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Grafting-Induced Phenotypic and Genomic Variations in Cassava (*Manihot esculenta* Crantz) through Interspecific Compatibility with *M. glaziovii*

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Abstract

Grafting is a promising approach to enhance cassava (*Manihot esculenta* Crantz) productivity, particularly in improving tuber yield and quality. Despite its technical simplicity, research on the morphological and molecular consequences of grafting in cassava is limited. This study aimed to quantitatively assess phenotypic differences between grafted and shoot-cutting plants and characterize genetic modifications in shoot apical meristems near the graft union. Three splice-grafting combinations were evaluated: *M. glaziovii* (cv. "Karet")/"Revita RV1" (KR), "Karet"/ "Carvita 25" (KC), and "Carvita 25"/ "Revita RV1" (CR), alongside shoot-cutting plants of each cultivar. Grafted seedlings and conventional cuttings were transplanted to the field, and growth was monitored up to five months after grafting (5 MAG). Shoot bud samples were collected for RAPD analysis at three months (3 MAG). Grafted plants showed differences in morphology compared to controls, especially in branching architecture, branch angle, stem diameter, and internode length. However, the overall plant form and primary stem type remained stable. The color of emerging shoots consistently reflected their genotypic origin, like scion or rootstock, as did the shoot buds nearest the graft union. RAPD analysis using multiple primers revealed polymorphic banding patterns, with OPE-12 producing the most diverse profiles. While specific bands were associated with each cultivar, grafted regenerants often exhibited altered or novel band profiles, suggesting somaclonal variation or graft-induced genetic/epigenetic changes. Some regenerants displayed unexpected band types, such as C1 in R-KR1 and R-KR3, which were absent from their known parental genotypes. Cluster analysis grouped 45 samples into five major clusters and eight subgroups, indicating genetic divergence among certain grafted combinations, particularly "Carvita 25"–"Revita RV1" and *M. glaziovii*–"Revita RV1". These results demonstrate that grafting can significantly impact cassava phenotype and genome stability. This study shows that interspecific grafting between cassava (*Manihot esculenta* Crantz) and *M. glaziovii* can induce significant phenotypic and genomic variations.

Keywords: graft union, RAPD, regenerant clone

Introduction

Cassava (*Manihot esculenta* Crantz) is a perennial crop capable of year-round cultivation, demonstrating remarkable adaptability to nutrient-deficient soils and drought conditions (Fathima et al., 2023). Its leaves and tubers are nutritionally valuable, with fresh tubers containing 25.3–35.7 g.100 g^{-1} carbohydrates (Mohidin et al., 2023), making them a significant energy source. Beyond direct consumption, cassava tubers are industrially processed into tapioca starch, mocaf (modified cassava flour) (Elida and Hamidi, 2009; Khasanah et al., 2022), animal feed, and derivative products.

While cassava is predominantly propagated via stem cuttings, grafting has emerged as a viable technique to combine desirable traits from scion and rootstock genotypes, generating novel phenotypes with enhanced characteristics (Wang et al., 2016). This method leverages the compatibility of vascular tissues to create chimeric plants with improved yield, stress tolerance, or disease resistance.

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Grafting has been successfully employed as a powerful horticultural technique for plant improvement, demonstrating significant benefits across multiple crop species. Notable applications include (1) the development of disease-resistant tomato varieties, (2) enhancement of watermelon fruit quality and yield, (3) creation of abiotic stress-tolerant grape cultivars, and (4) improvement of cassava productivity through increased flowering frequency and tuber development (weight and length parameters) (Rivard and Louws, 2008; Turhan et al., 2012; Serra et al., 2014; Souza et al., 2018; Bangthong et al., 2021; Hartati and Hartati, 2016; Gakpetor et al., 2017). This technique also shows potential for generating novel plant types through scion-rootstock combinations (Goldschmidt, 2014). The success of grafting depends fundamentally on effective vascular reconnection between scion and rootstock tissues (Junior et al., 2022). This biological fusion establishes nutrient translocation, hormonal signaling networks, and metabolic exchange - all critical for expressing the desired phenotypic traits in the grafted plant.

The grafting-mediated transfer process facilitates the movement of macromolecules and bioactive compounds that regulate physiological interactions and induce diverse phenotypic responses in the composite plant (Loupit and Cookson, 2020). The variation in responses observed in the scion-rootstock combination is thought to result from the movement of nucleus or chromatin cells, which is considered one of the mechanisms of grafting hybridization (Wang et al., 2016). Molecular characterization techniques, including DNA fingerprinting and next-generation sequencing approaches, can effectively trace the transmission of genetic material and differentiate plant genotypes within grafted populations. While grafting procedures are technically simple, the underlying molecular mechanisms governing scion-rootstock compatibility and long-term stability remain complex and poorly understood.

This study investigates whether grafting-induced genetic modifications occur in cassava (*Manihot esculenta* Crantz). Such modifications could be an alternative approach to produce improved cassava seedlings. Moreover, this study employed RAPD markers to evaluate the genetic identity of shoots developed from either scion or rootstock tissues proximal to the graft union, focusing on identifying potential genetic alterations. Initial screening establishes the frequency and reproducibility of detected genetic changes, providing crucial data for evaluating grafting as a possible breeding tool in cassava.

This study combines random amplified polymorphic DNA (RAPD) markers with comprehensive morphological characterization to investigate graft-induced variations in cassava. The RAPD markers utilize short, arbitrary primers to amplify random DNA segments through polymerase chain reaction (PCR), generating polymorphic banding patterns that serve as genetic fingerprints (Sulistyawati and Widiatmoko, 2017). This molecular analysis provides an early indication of potential genomic alterations at the graft union interface. Concurrently, we systematically evaluate morpho-agronomic traits, including growth architecture parameters and leaf morphology. This research aims to quantitatively compare phenotypic performance between grafted and stem-cutting (control) plants and molecularly characterize genetic modifications in shoot apical meristems derived from either scion or rootstock tissues developed proximal to the graft union.

