

Screenhouse Screening of Ten Cassava (*Manihot esculenta* Crantz) Varieties for Resistance to Cassava Mosaic Disease via Graft Inoculation in Sudan Savannah, Nigeria.

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Received 28 July, Accepted 20 August, Published 11 September

Direct Research Journal of Biology and Biotechnology



Vol. 12(2), Pp. 41-49, September 2026

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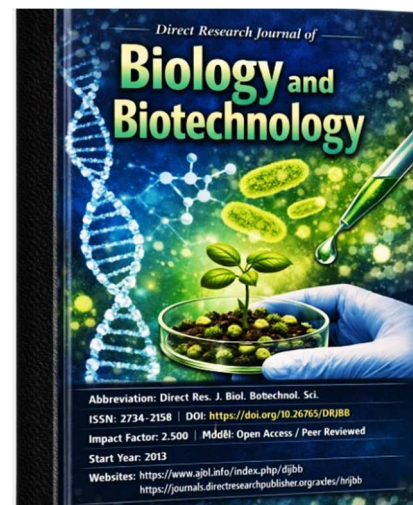
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Research Article
ISSN: 2734-2158

ABSTRACT

Cassava mosaic disease (CMD) is the most important viral constraint to cassava production in Africa. This study aimed to rigorously assess the phenotypic responses of ten cassava varieties, eight improved genotypes (IBA30572, OBASANJO 2, GAME CHANGER, IBA 164773, IBA 154810, IBA 961632, BABA 70, IBA 0505) and two local landraces (DANGWAMNATI and BAH AUSHE) to CMD under controlled graft inoculation, providing a benchmark for genotype selection under uniform high pathogen pressure. The experiment was laid out in a completely randomized design (CRD) with six replicates to ensure statistical robustness and to enable reliable discrimination among resistance phenotypes. Healthy rootstocks were graft-inoculated with scions from CMD-infected plants and monitored for disease incidence and severity at 2, 4, 6, 8, 10, and 12 weeks after inoculation (WAI). Data were analyzed using descriptive statistics (mean incidence and severity percentages), with no inferential statistical tests applied; this descriptive-only approach was chosen to characterize phenotypic patterns rather than test treatment differences, and its limitation lies in the absence of formal hypothesis testing or variance partitioning. Results revealed four distinct resistance phenotypes. Highly resistant varieties (OBASANJO 2, GAME CHANGER, BABA 70, IBA 0505) maintained 0% incidence and 0% severity throughout, demonstrating true immunity characteristic of CMD2 gene-mediated resistance. Tolerant varieties (IBA 30572, IBA 154810) showed 16.67% incidence but remarkably low severity (4.17%), indicating ability to contain infection and limit symptom expression. IBA 164773 exhibited partial resistance with 33.34% incidence and 8.33% severity. Susceptible varieties showed progressive disease development: IBA 961632 reached 66.67% incidence and 29.17% severity, while local landraces DANGWAMNATI and BAH AUSHE showed complete susceptibility (100% incidence by 6 WAI) with devastating severity (83.33% and 87.50%, respectively). Symptom expression in susceptible genotypes included severe mosaic, leaf distortion, and stunting, while resistant plants remained symptomless. These findings provide detailed information on resistance phenotypes under uniform high-pressure inoculation, revealing true genetic potential that may not be fully expressed under field conditions.

Keywords: CMD, graft inoculation, resistance, phenotypes, immunity, tolerance, CMD2, *Manihot esculenta*, *Bemisia tabaci*, screenhouse, Sudan Savannah



Citation: Bello, I., Mohammed, U. I., Alhassan, J., Magaji, M. D., Yusuf, I. J., Rabbi, I. Y. & Iluebbey, P. O. (2026). Screenhouse Screening of Ten Cassava (*Manihot esculenta* Crantz) Varieties for Resistance to Cassava Mosaic Disease via Graft Inoculation in Sudan Savannah, Nigeria. *Direct Research Journal of Biology and Biotechnology*. Vol. 12(2), Pp. 41-49. <https://doi.org/10.4314/djbb.v12i2.5>

