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Molecular Identification of Leafhoppers Infesting Okra, Eggplant, and Cotton

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ABSTRACT

Leafhoppers (Cicadellidae) are major pests of key crops, including okra, eggplant, and cotton, in tropical Africa. Several closely related species, which are often challenging to differentiate, infest these crops, yet little is known about their relative roles in causing crop damage. The study aims to clarify the taxonomy of the species and provide a preliminary assessment of their impact on eggplant, okra, and cotton production. A biomolecular analysis was conducted on 180 leafhopper individuals collected from 13 locations across the three crops during the 2021 and 2022 cropping seasons. The findings revealed that the same species were present on cotton, okra, and eggplant. Three primary species were identified: *Empoasca papayae*, *Jacobiasca lybica*, and *Amrasca biguttula*. The abundance of these species varied between the two years. In 2021, the predominant species found on okra, eggplant, and cotton were *J. lybica* and *E. papayae*; *J. lybica* was the most abundant, proportions on okra, eggplant, and cotton were 90, 95.8, and 91.7%, respectively. In contrast, by 2022, *A. biguttula* emerged as the most abundant species with proportions of 100, 100, and 85% on okra, eggplant, and cotton, respectively. Although *J. lybica* was present on cotton, it was less abundant. The introduction of *A. biguttula*, a species new to West Africa, marked a shift in the leafhopper community, replacing the local species on African eggplant, okra, and cotton. These results enhance our understanding of leafhopper species composition on these important crops and will inform the development of targeted pest management.

The Cicadellidae family is highly diverse, comprising more than 2,417 genera, 331 subgenera, and approximately 25,000 species and 500 subspecies (Fu et al., 2014; Roskov et al., 2020), many of which are significant agricultural pests. These leafhoppers cause substantial damage to export crops such as cotton and vines and food crops, including okra, kenaf, African eggplant, and chili peppers (Kouadio et al., 2022a, b, 2024; Ramila et al., 2016). In Côte d'Ivoire, leafhoppers were once considered secondary pests in cotton cultivation, mainly due to the use of hairy cotton varieties that deterred infestation (Vaissayre et al., 1997). However, since 2012, leafhopper populations have surged, becoming an emerging threat to cotton production (Koné et al., 2017). These infestations have been marked by severe attacks, resulting in significant crop losses. The 2022 cropping season witnessed widespread leafhopper outbreaks that caused extensive damage and considerable economic losses in both vegetable and cotton crops (Kouadio et al., 2022b, 2024). In response, the Ivorian government allocated more than 34 billion CFA francs to compensate for the damage caused by these pests (Kouadio et al., 2024).

An initial morphological survey identified the leafhopper species responsible for the damage, revealing the presence of *Amrasca biguttula* Ishida, previously unreported in Côte d'Ivoire (Kouadio et al., 2022b, c, 2024). Although morphological identification remains a valuable tool for species identification, it has inherent limitations. These include a shortage of experts trained in classical taxonomy (Hartop et al., 2022; Schlick-Steiner et al., 2010)

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and an inability to differentiate cryptic species based solely on morphological features (Dayrat, 2005; Hartop et al., 2022; Prata et al., 2018). To address these challenges, molecular identification methods were employed to confirm the species in question. This study aims to provide a clearer taxonomic understanding of the leafhopper species affecting eggplant, okra, and cotton, and to assess their economic significance to these vital crops.

MATERIALS AND METHODS

Study Site. Leafhopper samples were collected from 13 localities (Fig. 1) across the cotton-producing region of Côte d'Ivoire, spanning latitudes 7°5' N to 12° N and longitudes 3° W to 8.5° W. This area covering approximately 20,000 km^2, lies between central and northern Côte d'Ivoire, extending from 5.75° N to 10.75° N latitude and 3.5° W and 8.5° W longitude. The localities are geographically divided into two main regions by the 9th parallel: the southern zone, located below the 9th parallel, and the northern zone, situated above it. The northern zone experiences a Sudanian climate, characterized by a dry season from November to April and a rainy season from May to October, with peak rainfall occurring in August. In contrast, the southern zone has a transitional sub-equatorial climate, with two distinct rainy seasons (March to June, and September to October) and two dry seasons (July to August and November to February). Both okra and African eggplant are cultivated in this region and are heavily infested by leafhoppers. To investigate whether the leafhopper species found on cotton also infest other host plants, additional collections were made from okra and eggplant.