Materials and Methods

Grafting Protocol for Cassava: Scion-Rootstock Preparation and Seedling Establishment

This study examines graft compatibility and genetic stability in cassava (*Manihot esculenta* Crantz) using interspecific (*Manihot glaziovii* cv. “Karet”) and intraspecific (“Carvita 25” and “Revita RV1” cultivars) grafting combinations. Three distinct scion-rootstock configurations were evaluated: (1) “Karet” (scion) grafted to “Revita RV1” (rootstock), denoted as KR (S0-KR and R0-KR), (2) “Karet” (scion) grafted to “Carvita 25” (rootstock), denoted as KC (S0-KC and R0-KC), and (3) “Carvita 25” (scion) grafted to “Revita RV1” (rootstock), denoted as CR (S0-CR and R0-CR). The labels S0 and R0 were used to indicate the tissue origin of the observation, with S0 referring to the scion-derived portion and R0 referring to the rootstock-derived portion. Shoot-cutting controls were maintained for each genotype. The experimental design incorporated 15 biological replicates per combination to ensure robust statistical power. The splice grafting technique was meticulously executed using 25 cm scions and rootstocks of identical diameter to maximize cambial alignment, following established protocols (Melnyk and Meyerowitz, 2015). All graft unions were secured with plastic wrap and maintained in polybags (30 × 40 cm) under controlled nursery conditions for 30 days post-grafting before successful grafts were transplanted to field conditions alongside control plants (Figure 1). The experiment was conducted at the greenhouse of BRIN, Cibinong, Bogor, West Java. After the nursery period, the plants were transplanted into the field. The field is located at an elevation of 120–140 meters above sea level (m a.s.l.). The site had an average annual rainfall

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of 2,150–2,650 mm and temperatures ranging from 22°C to 31°C.

The phenotypic evaluation focused on 12 randomly selected grafted plants per combination, with systematic monitoring of the grafting outcomes. For molecular analysis, we specifically sampled five apical shoot buds from scion-derived (S0-) and rootstock-derived (R0-) tissues within 2 cm of the graft union. This targeted sampling strategy enables precise characterization for a deeper understanding of the genetic interactions between the scion and rootstock, potentially providing insights into graft compatibility and growth performance in cassava.

Growth Performance Evaluation of Grafted Cassava Plants

Twelve grafted specimens and their corresponding original genotypes were maintained under field conditions for phenotypic characterization 5 months after grafting (5 MAG). Comprehensive morphometric analysis was conducted through both qualitative and quantitative assessments, encompassing three primary trait categories: Plant Architecture (plant height, stem morphology, branching characteristics, nodal development, Foliar Characteristics (Phyllotaxis and leaf count, shoot pigmentation, venation architecture, petiole morphology, lamina dimensions, and lobe configuration) and Shoot System Development: (primary shoot length and number). All measurements were recorded following cassava phenotyping guidelines as described by Fukuda et al. (2010) and the DUS (Distinctness, Uniformity, and Stability) testing manual issued by the Indonesian Ministry of Agriculture, standardized protocols for cassava phenotyping to ensure data reliability.

Molecular Genetic Analysis Using RAPD Markers

Molecular analysis using RAPD markers was conducted to assess potential genetic variation between grafted and non-grafted cassava plants. The study aimed to explore general DNA variation rather than identify specific gene-level changes. RAPD was selected as a cost-effective and practical method to detect possible graft-induced polymorphisms. RAPD was suitable for this preliminary study due to its simplicity and the lack of need for prior genomic data. Similar graft-induced variation was reported in mungbean (Zhang et al., 2002).

Genomic DNA was isolated from leaf tissues of both controls (un-grafted) and grafted cassava plants, including control (cv. “Karet”, cv. “Revita RV1”, and cv. “Carvita 25”) and graft-derived samples: scion-originated shoots (S0-KR, S0-CR, S0-KC) and rootstock-originated shoots (R0-KR, R0-CR, R0-

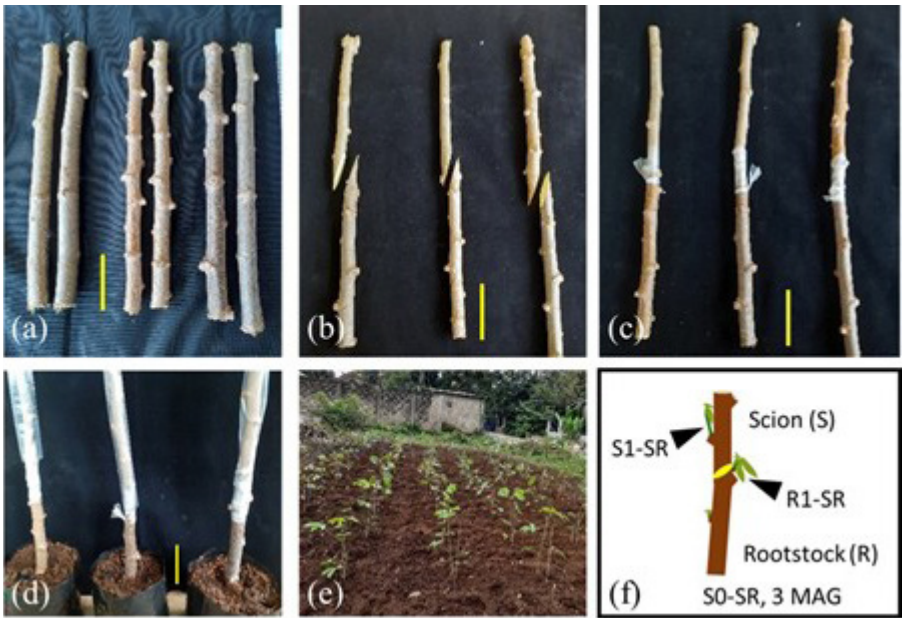

Figure 1. Schematic representation of cassava grafting methodology and experimental design. (a) Selection and preparation of healthy scion (25 cm) and rootstock materials; (b) Precision diagonal cutting of scion and rootstock stem to maximize cambial contact area; (c) Graft union formation using splice grafting technique; (d) Wrapping with plastic and establishment in nursery polybags; (e) Acclimatized grafted seedlings transplanted to experimental field plots; (f) Sampling strategy for molecular analysis, showing designated collection zones for scion (S) and rootstock (R) tissues at 3 months after grafting (3 MAG).

