TEMPORAL AND SPATIAL DYNAMICS OF *Bemisia tabaci* POPULATIONS AND CASSAVA VIRAL DISEASES ON SELECTED WHITEFLY RESISTANT CASSAVA GENOTYPES IN UGANDA

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ABSTRACT

Bemisia tabaci (Gennadius) (Hemiptera: Aleyrodidae) is a pest that causes widespread damage on cassava (*Manihot esculanta* Crantz), a staple food crop for millions of households in sub-Saharan Africa. *Bemisia tabaci* also acts as a vector responsible for spreading plant viruses that cause two of the most economically damaging diseases in cassava; namely cassava mosaic disease (CMD) and cassava brown streak disease (CBSD). The objective of this study was to determine the population dynamics of *B. tabaci* on whitefly resistant cassava genotypes in different agro-ecologies in Uganda. Data were collected once a month, for six months on adult whitefly populations, cassava mosaic disease (CMD) and cassava brown streak disease (CBSD) incidence and symptom severity. The results obtained indicated that cropping season (2015 and 2016), agro-ecology, cassava age and genotypes strongly (P≤0.001) influenced the population of adult whitefly. Moderate (47.44% ± 0.7821) and high (72.04% ± 0.6916) overall means incidences of CBSD recorded across agro-ecologies on the whitefly resistant genotypes in 2015 and 2016 trials, respectively, were likely due to use of cutting-infected planting materials that were not detected through visual inspection at trial establishment. The analysis further revealed that the interaction effect of genotype, agro-ecology and crop age (months after planting: MAP) had a highly significant influence (P≤ 0.001) on whitefly abundance and high significant effect (P≤0.05) on CMD incidence and severity. The CMD and CBSD incidence as well as symptom severity increased with crop age from 3 months after planting across agro-ecologies. The study demonstrates that whitefly population dynamics and viral disease incidence are influenced by cassava genotypes, agro-ecological differences and crop age (MAP). Information generated could be used to guide the development of appropriate area-specific control strategies to mitigate the effect of whitefly and whitefly-transmitted viral diseases in cassava.

Key Words: CBSD, CMD, incidence, severity

RÉSUMÉ

Bemisia tabaci (Gennadius) (Hemiptera : Aleyrodidae) est un ravageur qui cause des dégâts étendus sur le manioc (*Manihot esculanta* Crantz), une culture vivrière de base dans des millions de ménages en Afrique subsaharienne. *Bemisia tabaci* agit également en tant que vecteur responsable de la propagation de virus végétaux qui causent deux des maladies les plus dommageables sur le plan économique du manioc; à savoir la maladie de la mosaïque du manioc (CMD) et la maladie des stries brunes du manioc (CBSD). L'objectif de cette étude était de déterminer la dynamique des populations de *B. tabaci* sur les génotypes de manioc résistants aux aleurodes dans différentes agro-écologies en Ouganda. Des données ont été recueillies une fois par mois pendant six mois sur les populations d'aleurodes adultes, l'incidence de la maladie de la mosaïque du manioc (CMD) et de la maladie des stries brunes du manioc (CBSD) et la gravité des symptômes. Les résultats obtenus ont indiqué que la saison de culture (2015 et 2016), l'agro-écologie, l'âge et les génotypes du manioc ont fortement influencé (P≤0,001) la population d'aleurodes adultes. Les incidences moyennes globales modérées (47,44 % ± 0,7821) et élevées (72,04 % ± 0,6916) de CBSD enregistrées dans les agro-écologies sur les génotypes résistants aux aleurodes dans les essais de 2015 et 2016, respectivement, étaient probablement dues à l'utilisation de matériel de plantation infecté par des boutures qui n'ont pas été détectés par inspection visuelle dans l'établissement d'essai. L'analyse a en outre révélé que l'effet d'interaction du génotype, de l'agro-écologie et de l'âge de la culture (mois après la plantation: MAP) avait une influence hautement significative (P≤0,001) sur l'abondance des aleurodes et un effet significatif élevé (P≤0,05) sur l'incidence et gravité. L'incidence de CMD et de CBSD ainsi que la sévérité des symptômes ont augmenté avec l'âge de la culture à partir de 3 mois après la plantation dans toutes les agro-écologies. L'étude démontre que la dynamique des populations d'aleurodes et l'incidence des maladies virales sont influencées par les génotypes de manioc, les différences agro-écologiques et l'âge des cultures (MAP). Les informations générées pourraient être utilisées pour orienter l'élaboration de stratégies de contrôle appropriées et spécifiques à la zone pour atténuer l'effet des aleurodes et des maladies virales transmises par les aleurodes sur le manioc.

Mots Clés: CBSD, CMD, incidence, gravité

INTRODUCTION

Bemisia tabaci (Gennadius) (Hemiptera: Aleyrodidae) is a pest that causes widespread damage on cassava (*Manihot esculanta* Crantz), a staple food crop in millions of people in sub-Saharan Africa (Berry *et al.,* 2004; Colvin *et al.,* 2004). The damage is inflicted by direct phloem-feeding and excretion of sugar-rich honeydew, which acts as a substrate for the growth of sooty mould that causes the darkening of leaves, leading to reduced respiration and photosynthesis (Colvin *et al.,* 2004). *Bemisia tabaci* is also a vector responsible for spreading plant viruses that cause two most economically damaging diseases in cassava; namely cassava mosaic disease (CMD) and cassava brown streak disease (CBSD) Tumwegamire *et al.,* 2018).

