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PCR-Based Diagnosis of Cassava Mosaic Begomoviruses and DNA Satellites in Cassava Plants in Northern Ghana

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ABSTRACT

Cassava mosaic begomoviruses and DNA satellites are major threats to cassava production. In this study, 55 cassava farmers' fields in Northern Ghana were randomly assessed for cassava mosaic disease (CMD) incidence, severity, adult whitefly counts, and cassava mosaic begomoviruses. Also, DNA satellite status was determined for 203 asymptomatic and symptomatic cassava leaf samples using polymerase chain reaction involving primers that detect *Begomovirus manihotis* (formerly *African cassava mosaic virus*; ACMV) and *Begomovirus manihotisafrikaense* (formerly *East African cassava mosaic virus*; EACMV) and DNA satellites. CMD was recorded in 50 (90.9%) out of the 55 farms surveyed. Incidence of CMD ranged from 3.33% to 69.65%, with a mean of 46.3% in Northern Ghana. Also, CMD severity ranged from 2.0 to 3.1 and averaged 2.5. Adult *Bemisia tabaci* counts were generally low. Out of 168 symptomatic cassava leaf samples, ACMV only was detected in 64.3%; EACMV only was detected in 15.5%, and EACMV–ACMV coinfection was detected in 20.2% of these leaf samples. Out 63 EACMV positive cassava leaf samples, satIII and satII were, respectively, detected in 85.7% and 77.8% samples. This study indicates the presence of *Begomovirus manihotis*, *Begomovirus manihotisafrikaense*, and satellites (satII and satIII) in Northern Ghana. The data generated by this study could serve as potential resource in modeling to predict CMD and related satellites spread both in and outside Ghana.

1 | Introduction

Cassava (*Manihot esculenta* Crantz), largely cultivated in the tropics, is an essential food security crop for millions of people in America, Africa, and Asia [1, 2]. It serves as an important cash crop in sub-Saharan Africa (SSA) and an important crop to the vulnerable [2]. The major cassava-producing countries in SSA include Nigeria, the Democratic Republic of Congo, Ghana, Kenya, Côte d'Ivoire, Tanzania, Mali, and Togo [3]. The crop is cultivated across SSA all year round with Nigeria being the top global producer with production estimated at 59.5 million metric tons [3].

Cassava is ranked as the third-largest carbohydrate source with over 500 million people globally depending on its harvest for food consumption [4]. The production per annum is estimated at 290 million metric tons worldwide, of which Africa produced 163 million tons and Ghana produced 22 million metric tons in 2020 [3].

The crop is drought tolerant and cultivated in all 16 regions of Ghana with the Eastern Region having the highest production [5]. Cassava contributes to the socioeconomic development in SSA with its trade and economic use with products such as gari,

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tapioca, cassava chips, and cassava bread, and it is an increasingly accepted raw material for industrial use [6].

Amidst its importance, cassava production is threatened by cassava mosaic disease (CMD). In extreme conditions, 80%–100% yield loss has been reported to have affected economic projections in cassava production [5, 7].

Currently, 11 distinct *Begomovirus* species (nine from Africa and two from Asia) have been characterized and reported as CMD causal agents [4]. Transmission of cassava mosaic begomoviruses (CMBs) and satellite occurs via the vector, *Bemisia tabaci*, and vegetative propagation with infected stem cuttings [4, 8]. Farmer-to-farmer exchange accounts for CMD spread because of farmers' dependence on CMD-susceptible landraces as sources of planting materials [5]. Earlier CMD studies in Ghana confirmed cassava mosaic begomovirus (CMB) species existence and the high prevalence of *Begomovirus manihotisafrikaense* and *Begomovirus manihotis* [9].

DNA satellites are subviral particles (~1.3 kb) associated with CMGs that modulate and increase CMD susceptibility and severity and have been reported recently in cassava [10]. DNA satellites' first detection in Africa was due to infected cassava exhibiting unusual filiform-shaped leaves associated with bipartite CMBs in Central and East Africa [11–13], posing serious epidemiological implications to cassava production.

DNA satellites (satII and satIII) were confirmed in a recent study in Southern Ghana [14], and it was the first in the West Africa subregion. However, there is no up-to-date report on nationwide data on virus diversity and infectivity level of *Begomovirus*-satellite activities in the country [5].