INTRODUCTION

Cassava (*Manihot esculenta* Crantz) is one of the most important food security crops sustaining human populations across tropical and subtropical regions. Originating from the Amazon basin of South America, cassava was introduced to Africa by Portuguese traders during the sixteenth century and has since become integrated into agricultural systems across sub-Saharan Africa, where it serves as a primary caloric source for over 500 million people daily (Nassar & Ortiz, 2010). Nigeria is the world's leading cassava producer, contributing approximately 20% of global production with an annual output exceeding 60 million metric tons from nearly 7 million hectares (FAO, 2023). The crop is cultivated across all major agroecological zones, from the humid forests of the south to the Sudan Savannah in the north, each presenting unique production challenges (Ogbe *et al.*, 2003). Cassava exhibits remarkable versatility, with storage roots processed into traditional foods including gari, fufu, lafun, and tapioca, while leaves provide protein, vitamins, and minerals. Beyond subsistence, cassava has gained industrial importance in production of high-quality flour, starch for pharmaceuticals and textiles, sweeteners, and bioethanol (Li *et al.*, 2022).

Despite its importance, cassava production faces significant biotic constraints, with viral diseases representing the most economically damaging. Cassava mosaic disease (CMD), caused by cassava mosaic geminiviruses (CMGs) transmitted by whitefly (*Bemisia tabaci*), is the most widespread and devastating constraint across sub-Saharan Africa (Legg *et al.*, 2015). First reported in East Africa during the 1890s, the disease has spread across the continent, with Nigeria's Sudan Savannah experiencing intense pressure due to conditions favoring vector proliferation (Ogbe *et al.*, 2003). The causal agents include African cassava mosaic virus (ACMV) and East African cassava mosaic virus (EACMV), which frequently occur as mixed infections, exacerbating symptom severity and complicating resistance breeding (Naseem & Winter, 2016).

Recent studies have documented the emergence of novel begomoviral strains and shift in CMD epidemiology across West Africa, with implications for resistance durability. The deployment of CMD2-based resistance has been a cornerstone of breeding programs, yet the durability and stability of this resistance across agro-ecological zones remains an active area of investigation (Legg *et al.*, 2015). Contemporary graft-inoculation screening methodologies have proven valuable for distinguishing true genetic resistance from field escape, particularly in cassava breeding programs (Monde *et al.*, 2012). Infected plants exhibit chlorotic leaf mosaic, distortion, stunted growth, and reduced storage root formation, with yield losses ranging from 20% to 95% depending on cultivar susceptibility, viral strain virulence,

and environmental conditions (Chikoti *et al.*, 2019). Symptom expression varies among genotypes, with tolerant varieties exhibiting mild chlorosis while maintaining acceptable yields, whereas highly susceptible genotypes may experience complete crop failure. CMD management requires an integrated approach combining cultural practices, phytosanitary measures, and genetic resistance. Host plant resistance represents the most effective, economical, and sustainable strategy for smallholder farmers (Legg *et al.*, 2015). Cultural methods including roguing infected plants and using disease-free planting material can reduce incidence but are labor-intensive and difficult to sustain at scale. Phytosanitary regulations aim to limit spread of novel viral strains, though enforcement remains challenging. Biological control of whiteflies offers supplementary benefits but cannot alone achieve adequate disease suppression. Consequently, development and deployment of resistant varieties has emerged as the cornerstone of CMD management, with resistance breeding receiving sustained investment for over eight decades.

While several cassava varieties have demonstrated field resistance to CMD, it is not known whether this reflects true genetic immunity or merely disease escape under conditions of lower natural inoculum pressure. Field screening alone cannot reliably distinguish between varieties that are genuinely resistant and those that simply escaped infection due to insufficient vector pressure or unfavorable environmental conditions for disease development. The study was conducted to characterize the resistance phenotypes of ten cassava varieties to CMD under controlled graft inoculation in the Sudan Savannah agro-ecological zone, specifically to determine whether varieties exhibiting field resistance demonstrate true genetic immunity or merely disease escape. This was achieved through: graft inoculation of all varieties under uniform high pathogen pressure, monitoring of disease incidence and severity over a 12-week period, and classification of varieties into distinct resistance phenotype categories.

