WHITEFLY RESISTANCE IN AFRICAN CASSAVA GENOTYPES

C. GWANDU[1,2], M. OCHWO-SSEMAKULA[2] and P. SSERUWAGI[1]

[1]Tanzania Agricultural Research Institute - Mikocheni, P. O. Box 6226, Dar es Salaam, Tanzania
[2]College of Agricultural and Environmental Sciences, School of Agricultural Sciences,
Makerere University, P. O. Box 7062, Kampala, Uganda
Corresponding author: cathygwandu@yahoo.com

ABSTRACT

Whitefly (*Bemisia tabaci*), a major pest and vector of viruses in cassava, is the greatest current threat to cassava production in sub-Saharan Africa (SSA). Research efforts have focused on management of the two viral diseases: cassava mosaic disease (CMD) and cassava brown streak disease (CBSD), and have ignored the whitefly vector that is driving the spread of the viruses, causing CMD and CBSD in SSA. The objective of this study was to evaluate cassava genotypes for resistance to *B. tabaci* based on field infestation and damage in Uganda. The study was carried out in four sites with diverse agro-ecologies including: Namulonge, Kasese, Ngetta and Serere during 2015 and 2016.Whitefly nymph abundance and feeding damage were assessed on each test genotype from 3 to 6 months after planting (MAP). In 2015, the highest broad sense heritability estimates were 39% (4 MAP) and 53% (5 MAP) for whitefly nymph abundance and feeding damage, respectively. In 2016, broad sense heritability estimates were 23% (3 MAP) and 41% (4 MAP) for whitefly nymph abundance and feeding damage, respectively.Analysis of variance of whitefly nymph abundance showed a significant (P< 0.05) location × genotype × season interactions at 3, 4, 5 and 6 MAP. There were also significant (P< 0.05) location × genotype × season interactions at 3 and 4 MAP for whitefly feeding damage. Ten genotypes showed good levels of resistance to whitefly infestation and feeding damage including: UG120202, UG120174, NASE13, UG120160, UG120286, UG120293, UG130075, CSI-142, CS1-144 and UG130085. These genotypes may serve as parental materials for breeding programmes for whitefly and viral disease control.

Key Words: *Bemisia tabaci*, cassava brown streak disease, cassava mosaic disease

RÉSUMÉ

La mouche blanche (*Bemisia tabaci*), le ravageur et vecteur principal de virus du manioc, constitue actuellement la plus grande menace pour la production de manioc en Afrique Subsaharienne (AS). Les recherches ont porté sur la gestion des deux maladies virales: la maladie de la mosaïque du manioc (MMM) et la maladie de la striure brune du manioc (MSBM) , et ont ignoré le vecteur de la mouche blanche qui est à l'origine de la propagation des virus, causant le MMMet le MSBM en Afrique

subsaharienne. L'objectif de cette étude était d'évaluer la résistance de *B. tabaci* aux génotypes du manioc sur la base d'une infestation et de dégâts sur le champs en Ouganda. L'étude a été menée en 2015 et 2016 sur quatre sites présentant diverses agro-écologies, notamment Namulonge, Kasese, Ngetta et Serere. L'abondance des nymphes blanches et les dommages alimentaires ont été évalués sur chaque génotype testé 3 à 6 mois après la plantation (MAP). En 2015, les estimations les plus élevées de l'héritabilité au sens large étaient de 39% (4 MAP) et 53% (5 MAP) pour l'abondance des nymphes de la mouche blanche et les dommages causés par l'alimentation, respectivement. En 2016, les estimations de l'héritabilité au sens large étaient respectivement de 23% (3 MAP) et 41% (4 MAP) d'abondance des nymphes de la mouche blanche et des dommages causés par l'alimentation. L'analyse de la variance de l'abondance des nymphes de la mouche blanche a révélé une interaction significative (p <0,05) de lieu × génotype × interactions saisonnières à 3, 4, 5 et 6 MAP. Il y avait aussi des interactions significatives (P <0,05) de lieu × génotype × interactions saisonnières aux niveaux de 3 et 4 MAP pour les dommages causés par l'alimentation des mouches blanches. Dix génotypes ont montré de bons niveaux de résistance à l'infestation par mouches blanches et aux dommages causés par l'alimentation, notamment: UG120202, UG120174, NASE13, UG120160, UG120286, UG120293, UG130075, CSI-142, CS1-144 et UG130085. Ces génotypes peuvent servir de matériel parental pour les programmes de sélection visant à lutter contre mouches blanches et les maladies virales.