Regular monitoring and characterization are vital to update current CMB epidemiological data and bridge the information gap nationwide for efficient and reproducible CMD research to tackle the emergence of satellites [5, 15]. Periodic surveys are needed to ascertain CMB and satellite diversity and distribution for decisions on management of CMD. The objectives of this study were therefore to assess CMD incidence, symptom severity, and *B. tabaci* population in cassava growing areas in Northern Ghana with the aim to identify *Begomovirus manihotis*, *Begomovirus manihotisafrikaense*, and DNA satellites (satII and satIII).

2 | Materials and Methods

2.1 | Experimental Site Selection

CMD survey was conducted in fifty-five (55) cassava fields in cassava-producing districts across the five (5) regions in Northern Ghana (savannah agro-ecological zone of Ghana). These regions constitute two-thirds of Ghana's land area with an estimated 149,800 km², 957–1100 mm mean annual rainfall, and 28.1°C–28.6°C daily mean temperature [16]. The regions surveyed were Northern, North East, Savannah, Upper East, and Upper West regions in July, 2022 (major season), with a modal rainfall pattern. The savannah ecological zone of Ghana comprising the Guinea Savannah (GS) and Sudan Savannah (SS) constitutes dryland and desertification-prone areas with characteristic drought sensitivity and extreme weather conditions with an average humid climatic condition during the survey.

2.2 | Farmers' Field Sampling and Data Collection

A detailed list of major cassava-growing districts in each region was obtained from the Statistics, Research and Information Directorate (SRID) of the Ministry of Food and Agriculture. From the list, cassava-growing districts were selected, and communities were randomly sampled per availability and accessibility of cassava fields in each district for this study. Informal discussions, where possible, were held with the district AEAs to confirm the cassava-growing communities [17]. Sampling interval between fields was mostly 10–15 km along accessible roads based on available and suitable cassava fields, 3–6 months after planting (MAP) [18]. In each field, data were collected on the cassava cultivars, intercrops, number of visible cassava fields nearby, coordinates of the field (using Google Earth), CMD incidence and severity, adult whitefly counts.

Thirty (30) individual cassava plants (3–6 MAP) were randomly assessed and scored at regular intervals along two horizontals and a diagonal across each field [19] for CMD incidence and severity and adult whitefly counts. Two–five (2–5) plants were selected at approximately equidistant intervals in each half transect from the field's center based on the severity, and young leaf samples were collected from the top of the canopy into labeled zip lock bags and kept on ice. A total of 203 asymptomatic and symptomatic CMD-affected cassava leaf samples were collected from 55 farmer's fields, kept on ice during transit, and transferred to –20°C freezer at the Biotechnology Centre, University of Ghana, Legon, until DNA was extracted. Study sites were located between 2.480 W–0.44E longitude and 8.29–10.85 N latitude in Ghana. Field assessment of the fields surveyed was done with no record of seasonal changes.

2.3 | Assessment of CMD Incidence, Symptom Severity, and Adult Whitefly Counts

For each of thirty (30) cassava plants assessed, if present, CMD infection was categorized as either cutting-borne or whitefly-borne. Cutting-borne infection refers to those plants in which lower leaves through to the upper leaves of the cassava plants were affected by CMD, whereas whitefly-borne infections referred to those plants whose lower leaves were asymptomatic but upper leaves showed CMD symptoms [8]. CMD symptom severity of cassava plants in all sampled fields was assessed according to [20]. Mean symptom severity was calculated for scores 2–5 [21]. Adult *B. tabaci* count was assessed by counting adult whiteflies on the abaxial side of the topmost five expanded leaves of the tallest shoot.

2.4 | DNA Extraction and Quality Check

Genomic DNA was extracted using cetyltrimethylammonium bromide (CTAB) [22]. Quality of the genomic DNA was assessed by electrophoresis using 0.8% agarose gel.

2.5 | Polymerase Chain Reaction With CMB DNA Satellite Primers

PCR was performed using specific primer pairs designed to detect *Begomovirus manihotis*, *Begomovirus manihotisafrikaense*, and related satellites (Table 1). The reaction volume (25 µL) comprised of 12.5 µL Quick-Load Taq 2X Master Mix with Standard Buffer (New England Biolabs, NEB), 8.5 µL nuclease-free PCR

TABLE 1 | Primers and their respective target viruses for the *cassava mosaic begomoviruses* and associated satellites.

