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The Genetic Homogeneity of Uganda's East African Highland Bananas (Mutika/Lujugira) Does Not Match the Extensive Morphological Variation Identified in this Subgroup

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Abstract: The East African Highland banana (Mutika/Lujugira subgroup) is composed of triploid (AAA) cooking and beer banana varieties that are adapted to the high-altitude region of the Great Lakes region of East Africa. Banana production is affected by several biotic and abiotic factors. Breeding opportunities in bananas are limited due to female sterility and parthenocarpy. The genetic diversity of crops enables breeders to develop new germplasm. Molecular markers have been used widely to dissect crop plants' genetic diversity. This study assessed the genetic variation in 27 varieties from the Mutika/Lujugira subgroup using random amplified polymorphic DNA (RAPD). No genetic variation was observed among the banana varieties, and the 18 ten-mer primers produced monomorphic banding profiles. The genetic homogeneity of this banana subgroup is not congruent with their extensive morphological variation. Domestication and the bottleneck effect are often cited as the cause of reduced diversity in crop plants. On the other hand, several mechanisms, including somatic mutations, transposable elements, polyploidy, genome plasticity, and epigenetic mechanisms, are known to increase plant phenotypic variability. Further in-depth research is needed to explain the puzzle between the genetic and morphological diversity in the Mutika/Lujugira subgroup.

Keywords: diversity; Mutika/Lujugira subgroup; morphological characterization; RAPD

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1. Introduction

The East African Highland Banana (Mutika/Lujugira subgroup) [1] comprises approximately 120 locally adapted AAA-EA (or EAHB) cultivars and landraces used mainly for cooking and beer production. The three AAA genomes of these bananas (*Musa* spp.) originated from two wild subspecies, *M. acuminata* sp. *banksia* (AA) and *M. acuminata* sp. *zebrina* (A) [2,3]. However, sequencing data showed that the AAA-EA has large introgressions from another wild species, *M. schizocarpa* [4]. These bananas (*Musa* spp.) are cultivated in Uganda, Kenya, Western Tanzania, Rwanda, Burundi, and the Democratic Republic of Congo, where they make up the main carbohydrate staple and a source of income [5]. Bananas are also a good source of vitamins, sodium, potassium, calcium, and magnesium [6]. The East African Highlands and Great Lakes Region are zones of secondary diversity for bananas [7].

Monoculture and the narrow genetic base of bananas have increased their vulnerability to diseases such as black Sigatoka (*Pseudocercospora fijiensis*), Fusarium (*Fusarium oxysporum* foc *cubsense*), and *Xanthomonas campestris* pv *musacearum* [8] and several pests. Climate change and global warming are further threats to banana cultivation due to its uniform genetic background. Genetic diversity is an important component of plant breeding, which helps develop new and improved crop cultivars and address global challenges that affect food security, sustainability, and adaptation to climate change [9]. Molecular markers are widely used in plants to provide estimates of the genetic diversity of plants and genetic relationships within germplasm [6].

RAPD (random amplified polymorphic DNA) has been used to distinguish diverse *Musa* germplasms [6,10–12], assess the genetic stability of tissue-cultured plantlets [13], create a molecular linkage map using several marker systems including RAPD [14], and identify genomes in *Musa* [5]. Despite the criticism of the technique, it is still being reported in recent publications, as shown above.

The EAHBs are highly diverse in morphology and were divided into five phenotypic groups (Nfuuka, Musakala, Nakabululu, Nakitembe, and Mbidde) [15]. The Mbidde group is also biochemically different, with an astringent and bitter pulp used primarily to produce beer. Recent studies using SSR markers have shown that varieties in the Mutika/Lujugira subgroup displayed no genomic variation [16,17].

Several studies have used a combination of molecular markers to find the most effective indicator that provides the greatest diversity in a species [18]. For example, in maize, a comparison of RAPD, RFLP, AFLP, and SSR markers established that AFLP was the most suitable technique for fingerprinting and assessing genetic relationships in tropical maize inbred lines [19]. In *Dioscorea*, a vegetatively propagated crop, RAPD, ISSR, AFLP, and ISTR marker techniques provided similar levels of diversity [20].