Mots Clés: *Bemisia tabaci*, maladie de la striure brune du manioc, maladie de la mosaïque du manioc

INTRODUCTION

Whitefly, *Bemisia tabaci* (Gennadius) (Hemiptera: Aleyrodidae), is one of the world's most serious plant pests, and is a major vector of viral diseases in cassava (Legg, 2010). It is native to tropical and subtropical regions, but has spread rapidly around the world (Caro and Dumo, 2012). *Bemisia tabaci* is a polyphagous whitefly, colonising over 500 plant species from 74 families (Bellows *et al.,* 1994). However, the monophagous *B. tabaci* populations have also been reported on *Jatropha gossypifolia* and *Croton labatus* (Jatropha races) and cassava *B. tabaci,* colonising cassava and wild eggplant in Africa (Lisha *et al.,*2003); and five other non-cassava plant species: *Manihot glaziovii*, *Jatropha gossypifolia*, *Euphorbia heterophylla*, *Aspilia Africana* and *Abelmoschu sesculentus* in Uganda (Sseruwagi *et al.*, 2006).

Whitefly populations vary depending on the stage of plant growth of cassava (Fishpool *et al.,* 1995; Sseruwagi *et al.,*2003). Adults invade slowly and establish within a sufficiently grown crop; and a small population appears after 3 weeks of the initial colonisation.

This is followed by rapid build up at 3 to 4 months after planting (Sseruwagi *et al.,* 2004; Macfadyen *et al.,* 2018). Rapid whitefly population growth occurs during this period, due to appropriate foliage support. A steady population growth follows for a short period, followed by a rapid decline to low residual level maintained throughout the rest of the crop's growth period (Fishpool *et al.,* 1995).

Bemisia tabaci population dynamics and activity depend on nutritional quality of the host-plant, changes in the climatic factors (temperature, rain, wind and relative humidity), and natural enemy populations (Maria *et al.,* 2003). Food resources are devoted to aerial growth during the early growth period (1 to 3 months), and decline after 4 to 5 months when the process of root tuberisation begins. A greater whitefly population during the first 3 months is usually observed, than when the plants are more mature (Marmey *et al.,*1994). Boost in whitefly population is favoured by high temperatures and radiation, and low rainfall and relative humidity (Fargette *et al.*, 1985). The adults disperse mainly by the aid of wind, moving short and long distances (Blackmer *et al.*, 1995), and also by the aid of

humans who move immature and adult stages on planting material (Byrne and Bellows, 1991). Cropping practices such as planting date (Legg *et al.*, 2011), crop disposition (Chikoti *et al.,* 2013) and intercropping (Fargette *et al.,*1994) further influence whitefly population dynamics, and hence aid the spread of the whitefly-transmitted viruses.

In the initial stage of a whitefly infestation, the adults choose a host plant for feeding and/or oviposition. Selection of the host plant may depend on several factors, such as leaf colour and colour of apical leaves (Baran *et al.,* 1983), shape of central leaflet (Oriani *et al.,* 2011), orientation of petiole, and hairy and/or smooth leaf (Nombela *et al.,* 2000). For example, in cotton, whiteflies prefer light green leaves (Stansly, 1986). This color is believed to be the most important factor for whitefly host recognition (Berlinger, 1986).

A less open plant canopy is also preferred by whiteflies (Chen *et al.,* 2004). Several studies have evaluated the preference of *B. tabaci* among cultivars of cotton, tomato and cassava, and found that whiteflies show preference for cultivars with moderately hairy leaves (Mohd Rasdi *et al.,* 2009; Legg, 2010; Oriani *et al.,* 2010).

Characters that affect whitefly feeding also affect oviposition. It was suggested that whiteflies choose the most suitable host for oviposition, not only because they can feed on it, but also because the offspring should be able to survive on it (Sharma *et al.,* 2015). Therefore, growing cassava genotypes with genetic resistance (antixenosis) could be an effective, economic and ecofriendly method for controlling whitefly.

The direct feeding damage by whiteflies on cassava appears as chlorotic mottling and twisting or curling, particularly on upper leaves (Bellotti and Arias, 2001). If large populations develop early in the life of the crop, plant vigour and tuber sizes are reduced, and general plant stunting occurs. Another effect of the large whitefly populations is the production of honey dew, which falls onto the lower leaves. This is subsequently colonised by black sooty mould (Srinivasan *et al.,* 2012),which reduces the ability of the leaves to photosynthesize and contribute to yield losses by over 50% (Maruthi *et al.,* 2017). The occurrence of black sooty mould on the upper surface of the lower leaves of cassava plants is now commonplace in countries like Uganda, and this recent phenomenon is referred to by farmers as "black mosaic". This name suggests that farmers are aware of the reduced yields that result, because "mosaic" is a term closely associated with the cassava mosaic disease (CMD) pandemic that has devastated cassava production in the country since the late 1980s, causing famine and suffering to the people whose livelihood depend on the crop (Thresh *et al.*, 1994).