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KC). The extraction protocol was adapted from the CTAB method with optimized steps. 100 mg of young leaf tissue was flash-frozen in liquid nitrogen and mechanically pulverized. Ground tissue was mixed with 100 µL of pre-warmed CTAB buffer containing 0.2% β-mercaptoethanol, followed by the addition of 500 µL CTAB buffer. Incubation solution at 65°C for 30 min with periodic vortexing, cooled for 5 minutes, then mixed with 600 µL of chloroform: octanol (24:1 ratio), homogenized, and centrifuged at 6000 rpm at 4°C for 10 minutes, repeated three times. A 500 µL supernatant was mixed with 1 mL ice-cold isopropanol and incubated at -30°C for 1 hour. The supernatant was discarded after centrifugation at 12,000 rpm at 4°C for 15 minutes. The pellet was washed with 70% ethanol, centrifuged again, air-dried, and dissolved in 40 µL of DNase/RNase-free water. DNA quality and concentration were verified using spectrophotometric (Nanodrop™) and electrophoretic (0.8% agarose gel) methods before RAPD analysis.

RAPD Analysis of Genetic Variation

PCR amplification was performed in a 25 µL reaction containing 12.5 µL of 2 × myTaq Red Mix from *Bioline*, 10.5 µL of RNase-free water, 1 µL of primer, and 1 µL of DNA template. The primers used were OPE-14 (5'-TGCGGCTGAG-3'), OPQ-20 (5'-TCGCCCAGTC-3'), OPC-06 (5'-GAACGGACTC-3'), OPE-15 (5'-ACGCACAACC-3'), OPF-13 (5'-GGCTGCAGAA-3'), and OPE-12 (5'-TTATCGCCCC-3'). PCR conditions: initial denaturation (94°C for 3 minutes), 40 cycles of amplification (94°C for 20 seconds, 35°C for 40 seconds, and 72°C for 2 minutes), and a final extension (72°C for 7 minutes). PCR products were separated on 2% agarose gels at 70 volts for 1.5 hours and visualized under a UV transilluminator. DNA banding patterns from PCR results were analyzed for scion, rootstock, and control plants.

Data Analysis

Morphological data were analyzed using SPSS version 26. Non-parametric Kruskal-Wallis tests ($\alpha = 0.05$) were implemented in SPSS v26 (IBM Corp.) to accommodate non-normal data distribution and unbalanced design considerations (Zakiyah et al., 2017). Dunnett's post-hoc test was conducted with a 5% error rate to identify which treatments had a significant effect. The data collected from morphological observations are presented in tabular form. The DNA banding patterns were also analyzed using hierarchical cluster analysis with average linkage (between groups). The SPSS software produced a dendrogram (Widiyanti, 2007) to identify the genetic grouping of scion and rootstock shoots in grafted cassava plants.

Results and Discussion

Experimental Environment and Plant Growth

The study was conducted in the experimental field of the Research Area of the National Research and Innovation Agency (BRIN) in Cibinong District, Bogor Regency, West Java. Cibinong is 120–140 m a.s.l., with an average annual rainfall of 2,150–2,650 mm and temperatures ranging from 22°C to 31°C. For a recent study examining cassava performance at higher altitudes, Santanoo et al. (2024) investigated cassava growth at 195 m a.s.l. in a tropical savanna climate. Their findings indicated that cassava can maintain high productivity under such conditions, especially with appropriate irrigation and drought mitigation strategies. Additionally, according to Fathima et al. (2023), the optimal temperature for cassava (*Manihot esculenta*) growth ranges between 25–29°C; however, the plant can tolerate temperatures from 16°C to 38°C, as tuber crops generally tolerate high temperatures and drought. Such adaptation suggests that when proper management practices are applied, cassava is adaptable to various environmental conditions, including higher altitudes and varying temperatures.

The growth performance of the original genotypes and grafted cassava is presented in Table 1. At 5 weeks after planting, *M. glaziovii* exhibited the highest growth performance, followed by "Carvita 25" and "Revita RV1". "Carvita 25" recorded a branch length of 78.2 cm, 84.8 leaves, and 49.2 nodes, while "Revita RV1" produced a branch length of 64.3 cm, 67.8 leaves, and the highest node number at 78.6. In comparison, the graft combination CR exhibited markedly reduced growth performance. The CR graft only achieved 26.5 cm in branch length, 27.7 leaves, and 44.3 nodes. These values are substantially lower than those of both parental genotypes ("Carvita 25" and "Revita RV1"), suggesting that the CR combination may be physiologically incompatible or exhibit a weak graft union, resulting in impaired shoot development. Meanwhile, the KC graft produced moderate growth with 53.2 cm branch length, 57.5 leaves, and 46.7 nodes. The KR combination showed a slightly shorter branch length (46.0 cm) and fewer leaves (37.0). Still, it developed a relatively high number of nodes (59.5), potentially indicating a more active meristematic region despite reduced elongation.