Target virus, satellite	Primer	Primer sequence (5'-3') reference
ACMV*	JSP001	ATGTCGAAGCGACCAGGAGAT [23]
	JSP002	TGTTTATTAATTGCCAATACT [23]
EACMV**	JSP001	ATGTCGAAGCGACCAGGAGAT [23]
	JSP003	CCTTTATTAATTTGCTCACTGC [23]
satII	Sat IIF	GCCGCACCACTGGATCTC [12]
	Sat IIR	CAGCAGCCAGTCAGGAAGTT [12]
satIII	Sat IIIF	AGGCCTCGTTACTAAAAGTGC [11]
	Sat IIIR	ACCTGACGGCAGAAGGAAT [11]

Note: Synthesized by Inqaba Biotec Ltd, South Africa.

**Begomovirus manihotis*.

***Begomovirus manihotisafraicaense*.

water (Inqaba Biotec Ltd), 0.5 μ L each of forward and reverse primers (5 μ M), and 3.0 μ L DNA. PCR was performed in an Applied Biosystems 2720 thermal cycler with the following cycling conditions: initial denaturation at 94°C for 3 min, followed by 30 cycles of 94°C for 1 min, 55°C for 1 min 30 s, and 72°C for 1 min, with a final extension of 72°C for 5 min [12]. Amplicons were separated by electrophoresis on ethidium bromide (10 mg/mL)-stained 1.5% (w/v) agarose gel alongside a DNA ladder at 100 V for 1 h. The bands were visualized using a Syngene Gel documentation system.

2.6 | Data Analysis

CMD incidence was determined by calculating the percentage of plants with CMD symptoms per field. Mean severity was determined for each field using severity scores 2–5.

$$\text{CMD Incidence} = \frac{\text{Number of diseased plants}}{\text{Total number of plants assessed plants}} \times 100 \%, \quad (1)$$

$$\text{CMD Severity} = \frac{\sum(\text{all severity score of 2 and above})}{\text{Total number of diseased plants (score 2 – 5)}}. \quad (2)$$

Presence of amplified PCR bands was represented by (+), and (–) represented the absence of amplified PCR bands.

3 | Results and Discussion

3.1 | CMD Incidence, Severity, and Adult *B. tabaci* Count

CMD was widespread in the 55 farmers' fields surveyed in Northern Ghana. CMD incidence reached 100% in 10 (18.18%) out of 55 farmers' field surveyed (data not shown). Savannah region had the highest CMD incidence (69.65%; range: 66%–100%) followed by the North East region (65.56%), Northern region (57.37%), Upper East region (35.56%), and Upper West region (3.3%) (Table 2).

CMD incidence of between 81% and 100% was recorded in 19 farmers' fields, followed by 60%–80% in 12 farmers' fields. No CMD was recorded in 5 locations across the 55 locations sampled (Figure 1). High CMD incidence (66%–100%) was recorded in 5

cassava growing districts (North East Gonja, Sawla-Tuna-Kalba, Bole Central Gonja, East Gonja, and West Gonja) (Table 2).

CMD incidence of 34%–65% was recorded in East Mamprusi, Kassena Nankana East Municipal, Builsa North, Kassena Nankana West, Tamale Metro, Kpandai, Nanumba South, Yendi Municipal, and Gushegu Municipal.

This study represents the most extensive CMD survey in Northern Ghana to date. It gives a more current representation of CMD spread and satellite presence in Northern Ghana. Similar surveys on CMD incidence and severity done previously mainly focused on the southern regions of Ghana [9] except for a study by Oppong et al. [5], where fewer parts of the north were covered [5] than in the present study. CMD symptoms expressed included leaf distortion, twisted leaves, leaf mosaic patterns and chlorotic patterns, leaf reduction, and stunting of CMD diseased plants in cassava farmers' fields in Northern Ghana. CMD symptoms were consistent with previous report in Southern Ghana [9, 14].

High CMD incidence recorded in more than 50% of the farmers' fields concurs with the high CMD incidence reported in the country [5]. Mild-to-severe severity symptoms recorded in the present study could be attributed to the accumulated viral load because of recycling of infected cuttings and CMD-susceptible local cultivar use [24, 25]. Despite the moderate severity, CMD was widespread across cassava-growing districts which indicate the exposure of farmer's field to CMD [14, 21].

Widespread CMD distribution in infected fields can be attributed to the extensive CMD spread in cassava production areas through the practice of exchange of cuttings among farmers [25, 26]. This practice poses strong epidemic risk among cassava growing districts and regions of the country and the subregion especially through movement of infected cassava cuttings. Local farmers still cultivate highly susceptible low-yield local cultivars, and the unsurprising disregard for CMD is a limitation management of the disease [24, 27, 28].