The greatest economic threat is from whitefly acting as a vector of: cassava mosaic begomoviruses (CMBs) and cassava brown streak viruses (CBSVs), which cause cassava mosaic disease (CMD) and cassava brown streak disease (CBSD), respectively. These diseases severely reduce cassava productivity in sub-Saharan Africa, causing more than US$1 billion annually (Mbanzibwa *et al.,* 2011; Legg *et al*., 2013). In the late 1990s, CMD was rapidly spread by the whitefly vector through southern Uganda and into neighbouring countries in East Africa (Legg *et al.,* 2011). By the mid-2000s, 11 countries across East and Central Africa were affected by a severe CMD pandemic. Average yield losses of nearly 50% were reported due to CMD, causing food shortages and localised famine in the region.

Various control options were employed to manage the disease, although more emphasis was put on development of virus-resistant cassava varieties (Legg, 2010). Both conventional and transgenic breeding efforts were applied to identify sources of resistance and to incorporate these into farmer-preferred cassava varieties (Legg and Thresh, 2003). The International Institute of Tropical Agriculture (IITA) was the main source of

germplasm for resistant breeding materials, as well as diverse collections of West African landraces (Legg, 2010).

Areas affected by the severe CMD epidemic in northern and central Uganda and at the 'fronts', were characterised by high whitefly abundance than in unaffected areas (Gibson, 1996; Legg *et al.,* 2002). Since 2004, CMD and CBSD have spread over much of the Great Lakes Region of East and Central Africa (Alicai *et al.,* 1994). The key factor believed to drive the spread of these viruses was the dramatic increase in abundance of their whitefly vector (Legg *et al.,* 2013). Several resistant cassava varieties introduced to combat CMD and CBSD were later found to be highly suitable for *B. tabaci* and, thus exhibited limited whitefly resistance (Legg *et al.,* 2014). This undesirable trait adversely affected the effectiveness of CMD and CBSD control strategies, because adult *B. tabaci* are highly mobile. However, little attention was given to *B. tabaci* until 2012, when possible resistance sources to whitefly were found in several Ugandan cassava landraces and a South American genotype (Omongo *et al.,* 2012).

Recently, efforts in whitefly research have focused on understanding systematics, species diversity and ecology. Improved cassava genotypes have co-evolved with the virus and whitefly (Legg, 2010) and so an investigation into whitefly resistance is important to identify potentially useful genotypes for further resistance breeding and ultimately for development of effective management strategies for the increased whitefly populations now present in cassava production areas. In addition, whitefly resistance offers a low-cost, sustainable solution with the best chances of widespread adoption by subsistence farmers (Bellotti and Arias, 2001). The objective of this study was to determine sources of resistance of available cassava genotypes under high whitefly pressure in Uganda.

MATERIALS AND METHODS

Study sites and genetic materials. Field experiments were conducted in four diverse environments in Uganda, namely: Namulonge, Kasese, Ngetta and Serere (Table 1). The study was conducted for four months per cropping season from September to December 2015 (Season 1) and August to November 2016 (Season 2). Fifty diverse cassava genotypes that are part of a breeding population established in the Cassava Base genomic selection project (www.cassavabase.org) were used in the study (Table 2). The genotypes were selected based on parental diversity and agronomic performance.

Experimental design. The experiments were established in an augmented design, with the following five check clones: NASE 1 and TME 204 (highly susceptible and highly resistant to CMD and CBSD, respectively), TME14 and NASE 14 (highly susceptible and highly resistant to CMD and CBSD, respectively), and NASE 3 (resistant to CMD and susceptible to CBSD). At each location, the cassava genotypes were established in single un-replicate row plots of 10 plants, at a spacing of 1 m x 1 m according to Kawuki *et al.* (2011).

Phenotypic data collection. Whitefly infestation and damage levels were recorded on the test genotypes, for four months at 3, 4, 5 and 6 months after planting (MAP), the period of rapid whitefly build-up on cassava (Sseruwagi *et al.,* 2003). This was done using three traits; namely whitefly nymph abundance/counts, feeding damage and plant morphological parameters. Whitefly feeding damage was assessed in the field on four plants per genotype, using a severity score scale of 1–5; in which1 represents no leaf damage; 2 represents <25% of leaves damaged and with mild chlorosis on few apical leaves;

TABLE 1.   Agro-climatic description of the locations where test cassava genotypes were evaluated for whitefly cassava resistance in Uganda

Characteristics	Site			
	Namulonge	Serere	Ngetta	Kasese
Whitefly abundance	High	Low	Low	High
Temperature (min/max)	16 - 28 °C	19 - 31 °C	19 - 29 °C	18 -31 °C
Rainfall	Bimodal rainfall 1st September to November and 2nd March up to May of each year	Bimodal rainfall 1st September to December/January and 2nd February up to May/June of each year	Uni-modal rainfall 1st October/ November until April/May of each year	Uni-modal rainfall 1st March to May and 2nd August up to November of each year
Mean rainfall (mm)	1270	1419	1483	1200
Latitude	0.5297	1.5176	53.6947	0.1833
Longitude	0.1833	33.4579	22.9297	30.0833
Altitude (m.a.s.l)	1150	1080	1300	960
Vegetation	Transition forest with sandy clay loam	Moist savannah	Moist savannah	Moist savannah