Phloem-feeding, indirect damage caused by sooty mould and transmission of plant viruses by *B. tabaci* cumulatively reduce cassava crop yields by up to 80% (Dinsdale *et al.,* 2010). Eight species of cassava mosaic begomoviruses (CMBs) (Family Geminiviridae: Genus Begomovirus) (Legg and Fauquet, 2004) are associated with CMD in Africa. These include African cassava mosaic virus (ACMV), East African cassava mosaic Cameroon virus (EACMCV), East African cassava mosaic Kenya virus (EACMKV), East African cassava mosaic Malawi virus (EACMMV), East African cassava mosaic virus (EACMV), East African cassava

mosaic virus-Uganda (EACMV-UG), East African cassava mosaic Zanzibar virus (EACMZV), and South African cassava mosaic virus (SACMV). In the Asian sub-continent, Indian cassava mosaic virus (ICMV) and Sri Lankan cassava mosaic virus (SLCMV) were reported to be the key begomoviruses limiting cassava production (Dixon *et al.,* 2010; Wang *et al.,* 2020).

CBSD is caused by two distinct viruses: *Cassava brown streak virus* (CBSV) and *Ugandan cassava brown streak virus* (UCBSV), both of which belong to the genus Ipomovirus in the family Potyviridae. CMD and CBSD symptoms are usually variable and irregular, depending on many factors such as plant age, cultivar (genotypes), environmental conditions (altitude, temperature and rainfall quantity) and virus species (Navangi *et al.,* 2020).

Cassava mosaic disease and CBSD are both disseminated widely in infected planting materials (Legg and Thresh, 2014; Okul *et al.,* 2018). Therefore, repeated use of cassava planting materials obtained from the previous season's crop, some of which may already have been infected with cassava viruses, could result in the rapid deterioration of crop quality and yield (Legg and Thresh, 2014). Previous studies have shown the importance of factors such as cassava variety, proximity of other cassava fields or sources of inoculum, crop density and virus strains present in influencing the pattern of spread of CMD and CBSD within and between fields (Legg *et al.,* 2011). Wind also plays a big role in enhancing dispersal of whiteflies that carry the causal viruses for CMD and CBSD both within and between cassava fields (Gwandu *et al.*, 2019) as well as over long distances (Maruth *et al.,* 2017). Wind speed and direction influence distribution of whitefly populations in a field; it has been shown that incidence of disease is higher on the upwind side than on downwind side of fields (Sseruwagi *et al.,* 2003; MacFadyen *et al.,* 2018). Various factors thus, influence whitefly population dynamics (MacFadyen *et al.,* 2018) and the pattern of spread of CMD

(Colvin *et al.,* 2004; Legg *et al.,* 2017) and CBSD (Mware *et al.,* 2009; Legg *et al.,* 2011; Gwandu *et al.,* 2015) within and between cassava fields. Fluctuations in whitefly populations partly depend on climatic factors such as temperature, rainfall and wind (Fargette *et al.,* 1990). A number of studies suggested high temperature as the primary factor driving the increase in whitefly populations (Boissot *et al.,* 2003). This is, however, not always the case where drought limited plant growth or in the event of an epidemic such as occurred in Uganda in the 1990s, when the whitefly spread rapidly in cooler areas (Legg and Ogwal, 2009).

Whitefly populations increase after the rainy season largely due to the vigorous plant growth that support their development (Fargette *et al.,* 1994). In Tanzania, Legg *et al.* (2017) showed that regions with the highest whitefly populations were hot and wet coastal areas, as well as drier inland areas moderated by neighbouring lakes.

New plantings are soon colonised by immigrant whiteflies moving from older stands of cassava in the area. The immigrants then reproduce to reach peak populations within a few months, before populations decline and adults disperse to other younger cassava (Hu *et al.,* 2011; Legg *et al.,* 2014; Gwandu *et al.,* 2015). The objective of this study was to determine the population dynamics of *Bemisia tabaci* (Homoptera: Aleyrodidae) on whitefly resistant cassava genotypes in different agro-ecologies in Uganda.

MATERIALS AND METHODS

Study sites. A field experiment was conducted in four diverse agro-ecologies in Uganda, namely: Humid Lake Victoria Crescent (Namulonge), Rift Valley (Kasese), Tropical Savannah (Ngetta) and Moist Savannah (Serere) (Table 1) for two seasons, namely July to December 2015 (Season 1) and April to September 2016 (Season 2).

TABLE 1. Agro-climatic description of the locations where test cassava genotypes were evaluated for whitefly resistance in Uganda in 2015 and 2016

Characteristic	Site			
	Humid Lake Victoria Crescent (Wakiso District)	Moist Savannah (Serere District)	Tropical Savannah (Lira District)	Rift Valley (Kasese District)
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 with Sandy clay loam sand black clays	Moist savannah with Sandy loam	Moist savannah with Peaty sands and clay

Source: Sebuwufu *et al.* (2015)

The Lake Victoria Crescent (Namulonge) agroecology is located at 0° 31' 46" latitude and 32° 36' 9" longitude in central Uganda, at an altitude of about 1150 meters above sea level (masl). The area has a bimodial rainfall pattern, which peaks in March and April in the first rainy season and in October or November in the second season of each year.

The Rift Valley (Kasese) agro-ecology lies in the high ground of the southwest and the rift valley lakes at 0° 10' 60.00" latitude and 30° 04' 60.00" longitude. This zone is hot and dry with temperatures ranging from 18 to 31 °C to and mean annual rainfall of 875-1000 mm. Mean annual rainfall on the higher plateau of the zone rises to over 1250 mm.

The Tropical Savannah (Ngetta) agroecology is located in northern Uganda at 2° 16' 59" latitude and 32° 55' 59" Longitude. It stands at 1300 masl and experiences a uni-modal rainfall pattern with an average of 1483 mm annually, stretching from April to November with an extended dry period from December to March or each year.