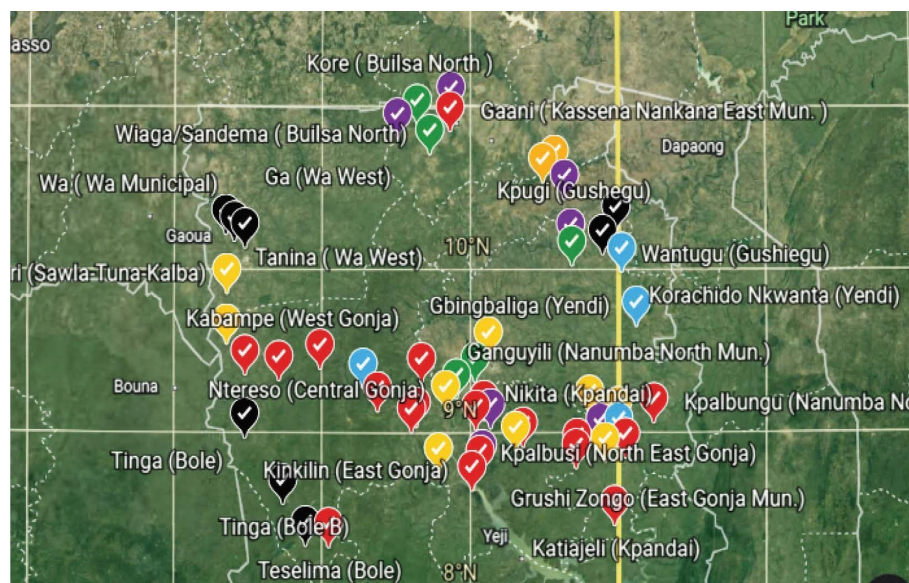
The overall mean CMD severity was 2.53 (Table 2). The predominant CMD severity was in the range of 2.6–3.5 (Figure 2). North East region had the highest CMD severity of 3.13, followed by Northern region (2.73), Savannah region (2.66), Upper East region (2.14), and Upper West region (2.00) (Table 2).

Asymptomatic cassava plants were frequent in the Upper West and Upper East regions, contrary to that of the Savannah, North

TABLE 2 | Average CMD incidence, CMD severity, and adult whitefly counts in farmers' cassava fields surveyed in Northern Ghana.

Region	District	No. of surveyed farms	Average disease incidence %	Average disease severity	Adult whitefly count
Northern	Tamale Metro	1	76.67	3.22	28
	Kpandai	5	88.66	2.87	104
	Nanumba South	3	58.34	2.43	54
	Nanumba North Municipal	4	71.67	2.90	79
	Yendi Municipal	3	22.22	2.64	0
	Gushegu Municipal	3	26.67	2.32	9
			57.37	2.73	274
Savannah	North East Gonja	5	60.00	2.50	52
	Central Gonja	4	70.67	2.36	0
	East Gonja Municipal	4	79.45	2.97	45
	Sawla-Tuna-Kalba	2	86.67	2.86	36
	West Gonja	6	86.67	2.90	39
	Bole	4	34.44	2.39	44
			69.65	2.66	216
North East	East Mamprusi Municipal	3	65.56	3.13	0
			65.56	3.13	0
Upper East	Kassena Nankana East Municipal	2	78.34	2.95	6
	Builsa North	2	28.34	2.47	0
	Kassena Nankana West	1	0.00	1.00	0
			35.56	2.14	6
Upper West	Wa Municipal	1	3.33	2.00	0
	Wa West	2	3.33	2.00	2
			3.33	2.00	2
Total Average			46.294	2.532	

Note: Bold values are totals.

**FIGURE 1** | CMD incidence in surveyed cassava fields in Northern Ghana mapped using Google Earth. Incidence scale: green—no CMD incidence; black—1%–20%; blue—21%–40%; violet—41%–60%; yellow—60%–80%; red—81%–100%.

East, and Northern regions. This observation could be ascribed to the low cassava production in the Upper West and Upper East regions with the associated reduced movement of cassava cuttings [5]. Similarly, the Upper East and Upper West regions recorded low CMD incidence and severity compared to the Savannah, North East, and Northern regions, and this could be

attributed to low level of farmer involvement in cassava production on a regional basis. Less than 10 healthy farmers' fields were found, mostly in North East, Upper East, and Upper West regions, which concurs with a similar report in Cameroon [29], making these regions suitable for multiplication of cassava planting materials.