This study used RAPD analysis to assess the genetic diversity in the Mutika/Lujugira subgroup from Uganda. The results are compared with those of recent studies that used other marker types. Recent advances in genomics make it possible to postulate why some plants show great morphological variation but no genetic variation. The paper also provides reasons for the possible reduced genomic diversity in the Mutika/Lujugira subgroup and potential mechanisms that could have increased diversity after domestication. This study emphasizes research areas that would increase our knowledge of banana diversity.

2. Materials and Methods

The plant material used in this study was obtained from the banana germplasm collection at Kawanda (0°24′28″ N, 32°31′54″ E) and Namulonge Research Stations (00°31′30″ N, 32°36′54″ E) in Uganda and consisted of 27 varieties from the Mutika/Lujugira subgroup (Table 1).

Table 1. Genotype, genome composition, clone set and uses of the East African Highland bananas used in this study.

Serial No.	Genotypes	Genome Composition	Clone Set	Use
1	Entukura	AAA	Nfuuka	Cooking
2	Enzirabahima	AAA	Nfuuka	Cooking
3	Nabusa	AAA	Nfuuka	Cooking
4	Namwezi	AAA	Nfuuka	Cooking
5	Nante	AAA	Nfuuka	Cooking
6	Ndyabalangira	AAA	Nfuuka	Cooking
7	Nfuuka	AAA	Nfuuka	Cooking
8	Tereza	AAA	Nfuuka	Cooking
9	Kabucuragye	AAA	Musakala	Cooking
10	Mayovu(e)	AAA	Musakala	Cooking
11	Mukazialanda	AAA	Musakala	Cooking
12	Nakibizzi	AAA	Musakala	Cooking
13	Namunwe	AAA	Musakala	Cooking
14	Siira	AAA	Musakala	Cooking
15	Kazirakwe	AAA	Nakabulu	Cooking
16	Kibuzi	AAA	Nakitembe	Cooking

Table 1. *Cont.*

Serial No.	Genotypes	Genome Composition	Clone Set	Use
17	Mbwazirume	AAA	Nakitembe	Cooking
18	Nakasabira	AAA	Nakitembe	Cooking
19	Nakawere	AAA	Nakitembe	Cooking
20	Nakyetengu	AAA	Nakitembe	Cooking
21	Nandigobe	AAA	Nakitembe	Cooking
22	Salalugazi	AAA	Nakitembe	Cooking
23	Enkara	AAA	Mbidde	Beer
24	Kabula	AAA	Mbidde	Beer
25	Nalukira	AAA	Mbidde	Beer
26	Murure	AAA	unknown	Unknown
27	Nsowe	AAA	unknown	Unknown

2.1. DNA Extraction

DNA was extracted according to [5] with minor adjustments. About 0.5 g of leaves were ground in liquid nitrogen with a mortar and pestle. Ten milliliters of extraction buffer (20 mM sodium EDTA, 100 mM Tris-HCL, pH adjusted to 8.0 with HCL; 1.4 M Sodium Chloride (NaCl), 2% CTAB (hexadecyltrimethylammonium bromide) and 0.2% of β-mercapto-ethanol) were added to the ground leaves and mixed in the mortar. The mixture was then poured into a clean 15 mL polypropylene centrifuge tube and incubated at 65 °C for 30 min. The mixture was then brought to room temperature before 6 mL of chloroform; octanol was added and mixed to form an emulsion. The mixture was centrifuged at 4000 rpm for 30 min. The top aqueous phase was then transferred to a new centrifuge tube, and 0.5 volume of 5 M NaCl was added to the aqueous phase and mixed well. Two volumes of cold absolute ethanol were added and refrigerated at 4–8 °C for 15–20 min until DNA strands appeared. The tube was centrifuged at 2500× *g* rpm for 5 min, and speed was increased to 4000 rpm for an additional 5 min. The supernatant was discarded, and the pellet was washed with cold 70% ethanol. The ethanol was completely removed by leaving the tubes uncovered at 65 °C for 30 min. The DNA pellet was then dissolved in 1000 uL TE (10 mM Tris-1 mM EDTA, pH 8) buffer. The RNA was removed by adding 6 uL RNAse (10 mg/mL) and incubated for 30 min. The DNA was re-precipitated.