MATERIALS AND METHODS

The greenhouse experiment was conducted at Abdullahi Fodio University of Science and Technology, Aliero (AFUSTA), Kebbi State, Nigeria, located within the Sudan Savannah agro-ecological zone (latitude 12°18'16.9"N, longitude 4°29'56.9"E). The agro-ecological conditions of Kebbi State are characterized by a single growing season with annual rainfall of 600-800 mm, predominantly occurring from June to September (Kebbi State Agricultural Development Project, 2022). The greenhouse provided controlled environmental conditions with temperatures ranging from 28-32°C and natural

photoperiod, protected from insect vectors and external environmental variability. The experiment was conducted from June to September 2024, coinciding with the rainy season when field conditions would normally favor disease development

Plant Materials

Ten cassava varieties were evaluated in this study, comprising eight improved genotypes obtained from the International Institute of Tropical Agriculture (IITA), Ibadan, and two farmer-preferred local landraces collected from Aliero, Kebbi State. The improved varieties included: IBA 30572, OBASANJO 2, GAME CHANGER, IBA 164773, IBA 154810, IBA 961632, BABA 70, and IBA 0505. The local landraces were DANGWAMNATI and BAHASHE. All planting materials were obtained as virus-free stem cuttings from certified sources

Preparation of Rootstocks

Stem cuttings of approximately 10 cm length with 5-6 viable buds were prepared from each of the ten varieties. To eliminate any possible latent virus infections, cuttings were submerged in hot water at 45-50°C for 30 minutes before planting, following the protocol described by Zinga *et al.* (2014). Treated cuttings were planted in polyethylene pots (25 cm diameter) filled with sterilized sandy loam soil (3 parts soil: 1-part well-decomposed organic matter). Pots were maintained under screenhouse conditions with regular watering to ensure optimal growth. Sixty cuttings of each variety were planted to allow for six replicates and to account for potential grafting failures.

Source of Inoculum and Graft Inoculation

CMD inoculum was sourced from field-grown susceptible plants of the local variety SARKIN FAWA exhibiting severe symptoms (severity score 5 on the 1-5 scale). These source plants were confirmed positive for cassava mosaic virus infection by PCR using primers JSP1/JSP2 and JSP1/JSP3 prior to use. Infected stems were collected and maintained in a separate screenhouse compartment to prevent contamination of healthy plants.

Graft inoculation was performed at 4 weeks after planting (WAP), when rootstocks had established vigorous growth and developed 6-8 fully expanded leaves, following the technique described by Mohammed (2012). Scions (5-7 cm long) were prepared from infected source plants, trimmed to retain the first unopened and second opened leaves, with buds intact. A wedge-shaped cut was made at the base of each scion using a sterile razor blade. A complementary "V"-shaped incision was made on the rootstock stem at approximately 10-15 cm above soil level. The scion wedge was inserted into the rootstock incision, ensuring cambial contact, and the graft union was wrapped with parafilm to maintain stability and prevent desiccation.

Grafted plants were covered with perforated transparent plastic bags for two weeks to maintain high humidity and promote graft union formation. Bags were gradually opened after 10 days and completely removed at 14 days after grafting. Plants were maintained under screenhouse conditions with regular watering and monitoring for graft take. Graft success rate was recorded for each variety, and successfully grafted plants (those showing scion survival and new growth) were retained for disease assessment; failed grafts were excluded from the experiment. Mock-inoculated control plants (subjected to the same grafting procedure but using healthy scions) were included for each variety to control for grafting stress effects.

Experimental Design

The experiment was laid out in a completely randomized design (CRD) with six replicates per variety. CRD was chosen because the screenhouse environment provided uniform conditions with no identifiable blocking factors, and this design maximizes the precision of treatment comparisons under homogeneous conditions. Each replicate consisted of one plant per variety, with plants arranged randomly on screenhouse benches. The six replicates for each of the ten varieties gave a total of 60 plants in the experiment, with an additional 10 mock-inoculated control plants (one per variety). Plants were spaced at 0.5 m between pots to allow adequate air circulation and light penetration. Six replicates were deemed adequate based on precedent studies using similar replicate numbers for graft-inoculation screening (Mohammed, 2012; Mukiibi *et al.*, 2019).

Disease Assessment

Disease assessments were conducted at 2, 4, 6, 8, 10, and 12 weeks after inoculation (WAI). At each assessment, all plants were visually examined for the presence of characteristic CMD symptoms, including leaf mosaic patterns, chlorosis, leaf distortion, vein clearing, and stunting.