The Moist Savannah (Serere) agroecology, on the other hand, is located at 1°29'57.85" latitude and 33°32'56.43" longitude; and lies approximately 1,080 meters above sea level. It is characterised by mean annual rainfall of 1419 mm, mean annual maximum temperature of 31 °C and mean minimum temperature of 19 °C.

Genetic materials. Fifty diverse cassava had previously been evaluated for key agronomic traits and response to CMD and CBSD at Namulonge (central Uganda), were selected from the training population and used for this study. The training population comprised of 429 clones that are part of the Next Generation Cassava Breeding Project that is exploring the usefulness of genomic selection (www.cassavabase.org) for cassava genetic improvement (Wolfe *et al.,* 2016). The initial evaluation of the 50 genotypes was done at a single site (Namulonge) characterised by high CMD and CBSD pressure and high whitefly

populations (Abaca *et al.,* 2012; Kaweesi *et al.,* 2014; Pariyo *et al.,* 2015), for two consecutive years (2013 and 2014). During each year, visual assessment for CMD and CBSD symptom expression on foliage was carried out for all plants in a plot on the basis of maximum severity score obtained per plot. A third CMD and CBSD field re-evaluation was undertaken in 2015 at three locations in Namulonge (central Uganda), Kamuli (eastern Uganda) and Kasese (western Uganda).

Treatments and design. Treatments comprised of the 50 genotypes of cassava (Table 2), four argoecological zones (humid Lake Victoria Crescent, rift valley, Tropical Savannah and Moist Savannah) and two seasons (2015 and 2016). Treatments were laid out in an augmented design, with the following five check clones: NASE 1 and TME204 (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-replicated row plots of 10 plants, at the recommended spacing of 1 m x 1 m (Kawuki *et al.,* 2011).

Data collection

Whitefly population assessment. Adult whiteflies were counted on the abaxial part of the top five fully expanded leaves on each plant in the plots. Each leaf was held by the petiole and gently turned upside down to count the number of adult whitefly. Counting was done during the relatively cooler periods (morning and late evening) when the insects were less active (Sseruwagi *et al.,* 2004). Data were collected per month for 6 months after planting.

Disease incidence and severity evaluation. CMD and CBSD incidence were determined

TABLE 2.   Selected cassava genotypes evaluated for whitefly resistance in Uganda in 2015 and 2016

SN	Genotype	Female	Male	Pedigree/source
1	UG120174	MM96/0686	MM96/0686	Full sib of IITA clone x IITA clone
2	UG120191	Introduction Tanzania	Unknown	Selection from Tanzania Seed Introduction-2005
3	UG120160	CR21-6	Unknown	Half sib of CIAT CR-Line
4	UG130008	TZ 140	Unknown	Half sib of Tanzania material
5	UG120024	MM96/4271	Namikonga	Full sib of IITA clone x Tanzania clone-Namikonga
6	UG130085	NASE 13	Unknown	Half sib of IITA Clone
7	UG120251	TMS 60142	NASE 13	Full sib of IITA clone x IITA clone
8	UG120170	CR24-8	Unknown	Half sib of CIAT CR-Line
9	UG120227	Njule red	Unknown	Half sib of Ugandan local
10	UG120124	MM96/4271	MH04/2767	Full sib of IITA clone x IITA clone
11	UG120127	TZ 130	TZ 130	Selfed progeny of Tanzanian material
12	UG120198	Introduction Tanzania	Unknown	Selection from Tanzania Seed introduction -2005
13	UG120070	TME 204	MH95/0414	Full sib of IITA clone x IITA clone
14	UG120133	TMS30572	Unknown	Half sib of IITA clone
15	UG120063	TME 204	SE95/00036	Full sib of IITA clone x IITA clone
16	UG120001	TMS30572	MH95/0414	Full sib of IITA clone x IITA clone
17	UG130006	TZ 140	Unknown	Half Sib of Tanzania material
18	UG120293	TME 204	Unknown	Half sib of IITA clone
19	UG120252	TMS 60142	NASE 13	Full sib of IITA clone x IITA clone
20	UG120286	Kibao	CR36-2	Full Sib of CIAT CR-Line x Ugandan local
21	UG120295	TME 204	Unknown	Half sib of IITA clone
22	UG120202	SE95/00036	MM96/4291	Full sib of IITA clone x IITA clone
23	UG120109	40	40	Selfed progeny of IITA clone
24	UG120267	TMS 60142	TME 14	Full sib of IITA clone x IITA clone
25	UG120198	Introduction Tanzania	Unknown	Selection from Tanzania Seed introduction -2005
26	UG120286	Kibao	CR36-2	Full Sib of CIAT CR-Line x Ugandan local
28	UG120050	TME 14	Namikonga	Full sib of IITA clone x Tanzania clone-Namikonga
29	UG120072	TME 204	MH95/0414	Full sib of IITA clone x IITA clone

TABLE 2. Contd.