2.2. DNA Quantification

The DNA was quantified with the Nanodrop^R (Thermo Scientific, Wilmington, DE, USA), following the manufacturer's instructions. DNA was standardized to 40 ng/uL by diluting with sterile TE buffer. The quality of the DNA was assessed by electrophoresis in 1% agarose gel dissolved in 1X TBE buffer. The gel was stained with ethidium bromide and visualized under UV light.

2.3. RAPD Analysis

The PCR reaction mixtures included 10× amplification buffer, 37.5 mM $MgCl_2$, 2.5 mM dNTPs, 0.5 uL *Taq* polymerase (GoTaq; Promega, Madison, WI, USA), 5 uL DNA, and 2 uL of each primer (Operon Technologies, Alameda, CA, USA). The eighteen primers used in this study are listed in Table 2. The following PCR conditions were used: 94 °C for 2.5 min initial denaturation, followed by 35 cycles of 50 s at 94 °C, 50 s at 40 °C, 1.5 min at 72 °C, and a final extension step of 7 min at 72 °C.

Table 2. List of RAPD primer sequences used in this study.

Primer No.	Primer	Primer Sequence
1	A17	5′-GACCGCTTGT-3′
2	A18	5′-AGGTGACCGT-3′
3	B5	5′-TGCGCCCTTC-3′
4	B10	5′-CTGCTGGGAC-3′
5	B17	5′-AGGGAACGAG-3′
6	B19	5′-ACCCCCGAAG-3′
7	C8	5′-TGGACCGGTG-3′
8	C12	5′-TGTCATCCCC-3′
9	C15	5′-GACGGATCAG-3′
10	C16	5′-CACACTCCAG-3′
11	C18	5′-TGAGTGGGTG-3′
12	C20	5′-ACTTCGCCAC-3′
13	D2	5′-GGACCCAACC-3′
14	D4	5′-TCTGGTGAGG-3′
15	D8	5′-GTGTGCCCCA-3′
16	D10	5′-GGTCTACACC-3′
17	D11	5′-AGCGCCATTG-3′
18	D13	5′-GGGGTGACGA-3′

2.4. Gel Electrophoresis

The PCR products were analyzed by electrophoresis in 1% agarose gel in 1X TBE buffer. Ten microliters of the PCR product were mixed with 1 uL of 0.1 mL 6X Orange DNA Loading Dye from Fermentas Life Sciences (Wilmington, DE, USA). Electrophoresis was carried out at 90 V for 2 h. The gel was stained with ethidium bromide and visualized under UV light. Representative RAPD banding profiles of the EAHB are shown in Figures 1–3.

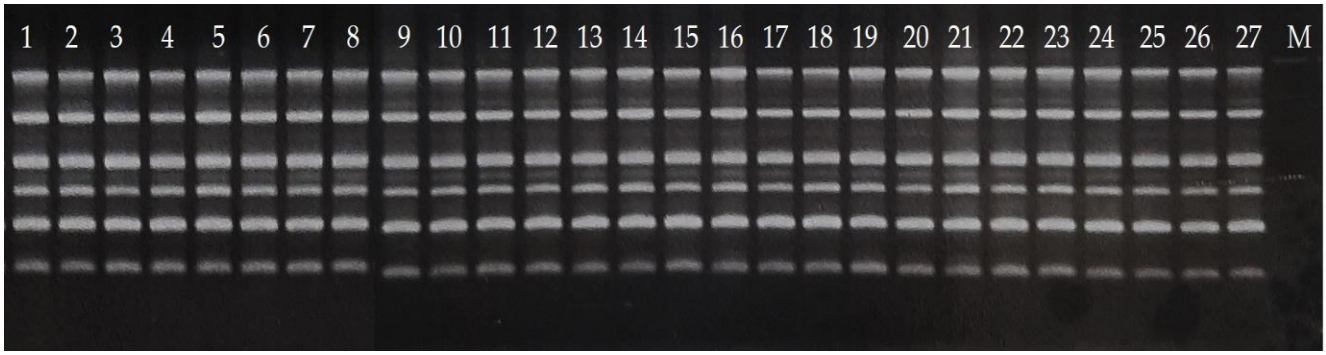

Figure 1. RAPD banding patterns of 27 East African Highland banana varieties with Operon primer C16.