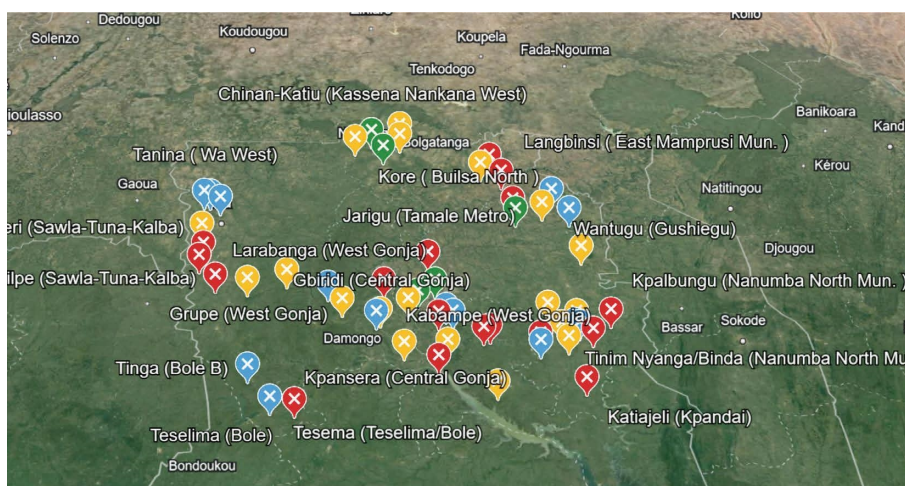


FIGURE 2 | Mean CMD severity in surveyed cassava fields in Northern Ghana mapped using Google Earth. Severity scale: green—1; blue—2.0 to 2.5; yellow—2.6 to 3.0; red—3.1 to 3.5.

The Northern region had the highest whitefly population of 274, and none was recorded in North East region. The rest were Savannah region (216), Upper East region (6), and Upper West region (2). No adult *B. tabaci* was recorded in 6 districts (Yendi Municipal, Central Gonja, East Mamprusi, Bulsa North, Wa Municipal, and Kassena Nankana West) while 104 adult *B. tabaci* (being the highest) were recorded in Kpandai District (Table 2).

No relationship was observed between CMD incidence and adult *B. tabaci* count per district. No adult *B. tabaci* was recorded in Central Gonja District, but it had high mean CMD incidence (70.67%). Also, relatively higher adult *B. tabaci* count (54) was recorded for Nanumba South, yet it had a mean CMD incidence of 58.34% (Table 2).

Similarly, Tamale Metro had low adult *B. tabaci* count (28) but high mean CMD severity (3.22), whereas Kpandai with the highest adult *B. tabaci* count (104) had relatively lower mean CMD severity (2.87) (Table 2). The main infection modes assessed visually were cutting-borne (contaminated cuttings) which accounted for more than 90% of sampled CMD-affected samples while 10% was due to whitefly-borne infection (supporting table).

Adult *B. tabaci* numbers per plant were generally low and followed recent reports in Ghana [5] and Burkina Faso [30] and were in contrast with reports in Cameroon [29]. Adult *B. tabaci* populations varied among the regions as similarly reported in other findings in Congo [31] and Ghana [9]. The low *B. tabaci* population could perhaps be due to the varied differences in climate, cultural practices, and cassava cultivars which influence *B. tabaci* activities in CMD infestation [32–34].

Also, low adult *B. tabaci* populations were observed in the high-altitude regions of North East, Upper East, and Upper West, which is similar to previous studies by the authors of [35, 36] on the correlation of high altitude and whitefly multiplication. The population of *B. tabaci* and CMD incidence varied such that there was no *B. tabaci* population in North East region; however, CMD incidence was the second highest in contrast to that of the Northern region. Cutting-borne CMD incidence was higher than whitefly-borne CMD incidence as similarly reported in Cameroon [25].

3.2 | Molecular Detection of CMBs and Related Satellites

Out of the two hundred and three (203) samples obtained from the Northern regions of Ghana, 168 cassava leaf samples were symptomatic; *Begomovirus manihotis* only was detected in 108 (64.28%) cassava leaf samples (Figure 3), *Begomovirus manihotisafrikaense* only was detected in 26 (15.47%) cassava leaf samples (Figure 4), and mixed infection by both *Begomovirus manihotis* and *Begomovirus manihotisafrikaense* was detected in 34 (20.23%) cassava leaf samples.

DNA satellite satIII (~306 bp) was detected in 54 (85.7%) out of the sixty-three (63) samples that tested positive for East African cassava mosaic virus (EACMV) either as single infection or in mixed infection with African cassava mosaic virus (ACMV) (Figure 5). Also, DNA satellite satII (~895 bp) was detected in 49 (77.8%) of these same 63 cassava leaf samples (Figure 6).