SN	Genotype	Female	Male	Pedigree/source
30	UG120161	CR21-6	Unknown	Half sib of C i8IAT CR-Line
32	UG120210	MH97/2961	Nyaraboke	Full sib of IITA clone x Ugandan local
33	UG120291	TME 14	Unknown	Unknown
34	UG130075	Unknown	Unknown	Unknown
35	UG130078	Unknown	Unknown	Unknown
36	UG130083	Unknown	Unknown	Unknown
39	CSI-144	Unknown	Unknown	Unknown
40	CSI-142	Unknown	Unknown	Unknown
41	UG130004	Unknown	Unknown	Unknown
42	UG130066	Unknown	Unknown	Unknown
43	UG120220	Unknown	Unknown	Unknown
44	UG120225	Unknown	Unknown	Unknown
45	UG130038	Unknown	Unknown	Unknown
46	TME 204 (Check)	Unknown	Unknown	Unknown
47	NASE 14 (Check)	Unknown	Unknown	Unknown
48	TME 14 (Check)	Unknown	Unknown	Unknown
49	NASE 1 (Check)	Unknown	Unknown	Unknown
50	NASE 13 (Check)	Unknown	Unknown	Unknown

by assessing the number of visibly diseased plants, as the proportion or percentage of plants in a stand with symptoms on a scale of 0-1 (P) or 0-100 (%) (Fargette *et al.,* 1985). Disease severity or the degree of symptom expression was assessed visually using an arbitrary scale of 1-5 , where 1 = no CMD symptoms and 5 = most CMD severe symptoms, including leaf distortion and stunting of plants (Hahn *et al.,* 1980). In addition, visual assessment of CBSD symptom expression was carried out on each plant per plot for six months; from July to December in 2015 (season 1) and April to September in 2016 (Season 2). The degree of CBSD infection was scored on a 1-5 scale, where for foliar: 1 = no symptom; 2 = mild symptom (1-10%); 3 = pronounced chlorotic mottle and mild stem lesion (11-25%); 4 = severe chlorotic mottle and stem lesion (26-50%) and 5 = very severe symptoms (>50%) (Patil *et al.,* 2014) (Table 3). Scores for symptomless plants were omitted when calculating the mean severity for each genotype.

Data analysis. Incidence values were subjected to ANOVA and means separated using the Least Significant Difference (LSD) test at 1% probability level in the GenStat Statistical Package 12th edition (Wang *et al.,* 2016). For calculating mean disease symptom severity for

CMD and CBSD, healthy cassava plants with score 1 were excluded, and the means generated based on the diseased plants only. Mean CMD and CBSD severity together with the whitefly population data were transformed using the logarithmic function. Means were separated using the LSD test at 1% probability level. Actual disease progress (incidence %) curves (based on obviously diseased plants at each time of assessment) were plotted to determine temporal spread of CMD and CBSD for each genotype and site.

Data on disease incidence, severity and whitefly abundance variance components were estimated based on the Generalised Mixed Effect Model, with genotype (G) declared as fixed effects and agro-ecology (A) (Humid Lake Victoria Crescent (*Namulonge),* Rift Valley (*Kasese)*, Tropical Savannah (Ngetta) and Moist Savannah (*Serere-)*, plus Months after Planting (T) time as random effects; using the following model:

$$Y_i = G + A + TA + GA + TGA$$

Where:

Y_i = observation (response variable);
A = Agroecology;
T = Months using R statistical software (R Core Team, 2013).

TABLE 3. The cassava mosaic disease severity scale used in evaluation

Scale	Symptom description
1	Unaffected shoots, no symptoms
2	Mild chlorosis, mild distortions at bases of most leaves, while the remaining parts of the leaves and leaflets appear green and healthy
3	Pronounced mosaic pattern on most leaves, narrowing and distortion of the lower one-third of the leaflets
4	Pronounced mosaic pattern on most leaves, narrowing and distortion of the lower one-third of the leaflets
5	Very severe mosaic symptoms on all leaves, distortion, twisting, mis-shapen and severe leaf reductions of most leaves accompanied by severe stunting of plants

Source: Sseruwagi *et al.* (2004)

RESULTS

Effect of interaction of genotype, crop age and agro-ecology. Combined analysis of variance for effect of interaction of genotype, agro-ecology, disease incidences, severity and whitefly abundance are shown in Table 4. In season 1 (2015), whitefly population, CMD incidence as well as CMD and CBSD severity, revealed the influence of genotype (P<0.05), agro-ecology (P<0.001) and crop age (P<0.001) to be significant and highly significant, respectively. The combined analysis of variance further revealed that interaction of genotype and agro-ecology had highly significant (P<0.001) effects on whitefly abundance, CMD and CBSD severity and significant (P<0.05) effects on CMD and CBSD incidences. Also, there were significant (P<0.05) interactions of genotype and crop age on whitefly abundance, CMD incidence and severity; effects on CBSD incidence and severity were however not significant at P>0.05. Analyses further revealed the interaction effect of genotype, agro-ecology and crop age to be highly significant (P< 0.001) on whitefly abundance and significant (P< 0.05) on CMD incidence and severity.

In season 2 (2016), there were highly significant (P<0.001) genotype and agro-ecology interactions on CMD incidence, CMD and CBSD severity; but significant (P<0.05) effects on whitefly abundance and CBSD incidence (Table 4). In addition, the interaction between genotype and crop was significant (P<0.05) on whitefly abundance; but not on disease incidences and severity. However, the genotype, agro-ecology and crop age interactions were highly significant (P<0.001) on whitefly abundance as well as on diseases incidences and severity (P<0.01).