Materials. The study focused on leafhopper specimens collected from cotton (*Gossypium hirsutum* L. [(Malvaceae]), the main species grown in Côte d'Ivoire; okra (*Abelmoschus esculentus* L. ([Malvaceae]); and African eggplant (*Solanum aethiopicum* L. [Solanaceae]).

Sample Collection. Samples were collected from June to November during the 2021 and 2022 crop years. Leafhoppers were collected using a mouth aspirator from 30 individual plants per locality. These plants were grouped into six sets of five consecutive plants, sampled sequentially from the same row, following the method described by Nibouche et al. (2002). Sampling took place between 7:30 a.m. and 1:00 p.m., within a 0.25-ha area at the center of each plot. The captured leafhoppers were placed in plastic tubes containing a naphthalene ball wrapped in cotton fiber to preserve them. In the laboratory, samples were transferred to high-grade alcohol (96%) and stored at 5 °C in a refrigerator.

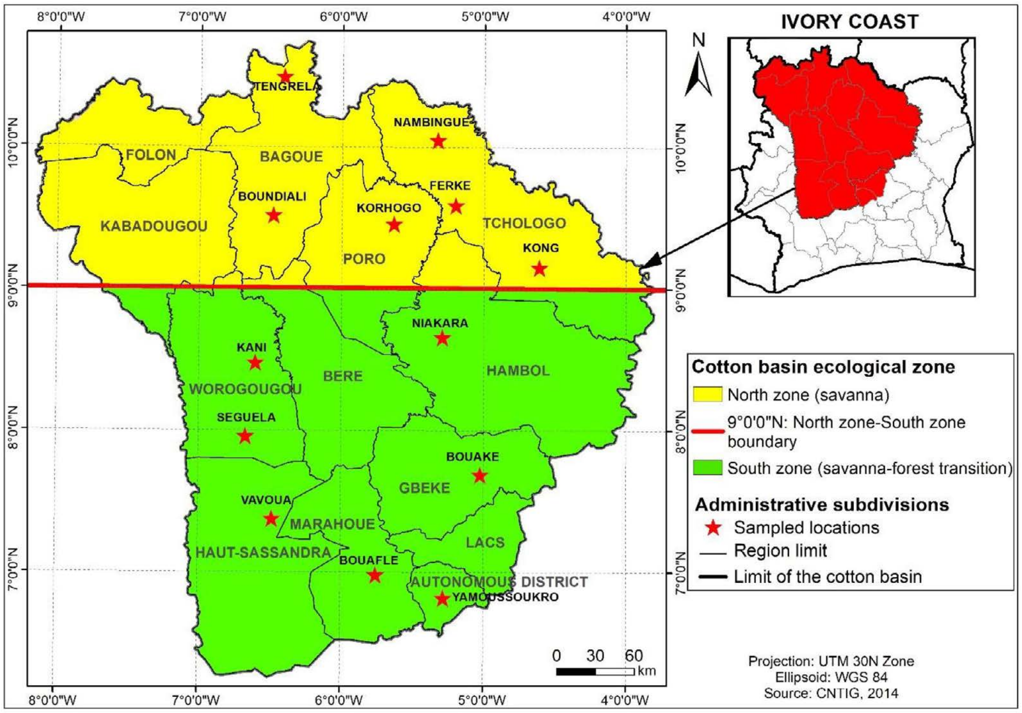

Figure 1. Species identification sample collection area in Côte d'Ivoire.

