Parasitism of the whitefly *Bemisia tabaci* by aphelinid parasitoids on cassava across five agro-ecological zones of Cameroon

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ABSTRACT

The whitefly *Bemisia tabaci* (Gennadius) is the vector of cassava mosaic viruses causing cassava viral diseases, which are the most important biotic constraints of cassava production in sub-Saharan Africa (SSA). Presently, *B. tabaci* management in cassava fields calls for the development of an integrated approach that relies on host plant resistance and biological control. Data on *B. tabaci's* natural enemies, particularly parasitoids, in Central Africa are limited. Field surveys were conducted from 2015 to 2017 to identify parasitoids associated with *B. tabaci* in 5 Cameroon agro-ecological zones. Additionally, population dynamics studies were conducted in replicated fields experiments were conducted from 2016 to 2018 to identify cassava genotypes that can best promote *B. tabaci* parasitism. Two parasitoids, *Encarsia sophia* (Girault & Dodd) and *Encarsia lutea* (Masi) were found parasitizing *B. tabaci* nymphs with higher parasitism by *E. lutea* compared with *E. sophia*. The average parasitism rate during the survey was 33.4% for *E. lutea* and 8.4% for *E. Sophia,* regardless of AEZ. The highest parasitism rates by *E. lutea* (48.2% and 24.2% from field trials and surveys, respectively) were observed in the Western Highlands (AEZ 3) while parasitism by *E. sophia* was less than 12.4%. Four cassava genotypes (I090590, I011797, I090574, and I070593) promoted higher parasitism rates of *B. tabaci* by *E. lutea* and *E sophia*. The contributions of the two parasitoids and their integration with cassava genotypes for the management of *B. tabaci* in cassava fields are discussed.

1. Introduction

The whitefly *Bemisia tabaci* (Gennadius) is arguably one of the most economically important pests worldwide, due primarily to its capacity to transmit numerous plant viruses that cause diseases across a wide range of field and horticultural crops, particularly in subtropical and tropical regions of the world (Zhang et al., 2007). Damage caused by virus infections and whitefly feeding on the host plant (Nelson, 2008) can lead to huge crop yield losses (Oliveira and Anderson, 2001; Brown and Czosnek, 2002; Jones, 2003; Stansly et al., 2010).

In sub-Saharan Africa (SSA), *B. tabaci* is a common and widespread pest of cassava (*Manihot esculenta* Crantz) (Stansly et al., 2010), one of the most important crops for food security and income generation on the continent, particularly in western and central Africa (FAOSTAT, 2018). The insect is the vector of at least nine begomovirus species, the causal agents of cassava mosaic disease (CMD), and two distinct ipomovirus species that cause the cassava brown streak disease (CBSD) (See Rey 2017for review). Both diseases can lead to substantial reductions in cassava root yield, quality of cassava stems used as planting material, and leaves that are widely consumed as fresh vegetables (Calvert et al., 2022; Legg and Hillocks 2002; Legg et al., 2015). Yield loss due to uncontrolled CMD infections can reach 82% depending on factors including virus strain, cassava genotype, and timing of plant infection (Owor et al., 2004; Macfadyen et al., 2018). In Cameroon, Akinbade

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et al. (2010) reported the occurrence of the African cassava mosaic virus (ACMV), the East African cassava mosaic (EACMV), and two EACMV strains, the Cameroon strain (EACM-CV) and the Ugandan strain (EACMV-UG). *Bemicia tabaci* biotypes from Cameroon belong to the SSA3 and SSA4 groups (Berry et al., 2004; Gnakiné et al., 2012; Mac-Fadyen et al., 2018). Although symptoms like CBSD have been observed in the country by our team, CBSD's presence in Cameroon is yet to be confirmed.

Management of *B. tabaci* often requires an integrated approach that considers one or more management options (Van den Elsen-van den et al., 2016). Pesticides are frequently used in temperate regions to control *B. tabaci* populations, but they are not widely used in SSA, except on susceptible high-value vegetable crops (Wilson and Tisdell, 2001; Aktar et al., 2009; Maitah et al., 2015; Mahmood et al., 2015; Fotso et al., 2017). Factors such as temperature, precipitation, relative humidity, altitude, host-plant resistance, and natural enemies are considered key factors in natural whitefly mortality and can, under certain conditions, limit the size of whitefly populations (Kedar et al., 2014; Swati and Rolania, 2017). Several parasitoids are known to be associated with *B. tabaci* nymphs and have been reported to contribute to reductions in *B. tabaci* populations (Li et al., 2011; Kalyebi et al., 2018). *Encarsia* spp. and *Eretmocerus* spp. (Hymenoptera: Aphelenidae) are the main genera of whitefly parasitoids; they parasitize the nymphal instars of whiteflies and often cause additional mortality through host feeding (Kedar et al., 2014; Swati and Rolania, 2017).

In the genus *Encarsia*, several studies have been conducted on the key importance of the species *Encarsia lutea* (Masi) and *Encarsia sophia* (Girault & Dodd) attacking *B. tabaci* in several agricultural systems in SSA (Asiimwe et al., 2007; Ntawuruhunga et al., 2007; Sangha et al., 2018). In Tanzania, based on molecular and morphological evidence, three *Encarsia* species and three *Eretmocerus* species were obtained from *B. tabaci* with *E. sophia*, *E. lutea*, and *Eretmocerus mundus* Mercet being the most common in decreasing order (Guastella et al., 2015). In Africa, plans are underway to combine cassava resistance to CMD and CBSD with that of *B. tabaci* (Legg et al., 2015; Kalyebi et al., 2018; Tumwegamire et al., 2018). Comparatively little attention has been given, however, to combining host-plant resistance with the use of biological control, especially with parasitoids that have been used effectively on other continents (Naranjo, 2001). Unlike in Europe and North America, information on parasitoids of *B. tabaci* on cassava and how they are affected by climate and cassava genotype in Africa are limited (Legg et al., 2014; Romba et al., 2018), and non-existent for Central Africa including Cameroon.

This study was undertaken to (1) identify parasitoids of *B. tabaci* from cassava farms and to determine their relative abundance and field parasitism rates of *B. tabaci* in various agro-ecological zones of Cameroon through field surveys, and (2) to determine the effect of cassava genotypes and environmental conditions on the dynamics of whiteflies and their associated parasitoids through cassava field trials.

2. Material and methods

2.1. Study area

Field surveys were conducted in five agro-ecological zones (AEZs) of Cameroon including nine administrative regions, during the dry season between December and January of 2015–2016, 2016–2017, and 2017–2018 to collect, identify, and determine the relative abundance and parasitism rate of *B. tabaci* parasitoids (Fig. 1). The surveys were conducted during the first half of the long dry season which corresponds to the period of high abundance of whiteflies (Swati and Rolania, 2017), especially on plants that are 3–6 months old, and that is also the time for easy road access to the fields. The surveys targeted five agro-ecological zones in Cameroon: (1) the Sudano- Sahelian (AEZ 1); (2) the High Guinea Savanna (AEZ 2); (3) the Western Highlands (AEZ 3); (4) the Humid Forest with Monomodal Rainfall (AEZ 4); and (5) the Humid

Forest with Bimodal Rainfall (AEZ 5) (Table 2). Over the 3 years of this study, a total of 518 cassava fields were surveyed in 189 villages (Table 1). In each village, the same cassava plot, or a plot nearby was sampled each year.

2.2. Sampling methods

The number of fields sampled during each survey was based on the frequency of cassava fields encountered at the time of sampling which reflected the level of cassava cultivation in the various regions (Table 2). Fields with cassava plants between 3- and 6-month-old were selected at regular intervals of at least 20–30 km along motorable roads running through each AEZ. Fields were accessed with the permission of their owner. Field geographic coordinates and altitude were obtained with a handheld GPS reader (Garmin eTrex 20 HC, Garmin Ltd, Kansas, and the USA).