Whitefly population dynamics. Whitefly population changes were not different between 2015 and 2016 growing seasons (Fig. 1). In 2015, Rift Valley-Kasese and Tropical Savannah-Ngetta recorded a mean population of 49 and 79, respectively at 1 MAP (July);

TABLE 4. Effect of interaction of genotypes, crop age and agro-ecology on whitefly abundance, diseases incidence and severity

Source of variation	DF	2015					2016				
		Whitefly population	CMD incidence	CBSD incidence	CMD severity	CBSD severity	Whitefly population	CMD incidence	CBSD incidence	CMD severity	CBSD severity
Genotype (G)	49	777213.69 **	2382.14 **	643.96	5.31 **	4.15 **	729507.12 **	2764.38 **	1929.38 **	6.02 **	2.62 **
Agro-ecology (A)	3	7351805***	37667***	3316.4***	76.673***	19.53***	5608167***	30269.0***	1994.4*	59.263***	22.99***
Blocks	4	585593.34	5270.1	1824.66	12.01	6.4	1170026.23	5922.46	1068.25	13.87	3.69
Crop age (C)	5	3589307***	16096***	30166.5***	34.85***	8.46***	8046556***	6218.6***	21519.1***	17.869***	88.04***
Checks	4	1180349.98	4768.32	810.56	4768.32	3	614367.18	4506.04	6924.22	5.53	15.3
G x A		216289***	1717**	618.5**	3.218***	1.39***	190685**	732.8***	1090.3**	1.121***	1.631***
G X C		191193**	534**	469.7	0.516**	0.396	211190**	494.8	830.5	0.336	0.472
G X A X C		163691***	563**	327.4	0.452**	0.380	76071***	513.7*	703.7*	0.241*	0.288*

Significance: * P < 0.05; ** P < 0.01; and *** P < 0.001

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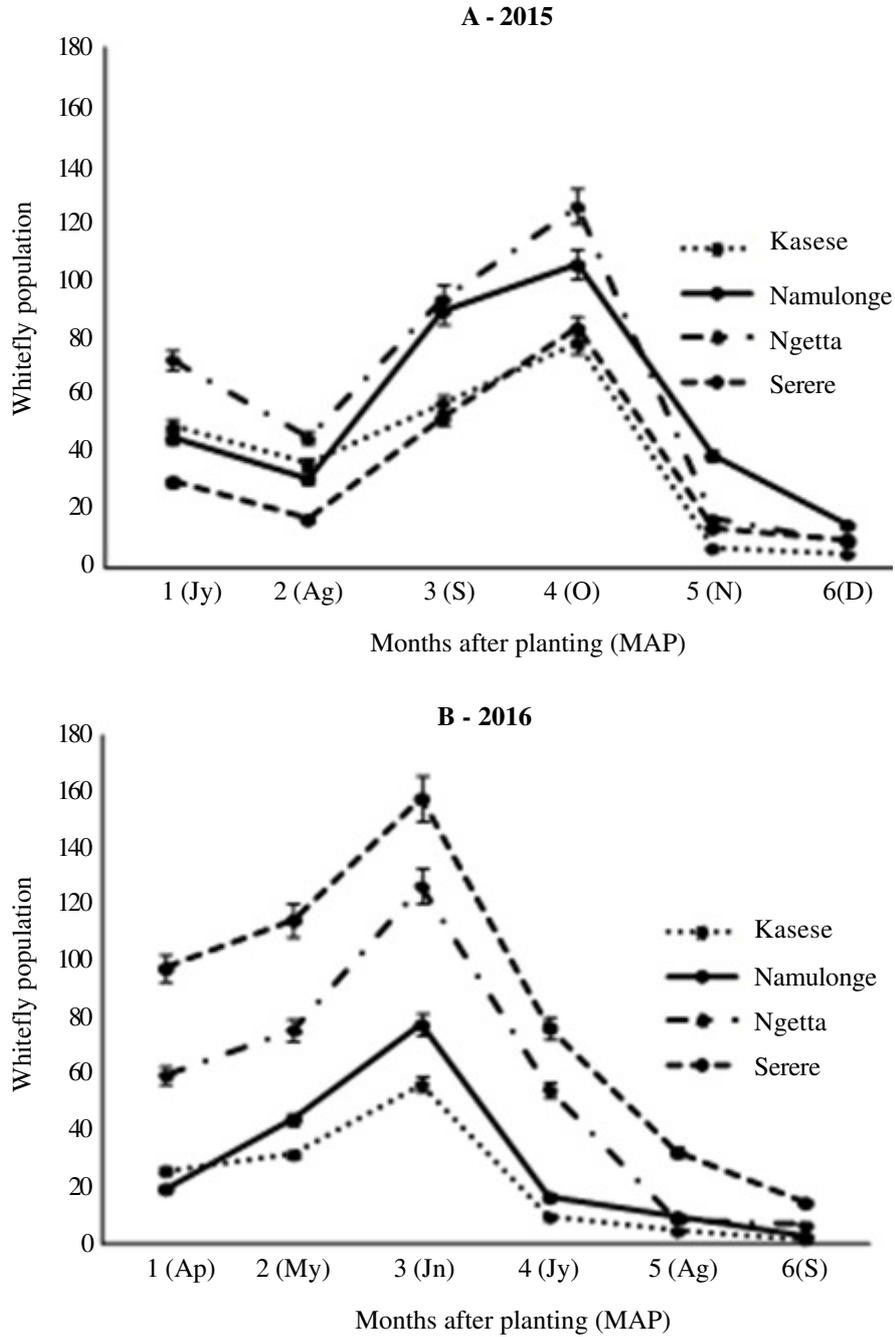
A - 2015

B - 2016

Figure 1. Mean adult whitefly population dynamics in the study locations in (A) 2015 and (B) 2016 in Uganda. Ap = April, My = May, Jn = June, Jy = July, Ag = August, S = September, O = October, N = November and D = December.

that initially declined before rising steadily to the maximum populations of 78 and 120 at 4 MAP (October). This was followed by a sharp decline to the lowest population of 7 and 17 at 5 MAP (November) and 5 and 10 at 6 MAP (December). A similar trend was observed in the Humid Lake Victoria Crescent-Namulonge and Moist Savannah-Serere zone, except that adult whitefly populations initially steadily increased at 1 MAP (July) and grew to the maximum of 105 (Humid Lake Victoria Crescent-Namulonge) and 125 (Tropical Savannah-Ngetta) at 4 MAP (October), before declining to the lowest of 15 (Humid Lake Victoria Crescent-Namulonge, Tropical Savannah-Ngetta and Moist Savannah-Serere) and 10 (Rift Valley-Kasese), respectively at 6 MAP (December) (Fig. 1A).