DNA Sequencing and Data Analyses. The genomes of 180 individuals were extracted, and each specimen was sequenced for the standardized 658 bp barcode fragment of the mitochondrial cytochrome c oxidase subunit I (COI) gene (Hebert et al., 2003). DNA was extracted from a leg or the entire specimen using the DNeasy Blood and Tissue kit (Qiagen, Hilden, Germany). Polymerase chain reaction (PCR) amplifications were performed using a cocktail of COI primers (Hansen et al., 2021), on a Mastercycler® Nexus (Eppendorf, Hamburg, Germany). Each 10 µL PCR reaction contained 5 µl of Multiplex Master Mix (Qiagen), 2µM of forward and reverse primers, and 2 µl of DNA template. The PCR protocol included an initial denaturation at 94 °C for 15 min, followed by 35 cycles of 30 s at 94 °C, 1 min at 52 °C, and 1 min at 72 °C, with a final extension at 72 °C of 20 min. PCR products were sequenced by Eurofins Genomics (Eurofins Genomics, France). Voucher specimens sequenced are deposited in the Continental Arthropod Collection at Centre de Biologie pour la Gestion des Populations, Montpellier, France (CBGP, 2020). Barcode sequences were aligned using Codon Code Aligner ver. 3.7.1. (Codon Code Corporation, Centerville, MA). Pairwise genetic distances (uncorrected p-distance values) between species were calculated with MEGA version 11 (Tamura et al., 2013).

Data Analysis. ***Determination of species proportions***. The overall proportion of species was calculated across both seasons of the study. Proportions were also analyzed by locality and crop year, allowing for the assessment of geographic and inter-annual variations. Frequencies were extracted, and percentages were calculated using the questionr package (Barnier et al., 2023). These analyses were carried out using R 4.1.2 (R Core Team, 2021).

Determining haplotypes. Haplotype networks provide intuitive insights into genealogical relationships at the intraspecific level and support interferences about biogeography and population history (Leigh and Bryant, 2015). Networks were constructed for the most abundant species to visualize the biogeography of haplotypes, highlighting common and specific haplotypes in a spatial context. This approach aims to uncover the processes driving the geographic distribution of genetic variation within species (Voet and Nicolas, 2022). A haplotype network was also generated for individuals collected from different host plants, aiming to explore molecular specificity among individuals across host plants and localities. These analyses were performed using PopART version 1 (Leigh and Bryant, 2015), employing the minimum spanning network method.

Determination of genetic diversity parameters. Tajima's D parameters and π-nucleotide diversity were determined to assess genetic diversity between species and within the most abundant species.

RESULTS

Main Species Identified. DNA sequence analysis using BLAST on GenBank identified species from okra, eggplant, and cotton that belonged to three genera: *Empoasca*, *Jacobiasca*, and *Amrasca* (Table 1). In 2021, two species were identified: *Jacobiasca lybica* (de Bergevin) and *Empoasca papayae* Oman. By 2022, *Amrasca biguttula* was the only species found on okra and eggplant. On cotton, three species were present: *A. biguttula*, *J. lybica*, and *E. papayae*. Notably, *A. biguttula* was absent from all samples collected during the 2021 season.

Phylogeny of Leafhopper Species Identified from Blast. By submitting the sequences to GenBank, we identified most individuals as belonging to three species, although some could not be assigned to a specific species. The identified species were: J. lybica (GenBank IDs: OQ381277.1, OQ381276.1 and OQ381273.1), with similarity percentages ranging from 95 to 98.09%; *A. biguttula* (GenBank

Table 1. Main leafhopper species identified on okra, eggplant, and cotton in the cotton production area of Côte d'Ivoire

		2021			2022		
Genus	**Species**	**Okra**	**Eggplant**	**Cotton**	**Okra**	**Eggplant**	**Cotton**
Empoasca	***papayae***	+^{z}	+	+	-	-	+
Jacobiasca	***lybica***	+	+	+	-	-	+
Amrasca	***biguttula***	-	-	-	+	+	+
Cicadellidae sp.		-	-	+	-	-	+

^{z} - : absence ; + : presence

IDs: MK293720.1 and MK391413.1), with similarity percentages ranging from 99.52 to 100%; and *E. papayae* (GenBank ID: KY931023.1), with a similarity percentage of 86.81%. Additionally, two specimens could be identified only at the family level (Cicadellidae): Cicadellidae sp. sc 07141 (GenBank ID: KX052128.1), with a similarity percentage of 99.52% and Cicadellidae sp. 3 AY-2013 (GenBank IDs: HF968653.1), with a similarity percentage of 100%.

