, Nase 1, Mkumba, Magana, Kizimba, Kiroba, Kibandameno, F10-30-R2, Aladu and 72-TME-14) had more SSA1-SG3 eggs laid, and nymphs developed. SSA1-SG3 had large numbers of eggs laid and nymphs developed on Kaleso and Kalawe but a few of these emerged as adults. On the other hand, Yizaso, Ofumbachai, PER 317, Nase 18, Nam 130, Mkumbozi, Eyope, Colicanana, and CHO5/203 had the fewest eggs laid on them, but the nymphs all developed and all emerged into adults (a-resistant for eggs, a-resistant for nymphs, but c-susceptible for adult emergence, Figure 3).

Three-way analysis of deviance from negative binomial GLM, by genotype, life stages, and whitefly populations when given a choice of only one cassava genotype to feed on to measure their non-preference (antixenosis) and development (antibiosis) indicated highly significant interactions between genotype and whiteflies population ($p < 0.00001$). There were also significant interactions between genotype and life stage, populations, and life stage ($p < 0.00001$), as well as between the three variables: genotypes, whitefly populations, and life stages ($p < 0.00001$) (Table 5). There were no significant differences between whiteflies population, life stages, or origin (Latin America or Africa) of the cassava genotypes screened in no-choice experiments (Table 6). However, the mean numbers of whiteflies counted were higher for African than Latin American genotypes (193.6 $\pm$ 10.2 b and 148.6 $\pm$ 14.1 a, respectively, $p = 0.0169$). African genotypes also had more life stages compared to Latin American genotypes. SSA1-SG3 (mean = 335.3 $\pm$ 13.8, $p = 0.0018$) was more prevalent compared to SSA1-SG1 (mean = 151.4 $\pm$ 9.9, $p = 0.0018$).

Table 5. Three-way analysis of deviance showing the relationship between genotypes, pooled counts of eggs, total nymphs, and adults (life stages) for the two *B. tabaci* populations in the no-choice experiment.

Interaction	Degree of Freedom	Deviance Chi-Square Units	*p*-Value
Genotype	46	983.02	<0.00001
Species	1	167.48	<0.00001
Life stage	2	1534.24	<0.00001
Genotype × populations	41	579.21	<0.00001
Genotype × life stage	92	272.42	<0.00001
Populations × life stage	2	213.65	<0.00001
Genotype × populations × life stage	82	207.46	<0.00001
Residual	520	916.89	

The Chi-square statistic was used to distinguish the interaction between cassava genotypes, the different whitefly stages, and two whitefly populations using a negative binomial generalized linear model.

Table 6. Three-way analysis of deviance by genotype origin (Latin America and Africa) life stages and whiteflies population in no-choice experiment.

Interaction	Degree of Freedom	Deviance Chi-Square Units	*p*-Value
origin	1	8.62	0.00332
Species	1	24.14	<0.00001
Life stage	2	372.08	<0.00001
Origin × populations	1	2.84	0.09194
Origin × life stage	2	0.31	0.85642
Species × life stage	2	69.55	<0.00001
Origin × populations × life stage	2	0.14	0.93239
Residual	775	940.5	

The Chi-square statistic was used to distinguish the interaction between cassava genotype's origin (Latin America and Africa), the different whitefly stages and two whitefly populations using a negative binomial generalized linear model.

Tajirika (8.4 ± 3.5, $p < 0.0001$) had the least mean number of whitefly life stages, but this was not significantly different from MECU72 (47.6 ± 13.4) (Table 7). Kiroba (435.4 ± 121.8, $p < 0.0001$) had the highest mean number of whitefly life stages, but this was not significantly different from Nase 1, F10-30-R2, TME 204, Oekhumelela, BRA 327, 72-TME-14, Kizimbani, Kaleso, Njule Red, PER 415, Nase 8, Mkumba, Magana, Aladu, ECU 64, Kibandameno, Nase 3, and the rest of the other genotypes (Table 7).

Table 7. Mean number of life stages (eggs, nymphs, and adults) for the two African whitefly populations on cassava genotypes in the no-choice experiment.