Similar trends were recorded in 2016, although the populations peaked one month earlier at 3 MAP (June) with 158, 127, 78 and 57 for Moist Savannah-Serere, Tropical Savannah-Ngetta, Humid Lake Victoria Crescent-Namulonge and Rift Valley-Kasese, respectively compared to 2015 (Fig. 1B). The highest peak populations were also recorded in Serere and Ngetta compared to Namulonge and Ngetta in 2015.

Diseases progression

Cassava mosaic disease progression. In 2015, the progression of CMD incidence exhibited similar trends in all four-study agro-ecological zones. Disease developed rapidly from a mean incidence of 1% (Humid Lake Victoria Crescent-Namulonge), 11% (Moist Savannah-Serere), 3% (Tropical Savannah-Ngetta) and 10% (Rift Valley-Kasese) at 1 MAP (July), to the maximum recorded incidence of approximately 97% at 6 MAP for Humid Lake Victoria Crescent-Namulonge, Tropical Savannah-Ngetta and Moist Savannah-Serere (December) (Fig. 2A). In contrast, in 2016, CMD incidence progressed relatively slowly, and remained lower than 10% from 1 MAP (April) until 3 MAP (June) with mean CMD

incidences of 3, 1, 2 and 6% at Moist Savannah-Serere, Tropical Savannah-Ngetta, Humid Lake Victoria Crescent-Namulonge and Rift Valley, respectively-Kasese (Fig. 2B). In both years, however, the highest disease incidence at 6MAP was realised in the Rift Valley-Kasese zone.

Cassava brown streak disease progression. In 2015, CBSD incidence developed rapidly in all four study agro-ecological zones (Fig. 2); from a mean CBSD incidence of 5, 15, 20 and 27% at Tropical Savannah-Ngetta, Rift Valley-Kasese, Humid Lake Victoria Crescent-Namulonge and Rift Valley-Kasese, respectively; to the maximum recorded mean incidence of 98% for all four agro-ecological zones (Fig. 2C). However, in 2016, disease progression was rather gradual in all the study locations, and reached different maxima of 47% (Rift Valley-Kasese), 76% (Humid Lake Victoria Crescent-Namulonge), 90% (Moist Savannah-Serere) and 93% (Tropical Savannah-Ngetta) (Fig. 2D).