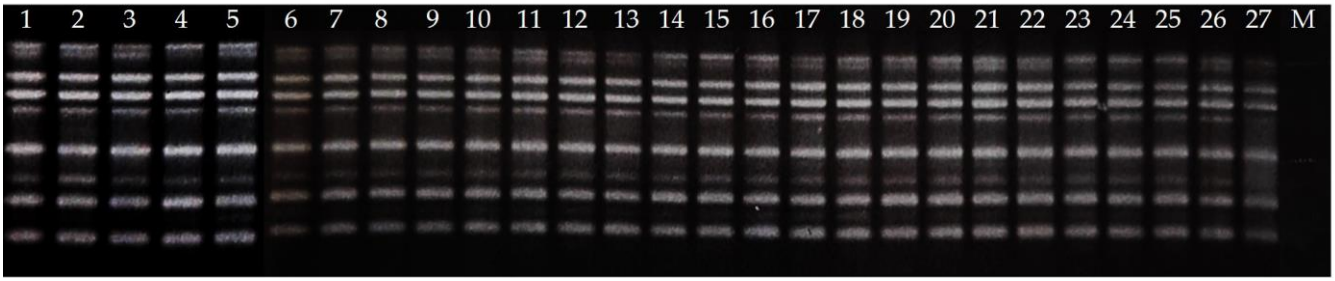

Figure 2. RAPD banding patterns of 27 East African Highland banana varieties with Operon primer B10.

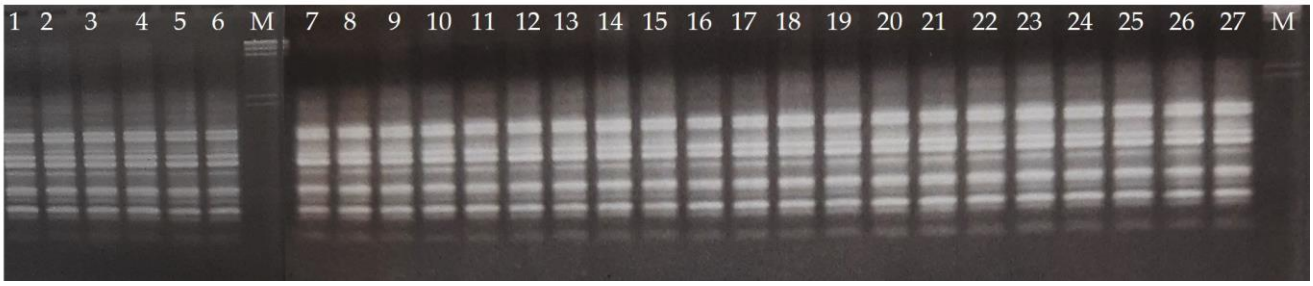

Figure 3. RAPD banding patterns of 27 East African Highland banana varieties with Operon primer D11.

3. Results and Discussion

The most significant result of this investigation is that the 18 RAPD primers produced monomorphic banding patterns amongst all the 27 landraces (Figures 1–3).

The sample size of this study represents a third of the approximately eighty landraces in the Mutika/Lujugira subgroup identified in Uganda [15]. Other studies of this banana subgroup by [21] using RAPD and AFLP and [16,17] using SSR markers also showed no genetic variation. The authors in [16] suggested that this banana subgroup is genetically homogeneous, with a monophyletic origin that underwent population expansion by vegetative propagation. The SSR and RAPD markers likely assessed only a small number of loci, and the genome coverage in these studies was low, as [22] suggested. The EAHB also varies in fertility and seed set [23], vitamin A, iron, and zinc content [24,25], and cytogenetic variation in the form of translocations, minor genome size variation, and aneuploidy [3].

Microsatellites have been propositioned as highly informative, codominant, multiallelic, and highly reproducible genetic markers [26]. They have been used widely for estimating gene flow, diversity, crossing-over rates, and evolution to uncover intraspecific genetic relatedness [27]. Despite the several advantages of SSR markers, they appear unsuitable for revealing genomic variability in this particular banana subgroup. However, SSR markers have been used to identify genetic diversity in other banana studies [6,28–31].