A phylogenetic tree was constructed to assess the relationships between the BLAST-matched sequences and the sequenced individuals. The analysis revealed five distinct groups. Notably, none of the sequenced individuals were closely related to *E. papayae*. The majority of individuals collected in 2021 were closely associated with *J. lybica*, whereas those collected in 2022 predominantly clustered with *A. biguttula* (Fig. 2).

Species Composition on Okra and Eggplant. Three primary leafhopper species were identified on okra and eggplant: *E. papayae*, *J. lybica*, and *A. biguttula*. Species proportions varied between crop years. In the 2021 season, two species were identified: *J. lybica* was the predominant species, comprising 93.2% of the total, with proportions of 95.8% on eggplant and 90% on okra; and *E. papayae* accounted for 6.8%, with proportions of 4.2% on eggplant and 10% on okra (Tables 2 and 3). During

Table 2. Main leafhopper species identified on okra and eggplant in Côte d'Ivoire

	Overall Proportion (%)	
Species	**2021**	**2022**
Amrasca biguttula	**0**	**100**
Empoasca papayae	**6.8**	**0**
Jacobiasca lybica	**93.2**	**0**

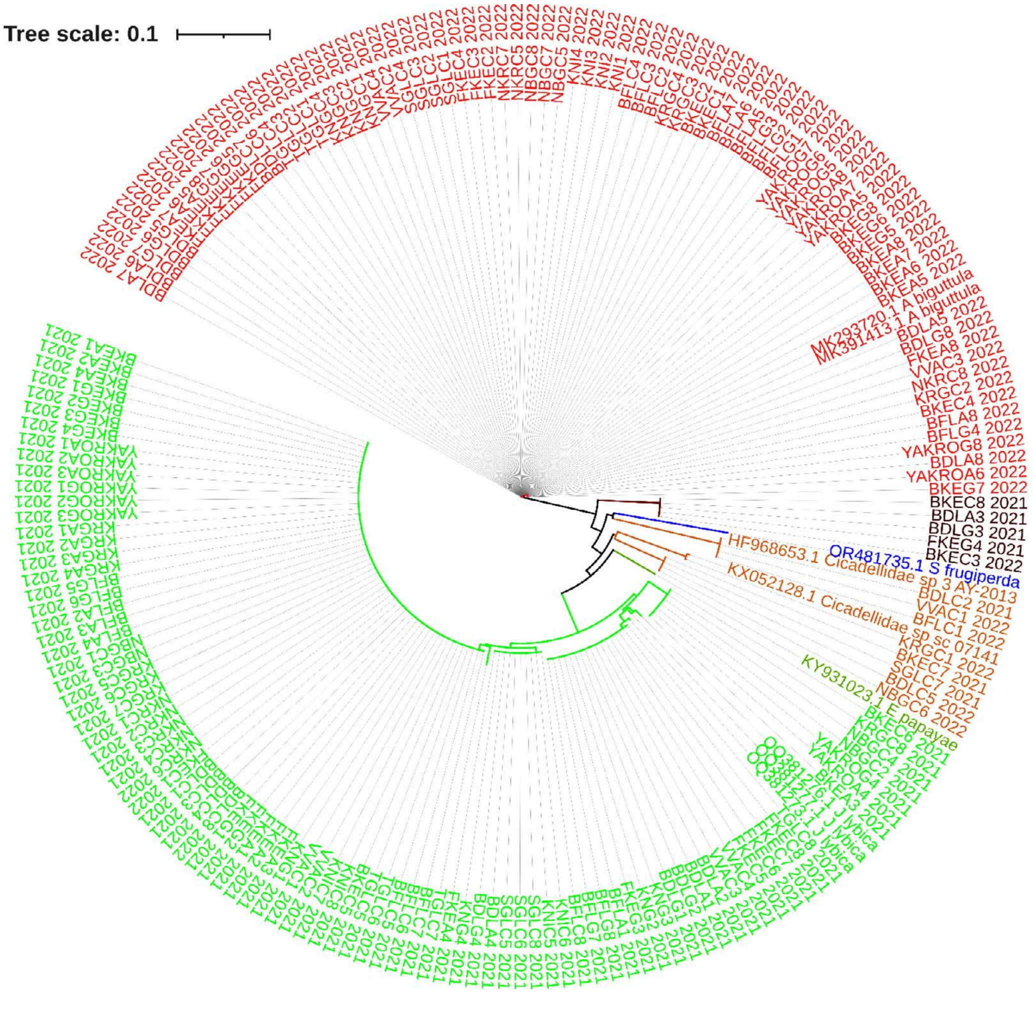

Figure 2. Phylogenic tree of blast results from leafhopper samples collected on okra, eggplant, and cotton in Côte d'Ivoire.

Table 3. Specific seasonal composition of leafhopper species identified on okra and eggplant in Côte d'Ivoire

	Overall Proportion (%)					
	2021			2022		
Host plant	***Amrasca biguttula***	***Empoasca papayae***	***Jacobiasca lybica***	***Amrasca biguttula***	***Empoasca papayae***	***Jacobiasca lybica***
Eggplant	0	4.2	95.8	100	0	0
Okra	0	10	90	100	0	0

the 2022 season, only *A. biguttula* was identified on both okra and eggplant, representing 100% of the samples collected (Table 3). Neither *E. papayae* nor *J. lybica* were found in 2022, whereas *A. biguttula* was absent during the 2021 season.