In previous studies, shoots developing from the rootstock region are generally considered minimally influenced by the adaptation processes and vascular communication between scion and rootstock. Such a condition suggests that their development proceeds relatively undisturbed. Melnyk (2017) explains that in incompatible grafts, once vascular connections are

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established, the graft interface is unlikely to affect scion development directly, implying a degree of developmental independence. Similarly, Warschefsky et al. (2016) note that while rootstocks can influence scion phenotypes via resource allocation and hormonal signaling, shoots originating from the rootstock tend to follow their inherent developmental pathways. These findings support that rootstock-derived shoots remain largely unaffected by the scion-rootstock interaction. The observed shoots may have originated from the rootstock, growing autonomously from the scion while maintaining complete physiological reliance on the rootstock system (Karaca et al., 2020).

Morphology of Grafted Plants and Original Genotypes

Observations revealed morphological differences between grafted cassava plants and controls, particularly in branching levels, branch angle variation (ranging from sharp to blunt), stem diameter, and internode length. However, plant type and primary stem type remained uniform across treatments.

Mature stem color varied among green, brown, and yellow, while young stems exhibited a brown, green, and reddish color mix. Stem parenchyma was consistently green in both young and mature stems. These findings are consistent with recent studies showing that grafting can influence shoot morphology, including stem diameter, color, and branching architecture, due to the interaction between scion and rootstock genotypes (Kouassi et al., 2019).

The observed morphological variations may reflect the influence of graft-induced physiological changes, possibly resulting from altered hormonal signaling, nutrient transport, or vascular integration between scion and rootstock. For example, differences in branch angle and internode length could affect light interception and canopy structure, with potential implications for photosynthetic efficiency and yield (Rodrigues et al., 2016). The consistent green coloration of the stem parenchyma suggests that core physiological functions, such as photosynthate transport and storage, remain unaffected by grafting. Additionally, color differences in the outer stem tissues could indicate altered secondary metabolite profiles or stress responses, potentially contributing to plant adaptability in varying environments (Omokolo et al., 2018; Baiyeri et al., 2022). Thus, while the core plant architecture remains stable, grafting may introduce subtle yet significant phenotypic shifts that warrant further investigation.

As shown in Table 2 and Figure 2, shoot buds located closest to the graft union also matched their respective origin (scion or rootstock), indicating that identity-specific traits were maintained after grafting. As all genotypes shared identical scores for these traits, the information was presented narratively in the text. In this study, cassava exhibited a monochotomous main stem type and an unbranched plant type across all genotypes. *M. glaziovii* exhibited the most robust shoot morphology, with two branching levels, wide branch angles (>65°), a thick stem diameter (25.8 cm), and the longest internode (6.9 cm). Its mature stems appeared yellowish green, while the young stems and parenchyma were dark green. “Carvita 25” formed three branch levels with moderate branch angles (35–50°), a stem diameter of 19.4 cm, and an internode length of 3.9 cm. The mature stems were yellowish brown, the young stems were light green, and the parenchyma was also light green. In contrast, “Revita RV1” exhibited no branching, had a narrower stem (17.7 cm), and the shortest internode length among the original genotypes (3.5 cm), with greenish brown mature stems, reddish green young stems, and dark green parenchyma. Notably, Revita did not produce any branches, and this unbranched phenotype was also observed in its graft-derived rootstock portions, namely R0-CR and R0-KR, as both rootstocks were derived from Revita, which inherently lacks branching.

In grafted combinations, the CR graft exhibited reduced morphological development. The S0-CR produced two branch levels and moderate stem characteristics (12.5 cm diameter; 2.4 cm

Table 1. The growth of original genotypes and grafted cassava plants at 5 months after grafting

Genotypes	Branch length (cm)	No. of leaves	No. of nodes
“Carvita 25”	78.2	84.8	49.2
M. glaziovii	96.8	93.3	61.8
“Revita RV1”	64.3	67.8	78.6
CR	26.5	27.7	44.3
KC	53.2	57.5	46.7
KR	46.0	37.0	59.5

Notes: S0 = scion, R0 = rootstock, CR = "Carvita 25" scion–"Revita RV1" rootstock, KC = *M. glaziovii* (cv. "Karet") scion–"Carvita 25" rootstock, KR = *M. glaziovii* (cv. "Karet") scion–"Revita RV1" rootstock.

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internodes), while the R0-CR remained unbranched and developed slightly larger stem diameter (13.0 cm) and longer internodes (2.8 cm). The KC combination showed more favorable shoot morphology. The S0-KC developed 2–3 branching levels with wide branch angles (>65°), a stem diameter of 20.0 cm, and an internode length of 5.3 cm. The R0-KC retained typical “Carvita 25” coloration and recorded moderate stem development (16.1 cm diameter; 4.2 cm internodes). In the KR graft, the S0-KR produced 2–3 branch levels, wide branch angles, a stem diameter of 17.0 cm, and relatively long internodes (6.4 cm). In contrast, the R0-KR remained unbranched, with a narrower stem (12.4 cm) and the longest internode length among all rootstocks (6.8 cm). These data support the idea that the morphological characteristics of scions and rootstocks at early stages after grafting remain strongly influenced by their genotype of origin, and that grafting combinations may impact structural development through compatibility interactions.

The coloration of emerging scion shoots, including young leaves, veins, and petioles, consistently reflected the original scion genotype. Similarly, shoots from the rootstock retained the characteristics of their source. As presented in Table 3, leaf morphology at 5 weeks after grafting demonstrated distinct characteristics between genotypes, particularly in terms of shoot color, young leaf color, vein, and petiole coloration, as well as petiole length and lobe size. *M. glaziovii* exhibited a light green shoot and leaf color, with yellowish green veins and dark reddish green petioles. It produced the longest petiole (41.7 cm) and the largest leaf lobes (29.7 × 11.2 cm), indicating vigorous foliage development. “Revita RV1” showed a brown shoot with brownish green young leaves, red veins and petioles, and a petiole length of 39.7 cm. Its leaf lobes were smaller (21.1 × 6.2 cm). “Carvita 25” had purple shoots, purplish green young leaves, light red veins, and red petioles, with a shorter petiole (30.9 cm) and lobe size of 21.9 × 6.4 cm.