Genotype	Mean ± Standard Error	CLD Code
72-TME 14	307.7 ± 86.1	h. . .p
Aladu	227.9 ± 63.8	k. . .p
Albert	188.9 ± 52.9	c. . .n
BRA 327	325.3 ± 112.2	mnop
CHO 5/203	74.4 ± 20.9	b. . .h
Col2246(Susceptible control)	86.2 ± 24.2	abc
Colicanana	100.1 ± 28.1	f. . .p
ECU 64	218.7 ± 61.2	h. . ..p
Eyope	80.9 ± 22.7	bcde
F10-30-R2	404.2 ± 116.4	op
Kalawe	138.8 ± 38.9	bcdef
Kaleso	258.1 ± 72.2	i. . .p
KBH 2002/066	70.6 ± 19.8	c. . .n
Kibandameno	215.2 ± 60.2	c. . .n
Kiroba	435.4 ± 121.8	p
Kizimbani	292 ± 81.7	g. . .p
Magana	245.3 ± 68.7	g. . .p
Mbundumali	178.4 ± 50	b. . .k
MECU72(Resistant control)	47.6 ± 13.4	ab
Mkumba	249.9 ± 69.9	lmnop
Mkumbozi	112.4 ± 31.5	b. . .j
Nam 130	68.6 ± 19.3	bcdef
Nase 1	436.1 ± 122	Mnop
Nase 14	103.9 ± 29.1	abc
Nase 18	250.6 ± 70.1	lmnop
Nase 3	194.1 ± 54.3	j. . .p
NGA11(Susceptible control)	125.6 ± 35.2	c. . .n
Njule Red	260.3 ± 72.8	i. . .p
Nziva	187.6 ± 52.5	d. . .o
Oekhumelela	358.6 ± 143.6	nop
Ofumbachai	91.5 ± 26.4	e. . .p
Orera	57.9 ± 23.3	b. . .i
PER 273	130.2 ± 36.5	c. . .m
PER 317	100.6 ± 28.2	b. . .i
PER 330	105.7 ± 52.6	b. . .h
PER 334	115.5 ± 32.4	bcdefg
PER 335	129.7 ± 36.3	g. . .p
PER 368	173.1 ± 69.4	c. . .o
PER 415	250 ± 70	j. . .p
PER 608	141.8 ± 43.6	c. . .n
Pwani	93.2 ± 26.2	abc
Sagonja	132 ± 37	f. . .p
Sauti	172.8 ± 48.4	c. . .n
Tajirika	8.4 ± 3.5	a
TME 204	399.1 ± 111.6	nop
Tongolo	79.1 ± 22.2	bcd
Yizaso	106.2 ± 29.8	c. . .l

Five plants per genotype for each whiteflies population screened. Multiple comparisons between means were from the Holm-corrected least significant difference method, using data from the negative binomial generalized linear model. Means with the same letter code are not significantly different at the $p = 0.05$ level.

3.3. Principal Components Analysis—Genotypes Used in Both Choice and No-Choice Experiments

Comparison of the life stages for SSA1-SG1 and SSA1-SG3 in choice and no-choice tests in the principal component analysis showed that some genotypes are susceptible or resistant in both experiments, but for others, their performance depended on the experimental protocol (Figure 4). The data used are genotype ranks for life stages in both experiments. The PC1 and PC2 axes account for 82.4% of the variance. Seven African genotypes: Tongolo, Mbundamali, Colicanana, Orera, Ofumbachai, Nam 130, Tajirika, and two Latin American genotypes, MECU72 and PER 317, were identified as resistant in both screening methods. While nine African genotypes—Kaleso, F10-30-R2, Nziva, Oekumelela, Mkumba, Nase 18, Albert, Kizimbani, and TME 204—were susceptible. The other genotypes had either antixenosis (non-preference) type of resistance (such as Kibandameno, Nase 1, Aladu, Kiroba, Sagonja, Magana, 72-TME-14, PER 415, Njule Red, and Sauti) identified in the choice test or antibiosis resistance (such as Nase 14, Pwani, CH05/203, Col2246, KBH 2002/066, Yizaso, Kalawe, Mkumbozi, Eyope, and NGA11) identified in the no-choice test.