Species Composition of Cotton Plants Identified. Three main leafhopper species were identified on cotton: *E. papayae*, *J. lybica*, and *A. biguttula*. Species proportions varied between crop years (Table 4). In the 2021 season, two species were accurately identified, whereas 2.1% of individuals could not be assigned to a specific species. The identified species were: *J. lybica*, the predominant species, representing 91.7% of individuals; and *E. papayae* accounting for 6.2% of individuals.

Table 4. Main leafhopper species identified on cotton in Côte d'Ivoire after blasting on GenBank

	Overall Proportion (%)	
Species	**2021**	**2022**
Amrasca biguttula	0	85.4
Empoasca papayae	6.2	4.2
Jacobiasca lybica	91.7	6.2
Cicadellidae sp	2.1	4.2

In the 2022 season, three species were accurately identified and 4.2% of individuals remained unidentified at the species level. The identified species included: *A. biguttula*, the most predominant species, comprising 85.4% of individuals; *J. lybica*, representing 6.2% of individuals; and *E. papayae*, accounting for 4.2% of individuals.

Intra- and Interspecies Genetic Variability. Genetic variability parameters were assessed for all samples, revealing 11 haplotypes with mutations ranging from 3 to 82, indicating genetic variability among individuals. Nucleotide diversity was 0.28. Haplotype distribution and mutation numbers varied across localities and host plants (Figs. 3 and 4). All identified haplotypes were present on cotton, whereas eggplant and okra shared similar haplotypic variations. Haplotype 1 and Haplotype 8 were the most abundant, found in most sampled localities.

For samples identified as *J. lybica*, five haplotypes were detected, with mutations ranging from 5 to 18, suggesting relatively low genetic variability within this species (Fig. 5). Nucleotide diversity was 0.26. Haplotype 1 was widespread, appearing in all

