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**SWEDISH UNIVERSITY
OF AGRICULTURAL
SCIENCES**

DOCTORAL THESIS

Alnarp 2023

Acta Universitatis Agriculturae Sueciae
2023:15

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Abstract

The production of East African highland bananas Eastern Africa is under threat by pests and pathogens. Improved banana cultivars with high and stable yield, suitable end use quality, host plant resistance to major pests and pathogens, and adaptation to target population of environments can help boost productivity when combined with sound crop husbandry practices. This study evaluated 24 primary and secondary 'Matooke' banana triploid hybrids [NARITA (N)], six triploid local 'Matooke' cultivars, and one exotic cultivar over three years at three highland sites in Uganda's western and central regions, as well as three sites in Tanzania's northeastern and southern highlands regions. The aim of this investigation was to; (1) assess the relative importance of characteristics used by farmers in Uganda and Tanzania to select improved 'Matooke' banana cultivars, (2) identify high-yielding banana genotypes with specific and broad adaptation potential, (3) contribute to the release of four 'Matooke' hybrids banana cultivars with the potential of adoption by farmers in East Africa, and (4) carry out molecular verification of newly bred cultivars, ensuring the release and supply of true-to-type banana cultivars to farmers. We used farmer participatory approaches to understand farmers' preferences for cultivar characteristics, as well as mixed models (i.e., restricted maximum likelihood/best linear unbiased prediction), and additive main effect multiplicative interaction model biplots to dissect and visualize genotype-by-environment patterns. Large fruit, a large bunch, market acceptability of the banana bunch, a sturdy stem, and an attractive appearance of the banana plant were the characteristics that Tanzanian and Ugandan farmers preferred the most. Farmers of both genders were more focused with production-related characteristics, but men valued marketing-related characteristics more while women preferred use-related characteristics. The highly significant effects of both genotype and interaction of the likelihood ratio test indicated the influence of genotype and site heterogeneity in selecting specific and broadly adapted cultivars. N23 had the highest yield at all sites related to adaptability and stability, outperforming the mean genotype-wide yield by 34.2%. N27 (2nd), N7 (3rd), N18 (4th), N4 (5th), N12 (6th), and N13 (7th) in Tanzania, as well as N17 (2nd), N18 (3rd), N2 (4th), N8 (5th), N13 (6th), N12 (7th), N4 (8th), and N24 (9th) in Uganda, had high yield, stability, and adaptability. Lyamungo in Tanzania and Sendusu in Uganda were the best sites for discriminating breeding clones. As a result, these testing locations are suggested as prime examples of locations to test and choose superior genotypes. Furthermore, *Pseudocercospora fijiensis*, a fungal pathogen, causing black leaf streak (BLS) did not have a significant effect ($P > 0.05$) on the hybrids' yield, stability, or adaptability. The four released 'Matooke' hybrids (TARIBANs) have the potential to improve the quality of life of millions of people in the East African region and ensure food security because they combine high yield, farmer desired characteristics (including cooking attributes), and host plant resistance to the BLS pathogen. Over 90% of the 'Matooke' cultivars were be true-to-type, and the microsatellites markers used in this study produced repeatable polymorphic bands in 26 'Matooke' and exotic banana cultivars, thus demonstrating their value as a powerful tool for investigating genetic diversity and establishing relationships among 'Matooke' cultivars. This demonstrates genotyping's ability to precisely identify and validate clones.

Keywords: *Musa* sp., farmers' characteristic preferences, genotype $\times$ environment interaction, 'Matooke', *Pseudocercospora fijiensis*, simple sequence repeats, TARIBAN

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Abstract

Produktionen av östafrikanska höglandsbananer är hotad av skadedjur och sjukdomar. Förbättrade banansorter med hög och stabil avkastning, lämplig slutanvändningskvalitet, resistens mot skadedjur och sjukdomar och anpassade till specifika miljöer kan hjälpa till att öka produktiviteten i kombination med sunda växtodlingsmetoder. Denna studie utvärderade 24 primära och sekundära "Matooke"-banan triploida hybrider [NARITA (N)], sex triploida lokala "Matooke"-sorter och en exotisk sort under tre år på tre höglandsplatser i Ugandas västra och centrala regioner, samt tre platser i Tanzanias nordöstra och södra höglandsregioner. Syftet med denna undersökning var att; (1) bedöma den relativa betydelsen av egenskaper som används av bönder i Uganda och Tanzania för att välja förbättrade "Matooke"-banansorter, (2) identifiera högavkastande banangenotyper med specifik och bred anpassningspotential, (3) introducera fyra nya 'Matooke'-hybridsorter med potentialen att användas av bönder i Östafrika, och (4) utföra molekylär verifiering av nya sorter, vilket säkerställer introduktionen och leverans av typtrogna banansorter till jordbrukare. Vi använde "farmer participatory approaches" för att förstå bönders preferenser för sortegenskaper, såväl som "restricted maximum likelihood/best linear unbiased prediction", och "additive main effect multiplicative interaction model biplots" för att granska och visualisera genotyp-miljö-mönster. Stor frukt, stort klase, marknadsacceptans för bananklasen, en robust stjälk och ett attraktivt utseende på bananplantan var de egenskaper som tanzaniska och ugandiska lantbrukare föredrog mest. Bönder av båda könen fokuserade mest på produktionsrelaterade egenskaper, men män värderade marknadsföringsrelaterade egenskaper i högre utsträckning medan kvinnor föredrog användningsrelaterade egenskaper. De betydande effekterna av både genotyp och "interaction of the likelihood ratio test" indikerade vikten av genotyp och platsheterogenitet vid val av specifika och brett anpassade sorter. N23 hade den högsta avkastningen på alla platser relaterade till anpassningsförmåga och stabilitet, och överträffade det genomsnittliga genotypomfattande avkastningen med 34,2 %. N27 (2:a), N7 (3:a), N18 (4:a), N4 (5:a), N12 (6:a) och N13 (7:a) i Tanzania, samt N17 (2:a), N18 (3:a), N2 (4:a) , N8 (5:a), N13 (6:a), N12 (7:a), N4 (8:a) och N24 (9:a) i Uganda, hade högt utbyte, stabilitet och anpassningsförmåga. Lyamungo i Tanzania och Sendusu i Uganda var de bästa platserna för att urskilja förädlingskloner. Som ett resultat föreslås dessa testplatser som utmärkta exempel på platser att testa och välja överlägsna genotyper. Dessutom hade *Pseudocercospora fijiensis*, en svamppatogen, som orsakar svarta bladstrimmor (BLS) ingen signifikant effekt (P > 0,05) på hybridernas avkastning, stabilitet eller anpassningsförmåga. De fyra släppta "Matooke"-hybriderna (TARIBAN) har potential att förbättra livskvaliteten för miljontals människor i den östafrikanska regionen och säkerställa livsmedelssäkerhet eftersom de kombinerar hög avkastning, odlarens önskade egenskaper (inklusive matlagningsegenskaper) och resistens mot BLS-patogenen. Över 90 % av "Matooke"-sorterna var sortäkta, och mikrosatellitmarkörerna som användes i denna studie producerade repeterbara polymorfa band i 26 "Matooke" och exotiska banansorter, vilket visade deras värde som ett kraftfullt verktyg för att undersöka genetiska mångfald och släktskap mellan "Matooke"-sorter. Detta visar genotypningens förmåga att exakt identifiera och validera kloner.

Dedication

To men and women who work tirelessly in rural agriculture to better their lives and ensure the survival of their families

"I can do all things through Christ who strengthens me"

 Philippians 4:13

Contents

List of publications

This thesis is based on the work contained in the following papers, referred to by Roman numerals in the text:

I.   Noel A. Madalla, Rony Swennen, Allan Brown, Sebastien Carpentier, Inge Van den Bergh, Rhiannon Crichton, Pricilla Marimo, Eva Weltzien, Cornel Massawe, Mpoki Shimwela, Daud Mbongo, Grace Kindimba, Jerome Kubiriba, Robooni Tumuhimbise, Asher W. Okurut, Martina Cavicchioli, Rodomiro Ortiz. Farmers' Preferences for East African Highland Cooking Banana 'Matooke' Hybrids. (Accepted)

II. Noel A. Madalla, Rony Swennen, Allan F. Brown, Cornel Massawe, Mpoki Shimwela, Daud Mbongo, Grace Kindimba, Jerome Kubiriba, Robooni Tumuhimbise, Asher W. Okurut, Sebastien Carpentier, Inge Van den Bergh, Rhiannon Crichton, Lewis Machida, Eva Weltzien, Rodomiro Ortiz (2022). Yield Stability of East African Highland Cooking Banana 'Matooke' Hybrids. *Journal of the American Society for Horticultural Science.* 147(6), 334–348. https://doi.org/10.21273/JASHS05246-22

III. Noel A. Madalla, Cornel Massawe, Mpoki Shimwela, Daud Mbongo, Grace Kindimba, Jerome Kubiriba, Ivan Arinaitwe, Kephas Nowakunda, Priver Namanya, Robooni Tumuhimbise, Asher W. Okurut, Adolf Saria, Munguatosha Ngomuo, Rony Swennen, Allan F. Brown, Michael Batte, Sebastien Carpentier, Inge Van den Bergh, Rhiannon Crichton, Pricilla Marimo, Eva Weltzien, Rodomiro Ortiz (2022). TARIBAN1, TARIBAN2, TARIBAN3, and TARIBAN4

'Matooke' Cooking Banana Cultivars for the Great Lakes Region of Africa. *HortScience*. 57(12), 1-5. https://doi.org/10.21273/HORTSCI16854-22

IV. Noel A. Madalla, Rony Swennen, Allan Brown, Moses Nyine, Michael Batte, Brigitte Uwimana, Sebastien Carpentier, Inge Van den Bergh, Rhiannon Crichton, Eva Weltzien, Pavla Christelová, Eva Hřibová, Cornel Massawe, Mpoki Shimwela, Daud Mbongo, Grace Kindimba, Jerome Kubiriba, Robooni Tumuhimbise, Asher W. Okurut, Rodomiro Ortiz. Microsatellite verification of East African Highland Cooking Banana 'Matooke' Hybrids. (Manuscript)

List of figures

Abbreviations

AMMI	Additive Main Effects Multiplicative Interaction
ANOVA	Analysis of Variance
AYT	Advanced Yield Trials
BLS	Black Leaf Streak
BLUP	Best Linear Unbiased Prediction
BW	Bunch Weight
DUS	Distinctiveness, Uniformity, and Stability
EAHBs	East African Highland Bananas
EET	Early Evaluation Trials
FGDs	Focus Group Discussions
GEI	Genotype-by-Environment Interaction
GS	Genetic Similarity
HMGV	Harmonic Mean of Genotypic Values
HMRPGV	Harmonic Mean of Relative Performance Genotypic Values
IITA	International Institute of Tropical Agriculture
INSL	Index of Non-Spotted Leaves
KASP	Kompetitive Allele Specific PCR
LRT	Likelihood Ratio Test
MET	Multi-Environments Trials
MMs	Mixed Models
NARO	Uganda's National Agriculture Research Organization
NPT	National Performance Trials
NSL	Number of Standing Leaves
PA	Preference Analysis
PCoA	Principal Coordinate Analysis
PCR	Polymerase Chain Reaction
PS	Preference Score

PVS	Participatory Varietal Selection
PYT	Preliminary Yield Trial
REML	Restricted Maximum Likelihood
RAPD	Random Amplified Polymorphic DNA
RFLP	Restriction Fragment Length Polymorphism
RPGV	Relative Performance of Genomic Values
SGD	Sustainable Development Goals
SPSS	Statistical Package for Social Science
SSR	Simple Sequence Repeats or Microsatellites
UPGMA	Unweighted Pair Group Method with Arithmetic Mean
VCU	Value for Cultivation and Use
WAASB	Weighted Average of the Absolute Scores
YLD	Yield Potential
YLS	Youngest Leaf Spotted

1. Introduction

The global human population is expected to increase by 1 billion people every 14 years, reaching 10 billion within 20 to 25 years, thereby necessitating 70 to 100% more crop production by that time to maintain a stable food supply (FAO, 2018). Furthermore, this goal must be achieved in the face of climate change (Foley et al., 2011). Breeders should use all possible technologies to improve yield to overcome these challenges. Improved cultivars with high edible yield, suitable end use quality, host plant resistance to major pests and pathogens, and adaptation to the target population of environments can help boost productivity when combined with sound crop husbandry practices. Banana (*Musa* sp.) –including dessert and cooking cultivars– is one of the 10 most important food crops grown in the world (FAO, 2014; Ortiz and Swennen, 2014). The crop feeds millions of people worldwide and is grown in more than 135 countries (Lescot, 2018). Approximately 145 million metric tons (MMT) of bananas and plantains are harvested annually throughout the world, with a market value of € 26.5 billion (Ortiz and Swennen, 2014; Brown et al., 2017). In sub-Saharan Africa, banana production is projected to reach over US$ 30 billion over the next 30 years, thereby approaching production of roots, tubers, and cereal crops, with local consumption expected to rise by 40 MMT (IFPRI, 2022).

East African highland bananas (EAHBs or designated as *Musa* AAA-EA), which include the cooking types ('Matooke') and brewing types ('Mbidde'), dominate production in the region and provide 3 to 22% of daily caloric intake, which is estimated to be 147 kilocal/person. They are also grown on about 30 to 40% of used agricultural land (Kalyebara et al., 2007; FAO, 2014; Tinzaara et al. 2018). EAHB plants thrive at elevations of 1,000 to

2,000 meters above sea level and are known as the second centre of banana diversity (the first being the Indo-Malaysian region of Asia) (Karamura, 1998). Most farmers in East Africa practice intercropping due to shrinking land sizes and the need for food security (Ouma 2009). When a banana plantation is established, it is frequently intercropped with beans (*Phaseolus vulgaris*), coffee (*Coffea arabica*), maize (*Zea mays*), and sweetpotatoes (*Ipomoea batatas*) (Gambart et al., 2020). Tree crops like ficus (*Ficus nataliensis*), jack fruit (*Artocarpus heterophillus*), and pawpaw (*Carica papaya*) are frequently left in banana fields to act as wind barriers (Gambart et al., 2020).

Several pathogens and pests threaten the long-term viability of EAHB production throughout the region (Stover and Simmonds, 1987; Swennen et al., 1989, 2013; Tushemereirwe et al., 2015), which must be considered for banana improvement. Pests such as the banana weevil *Cosmopolites sordidus* (Gold and Tinzaara, 2008), the burrowing nematode *Radopholus similis* (Dochez, 2004), the black leaf streak (BLS) pathogen *Pseudocercospora fijiensis* (Ortiz and Vuylsteke, 1994a), the fusarium wilt fungus *Fusarium oxysporum* f. sp. *cubense* (Arinaitwe et al., 2019), the banana bacterial wilt *Xanthomonas campestris* pv. *Musacearum* and *Banana bunchy top virus* (Tushemereirwe et al. 2015; Nakato et al., 2018) have had severe consequences for most of East Africa's major banana producing regions, with the potential to further destabilize both food security and household incomes (Van Asten et al., 2005; Barekye, 2009; Tushemereirwe et al., 2015).

EAHBs are quite susceptible to BLS (Kimunye et al., 2021). The pathogen negatively impacts the quality of the fruit after harvest, which is the main reason why importers reject banana fruit (Gold et al., 1993; Arias et al., 2003). BLS arrived in Africa in the late 1970s and quickly spread throughout the continent (Wilson and Buddenhagen, 1986). When left unchecked, the disease causes leaf decay, reducing photosynthetic area and potentially resulting in a significant reduction in yield or crop failure (Mobambo et al., 1993). These production limitations are further exacerbated by shorter fallow periods and a general decline in soil fertility as a result of increasing population pressure on available land resources (Bakry et al., 2009).