2.3. Whitefly and parasitoid sampling

Selected fields were scouted by inspecting 10 plants at 3 locations along the field's longest diagonal, for a total of 30 plants per field (Sseruwagi et al., 2004; Legg, 2010). Two consecutive sampled plants at each location along the diagonal were separated by 3–5 non-sampled plants depending on the length of the diagonal. *Bemisia tabaci* adults and nymphs were counted on each of the selected cassava plants with the help of an optical lens binocular magnifier (OptiVISOR®, Model DA-5 Blue, and 3.5 x). Adults were counted on the first five expanded leaves at the tip of the tallest shoot, by gently turning over the leaves while they hide from the sun to minimize adult whitefly disturbance (IITA, 1990; Sseruwagi et al., 2004). Whitefly nymphs (all four instars) were counted on 10–14 fully expanded leaves, preferably collected from the middle part (not at the growing point nor the basal developed leaves) of cassava plants (Legg, 2010). This is the position on the cassava plant where the whitefly nymphs are known to occur the most frequently (Sseruwagi et al., 2004). The selection of the leaf position to count whitefly nymphs was done considering the shape and the height of each plant since the same variety could have differences in growth rate depending on rainfall and temperature. In addition, different genotypes have different growth rates and thus the distribution of nymphal stages could vary with genotype. Whitefly eggs, which are found on the youngest leaves, were not counted. Whitefly nymphs were categorized into non-parasitized (yellow green) and parasitized individuals. The loss of the asymmetry of the mycetomes in nymphs is an early parasitism sign, but parasitoid species cannot be determined at this stage. The most reliable sign of a parasitized nymph is their change in color which turns black or yellow. Parasitized nymphs were classified into black nymphs with posterior red meconia or dark yellow nymphs with no visible meconia. The two-color classification, which is most visible in 4th instar whitefly nymphs, has been successfully used by other studies to distinguish parasitized from unparasitized nymphs (Otim et al., 2006; Gould et al., 2008). Parasitized nymphs were kept in bottles for adult parasitoid emergence and the emerged adults were collected and kept for identification.

2.4. Population dynamics study

Field trials were established for three consecutive years (2015–2016, 2016–2017, and 2017–2018) corresponding with the years of the surveys. Eleven improved cassava genotypes, developed in Nigeria by the IITA Cassava Breeding Unit and previously tested in Cameroon for their high yield and resistance to cassava mosaic disease (Tize et al., 2021), were used to evaluate their effect on the dynamics of whiteflies and their associated parasitoids and to identify genotypes which promote biological control. The local and widespread Cameroon farmer variety – LMR – was used as the control. Accession names and their pedigree are available in the cassava database (Table 3) (https://www.cassavabase.
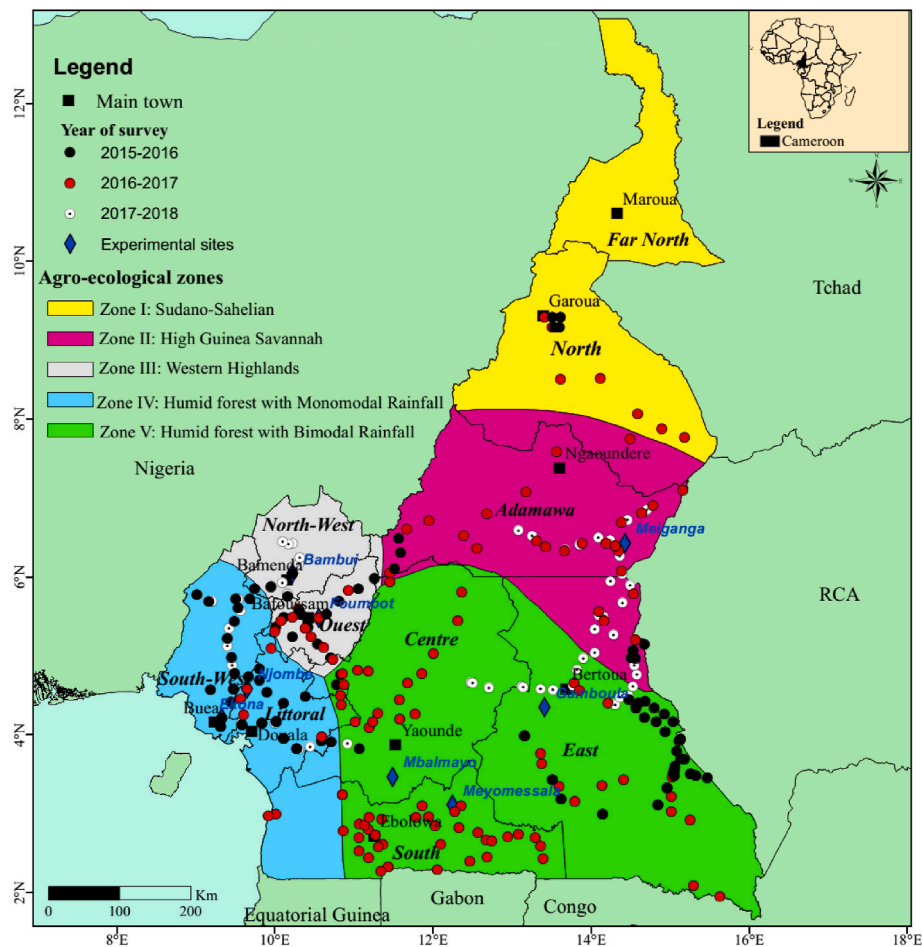
Fig. 1. Cameroon map including survey fields' locations (black-filled circle – 2015–2016; red-filled circle – 2016–2017; black-dot circle – 2017–2018) and the cassava field experimental site (blue diamond) in Foumbot and Bambui – agro-ecological zone (AEZ) 3; Ekona and Njombe - AEZ 4; Mbalmayo, Meyomessala, and Gamboula – AEZ 5, and Meiganga in AEZ 2.

org/). A total of eight field sites were established, two fields in each of AEZ 3 (Foumbot and Bambui) and AEZ 4 (Ekona and Njombe), three in AEZ 5 (Mbalmayo, Meyomessala, and Gamboula), and one in AEZ 2 (Meiganga). At each site, a randomized complete block design was used, with 3 replicate blocks of 94 × 5 m excluding the borders. Plots within blocks measured 6 × 5 m (7 x 6 rows of plants) with plants spaced at 1 × 1 m, and 2 m alleys between plots.

Sampling for *B. tabaci* nymphs and parasitoids was conducted at 3, 6, and 9 months after planting (MAP) (IITA, 1990; Fotso et al., 2018). According to (IITA (1990), Fukuda et al. (2010), and Kalyebi et al. (2018), the fourth to sixth months after planting generally correspond to peak whitefly populations on cassava. On each sampling, 10 cassava plants were randomly selected from each of the 3 replicate plots for inspection, for a total of 30 plants per genotype, excluding the border rows, and avoiding adjacent plants within and between rows.

On each plant, the number of parasitized and non-parasitized whitefly nymphs was counted on the 14th leaf (IITA, 1990). All sampled leaves with parasitized nymphs were removed from the plants, bundled together with their petioles, and placed in 250 ml water-filled vials to maintain leaf freshness. The vial and the leaves were then placed inside a 1.5-L transparent plastic bottle with ~50% of the side cut out and replaced with a muslin cloth for aeration (Supplementary Fig. 1). Each bottle was equipped at the top with an inverted funnel and a tube to collect emerging parasitoids and whiteflies. Bottles were kept at room temperature for 15 days after which cassava leaves dried off and could no longer support nymphs' development to allow for the

emergence of adult parasitoids. The bottles were then frozen for 5 min, and all emerged adult parasitoids were removed and conserved in vials with 95% ethanol. Collected parasitoids were identified by Dr. Andy Polaszek from the Centre for Biodiversity of the Natural History Museum, United Kingdom (Ref: IAS, 2019–8171). Duplicates in vials were kept at the insect collection of the International Institute of Tropical Agriculture (IITA) in Yaoundé, Cameroon.

2.5. Data analysis

For the survey data, *B. tabaci* adults and nymphs were evaluated as the average number (± standard error) per plant and leaf, respectively. Total parasitism rates, percentage of parasitized nymphs by each parasitoid, and *B. tabaci* abundance were log-transformed to reduce

Table 1
Number of fields sampled during the 3 surveys in the 5 targeted agro-ecological zones (AEZs).