Out of the thirty-five (35) asymptomatic cassava leaf samples, more than half (20; 57.1%) were negative, 11 (31.4%) tested positive for *Begomovirus manihotis* only, 3 (8.5%) tested positive for *Begomovirus manihotisafrikaense* only, and 1 (3%) was positive for *Begomovirus manihotis* and *Begomovirus manihotisafrikaense*. Distribution of *Begomovirus manihotis*, *Begomovirus manihotisafrikaense*, satII, and satIII in Northern Ghana is presented in Figure 7.

3.3 | Legend

Red: *Begomovirus manihotis*, *Begomovirus manihotisafrikaense*, and satellites.

Light red: *Begomovirus manihotis*, *Begomovirus manihotisafrikaense*, and sat III only.

Violet: *Begomovirus manihotisafrikaense* and satellites.

Brown: *Begomovirus manihotis* and *Begomovirus manihotisafrikaense* without satellites.

Yellow: *Begomovirus manihotis* only.

Green: *Begomovirus manihotisafrikaense* only.

White: no virus detected.

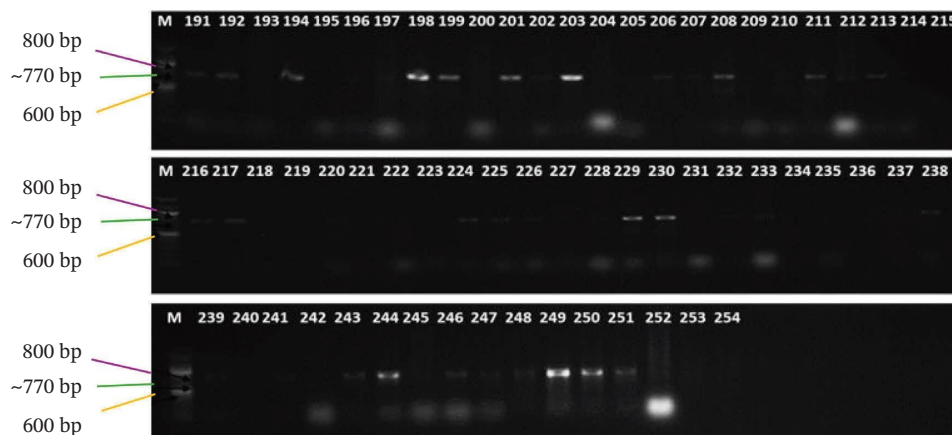


FIGURE 3 | Agarose gel electrophoresis image of total PCR product (770 bp) on 1.5% agarose gel generated using primer pair JSP001/002 for *Begomovirus manihotis*. M—1.0-kb DNA ladder; Lane 254—negative control. Lanes 191–263 represent cassava samples from various locations.

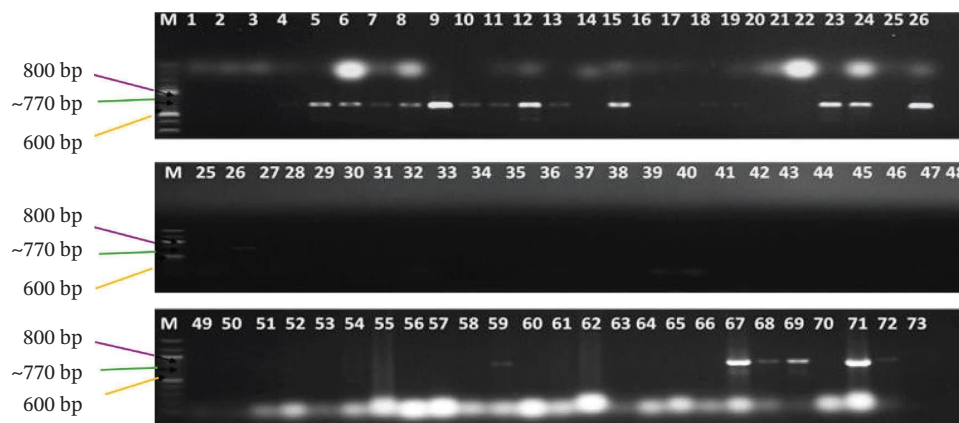


FIGURE 4 | Agarose gel electrophoresis of total PCR products (770 bp) on 1.5% agarose gel generated using primer pair JSP001/003 for *Begomovirus manihotisafricaense*. M—1.0-kb DNA ladder; Lane 73—negative control. Lanes 1–72 are samples of cassava leaf.