Banana on farm yields are low in comparison to their potential; Tanzania could produce up to 40 t·ha^{-1} per year, but only 5.7 to 7.5 t·ha^{-1} per year is the on farm harvest, and Uganda could produce up to 70 t·ha^{-1} per year, but only 5 to 20 t·ha^{-1} per year is being produced (van Asten et al., 2005; BMGF, 2014). The weight of a banana bunch has decreased from 60 kg to less than 10 kg (Barekye, 2009). Furthermore, plantation life has been reduced to less than five years, particularly in low-altitude areas, compared to 25 or 50 years or more in southwestern Uganda and southern Tanzania (Kikulwe et al., 2007; Nkuba, 2007). As a result, genetic improvement has become the most viable option, with a primary focus on developing cultivars resistant to major pests and pathogens. Banana hybridization is currently being pursued at seven research institutions worldwide, including Uganda's National Agriculture Research Organization (NARO) and the International Institute of Tropical Agriculture (IITA). Beginning in the mid-1990s, the goal of EAHBs hybridization was to find genotypes with a consistent high yield, host plant resistance to BLS, and other desirable qualities for farmers.

Evaluating improved banana cultivars in the target population of environments is a critical stage for increasing crop productivity, influencing adoption and informing breeding strategies. The main objective of this thesis was to increase understanding of the crucial factors that should be considered when evaluating and releasing improved 'Matooke' banana cultivars in East Africa. The study was able to identify adapted, stable, high-yielding, pathogen and pest resistant and farmers' preferred 'Matooke' hybrids in Uganda's western and central highlands, as well as Tanzania's northeastern and southern highlands. The findings of this study contributes to the Sustainable Development Goals (SGD), specifically SGD 2 and 1, which are about eradicating hunger and poverty in all of its forms, respectively, by 2030. This is because smallholder farmers in sub-Saharan Africa, where poverty and hunger are at their peak, grow bananas as both food and income crops. The farmers' livelihoods will therefore be improved by the efficient cultivation of new banana cultivars that are high yielding and suitable to grow in the target population of environments.
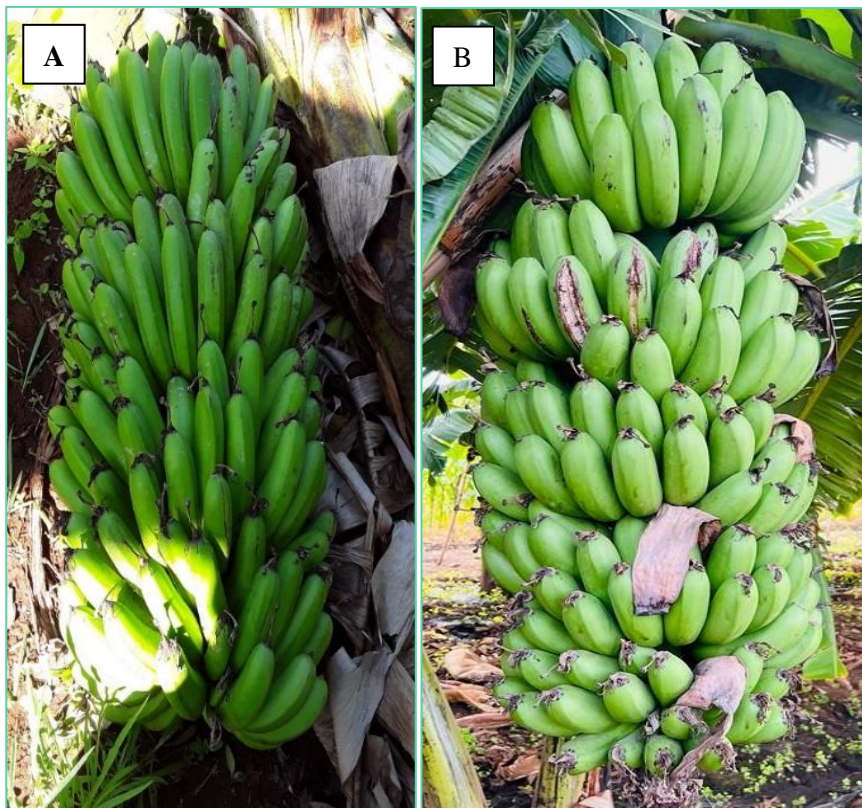
Figure 1. Bunches of 'Matooke' cooking banana cultivars (A: NARITA 7 and B: NARITA 23). These banana hybrids were evaluated for BLS resistance, yield stability and consumer acceptance in Tanzania and Uganda.

2. Background

2.1 Origin, domestication and genetic diversity

There has been conjecture regarding the origin of the first domesticated bananas in Africa for more than a century. Although other researchers such as De Langhe and colleagues (1994-1995, 1999, 2000) hypothesized that this occurred around 3,000 years ago based on biological, linguistic, and prehistoric evidence, Beed et al. (2012) believe that bananas were introduced to Africa between 2,000 and 6,000 years ago, much earlier than other important crops such as maize and cassava (Nayar, 2010). A recent discovery of banana phytoliths in Cameroon dating back to the first millennium BC has sparked debate about when this vital food crop was introduced to the continent (Mbida et al., 2000; Mbida et al., 2001; Lejju et al., 2006). A comparison of *Musa* and *Ensete* phytoliths revealed for the first time in Africa that those recovered from refuse pits excavated in central Cameroon and dated to around 2500 B.P. descended from the cultivated banana.

Edible bananas would have arrived from Southeast Asia via several introductions in the Great Lakes Region of East Africa, which includes Burundi, Democratic Republic of the Congo, Kenya, Rwanda, Uganda, and Tanzania, between the first and sixteenth centuries A.D. (Price, 1995; Karamura, 1998; Nayar, 2010). This region is considered as the secondary center of *Musa* genetic diversity, where the EAHBs underwent phenotypic diversification (Tugume et al., 2002). They are thought to have evolved from a single ancestor by clonal selection, and the phenotypic diversity of these cultivars is thought to be the result of an accumulation of somatic mutations (Shepherd, 1957; De Langhe, 1961; Ude et al., 2003; Kitavi et al., 2016).

According to recent research on the genetic diversity of EAHB, the diploid *M. acuminata* subspecies *zebrina* and *banksii* are putative parents of EAHBs (Pillay et al., 2001; Li et al., 2013; Kitavi et al., 2016; Němečková et al., 2018). This was also recently validated by Christelová et al. (2017) using simple sequence repeat (SSR) markers on more than 600 populations of wild diploid and cultivated triploid clones of bananas and plantains from East Africa.

There are more than 70 highland banana cultivars in East Africa (Baker and Simmonds, 1952; Swennen and Vuylsteke, 1991; Gold et al., 2002a). The population of Uganda and Tanzania enjoys the widest variety of specially adapted bananas. Banana cultivars have a significant degree of variation at the micro level, or on individual farms (Edmeades et al., 2006). At least seven banana cultivars are typically grown concurrently in a normal Ugandan household, as opposed to an average of 10 cultivars per household in Tanzania (Edmeades et al., 2007). The majority of cultivars grown by farmers are native to East Africa, and their distribution appears to be rather uniform across households. Farmers keep so many cultivars on their farms because they believe that each cultivar of banana has specific benefits and disadvantages in terms of both production and consumption requirements.

2.2 Ecology

Banana is widely distributed throughout the tropical and subtropical regions of the world between 30º North and 30º South of the equator. Fruits are harvested all year in suitable climates although some cultivars are photoperiod sensitive (Tixier et al., 2004; Zeller, 2005; Fortescue et al., 2011; Brown et al., 2017). Bananas can be grown in soils ranging from very sandy to very clayey, though the former may necessitate more frequent watering or a mulching system to maintain water content, while the latter causes aeration problems. A fruiting cycle can last up to two years.

Depending on climate, cultivation conditions, and cultivar, vegetative growth can last 6 to 12 months, and the time between inflorescence emergence and bunch harvesting can range from 2.5 to 10 months (Stover and Simmonds, 1987; Turner et al., 2007). The time it takes from planting to

shooting (inflorescence emergence) ranges between 180 and 250 days. Shoot to harvest time in most tropical areas below 500 m elevation ranges from 75 to 125 days, and in most subtropical areas ranges from 110 to 250 days. Temperature is the primary determinant of plant growth and fruit maturity. The optimal temperature for foliar growth is 26–28ºC (Ganry, 1980), and the optimal temperature for fruit development is slightly higher at 29–30ºC. Leaf scorch occurs at temperatures of 37ºC or higher, and growth ceases at 38–40ºC. In terms of low temperatures, foliar emergence, and all growth ceases around 10ºC (Aubert, 1971; Stover and Simmonds, 1987).

The hydric state of the banana plant, which is especially significant at 20ºC, is typically regarded as the second most essential component responsible for growth, development, and fruit production (Turner et al., 2007; Stevens et al., 2020). The plant needs a lot of water because of its rapid growth and wide foliar area, but it can tolerate a certain amount of drought by closing its stomata and maintaining a strong root pressure (Turner et al., 2007). According to estimates from Turner et al. (2007), a plant's typical daily water transpiration ranges from 5.6 mm when exposed to direct sunlight to 1.9 mm when completely cloudy. As the temperature rises, the amount required grows as well, and beyond 30°C, the water consumption can double. Cultivars more suited to subtropical climates are also better able to withstand winds up to 40 km/h. However, at greater speeds, crops suffer substantial losses, and winds of more than 55 km/h can destroy a plant.

2.3   Nutritional value and uses

Banana are good source of carbohydrates and fibre. They are high in essential vitamins A1, B1, B2 and C, as well as minerals such as potassium (Chandler, 1995). They have many nutritional benefits as a food, including starchy, pro-vitamin A carotenoids ranging from 0.23 to 59.56 g/g dry weight (Ekesa et al., 2012). Tanzania and Uganda population's uses banana fruit and stem in a variety of ways, however customer preferences vary according to different customs, palate preferences, and relative shortage (Kalyebara et al., 2007). As a result, a single cultivar can be used in numerous and varied ways both within and between communities (Nkuba et al., 2003). Compared to Uganda, Tanzania has consumption preferences that are less tied to the type of usage.

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Unlike Uganda, where the main dish is steamed, mashed banana or 'Matooke', Tanzania's main dish is a combination of banana, meat or beans, and vegetables. They can also be boiled, baked, dried, and pounded in a variety of ways (FAO, 1990; De Langhe et al., 2001).

Banana can also be used to make ropes, covers for fermenting cassava, nesting materials for egg-laying poultry, building materials for temporary shelters, sponges, and roofing material, all of which are made from dried leaves, leaf sheaths, and petioles, as well as the stalk that connects the leaf blade to the stem (De Langhe et al. 2001; Kamira et al., 2015). Furthermore, banana leaves are utilized for food wrapping, packaging, marketing, and serving (i.e., as plates) (Karamura, 1993; Kamira et al., 2015). Fruit peels are fed to animals as fodder, while dried peels are used to make soap (Akinyemi et al., 2010; Kamira et al., 2015). The banana plant serves as a source of food, medicine, and ornaments in Tanzania. The fruit's starch may be utilized for industrial purposes and the leaves can be used to make utensils, carpets, and thatch (Nkuba and Byabachwezi, 2003).

2.4 Crossbreeding

Since the 1920s, the development of cultivars resistant to pathogens and pests has been a top priority in all banana breeding programs. Banana genetic improvement formally began in the mid-1980s in Africa in response to an outbreak of BLS, and the rising financial and environmental costs of chemical treatment provided additional impetus for genetic improvement because no existing cultivar had innate resistance to this then new disease in sub-Saharan Africa (Tenkouano et al., 2011). The first banana breeding in East Africa, which began as a collaboration activity between NARO and IITA took a holistic approach, combining breeding pathogen-resistant cultivars and integrated pest management, which includes clean propagules and biological control, as well as better crop husbandry techniques for stable and sustainable 'Matooke' production. The primary goal was to improve EAHBs by identifying and incorporating host-plant resistance to BLS, weevils, and nematodes from wild diploid progenitors (Bakry et al., 2009).

Triploid female reproductive EAHB (AAA genome group) cultivars were crossed with the wild diploid accession 'Calcutta 4', which belongs to the AA subgroup *M. acuminata*. The chosen tetraploid hybrids were then crossed with improved diploids, and the resulting secondary triploid hybrids were selected after early evaluation trials, and further thoroughly evaluated during preliminary yield trials. A preliminary yield trial involves analysing a row of clonal hybrids, whereas an early evaluation involves evaluating single plants from a large population of hybrids. Selection was done with an emphasis on yield, resistance to BLS, and bunch orientation at each stage of evaluation. Identification of seed-producing 'Matooke' cultivars, which are rare and difficult to find, was one of the initial steps in the genetic improvement of EAHBs (Batte et al., 2019; Batte et al., 2021). This led to the initial assumption that crossbreeding of EAHBs was not feasible (Rowe, 1984). Parthenocarpy, low male fertility in some cultivars, low seed viability, irregular meiotic behaviour, lengthy generation times, and a diversity of genomic configurations were challenges to overcome for genetic improvement in this crop (Ortiz and Vuylsteke, 1994b; Ortiz and Swennen, 2014; Ortiz, 2015).

Often, it takes 1000 seeds from more than 1000 hand pollinations of 200 plants (0.12 ha) in the *Musa* breeding process to produce one chosen tetraploid banana/plantain-derived hybrid each year (Vuylsteke et al., 1997). The ABB cooking bananas have the highest seed set rates, followed by some French plantains and a few EAHBs from the Nfuuka clone set (Vuylsteke et al., 1993). Diploid bananas, on the other hand, are essential for genetic advancement due to the constrained genetic variability and low fertility of cultivated triploid bananas. *M. acuminata* accessions such as the wild 'Calcutta 4' –a source of resistance to BLS, yellow Sigatoka, fusarium wilt, banana weevil, and burrowing nematodes– have been used almost exclusively to improve diploid bananas (Ortiz, 2015). IITA and Fundación Hondureña de Investigación Agrícola (FHIA) in Honduras have released several improved fertile diploids with varying degrees of pathogen resistance (Rowe and Rosales, 1993; Tenkouano et al., 2003; Tenkouano et al., 2019).

It takes around 15 to 20 years to complete the breeding cycle from crossing to cultivar release. Some barriers to *Musa* genetic enhancement were solved

through ploidy manipulation, tissue culture techniques, and fertility screening of the germplasm. It is against this background that *Musa* breeders were able to develop novel EAHB 'Matooke' hybrids, specifically the primary and secondary triploid NARITA hybrids to be grown by farmers in the East African region. They were given the name NARITA to honour NARO and IITA's collaboration in breeding the hybrids.

2.5   Participatory farmers evaluation and cultivar release

Farmers' slow adoption of improved cultivars has continued to minimize benefits and impacts spill over to local communities, increasing the risk of food insecurity and vulnerability. Breeders' selection criteria have primarily focused on high yield, early maturity, and host plant resistance to pathogens and pests (Matooke breeding profile, 2018; Akankwasa et al., 2020; Gold et al., 2002b). However, many other desirable characteristics by end users, such as *inter alia* pulp colour, ease of peeling, or feed for animals, influence the acceptance and adoption of a banana cultivar (Thiele et al., 2021; Madalla et al., 2021). These characteristics can be difficult for breeders to assess meaningfully unless there is a research collaboration with farmers and social scientists. Incorporating farmer needs is critical not only for influencing adoption, but also for improving the efficiency and effectiveness of breeding efforts, especially in variable and marginal environments where adoption of improved cultivars from plant breeding programs has been limited.

Some researchers (Maru-Aduening et al., 2006) argued that farmers have their own performance and quality indicators, which are not always well anticipated by researchers. They are relatively consistent in their choices, and their choices correspond to their needs, preferences, cultural values, and local environments. As a result, most technologies developed without the participation of farmers have failed to adequately address the issues of rural poverty in Africa (Pretty et al., 2003). Furthermore, the selection criteria used by the researchers may not be applicable to the target population of environment. These differ in terms of soil type, moisture and temperature regimes, fertility, and the onset, intensity, and duration of rain, as well as social, cultural, and economic dimensions, where farmers thrive to grow their bananas. A variety of socioeconomic and institutional factors also impede

adoption. Farmers' low income and lack of education, poor promotion and weak extension systems, expensive and insufficient quantities of planting material, and delays in distributing approved planting materials all contribute to low adoption.