Agro-ecological Zone	Survey year			Total by AEZ
	2015–2016	2016–2017	2017–2018	
AEZ 1	13	13	12	38
AEZ 2	30	30	30	90
AEZ 3	25	25	20	70
AEZ 4	27	26	25	78
AEZ 5	81	81	80	242
Total by year	**176**	**175**	**167**	**518**

Table 2

Range of geographic locations (longitude, latitude, and elevation) and climate characteristics (minimum and maximum annual Rainfall, relative humidity, and temperature) of the 5 agro-ecological zones covered in the study.

Agro-ecological Zones (AEZ)	Longitude	Latitude	Elevation (masl)*	Rainfall (mm)	Humidity (%)	Temperature (°C)
AEZ 1	12°30 - 15°42	08°36 - 12°54	250–700	650–1200	17.1–74.9	24.1–33.5
AEZ 2	11°24 - 14°36	05°42 - 08°36	500–1500	1500–1742	76.4–84.5	13.3–30.3
AEZ 3	09°18 - 11°24	04°54 - 06°36	1500–2500	1800–2135	76.4–84.5	22.6–33.1
AEZ 4	08°48 - 10°30	02°6 - 06°12	0–900	2000–3653	66.1–86.2	22.6–33.6
AEZ 5	10°30 - 06°12	02°6 - 05°48	400–900	1500–2000	60–90	17.3–31.6

heteroscedasticity inherent in insect counts (Durner, 2019). The total number of *B. tabaci* nymphs was calculated as a sum of parasitized and unparasitized nymphs. The relative abundance of each parasitoid was calculated as a percentage of the total number of nymphs parasitized by each parasitoid divided by the total number of parasitized nymphs. The apparent parasitism rate was calculated as a percentage of parasitized nymphs divided by the total number of nymphs (sum of parasitized and unparasitized nymphs). We used variance components structure in the repeated-measures ANOVA (general linear mixed models (GLM) to evaluate the effects of years (Y), agro-ecological zones (AEZ), month after planting (MAP), genotypes and their interactions on the abundance of *B. tabaci* nymphs and parasitism rate in the combined experiments from the survey and field trial, considering plots as experimental units for the field trial. The block was considered as a replicate in this analysis. Tukey's test was used for post-hoc separation of means where treatment tests showed statistical significance ($P < 0.05$).

The climate variables were summarized using a 7-day running average and Pearson's correlation analysis was performed to determine which variables were associated with the variation in *B. tabaci* nymphs, *E. lutea,* and *E. sophia* parasitism in each agro-ecological zone.

For the trial data, the relative abundance of *B. tabaci* nymphs, total parasitism rates, and parasitism rates for each parasitoid were analyzed as described previously for the analysis of survey data. We used the metan package in R software to perform a stability analysis of multi-environment trial data (MET) using parametric and non-parametric stability statistics (Olivoto, 2019). MET allows us to identify the cassava genotypes on which the parasitism rate is either high or low and provides valuable information on the potential contribution of the parasitoid fauna on each genotype for the biological control of *B. tabaci* (Yan and Kang, 2003; Guastella et al., 2015). The best linear unbiased prediction (BLUP) was used to predict Breeding Values (BV) of each genotype for total count of *B. tabaci* nymphs and parasitoids, and parasitism rate (%). The BLUP was performed by pooling all three years using the linear mixed model approach that considered cassava genotype as a fixed factor and the AEZ (environment) as random factors. The time factor (years) was nested into location to determine whether each factor has a statistically significant effect on whitefly population or

parasitism rate. The model also included genotype by environment (G x E) interactions. Data were analyzed using the statistical software R v. 4.1.2 (R Development Core R Core Team, 2021).

3. Results

3.1. Identity, diversity, and relative abundance of parasitoids recorded during the survey

The two parasitoid species *E. sophia* and *E. lutea* emerged from parasitized whitefly nymphs. Both parasitoids occurred across all agro-ecological zones of Cameroon. There was a significant difference in the relative abundance of the two parasitoids among the AEZs ($F_{4, 195} = 35.1$; $P < 0.001$). *Encarcia lutea* was the most abundant of the two parasitoids across AEZs, with 90.8% in AEZ 1, 81.7% in AEZ 2, 87.6% in AEZ 3, 92.4% in AEZ 4, and 70.7% in AEZ 5 (Fig. 2).

The highest total number of parasitoids was recorded during the 1st survey in 2015–2016 (n = 7001). This number dropped by 76.2% in 2016–2017 (n = 1644) and by 78% in 2017–2018 (n = 1501) (Supplementary Table 1).

3.2. *Bemisia tabaci* **adults, nymphs, and parasitism rates during field surveys**

There were significant variations in *B. tabaci* adults and nymph counts among AEZs averaged across years (Table 4). The highest average number of *B. tabaci* adults per plant (6.6 ± 0.6) was recorded in the Humid Forest with Monomodal Rainfall zone (AEZ 4), while the lowest (1.4 ± 0.2) was observed in the Western Highlands zone (AEZ 3) (Table 4). The highest *B. tabaci* nymphs per plant (12.4 ± 2.1) was observed in the Sudano Sahelian zone (AEZ 1) while the lowest (3.6 ± 0.1) was recorded in the Humid Forest with Bimodal Rainfall zone (AEZ 5).

There was no difference in *E. lutea* parasitism among AEZs; however, *E. sophia* parasitism rate (11.9%) was significantly higher in Western Highlands (AEZ3) compared with the other AEZs (Table 4).

We found a significant effect among years across agro-ecologies

Table 3

List of cassava genotypes (accessions) used in the multilocational trials with their associated names in the Cassava Base, breeding pedigree, and root flesh color.

| Accession	Cassava Base name	Pedigree	Flesh color
I070593	IITA-TMS-IBA070593	IITA-TMS-IBA011277/IITA-TMS-IBA990067	Yellow
I010040-27	IITA-TMS-CAM090027	IITA-TMS-IBA010040 HS*/?	Yellow
I011797	IITA-TMS-IBA011797	IITA-TMS-IBA950379/TMEB117	Yellow
I070557	IITA-TMS-IBA070557	IITA-TMS-IBA011663/IITA-TMS-IBA940330	Yellow
I070738	IITA-TMS-IBA070738	IITA-TMS-IBA011649/IITA-TMS-IBA051237	Yellow
I071026	IITA-TMS-IBA071026	IITA-TMS-IBA011277/IITA-TMS-IBA011412 (4X)	Yellow
I090521	IITA-TMS-IBA090521	IITA-TMS-IBA974763/MAUNJILI	White
I090537	IITA-TMS-IBA090537	IITA-TMS-IBA961569/IITA-TMS-IBA961569	White
I090574	IITA-TMS-IBA090574	IITA-TMS-IBA961632/CM5306-8	White
I090590	IITA-TMS-IBA090590	IITA-TMS-IBA972205/MCOL 1468	White
I090616	IITA-TMS-IBA090616	IITA-TMS-MOK980068/CM6921-3	White
LMR	LMR	Unknown	White

HS*/? Denotes half-sibling.
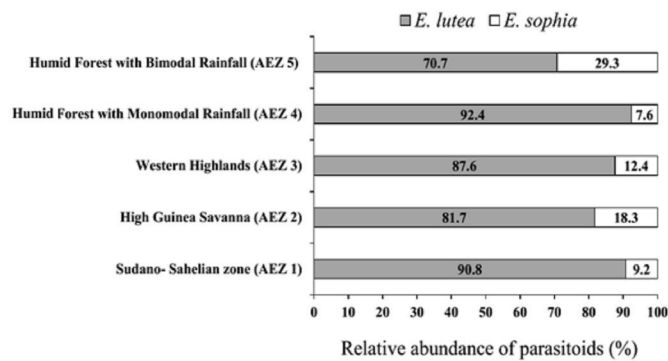
Fig. 2. Relative abundance of *Bemisia tabaci* parasitoids *Encarsia lutea* and *Encarsia sophia* across AEZs during the 2015–2018 surveys.