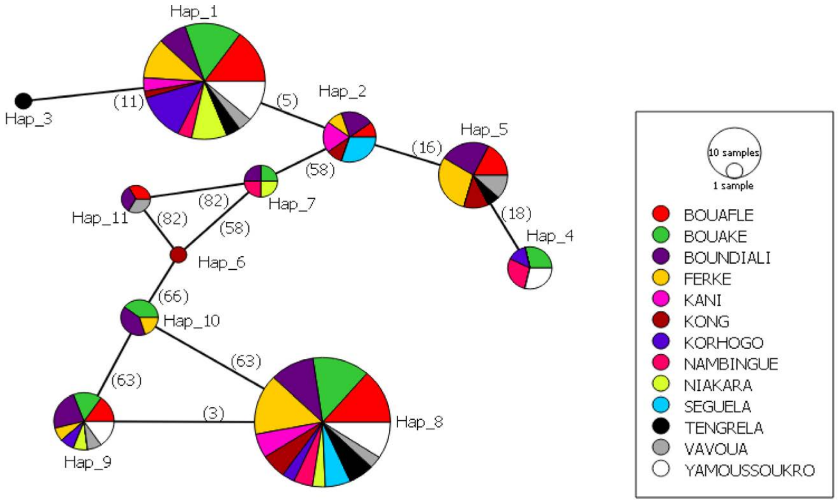

Figure 3. Haplotypic mutations observed in all sequenced individuals from sampled localities in Côte d'Ivoire.

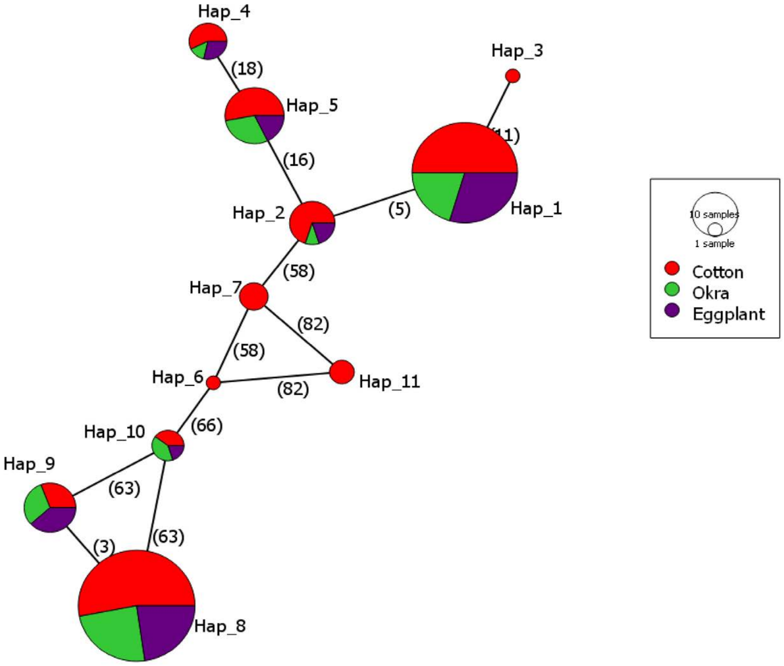

Figure 4. Haplotypic mutations observed between all sequenced leafhopper individuals from host plants sampled in Côte d'Ivoire.

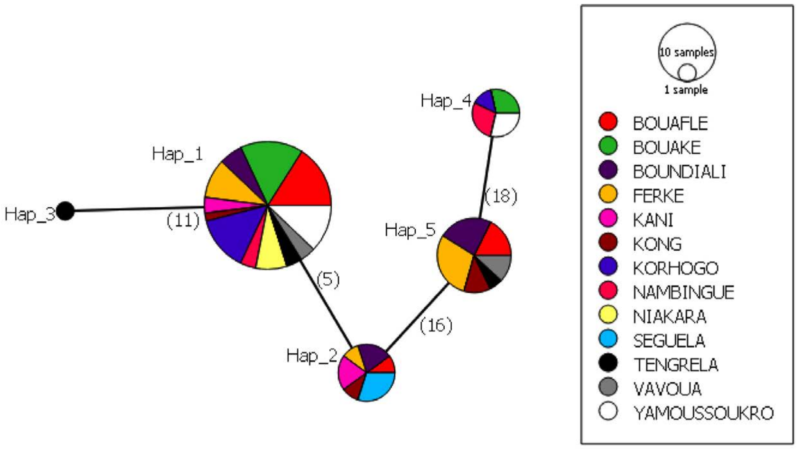

Figure 5. Haplotypic mutations observed in *Jacobiasca lybica* individuals collected in 13 localities from Côte d'Ivoire.

sampled localities except Séguéla (Fig. 6). Cotton samples contained all five haplotypes.