Participatory approaches are critical for better understanding on farm variation and increasing the chances of bred-germplasm adoption. Differences in characteristic preferences are also influenced by gender-specific needs and priorities (Teeken et al., 2018). According to Christinck et al. (2017), men prioritize production-related characteristics, whereas women prioritize gastronomic and post-harvest aspects. Breeders need to gain a thorough understanding of the needs and preferences of men and women farmers to develop cultivars that meet the needs of both genders (Miriti et al., 2013; Christinck et al., 2017). They also need to be able to prioritize these characteristics based on socioeconomic and environmental factors (Paris et al., 2011). Participatory varietal selection (PVS) techniques are frequently used to help identify new cultivars that farmers prefer to grow for the traits they value (Weltzien et al., 2019), as well as to facilitate their adoption and dissemination, all of which have positive effects. Thapa et al. (2009) assert that by using overall preference scores when choosing cultivars, farmers' preferences and preferred quality can be incorporated into the breeding program because these overall scores account for and balance out the effects of all pertinent characteristics. Bellon (2002) emphasizes the significance of a breeding strategy that considers characteristics that are essentially "products of human perception," or "subjective".

The seed certification institutes, on the other hand, are typically involved in a series of nationally performance trials (NPT) for at least three seasons of value for cultivation and use (VCU) as well as for distinctiveness, uniformity, and stability (DUS) tests to comply with requirements for official cultivar release in countries with varietal release systems. As a result, a variant of the multi-environment testing (MET) over several cropping cycles or years is usually conducted before the official release of the best bet selections.

2.6 Genotype-by-environment interaction

Researchers and farmers in any crop strive for more stable and high-yielding cultivars. Similarly, a banana breeder aims to develop a cultivar that thrives in a variety of settings. As a result, the primary goal of every plant breeding program is to direct cultivar selection onto its growing surroundings, which is a prerequisite for recommending novel selections for large-scale production (Annicchiarico, 2002). To accomplish this, breeding programs typically conduct a thorough evaluation of a group of diverse genotypes across locations and years, typically near the end of the cultivar development process. MET allows for the evaluation of genotypes' relative performance and stability in terms of yield and yield-related characteristics (Annicchiarico, 2002; Kang, 2004; Vaezi et al., 2019).

Likewise, MET analysis is used to determine the genotype-by-environment interaction (GEI), which is critical for proper discriminating and ranking of bred-germplasm, identifying top-yielding and stable genotypes for advancing or cultivar recommendations, and identifying the best breeding environments (Yan and Tinker, 2006). The genotype-by-location and genotype-by-crop cycle (or year or season) interactions are included in the GEI and may influence how well a genotype performs in different environments. For example, a clonal phenotype that corresponds to a particular genotype may change from year to year in the same location or from location to location within the target population of environments in the same year. Yield is a complex and multidimensional trait influenced by genotype (G), environment (E), and GEI. The GEI effect is important for breeders because it reflects yield variation that is not explained by individual G and E effects (Yan and Hunt, 2001; Ebdon and Gauch, 2002).

The genotype by environment interaction can provide useful information to breeders despite causing inconsistency in performance across environments and complicating cultivar selection (Busey, 1983; Magari and Kang, 1993; Kang, 1998). For example, a significant GEI may justify the need for additional broad-based testing in various environments and forecast the expected variability among testing sites (Busey, 1983). Yield and other quantitative traits also vary in heritability due to genotypic differences, environmental influences, and GEI (Bradshaw, 1965; Crossa et al., 1990).

The magnitudes of these variations are critical for designing a breeding strategy and improving selection responses. A variety of statistical models is reported in the literature because of numerous investigations have been conducted to address GEI in breeding (Smith et al., 2005; Malosetti et al., 2013).

The use of mixed models (MMs) in evaluating genotypic performance and stability for plant breeding is of particular interest because it combines estimation procedures such as restricted maximum likelihood (REML) to estimate variance components and best linear unbiased prediction (BLUP) to predict random effects. They enable non-biased genotypic value prediction as well as more accurate and reliable estimation of genetic and environmental parameters (Searle et al., 1992; Smith et al., 2005). The analyses treat genetic values as random effects, resulting in a more precise genetic value prediction for the candidates that is both unbiased and has a low prediction error variance (Henderson, 1985; Robinson, 1991; Piepho et al., 2008). The biggest advantage of MMs is the ability to combine data from various sources with varying degrees of unbalance into a complex model that will maximize the use of this data to estimate genetic parameters. For instance, MET analysis uses data from multiple trials where not every genotype is present at every site and where there may be variation in the number of replicates, precision, and consequently heritability for each site.

Predicted genotypic values can be used to determine the harmonic mean of relative performance of genotypic values (HMRPGV). The HMRPGV method put forth by Resende (2007a) in the context of MMs is one of the few methods that uses REML and BLUP, with the advantage of allowing analysis of unbalanced data. The genotypes can be simultaneously sorted by genotypic values (yield) and stability using the harmonic means of the BLUP in the HMRPGV method for stability analysis. As a result, the harmonic mean of genotypic values (HMGV) increases with decreasing standard deviation of genotypic performance among the locations. The relative performance of genotypic values (RPGV), which is measured across environments, is used for adaptability analysis. To obtain the average value of these ratios across all locations, the predicted genotypic values in this instance are expressed as a percentage of the general mean for each location.

The HMRPGV allows therefore for the simultaneous genotypic analysis of yield, adaptability, and stability (Resende, 2007a).

2.7 Genomic verification of EAHBs

DNA markers are helpful for population and quantitative genetics research in *Musa*, as well as taxonomy and cultivar true-to-type evaluation (Manzo-Sánchez et al., 2015). Several molecular markers, especially those linked to PCR-based methods, have been extensively used to estimate genetic variability and perform phylogenetic analyses in the banana (Ssebuliba et al., 2006; Kitavi et al., 2016). DNA markers include simple sequence repeats (SSR) or microsatellites, restriction fragment length polymorphisms (RFLP), random amplified polymorphic DNA (RAPD), expressed sequence tags (ESTs), single nucleotide polymorphisms (SNPs) and Kompetitive allele specific PCR (KASP). Microsatellite markers, with their high reproducibility and simple interpretation, has the greatest potential for use in the banana due to their ability to detect higher levels of polymorphism and their codominant inheritance (Selvi et al., 2003; Ortiz, 2015). They have been successfully used to analyse the genetic diversity of EAHBs local germplasm, widely cultivated cultivars, and some wild germplasm (Karamula, 1998; Ssebuliba et al., 2006; Kitavi et al., 2016; Nmeková et al., 2018). Little is known, however, about the recently developed hybrid "Matooke" germplasm, which possesses crucial adaption qualities for regional climatic settings and smallholdings. Only Nyine et al. (2017) and Batte et al. (2019) characterized with DNA markers the newly bred 'Matooke' germplasm (or NARITAs).

3. Thesis Aims

This thesis' main objective was to improve the understanding of the critical factors to consider when evaluating and releasing improved banana cultivars in East Africa. This is an important step for increasing crop productivity, influencing adoption, and informing breeding strategies.

Specific aims:
- To investigate the relative importance of characteristics used by farmers in Uganda and Tanzania to select improved 'Matooke' banana cultivars, and if there were differences in cultivars and characteristic preferences between men and women farmers.
- To identify high-yielding improved 'Matooke' banana cultivars with specific and broad adaptation potential across the East Africa region.
- To contribute to the release of four 'Matooke' hybrids banana cultivars with the potential of adoption by farmers in East Africa.
- To carry out molecular verification of newly bred cultivars, ensuring the release and supply of true-to-type banana cultivars to farmers.

4. Materials and Methods

Multisite evaluation trials were conducted in Uganda and Tanzania with the goal of selecting clones that combine host plant resistance to black leaf streak with stable high yield and other desirable quality characteristics, as well as assessing their adoption potential with farmers and consumers in comparison to their parental landraces and exotic cooking bananas (Fig. 2). Over a three-year period (from 2016 to 2019), 24 'Matooke' primary and secondary triploid hybrids NARITA, six 'Matooke' triploid local cultivars, and one exotic cultivar were evaluated for yield and other related traits across six sites in Uganda's western and central regions, as well as Tanzania's northeastern and southern highlands regions. The selected sites (Kawanda, Mbarara, and Sendusu in Uganda; and Maruku, Mitalula, and Lyamungo in Tanzania) are the key banana producing zones in both countries. In each block, 12 plants of each genotype were cultivated in a randomized complete block design with four replications. Sites in Tanzania and Uganda were planted in April and May of 2016, respectively. Farmers' site-specific landraces, as well as the widely cultivated 'Mbwazirume' (used as a common local cultivar check), were planted alongside a Cavendish 'Williams' (*Musa* AAA) banana cultivar, all of which are BLS susceptible. Local checks selected are a fair representative of what farmers are currently cultivating. The plants were placed 3 m apart, resulting in a 1152 plant/ha plant density. The planting hole had a diameter of 100 cm. Similar crop husbandry practices were used at Sendusu, where plant density was 1667 plants/ha.
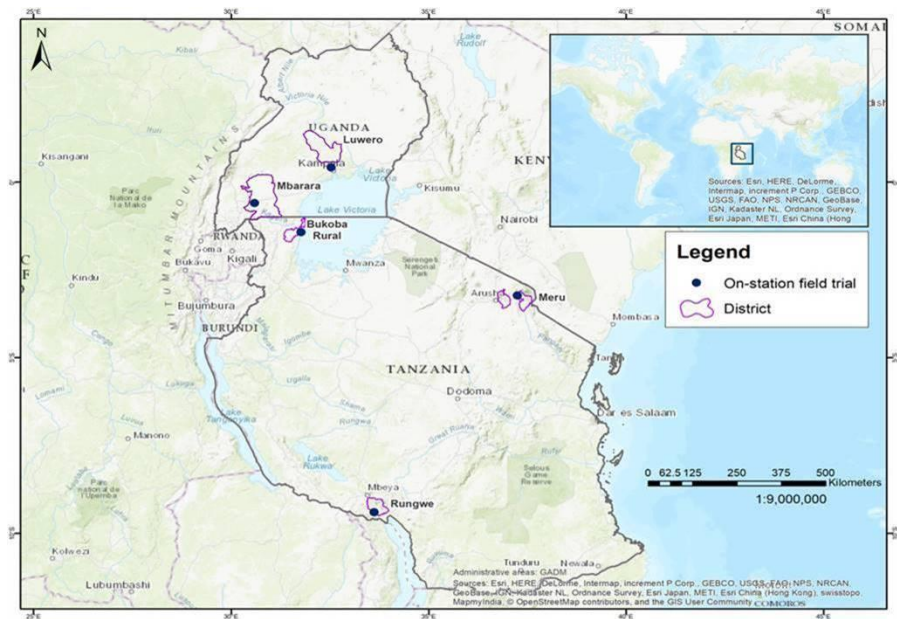
Figure 2. A map of the study sites in East Africa, including three highland sites in Uganda's western and central regions, as well as three sites in Tanzania's northeastern and southern highlands regions (Photo: David Brown).

4.1 Farmers preference analysis

During a field day in 2018, a group of 80 to 120 farmers visited the trial sites to visually assess the most desirable cultivars, which were then categorized on a quantitative scale to find the best ones based on the preference analysis score. Maruku had 34 men and 44 women, Mitalula had 88 men and 43 women, Lyamungo had 51 men and 51 women, Kawanda had 21 men and 79 women, and Mbarara had 62 men and 54 women. Along with the local village farmers, the group of farmers included farmers from nearby villages. District officials, extension personnel, and village leaders were used for farmer mobilization activities at each site three weeks before each exercise, identifying and listing banana-growing households with members of both genders and ages who voluntarily agreed to participate in the preference ranking exercise. One day prior to the exercise, the village leaders reminded

all farmers who had been chosen as participants. A total of 120 farmers were urged to participate at each site.

The preference analysis (PA) was carried out during the pre-harvest period, when most cultivars had attained approximately 80% physiological maturity (Paris et al., 2011). Because banana is a perennial crop that produces bunches all year, the investigation was undertaken during the peak season (from July to October 2018), when mother plants with advanced agronomic growth and a diverse range of plants with mature bunches were available. This exercise allowed men and women farmers to vote on their "most- and least-preferred" cultivars. Initially, farmers were asked to move around the field in groups, look at genotypes that had been coded and labelled, and classify the ideal visual characteristics for each cultivar, such as bunch size, leaves, stems, pathogen resistance, plant height, suckering potential and general plant appearance, with the aid of a researcher. Farmers were also allowed to discuss about cultivar appearance and traits they liked or disliked with other farmers. They could also ask the researchers for clarification on characteristics they could not see but were curious about, such as maturation period, or chop and peel a banana fruit to rate the pulp and sap colour and peeling difficulty. Farmers were then given three types of ballots to vote on 'like,' 'don't like,' and 'don't know,' each with the same number of cultivars to be voted on. They were instructed to vote for each cultivar individually by placing their ballots in a bag or envelope placed in front of each cultivar. Male and female farmers cast different coloured votes to highlight any gender differences in varietal preferences.

The preference score (PS) for each cultivar was calculated by adding the number of "liked" ballots (weight = 1), "do not know" ballots (weight = 0.5), and "do not like" ballots (weight = 0), multiplying by 100, and dividing by the total number of "liked," "do not know," and "do not like" ballots. The PS is a number between 0 and 100 that indicates how much the group of respondents liked the cultivar in question (0 – no one liked it; 100 – everyone liked it). A pre-formatted excel sheet was used to quickly enter the votes of the participating farmers and calculate the PS for each cultivar, disaggregated by gender.

$$PS(\%) = \frac{[(n_1 * 1) + (n_2 * 0.5) + (n_3 * 0)] * 100}{(n1 + n2 + n3)}$$

with n_1 = the number of 'like' ballots, n_2 = the number of 'do not know' ballots, n_3 = the number of 'do not like' ballots

The PS computation results were presented to the farmers for discussion of their reasons for selecting the most- and least-preferred cultivars. The names of the three most preferred and three least preferred cultivars for each gender were given to the participants. The group was then divided by gender, and participants discussed what they liked and disliked about the three most preferred cultivars and the three least preferred cultivars. The participants returned to the field to examine the characteristics of the selected cultivars. Enumerators facilitated the discussions, and a note taker jotted down observations on flipcharts. The participants, who were divided into two groups—one for men and one for women—then listed the most important criteria they consider when selecting a new banana cultivar, in order of importance. They also provided a short explanation for each. In the end, the PA usually generated two types of data: (a) a quantitative preference score for each cultivar, and (b) a list of characteristics that farmers liked about the preferred cultivars.

The quantitative data was analysed using the Statistical Package for Social Science (SPSS). Using content analysis, the qualitative information from farmers' focus group discussions (FGDs) was described. Based on each farmer's positive or negative votes assigned to each cultivar, the preference scores for local and hybrid cultivars at each location were calculated, and the Mann-Whitney U test was used to confirm the difference in farmer preference between local and hybrid cultivars at each location. To determine whether gender affected cultivar preferences, Wilcoxon's signed rank test was also used. Additionally, the relationship between male and female farmers' scores for cultivar preference as a selection criterion was examined using Spearman's rank correlation.

4.2   Yield potential and BLS resistance

Using mean data from the first two crop cycles, the yield potential [YLD (tonnes/hectare per year)] was calculated using the formula:

$$YLD = BW \times 365 \times PD/(DH \times 1000),$$

where BW and DH stand for bunch weight (fresh) and days to harvest, respectively, and 365 and PD stand for days per year and plant density per hectare, respectively (Swennen and De Langhe, 1985; Ortiz, 1997a; Tenkouano et al., 2019).