(AEZ), among agro-ecologies (AEZ) across year, and for the interaction between AEZ and years for *B. tabaci* nymphs, *E. sophia,* and overall parasitism rate. The AEZ effect was not significant for *E. lutea* parasitism (Table 5).

3.3. *B. tabaci* nymphs and parasitism rate in the field trials

There was a significant difference in the abundance of *B. tabaci* nymphs among AEZs averaged across years ($F_{3, 471} = 4.05$; $P = 0.01$), among years averaged across AEZs ($F_{2, 469} = 17.06$; $P = 0.001$), and among months after planting ($F_{2, 472} = 19.3$; $p < 0.001$) (Table 6, Fig. 3). The interactions between years and AEZ, and between month after planting (MAP) and AEZ were significant for *B. tabaci* nymphs ($F_{6, 469} = 4.45$; $P = 0.001$; $F_{6, 469} = 3.22$; $P = 0.01$, respectively*)*. The highest abundance of *B. tabaci* nymphs per leaf (48.9 ± 4.9) was recorded during 2016–2017 in the Humid Forest with monomodal rainfall (AEZ 4) while the lowest (3.5 ± 1.2) was recorded during 2017–2018 in the High Guinea Savanna zone (AEZ 2) (Fig. 5) (see Fig. 4).

We found a significant interaction between years averaged across AEZs only for *E. lutea* parasitism rates. The interaction between AEZ and year was not significant for parasitism rates. The interaction between MAP and AEZ was significant only for *E. sophia* (Table 6, Fig. 6). Regardless of AEZ, the parasitism rate was higher at 3 MAP ($33.4 \pm 4.5\%$ for *E. lutea* and, $8.4 \pm 2.2\%$ for *E. sophia*) compared with 6 and 9 MAP (Supplementary Table 2).

3.4. Association between the abundance of parasitoids and B. tabaci nymphs with temperature, rainfall, relative humidity, and elevation

In High Guinea Savanna (AEZ 2), only *E. lutea* was positively associated with mean temperature ($r = 0.7$; $P = 0.001$), rainfall ($r = 0.7$; $P =$

0.001) and mean relative humidity ($r = 0.85$; $P = 0.002$). In the Western Highlands (AEZ 3), *E. sophia, E lutea,* and *B. tabaci* nymphs were negatively associated with mean temperature ($r = -0.77$, $P = 0.001$; $r = -0.69$, $P = 0.001$; and $r = -0.91$, $P = 0.001$, respectively). In the Humid Forest with Monomodal Rainfall (AEZ 4), *B. tabaci* nymphs and *E sophia* were negatively associated with maximum temperature ($r = -0.60$, $P = 0.03$; $r = -0.87$, $P = 0.005$, respectively), while in the Humid Forest with Bimodal Rainfall (AEZ 5), only *E. lutea* was negatively associated with maximum temperature ($r = -0.8$; $P = 0.003$) (Table 7). *B tabaci* nymph count was negatively correlated with altitude except in Humid Forest with Bimodal Rainfall (AEZ 5).

3.5. *Best linear unbiased predictors (BLUPs) for total B. tabaci nymphs, E. sophia, and E. lutea parasitism*

Genotype I090521 had the highest total number of nymphs among all genotypes and no significant difference was recorded between years. The predicted breeding values for *B. tabaci* nymphs ranged from -17.2 ± 2.2 for genotype I070593 to $+104.5 \pm 2.2$ for genotype I090521, which was the most infested. Results from all genomic prediction methods showed higher estimates of genomic heritability for total nymphs (0.8) than phenotypic heritability for total counts of parasitoids, parasitism of *E. lutea, E. sophia,* and combined parasitism. The linear mixed model test indicated highly significant effects for *B. tabaci* nymphs ($F_{11, 402} = 36.4$; $P < 0.001$).

The predicted breeding values for *E. lutea* parasitism ranged from $-10.6 \pm 0.9\%$ for genotype I090521, which had low numbers of parasitized nymphs, to $+14.4 \pm 0.9\%$ for I090590, which had high numbers of parasitized nymphs (Table 8). For *E. sophia,* the breeding values in parasitism rate ranged from $-2.2 \pm 0.5\%$ for genotype I090521, which had low rates of parasitism, to $+3.9 \pm 0.5\%$ for I070593 which had the highest parasitism rate (Table 8). Overall, *B. tabaci* parasitism on four cassava genotypes that were above the BLUP means parasitism was considered for genotypes that promoted a higher parasitism rate compared with genotypes with parasitism rates lower than the BLUP mean (Fig. 7).

The quadrants in Fig. 8 represent the four classes (I, II, III, and IV) of cassava genotypes/environment for the combined parasitism rate (%) of *B. tabaci* and stability using the weighted average of absolute scores for the BLUP of the genotype and environment interaction (WAABS). The 1st quadrant shows that genotype I090521 was the most unstable genotype. The Western Highlands (AEZ3), which is displayed in that quadrant, had a high discriminative ability for parasitism rate. The 2nd quadrant did not include any genotypes on which the parasitism rate could be high, but unstable. The Humid Forest with Monomodal Rainfall (AEZ 4) included on that quadrant, in addition to providing a high parasitism rate, could have also provided good discrimination ability for the genotypes. Most genotypes fell in the 3rd quadrant and were

Table 4
Average number ($\pm$SE) of *B. tabaci* adults and nymphs, and parasitism rate ($\% \pm$ SE) by *Encarsia lutea* and *Encarsia sophia* in five agro-ecological zones (AEZ) combined over the three survey years.

AEZ	*Bemisia tabaci*		Parasitism rate (%)		
	Adults	Nymphs	*E. lutea*	*E. sophia*	Overall
AEZ 1	5.8 ± 1.2 ab	12.4 ± 2.1 a	4.1 ± 2.8 a	1.5 ± 0.2 ab	5.6 ± 2.5 c
AEZ 2	3.4 ± 0.4 ab	8.3 ± 1.0 b	15.5 ± 3.6 a	2.7 ± 1.5 b	18.2 ± 3.9 ab
AEZ 3	1.4 ± 0.2 b	3.7 ± 0.4 cd	24.2 ± 5.4 a	11.9 ± 2.2 a	36.1 ± 5.9 a
AEZ 4	6.6 ± 0.6 a	6.2 ± 0.9 bc	14.6 ± 4.4 a	4.6 ± 1.8 ab	19.1 ± 4.8 ab
AEZ 5	3.9 ± 0.2 ab	3.6 ± 0.1 d	15.0 ± 2.2 a	3.1 ± 0.9 b	18.1 ± 2.4 ab
AEZ Mean	$\mathbf{4.2 \pm 0.5}$	$\mathbf{6.8 \pm 0.9}$	$\mathbf{14.7 \pm 3.7}$	$\mathbf{4.8 \pm 1.3}$	$\mathbf{19.4 \pm 3.9}$
F-value	3.57	23.1	1.20	3.73	2.78
Df	4, 300	4, 300	4, 284	4, 284	4, 284
P-value	0.007	0.001	0.308	0.005	0.027

Means in a column followed by the same lower-case letter are not significantly different at $\alpha = 0.05$; SE = Standard error.

Table 5
Repeated measures analyse of the effects of years (Y), agro-ecological zones (AEZ), and their interactions on *B. tabaci* nymphs and parasitism rate in the combined experiments from the survey.

Source of variation	df	*B. tabaci*		Parasitism rate (%)					
		nymphs		*E. sophia*		*E. lutea*		Overall	
		F	*P*	F	*P*	F	*p*	F	*P*
Year	2, 290	19.2	<0.001	21.9	<0.001	17.4	<0.001	38.4	<0.001
AEZ	4, 290	5.3	0.004	6.9	<0.001	2.2	0.066	6.4	<0.001
Year*AEZ	8, 290	5.8	<0.001	5.5	<0.001	1.3	0.233	4.2	<0.001

df = degrees of freedom; AEZ = Agro-ecological zones.