In samples identified as *A. biguttula*, seven haplotypes were identified, with mutations ranging from 1 to 82, indicating considerable genetic variability within the species (Fig. 7). Cotton samples showed the highest genetic variability with 11 haplotypes identified. Nucleotide diversity was 0.10. Haplotype 1 was the most common, found across all sampled locations (Fig. 8).

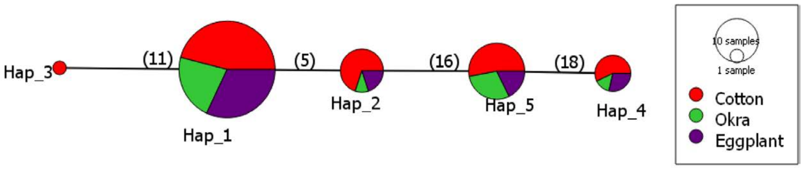

Figure 6. Haplotypic mutations observed in *Jacobiasca lybica* individuals collected on 3 host plants in Côte d'Ivoire.

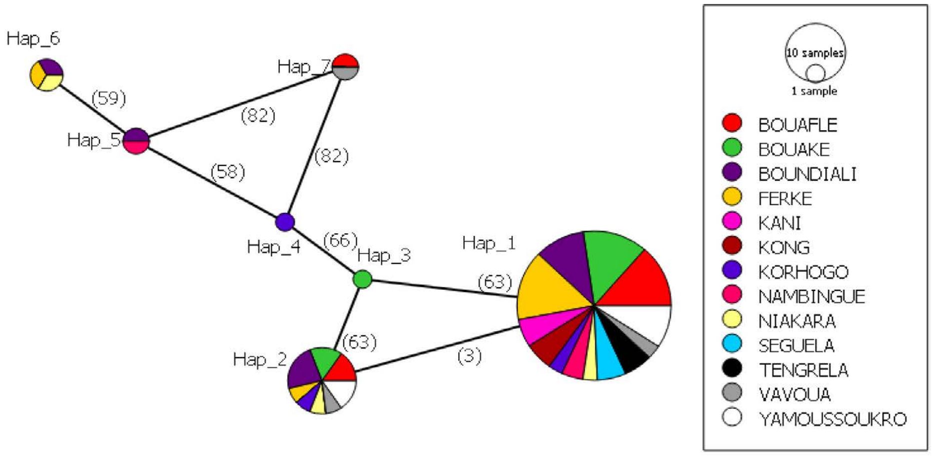

Figure 7. Haplotypic mutations observed in *Amrasca biguttula* individuals collected in 13 localities from Côte d'Ivoire.

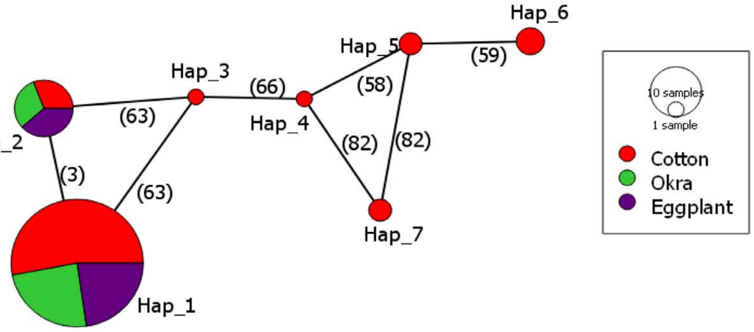

Figure 8. Haplotypic mutations observed in *Amrasca biguttula* individuals collected on 3 host plants in Côte d'Ivoire.