The CR graft displayed marked reductions in leaf morphology. The S0-CR showed purple pigmentation, similar to “Carvita 25”, with a shorter petiole (20.2 cm) and smaller lobe size (16.7 × 5.0 cm). The R0-CR retained “Revita RV1” like coloration with red and petiole length (37.8 cm) but also showed reduced

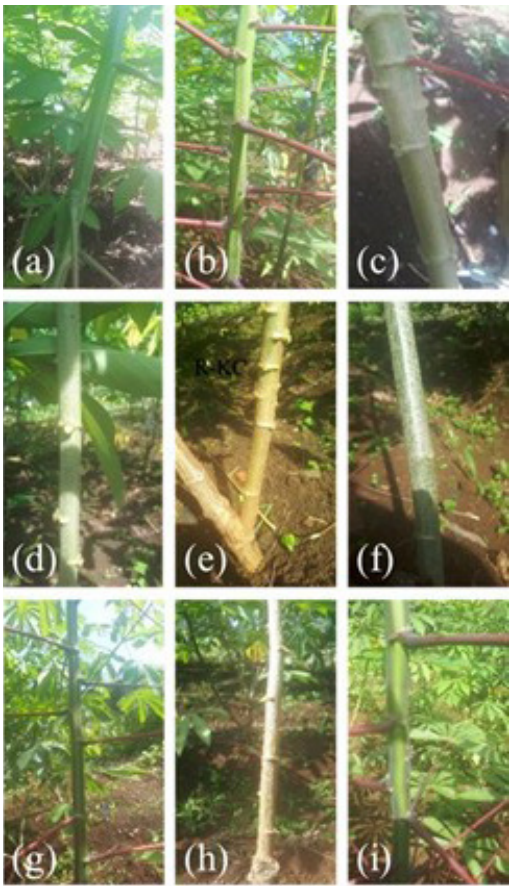

Figure 2. Stem morphology of the original genotype cassava and shoot growth of scion and rootstock in grafted plants. a) *M. glaziovii*, b) "Revita RV1", c) "Carvita 25", d) S0-KC, e) R0-KC, f) S0-KR, g) R0-KR, h) S0-CR, i) R0-CR. CR = "Carvita 25" scion–"Revita RV1" rootstock, KC = *M. glaziovii* (cv. "Karet") scion–"Carvita 25" rootstock, KR = *M. glaziovii* (cv. "Karet") scion–"Revita RV1" rootstock.

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Table 2. Morphology of the shoot of scion (S), rootstock (R), and control at 5 months after grafting

Genotypes	Number of branch levels	Branch angle (°)	Stem diameter (cm)	Internode length (cm)	Mature stem color	Young stem color	Parenchyma color
M. glaziovii	2	> 65	25.8	6.9	Yellowish green	Dark green	Dark green
“Revita RV1”	0	-	17.7	3.5	Greenish brown	Reddish green	Dark green
“Carvita 25”	3	35–50	19.4	3.9	Yellowish brown	Light green	Light green
S0-CR	2	35–50	12.5	2.4	Yellowish brown	Light green	Light green
R0-CR	0	-	13.0	2.8	Greenish brown	Reddish green	Dark green
S0-KC	2–3	> 65	20.0	5.3	Yellowish green	Dark green	Dark green
R0-KC	3	35–50	16.1	4.2	Yellowish brown	Light green	Light green
S0-KR	2–3	> 65	17.0	6.4	Yellowish green	Dark green	Dark green
R0-KR	0	-	12.4	6.8	Greenish brown	Reddish green	Dark green

Notes: S0 = scion, R0 = rootstock, CR = "Carvita 25" scion–"Revita RV1" rootstock, KC = *M. glaziovii* (cv. "Karet") scion–"Carvita 25" rootstock, KR = *M. glaziovii* (cv. "Karet") scion–"Revita RV1" rootstock.

Table 3. Leaf morphology of the control and grafted cassava

Genotype	Shoot color	Young leaf color	Vein color	Petiole color	Petiole length (cm)	Lobe size (length x width) (cm)
M. glaziovii	Light green	Light green	Yellowish green	Dark reddish green	41.7	29.7 x 11.2
“Revita RV1”	Brown	Brownish green	Red	Red	39.7	21.1 x 6.2
“Carvita 25”	Purple	Purplish green	Light red	Red	30.9	21.9 x 6.4
S0-CR	Purple	Purplish green	Light red	Red	20.2	16.7 x 5
R0-CR	Brown	Brownish green	Red	Red	37.8	16.7 x 5
S0-KC	Light green	Light green	Yellowish green	Dark reddish green	27.1	22.7 x 9
R0-KC	Purple	Purplish green	Reddish yellow	Reddish yellow	27.5	18.7 x 5.4
S0-KR	Light green	Light green	Yellowish green	Dark reddish green	18.9	18.5 x 7.6
R0-KR	Brown	Brownish green	Red	Red	36.3	17.2 x 5.2

Notes: S0 = scion, R0 = rootstock, CR = "Carvita 25" scion–"Revita RV1" rootstock, KC = *M. glaziovii* (cv. "Karet") scion–"Carvita 25" rootstock, KR = *M. glaziovii* (cv. "Karet") scion–"Revita RV1" rootstock.