Table 6
Repeated measures analyse of the effects of years (Y), agro-ecological zones (AEZ), and their interactions on *B. tabaci* nymphs and parasitism rate in the combined experiments from the field trial.

Sources of variation	df	*B. tabaci*		Parasitism rate (%)					
		nymphs		*E. sophia*		*E. lutea*		Overall	
		F	*P*	F	*P*	F	*P*	F	*P*
Years	2, 436	17.1	0.001	0.57	0.57	5.51	0.01	2.86	0.06
AEZ	3, 452	4.05	0.01	1.67	0.18	1.66	0.18	1.89	0.13
MAP	2, 436	19.3	0.001	6.23	0.001	6.61	0.001	9.98	0.001
Years*AEZ	6, 436	4.45	0.001	1.91	0.08	1.02	0.42	0.98	0.44
AEZ*MAP	6, 436	3.22	0.01	4.11	0.001	1.58	0.16	1.13	0.35

df = degrees of freedom; AEZ = Agro-ecological zones.

considered low productive genotypes because of the low WAABS values. The High Guinean savannah AEZ2 and the humid forest with bimodal rainfall (AEZ5) included in this quadrat displayed a low parasitism rate and low discrimination ability. Four genotypes I090590, I070593, I090574, and I011797 broadly promoted the parasitism rate and are displayed in the fourth quadrant. No location displayed high parasitism rates with a low discriminative ability (Quadrant IV) (Fig. 8).

4. Discussion

Two aphelinid parasitoid wasps, *E. lutea* and *E. sophia*, were collected on cassava in varying numbers in all surveyed sites during three cropping cycles, with *E. lutea* being consistently more abundant than *E. sophia*. Similar studies from Uganda, Nigeria, Mexico, and Tanzania also reported a higher abundance of *E. lutea* compared with other parasitoids that included *E. sophia*, *E. formosa* (Gahan), *Eretmocerus mundus* (Mercet), and *Eretmocerus eremicus* (Rose & Zolnerowich) (Asiimwe et al., 2007; Sánchez-Flores et al., 2017; Otim et al., 2018). The
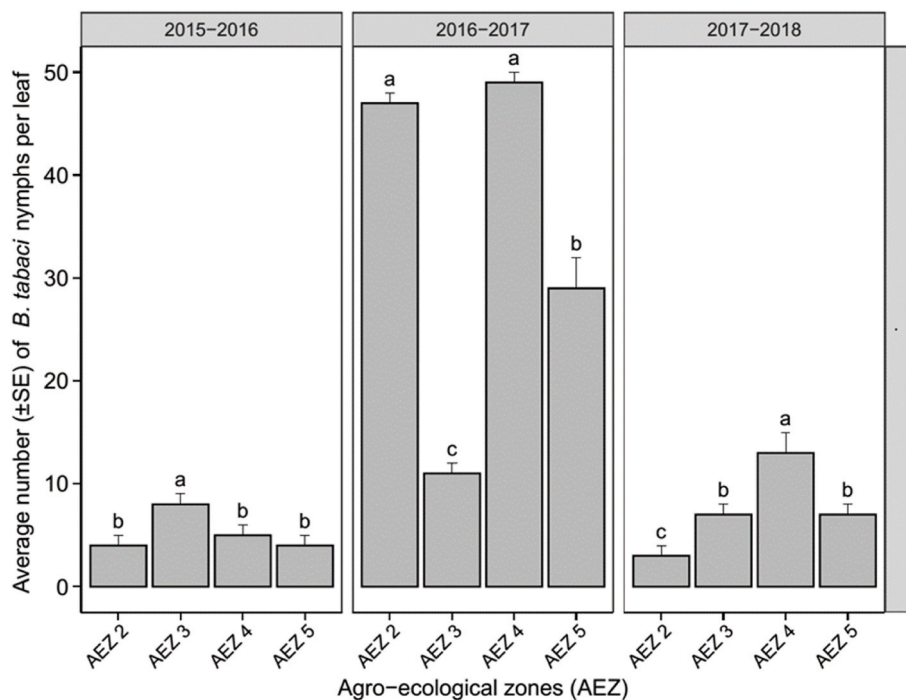

Fig. 3. Mean number of *B. tabaci* nymphs per leaf by AEZ. Vertical bars represent the standard error of the mean (SEM). Means followed by the same letter for each year separately are not significantly different at the 0.05 level. The agro-ecological zones are AEZ 2 = High Guinea Savanna, AEZ 3 = Western highlands, AEZ 4 = Humid Forest with Monomodal Rainfall, and AEZ 5 = Humid Forest with Bimodal Rainfall.
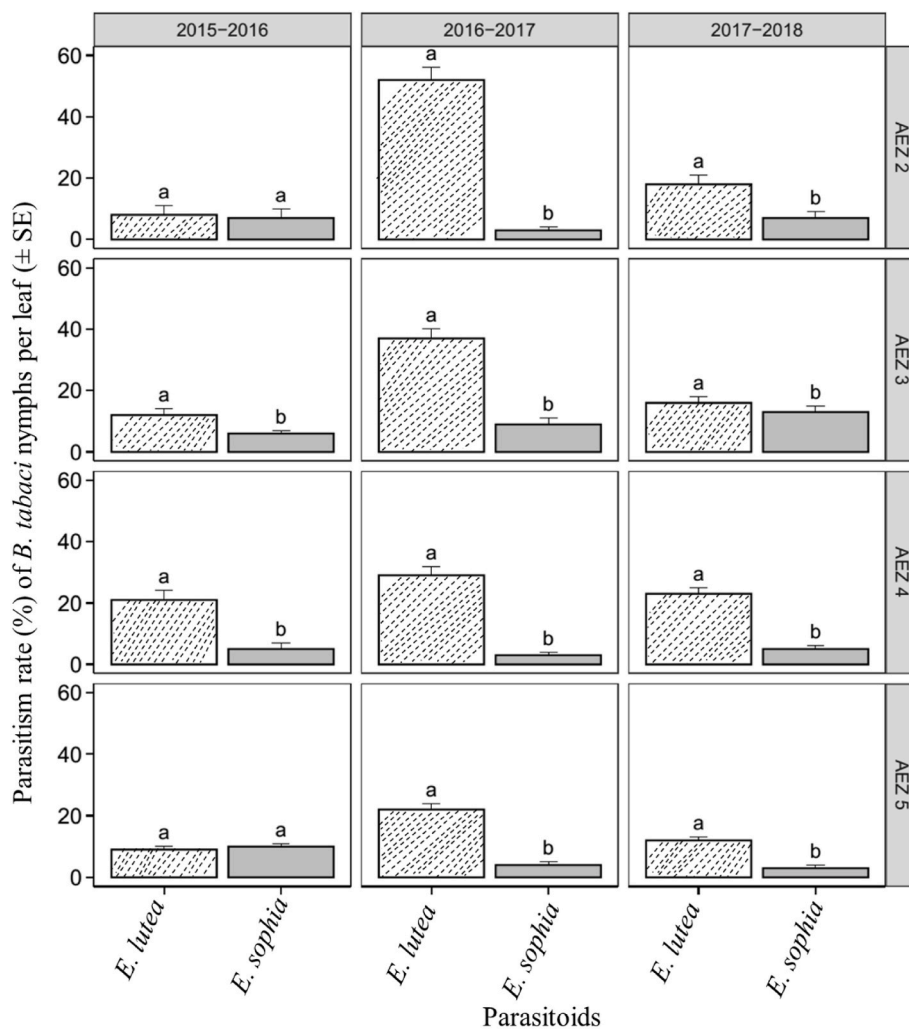
Fig. 4. Parasitism rates (mean ± SE) in cassava cropping seasons per agro-ecology. AEZ 2 = High Guinea Savanna, AEZ 3 = Western highlands, AEZ 4 = Humid Forest with Monomodal Rainfall, and AEZ 5 = Humid Forest with Bimodal Rainfall. Means followed by the same letter for each year and AEZ separately are not significantly different at the 0.05 level. Vertical bars represent the SEM.

mechanisms underlying the variability in the relative abundance of parasitoid species likely involve a combination of direct and indirect effects covering a range of factors including the prevalence of favorable conditions that affect each parasitoid species and the effect of the availability of host plants (Sánchez-Flores et al., 2017; Otim et al., 2018).