To evaluate the responsiveness of banana hybrids to BLS, the index of non-spotted leaves (INSL), which indirectly measures host plant resistance to BLS, was calculated using the following formula:

$$INSL = [(YLS - 1)/NSL] \times 100$$

YLS and NSL stand for the youngest leaf spotted and the number of standing leaves, respectively. When YLS is 0, YLS equals NSL plus 1. According to Viljoen et al. (2017), this index measures resistance and estimates the amount of photosynthetic leaf area that is available before the fruit fills.

4.3   Consumer acceptability test of 'Matooke' hybrids

On a scale of 1 to 5, with 1 denoting extreme dislike (i.e., very bad) and 5 denoting extreme liking (i.e., very good), a panel of more than 300 banana farmers from three Tanzanian sites completed the consumer acceptability tests of the cooked hybrid and common local cultivars based on the sensory qualities of taste, aroma, mouth feel (or texture in the mouth), color, texture in the hand, and overall acceptability (Marimo et al., 2020; Nowakunda and Tushemereirwe, 2004). Fruit that had been boiled was the main product that Tanzanian farmers evaluated. Farmers in Lyamungo evaluated the fruit as mtori, a local dish made by boiling banana fruits, mixing them with meat, and then smashing them to make a thick porridge, as well as machalari,

which is made by chopping bananas into pieces and mixing them with meat and other ingredients.

4.4 Variance components and genetic parameters

Using the R package multi-environmental trial analysis 'Metan,' the REML/BLUP mixed model approach was used to estimate variance components and genetic parameters for yield, assuming the effects of GEI to be random and the effects of environment and block/replicates within-environment to be fixed effects (Olivoto and Lúcio 2020; R Core Team 2021). The BLUP of the ith genotype was:

$$BLUP_i = \mu + \hat{g}_i$$

The effect of the ith genotype in the jth environment $\left(\hat{g}_{ij}\right)$ within $\mathbf{u}_{ge}$ was given as:

$$\hat{g}_{ij} = h_g^2(\bar{y}_{i.} - \bar{y}_{..}) + h_{ge}^2\left(y_{ij} - \bar{y}_{i.} - \bar{y}_j + \bar{y}_.\right)$$

where h_g^2 is the shrinkage effect for the genotype effect given by $h_g^2 = (\hat{\sigma}_{\alpha t}^2 + e\hat{\sigma}_\alpha^2)/(\hat{\sigma}_{\alpha t}^2 + \hat{\sigma}_\delta^2 + e\hat{\sigma}_\alpha^2)$, and $h_{ge}^2 = \hat{\sigma}_{\alpha \tau}^2/(\hat{\sigma}_{\alpha \tau}^2 + \hat{\sigma}_\varepsilon^2)$ is the shrinkage effect for GEI.

The BLUP of the ith genotype in the jth environment following Olivoto and Lúcio (2020) and Yang (2007) was:

$$\text{BLUP}_{ij} = \bar{y}_j + \hat{g}_{ij}$$

This methodology is an optimal procedure for unbalanced data.

The significance of the main effects and interactions was determined using a combined analysis of variance (ANOVA) on the mean yield data. To determine the significance of the model's genotypic effects, the likelihood ratio test (LRT) was used. The following genetic parameters were considered in the analysis of variance component: genotypic variance, variance of GEI, residual variance, phenotypic variance, broad-sense heritability, coefficient of determination for the genotype-vs-environment interaction effects,

heritability of the genotypic mean, accuracy of genotype selection (As), correlation between genotypic values across environments, genotypic coefficient of variation, and residual coefficient of variation.

4.5 Stability and adaptability analysis

The HMGV, RPGV, and HMRPGV were used to evaluate genotypes stability, adaptability, and yield. The HMGV is a stability indicator that compares predicted genotypic yield values (tonnes/hectare per year) that have been penalized for instability, enabling for the identification of both stable and high-yielding genotypes. Because of their low temporal and spatial variability, the best genotypes based on their HMGV must exhibit consistency in performance year after year/cycle, and across regions. In other words, the best genotypes are the ones that respond in a predictable manner when environmental conditions change. The RPGV, which refers to genotypes' ability to respond favourably to environmental changes, can be calculated on the same scale as yield (tonnes/hectare per year) by multiplying the RPGV value by the general mean to obtain the mean μ genotypic value (RPGV × μ). The HMRPGV is a simultaneous selection index for stability, adaptability, and mean performance that is expressed as a unique value that can be multiplied by to produce genotypic values for each genotype (HMRPGV × μ) that is penalized for instability and capitalized for GEI (Resende, 2007a, 2007b).

To evaluate genotypic stability using additive main effects multiplicative interaction (AMMI) biplots and to visualize the relationships between the performance of candidate genotypes and selection sites, we used the singular value decomposition of the matrix of BLUPs for the GEI effects generated by a liner mixed model (Gauch and Zobel, 1988; Gauch, 2013; Olivoto et al., 2019a). The biplots were generated by applying an AMMI-like analysis using the singular value decomposition (SVD) method to the shrunken GEI effects matrix of a BLUP-based mixed model. The linear mixed model with symmetric singular value partitioning ($\alpha = 1/2$) produced the double centered BLUP interaction effects matrix, from which the interaction principal components (IPCs) were obtained by fitting the SVD. The weighted average of the absolute scores (WAASB) from the singular value decomposition of

the matrix of BLUPs for the GEI effects produced by a linear mixed-effect model was used to quantify the genotypic stability of each genotype. According to Olivoto et al. (2019a, 2019b), the genotype with the lowest WAASB value —i.e., the one that deviates the least from the mean performance across sites— is the most stable.

4.6 Microsatellite verification of 'Matooke' hybrids

Sample for molecular characterization were collection only from plants that were visually identified as true-to-type for the purposes of verification. In each of the five field sites, 3 to 7 plant samples were collected for each cultivar depending on the number of available plants in a plot. This resulted in a total of 1002 banana samples, including triploid local cultivars, exotic cultivars, and primary and secondary triploid hybrids of the 'Matooke' called NARITA, were collected from three sites in Tanzania (Lyamungo, Maruku, and Mitalula) and two in Uganda (Kawanda and Mbarara). Fresh 10 cm long cigar-shaped banana leaves were plucked from young banana plants and delivered to the Institute of Experimental Botany in Olomouc, Czech Republic. Using flow cytometry, the ploidy level of each accession was determined to strengthen the characterization prior to SSR genotyping (Doležel et al., 1997). Genomic DNA was isolated from roughly 20 mg of lyophilized leaf tissues of young banana plants using a NucleoSpin Plant II kit (Macherey-Nagel, Duren, Germany) according to the manufacturer's protocol. Each sample replication was treated as an individual sample throughout the downstream analysis, with its own quality control code. The NanoDrop ND-1000 spectrophotometer was used to evaluate the concentration and purity of DNA. The accessions were genotyped using 19 informative *Musa* SSR primers. The primer list, polymerase chain reaction (PCR) parameters, and fragment analysis procedure were all based on Christelova et al. (2011). Two rounds of PCR were carried out independently on each sample. The SSR profile for each sample was determined using capillary electrophoresis on an ABI3730xl DNA analyzer.

The data were then analyzed using GeneMarker v1.75 software (Softgenetics, State College, PA, USA), manually checked, and then included in marker panels (Christelova' et al., 2011). Each sample's

concordance of alleles was meticulously reviewed and assessed. Only samples with discrepancy between the two results received a third round of PCR. To allow for joint analysis of all ploidy levels, alleles were rated as dominant markers for presence and absence (1/0). SSR data from NARITAs previously generated by Batte et al. (2019) using the same set of SSR markers were utilized as benchmarks for distinguishing true-to-type clones from separate field trials. The major allele frequency, number of alleles per marker, and polymorphism information content (PIC) were estimated using PowerMarker v3.25 software on the combined dataset. To determine the degree of genetic diversity among all samples, data were imported into R and Nei's genetic distance coefficients were calculated (Nei, 1973). The unweighted pair group method with arithmetic mean was then used to perform hierarchical clustering (UPGMA; Michener and Sokal, 1957). A dendrogram was created and shown using the R package 'ggtree' based on the findings of the UPGMA analysis. The merged dataset's principal components (PCs) were calculated using the R function prcomp. The first two PCs were plotted using 'ggplot2' algorithms to demonstrate sample clustering, and the subgroups were identified using different colours.

5. Results and discussion

5.1 Farmers' cultivar preferences

The trade-offs farmers make when choosing which cultivars to grow are influenced by their perceptions of the relative importance of various characteristics, which in turn affects their consumption and preferences. During the preference ranking, farmers were asked to vote for the cultivars they liked and disliked the least. The local cultivars 'Enyoya' (PS = 95), 'Nshakala' (PS = 93), 'Mbwazirume' (PS = 77), and 'Nakitembe' (PS = 76) were the most preferred cultivars by farmers. The PS values of the hybrids N2 and N23, which tied for the highest PS score of 75, were very close to those of local cultivars. N4 and N12 tied for the PS score (68) and were ranked among the top 10 most preferred cultivars. Numerous factors went into the selection of these cultivars, including large bunch size and related characteristics such as bunch marketability, medium plant stature, pathogen resistance, consumption, and animal feed attributes. Additionally, banana plant leaves and pseudostem vigour were mentioned. Farmers believe that a robust pseudostem and many leaves suggest a healthy plant that will generate a large yield, but the cultivar's capacity to endure environmental shocks while providing a constant production is believed to be connected to the host plant's resilience to pathogens.

Of the 30 hybrids and cultivars tested, N17 was the least liked (PS = 25), followed by the local cultivar 'Ndizi Uganda' (PS = 34), the hybrids N20 (PS = 35), N19 (PS = 39), and N10 (PS = 39). Farmers disliked these cultivars for a variety of reasons, including low yields, few short, compact fruits

despite maturation, difficulty in peeling, small bunch sizes, unsuitability for commercial use, small pseudostems, an unattractive overall appearance, and resemblance to a juice cultivar due to its excessively dark pseudostem. The wide range of farmers' perceptions of cultivar preferences demonstrates the diversity of opinions within the farming community as well as the factors that, if not considered during the breeding process, may be central to cultivar rejection. This disparity suggests that the variances are not random, but rather reflect the preferences of specific farming groups (Weltzien et al., 2008; Christinck et al., 2017).

Based on the preference scores established by each farmer's positive or negative votes assigned to each cultivar, the Mann-Whitney U test was used to confirm the difference in farmers' preference between local and hybrid cultivars at each site. The results showed that the local and hybrid cultivar preferences differed significantly ($P < 0.05$) at the Maruku site in Tanzania and the Kawanda site in Uganda. The differences were not significant ($P > 0.05$) at Mitalula and Lyamungo in Tanzania, as well as at Mbarara in Uganda. Farmers value both local and hybrid cultivars due to the benefits from their unique characteristics, as evidenced by the non-significant preference differences between local and hybrid cultivars at three of the five sites.

5.2   Farmers' characteristic preference

Farmers used a variety of approaches to define characteristics, with different sites and countries favouring different characteristics. This was particularly true for characteristics such as yield, marketability, cultural relevance, and host plant resistance to pests and pathogens, and abiotic stress tolerance. It was interesting to observe that farmers selected multiple characteristics, which is consistent with earlier research showing that smallholder farmers take a variety of factors into account when choosing and further adopting cultivars (Mulatu and Zelleke, 2002; Kolech et al., 2017; Acheampong et al., 2018). Tanzanian farmers preferred large bunches over other attributes such as bunch marketability and robust stem. Large fruit, drought tolerance, a strong stem, and phenotypic similarity to local cultivars were given priority over all other characteristics by Ugandan farmers. Large fruit, a large bunch,

market acceptability of the banana bunch, a sturdy stem, and an attractive appearance of the banana plant were the characteristics that mattered most to farmers in both countries. Farmers also preferred regulated suckering, pathogen resistance, early maturity, banana leaf suitability for animal feeds, medium plant stature, cultural relevance, and local uses such as the ability of banana plant residues to be used to make rope, food covers, or items to carry water, as well as the plant's ability to sustain leaves.

As bananas became more commercial, farmers' desire for large bunch size, which indicates a cultivar's marketability, was anticipated. Banana pests and pathogens are important problems in the region, but farmers did not consider them to be a crucial factor. This could be because hybrid bananas had few infections, indicating that new banana cultivars are pest- and pathogen-resistant, or it could be because farmers are having difficulty identifying pathogens, which could be related to farmers misidentifying the cause and effect of pests or pathogens. Farmers can select preferred genotypes to suit their environment as well as to meet quality and other consumer criteria (Hardon, 1995), but they may be limited in selecting for specific characteristics such as pathogen resistance due to a lack of knowledge. Hence, it has been suggested that local knowledge systems (farmers' knowledge) and science-based knowledge (breeders' knowledge) be combined in agricultural research and development through participatory approaches (Haverkort et al., 1991).

The fact that farmers valued the appearance of banana plants as a desirable characteristic, implying that they value the total value of a cultivar's characteristics more than individual attributes because it allowed them to predict how it would perform in different situations. The initial purchase price influences the market value of the cultivar, which is also significantly influenced by the appearance of the plant product.

5.3   Gender characteristic preferences

Knowing which characteristics men and women farmers as well as other value chain participants prefer allows for the development of novel cultivar product profiles with a higher likelihood of being accepted. Production

systems and the farmers' production objectives are two examples of several factors that affect how genders choose certain characteristics. Across sites, men preferred a large bunch, marketability, lots of suckers, large fruit, and vigorous stems. On the other hand, women valued a large bunch, followed by the appearance of the plant, the bunch, and the fruit, a robust stem, an early maturity, and pathogen and pest resistance. According to Weltzien et al. (2019) women's preferences for varietal characteristics are more frequently linked to aspects of food security such early maturation, postharvest processing, and food preparation. Farmers are conscious of their local environment as well as the crucial characteristics that new cultivars must possess, particularly as they strive to adapt to their demanding surroundings and production techniques. Thus, a sound methodology and gender-inclusive participation approaches are required for cultivar improvement programs at many levels, including internationally, regionally, nationally, and locally.

5.4 Analysis of variance and site mean performance.

Selection based on yield assessments in multiple environments is a critical step of cultivar development. GEI, or the differential response of test genotypes across target test environments, influences the effectiveness of selecting superior genotypes. The pooled analysis of variance validated the importance of multilocational testing of bred banana genotypes at six sites in Tanzania and Uganda prior to release, with statistical significance for yield variation of 41%, 28.7%, and 11.2% for E, G, and GEI, respectively. The average site's yield potential ranged widely, from 9.7 t·ha^{-1} per year in Maruku, Tanzania, to 24.3 t·ha^{-1} per year in Sendusu, Uganda, thereby demonstrating the influence of different environments on genotype performance.

5.5 Estimates of heritability and variance components

To plant breeders the question of what proportion of phenotypic variability is attributable to genetic factors is of central importance in allocating resources and designing breeding strategies to optimize cultivar development. Improving the estimation of trait heritability is critical for

increasing the rate of genetic gain. According to Ortiz and Tenkouano (2011), yield is a multigenic trait with continuous phenotypic variation, making it challenging to evaluate the effects of the underlying genes and ascertain how they are inherited. This study found that genetic variation between the 30 genotypes tested accounted for 40% of the variance in mean yield, with broad sense heritability for yield estimated as 0.33 in Uganda, 0.39 in Tanzania, and 0.4 across all sites. These findings demonstrated a reasonable gain associated with genetic difficulties of improving EAHB due to their low fertility, vegetatively propagated, hybrid-prone, and polyploidy nature.

The improvement of genetic gains in banana breeding programs and their implementation in farmers' fields, however, necessitates the integration of several factors, including germplasm resources, genomics, breeding, and agronomic practices, as well as improved seed delivery systems. Breeding programs can raise heritability estimates by a variety of means, including the use of partially repeated trials (p-rep) or non-replicated designs in cases when spatial changes can be made properly, as well as increasing the number of target locations for evaluations. Ssali et al. (2016) and Ortiz (1997b) found that the broad sense heritability of bunch weight of the secondary triploid banana 'Matooke' (*Musa* sp., AAA-EA) in Uganda and *Musa* germplasm in Nigeria, respectively, was 0.48 and 0.66.