Disease Incidence: Disease incidence was calculated as the percentage of plants showing visible CMD symptoms for each variety at each assessment period using the formula (Chaube & Pundhir, 2005).

$$\text{Disease incidence (\%)} = \frac{\text{Number of diseased plants}}{\text{Total number of plants examined}} \times 100$$

Disease Severity: Disease severity was assessed on a 1-5 scale following the standard protocol established by the International Institute of Tropical Agriculture (IITA, 1990):

Disease severity index =

$$\frac{[\text{Sum (class frequency} \times \text{score of rating class)}]}{(\text{Number of plants assessed} \times \text{Maximum scale})} \times 100$$

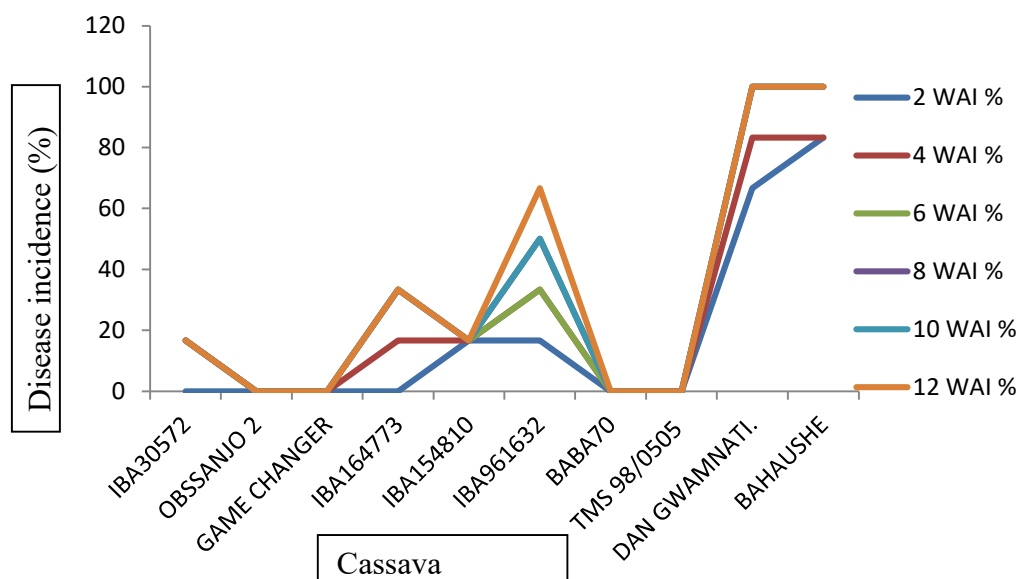


Figure 1: Disease Incidence of Viruses Infecting Cassava in Screenhouse at Abdullahi Fodio University of Science and Technology, Aliero in 2023/2024.

1 = No symptoms (healthy plant)

2 = Mild chlorotic spots on most leaves, with the remaining parts of leaves and leaflets appearing green and healthy

3 = Pronounced mosaic pattern on most leaves, with distortion of the lower one-third of most leaves

4 = Severe mosaic pattern on most leaves, with significant distortion and reduction in leaf size

5 = Very severe mosaic symptoms on all leaves, often accompanied by severe leaf distortion, shoe-string appearance, and overall plant stunting

Statistical Analysis

Data were analyzed using both descriptive and inferential statistics. Descriptive statistics (means and standard errors) were calculated for disease incidence and severity at each assessment time point for each variety. For inferential analysis, disease severity data were subjected to analysis of variance (ANOVA) with repeated measures across WAI, followed by Duncan's Multiple Range Test (DMRT) for mean separation among varieties (Duncan, 1955). Disease incidence data (proportions) were analyzed using chi-square test for independence of infection rates among varieties. All analyses were performed using SAS version 9.4 (SAS Institute, Cary, NC, USA). Statistical significance was declared at $P < 0.05$. Varieties were categorized into resistance phenotype groups based on their final (12 WAI) incidence and severity values using hierarchical clustering (Lokko *et al.*, 2005).

RESULTS

Graft Success Rate

Graft success rates varied among varieties, ranging from 75% to 100%. The mean graft success rate across all varieties was 91.7%. Varieties with higher vegetative vigor (IBA 30572, GAME CHANGER) showed slightly higher graft success rates (100%), while the local landraces DAN GWAMNATI and BAHAUSHE showed slightly lower rates (83.3%). No systematic relationship was observed between graft success rate and subsequent disease resistance phenotype.