Our RAPD study of similar bananas (AAA) from Rwanda did show a moderate amount of genetic diversity [5]. However, insignificant or no genetic diversity was reported for studies that assessed the molecular genetic diversity of homogenomic subgroups of bananas, including an AFLP analysis of the EAHB with two primer combinations [32], AFLP assessment of plantains (AAB) [33], and AFLP and SSR of plantains [22]. The only study that showed within-group variation in the AAA Cavendish bananas was reported by Ermini et al. (2018) [34]. On the contrary, as expected, greater genetic diversity has been described for studies that used a mixed group of species or subgroups of bananas [6,10,29,35–41].

The phenotype of an organism is dependent not only on its genetic constitution but is a product of its genotype, the environment, genotype-by-environment interactions, and perhaps other unknown effects [42]. This may be true for the EAHB. It has been postulated that most of the variability in the EAHB is due to somatic mutations and chimerism [15].

Recent evidence suggests that transposons and epigenetics, individually or in combination, can influence a plant's phenotype. Furthermore, polyploidy, which was once considered an evolutionary dead end, is now widely proposed as another mechanism that influences plant phenotypic variation [43]. Several lines of evidence from different research fields suggest that the organellar genomes also contributed to plant adaptation [44].

Since vegetative propagation bypasses the meiotic step, the offspring are expected to be identical to the progenitor except when mutations occur [45]. However, some clonally propagated crops, including *Agave fourcroydes* [46] and *Vitis* [47], show high genetic diversity. Despite its clonal reproduction, bananas also exhibit a high level of morphological diversification in pseudostem color, fruit size, shape and color of petiole bases, plant height, and growth habit [15,48].

Many mechanisms can intensify the genetic diversity in clonally propagated plants to enhance variation and provide an open system for adaptation and selection [42,45]. Mutation types that usually affect a single gene include point mutations that result in single nucleotide polymorphisms (SNPs) and insertions or deletions (InDels) of base pairs. Entire genes can be deleted or duplicated (gene loss or gain). Larger-scale mutations occur at the chromosomal level, including deletions and duplications of chromosomal regions, whole chromosomes (aneuploidy), or entire genomes (polyploidy). In addition, recombination between homologous chromosomes results in the shuffling of genes during meiosis, resulting in new combinations of genes in the progeny. Inversions, homologous recombination, and reciprocal translocations have been reported in bananas [49–51]. Domestication is one of the factors that is considered to have reduced the genetic diversity of the EAHB.

3.1. Reduced Diversity of Bananas via Domestication

Domestication introduces major germplasm changes and reduces crop species diversity [52,53]. The domestication bottleneck effect has been proposed for bananas [2]. Reduced genetic diversity due to domestication is ascribed to the genetic bottleneck effect, in which the population size of a crop is diminished [54]. Unlike crops such as maize or wheat, domestication of bananas did not completely change the plant's phenotype since cultivated bananas maintain the genetic signature of the wild diploid species *Musa acuminata* and *M. balbisiana*. This is plausible because domestication involved a limited number of major genes under monogenic recessive control [55]. Conscious and unconscious selection of a few "domestication traits", including parthenocarpy, seedlessness, increased fruit pulp content, increased number of useful nutrients, and perhaps increased palatability from wild diploid species about 7000 years ago, is considered to have reduced genetic diversity in edible bananas [56]. Initially, the admixture of still fertile domesticates allowed mating with other fertile diploids among the subspecies to produce the vast diversity of extant bananas [57].

On the other hand, fertile diploid bananas produced triploid bananas through diplogametes and meiotic restitution [1,58]. Vegetative propagation made these selections less fertile or to lose their ability for sexual reproduction but conferred several advantages as a method of reproduction [56]. This led to a gradual reduction in the initial diversity of the selections. Additional bottlenecks may have occurred when human migrations took these bananas to different regions of the world far away from the point of origin [54]. This has been proposed for this banana subgroup by Kitavi et al. (2016) [16].