Cassava mosaic disease severity progression. In 2015, progression of CMD foliar symptom severity displayed a similar trend in all four study locations (Fig. 3A). Mean CMD severity gradually increased from 2.0 at 1 MAP (July) in all four study sites to the maximum recorded mean severity of 4.5, 4.3, 4.0 and 3.9 at Rift Valley-Kasese, Moist Savannah-Serere, Humid Lake Victoria Crescent-Namulonge and Tropical Savannah-Ngetta, respectively (Fig. 3A). Conversely, CMD symptom severity followed diverse trends in each of the four study locations in 2016 (Fig. 3B). Severity developed rapidly in Humid Lake Victoria Crescent-Namulonge and Moist Savannah-Serere, and gradually in Tropical Savannah-Ngetta and Rift Valley-Kasese. Ultimately, CMD symptom severity developed to the highest mean of 5.0 in Humid Lake Victoria Crescent-Namulonge, Rift Valley-Kasese and Moist Savannah-Serere, and
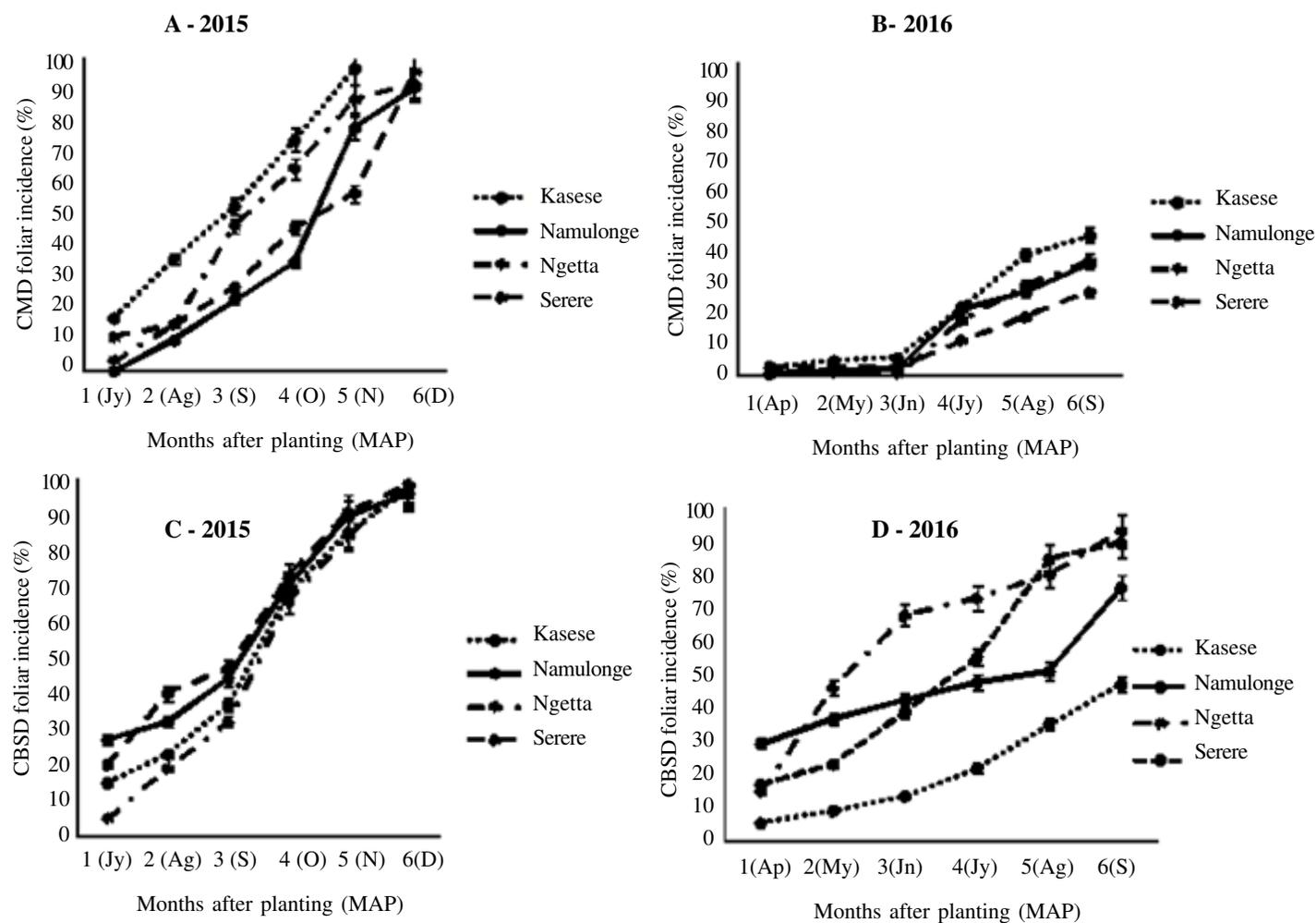
Figure 2. Progression of cassava mosaic disease in (A) 2015 and (B) 2016 and cassava brown streak disease in (C) 2015 and (D) 2016 in different study locations of Uganda. Ap = April, My = May, Jn = June, Jy = July, Ag = August, S = September, O = October, N = November and D = December.
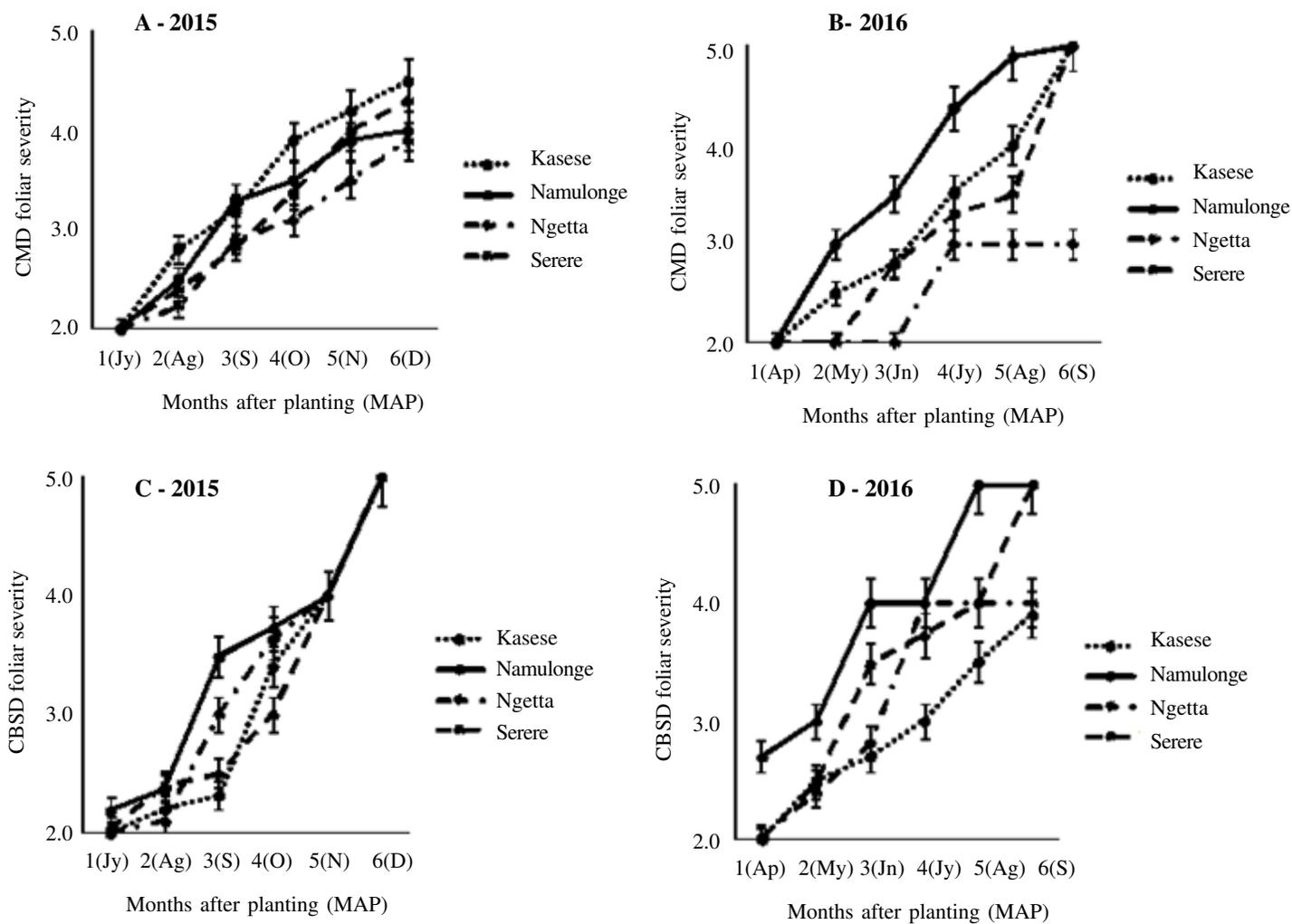
Figure 3. Progression of foliar severity of cassava mosaic disease in (A) 2015 and (B) 2016, and cassava brown streak disease in(C) 2015 and (D) 2016 in different study locations of Uganda. Ap = April, My = May, Jn = June, Jy = July, Ag = August, S = September, O = October, N = November and D = December.

only to a maximum mean of 3.0 at Tropical Savannah-Ngetta at 6 MAP (Fig. 3B).