Both the G and GEI effects were highly significant ($P < 0.001$) with reference to the LRT. G variation and GEI together accounted for 40.1% and 7.8%, respectively, of the phenotypic variation in yield across sites. In Tanzania, 39.2% of phenotypic yield variation was explained by G variation and 2.2% by GEI variation. In Uganda, G variation made up 33% of all phenotypic variation, while GEI made up a higher percentage (22.2%). The residual variance accounted for 58.6%, 44.9%, and 51.8%, respectively, of the phenotypic yield variation in Tanzania, Uganda, and across sites. In banana breeding, genetic variation provides the basis for selection. Because of its multigenic inheritance and phenotypic plasticity, the median genotypic variance reported in this study, as well as the significant residual variation, highlighted the complexity of the genetic architecture of yield in banana.

5.6   Cultivar stability and adaptability

Cultivars with dynamic stability are able to adapt to changes in the environment and significantly increase the expression of their yield, whereas those with static stability continue to perform nearly the same in diverse environments (Becker and Leon, 1988). As a result, it is critical to assess the GEI effect's magnitude, identify genotypes with known stability types to facilitate cultivar selection, and determine whether these are adapted to a variety of environments or to specific ones. Using BLUP-based indices, HMGV, RPGV, and HMRPGV, for selecting genotypes with high mean performance, stability, and adaptability, N23 had the highest yield associated with adaptability and stability across all sites. With an HMRPGV value of 22.5 t·ha^{-1} per year, this hybrid outperformed the average performance of all genotypes tested in Tanzania and Uganda by 34.2%. N17 was ranked second overall and second in Uganda, outperforming the overall average yield by 29.5%. The consistent performance of N23 and N17 indicate that they can be made available to farmers for growing in different target population of environments where they were tested while still yielding enough produce to supplement farmers' income and guarantee food security for rural livelihoods.

Hybrids N27, N18, N13, and N4 were ranked third, fourth, fifth, and sixth, respectively, in terms of yield, stability, and adaptability across all sites. Tanzania's top five for yield, stability, and adaptability were N23, N27, N7, N18, and N4, while Uganda's top five were N23, N17, N18, N2, and N8. Thus, the shared top five genotypes in both countries are N23 and N18, with the rest being specific to Tanzania and Uganda. Tanzania's N12, N13, N8, N9, and N25, as well as Uganda's N13, N12, N4, N24, and N11, performed well but did not make the top five. 'Mbwazirume', a local check, ranked 23rd out of 30 genotypes evaluated across sites, 20th out of 24 in Tanzania, and 16th out of 22 in Uganda. In Tanzania, the N23, N18, and N4 genotypes, as well as the N7 genotype in both Tanzania and Uganda, are four of the top 10 genotypes released in the last six years. These cultivar releases demonstrate the current success of banana breeding in East Africa.

5.7 Genotype-by-environment interaction biplot analyses

The magnitude of GEI has a direct impact on cultivar recommendation for large-scale production. Breeding for maximum yield is only possible in the presence of a suitable test environment. GEI allows for the identification of superior genotypes adapted to specific environments as well as the selection of genotypes with stability adapted to multiple environments. The first (PC1) and second (PC2) principal components accounted for ca. 100% of the variation in yield in Tanzania, 100% of the variation in Uganda, and 88.5% of the variation across sites. In Tanzania, PC1 explained 76.56% of the variance in G and GEI (GGE), while PC2 explained 23.44%. In Uganda, PC1 accounted for 88% of the GGE variance in yield, while PC2 accounted for 11%. PC1 was responsible for 81.9% of the GGE variance in yield across sites, while PC2 was responsible for 6.7%.

The genotypes with a high mean yield and stability are the best for broad adaptation. They are above the overall mean of main effect yield and located near the centre of the biplot. Genotypes N2, N4, N8, N12, N13, N18, N25, and N27 in Tanzania and N2, N4, N8, N12, N18, N13, N24, and 'Mpologama' in Uganda were deemed to be the best because banana breeders are frequently drawn to genotypes that are high-yielding and relatively more stable. The results of the biplots across sites supported the findings of the individual country analysis, which showed that N12, N8, N4, N18, N24, and 'Mpologoma' maintained a high level of stability among the genotypes that were stable in the individual country analysis. According to Yan and Kang (2003), stable genotypes guarantee consistent yields with little variation. The genotypes with the highest yields and average stability were N17 and N23 in Uganda and N7 and N23 in Tanzania, and they were adapted to Lyamungo and Sendusu, respectively. Similarly, N23 and N17 remained the top performing genotypes adapted to Lyamungo and Sendusu, respectively, in the cross-site analysis. Most genotypes, including N18, N4, and N13, were close to the biplot origin and above the grand mean in both the cross-site and individual country analyses, indicating high-yield and stability.

Tanzanian cultivars N19, N15, and 'Ndizi Uganda,' as well as Ugandan cultivars 'Kisansa,' 'Nakitembe,' and 'Mbwazirume,' had the lowest yield and

stability. N19, N15, 'Ndizi Uganda,' 'Enyoya,' 'Kisansa,' N16, 'Nakitembe,' and N14, all lower yielding genotypes, retained their position in the cross-site analysis. These findings show that most farmers' check cultivars had low and unstable yields, which may be related to their poor ability to withstand unpredictable weather conditions along with more severe pathogen effects. Similarly, Mitalula, Maruku, and Kawanda remained low yielding sites in both cross-site and individual country analyses. Due to poor genotype discrimination ability, Mitalula in Tanzania, as well as Kawanda and Mbarara in Uganda, contributed little to GEI. At the Tanzanian sites of Maruku and Lyamungo, as well as Sendusu in Uganda, the vectors were significantly longer, contributing significantly to the GEI. As a result, they have the ideal conditions for cultivar differentiation. Cross-site analysis confirmed that Sendusu and Mbarara in Uganda, as well as Lyamungo in Tanzania, provided an optimal environment for cultivar differentiation, i.e., discrimination ability.

5.8 Releasing 'Matooke' banana cultivars (TARIBANs)

TARIBAN1 (NARITA 4), TARIBAN2 (NARITA 7), TARIBAN3 (NARITA 18), and TARIBAN4 (NARITA 23) were released in Tanzania in 2021 and registered on Tanzania's national cultivar list, allowing them to be multiplied and distributed to farmers. They were tested in five Tanzanian and Ugandan locations over three cropping cycles (mother plant and at least two ratoons), with the final selection of prospective 'Matooke' hybrids guided by a product profile that includes host plant resistance to BLS, culinary acceptability, and bunch weight significantly higher than the standard local check 'Mbwazirume'. Four triploid hybrids had an average bunch weight of 26.0 to 34.0 kg across all sites, with potential yields of 16.0 to 20.0 t·ha^{-1} per year. Of the four hybrids, "TARIBAN2" had the heaviest bunch weight (34.2 kg), followed by "TARIBAN4", "TARIBAN1," and "TARIBAN3". The check cultivar, "Mbwazirume," had a bunch weight of 15.8 kg, proving that the "TARIBAN" hybrids have a heavier bunch weight. To increase family income, cultivars with a large bunch are preferred by banana growers, traders, and domestic users.

Three of the four "TARIBAN" hybrids had higher levels of BLS resistance than their susceptible EAHB parents and their reference genotypes, as measured by the proportion of INSL, according to the analysis of the YLS at flowering in the three Tanzanian sites. Although 'TARIBAN3' INSL score was lower than 'Mbwazirume', it still met the requirement of 70% to be deemed a resistant banana cultivar. In terms of colour, aroma, taste, mouthfeel, texture, and general acceptability, the sensory qualities of the hybrids were mostly like those of 'Mbwazirume'. Due to the superior quality of its cooked food, the 'Mbwazirume' cooking banana cultivar is one of the most well-liked by consumers.

5.9   Microsatellite verification of 'Matooke' hybrids

The true-to-type and phylogenetic relationships of 26 East African highland banana cultivars, exotic cultivars, and primary and secondary triploid hybrids of the 'Matooke' germplasm were confirmed using SSR markers. Based on genetic similarity (GS), cluster analysis using the unweighted pair group method with arithmetic mean (UPGMA) identified distinct germplasm clades. Clade II consisted of triploid local 'Matooke' cultivars such as 'Ndizi Uganda,' 'Mbwazirume,' 'Nakitembe,' and 'Kisansa,' all of which had 100% GS. These cultivars have some morphological similarity, which could be linked to a common ancestor. Clades I and III were made up of NARITAs, with most samples being true-to-type for each cultivar. N26 and N2, as well as the hybrids N11 and N12, were closely related and hence clustered together due to shared male or female parents. The Cavendish cultivar 'Williams' formed Clade IV. Principal component analysis (PCA) was then used to validate the UPGMA results. The PCA combined the two NARITA clusters into one, resulting in three primary clusters (EAHB, NARITAs and Cavendish). Despite the existence of several morphologically distinct types, there is very little genetic variation among all EAHBs. Similarly, SSR markers have shown to be very helpful for determining and validating authentic East African highland bananas as well as for studying genetic relationships. This demonstrates how useful genotyping can be for precisely identifying and validating clones. As a result, combining the use of QR codes at all stages of field banana clone management with genotype verification using a feasible and reproducible genotyping technique, such as SSR

markers, is a recommended practice to ensure the purity of cultivars provided to farmers. That is, before new cultivars or suckers are released or planted in the field, their DNA must be fingerprinted. Each clone must be kept true-to-type both on the farm and in *ex situ* genebanks.

6. Conclusions and future perspectives

This study found that farmers in Uganda and Tanzania prefer a combination of criteria other than yield-related attributes when adopting improved 'Matooke' banana cultivars. Yield, plant growth, bunch marketability, culinary features, and stem vigorousness were the key drivers of farmer preference selections in this study. Farmers in Uganda and Tanzania evaluate the cultivar's entire worth as they see it, allowing them to estimate how it will perform under different conditions. These findings suggest that breeding for productivity and consumption characteristics should continue to be a major priority for banana development. According to gender preferences analysis, women and men do not require different cultivars, but rather cultivars with characteristics that both genders desire. Breeding will contribute more successfully to resolving gender-differentiated trait preferences if it is based on a complete examination of the diverse goals, and priorities of men and women cultivating bananas in their plots. The study also found that the hybrids N23, N7, N4, N27, and N18 in Tanzania and N18, N4, N12, N24, N17, N2, and N23 in Uganda combine high yield, stability, and adaptability. As a result, it is recommended that these hybrids be released for cultivation of "Matooke" bananas in the target populations of environments in the East African region, which is where the testing sites were selected. These hybrids were ranked similarly across the three BLUP-based indices, thereby demonstrating their superior performance. The low association of INSL scores with yield, stability, and adaptability is evidence of these hybrids' high host BLS resistance. They can therefore be introduced with confidence in areas where BLS has a serious impact and imperils farmers' livelihoods. The ideal sites for future breeding evaluation are Lyamungo in Tanzania and Sendusu in Uganda since they have the highest mean yield productivity and good discrimination abilities. The six sites were also found to be different,

and their clustering suggested distinct groups that may be employed as discrete zones for cultivar evaluations and regional cultivar deployment.

The results of this investigation showed that, after more than 20 years of breeding, a reasonable level of genetic advancement for the yield trait was attained. The four recently released "Matooke" banana cultivars, which have the potential to yield twice as much as the widely used local check 'Mbwazirume', along with the farmers' preferred cooking quality and resistance to the BLS pathogen, could enhance the quality of life of millions of people in the East African region and ensure food security. This may be the best alternative because most other banana cultivars, such as "Mshare" and dessert banana cultivars like "Sukari Ndizi," are facing increasing pest and pathogen threats.

More than 90% of the cultivars were true-to-type following SSR molecular analysis, with some cultivars clustering together due to parental ties. The markers employed in the study were found to distinguish genotypes reasonably well, but they did not reveal any variation within the high similarity cultivars. The results of this study are anticipated to support *Musa* genetic resource preservation and impact assessment of bred banana cultivars. This shows even further how precise genotyping may allow for clone identification and verification. Therefore, combining the use of QR codes with genotype verification using a practical and repeatable genotyping technique, such as SSR markers, at all stages of handling banana clones is recommended as a strategy to ensure that the purity of cultivars is upheld and provided to farmers. Before new cultivars are made public or plantlets are planted in the field, genotyping is a vital step.

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Popular science summary

One of the biggest problems facing humanity is the eradication of poverty in all its manifestations. The Sustainable Development Goals (SDGs), were enacted by the United Nations in 2015 as a global call to action to eradicate poverty, safeguard the environment, and guarantee that by the year 2030, peace and prosperity will be experienced by everyone. The findings of this study will contribute to achieving Sustainable Development Goals (SDGs) 1 and 2, which are about eradicating poverty and hunger in all its forms by 2030. This is because smallholder farmers in sub-Saharan Africa, where poverty and hunger are at their peak, grow bananas as both food and income crops. The farmers' livelihoods will therefore be improved by the efficient cultivation of novel banana cultivars that are high yielding, stable and resistant to production constraints (i.e., pests and pathogens), while also meeting consumer acceptability qualities.

East African highland bananas (EAHBs or often referred to as 'Matooke,' designated *Musa* AAA-EA), which include the cooking types ('Matooke') and brewing types ('Mbidde'), dominate production in the region and provide 3 to 22% of daily caloric intake, which is estimated to be 147 kilocalories per person. Several pathogens (black leaf streak (BLS) *Pseudocercospora fijiensis*, fusarium wilt *Fusarium oxysporum* f. sp. *cubense*) and pests (burrowing nematode *Radopholus similis,* banana weevil *Cosmopolites sordidus*) threaten the long-term viability of EAHB production throughout the region (Stover and Simmonds 1987; Jones 1999), which must be considered for banana improvement. EAHBs are quite susceptible to BLS. The pathogen negatively impacts the quality of the fruit after harvest, which is the main reason why importers reject banana fruit (Gold et al., 1993; Arias et al., 2003). The main objective of this study was to improve understanding

of the critical factors to consider when evaluating improved banana cultivars in East Africa (EA). This is an important step for increasing crop productivity, influencing adoption, and informing breeding strategies. The study took four approaches to accomplish this: 1) investigated the relative importance of characteristics used by farmers in Uganda and Tanzania to select improved 'Matooke' banana cultivars, as well as whether there were cultivar and characteristic preferences differences between men and women farmers; 2) identified high-yielding improved 'Matooke' banana cultivars and selected cultivars with specific and broad adaptation potential in EA; 3) contributed to the release of four 'Matooke' banana cultivars with EA adoption potential by farmers; and 4) concluded by carrying out molecular verification of newly bred cultivars, ensuring the release and supply of true-to-type banana cultivars to farmers. Large fruit, a large bunch, market acceptability of the banana bunch, a sturdy stem, and an attractive appearance of the banana plant were the characteristics that preferred most to farmers in Tanzania and Uganda. Both men and women farmers were more concerned with production-related characteristics, but the former valued marketing-related characteristics more while the latter preferred use-related characteristics. Out of the 30 genotypes investigated, N23 outperformed the mean genotype-wide yield by 34.2% and had the highest yield at all sites related to adaptability and stability. N27 (2nd), N7 (3rd), N18 (4th), N4 (5th), N12 (6th), and N13 (7th) in Tanzania and N17 (2nd), N18 (3rd), N2 (4th), N8 (5th), N13 (6th), N12 (7th), N4 (8th), and N24 (9th) in Uganda showed high yield and good adaptability. Lyamungo in Tanzania and Sendusu in Uganda were the best sites for discriminating breeding clones. As a result, these testing locations are suggested as prime examples of locations to test and choose superior genotypes. Furthermore, *Pseudocercospora fijiensis*, a BLS fungal pathogen, had no significant effect ($P > 0.05$) on the hybrids' yield, stability, or adaptability. To meet end-user demand, hybrids must balance high production, host plant tolerance to pests and diseases, and desired culinary quality. As a result, four 'Matooke' hybrids were chosen and released in Tanzania in June 2021 in accordance with the requirements of a national varietal release system and the standards established for a 'Matooke' product profile, which included host plant resistance to BLS, culinary acceptability, and a high potential yield that was significantly higher than the standard local check 'Mbwazirume'.