The domestication of several crops, including bananas, was not a single-step event but a multistep process over some time [59,60]. The reticulate nature of banana domestication is also supported by other researchers [60,61]. It is assumed that each of these domestication steps introduced further changes to the germplasm, and the more domesticated germplasm pools had a narrower range of genotypic diversity [62]. Although reduced diversity during domestication is true for most crops, it is important to mention that it is not the general rule. For example, broader phenotypic diversity of fruit shape, size, and color is observed in domesticated tomatoes [63]. In maize, cultivars have narrower phenotypic diversity relative to the less domesticated landraces [64].

3.2. Probable Mechanisms for Increased Phenotypic Diversity in the EAHB

Several mechanisms could have increased phenotypic variability in bananas. They include somatic mutations, somaclonal variation, the activity of transposable elements, new genome combinations, polyploidy, genome duplications, mitotic recombination, and recombination of novel alleles [21]. For example, somatic mutations, somaclonal variation, retrotransposition, chimerism, and epigenetic changes are the main sources of genetic variation in grapevine clones [45]. Recently, the role of genome plasticity and epigenetic mechanisms are also implicated in inducing changes in the phenotype of organisms [65]. Phenotypic changes in the EAHB are due to the accumulation of somatic mutations [66].

3.3. Somatic Mutations

Somatic mutations are an important source of variation in clonally propagated crops [59]. Bananas are good examples of the power of somatic mutations to provide genetic variation that contributes to adaptive evolution and increased phenotypic variability [67,68]. There is consensus that the phenotypic variability in the EAHB, and bananas in general, is a result of the accumulation of somatic mutations [33,66] and human selection [17]. The phenotypic diversity of the EAHB results from somatic mutations in the meristems of the lateral rhizomes, which produce suckers that mature into plants [15]. While some somatic mutations may be deleterious, others may offer a direct selective advantage or create a novel phenotype [59].

Plants with obligate vegetative reproduction have higher rates of somatic mutations than those that reproduce sexually [69,70]. For instance, in Bermuda grass, a plant with obligate vegetative reproduction, the level of somatic mutations was high (10 per triploid genome). Many morphology characteristics in bananas, including plant stature, pseudostem color, the shape of the petiolar canal, plant height, growth habit, bunch and fruit shape, astringency, and fruit pulp color, are prone to mutations [48,71]. However, currently, no direct link has been associated with any character or specific mutation. Recently, cultivar cultivar-specific markers, mutations, and chimerism were reported in Cavendish banana somaclonal variants [72]. Segregation tests, cloning, and sequencing of relevant genes are necessary to prove that any character is due to mutations or epigenetic variation [73].

Plants grown under in vitro conditions are subject to stress [74]. Oxidative stress is one of the main reasons for both spontaneous and induced mutations and a driving force for improving crops [75]. The EAHB could have undergone similar stresses when they were transported from their origin to different regions of the world. Although the climate in the East African highlands and South East Asia is described as tropical, the East African highlands perhaps have a different microclimate that influences the phenotypes of the plants, leading to variation. Plastic adaptation to different growth environments is reported to initiate phenotypic variation, especially in vegetatively propagated crops [56]. Bananas that were introduced into the subtropical zone of Argentina in the 1920s showed broader genetic variation to increase the genetic homeostasis necessary for adapting the crop to the suboptimal environment of Northeastern Argentinean Formosa Province [34].

3.4. Transposable Elements as Agents of Diversity

Transposable elements (TEs) are a major driving force in genome evolution and gene duplication, resulting in rapid plant phenotypic changes [76,77]. The mutating potential, genomic, and phenotypic changes due to transposable elements are discussed adequately in several publications [78–80]. Similarly, the key roles of TEs in fine-tuning the regulation of gene expression leading to phenotypic plasticity have been reviewed by several researchers [78,80,81]. Researchers agree that TEs are agents of genetic diversity on which selection can act [79]. The contribution of TEs to genetic diversity may be underestimated since TEs can be more active when organisms are under stress, such as in their natural environment [82,83]. Plants in any environment are constantly under environmental changes and are affected by abiotic (light, water, and temperature) and biotic factors such as pathogens and pests. They develop various genetic mechanisms to