In this study, we observed that differences in *E. lutea, E. sophia,* and *B. tabaci* abundance and their dynamics in the five agro-ecologies were associated with differences in temperature, rainfall, relative humidity, and altitude. For example, when we observed elevated temperature, high rainfall, and high *E. lutea* parasitism rate in AEZ 4 during 2016–2017, a significant decrease in *B. tabaci* numbers was noted during the following years (2017–2018). These factors therefore can likely affect the parasitoids and their host whitefly. In general, *B. tabaci* populations are favored by elevated temperatures and moderate rainfall (Sseruwagi et al., 2004). Similarly, high rainfall amounts can also cause high mortality of whiteflies and other insect and mite pests – largely through a washing-away effect (Leite et al., 2005; Katono et al., 2021; Amjad-Bashir et al., 2022; Zsögön et al., 2022) which in turn reduces pest and natural enemy. We observed a strong positive relationship between *B. tabaci* nymph abundance and parasitism rate by *E. lutea* in all the AEZs, similar to the findings of Kalyebi et al. (2021) in Burkina Faso, Benin, and Togo, which all together support the assumption that the

action of parasitoids on *B. tabaci* is density-dependent (Otim et al., 2006, 2018). However, a negative association was observed between elevated temperature and *B. tabaci* abundance as well as *E. lutea* parasitism. Higher temperatures, together with low rainfall can affect the survival and development of whitefly by desiccating older leaves before the pest completes its life cycle. These conditions, which are most prevalent during the dry season, can reduce *B. tabaci* populations. Other studies have shown that altitude influences the abundance of *B. tabaci*; however, the mechanisms explaining these effects have not been elucidated. It has been noted that, at higher altitudes (>1000 m above sea level), there are fewer plant disease problems and an absence of *B. tabaci* in cassava (Jeremiah et al., 2015; Doungous et al., 2022), probably due to low whitefly reproductive success and high mortality at lower temperatures at higher altitudes (Katono et al., 2021; Amjad-Bashir et al., 2022; Zsögön et al., 2022).

Overall, parasitism rates of *B. tabaci* were highest at three MAP, coinciding with the higher abundance *B. tabaci* (Liebhold and Tobin, 2008; Sambo et al., 2022). By visiting younger plants, parasitoids are more likely to find host insects which enhances parasitoid population growth and survival before the onset of elevated temperatures (or low temperatures at higher altitudes) and droughts during the long dry seasons. Consequently, the first three months of cassava growth could be the period for the field release of parasitoids for pest biological control
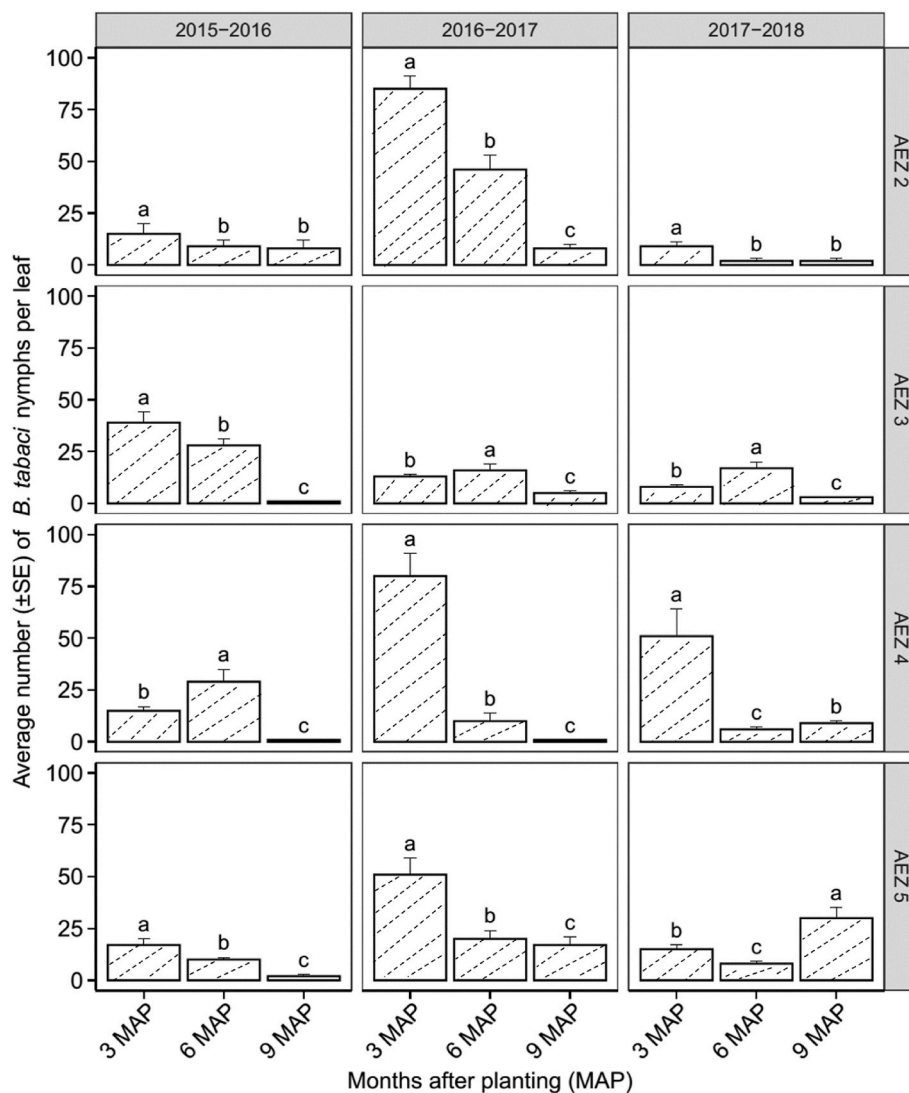
Fig. 5. Mean number of *B. tabaci* nymphs per leaf with the cassava crop age band in 4 agro-ecological zones. Vertical bars represent the SEM. Means followed by the same letter for each year and AEZ separately are not significantly different at the 0.05 level.

over a prolonged period (Kityo, 2016).

Applying the BLUP analysis approach to parasitoids on cassava is an interesting extension of the approach for genotype selection to promote biological control. To our knowledge, this is the first application of BLUP of mixed models for parasitoids of insect pests in agriculture, since BLUP was used for host range determination in weed biological control (Berner, 2010). Most breeding programs aim to select cassava genotypes at an early stage of the breeding process to optimize genetic gains and develop new genotypes that combine resistance to pests/diseases (Kalyebi et al., 2021) and high yields (Brown et al., 2016). Indeed, *E. lutea* and *E. sophia* showed a high parasitism rate on four cassava genotypes, with a BLUP value beyond the overall mean. These genotypes can promote a high parasitism rate for the control of *B. tabaci* populations. Moreover, I070593 is a genotype with higher total carotenoid content (>11 μl/mg) while I090590 and 071797 are among the high-yielding genotypes (Tize et al., 2021). The agronomic and nutritional traits of these genotypes should be explored further to determine their contribution to the observed higher parasitism rate which could be useful for the multiplication and conservation of parasitoids.