Source: Sebuwufu *et al.* (2015)

TABLE 2.   Selected cassava genotypes for investigation for whitefly resistance in Uganda

SN	Genotype	Female	Male	Pedigree/source
1	UG120174	MM96/0686	MM96/0686	Full sib of IITA clone x IITA clone
2	UG120191	Introduction Tanzania		Selection from Tanzania Seed Introduction-2005
3	UG130004	Unknown		Unknown
4	UG120160	CR21-6		Half sib of CIAT CR-Line
5	UG130008	TZ 140		Half sib of Tanzania material
6	UG130018	Unknown		Unknown
7	UG120024	MM96/4271	Namikonga	Full sib of IITA clone x Tanzania clone-Namikonga
8	UG130085	NASE 13		Half sib of IITA Clone
9	UG120251	TMS 60142	NASE 13	Full sib of IITA clone x IITA clone
10	UG120170	CR24-8		Half sib of CIAT CR-Line
11	UG120227	Njule red		Half sib of Ugandan local
12	UG120124	MM96/4271	MH04/2767	Full sib of IITA clone x IITA clone
13	UG130068	Unknown		Unknown
14	UG120127	TZ 130	TZ 130	Selfed progeny of Tanzanian material
15	UG130083	Unknown		unknown
16	UG120198	Introduction Tanzania		Selection from Tanzania Seed introduction -2005
17	UG120071	TME 204	MH95/0414	Full sib of IITA clone x IITA clone
18	UG120133	TMS30572		Half sib of IITA clone
19	UG120063	TME 204	SE95/00036	Full sib of IITA clone x IITA clone
20	UG120001	TMS30572	MH95/0414	Full sib of IITA clone x IITA clone
21	UG130006	TZ 140		Half Sib of Tanzania material
22	UG130075	Unknown		unknown
23	UG130078	Unknown		unknown
24	UG120293	TME 204		Half sib of IITA clone
25	UG120252	TMS 60142	NASE 13	Full sib of IITA clone x IITA clone
26	UG120286	Kibao	CR36-2	Full Sib of CIAT CR-Line x Ugandan local
27	UG130038	Unknown		Unknown
28	UG120295	TME 204		Half sib of IITA clone
29	UG120202	SE95/00036	MM96/4291	Full sib of IITA clone x IITA clone
30	UG120109	40	40	Selfed progeny of IITA clone
31	UG120267	TMS 60142	TME 14	Full sib of IITA clone x IITA clone
32	NAM 130	Check		
33	UG120190	Introduction Tanzania		Selection from Tanzania Seed introduction -2005
34	CS1-114	Check		
35	UG120193	Introduction Tanzania		Selection from Tanzania Seed introduction -2005
36	UG120283	NASE 13	TMS30572	Full sib of IITA clone x IITA clone
37	UG120291	TME 14		Half sib of IITA clone

TABLE 2. Contd.

SN	Genotype	Female	Male	Pedigree/source
38	UG120050	TME 14	Namikonga	Full sib of IITA clone x Tanzania clone-Namikonga
39	UG120072	TME 204	MH95/0414	Full sib of IITA clone x IITA clone
40	UG120161	CR21-6		Half sib of CIAT CR-Line
41	TP 294	Check		
42	CSI-75	Check		
43	TME 14	Check		
44	UG120220	Unknown		Unknown
45	UG120189	Introduction Tanzania		Selection from Tanzania seed introduction -2005
46	TME 204	Check		
47	UG130029	Unknown		Unknown
48	NASE 13	Check		
49	UG120210	MH97/2961	Nyaraboke	Full sib of IITA clone x Ugandan local

3 represents 25–50% of leaves damaged with mild chlorosis, curled and twisted; 4 represents 50–75% of leaves damaged with moderate chlorosis and/or wilting; and 5 represents >75% leaves damaged with defoliation (Sseruwagi *et al*., 2004).From each assessed plant, the 14th leaf from the apex was detached from the plant as per Taylor *et al*. (2008) and the leaf gently dried with tissue to remove the moisture/water, and then placed in sealable plastic bags. Thereafter, the leaves were stored at 4 °C at the National Crops Resources Research Institute (NaCRRI), Namulonge. The nymphs were counted with the aid of a×10 magnifying hand lens. The following morphological parameters were assessed using a cassava descriptor protocol (Fakudo *et al*., 2010): (i) leaf colour, (ii) colour of apical leaves, (iii) shape of central leaflet, (iv) orientation of petiole and (v) hairy and/or smooth leaf.