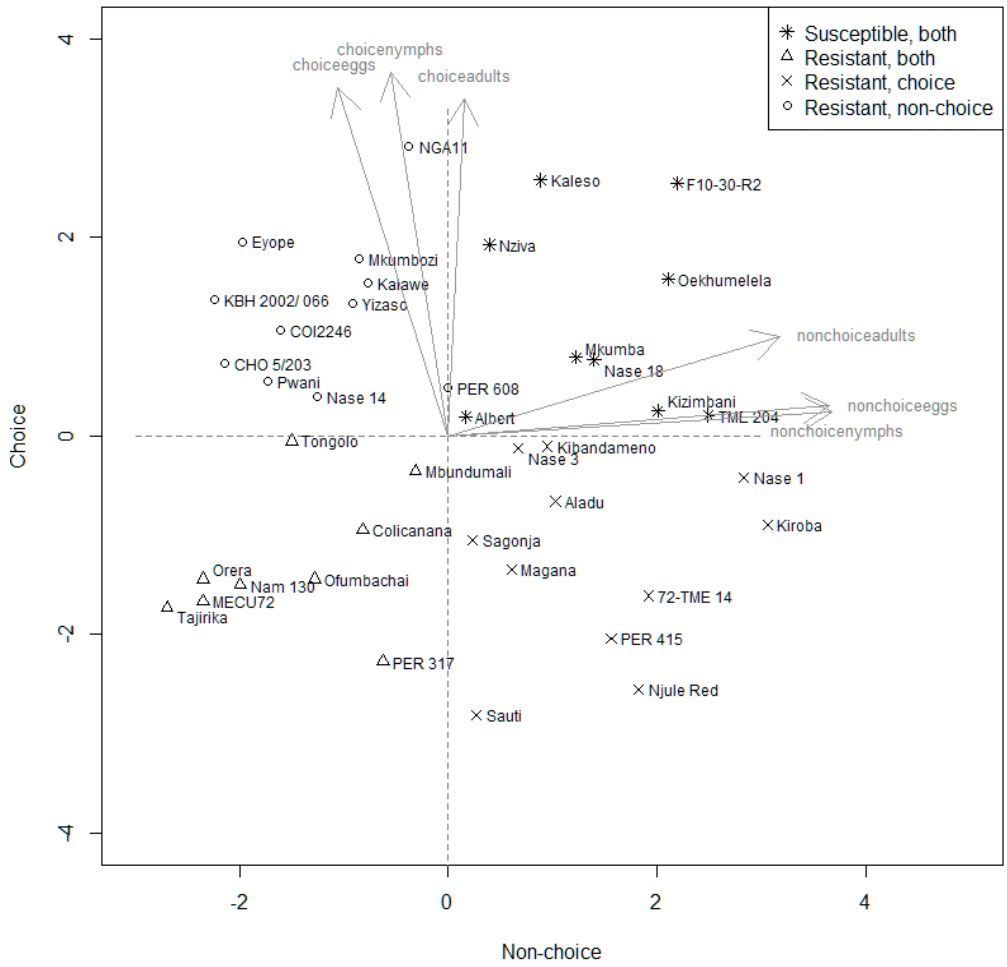

Figure 4. Biplot for PCA. Arrows indicate weights for the six parameters and point to the genotype scores on the first and second PCA axes (x and y axes, respectively).

4. Discussion

This study identified the sources of resistance from both Latin American and African cassava genotypes to the four African *B. tabaci* populations in choice (SSA1-SG1, SSA1-SG2, SSA1-SG3, and SSA2) and no-choice (SSA1-SG1, and SSA1-SG3) tests. A significant interaction was found between the whiteflies population and cassava genotypes, with some genotypes being more preferred for oviposition than others.

Based on the mean number of whitefly life stages on the test plants, three categories of cassava genotypes were recognized: susceptible, tolerant, or resistant. Latin American genotypes and Ugandan landraces were found to be either resistant or tolerant to oviposition, while some 5CP lines were susceptible. Because of the genotype–whiteflies population interaction, preferences for the cassava genotype were variable and dependent on the whitefly population. For example, the genotype NGA11 was highly preferred for oviposition by the SSA1-SG1 and SSA1-SG3 populations, while Mkumbozi was preferred by the SSA1-SG2 and SSA2 populations. While SSA1-SG1 and SSA1-SG2 belonged to the same biological species [16], in certain cases, they preferred different cassava genotypes. Generally, there were no significant differences between the 5CP genotypes, possibly because of the inbreeding pressure among the cassava national stocks due to limited genetic diversity [30]. Significant differences existed between LA and African genotypes, which present the diversity required for whitefly resistance breeding [17].