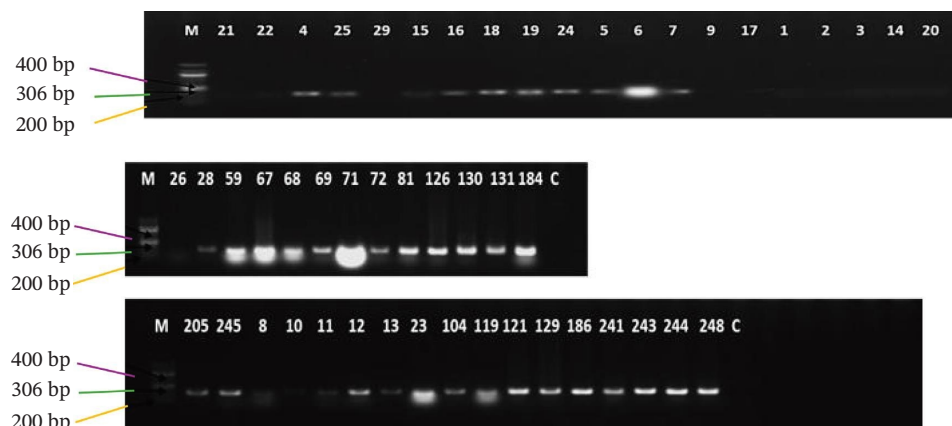


FIGURE 5 | Agarose gel image of amplicons generated using primer pair satIII F/R on 1.5% agarose gel; M—1.0-kb DNA ladder; Lane C—negative control; Lanes 21–248 represent cassava leaf samples.

Prevalence and spread of *Begomovirus manihotis*, *Begomovirus manihotisafricaense*, mixed infections by both begomoviruses, and related satellites (satII and satIII) in Northern Ghana were established in this present study. This finding has epidemiological

implications for cassava production in this part of the country. This finding concurs with previous reports that confirmed *Begomovirus manihotis* and *Begomovirus manihotisafricaense* incidence in West Africa and that of satellites in Ghana [5, 14, 21].

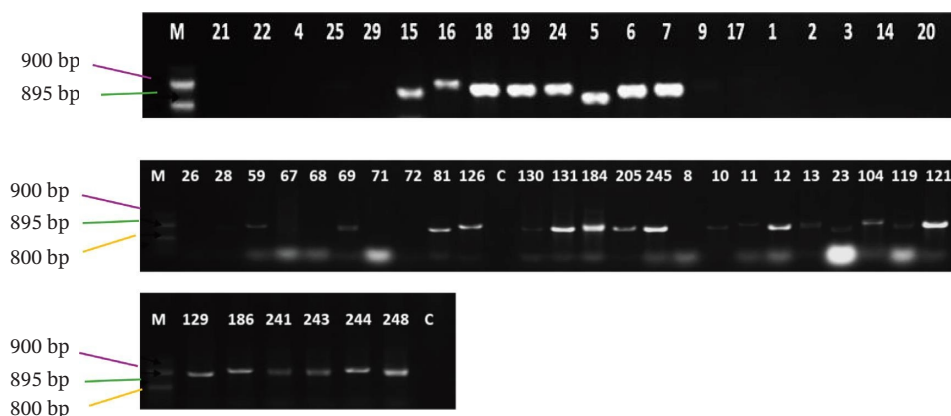


FIGURE 6 | Agarose gel image of amplicons generated using primer pair satII F/R on 1.5% agarose gel; M—1.0-kb DNA ladder; C—negative control; 21–248 represent cassava leaf samples.