Data analysis. Whitefly nymph abundance and feeding damage data were statistically analysed using R software (R Core Team, 2013). Nymph count data were logarithmically transformed to normalise it. Analysis of variance (ANOVA) was conducted to determine significant differences among treatments. The ANOVA was conducted using a mixed linear model (MLM) with genotypes as fixed effects. Mean squares generated from ANOVA were used to test the significance of the different sources of variation and to calculate variance components. In addition, variance components extracted were used to estimate broad-sense heritabilities for the assessed traits determined by estimating the amount of genetic variance among the genotypes as a proportion of the total phenotypic variance.

The MLM used to extract the variances was as follows:

$$Y_{ijk} = \mu + G_i + L_j + GL_{ij} + S_k + GS_{ik} + GSL_{ijk} + \varepsilon_{ijk}$$

Where:

Y_{ijk} is the observed phenotype for the kth season in the jth location of the ith genotype evaluated in the experiment; μ is grand mean; L_j is effect of location; GL_{ij} is effect of interaction between genotype and location; GS_{ik} is effect of interaction between genotype

and season; GSL_{ijk} is effect of interaction between genotype, season and location, and ε_{ijk} is residual.

The estimation of broad-sense heritability (H^2) was as follows:

$$H^2 = (G_i)/[(G_i) + (GL_{ij}/n_l) + (GS_{ik/ns}) + (GSL_{ijk/nl*ns}) + \varepsilon_{ijk}/n_l \times n_s \times n_b]$$

Where:

nl is number of locations, n_s is number of seasons and n_b is number of blocks.

Pearson's correlation coefficients (r_{xy}) were computed to determine the degree of association between whitefly feeding damage and nymph counts, using the following formula:

$$r_{xy} = \sum_{i=n}^{n} \frac{(x_i - \bar{x})(y_i - \bar{y})}{(n-1)s_x s_y}$$

Where:

x_i and y_i are the genotype means of the two variables being analysed and n is the total number of observations of each variable.

RESULTS

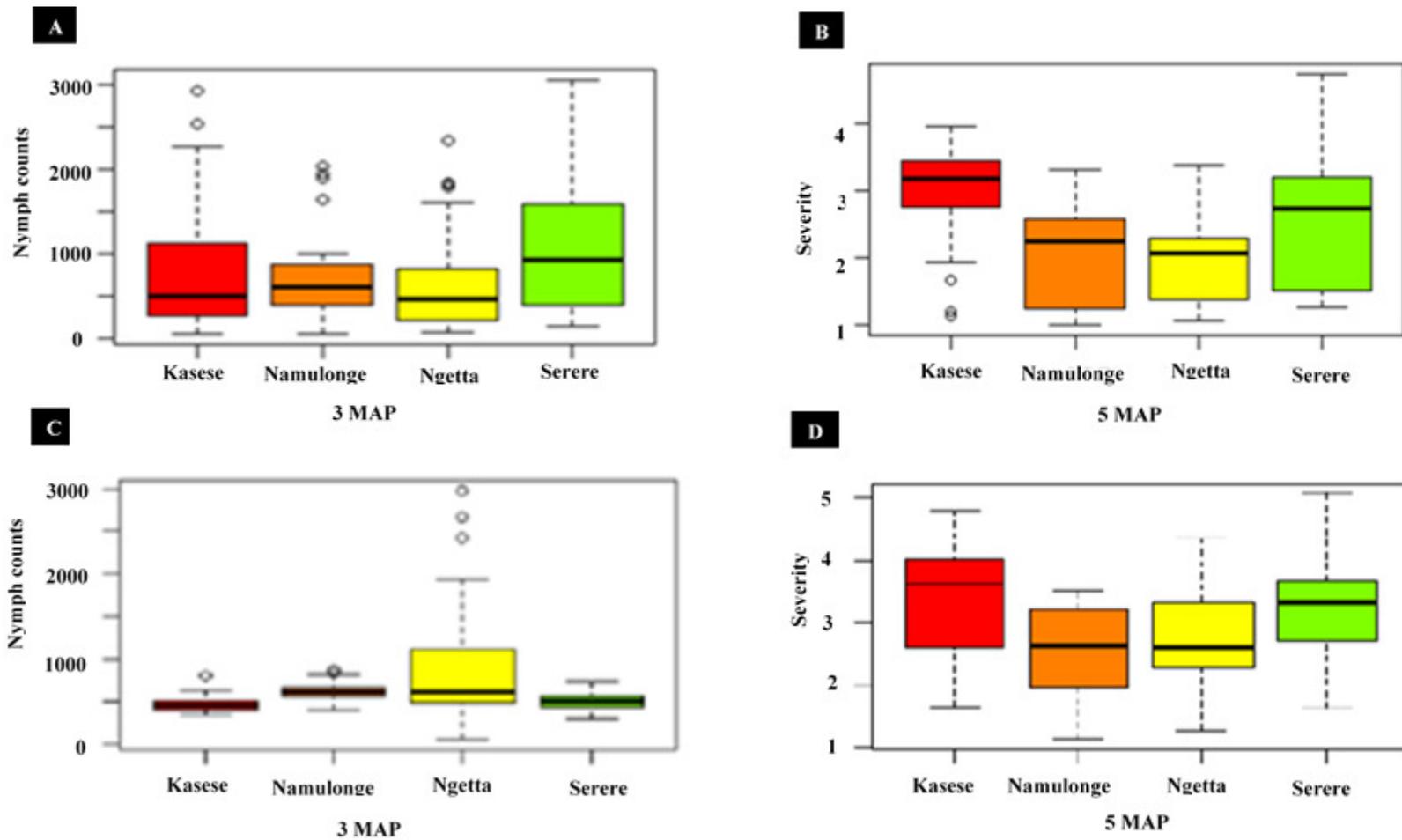**Whitefly nymph abundance and feeding damage.** In season 1 (2015), the highest variability for nymph abundance (>0<2000) was recorded at 3 MAP in Kasese and Serere (Fig. 1A). Nymph populations were normally distributed at Namulonge (NaCRRI), Ngetta and Serere (Fig. 1A).The highest variability for whitefly damage (severity scores >2<4) was recorded at 5 MAP in Namulonge and Serere (Fig. 1B). Whitefly feeding damage data were only normally distributed at Kasese (Fig. 1B). In season 2 (2016), the highest variability for nymph abundance (>0<1500) occurred at 3MAP in Ngetta only (Fig. 1C). Whitefly nymph populations were not normally