DISCUSSION

Molecular analysis conducted during the 2021 and 2022 cropping seasons revealed that the leafhopper species collected from cotton were identical to those found on eggplant and okra. These species, *J. lybica*, *E. papayae*, and *A. biguttula*, have the ability to feed on multiple host plants within the same environment, particularly cotton, eggplant, and okra (Barroga and Bernardo, 1993; Bernardo and Taylo, 1990; Jayasimha et al., 2012; Kouadio et al., 2022b; Ramila et al., 2016). This study supports prior findings based on morphological identification (Kouadio et al., 2022b, c, 2024), providing crucial information for developing effective phytosanitary protection programs.

The presence of multiple host plants in the same environment can contribute to the persistence of leafhoppers populations in cotton crops (Koné et al., 2017). Okra and eggplant are grown during the cotton season and in the off-season for market gardeners, potentially serving as both a food source and refuge for these insects during the intercrop period. Analysis of the annual species composition revealed cohabitation of these species based on host plant preference. However, during the 2022 season, only *A. biguttula* was observed on both okra and eggplant. The dominant species shifted between crop years. In 2021, two species were identified: *J. lybica* (93.2% on vegetable crops, 91.7% on cotton) and *E. papayae* (6.8%). This aligns with previous observations in Côte d'Ivoire (Kouadio et al., 2022b, 2024) suggesting *J. lybica* was primarily responsible for the attacks observed during the 2020-2021 season (Kouadio et al., 2024).

In 2022, *A. biguttula* was reported in Côte d'Ivoire for the first time. Previously identified as a minor pest on okra in Ghana (Obeng-Ofori and Sackey, 2003), *A. biguttula* represented 100% of individuals collected on okra and eggplant, and 85.4% on cotton. Its dominance corroborates findings by Kouadio et al. (2022b, 2024), with *A. biguttula* identified as the primary pest causing significant damage to cotton crops during the 2022 season. Its exclusive presence on okra and eggplant suggests a strong capacity to occupy the ecological niches previously dominated by local species. This species is highly prolific, as indicated by its rapid spread and the extensive damage caused on cotton crops, surpassing the economic damage threshold.

The shift in species dominance between the two crop years highlights the potential for species substitution. *A. biguttula*, also known as the Indian leafhopper *Amrasca devastans* (Ishida), or *Amrasca biguttula biguttula* (Ishida) (Xu et al., 2017), is native to regions including India, Pakistan, China, Japan, and western Asia (Cabrera-Asencio et al., 2023). Its economic impact on cotton farming in Côte d'Ivoire has been estimated at more than 34 billion FCFA, with crop losses exceeding 60% of the production potential (Kouadio et al., 2024). The damage is similarly significant on market gardening, with losses surpassing 50% (Devi et al., 2018).

Beyond its financial threat, *A. biguttula* poses a major risk to food security due to its impact on key vegetable crops like eggplant and okra, which are stapple crops in Côte d'Ivoire. Additionally, this species exhibits metabolic resistance to chemical insecticides, characterized by oxidase and glutathione-S-transferase activity, which complicates pest management (Halappa and Patil, 2016; Sagar and Balikai, 2014). To control this pest, insecticides from classes organophosphorus (1B), organochlorine cyclodiene (2A), pyrethroid-pyrethrin (3A), and neonicotinoid (4A) classes should be avoided-

Genetic diversity parameters revealed that *J. lybica* exhibited haplotypic mutations ranging from 5 to 18, with relatively high nucleotide diversity. In contrast, *A. biguttula* showed haplotypic mutations ranging from 3 to 82, but with low nucleotide diversity, suggesting limited genetic evolution despite the high number of mutations. This discrepancy could be attributed to the low nucleotide diversity within this invasive population in West Africa.

CONCLUSION

This study demonstrates that the leafhopper species found on cotton are identical to those present on eggplant and okra, with the main species identified as *E. papayae*, *J. lybica*, and *A. biguttula*. The dynamics of these species were observed in relation to the agricultural seasons. Notably, the study highlighted a shift in species composition, with a historically dominant local species being replaced by a more prolific newcomer. In 2021, *J. lybica* was the predominant species, but by 2022, it was replaced by *A. biguttula*, which showed increased dominance.

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