Disease Incidence Under Graft Inoculation

The screenhouse evaluation under controlled graft inoculation revealed distinct patterns of disease incidence progression among the ten cassava varieties over the 12-week assessment period (Figure 1). The uniform and aggressive virus challenge provided by graft inoculation revealed the true genetic potential of each variety to resist or succumb to infection.

Highly Resistant Varieties: The most striking outcome was the identification of four varieties exhibiting exemplary resistance. OBASANJO 2, GAME CHANGER, BABA 70, and IBA 0505 maintained a pristine disease incidence of 0.00% throughout the entire 12-week observation period. This complete absence of symptoms under the most aggressive virus challenge—direct vascular introduction of the pathogen—strongly indicates the presence of highly effective resistance genes. These varieties possess mechanisms that either prevent viral entry into plant cells, inhibit viral replication once inside, or impede the systemic movement of the virus through vascular tissues, thereby containing any potential initial infection. This phenotype is

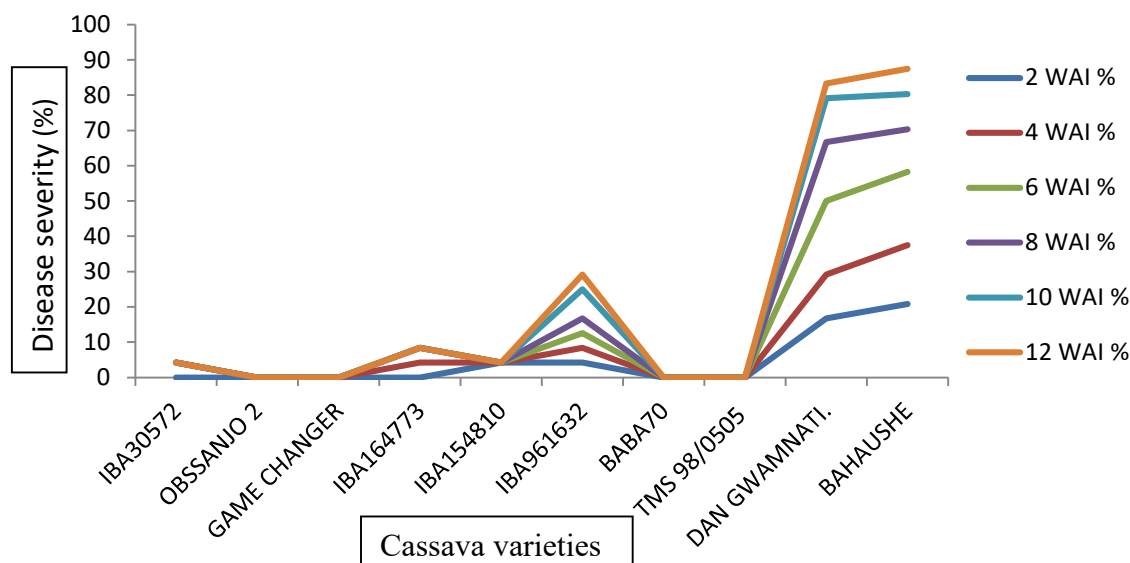


Figure 2: Disease Severity of Viruses Infecting Cassava in Screenhouse at Abdullahi Fodio University of Science and Technology, Aliero in 2023/2024.

characteristic of major gene resistance, specifically the CMD2 gene, which confers immunity through mechanisms that block virus establishment and spread.

Tolerant Varieties: A second group of varieties demonstrated what is known as tolerance or quantitative resistance. IBA 30572 and IBA 154810 both reached a disease incidence of 16.67% and, importantly, plateaued at this level for the remainder of the trial (from 4 WAI through 12 WAI). This pattern indicates that while the virus successfully established infection in a limited number of stems (one out of six replicates), the plants' innate defense mechanisms were effective in containing the pathogen and preventing its spread to the rest of the plant or to additional plants. The plateauing effect, with no new infections after 4 WAI, suggests that once the initial infection was contained, the resistance mechanisms prevented further systemic movement and secondary spread.

Partially Resistant Variety: IBA 164773 displayed a higher but still contained level of infection, with disease incidence reaching 33.33% (two out of six replicates) by 4 WAI and stabilizing at this level through 12 WAI. This indicates that the virus established infection in two out of six replicates, but the plants' defense mechanisms effectively contained the pathogen and prevented additional infections. ANOVA confirmed that this incidence rate was significantly lower than that of susceptible varieties but higher than that of tolerant varieties ($P < 0.05$).