distributed across all the locations. The highest variability for whitefly damage (severity scores >2<5) occurred at 5 MAP across all locations (Kasese, Namulonge, Serere and Ngetta). However, whitefly feeding damage data were normally distributed only at Namulonge (Fig. 1D).

Broad-sense heritability. In 2015, the highest broad sense heritability estimates were 39% (4 MAP) and 53% (5 MAP) for whitefly nymph abundance and feeding damage, respectively. In 2016, broad sense heritability estimates reduced to 23% (3 MAP) and 41% (4 MAP) for whitefly nymph abundance and feeding damage, respectively.

Whitefly resistance traits. There were significant differences in whitefly nymph abundance between genotypes at 3, 4 and 6 MAP (P<0.001) and at 5 MAP (P<0.01) (Table 3). Nymph abundance was highly significantly different between locations at 4 and 5 MAP (P<0.001), and at 3 (P< 0.05) and 6 MAP (P<0.01). Furthermore, there were significant genotype× season interactions for nymph abundance at 3, 4, 5 (P< 0.05) and 6 (P<0.001) MAP. Location x genotype interaction for nymph abundance was not significant. However, the location x genotype x season interactions were significantly different at 4, 5 and 6 MAP (P<0.001) and at 3 MAP (P<0.05).

There were similarly significant differences in whitefly feeding damage among genotypes at 3 and 5 MAP (P<0.001; Table 3). There were highly significant differences in whitefly feeding damage among genotypes (P<0.01) at 4 and 6 MAP, and among locations (P<0.001) at 3, 4, 5 and 6 MAP. Whitefly feeding damage was highly significant between seasons (P< 0.001) at 6 MAP, with similar results at 4 and 5 MAP (P<0.01). In addition, there were significant location × genotype interactions for whitefly feeding damage eat 3 MAP (P < 0.05) and 5 MAP (P<0.01). At 3 and 4 MAP, significant genotype ×season (P<0.01) and

Figure 1.   Stage of crop growth with highest variability and distribution of whitefly nymphs and damage across locations in 2015 (A & B) and 2016 (C & D) in Uganda.

TABLE 3.   Mean squares associated with whitefly resistance evaluations at different growth stages, across locations and seasons in Uganda

Source of variance	d.f	Nymph counts (logarithmic transformed)				Whitefly damage			
		3 MAP	4 MAP	5 MAP	6 MAP	3 MAP	4 MAP	5 MAP	6 MAP
Genotype	49	0.179***	0.198***	0.166**	0.234***	0.699***	0.821**	1.115 ***	1.003**
Location	3	0.270*	1.468***	5.119***	0.592**	10.832***	11.393***	22.976***	27.484***
Blocks	4	0.322	0.296	0.219	0.446	0.668	1.129	0.751	0.427
Season	1	0.030	0.612**	0.976***	1.794**	1.113	3.0624**	39.982 **	64.853***
Checks	5	0.462	0.439	0.137	0.132	1.235	1.022	2.135	1.297
Location: Genotype	159	0.035	0.035	0.070	0.083	0.389*	0.486	0.746 **	0.78
Genotype: Season	54	0.089*	0.066*	0.130**	0.181***	0.392**	0.334**	0.425	0.506
Location: Genotype: Season	122	0.103*	0.159***	2.752***	0.282***	0.376*	0.531*	0.474	0.816
Residual	124	0.074	0.079	0.066	0.088	0.289	0.378	0.446	0.522
s.e.d		0.019	0.020	0.018	0.021	0.038	0.043	0.047	0.022