In conclusion, this research provides additional evidence to support the positive impact of natural enemies and CMD-resistant cassava genotypes on the success of biological control of *B. tabaci*. Two species of parasitoids that emerged from whitefly nymphs were identified as

E. sophia and *E. lutea*. Regardless of AEZs and years, *E. lutea* was the most abundant parasitoid in the surveyed sites and field trials, compared with *E. sophia*. Four cassava genotypes on which parasitism rates were higher can be used to promote abundance and persistence of the parasitoids and could be useful in mixed cassava genotype systems to promote parasitism of whiteflies on less preferred genotypes as in the case of biological control of *Mononychellus tanajoa* (Bondar) with the predatory mite *Typlodromalus aripo* De Leon on cassava (Onzo et al., 2014). Although the present findings demonstrate that *E. sophia* and *E. lutea* can cause up to 60.5% of parasitism of *B. tabaci* under certain circumstances, such important levels of parasitism are not typical. It is therefore important to look at ways to increase the abundance of parasitoids. Studies on the biology and behavior of the main parasitoids under different whitefly population pressure in the targeted AEZs, as well as the effect of other natural enemies of *B. tabaci*, will be needed to boost the diversity and efficiency of natural enemies in sustaining low whitefly populations. This will contribute to reducing the transmission of cassava viruses and in turn improve cassava productivity. Further studies should focus on the potential of augmentative biological control of *B. tabaci* through the release of mass-reared parasitoids and their integration with other control methods including intercropping, cassava genotype mixtures, crop rotation, altered planting dates, destruction (burning) of plant debris after harvest and fertilization.
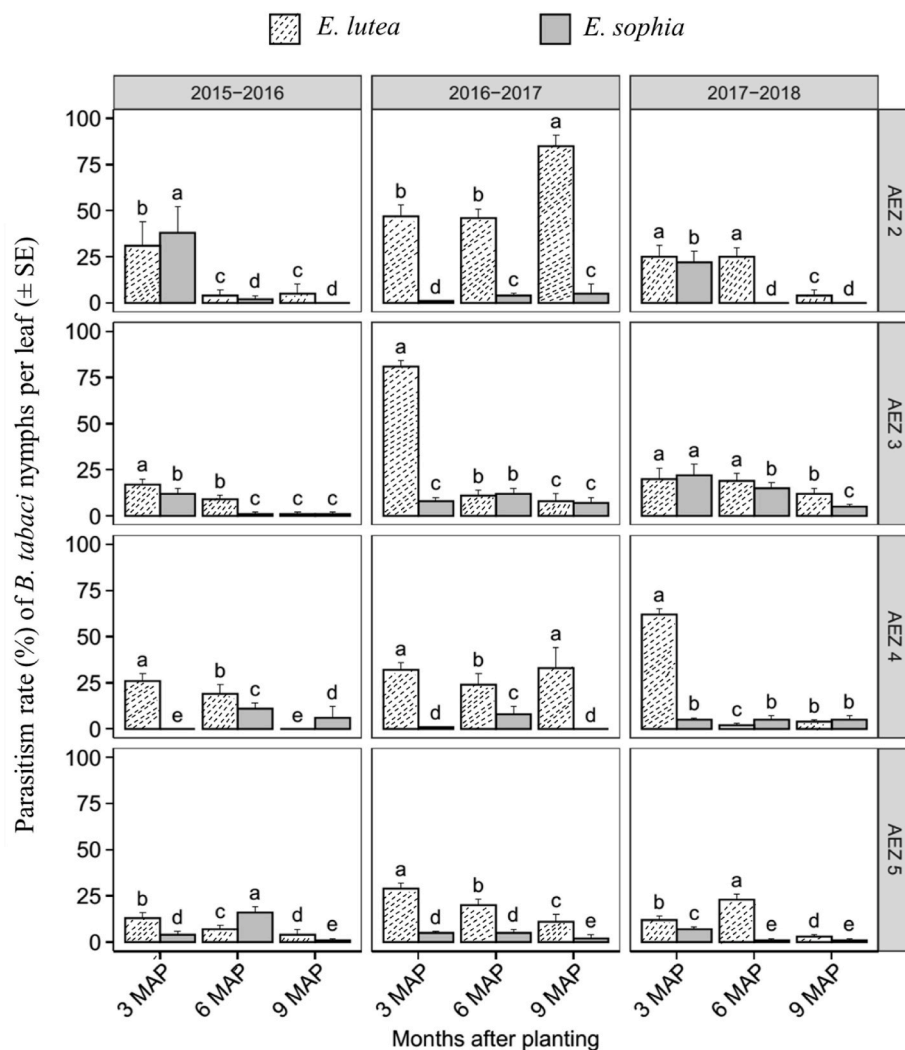
Fig. 6. Parasitism rates (mean ± SE) of the associated parasitoids on cassava with the cassava crop age in 4 agro-ecological zones: AEZ 2 = High Guinea Savanna, AEZ 3 = Western highlands, AEZ 4 = Humid Forest with Monomodal Rainfall, and AEZ 5 = Humid Forest with Bimodal Rainfall. The Sudano-Sahelian zone (AEZ 1) was not included since cassava is grown only in some marginal areas. Mean followed by the same letter for each year and AEZ are not significantly different at the 0.05 level with month after planting. Vertical bars represent the standard error of the mean.

Table 7

Spearman's correlation coefficient between environmental variables and the number of *B. tabaci* nymphs, *E. sophia,* and *E. lutea* parasitism per leaf, during the field trial in the four agro-ecologies (AEZs) from 2016 to 2018.

Variables	AEZ 2			AEZ 3			AEZ 4			AEZ 5		
	B. tabaci	E.	E.	B. tabaci	E.	E.	B. tabaci	E.	E.	B. tabaci	E.	E.
	nymphs	*lutea*	*sophia*	nymphs	*lutea*	*sophia*	nymphs	*lutea*	*sophia*	nymphs	*lutea*	*sophia*
TMax. (°C)	−0.29	−0.39	0.07	−0.47	−0.58	−0.65	−0.60	−0.41	−0.87	−0.46	−0.80	−0.21
	(0.004)	(0.359)	(0.907)	(0.094)	(0.002)	(0.004)	(0.03)	(0.267)	(0.005)	(0.412)	(0.003)	(0.596)
Mean T	0.40	0.70	0.41	−0.77	−0.69	−0.91	−0.52	−0.14	−0.62	−0.04	−0.33	−0.71
(°C)	(0.305)	(0.001)	(0.333)	(0.001)	(0.001)	(0.001)	(0.275)	(0.426)	(0.173)	(0.499)	(0.456)	(0.001)
TMin. (°C)	0.45	0.63	0.14	−0.22	−0.10	−0.58	0.19	0.20	−0.05	0.64	0.87	0.57
	(0.182)	(0.146)	(0.308)	(0.946)	(0.872)	(0.038)	(0.526)	(0.530)	(0.790)	(0.198)	(0.001)	(0.377)
Rainfall	0.33	0.70	0.33	−0.83	−0.77	−0.84	0.03	0.03	0.27	0.32	0.18	0.32
(mm)	(0.447)	(0.001)	(0.685)	(0.002)	(0.001)	(0.001)	(0.493)	(0.530)	(0.493)	(0.139)	(0.153)	(0.156)
RHMax	0.53	0.84	0.48	0.37	0.46	0.53	0.31	0.19	0.32	0.34	−0.25	0.25
(%)	(0.105)	(0.002)	(0.259)	(0.203)	(0.227)	(0.001)	(0.425)	(0.404)	(0.283)	(0.278)	(0.409)	(0.492)
Mean RH	0.57	0.85	0.48	0.69	0.68	0.70	0.12	0.20	0.40	0.25	−0.07	0.07
(%)	(0.105)	(0.002)	(0.206)	(0.269)	(0.298)	(0.003)	(0.360)	(0.354)	(0.282)	(0.466)	(0.746)	(0.732)
RHMin	0.50	0.79	0.44	0.85	0.78	0.83	0.10	0.21	0.46	0.23	0.17	0.06
(%)	(0.121)	(0.008)	(0.334)	(0.001)	(0.174)	(0.001)	(0.450)	(0.426)	(0.294)	(0.258)	(0.296)	(0.418)
Altitude	−0.65	−0.46	−0.59	−0.72	−0.61	−0.40	−0.70	0.48	0.70	0.31	0.10	0.59
(m)	(0.001)	(0.132)	(0.165)	(0.001)	(0.001)	(0.162)	(0.005)	(0.163)	(0.005)	(0.162)	(0.167)	(0.137)

The p-values of all coefficients are presented in parentheses. Min = Minimum, Max = maximum; T = temperature, RH = relative humidity; the P-values of all coefficients are presented in parentheses. Min = Minimum, Max = maximum; T = Temperature, RH = Relative Humidity. AEZ 2 = High Guinea Savanna, AEZ 3 = Western Highlands, AEZ 4 = Humid Forest with Monomodal Rainfall, and AEZ 5 = Humid Forest with Bimodal Rainfall.