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lobe size (16.7 × 5.0 cm). In the KC combination, the S0-KC resembled *M. glaziovii* in coloration, with light green leaves and yellowish green veins. It produced a petiole length of 27.1 cm and a lobe size of 22.7 × 9.0 cm. The R0-KC showed purple pigmentation consistent with "Carvita 25", with reddish-yellow veins and petioles, and a lobe size of 18.7 × 5.4 cm. The KR graft showed clear differentiation between scion and rootstock. The S0-KR maintained *M. glaziovii* traits with light green leaves, yellowish green veins, dark reddish green petioles, and shorter petiole length (18.9 cm). In comparison, the R0-KR expressed "Revita RV1" like coloration with red petioles and smaller lobes (17.2 × 5.2 cm).

Shoot buds closest to the graft union matched their respective origin (scion or rootstock). These findings contrast with Gakpetor et al. (2017), who reported that leaf coloration in grafted cassava followed the rootstock rather than the scion. Quantitatively, leaf petiole length and lobe size in grafted plants did not fully resemble the scion or rootstock parent. In general, grafted plants exhibited shorter petioles and smaller lobes than controls (Table 3, Figure 3), suggesting that scion-rootstock interactions influence these traits. Gakpetor et al. (2017) reported that petiole length in scion shoots typically follows the scion control plant, while Wang et al. (2017) emphasized that scion-rootstock interactions can alter morphological traits in grafted plants.

Genetic Analysis of Grafted Plants and Original Genotypes

DNA banding pattern variation

RAPD analysis revealed that all primers produced variable banding patterns, indicating their polymorphism (Table 4). Primer OPE-12 generated the highest number of DNA band profiles (A, A1, A2, B, B1, B2, C, C1, C2), followed by OPE-15 (A, B, B1, C, C1, C2), OPC-6 (A, B, B1, B2, C), OPF-13 (A, A1, B, C, C1), and OPE-14/OPQ-20 (A, B, C, C1). Band profile A was characteristic of the "Karet" (K) genotype, and band profile B identified cv. "Revita RV1" and C marked cv. "Carvita 25". For primer OPE-12, the cv. "Karet" (K) exhibited band A, also in some scion-derived regenerants (S-KC1 and a subset of S-KR). However, other S-KR regenerants displayed altered banding patterns: A1 (S-KR1, S-KR4) and A2 (S-KR3). Similarly, rootstock-derived shoots ("Revita RV1") showed modified B patterns: B1 (R-KR1-4) and B2 (R-KR5). Band profile C, typical of "Carvita 25", appeared in grafted shoots carrying its genotype, with variants C1 (S-CR1, S-CR3, S-CR4) and C2 (S-CR5). This phenomenon occurred across five other primers, where regenerant band patterns deviated from their original genotypes, suggesting potential somaclonal variation.

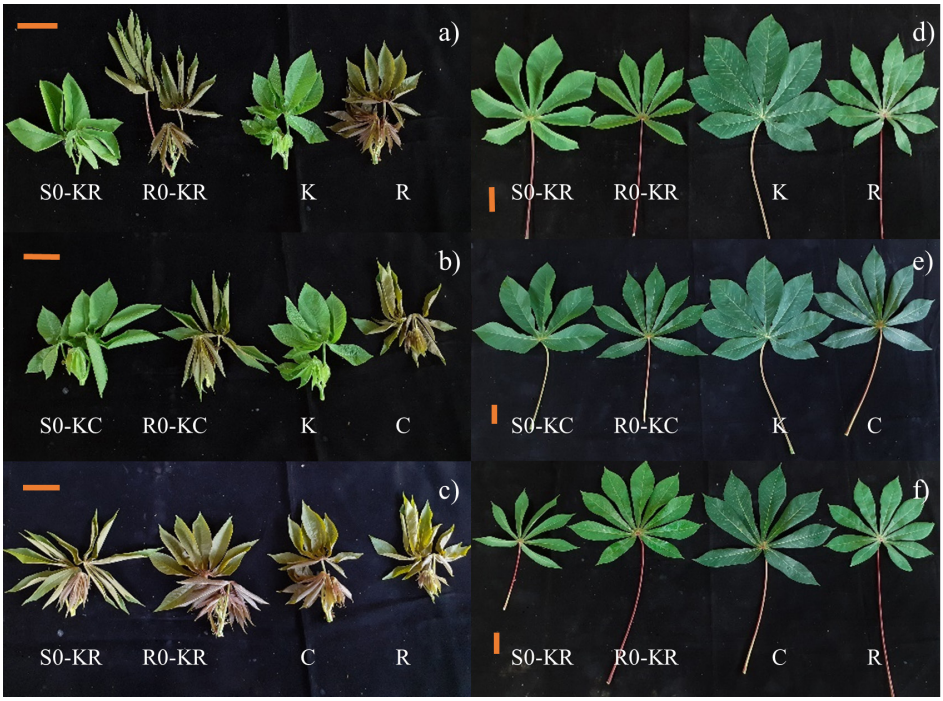

Figure 3. Morphological traits of shoot color (a–c), petiole length, and lobe size (d–f) in original and graft-derived (S0- and R0-) cassava plants.CR = "Carvita 25" scion–"Revita RV1" rootstock, KC = *M. glaziovii* (cv. "Karet") scion–"Carvita 25" rootstock, KR = *M. glaziovii* (cv. "Karet") scion–"Revita RV1" rootstock. Bar = 5 cm.