D.f = degrees of freedom; 3 MAP, 4 MAP, 5MAP and 6MAP are three, four, five and six months after planting, respectively. *, ** and *** represents significance at P<0.05, 0.01, and 0.001, respectively

location × genotype × season (P<0.05) interactions were observed for whitefly feeding damage.

Correlations among traits. In 2015, there were high correlations between whitefly nymph abundance and feeding damage 3 (r = 0.789) and 4 (r = 0.656) MAP, respectively. However, the correlations between nymph abundance and feeding damage at 5 (r = 0.469) and 6 (r = 0.221) MAP were weak. Similarly, in 2016 high correlation coefficients (r = 0.656 and r = 0.639) were observed between whitefly nymph abundance and feeding damage at 3 and 4 MAP, respectively. However, the correlation coefficients were similarly weak at 5 (r = 0.232) and 6 (r = 0.295) MAP, respectively.

Categorising genotype for whitefly resistance. Whitefly nymph abundance and feeding damage were used to categorise cassava genotype responses to whitefly resistance (Table 4). The ten most whitefly resistant genotypes were: UG120202, UG120174, NASE13, UG120160, UG120286, UG120293, UG130075, CSI-142, CS1-144

and UG130085, with mean whitefly nymph abundance of 2.689–3.624 and feeding damage of 2.017–2.989. Genotypes UG120189, UG130066, UG120133, UG120170, UG120198, UG130038, UG130078, UG120161, UG120220 and UG120251 were the most susceptible, based on mean scores of 2.25–2.89 for whitefly nymph abundance and 3.759–4.624 for whitefly feeding damage (Table 4).

Out of the ten whitefly resistant genotypes identified in this study, UG120202, UG120174, NASE13, UG120160, UG120286, UG120293 and CSI-142 recorded the least whitefly damage, with mean feeding damage scores of >2.017<2.478, with corresponding mean nymph abundance of >1.296<1.780. Genotypes UG130075, CS1-144 and UG130085 had mean nymph abundance of >1.840< 2.396 and mean whitefly feeding damage of>2.527<2.989.

Of the most whitefly susceptible genotypes, UG130078, UG120161, UG120220 and UG120251 had mean nymph abundance of >2.786<2.892, and the highest mean whitefly feeding damage scores of >4.033<4.624. Similarly, genotypes

TABLE 4. Ten most whitefly (*Bemisia tabaci*) resistant cassava genotypes evaluated in Uganda

	Resistant			Susceptible	
Genotype	Whitefly damage	Nymph counts (log)	Genotype	Whitefly damage	Nymph counts (log)
1. UG120202	2.017	1.296	UG120189	2.689	2.248
2. UG120174	2.364	1.332	UG130066	2.804	2.297
3. NASE13	2.369	1.402	UG120133	2.835	2.315
4. UG120160	2.406	1.425	UG120170	2.908	2.403
5. UG120286	2.418	1.703	UG120198	2.938	2.736
6. UG120293	2.478	1.748	UG130038	2.981	2.767
7. CSI-142	2.478	1.780	UG130078	3.033	2.786
8. UG130075	2.527	1.840	UG120161	3.134	2.791
9. CS1-144	2.567	2.384	UG120220	3.624	2.860
10. UG130085	2.579	2.396	UG120251	3.624	2.892
LSD (0.05)	0.076	0.048	LSD (0.05)	0.047	0.051

UG120189, UG130066, UG120133, UG120170, UG120198 and UG130038 had mean nymph abundance of >2.248<2.767 and relatively high mean whitefly feeding damage of >3.759<3.981.

Morphological characterisation of genotypes. The morphological characterisation of cassava genotypes for whitefly preference and colonisation was based on leaf colour, colour of apical leaves, and shape of the central leaflet, orientation of petioles and hairiness and/or smoothness of leaves. Apical leaves of the whitefly resistant genotypes: UG120202, UG120174, NASE13, UG120160, UG120286, UG120293 and CSI-142 were dark green, and UG130075, CS1-144 and UG130085 had light green foliage. The central leaflets of UG120202, UG120174, NASE13, UG120286, UG120293 and CS1-144 were elliptic-lanceolate shaped and straight; and linear for UG120160, CSI-142 and UG130075. The petioles for genotypes NASE13, UG120160, CSI-142, UG120202, UG120174, CS1-144 and UG130085 were inclined upwards; and reflexed downwards for UG120286 and UG120293. Genotypes UG120202, UG120174, NASE13, UG120286, UG120293 and CS1-144 had smooth leaves, while UG120160, CSI-142, UG130075 and UG130085 possessed hairy leaves.