Table 8
Best linear unbiased predictors (BLUPs) of breeding values with standard errors for a total count of whitefly nymphs and parasitoids, *E. sophia,* and *E. lutea* parasitism (%), and overall parasitism (%).

Genotype	Total count		Parasitism rate (%)		Combined parasitism (%)
	Nymphs	Parasitoids	*E. sophia*	*E. lutea*	
I090521	+104.5 ± 2.2*	+5.9 ± 0.6*	−2.2 ± 0.5*	−10.6 ± 0.9*	−12.8 ± 1.0*
I070557	−3.8 ± 2.2	+0.3 ± 0.6	−0.8 ± 0.5	−5.5 ± 0.8*	−6.3 ± 0.9*
I070593	−17.2 ± 2.2*	−2.5 ± 0.6*	+3.9 ± 0.5**	−0.1 ± 0.9	+3.6 ± 1.0*
I010040-27	−10.8 ± 1.9*	−1.4 ± 0.5*	+0.1 ± 0.5	−0.8 ± 0.8	−0.6 ± 0.9
I090590	−13.8 ± 2.1*	+0.3 ± 0.5	−1.3 ± 0.5*	+14.4 ± 0.9**	+13.0 ± 1.0**
I071026	−10.2 ± 2.2*	−1.7 ± 0.6*	−1.5 ± 0.5*	+1.3 ± 0.9	−0.1 ± 1.0
I011797	−7.3 ± 2.1*	+0.0 ± 0.5	+1.2 ± 0.5*	+2.1 ± 0.9*	+3.3 ± 1.0*
I090574	−12.3 ± 2.1*	−0.8 ± 0.5	−0.3 ± 0.5	+2.1 ± 0.9*	+1.9 ± 1.0
I090537	−5.9 ± 2.2*	−0.6 ± 0.6	+0.1 ± 0.5	−0.3 ± 0.9	−0.2 ± 1.0*
I090616	−5.9 ± 2.2*	+1.0 ± 0.6	−0.2 ± 0.5	+0.0 ± 0.9	−0.2 ± 1.0
I070738	−10.3 ± 2.2*	−1.0 ± 0.5	+0.3 ± 0.5	−1.5 ± 0.9	−1.1 ± 1.0
LMR	−7.1 ± 2.1*	+0.5 ± *	+0.7 ± 0.2*	+1.1 ± 0.1*	+0.4 ± 0.1*
BLUP Statistics					
Heritability (H2)	0.8	0.1	0.04	0.2	0.2
Phenotypic variance (Vp)	1292	16.2	31.7	84.5	91.4
Environment variance (Ve)	1209	7.3	11.1	60.8	65.6
Genotype variance (Vg)	83.4	8.9	20.0	23.7	25.8
Gen × Loc variance	0.2	65.2	46.8	55.5	47.9
Residual variance	16.4	25.8	17.6	20.8	26.3
Grand mean	25.9	5.4	4.6	22.9	27.5
SE	2.9	0.3	0.3	1.8	1.6
Minimum	−17.2	−2.5	−2.2	−10.6	−12.8
Maximum	+104.5	+5.9	+3.9	+14.4	+13.0
SD	25.8	4.0	3.7	21.0	20.1
CV (%)	99.6	74.1	79.9	92.0	73.0
n Replicates	3	3	3	3	3
n Environment	8	8	8	8	8
n Agro-ecologies	4	4	4	4	4
n Genotypes	12	12	12	12	12

$P < 0.01$**; $P < 0.05$*. The statistics listed for every variable are broad-sense phenotypic variance (Vp), heritability (H2), genotype variance (Vg), residual variance, grand mean, SD = standard deviation, coefficient of variation (CV%), the number of replications, environment, agro-ecology, and genotypes (n). The statistics shown are the estimates derived.

CRediT authorship contribution statement

Isaac Tize: Investigation, Software, Data Analysis, Writing- Original draft preparation. **Elias Nchiwan Nukenine:** Conceptualization, Supervision and Validation. **Apollin Fotso Kuate:** Supervision, Software, Data curation and analysis, Writing- Original draft preparation, Validation, Funds Acquisition, and Editing. **Armand Doumtsop Fotio:** Visualization, Reviewing. **Samuel Nanga Nanga:** Visualization, Reviewing, and Data analysis. **Francis Ngome Ajebesone:** Visualization, Reviewing. **Peter Kulakow:** Visualization, Reviewing. **P. Lava Kumar:** Visualization, Reviewing. **Komi Kouma Mokpokpo Fiaboe:**
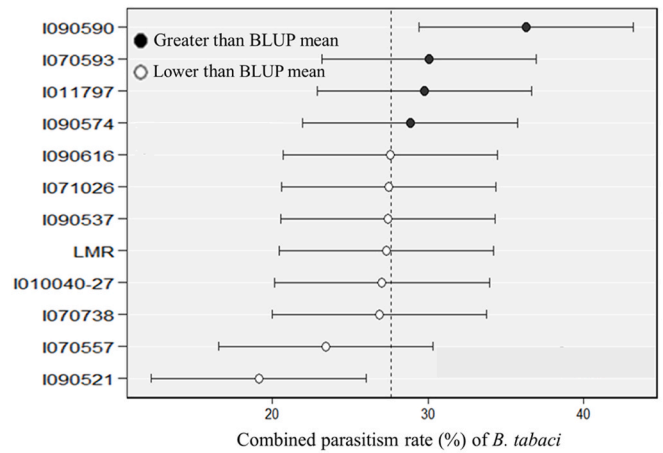

Fig. 7. Best linear unbiased prediction (BLUP) for combined parasitism rate (%) of *B. tabaci* recorded on 12 cassava genotypes. Black and grey circles represent the genotypes that had BLUP above and below of BLUP mean, respectively. Horizontal error bars represent the 95% confidence interval of a prediction considering a 2-tailed *t*-test.

Supervision, Writing– Reviewing & Editing and Validation. **Rachid Hanna:** Conceptualization, Methodology, Supervision, Validation, Writing – Reviewing, Editing, and Funds Acquisition.

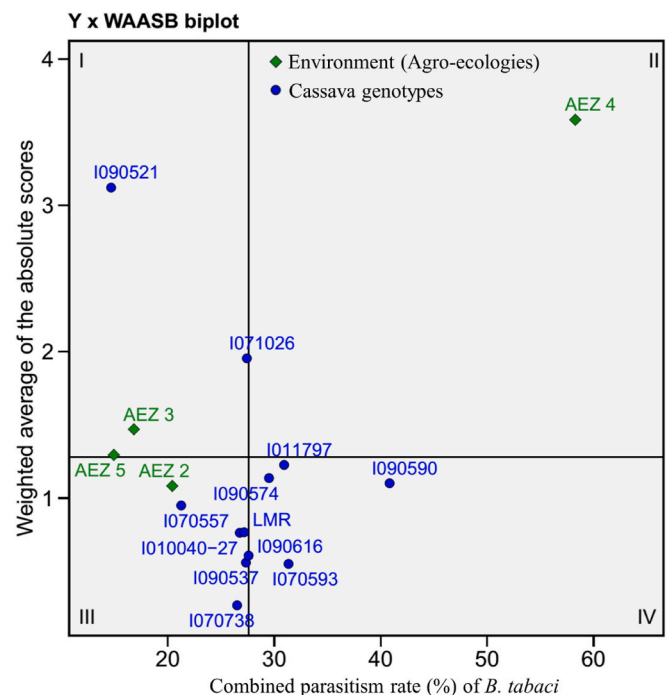## Declaration of competing interest

Fig. 8. Biplot of the combined parasitism rate (%) of *B. tabaci* vs. a weighted average of absolute scores for the best linear unbiased predictions of the genotype vs. environment interaction (WAASB) on 12 cassava genotypes evaluated in four agro-ecologies. A parasitism rate on cassava genotypes is depicted by a blue circle.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.cropro.2023.106241.

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