In cases where measurement of resistance involved the entire whitefly life stages, the four whiteflies population least preferred for oviposition genotypes were Kibandameno, Nase 3, Aladu, Nase 1, Kiroba, Sagonja, Magana, 72-TME-14, PER 415, Njule Red, and Sauti. Some Ugandan landraces, 5CPs, and Latin American genotypes, including Sauti, Njule Red, PER 368, PER 415, PER 335, PER 317, 72-TME14, MECU72, LM2008/363, Kiroba, Orera, Nase 1, Ofumbachai, and Sagonja, were also least preferred for oviposition, nymph development, and adult emergence. Most of these genotypes screened in the insectary also showed resistance when evaluated in the field, where one might find mixed whitefly population [34]. These were considered resistant and could directly be promoted for cultivation as they are already found among farmers or recommended for breeding purposes.

In general, the LA genotypes MECU72, PER 415, PER 317, PER 335, and PER 368 exhibited antixenosis mechanism resistance since fewer eggs were laid on them compared to African genotypes. Other studies [17,19–21] also found MECU72 and Njule Red to be least preferred for oviposition by *A. socialis* and *B. tabaci*, respectively, further indicating that these genotypes have antixenosis against the two whiteflies population. MECU72 has previously been shown to have both antibiosis and antixenosis mechanisms for both *A. socialis* and *B. tabaci* from Uganda [17,19,20]. However, a few of the other LA genotypes had antibiosis resistance, as the few eggs laid took longer to emerge as adults.

In this study, SSA1-SG2 and SSA2 did not differ in numbers of eggs laid and total nymphs, even though the two species favored/unfavored some genotypes. A similar study did not find significant differences between the same species in fecundity (nymph and emerged adults), development time, or proportion of females that emerged as adults on both cassava and eggplants [31].

The Tongolo, Mbundumali, Colicanana, Ofumbachai, Orera, Nam 130, MECU72, PER 317, and Tajirika genotypes that showed antixenosis or antibiosis resistance mechanisms both in choice and no-choice tests had fewer eggs, nymphs, and adults of SSA1-SG1 and SSA1-SG3. Tajirika and Orera belong to the same genetic and biochemical cluster, meaning they might exhibit the same resistance mechanism [30]. Such genotypes with both antixenosis and antibiosis resistance mechanisms may be ideal for the promotion of whitefly resistance. Njule Red and NGA11 exhibited contrasting behavior patterns in choice and no-choice tests for the two whiteflies population (SSA1-SG1 and SSA1-SG3), meaning that given a choice, the genotype Njule Red is not a preferred genotype by the populations, but when the whiteflies are restricted, they would still lay eggs and feed on it. Omondi [35] noted that whiteflies were capable of ovipositing on marginal and non-hosts when preferred hosts were not available, and this could be the case with Njule Red. This variety has a large leaf surface area, and this morphology is attributed to its high leaf lobe number and leaf lobe length and might attract high *B. tabaci* numbers, thus the high preference [36].

Some genotypes, such as CH05/203, Pwani, NGA11, Mkumbozi, Kalawe, Yizaso, Eyope, KBH2002/006, CoI2246, and Nase 14, had low numbers of whitefly life stages,

indicating they possess antibiosis resistance mechanisms. Col2246 (LA variety) is susceptible to the Latin American whitefly species *A. socialis* [20], which was used in this study as a susceptible control, but identical results were not obtained with the African species *B. tabaci*, the one used in this study. Our results showed that Col2246 has certain levels of resistance (antibiosis mechanism) to *B. tabaci*. The resistance in these genotypes may be attributable to the presence of some metabolites, such as cyanogenic glucosides [30,37,38]. It has been shown in another study that Nase 3, Nase 14, and Mkumba had an increase in cyanogenic compounds in response to whitefly as well as phenolic acid derivatives in Mkumba [39]. In another study, Nam 130 recorded high levels of peroxidase and tannin that are linked to whitefly feeding damage indicating they are involved in whitefly resistance [40]. However, according to Martinez and Diaz 2024,, there are species of *B. tabaci* that have detoxification mechanisms for the cyanogenic glycoside metabolites that some cassava possesses [41]. Therefore, other metabolites, such as lignin, that were found in higher deposition in the resistant MECU72, are vital [30]. We conclude that antibiosis in cassava could also be attributable to other mechanisms, such as the morphological characteristics of a variety [36].