Microsatellite (SSR) analysis revealed that more than 90% of the cultivars were true to type, with certain cultivars grouping together due to parental ties. The SSR markers used in this study produced repeatable polymorphic bands in 26 'Matooke' and 'Cavendish' banana cultivars, proving their utility as a powerful molecular tool for investigating genetic diversity and relationships among 'Matooke' cultivars. This demonstrates genotyping's potential for precisely identifying and validating clones.

Populärvetenskaplig sammanfattning

Ett av de största problemen som mänskligheten står inför är utrotning av fattigdom i alla dess yttringar. De hållbara utvecklingsmålen (Sustainable Development Goals, eller SDGs), antogs av FN 2015 som en global uppmaning till handling för att utrota fattigdom, skydda miljön och garantera att till år 2030 kommer alla att leva i fred och välstånd. Resultaten av denna studie kommer att bidra till att uppnå utvecklingsmål 1 och 2, som handlar om att utrota fattigdom och hunger i alla dess former till 2030. Detta beror på att småbrukare i Afrika söder om Sahara, där fattigdom och hunger råder, odlar bananer som både mat- och inkomstgrödor. Böndernas försörjning kommer därför att förbättras genom effektiv odling av nya banansorter som är högavkastande, stabila och resistenta mot produktionsbegränsningar (d.v.s. skadedjur och sjukdomar), samtidigt som de uppfyller egenskaper kopplade till konsumentpreferenser.

Östafrikanska höglandsbananer (EAHBs eller "Matooke", betecknad *Musa AAA-EA*), som inkluderar matlagningstyperna ("Matooke") och bryggtyperna ("Mbidde"), dominerar produktionen i regionen och ger 3 till 22% av det dagliga kaloriintaget, vilket uppskattas till 147 kilokalorier per person. Flera patogener ("black leaf streak" (BLS) *Pseudocercospora fijiensis*, "fusarium wilt" *Fusarium oxysporum* f. sp. *cubense*) och skadedjur (den grävande nematoden *Radopholus similis*, bananvivel *Cosmopolites sordidus*) hotar den långsiktiga livskraften för EAHB-produktionen i hela regionen (Simmonds 1987; Jones 1999), vilket måste tas i beaktande vid utvecklingen av nya banansorter. EAHB är relativt mottagliga för BLS. Patogenen påverkar kvaliteten på frukten negativt efter skörd, vilket är huvudorsaken till att importörer avvisar bananfrukt (Gold et al., 1993; Arias et al., 2003). Huvudsyftet med denna studie var att öka förståelsen för de

kritiska faktorer som bör beaktas vid utvärdering av förbättrade banansorter i Östafrika (ÖA). Detta är ett viktigt steg för att öka grödans produktivitet, påverka användningen och informera om förädlingsstrategier. Studien riktade in sig på fyra tillvägagångssätt för att åstadkomma detta: 1) genom att undersöka den relativa betydelsen av sortegenskaper som används av bönder i Uganda och Tanzania för att välja förbättrade "Matooke"-banansorter, samt om det finns skillnader mellan olika sort- och karaktärpreferenser mellan manliga och kvinnliga jordbrukare; 2) genom att identifiera högavkastande förbättrade "Matooke"-banansorter samt sorter med specifik och bred anpassningspotential i ÖA; 3) genom att bidra till att lantbrukarna fick tillgång till fyra nya "Matooke"-banansorter med ÖA-adoptionspotential; och 4) samt genom att utföra molekylär verifiering av nyframtagna sorter, för att säkerställa introduceringen och leveransen av typtrogna banansorter till jordbrukare.

Stor frukt, en stor klase, marknadsacceptans för bananklasen, en robust stjälk och ett attraktivt utseende på bananplantan var de egenskaper som föredrogs mest av jordbrukare i Tanzania och Uganda. Både manliga och kvinnliga jordbrukare var mer angelägna om produktionsrelaterade egenskaper, men de förra värderade marknadsföringsrelaterade egenskaper mer medan de senare föredrog användningsrelaterade egenskaper. Av de 30 undersökta genotyperna överträffade N23 den genomsnittliga genotypomfattande avkastningen med 34,2 % och hade den högsta avkastningen på alla platser relaterade till anpassningsförmåga och stabilitet. N27 (2:a), N7 (3:a), N18 (4:a), N4 (5:a), N12 (6:a) och N13 (7:a) i Tanzania och N17 (2:a), N18 (3:a), N2 (4:a), N8 (5:a), N13 (6:a), N12 (7:a), N4 (8:a) och N24 (9:a) i Uganda visade hög avkastning och god anpassningsförmåga. Lyamungo i Tanzania och Sendusu i Uganda var de bästa platserna för att urskilja förädlingskloner. Som ett resultat föreslås dessa som testplatser för att testa och välja överlägsna genotyper. Dessutom hade *Pseudocercospora fijiensis*, en BLS-svamppatogen, ingen signifikant effekt (P > 0,05) på hybridernas avkastning, stabilitet eller anpassningsförmåga. För att möta slutanvändarnas efterfråga måste hybrider balansera hög produktion, tolerans mot skadedjur och sjukdomar och önskad kulinarisk kvalitet. Som ett resultat valdes fyra "Matooke"-hybrider ut och släpptes i Tanzania i juni 2021 i enlighet med kraven i ett nationellt sortintroduktionssssystem och de standarder som fastställts för en "Matooke"-produktprofil, som inkluderade resistens mot

BLS, kulinarisk acceptans och en hög potentiell avkastning som var betydligt högre än den lokala standarden "Mbwazirume". Mikrosatellitanalys (SSR) visade att mer än 90 % av sorterna var typtrogna, där vissa sorter grupperade sig utifrån föräldraband. SSR-markörerna som användes i denna studie producerade repeterbara polymorfa band i 26 "Matooke" och "Cavendish" banansorter, vilket bevisar deras användbarhet som ett kraftfullt molekylärt verktyg för att undersöka genetisk mångfald och relationer mellan "Matooke" sorter. Detta visar genotypningens potential för exakt identifiering.

Acknowledgements

First, I would like to thank God Almighty for giving me the strength, knowledge, ability and opportunity to undertake this study and to persevere and complete it satisfactory. This achievement would not have been possible without his blessing. My profound gratitude goes to my supervisors, Prof. Rodomiro Ortiz, Prof. Rony Swennen, Prof. Sebastien Carpentier, Dr. Eva Weltzien, and Dr. Allan Brown, for their guidance throughout this monumental undertaking. They gave me invaluable advice and supported me during difficult times. Their motivation and assistance were enormously helpful in completing my studies successfully.

This work would not have been possible without the collaboration of the International Institute of Tropical Agriculture (IITA), The Alliance of Bioversity International and Centro Internacional de Agricultura Tropical (ABC), The Swedish University of Agriculture Science (SLU), Tanzania Agricultural Research Institute (TARI), and Uganda's National Agricultural Research Organization (NARO). In relation to that, I would like to thank IITA for funding my PhD education and reseach through the project "Accelerated breeding better bananas". Special thanks also goes out to ABC, my employer, for helping me out throughout the entirety of my PhD education.

I would like to express my gratitude to SLU, in particular the department of plant breeding, for providing me with a favourable learning and working environment that included highly qualified and competent teachers, highly experienced researchers, and a welcoming staff. Such a setting was essential for me to finish my research in the time allotted and to obtain the results of

the PhD. education. I would like to end by saying how much I appreciate my family's love and support. The focal point of my life is you.

Yield Stability of East African Highland Cooking Banana 'Matooke' Hybrids

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Abstract. East African banana (*Musa* sp.) breeding efforts have focused mainly on enhancing 'Matooke' productivity through the development of high-yielding, pathogen-resistant cultivars with adequate stability to contribute to regional food security. Before a breeding program can recommend promising cultivars for release, they must pass the sensory screens; be evaluated in the target population environments; and the data analyzed for yield, adaptability, and stability. Twenty-four primary and secondary triploid hybrids [NARITA (N)] derived from 'Matooke' bananas, six triploid local 'Matooke' cultivars, and one exotic cultivar were evaluated for their yield, adaptability, and stability across the East African region at three highland sites in Uganda's western and central regions, as well as at three sites in Tanzania's northeastern and southern highlands regions, from 2016–19. A randomized complete block design with four replicates was used for multisite trials. The mixed-model restricted maximum likelihood/best linear unbiased prediction approach, along with additive main effect multiplicative interaction model biplots, were used to dissect and visualize genotype-by-environment patterns. Following the likelihood ratio test, both genotype and interaction effects were highly significant, confirming the influence of genotype and site heterogeneity for selecting specific and broadly adapted cultivars. N23 had the greatest yield across all sites associated with adaptability and stability, outperforming the overall mean yield of all genotypes by 34.2%. In Tanzania, N27 (second), N7 (third), N18 (fourth), N4 (fifth), N12 (sixth), and N13 (seventh); and in Uganda, N17 (second), N18 (third), N2 (fourth), N8 (fifth), N13 (sixth), N12 (seventh), N4 (eighth), and N24 (ninth) demonstrated good adaptability and stability, as well as high yield. Furthermore, the fungal pathogen *Pseudocercospora fijiensis* had no significant effect ($P > 0.05$) on yield, stability, and adaptability of the hybrids. As a result, they can be introduced into areas where black leaf streak constrains banana production significantly and threatens farmers' livelihoods. The average site yield potential ranged from 9.7 to 24.3 t·ha⁻¹ per year. The best discriminating sites for testing breeding clones were Lyamungo in Tanzania and Sendusu in Uganda. Hence, these testing sites are recommended as ideal examples of locations for selecting superior genotypes.

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Bananas (*Musa* sp.) are among the 10 most important food crops worldwide. They include dessert, beer, and cooking cultivars (Food and Agriculture Organization of the United Nations 2014; Ortiz and Swennen 2014). They are popular in more than 150 nations because of their year-round production and high demand (Uma et al. 2011). With a global production of 145 million tonnes, worth $26.3 billion, the crop feeds millions of people worldwide (Brown et al. 2017; Lescot 2018). Most banana and plantain cultivars grown are intraspecific or interspecific triploid (2n = 3× = 33) hybrids derived from the diploid (2n = 2× = 22) *Musa acuminata* and *Musa balbisiana*, respectively (Ortiz and Vuylsteke 1994b). Wild species are diploid, whereas cultivars are diploid, triploid, and tetraploid (2n = 4× = 44) after natural or artificial hybridization (Robinson 1996).

The AAA triploids of the 'Mutika' subgroup, originally named 'Mutika-Lujugira' by Shepherd (1957), and often referred to as East African Highland bananas (EAHBs), are the edible derivatives of the wild species *M. acuminata* ssp. *zebrina* and ssp. *banksii* (Karamura and Pickersgill 1999; Kitavi et al. 2016; Li et al. 2013). They are farmer-selected cultivars that dominate the East African Great Lakes region (Karamura 1998; Perrier et al. 2019; Pillay et al. 2001). Their fruit provide between 3% to 22% of daily caloric intake, estimated to be 147 kilocal/ person, and generate more than $4.3 billion per year, or roughly 5% of the region's gross domestic product (Food and Agriculture Organization of the United Nations 2014; Kalyebara et al. 2007; Tinzaara et al. 2018).

Primary and secondary triploid EAHB hybrids, as well as their parental landraces and exotic cooking bananas, developed by Uganda's National Agriculture Research Organization and the International Institute of Tropical Agriculture, have been evaluated across Uganda's and Tanzania's diverse agroecozones (Tushemereirwe et al. 2015). The goal of this set of multilocational trials was to find genotypes with resistance to the leaf spot disease black leaf streak (BLS) caused by the airborne fungal pathogen *Pseudocercospora fijiensis*, as well as genotypes that demonstrate a consistent high yield and other desirable characteristics for farmers and consumers. The impetus was a significant drop in EAHB productivity resulting from several biotic constraints including BLS (Ortiz and Vuylsteke 1994a; Swennen and Vuylsteke 1993; Swennen et al. 1989, 2013; Tushemereirwe et al. 2015; Vuylsteke et al. 1993). As a result, female fertile triploid EAHB cultivars were crossed with a BLS-resistant male wild diploid banana ['Calcutta 4', AA (Tushemereirwe et al. 2015)]. The hybrid progeny produced ranged in ploidy level, with the vast majority being tetraploids. Because these primary tetraploids were more fertile than their triploid parents, they were crossed with improved diploids to produce the BLS-resistant triploid hybrids known as NARITA (N) (Batte 2019; Tushemereirwe et al. 2015).

In any crop, researchers and farmers aspire for more stable and high-yielding cultivars. Similarly, for banana, a breeder generally desires to develop a cultivar that thrives adequately in different environments. As a result, targeting cultivar selection onto its growing environment is the prime interest of any plant breeding program and a prerequisite for the recommendation of novel selections for large-scale production (Annicchiarico 2002). To achieve these goals, breeding programs usually undertake a rigorous evaluation of the performance of a set of diverse genotypes across locations and over years, mostly during the final stage of the cultivar development process. Multi-environment trials (METs) allow for the assessment of genotypes' relative performance and stability for yield and yield-related traits (Annicchiarico 2002; Kang 2004; Vaezi et al. 2019).

Yield is a complex trait that is influenced by genotype, environment (E), and genotype-by-environment interactions (GEIs). For breeders, the GEIs effect is important because it reflects yield variation not explained by individual genotypic and environmental effects (Ebdon and Gauch 2002; Yan and Hunt 2001). Although GEIs cause inconsistency in performance across environments and complicate cultivar selection, they can provide useful information to breeders (Busey 1983; Kang 1998; Magari and Kang 1993). For example, they justify the need for additional wide-based testing in different environments and predict the variability expected among testing sites (Busey 1983). The heritability and phenotypic expression of yield and other quantitative traits also vary as a result of genotypic differences, environmental influences, and GEIs (Bradshaw 1965; Crossa et al. 1990). The magnitudes of these variations are important when designing a breeding strategy and improving selection responses. Several numerical and graphical stability analyses are available that determine GEIs to recommend better performing and higher yielding genotypes across different environments (Ortiz and Ekanayake 2000).

Mixed models' restricted maximum likelihood and best linear unbiased prediction (BLUP) have been shown to be effective in evaluating genotypic performance and stability (Henderson 1975; Patterson and Thompson 1971). They allow for more accurate and reliable estimation of genetic and environmental parameters, as well as nonbiased genotypic value prediction (Searle et al. 1992; Smith et al. 2005). The analyses treat genetic values as random effects, resulting in a more accurate prediction of the candidates' genetic value, which is both unbiased and has a low prediction error variance (Henderson 1985; Piepho et al. 2008; Robinson 1991). Furthermore, mixed-model approaches reduce the noise caused by unbalanced designs and non-additive traits, both of which are common problems with MET data (Hu 2015; Piepho 1994). Predicted genotypic values, on the other hand, can be used to calculate the harmonic mean of relative performance of genotypic values (HMRPGV). This method has been used to evaluate the adaptability and genotypic stability of crops such as winter oilseed rape [*Brassica napus* (Bocianowski and Liersch 2021)], sugarcane [*Saccharum officinarum* (Bajpai and Kumar 2005)], and wheat [*Triticum aestivum* (Mohammadi and Amri 2008)]. It allows for simultaneous selection of stability, adaptability, and mean performance, which are expressed as a unique value that can be multiplied by the general mean (μ) to produce genotypic values for each genotype (HMRPGV × μ) that are penalized for instability and capitalized for GEIs.

The objectives of our research were to identify high-yielding banana genotypes and estimate variance components as well as broad sense heritability for yield, and to select cultivars with specific and wide adaptation potential across the East African region. Our results should assist banana breeders in East Africa

Table 1. Code, name, and origin of 30 banana genotypes evaluated for yield potential and stability in six Tanzanian and Ugandan sites between 2016 and 2019, as well as their use, cultivar type, and ploidy level.