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Table 4. DNA band profiles of the original genotype and regenerated shoots originating from the scion (S) and R= rootstock (R)

Banding patterns	Primer OPE-12	Primer OPE-15	Primer OPC-06	Primer OPF-13	Primer OPE-14	Primer OPQ-20
A	26.67 (%) K1, K2, K3, K4, K5, S0-KC1, S0-KC2, S0-KC3, S0-KC4, S0-KC5, S0-KR2, S0-KR5	33.33 (%) K1, K2, K3, K4, K5, S0-KC1, S0-KC2, S0-KC3, S0-KC4, S0-KC5, S0-KR1, S0-KR2, S0-KR3, S0-KR4, S0-KR5	33.33 (%) K1, K2, K3, K4, K5, S0-KC1, S0-KC2, S0-KC3, S0-KC4, S0-KC5, S0-KR1, S0-KR2, S0-KR3, S0-KR4, S0-KR5	31.11 (%) K1, K2, K3, K4, K5, S0-KC1, S0-KC2, S0-KC3 S0-KC5, S0-KR1, S0-KR2, S0-KR3, S0-KR4, S0-KR5	33.33 (%) K1, K2, K3, K4, K5, S0-KC1, S0-KC2, S0-KC3, S0-KC4 S0-KC5, S0-KR1, S0-KR2, S0-KR3, S0-KR4, S0-KR5	33.33 (%) K1, K2, K3, K4, K5, S0-KC1, S0-KC2, S0-KC3, S0-KC4, S0-KC5, S0-KR1, S0-KR2, S0-KR3, S0-KR4, S0-KR5
A1	4.44 (%) S0-KR1, S0-KR4	-	-	2.22 (%) S0-KC4	-	-
A2	2.22 (%) S0-KR3	-	-	-	-	-
B	11.11 (%) R1, R2, R3, R4, R5	31.11 (%) R1, R2, R3, R4, R5, R0-CR1, R0-CR2, R0-CR3, R0-CR4, R0-CR5, R0-KR1, R0-KR2, R0-KR3, R0-KR5	20.00 (%) R1, R2, R3, R4, R5, R0-CR1, R0-KR2, R0-KR4, R0-KR5	28.89 (%) R1, R2, R3, R4, R5R0-CR1, R0-CR2, R0-CR3, R0-CR4, R0-CR5, R0-KR2, R0-KR4, R0-KR5	22.22 (%) R1, R2, R3, R4, R5R0-KR1, R0-KR2, R0-KR3, R0-KR4, R0-KR5	33.33(%) R1, R2, R3, R4, R5, R0-CR1, R0-CR2, R0-CR3, R0-CR4, R0-CR5, R0-KR1, R0-KR2, R0-KR3, R0-KR4, R0-KR5
B1	8.89 (%) R0-KR1, R0-KR2, R0-KR3, R0-KR4	2.22 (%) R0-KR4	11.11 (%) R0-CR2, R0-CR3, R0-CR4, R0-CR5, R0-KR3	-	-	-
B2	2.22 (%) R0-KR5	-	2.22 (%) R0-KR1	-	-	-
C	35.56 (%) C1, C2, C3, C4, C5, S0-CR2, R0-CR1, R0-CR2, R0-CR3, R0-CR4, R0-CR5, R0-KC1, R0-KC2, R0-KC3, R0-KC4, R0-KC5	17.78 (%) C1, C2, C3, C4, C5, S0-CR3, S0-CR4, R0-KC3	33.33 (%) C1, C2, C3, C4, C5, S0-CR1, S0-CR2, S0-CR3, S0-CR4, S0-CR5, R0-KC1, R0-KC2, R0-KC3, R0-KC4, R0-KC5	26.67 (%) C1, C2, C3, C4, C5, S0-CR2, S0-CR4, S0-CR5, R0-KC1, R0-KC2, R0-KC3, R0-KC5	33.33 (%) C1, C2, C3, C4, C5, S0-CR1, S0-CR2, S0-CR3, S0-CR4, S0-CR5, R0-KC1, R0-KC2, R0-KC3, R0-KC4, R0-KC5	26.67 (%) C1, C2, C3, C4, C5, S0-CR1, S0-CR5, R0-KC1, R0-KC2, R0-KC3, R0-KC4, R0-KC5
C1	6.67 (%) S0-CR1, S0-CR3, S0-CR4	11.11(%) S0-CR2, S0-CR5, R0-KC2, R0-KC4, R0-KC5	-	11.11 (%) S0-CR1, S0-CR3 R0-KC3, R0-KR1, R0-KR3	11.11 (%) R0-CR1, R0-CR2, R0-CR3, R0-CR4, R0-CR5	6.67 (%) S0-CR2, S0-CR3, S0-CR4
C2	2.22 (%) S0-CR5	4.44(%) S0-CR1, R0-KC1	-	-	-	-
Total	100	100	100	100	100	100

Notes: Banding pattern codes (A–C2) are arbitrary and do not correspond to variety names. S0 = scion, R0 = rootstock, CR = "Carvita 25" scion–"Revita RV1" rootstock, KC = *M. glaziovii* (cv. "Karet") scion–"Carvita 25" rootstock, KR = *M. glaziovii* (cv. "Karet") scion–"Revita RV1" rootstock. C1-C5 = "Carvita 25" replicates (n = 5), K1-K5 = *M. glaziovii* (cv. "Karet") replicates (n = 5), R1-R5 = "Revita RV1" replicates (n = 5).

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Notably, Table 4 highlights an unexpected result: primer OPF-13 produced band profile C1 in regenerants R-KR1 and R-KR3 despite the absence of “Carvita 25” in their grafting parentage. This warrants further investigation using additional primers (e.g., SSR markers) or expanded sampling. Similarly, regenerants exhibiting band profile deviations from their parental genotypes require in-depth analysis to elucidate underlying genetic or epigenetic mechanisms. This study highlights the use of RAPD markers as a simple, cost-effective, and rapid tool to assess genetic relationships between scion and rootstock in grafted plants, especially in species with limited genomic resources (Babu et al., 2014). Polymorphic banding patterns served as genetic fingerprints, revealing variation among regenerants and controls, supporting diversity and clustering analyses (Probojati et al., 2019). However, as a dominant marker system, RAPD cannot distinguish homozygous from heterozygous states, limiting its resolution for breeding (Panchariya et al., 2024). Band patterns may suggest heterozygosity, but this is indirect and sensitive to factors like DNA quality, primer specificity, and PCR conditions. Combining RAPD with co-dominant markers like SSRs or SNPs could improve genotypic precision (Jones et al., 2007; McIntyre et al., 2009). Despite limitations, RAPD effectively detected genetic differences among graft components, supporting its role in early screening of compatible graft pairs (Chen and Wang, 2006).