DISCUSSION

At least 10 cassava genotypes showed good levels of resistance to whitefly infestation and damage, including: UG120202, UG120174, NASE13, UG120160, UG120286, UG120293, UG130075, CSI-142, CS1-144 and UG130085 (Table 4).

Variability in whitefly nymph abundance and feeding damage at different crop growth stages and across locations (Fig. 1) suggests that evaluation should be conducted across multiple environments. Low broad-sense heritability estimates were obtained at different crop growth stages and across different locations for whitefly nymph abundance and feeding damage. The low estimates for broad-sense heritability may indicate that inheritance of whitefly resistance traits is complex.

The significant differences observed among genotypes in the current study, both within and across seasons (Fig. 1A), suggest high genetic variability among the tested cassava genotypes. It seems therefore, that the 10 genotypes identified in our study may serve as good candidate parental materials for breeding programmes aimed at developing whitefly and viral disease resistant cassava. However, research is still required to fully understand the mechanisms and genetic bases of the resistance in these genotypes, which will aid in the retrogression of the whitefly resistant genes into the available viral disease resistant cassava cultivars.

The significant location effects associated with whitefly resistance traits within and across seasons (Table 3) showed that the field conditions in these locations differed and strongly affected whitefly resistance assessments. This suggests that future evaluation of cassava genotypes for whitefly resistance should be conducted in areas with high whitefly abundance. Resources should not be wasted on screening for whitefly resistance in low whitefly abundance areas. Conversely, the significant difference observed for season × genotype interactions at different crop growth stages, implied that season influenced genotype performance in relation to whitefly nymph abundance and feeding damage. The results show that the field conditions in all the study locations and seasons significantly affected genotype performance with regards to whitefly nymph abundance and feeding damage. Whitefly gradually infest and colonise cassava crops starting at 2 until 5 months after planting (MAP); and often peak at 3 and 4 MAP (Sseruwagi *et al.*, 2003). This was evident in the present study as supported by the significant positive correlations between whitefly nymph abundance/infestation and

feeding damage at 3 and 4 MAP. The effect was more evident in the 2015 than 2016 at 4, 5 and 6 MAP cropping seasons; emphasizing the importance of seasonal effects on whitefly infestation and damage on cassava.

Morphological characterisation of cassava genotypes with respect to whitefly preference and colonisation confirmed the characteristic traits of resistant genotypes to include: leaf and apical leaves colour. These are the traits that defined genotypes UG120174, UG120191 and UG130004 that had the lowest nymph abundance and feeding damage. Our findings are consistent with those reported by Legg (2010).

Genotypes UG130075, CS1-144 and UG130085 that had light green foliage were better hosts to *B. tabaci* , than cultivars UG120202, UG120174, NASE13, UG120160, UG120286, UG120293 and CSI-142 with dark green foliage. Our results are consistent with those of Stansly (1995), who showed that *B. tabaci* adults preferentially fed and oviposited more on light green than on dark green leaf cultivars. Elsewhere, studies evaluating poinsettia cultivars in relation to *B. tabaci* preference and performance also showed that light green leaf cultivars were more susceptible than dark green leaf cultivars (Berlinger, 1986).

Dark green leaf cultivars have higher phenolic content and thickness of the leaves, which may be the resistance mechanism playing a major role in relation to *B. tabaci* performance and behaviour (Shibuya *et al.,* 2010). Phenols are plant secondary metabolites involved in plant defense against insects such as *B. tabaci* (Mwila *et al*., 2017). The phenols are directly toxic to the insects and/or act as feeding deterrents (Chu *et al.,* 2017). These effects were also reported by Mwila *et al.* (2017),who showed the phenolic compounds to constitute a diverse group of plant secondary metabolites involved in plant defense against insect pests. The phenolics containan a stringent (mouth puckering) and bitter taste that deters insect pests. These compounds bind to the insect midgut proteins and digestive enzymes and precipitate them through hydrogen or covalent bonds, thereby limiting their availability to the insect pests, ultimately reducing insect growth and development. Therefore, we recommend that cassava farmers should grow darker green leaf cultivars because they are inherently less preferred by *B. tabaci* compared to the lighter green leaf foliage. Leaf orientation also seemed to be important, as genotypes with leaflets reflexed upward about the midrib supported fewer whiteflies than those reflexed downwards. Similar results were reported by Butler *et al.* (1983) in cotton plants. Byrne and Bellows (1991) reported leaf hairs to interfere with whitefly landing and feeding on cassava and proposed it to be a likely trait of whitefly resistance.

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