Susceptible Varieties: IBA 961632 showed a steady and concerning climb in infection rates, progressing from 16.67% at 2 WAI to 66.67% by 12 WAI. The progressive

increase throughout the season indicates a clear inability to halt the systemic movement of the virus within its tissues, with new infections continuing to appear even at 10-12 WAI. Highly Susceptible Varieties: The local landraces DAN GWAMNATI and BAHAUSHE proved to be exceptionally susceptible. BAHAUSHE displayed a very high infection rate (83.33%) at the first observation point (2 WAI), and both varieties reached 100% incidence by just 6 WAI, maintaining complete infection through 12 WAI. This rapid and complete systemic infection is consistent with an absence of functional resistance genes, rendering these varieties extremely vulnerable to infection under any conditions where virus inoculum is present. Statistical analysis confirmed that the final incidence of these varieties was significantly higher than all other varieties ($P < 0.05$).

Disease Severity Under Graft Inoculation

Disease severity data provided a more nuanced understanding of host-virus interactions than incidence data alone (Figure 2). Severity, which measures the intensity of symptom expression on infected plants, reveals not only which varieties become infected but also how effectively they can tolerate and limit the damage caused by the virus. ANOVA with repeated measures revealed significant effects of variety ($F = 45.82$, $df = 9$, $P < 0.001$), time ($F = 28.47$, $df = 5$, $P < 0.001$), and variety $\times$ time interaction ($F = 15.63$, $df = 45$, $P < 0.001$), indicating that varieties differed in both their overall severity levels and their patterns of severity progression over time.

Highly Resistant Varieties: The results confirmed the exceptional performance of the four highly resistant

Table 1: Disease incidence and severity recorded at 12 WAI in Screenhouse at Abdullahi Fodio University of Science and Technology, Aliero in 2023/2024.

Variety	Incidence (%)	Severity (%)	Resistance Category
OBASANJO 2	0.00 ± 0.00	0.00 ± 0.00	Highly Resistant
GAME CHANGER	0.00 ± 0.00	0.00 ± 0.00	Highly Resistant
BABA 70	0.00 ± 0.00	0.00 ± 0.00	Highly Resistant
IBA 0505	0.00 ± 0.00	0.00 ± 0.00	Highly Resistant
IBA 30572	16.67 ± 0.17	4.17 ± 0.04	Tolerant
IBA 154810	16.67 ± 0.17	4.17 ± 0.04	Tolerant
IBA 164773	33.34 ± 0.22	8.33 ± 0.06	Partially Resistant
IBA 961632	66.67 ± 0.19	29.17 ± 0.11	Susceptible
DANGWAMNATI	100.00 ± 0.00	83.33 ± 0.09	Highly Susceptible
BAHAUSHE	100.00 ± 0.00	87.50 ± 0.08	Highly Susceptible

Means within columns followed by different letters are significantly different at $P < 0.05$ (DMRT).

varieties identified through incidence data. OBASANJO 2, GAME CHANGER, BABA 70, and IBA 0505 maintained a disease severity of 0.00% throughout the 12-week period. This complete absence of visible symptoms reinforces the conclusion that these varieties possess robust resistance mechanisms, potentially involving a hypersensitive response where infected cells die rapidly to contain the virus, or extreme resistance that prevents viral replication entirely.

Tolerant Varieties: A second group of varieties, including IBA 30572 and IBA 154810, demonstrated a high degree of tolerance. While the incidence data showed these varieties became infected (16.67%), the severity data revealed the infection was remarkably contained. Both varieties plateaued at a very low severity of 4.17% from 4 WAI through 12 WAI. This suggests that although the virus is present and systemic in infected plants, the plants' physiology is largely unaffected. The mechanisms behind this tolerance could include an ability to maintain photosynthetic and metabolic function despite infection, or the production of compounds that mitigate viral damage without eliminating the virus entirely.

Partially Resistant Variety: IBA 164773 also displayed this characteristic of plateauing, though at a moderately higher level of 8.33% severity from 4 WAI onward. This indicates a slightly lower but still significant level of tolerance, with infected plants showing mild symptoms but containing damage to acceptable levels.