cope with habitat heterogeneity supplemented by phenotypic plasticity [83]. TEs have influenced phenotypic traits such as fruit shape, leaf variegation, inflorescence structure, skin color, seedless fruit development, plant height, response to disease and pest resistance, apical dominance, variation in flowering time, fruit variation, vitamin E accumulation, leaf angle, parthenocarpy, etc., of many crop plants [79,81]. Although transposable elements and retrotransposons are present in the banana genome [84–86], no association has been identified between any transposable element and trait. Several of the traits mentioned above are known to be highly variable in the EAHB [15]. It is known that TEs can induce spikes in mutation rates, as shown for wild populations of three sunflower species, barley, and some rice cultivars [78]. Further evidence is required to establish whether the somatic mutations observed in bananas are due to TEs. New technologies such as NGS and improved statistical tools may make it possible to confirm whether TE-mediated polymorphisms can be linked with phenotypes and or/environmental variation.

3.5. Epigenetic Variations Contribute to Plant Evolution

There is strong support that epigenetic mechanisms, including DNA methylation and histone modifications, generate genome rearrangements in response to biotic and abiotic environmental stresses [65]. Epigenetic mechanisms can bring about both genomic and phenotypic plasticity and produce different phenotypes when exposed to environmental variation [65]. It is likely to assume that the movement of bananas from their origin to different ecological zones, including the East African Highlands, was accompanied by abiotic and biotic stresses that influenced phenotypic variation.

Ref. [22] were the first to report on epigenetic marks in the form of a high degree of methylation polymorphism in plantains (AAB). However, no correlation was observed between the phenotypic classification and methylation diversity. Epigenetic variation is due to genomic changes that do not affect an organism's DNA sequence but can bring about several changes in gene expression [87]. This may be the reason why, despite the phenotypic variation in this subgroup of EAHB, no genome sequence changes were detectible with molecular marker technology such as SSR and RAPDs. Perhaps sequencing of these genomes may be useful in this regard.

Epigenetic variation in crop plants has affected several phenotypic characteristics such as modification of plant stature, fruit development and ripening, fertility, leaf shape, seed size, flowering time, floral symmetry, and anthocyanin pigmentation [88]. Considerable variation in the pseudostem height, color, and other characteristics occurs in bananas and is used to distinguish cultivars [48,71]. The role of epigenetics in determining these traits in bananas is unknown. The EAHB harbors significant epigenetic diversity with heritable epialleles that can contribute to morphological diversity [89]. The authors [48] proposed that DNA methylation plays an important role in bananas' pathogenic response to Foc TR4. DNA methylation changes in response to salt stress have been reported in *Musa acuminata* [90], suggesting that DNA methylation could be used to fine-tune gene expression. High-throughput sequencing techniques and biochemical techniques to manipulate epigenetic marks will allow us to see the influence of epigenetics on phenotype, plasticity, and evolution [65].

3.6. Polyploidy

Polyploidy or genome doubling is a prominent characteristic of plant genomes, including bananas, and results in high levels of gene duplication [91,92]. The duplicated genes can acquire new or slightly varied functions and provide the basis for gene sub-/neofunctionalization, further promoting plant species' adaptation and genome plasticity [93,94]. New genome combinations created via polyploidy can influence the morphological, ecological, physiological, biochemical, and cytological characteristics associated with diversifying traits and adapting plants to new environments [95,96].

Compared to their diploid ancestors, polyploid plants outperform their diploid relatives in many aspects and exhibit superior traits such as larger organs, increased vigor,

etc. [97]. This may be true in the case of the allopolyploid EAHB with three A genomes. Two studies have shown that polyploidy can affect morphological traits in bananas. Author [98] compared petiole strength in diploid and polyploid bananas and observed that the tetraploids had the weakest petiole-breaking strength compared to the triploids and the diploids. The authors [99] reported that ploidy affected fruit traits and plant height in plantain (ABB) hybrids. Induced polyploidy in bananas has shown that many features, including anthocyanin concentration and leaf pigmentation, female sterility, mitotic chromosomal irregularities, the root system, number of suckers, plant height, leaf morphology, number of living leaves at flowering and harvest, pseudostem diameter, length and diameter of fruits, greater fruit and bunch weights, and disease resistance differed compared with the original diploids [100,101]. Recently, ten induced tetraploids generated from six diploid banana AA genotypes showed that the tetraploids generally displayed inferior vegetative characteristics than the original diploids and had about 20% lower bunch weights [102]. The same study also reported a 50% decrease in fruit provitamin A carotenoids but increased lutein in the induced tetraploids. Further, pollen viability tests indicated over 70% viability for the induced tetraploids compared to the diploid controls.