Genotype code[i]	Genotype[ii]	Origin	Use	Type	Ploidy level
N2	NARITA 2	IITA/NARO	Food	Hybrid	3×
N4	NARITA 4	IITA/NARO	Food	Hybrid	3×
N6	NARITA 6	IITA/NARO	Food	Hybrid	3×
N7	NARITA 7	IITA/NARO	Food	Hybrid	3×
N8	NARITA 8	IITA/NARO	Juice	Hybrid	3×
N9	NARITA 9	IITA/NARO	Juice	Hybrid	3×
N10	NARITA 10	IITA/NARO	Juice	Hybrid	3×
N11	NARITA 11	IITA/NARO	Food	Hybrid	3×
N12	NARITA 12	IITA/NARO	Food	Hybrid	3×
N13	NARITA 13	IITA/NARO	Juice	Hybrid	3×
N14	NARITA 14	IITA/NARO	Food	Hybrid	3×
N15	NARITA 15	IITA/NARO	Food	Hybrid	3×
N16	NARITA 16	IITA/NARO	Juice	Hybrid	3×
N17	NARITA 17	IITA/NARO	Food	Hybrid	3×
N18	NARITA 18	IITA/NARO	Food	Hybrid	3×
N19	NARITA 19	IITA/NARO	Food	Hybrid	3×
N20	NARITA 20	IITA/NARO	Food	Hybrid	3×
N21	NARITA 21	IITA/NARO	Juice	Hybrid	3×
N22	NARITA 22	IITA/NARO	Food	Hybrid	3×
N23	NARITA 23	IITA/NARO	Food	Hybrid	3×
N24	NARITA 24	IITA/NARO	Food	Hybrid	3×
N25	NARITA 25	IITA/NARO	Food	Hybrid	3×
N26	NARITA 26	IITA/NARO	Food	Hybrid	3×
N27	NARITA 27	IITA/NARO	Food	Hybrid	3×
Mbwaz	Mbwazirume	Farmer selection	Food	Local cultivar	3×
Kisa	Kisansa	Farmer selection	Food	Local cultivar	3×
Nak	Nakitembe	Farmer selection	Food	Local cultivar	3×
Mpolo	Mpologoma	Farmer selection	Food	Local cultivar	3×
NdizUg	Ndizi Uganda	Farmer selection	Food	Local cultivar	3×
Eny	Enyoya	Farmer selection	Food	Local cultivar	3×
Wil	Williams	Farmer selection	Dessert	Exotic cultivar	3×

[i] Entry N22 was eliminated from analysis because of a very low number of plants stand in all sites.
[ii] NARITA are primary and secondary triploid hybrids. 'Mbwazirume' is a standard local cultivar planted in five sites, excluding Sendusu. Site-specific local cultivars Kisansa and Nakitembe were planted in Kawanda and Mbarara, 'Ndizi Uganda' in Lyamungo and Mitalula, 'Enyoya' in Maruku, and 'Mpologoma' in Sendusu. 'Williams' is giant Cavendish and a black leaf streak–susceptible cultivar.
IITA = International Institute of Tropical Agriculture; NARO = National Agriculture Research Organization (in Uganda).

and other similar environments in planning large-scale evaluation trials of promising cultivars or breeding lines before their official release to target environments.

Materials and Methods

Twenty-four 'Matooke' primary and secondary triploid NARITA hybrids, six 'Matooke' triploid local cultivars, and one exotic cultivar were evaluated for yield and other related traits across six sites in Uganda's western and central regions, as well as in Tanzania's northeastern and southern highlands regions (namely, Kilimanjaro, Kagera, and Mbeya) spanning a 3-year period (2016–19). The selected areas are the main banana-producing zones in both countries and were Kawanda, Mbarara, and Sendusu in Uganda; and Maruku, Mitalula, and Lyamungo in Tanzania. Tables 1 and 2 provide detailed information on the genotypes tested, the six sites, their rainfall, and other environmental characteristics. Twelve plants of each genotype were raised in each block in a randomized complete block design with four replications. Tanzanian and Ugandan sites were planted in April and May 2016, respectively. Farmers' site-specific landraces,

as well as the widely grown 'Mbwazirume' (used as a common local cultivar check), were planted alongside a reference banana Cavendish 'Williams' (*Musa* AAA), which are all BLS-susceptible cultivars. The selected local checks are a good representation of what farmers are currently growing.

The plants were spaced 3 m apart, yielding a plant density of 1152 plants/ha. The planting hole was 100 cm in diameter. Some plants died after planting because of a variety of factors, including drought, and were replaced with suckers from surviving mats of the same cultivar in the trial. To reduce competition for food and water, three plants were kept per mat (i.e., mother plant, daughter, and granddaughter). Farmyard manure was placed in the holes before planting at a rate of 10 kg/plant. Weeding was done every 2 to 3 months. Dead leaves were removed on a regular basis. Mulching was performed at the start of each dry season in the Ugandan sites and in Maruku, whereas furrow and basket irrigation were used in Lyamungo and Mitalula, respectively. Staking was done to keep the plants upright. The other trial management practices were consistent with good crop husbandry practices undertaken by farmers. Similar crop husbandry practices were used at Sendusu, where plant density

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Table 2. Description of agroclimatic characteristics (altitude, rainfall, temperature, soil type, and sites' global position), site mean yield potential (YLD), and broad sense heritability (H^2) of six testing sites in Tanzania and Uganda used to evaluate 30 banana genotypes for yield potential and stability.

Site	Country	Global position Lat.	Global position Long.	Altitude (m)	Rainfall (mm·year^{-1})	Temp (°C) Min.	Temp (°C) Max.	Temp (°C) Avg.	Soil type	YLD (t·ha^{-1}·year^{-1})	H^2
Mitalula	Tanzania	9°23′51.69″S	33°37′39.14″E	1,517	2,200	16	25	21	Clay loam	9.8	0.88
Maruku	Tanzania	1°25′28.05″S	31°46′24.91″E	1,300	2,000	16	30	23	Sand/silt loam	9.7	0.65
Lyamungo	Tanzania	3°13′48.27″S	37°14′54.40″E	1,270	2,389	14	27	21	Loam	19.5	0.60
Mbarara	Uganda	0°36′1.16″S	30°35′54.35″E	1,430	1,219	14	31	23	Sandy loam	14.7	0.76
Kawanda	Uganda	0°24′53.39″N	32°31′56.57″E	1,210	1,190	16	29	23	Sandy clay loam	13.6	0.80
Sendusu	Uganda	0°31′47″N	32°36′9″E	1,167	1,264	17	27	22	Sandy clay loam	24.3	0.63

Max. = maximum; Min. = minimum.

was 1667 plants/ha. When at least one fruit finger on a bunch began to ripen, the bunch was harvested, and the bunch weight was measured in kilograms per plant.

The yield potential (YLD; measured in tonnes/hectare/year) was calculated using mean data from the first two crop cycles with the formula

$$YLD = BW \times 365 \times PD/(DH \times 1000),$$

where BW and DH are bunch weight (fresh) and days to harvest, respectively; and 365 and PD refers to days per year and plant density per hectare, respectively (Ortiz 1997b; Swennen and De Langhe 1985; Tenkouano et al. 2019).

The index of nonspotted leaves (INSL), which measures indirectly host plant resistance to BLS, was calculated to assess the responsiveness of banana hybrids to BLS with the formula

$$INSL = \left[\frac{(YLS - 1)}{NSL}\right] \times 100,$$

where YLS and NSL indicate the youngest leaf spotted and the number of standing leaves, respectively. YLS = NSL + 1 when YLS is zero. This index estimates available photosynthetic leaf area before fruit filling and serves as a measure of resistance (Carlier et al. 2003; Gauhl 1994; Viljoen et al. 2017). It reveals a completely susceptible cultivar with a 0% INSL score and a completely resistant cultivar with a 100% INSL score. In addition, we used simple linear regression to examine the effect of BLS on hybrid yield, adaptability, and stability.

Variance components and genetic parameters. The restricted maximum likelihood/BLUP mixed-model approach was used to estimate variance components and genetic parameters for yield using R version 4.1.2 (R Foundation for Statistical Computing, Vienna, Austria) multi-environmental trial analysis "Metan," assuming the effects of GEIs to be random and the effects of environment and block/replicates within environment to be fixed effects (Olivoto and Lúcio 2020). The linear mixed model was defined as

$$y = Xb + Zu + e,$$

where y is an $n[= \sum_{j=1}^{e}(gb)] \times 1$ vector of observations in the kth block of the ith genotype in the jth year ($i = 1, 2, \ldots, g$; $j = 1, 2, \ldots, e$; $k = 1, 2, \ldots, b$), b is an $eb \times 1$ vector of fixed effects, u is an $m [= g + ge] \times 1$ vector of random effects, X is an $n \times eb$ design matrix relating y to b, Z is an $n \times m$ design matrix relating y to u, and e is an $n \times 1$ vector of within-group errors (Olivoto and Lúcio 2020; Yang 2007). The vectors b and u

were estimated using the well-known mixed model equation (Henderson 1975)

$$\begin{bmatrix} \hat{b} \\ \hat{u} \end{bmatrix} = \begin{bmatrix} X'R^{-1}X & X'R^{-1}Z \\ Z'R^{-1}X & Z'R^{-1}Z + G^{-1} \end{bmatrix} \begin{bmatrix} X'R^{-1}y \\ Z'R^{-1}y \end{bmatrix},$$

where G and R are the variance–covariance matrices for random-effect vector u and residual vector ε, respectively. The variance component estimates in G and R were obtained by restricted maximum likelihood using the expectation–maximization algorithm (Dempster et al. 1977). The BLUP of the ith genotype was

$$BLUP_i = \mu + \hat{g}_i.$$

The effect of the ith genotype in the jth environment $(\hat{g}_{ij})$ within u_{ge} was given as

$$\hat{g}_{ij} = h_g^2(\bar{y}_{i.} - \bar{y}_{.}) + h_{ge}^2(y_{ij} - \bar{y}_{i.} - \bar{y}_j + \bar{y}_{.}),$$

where h_g^2 is the shrinkage effect for the genotype effect given by $h_g^2 = (\hat{\sigma}_{\alpha t}^2 + e\hat{\sigma}_\alpha^2)/(\hat{\sigma}_{\alpha t}^2 + \hat{\sigma}_\delta^2 + e\hat{\sigma}_\alpha^2)$, and $h_{ge}^2 = \hat{\sigma}_{\alpha\tau}^2/(\hat{\sigma}_{\alpha\tau}^2 + \hat{\sigma}_\varepsilon^2)$ is the shrinkage effect for GEIs.

The BLUP of the ith genotype in the jth environment, according to Olivoto and Lúcio (2020) and Yang (2007), was

$$BLUP_{ij} = \bar{y}_j + \hat{g}_{ij}.$$

This methodology is an optimal procedure for unbalanced data.

A combined analysis of variance (ANOVA) on the mean yield data was used to determine the significance of the main effects and interactions. To determine the validity of the analyses of variance on the data, Bartlett's test was used to test the homogeneity of variances among sites. The likelihood ratio test was used to determine the significance of the model's genotypic effects. The analyzed genetic parameters were genotypic variance $(\hat{\sigma}_\alpha^2)$, variance of GEIs $(\hat{\sigma}_{\alpha\tau}^2)$, residual variance (σ_ε^2), phenotypic variance (σ_p^2), broad-sense heritability (H^2), coefficient of determination for the genotype-vs.-environment interaction effects (r_i^2), heritability of the genotypic mean (H_m^2), accuracy of genotype selection (As), correlation between genotypic values across environments (r_{gei}), genotypic coefficient of variation (CV_g, measured as a percentage), and residual coefficient of variation (CV_r, measured as a percentage). H^2, based on the plot level, was estimated as

$$H^2 = \frac{\hat{\sigma}_g^2}{\hat{\sigma}_g^2 + \hat{\sigma}_i^2 + \hat{\sigma}_e^2},$$

where $\hat{\sigma}_g^2$ is the genotypic variance, $\hat{\sigma}_i^2$ is the GEI variance, and $\hat{\sigma}_e^2$ is the residual variance. r_i^2 was estimated as

$$r_i^2 = \frac{\hat{\sigma}_i^2}{\hat{\sigma}_g^2 + \hat{\sigma}_i^2 + \hat{\sigma}_e^2},$$

where H_m^2 was estimated as

$$H_m^2 = \frac{\hat{\sigma}_g^2}{\left[\hat{\sigma}_g^2 + \hat{\sigma}_i^2/e + \hat{\sigma}_e^2/(eb)\right]}.$$

As was estimated as

$$As = \sqrt{H_m^2}$$

and r_{ge} was according to McCulloch and Searle (2001):

$$r_{ge} = \frac{\hat{\sigma}_g^2}{\hat{\sigma}_g^2 + \hat{\sigma}_i^2}$$

STABILITY AND ADAPTABILITY ANALYSIS. The harmonic mean of the genotypic values (HMGV) was calculated for the evaluation of stability. The relative performance of the genotypic values (RPGV) was used for the evaluation of adaptability, and the HMRPGV was used for the evaluation of stability, adaptability, and yield. All three parameters were calculated simultaneously for all genotypes according to the methods of Resende (2007a, 2007b). The HMGV is a stability indicator that compares predicted genotypic values for yield (tonnes/hectare/year) that have been penalized for instability, allowing the detection of both stable and high-yielding hybrids and cultivars. Because of their low temporal variability and the spatial variability, the best hybrids according to their HMGV must display consistency in performance year/cycle after year/cycle, and across locations. In other words, the best hybrids are those behaving in a highly predictable manner when environmental circumstances change. The HMGV was given by

$$HMGV_i = \frac{n}{\sum_{j=1}^{n} \frac{1}{GV_{ij}}},$$

in which n is the number of crop years in which the ith genotype was evaluated and GV_{ij} is the genetic value of ith family in jth crop year expressed by the ratio of the mean in this crop year. The RPGV, which refers to genotypes' ability to respond favorably to environmental changes, can be measured on the same scale as yield (tonnes/hectare/year) by multiplying the RPGV value by the general mean μ to obtain the mean genotypic value (RPGV $\times$ μ). The RPGV was

$$RPGV_i = \frac{1}{n} \sum_{j=1}^{n} \frac{GV_{ij}}{M_j},$$

where M_j is the mean yield in jth crop year.

The HMRPGV is a simultaneous selection index for stability, adaptability, and mean performance expressed as a unique value that can be multiplied by μ to produce genotypic values for each genotype (HMRPGV $\times$ μ) penalized for instability and capitalized for GEIs. The HMRPGV was calculated according to Resende (2004) as

$$HMRPGV_i = \frac{n}{\sum_{j=1}^{n} \frac{1}{RPGV_{ij}}}.$$

We used the singular value decomposition of the matrix of BLUPs for the GEIs effects generated by a linear mixed model to evaluate genotypic stability by additive main effects multiplicative interaction (AMMI) biplots and visualized the relationships among selection sites and the performance of candidate genotypes (Gauch 2013; Gauch and Zobel 1988; Olivoto et al. 2019a). The biplots were generated by subjecting a BLUP-based mixed model's shrunken GEIs effects matrix to an AMMI-like analysis using the singular value decomposition method. The interaction principal components were obtained by fitting the singular value decomposition to the double centered BLUP interaction effects matrix produced from a linear mixed model with symmetric singular value partitioning (α = 1/2).

The genotypic stability of each genotype was quantified by the weighted average of absolute scores (WAASB) from the singular value decomposition of the matrix of BLUPs for the GEIs effects generated by a linear mixed-effect model, estimated as follows:

$$WAASB_i = \sum_{k=1}^{p} |IPCA_{ik} \times EP_k| / \sum_{k=1}^{p} EP_k,$$

where $WAASB_i$ is the weighted average of absolute scores of the ith genotype, $IPCA_{ik}$ is the score of the ith genotype in the kth interaction principal component axis (IPCA), and EP_k is the amount of the variance explained by the kth IPCA (Olivoto et al. 2019a, 2019b). The genotype with the lowest WAASB value is considered the most stable (Olivoto et al. 2019a, 2019b)—in other words, the one that deviates least from the average performance across sites.