Susceptible Varieties: IBA 961632 showed a steady and progressive increase in symptom severity, climbing from 4.17% at 2 WAI to 29.17% by 12 WAI. This progressive worsening indicates that the virus is not only moving systemically but is also increasingly disrupting plant functions, leading to stunting, chlorosis, and leaf distortion that would directly impact root yield potential. DMRT indicated that the final severity of IBA 961632 was significantly higher than that of tolerant and partially resistant varieties ($P < 0.05$).

Highly Susceptible Varieties: The local landraces DANGWAMNATI and BAHAUSHE exhibited a trajectory of severe and devastating infection. Both started with high severity scores at 2 WAI (16.67% and 20.83%, respectively) and escalated to 83.33% and 87.50% by 12 WAI. A severity score exceeding 80% suggests near-total loss of photosynthetic capacity and plant function. Plants with this level of infection would be severely stunted, exhibit widespread mosaic and chlorosis covering most leaf surfaces, and would likely produce negligible root yield. DMRT confirmed that the final severities of these two varieties were significantly higher than all other varieties ($P < 0.05$) but not significantly different from each other.

Disease Incidence and Severity Recorded at 12 WAI in Screenhouse at Abdullahi Fodio University of Science and Technology, Aliero in 2023/2024

The evaluation of ten cassava varieties at 12 weeks after inoculation revealed a clear spectrum of resistance phenotypes, ranging from complete immunity to extreme susceptibility (Table 1). These categories provide critical insights into the genetic potential of each variety for managing cassava mosaic disease under controlled conditions.

Category 1: Highly Resistant (Complete Immunity). Four varieties—OBASANJO 2, GAME CHANGER, BABA 70, and IBA 0505—exhibited a combination of 0% incidence and 0% severity, indicating a complete absence of both infection and symptoms. This phenotype is strongly suggestive of true, high-level immunity governed by major gene resistance.

Category 2: Tolerant (Infection with Minimal Symptoms). Two varieties—IBA 30572 and IBA 154810—showed infection in a limited number of plants (one out of six), but the remarkably low severity score reveals a powerful capacity for tolerance. The contrast between infection rate and minimal symptom expression makes these varieties valuable for sustainable agriculture,

as they can host the virus without suffering significant physiological damage or economic loss.

Category 3: Partially Resistant. IBA 164773 presented an intermediate profile, with higher infection rate and correspondingly higher but still moderate severity. The virus is more widespread within the plant population and causes more noticeable symptoms, though the damage remains relatively contained.

Category 4: Susceptible. IBA 961632 showed extensive infection and significant symptomatic damage that would compromise photosynthesis and root development. The progressive increase in both parameters throughout the season indicates inability to contain viral spread.

Category 5: Highly Susceptible. The local landraces DANGWAMNATI and BAHAUSHE showed the most severe response, with complete infection rates coupled with devastating severity. This indicates complete systemic infection where the virus has overwhelmed the plants' defenses, leading to extreme stunting, severe leaf mosaic, and chlorosis. Plants with this level of infection would suffer near-total yield loss.

DISCUSSION

The greenhouse evaluation using controlled graft inoculation characterized resistance phenotypes of ten cassava varieties to cassava mosaic disease (CMD), revealing genetic potential not fully expressed in the field. Responses ranged from complete immunity to extreme susceptibility, with implications for breeding, deployment, and host–virus interactions in the Sudan Savannah.

Complete Immunity: The CMD2 Phenotype

Four varieties (OBASANJO 2, GAME CHANGER, BABA 70, and IBA 0505) maintained zero incidence and severity over 12 weeks, indicating true genetic immunity. This absence of infection under aggressive graft inoculation is consistent with CMD2-type resistance (Fondong, 2017; Sheat & Winter, 2023). CMD2 hinders viral replication and systemic movement, actively preventing establishment via effector recognition and defense activation, unlike tolerance (Fondong, 2017). Stability under high pressure confirms functional resistance genes. OBASANJO 2 is a known CMD2 carrier and key resistance source in West Africa (Olasanmi *et al.*, 2021). Other immune varieties align with this phenotype, though molecular confirmation would validate CMD2 status. Their performance supports deployment in the Sudan Savannah and suggests CMD2 resistance is not environmentally labile. CMD2 may confer broad-spectrum protection against begomoviruses (Sheat & Winter, 2023), adding strategic value. These four varieties should be prioritized for multiplication and distribution.