Cluster Analysis of Genetic Relationships Based on RAPD Markers

The DNA banding patterns obtained from RAPD analysis were scored and subjected to cluster analysis, generating a dendrogram illustrating the genetic relationships among all genotypes (original and regenerated shoots) (Figure 4). Clustering analysis using six primers produced a dendrogram at a genetic distance scale of 10, segregating the 45 samples into five major clusters (Groups I–V) and eight subgroups. Each cluster reflected the genetic affinities between samples, particularly between grafted plants and their respective controls: Group I comprised "Carvita 25" grafted onto *M. glaziovii*–"Carvita 25", "Carvita 25", and "Revita RV1" grafted onto "Carvita 25"–"Revita RV1", indicating a close genetic relationship between "Carvita 25" and "Revita RV1" when grafted onto "Carvita 25". Group II included *M. glaziovii* grafted onto *M. glaziovii*–"Revita RV1", "Revita RV1", *M. glaziovii* grafted onto *M. glaziovii*–"Carvita 25", and *M. glaziovii*, suggesting genetic proximity between *M. glaziovii* and "Revita RV1". Groups III–V revealed that specific graft combinations (e.g., "Carvita 25"–"Revita RV1" and *M. glaziovii*-"Revita RV1" were genetically divergent from their controls, as evidenced by their segregation into distinct clusters. Samples within the same group/subgroup shared close genetic relationships, consistent with findings by Pramudi et al. (2014) and

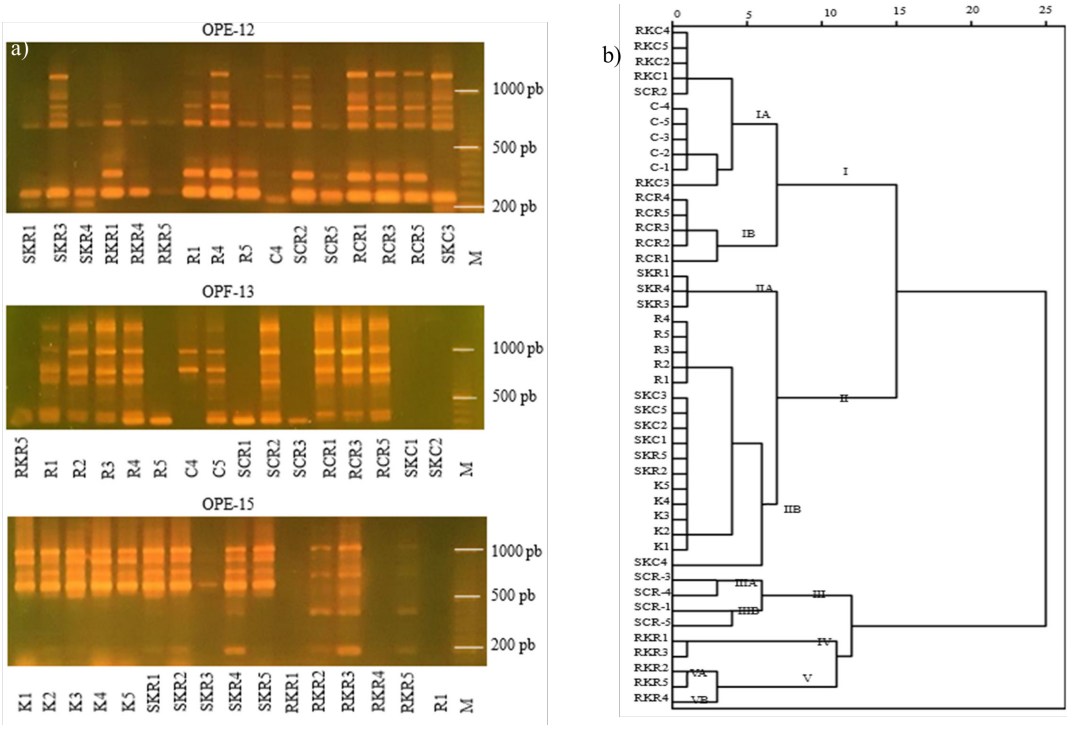

Figure 4. Displays the electrophoretic profiles of RAPD analysis using primer OPE-12, OPF-13, and OPE-15, representing scion/rootstock, regenerated shoots, and original genotype (control) (a) and Cluster Analysis of genetic relationship based on RAPD markers (b).

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Andriani (2016), who reported that genetically similar genotypes cluster on the same dendrogram branch, while distant genotypes occupy separate branches. Notably, DNA banding patterns were prioritized over morphological traits due to their higher stability in genetic discrimination.

Conclusions

This study demonstrates that interspecific grafting between cassava (*M. esculenta* Crantz) and *M. glaziovii* induces phenotypic and genetic variation. Grafting significantly affected the number of leaves and shoot length, while plant height and shoot number remained unaffected. Notably, grafting did not alter the plants' yield potential. Morphological differences were observed in the leaves, stems, and tubers of both scion and rootstock portions of grafted plants compared to the original genotypes. Distinct DNA banding patterns in grafted cassava plants, relative to their parental genotypes, highlight the genetic variation induced by grafting. The compatibility between cassava and *M. glaziovii* makes grafting a powerful tool for enhancing desirable traits and broadening genetic diversity in cassava breeding. These findings emphasize the potential of interspecific grafting as a novel approach to crop improvement and a valuable system for studying graft-induced genomic plasticity.

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