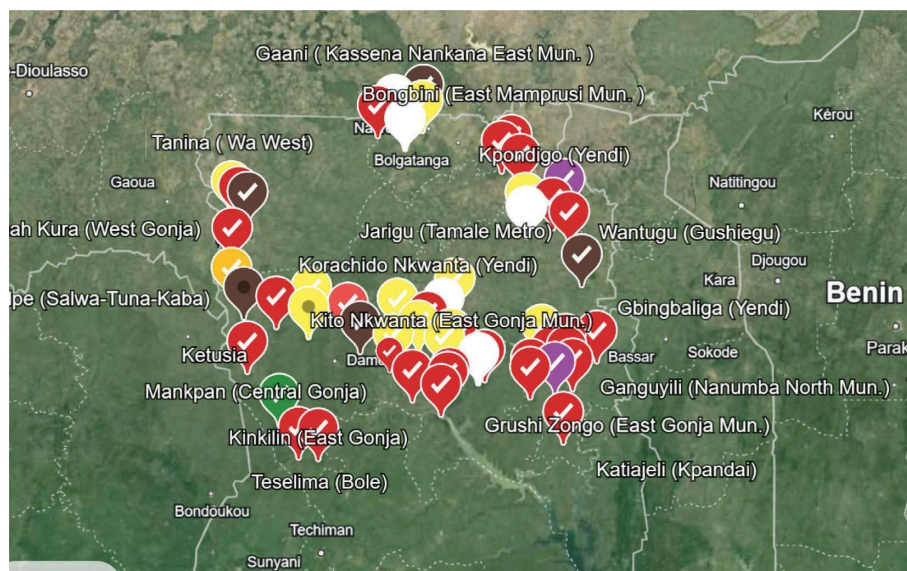


FIGURE 7 | Locations in Northern Ghana where *Begomovirus manihotis*, *Begomovirus manihotisafrikaense*, and satellites were detected from cassava leaf samples.

Begomovirus manihotis was more dominant compared to *Begomovirus manihotisafrikaense* in all the sampled locations in Northern Ghana as similarly confirmed by Ndomba [14] in Southern Ghana. The presence of *Begomovirus manihotis* and *Begomovirus manihotisafrikaense* confirms reports in Tanzania [13] and in Kenya [12]. Detection of mixed infections by *Begomovirus manihotis* and *Begomovirus manihotisafrikaense* with its associated severe symptoms concurs with reports by the authors of [5, 14, 37–39]. Severe symptoms have been reported to be associated with higher sustained yield losses; therefore, cassava growing areas with these infections could suffer more devastated damage than areas with single infections of either *Begomovirus manihotis* or *Begomovirus manihotisafrikaense*. Mixed infections present opportunities for viruses to recombine; as a result, new species or strains of these viruses could emerge in the future. Similarly, mixed infections could present higher virus titer in plants, thereby enhancing transmission by the whitefly vector. Nevertheless, the report of *Begomovirus manihotisafrikaense* only (single infections) in some sampled locations contradicts the findings in the country [9].

Interestingly, many CMD-affected cassava leaf samples tested positive for satIII and satII, confirming apparent incidence and widespread distribution of satellites in Northern Ghana, the first report in the five Northern regions. The present study revealing satII and satIII presence in Northern Ghana for the first time relates with the reports in Tanzania [11, 40], Kenya [12], and Southern Ghana [14]. Occurrence of satellites together with cassava mosaic could equally lead to successful transmission of these agents. Satellites have been reported to cause the breakdown of the dominance conferred by CMD2 to cassava plants [13]. One could expect a similar effect on cassava plants in the Northern parts of the country.

4 | Conclusions

The present finding demonstrates the wide distribution of CMD and related satellites in Northern Ghana and the main dissemination source being infected cuttings. The data generated by this study could serve as a potential resource in helping modelers to predict CMD and related satellites' spread and current

distribution in Ghana and possibly the West African subregion, which could be a valuable resource in managing CMD. The current study relied on PCR with primers for detection of the CMBs. It is recommended that future studies on CMD in Northern Ghana (as covered by the present work) should include additional primers for other species of viruses associated with CMD, Sanger sequencing of selected viral and satellite fragments, and the use of high-throughput sequencing.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

All data that support the findings of this study are in the article (including the supporting information).

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Supporting Information

Additional supporting information can be found online in the Supporting Information section.

Supporting Information 1. The manuscript has additional information such as supporting table and figure. The supporting table has farm-level data of cassava mosaic disease (CMD). These data as presented revealed the name of each location (town/village) where cassava farm was assessed. It contained mean CMD incidences, severity, infection type (whether cutting-borne or whitefly-borne), and adult whitefly counts. CMD incidence ranged from zero (0) to 100% on farmers' fields. Similarly, cutting-borne infection ranged from zero (0) to 100% on farmers' fields. Whitefly-borne infection, on the other hand, was between zero (0) and 33.3%. CMD severity also ranged from 1 to 3.4 on the farmers' cassava fields. The highest adult whitefly count per field was 28.

Supporting Information 2. The supporting figure presents pictures on CMD severity taken during the survey. These pictures were representative of asymptomatic cassava plants; mildly CMD-affected cassava plants; C, moderately CMD-affected cassava plants; D, severely CMD-affected cassava plants; and E, very severely CMD-affected cassava plants.