Tolerance: A Valuable Resistance Phenotype

IBA 30572 and IBA 154810 showed low incidence and severity, a classic tolerance phenotype: virus replication occurs but damage is minimized, preserving yield (Ntui *et al.*, 2024). This differs from immunity (no infection) and partial resistance (reduced symptoms). Mechanisms may include maintained photosynthesis, damage-mitigating compounds, altered resource allocation, or virus compartmentalization (Fondong, 2017; Sheat & Winter, 2023). Mild symptoms indicate effective damage limitation. Tolerance offers advantages: acceptable yields without complete virus exclusion, potentially more evolutionarily stable than immunity due to less selection pressure for resistance-breaking strains (Ntui *et al.*, 2024). However, tolerant plants may be inconspicuous virus reservoirs, serving as sources for vectors (Mware *et al.*, 2023). Deployment requires monitoring and integrated management. Understanding virus reservoirs in cassava systems is crucial (Munguti *et al.*, 2023).

Partial Resistance: Quantitative Defense Mechanisms

IBA 164773 showed partial resistance: moderate incidence, low severity. This suggests quantitative resistance, possibly the CMD1 gene from *Manihot glaziovii*, involving multiple minor genes (Fondong, 2017). It slows replication, limits movement, and reduces symptoms rather than preventing infection. The plateau in incidence and severity after 4 weeks indicates defense contained infection. Partial resistance is often more durable than major gene resistance due to less directional selection (Ntui *et al.*, 2024), though less complete.

Susceptibility and Extreme Susceptibility

IBA 961632 showed progressive disease, indicating ineffective containment. DANGWAMNATI and BAHAUSHE were extremely susceptible, with rapid complete infection and severe symptoms, indicating absent functional resistance genes—typical of unimproved landraces (Combala *et al.*, 2024). Such plants yield negligibly and act as potent virus reservoirs, amplifying inoculum and threatening neighboring fields (Combala *et al.*, 2024).

Comparison with Field Performance and Implications for Breeding

Field trials previously showed six varieties with complete resistance, but greenhouse evaluation revealed only four with true immunity. IBA 164773 and IBA 154810, despite zero field incidence, became infected under controlled inoculation. This underscores the importance of controlled inoculation to distinguish genetic resistance from field escape. IBA 154810 exemplifies field escape: no natural infection but susceptible when grafted. Field-only evaluation would misclassify it as resistant. This aligns

with research showing graft inoculation is robust for early elimination of susceptible genotypes (Houngue *et al.*, 2019). Houngue *et al.* (2019) found only 12 of 24 cultivars showed morphological resistance, and only 8 carried CMD2 markers, highlighting phenotype–genotype mismatch and the need for molecular confirmation. Controlled inoculation is indispensable; breeding programs should incorporate graft inoculation before variety release.

Implications for the Sudan Savannah and Regional CMD Management

The four immune varieties can be deployed confidently in high CMD pressure areas, including where EACMV-UG occurs (Combala *et al.*, 2024). They provide the highest protection and should anchor resistance-based management. Tolerant and partially resistant varieties suit moderate pressure areas, but their reservoir potential requires awareness. Extreme susceptibility of local landraces urges replacement, with extension programs demonstrating resistant vs. susceptible varieties under local conditions (Combala *et al.*, 2024).

Conclusion

This screenhouse study was conducted to characterize the resistance phenotypes of ten cassava varieties to cassava mosaic disease under controlled graft inoculation in Nigeria's Sudan Savannah, specifically to determine whether varieties exhibiting field resistance demonstrate true genetic immunity or merely disease escape. The study successfully achieved this objective. Four varieties (OBASANJO 2, GAME CHANGER, BABA 70, and IBA 0505) demonstrated complete immunity, maintaining zero incidence and severity throughout the trial, at par with CMD2-mediated resistance. Tolerant varieties (IBA 30572, IBA 154810) showed limited infection with remarkably low severity, while IBA 164773 exhibited partial resistance. In contrast, IBA 961632 showed progressive susceptibility, and local landraces DANGWAMNATI and BAHASHHE demonstrated catastrophic susceptibility with complete infection and devastating severity. The discrepancy between field performance and screenhouse results highlights the critical importance of controlled inoculation for distinguishing true genetic resistance from field escape.

Acknowledgments

We sincerely thank the West African Virus Epidemiology (WAVE) program for funding this research, and the International Institute of Tropical Agriculture (IITA), Ibadan, for providing the improved cassava varieties.

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