Polyploid induction in other plants also reported cytological, morphological, anatomical, phytochemical characteristics, yield, and qualitative characteristic differences between the polyploids and their respective diploids [103,104]. Combining multiple sets of chromosomes from different subspecies may increase the probability of accumulating alleles and novel epistatic interactions. This may be true in the case of the EAHB. A panel of genes showing highly significant differential expression was identified in one of the cultivars, Mbwazirume, used in this study by [105]. The study states that 13 of these differentially expressed genes could potentially influence the phenotype.

3.7. Chimerism

Chimerism also appears to have affected trait variability in the EAHB [71,72]. Chimerism is common in plants propagated vegetatively for a long period [106]. The presence of chimerism has been alluded to and described in bananas, although there is no in-depth investigation. A common feature in the EAHB is that during vegetative propagation, not all the suckers produced from a single mat are identical as expected in a vegetative crop [71]. It is believed that the meristem of the mother plant may give rise to highly variable suckers due to chimerism. Chimerism is common in vitro propagated banana plants due to the primary explants' chimeric heterogeneity [107]. Chimerism has influenced genetic variability in the grapevines [108,109].

3.8. Genomic and Phenotypic Plasticity

Since the genotype determines the phenotype, genotypic and phenotypic plasticity must be considered together in any discussion. Phenotypic plasticity has been documented in bananas [110,111]. Polyploidy introduces a high degree of plant genomic plasticity [112]. Perhaps polyploidy in the EAHB provides indirect evidence for genome plasticity in bananas. Like other plants, the EAHB has demonstrated tolerance to changing chromosome numbers (aneuploidy and polyploidy), genome size, transposable elements, insertions, deletions, and epigenome restructuring factors that induce genome plasticity [113]. These large-scale genomic changes restructure the transcriptome, metabolome, and proteome, resulting in altered phenotypes [113].

4. Conclusions

This study showed that an RAPD analysis of the varieties in the Mutika/Lujugira subgroup did not uncover any DNA sequence variation, similar to the results of two studies that used SSR markers. This is intriguing, considering that the genomes of these polyploid (AAA) bananas came from two different subspecies, and polyploidy is known to induce changes in genome structure [105]. There is no clear correspondence between the genomic and morphological variation in this group of bananas. While domestication is known to

narrow the genetic diversity of a population through bottleneck events, several mechanisms can increase phenotypic variability in plants. While the different mechanisms inducing variability in plants have been categorized in this paper for discussion purposes, there is a consensus that many of these mechanisms work in a reticulate manner. Separating the effects of epigenetics and TE on a plant's phenotype is very difficult [114]. TEs are now regarded as a link between the genome and the epigenome and as agents for genome and epigenome evolution [78]. Similarly, polyploidy induces many epigenetic modifications, including DNA methylation, histone modifications, and chromatin remodeling [115]. Further functional studies could reveal the relationship between genetic variation and the morphological and biochemical characteristics of bananas.

Further in-depth research is needed to identify the role of epigenetics, TEs, and polyploidy in banana evolution. Advances in sequencing technologies may generate new data to bridge the gap between the apparent discrepancy between the molecular and morphological diversity in the EAHB. The diversification of bananas results from processes much more complex than expected for a clonal crop [116]. Diminishing farm diversity has been reported in the EAHB in Burundi since the outbreak of banana bunchy top disease in the 1980s [7]. Plant breeding and the development of new disease and pest-resistant cultivars depend on knowing the genetic diversity of a crop. Further in-depth studies are required to decipher the genetic diversity in the Mutika/Lujugira banana subgroup. Currently, the phenotypic richness of the EAHB cannot be predicted from its genetic composition.

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