Cassava brown streak disease foliar severity progression. Generally, CBSD foliar symptom severity progression displayed different trends in all four study sites in both the 2015 and 2016 growing seasons (Fig. 3). However, in 2015 mean CBSD severity developed to a maximum of 5.0 in all four sites (Fig. 3C); while CBSD mean severity developed to the highest mean of 5.0 in Humid Lake Victoria Crescent-Namulonge and Moist Savannah-Serere, and 4.0 and 3.9 for Tropical Savannah-Ngetta and Rift Valley-Kasese, respectively at 6 MAP in 2016 (Fig. 3D).

DISCUSSION

Effect of interaction of genotype, crop age and agro-ecology. The significant differences observed among genotypes with respect to whitefly abundance, diseases incidences and severities, suggest high genetic variability among the tested cassava genotypes. This implies that the cassava genotypes responded differently in different agro-ecologies with regards to whitefly abundance, CMD and CBSD incidence and severity. This was also evident in Gwandu *et al.* (2019) as supported by the significant important of genotypes effects on whitefly population. The significant agro-ecology effects on whitefly abundance, diseases incidences and severity demonstrated that the field conditions in these agro-ecologies differed and thus affected the whitefly populations. This suggests that future evaluation of cassava genotypes for whitefly population dynamics should be conducted in areas with high whitefly abundance. This phenomenon was similar to work of other researchers (Gwandu *et al.,* 2019; Navangi *et al.,* 2020), who reported significant variation among genotypes and agro-ecologies for whitefly abundance.

The significant difference observed for agro-ecology × genotype interactions at different crop growth stages, implied that all three factors worked together to mediate whitefly populations, diseases incidences and whitefly population. Depending on the crop age and for a specific genotype, it would thus be expected that field conditions would have a different effect on the variables measured. Navangi *et al.* (2020) and Katono *et al.* (2021) confirmed that susceptibility levels, predominant virus species and climatic factors influence abundance of whitefly vectors and/ or growth rate of the crop as previously indicated by Legg *et al.* (2014). The population of *B. tabaci* builds up starting at three MAP and peaks between four and five MAP, when the foliage is very well formed and succulent after which it drops drastically as plants grow taller, become more woody (less succulent) and shade the leaves (Sseruwagi *et al.,* 2003). The environmental conditions differences in the studies area the differences in whitefly population may be due to differences in temperature, rainfall, or relative humidity conditions. High rainfall amounts is known to wash away whiteflies and other insect pests, thus causing significant mortality and population reduction (Katono *et al.,* 2021). The positive relationship between *B. tabaci* abundance and temperature possibly resulted from increased adult longevity and increase reproductive success at high temperature (Mugerwa *et al.,* 2012).

Whitefly population dynamics. There were significant variations in the population of adult whitefly on the diverse cassava genotypes used in the current study. This was expected since cassava genotypes differ in morphology and plant biochemistry, which determine the suitability of the host plant to whitefly colonisation (Mwila *et al.,* 2017; Kalyebi *et al.,* 2018; Gwandu *et al.,* 2019). However, despite the variations in adult whitefly populations recorded on cassava plants in the current study, the populations were not highly (super) abundant as was reported earlier in Uganda in the late 1990s (Legg *et al.,* 2002).

This is evidence that these cassava genotypes support less whitefly and can be considered to be relatively more tolerant genotypes. Throughout the study, genotype UG130075 exhibited the highest and UG120210 the lowest CMD incidences; while UG130075 and UG120174 exhibited high CBSD incidence and UG130085 was the most affected.

Diseases progression. Although all the experimental plants were obtained from CMD and CBSD-screened mother plants (using visual and not molecular assessments) and grown in the different environments, disease incidence data suggested that the disease was influenced by the inherent susceptibility and resistance or tolerance to the causal viruses for CMD and CBSD as was similar to the reports of Hillocks *et al.* (2001) and Wudil *et al.* (2019) who noted that different cultivars respond differently to CMD and CBSD. Additionally, the low (<10%) and relatively high (>50%) mean CMD and CBSD incidences, respectively; recorded on the trials throughout the study period confirm that the genotypes are highly resistant to CMD, but highly susceptible to CBSD. The magnitude of increase of CMD incidence and symptom severity were more likely associated with inherent resistance to disease (Otim-Nape *et al.,* 1997; Sseruwagi *et al.,* 2003). The generally consistent behaviour of the whitefly resistant cassava genotypes in all four study agroecologies suggests that their resistance is stable over a wide range of environments and can be exploited as a means of decreasing - losses caused by CMD and CBSD in all areas of Uganda.

CONCLUSION

This study demonstrates that whitefly population dynamics and viral disease incidence are influenced by cassava genotypes, agro-ecological differences and crop age. Information generated could be used to guide the development of appropriate area-specific control strategies to mitigate the effect of whitefly and whitefly-transmitted viral diseases in cassava.

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