For effective management of whitefly infestations, both antixenosis and antibiosis resistance mechanisms are preferred since antixenosis alone may be insufficient in case the whitefly increases the number of eggs laid, as most of these will emerge as adults. This is likely to render the genotype susceptible, as the long growth period of cassava will support an increase in the whitefly population [42,43].

The fact that some of the 5CP lines showing whitefly resistance are also resistant to both CMD and CBSD would provide a double benefit to farmers who are currently growing these genotypes. These genotypes would only need to be popularized for adoption. Although landraces such as Njule Red, Aladu, Ofumbachai, Magana, Tongolo, and LA genotypes showed prominent levels of resistance against the whitefly, their susceptibility to the two cassava viruses would hinder their promotion. These genotypes could be used as parents in breeding programs and crossed with CMD- and CBSD-resistant genotypes to generate progenies that may have resistance or tolerance to both whitefly and viral diseases.

The genotypes Kizimbani, Kalawe, Tajirika, Eyope, and Yizaso that were found resistant to CMD/CBSD were found susceptible to some whiteflies population in this study, corroborating previous studies that reported *B. tabaci* having preference for CMD-resistant varieties [17]. Interestingly, some CMD-susceptible genotypes, such as Kibandameno, Mbundumali, Colicanana, Nziva, and Orera, were still found susceptible to some whiteflies population evaluated in this study owing to whitefly species differences.

It is important to note that defining whitefly resistance is complicated since a small event such as oviposition is made up of many factors that include the selection and feeding behavior of the whitefly [20,24]. Similarly, antixenosis, or non-preference to egg-laying that involves oviposition, is represented by the presence of morphological and chemical factors of the host plant that adversely affect the behavior of whiteflies [22–24]. The big variation in the biological data can cause interpretation challenges. Additionally, whitefly resistance is a quantitative trait with many contributing factors that may be inconsistent. Only consistent data, such as the number of eggs laid/emerged, is used to define and select genotypes with antixenosis and antibiosis resistance mechanisms. The variability in such data owing to differences in genotypes screened demonstrates that sources of resistance to African cassava *B. tabaci* exist within cassava genotypes.

5. Conclusions

The present study identified 13 cassava genotypes that were resistant to whitefly, of which 11 exhibited antixenosis and 10 exhibited antibiosis (nymph mortality). Interestingly, eight (Tongolo, Mbundumali, Colicanana, Orera, Ofumbachai, Nam 130, Tajirika, and MECU72) demonstrated resistance through a combination of antixenosis and antibiosis against SSA1-SG1 and SSA1-SG3, and these can be considered the best sources of resistance for the rapid development of whitefly-resistant cassava genotypes in African countries.

However, field trials are recommended for the future variety development of these eight genotypes. This study has greatly contributed to our understanding of cassava-whitefly resistance mechanisms and the potential for managing African *B. tabaci*, as more is known about the whitefly species.

Author Contributions: Conceptualization, J.A., M.N.M. and J.C.; methodology, J.A., M.N.M., C.A.O., A.B.-C.,L.A.B.L.-L. and J.C.; formal analysis, J.A., M.N.M. and J.C.; investigation, J.A., M.N.M. and J.C.; resources, M.N.M., A.B.-C., L.A.B.L.-L. and J.C.; data curation, J.A.; writing—original draft preparation, J.A.; writing—review and editing, J.A., M.N.M., A.K., C.A.O., A.B.-C. and J.C.; visualization, J.A.; supervision, M.N.M. and J.C.; project administration, J.C.; funding acquisition, J.C. All authors have read and agreed to the published version of the manuscript.

Funding: This work was supported through the Natural Resources Institute, University of Greenwich from a grant provided by the Bill & Melinda Gates Foundation; The African Cassava Whitefly Project, (OPP1058938).

Data Availability Statement: The original contributions presented in the study are included in the article, further inquiries can be directed to the corresponding authors.

Acknowledgments: We are grateful to Stephen Young, who guided J.A. in developing her statistical skills. In addition, we would like to thank the anonymous referees for their remarks that helped us greatly improve this manuscript.

Conflicts of Interest: The authors declare no conflicts of interest. The funders had no role in the design of the study; in the collection, analyses, or interpretation of data; in the writing of the manuscript, or in the decision to publish the results.

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