Results and Discussion

One of the first decisions farmers must make is which cultivar to grow in a field based on its anticipated economic and social benefits, which are typically defined in terms of the greatest yield potential and performance stability. This critical decision determines how long their banana production can be sustained. However, determining the best cultivars across a diverse set of environments exposed to intricate biotic and abiotic patterns and interactions that frequently result in significant variations in cultivar rank is far from trivial. As a result, one of the primary goals of plant breeding programs is to identify the ability of advanced bred germplasm to adapt to different agroecological settings.

COMBINED ANOVA. Table 3 gives the results of the combined ANOVA for a yield of 30 banana genotypes studied across six locations in Tanzania and Uganda. Genotype and environment, as well as their GEIs, were statistically significant ($P < 0.001$). The environment effect accounted for 41.7% of variation in yield, whereas the genotype and GEIs effects accounted for 28.7% and 11.2%, respectively. The significance of GEIs highlighted the importance of studying phenotypic stability by revealing differences in genotypic responses to agroecological differences in years and locations. This result suggests that some genotypes or groups of genotypes have specific adaptation to sites, whereas others may show broad adaptation, thereby confirming the importance of multilocational testing of cultivars before release. METs are critical for identifying cultivars that perform consistently year after year (with little temporal variation), as well as cultivars that perform consistently from location to location (small spatial variability). Farmers value and benefit

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Table 3. Combined analysis of variance of 30 banana genotypes evaluated for yield potential and stability across six sites in Tanzania and Uganda.

Source of variation	df	Sum of squares	Mean square	F value	P value	Yield potential (% TSS)
Environment	5	6,670	1334.0	96.7	$<3.46E^{-50}$**	41.7
Replication	16	332	20.8	1.5	0.10^{NS}	2.1
Genotype	29	4,590	158.1	11.5	$2.71E^{-28}$**	28.7
Genotype-by-environment interaction	86	1,790	20.8	1.5	0.01*	11.2
Residual	189	2,610	13.8	—	—	16.3
Total	325	15,992	—	—	—	—
Coefficient of variation (%)	—	—	25.2	—	—	—

TSS = total sum of squares.
NS indicates nonsignificant at $P > 0.05$, while * and ** indicate significant at $P < 0.01$ and $P < 0.001$, respectively.

from temporal stability, whereas breeders and seed producers value and benefit from spatial stability (Crossa et al. 1990; Kang 1990; Kang and Gauch 1996).

The mean site yield potential varied greatly, ranging from 9.7 t·ha^{-1} per year in Maruku, Tanzania, to 24.3 t·ha^{-1} per year in Sendusu, Uganda (Table 2). The wide range of yield potential confirmed, among other factors, the impact of different environments on genotype performance. Farmers in the developing world often have limited inputs and grow bananas in harsh and unpredictable environments, so a diverse set of conditions is required to conduct an accurate evaluation of yield stability.

Estimates of heritability, variance components, and genetic parameters. Estimates of the degree of phenotypic variation and heritability of yield must be reliable and accurate to optimize banana breeding selection efficiency. The components

of hybrid phenotypic variation, as well as trait heritability and other important genetic parameters, are listed in Table 4. The likelihood ratio test revealed highly significant effects ($P < 0.001$) for both genotype and GEI effects (Table 4). Genotypic variation accounted for 40.1% of the phenotypic variation in yield across sites, whereas GEIs accounted for 7.8%. In Tanzania, genotypic variation accounted for 39.2% of phenotypic yield variation, whereas GEI variation accounted for 2.2%. Genotypic variation accounted for 33% of total phenotypic variation in Uganda, with GEIs accounting for a greater proportion (22.2%). The residual variance represented 58.6% of the phenotypic yield variation in Tanzania, 44.9% in Uganda, and 51.8% across sites.

Genetic variation provides the grounds for selection in banana breeding. The median genotypic variance obtained in our study, as well as the considerable residual variation, underlined the

Table 4. Likelihood ratio test, estimated variance components, and genetic parameters for yield potential (tonnes/hectare/year) of 30 banana genotypes evaluated for yield and stability across six sites in Tanzania and Uganda.

	Likelihood ratio test	
Statistics	Genotype	Genotype-by-environment interaction
χ^2	39.7	2.76
P value	2.92×10^{-10}	9.64×10^{-6}

	Variance components[i]		
REML[ii]	Across sites	Tanzanian sites	Ugandan sites
$\hat{\sigma}^2_\alpha$	11.00 (40.1% of σ^2_p)[iii]	10.30 (39.2% of σ^2_p)	9.03 (33.0% of σ^2_p)
$\hat{\sigma}^2_{\alpha\tau}$	2.10 (7.8% of σ^2_p)	0.60 (2.2% of σ^2_p)	6.07 (22.2% of σ^2_p)
σ^2_ε	14.20 (51.8% of σ^2_p)	15.40 (58.6% of σ^2_p)	12.30 (44.9% of σ^2_p)
σ^2_p	27.40	26.36	27.36
H^2	0.40	0.39	0.33
r^2_i	0.08	0.02	0.22
H^2_m	0.92	0.87	0.74
As	0.96	0.93	0.86
r_{ge}	0.23	0.04	0.33
CV$_g$ (%)	22.50	24.19	18.19
CV$_e$ (%)	25.50	29.69	21.19
CV ratio	0.88	0.81	0.85
μ, μ_T, and μ_g[iv]	14.81	13.23	16.53

[i] $\hat{\sigma}^2_\alpha$ = genotypic variance; $\hat{\sigma}^2_{\alpha\tau}$ = variance of GEI; σ^2_ε = residual variance; σ^2_p = phenotypic variance; H^2 = broad-sense heritability; r^2_i = coefficient of determination for the genotype-vs-environment interaction effects; H^2_m = heritability of the genotypic mean; As = accuracy of genotype selection; r_{ge} = correlation between genotypic values across environments; CV$_g$ (percent) = genotypic coefficient of variation; CV$_e$ (percent) = residual coefficient of variation; CV ratio = the relative coefficient of variation.
[ii] Restricted maximum likelihood.
[iii] Parenthetical values indicate the percentage of the observed phenotypic variance.
[iv] μ = general mean for six sites in Tanzania and Uganda; μ_T = mean for three Tanzanian sites; μ_g = mean for three Ugandan sites.

Table 5. Best linear unbiased predictions (BLUPs) for yield potential [YLD (tonnes/hectare/year)] of 30 banana genotypes evaluated for yield and stability in six Tanzanian and Ugandan sites, along with the stability of their genotypic values [harmonic mean of the genotypic values (HMGV)], adaptability of genotypic values [relative performance of the genotypic values (RPGV)], genotypic values capitalized by the interaction (RPGV × μ), stability and adaptability of genotypic values [harmonic mean of relative performance of genotypic values (HMRPGV)], and mean genotypic values (HMRPGV × μ).

Genotype code	Genotype[i]	YLD_{BLUPs}	HMGV	RPGV	RPGV × μ	HMRPGV	HMRPGV × μ
N23	NARITA 23	23.40	21.10	1.51	22.70	1.50	22.50
N17	NARITA 17	26.10	22.80	1.40	21.00	1.40	21.00
N27	NARITA 27	16.60	15.30	1.27	19.10	1.27	19.00
N18	NARITA 18	18.70	16.60	1.20	18.10	1.20	18.00
N13	NARITA 13	17.40	15.70	1.15	17.20	1.14	17.10
N4	NARITA 4	17.10	15.70	1.13	16.90	1.12	16.80
N12	NARITA 12	16.50	15.20	1.10	16.50	1.10	16.50
N8	NARITA 8	16.50	14.90	1.08	16.20	1.08	16.20
N25	NARITA 25	14.50	13.10	1.08	16.30	1.07	16.10
N2	NARITA 2	16.60	14.80	1.07	16.00	1.06	15.90
N24	NARITA 24	17.60	17.00	1.04	15.60	1.04	15.50
Eny	Enyoya	10.30	10.10	1.02	15.40	1.02	15.40
N7	NARITA 7	17.10	15.40	1.02	15.30	1.01	15.20
N26	NARITA 26	13.00	11.90	1.00	15.10	1.00	15.00
N9	NARITA 9	13.90	12.50	0.99	14.90	0.99	14.80
N21	NARITA 21	14.40	13.40	0.97	14.50	0.96	14.50
N11	NARITA 11	15.10	11.80	0.95	14.30	0.91	13.70
N10	NARITA 10	13.30	12.60	0.91	13.70	0.91	13.60
N20	NARITA 20	11.50	10.20	0.87	13.10	0.87	13.00
N6	NARITA 6	13.50	11.40	0.88	13.10	0.86	13.00
Wil	Williams	11.80	10.60	0.86	13.00	0.86	12.90
Mpolo	Mpologoma	18.90	20.40	0.84	12.60	0.84	12.60
Mbwaz	Mbwazirume	11.80	10.30	0.83	12.50	0.82	12.30
Nak	Nakitembe	10.60	10.90	0.78	11.80	0.78	11.80
N16	NARITA 16	12.70	12.70	0.75	11.20	0.75	11.20
Kisa	Kisansa	9.59	10.10	0.728	10.90	0.73	10.90
N14	NARITA 14	11.00	9.41	0.726	10.90	0.72	10.80
NdizUg	Ndizi Uganda	9.65	8.71	0.675	10.10	0.67	10.10
N15	NARITA 15	7.73	6.45	0.59	8.86	0.57	8.48
N19	NARITA 19	6.12	4.95	0.474	7.11	0.44	6.63

[i] NARITA are primary and secondary triploid 'Matooke' hybrids. 'Mbwazirume' is a standard local cultivar planted in five sites, excluding Sendusu. Site-specific local cultivars Kisansa and Nakitembe were planted in Kawanda and Mbarara, 'Ndizi Uganda' in Lyamungo and Mitalula, 'Enyoya' in Maruku, and 'Mpologoma' in Sendusu. 'Williams' is a giant Cavendish and a black leaf streak–susceptible cultivar.

complexity of the genetic architecture of yield in banana, resulting from its multigenic inheritance, and phenotypic plasticity. As a consequence, quantitative traits are more vulnerable than qualitative traits to alteration by the variation in environmental conditions to which plants in the population are subjected (Acquaah 2012). Tenkouano (2001) reported that the multiploidy and heterogenomic structure of breeding populations result in unpredictable variation in genome size and structure across and within generations. Usually this complicates phenotypic selection for most yield and growth-related traits (Ortiz and Vuylsteke 1996). Breeders would gain in efficiency if they could assign segregating offspring to ploidy and genome classes putatively predictive of their prospective use before field evaluation (Tenkouano 2001).

The heritability of a trait broadly expresses the proportion of phenotypic variance within a population that can be attributed to heritable genetic factors. Its estimation is critical because it shows how much of a trait is genetically based and allows the best improvement approach to maximize the selection response (Falconer and Mackay 1996). The estimate of broad sense heritability was 0.33 for Uganda, 0.39 for Tanzania, and 0.4 across

all sites, implying that genetic differences accounted for 40% of the variance in mean yield observed among the 30 genotypes tested (Table 4). The heritability of the genotypic mean, commonly estimated when means are used as selection criteria, was 0.87 and 0.74 for Tanzania and Uganda, respectively, whereas 0.92 was achieved across all sites.

The development of new banana hybrid cultivars should optimize breeding initiatives that strike a balance between population size and selection intensity (Xu et al. 2017). Improved estimation of trait heritability remains critical for increasing the rate of genetic gain. Because yield is a multigenic trait with continuous phenotypic variation (Ortiz and Tenkouano 2011), analyzing the effects of the underlying genes and determining their inheritance mode is difficult. As a result, their estimated heritability is low, necessitating indirect selection based on highly heritable component traits to aid in the accumulation of desirable genes. According to Batte et al. (2021), the main traits contributing to bunch weight (which is a proxy for edible yield) in EAHBs are fruit length, number of fruit in a bunch, fruit circumference, and number of hands in a bunch. As a result, when

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selecting parents for use in breeding for yield in EAHBs, these traits should be evaluated to guarantee they are passed on to the new hybrids targeted for release to farmers.

Experimental designs could contribute to improving heritability estimates. Increasing the number of replications and locations has been reported to contribute toward an increase in heritability estimates (Schmidt 2019; Xu et al. 2017). Because the heritability estimates do not respond linearly to an increase in replications, increasing the number of target locations for evaluations is considered a better option to increase heritability estimates (Cobb et al. 2019; Weikai 2014). Usually, this results in additional costs. However, with additional testing environments, a breeder–agronomist can identify cultivars with specific adaptation as well as those with a broad adaptation, which would not be possible from testing in a single environment. In this context, the adoption of partially replicated trials or nonreplicated designs may be beneficial in cases in which spatial adjustments can be done properly (Cullis et al. 2006; Schmidt 2019; Williams et al. 2011).

Ssali et al. (2016) and Ortiz (1997a) reported broad sense heritability of bunch weight of secondary triploid banana 'Matooke' (*Musa* sp., AAA-EA) in Uganda and *Musa* germplasm in Nigeria to be 47.8% and 66%, respectively. Batte (2019) observed a high heritability of 84% for EAHB yield and 76% for bunch weight; however, his study, although using multi-generation trials, was conducted in a single site in Uganda (Sendusu), so the estimated heritability could be overestimated because of a lack of GEIs—in other words, across site variation. This is further supported by the investigation of broad sense heritability for individual sites in our study, the values of which are more than 60% because single-site heritability estimates do not account for GEIs (Table 2).

In addition to genetic gain, recent emphasis in plant breeding has also been on the genotypes with premium value and quality to satisfy consumer preferences (Akankwasa et al. 2020; Thiele et al. 2021). For example, superior banana cultivars should achieve genetic gain linked with fruit quality attributes and sensory perception (Cobb et al. 2019; Nowakunda and Tushemereirwe 2004). The concept of genetic gain may also be extended to cover the gain farmers can achieve in their income with unit cost or input—a trait that is also linked to the environment in banana (Meya 2021). Decentralized selection has been conceptualized more systematically during the past two decades, with the goal of increasing selection gains for marginal, low-input farming systems. Ceccarelli (1996) concluded that cultivar selection and testing for marginal production circumstances and resource-limited farmers should be conducted more intensively in farmers' field target environments. By determining the optimal genotypes for each target environment, it is possible to exploit favorably the interaction between plant populations and specific environmental conditions (i.e., GEI).

The genotypic correlation of genotype performance across sites was 0.2, thereby indicating the presence of GEIs that change genotype ranking across environments (Table 4). The result emphasizes the importance of assessing genotype adaptability and stability to provide accurate recommendations to farmers and breeders in various target regions (Yan and Tinker 2006). Inconsistency in genotype performance across locations or years provides additional information for breeders and suggests that, along with justifying the need for more broad-based testing in different environments, the degree of inconsistency could help

predict the variability expected among different fields (Busey 1983). The genotypic variation coefficients across locations were greater than 10%, indicating the presence of genetic variability and the possibility of effective clonal selection (Table 4). Ssali et al. (2016) obtained similar results using the same method and mixed models for 11 secondary triploid banana 'Matooke' hybrids.

The high cross-site selection accuracy (0.9) indicates that the experimental design was effective in reducing potentially disruptive effects. It also shows that the predicted and true genotypic values are highly correlated, implying a high precision in the identification and the possibility of success in the selection of individuals with specific or broad adaptation. Resende and Duarte (2007) recommended accuracy values greater than 0.7 for intermediate stages of the breeding program and greater than 0.9 for cultivar recommendations. A medium to high CV was observed ($CV_e = 25.5$), but CV_e estimates alone cannot judge experimental quality. Instead, the CV_r ($= CV_g/CV_e$) must be estimated, with magnitudes close to or greater than one being preferred (Olivoto et al. 2017). Yield had $CV_r \geq 0.9$ across sites, thus indicating the possibility of achieving selection gain.

GENOTYPE YIELD, STABILITY, AND ADAPTABILITY. Breeding programs must test hybrids in target environments and analyze data for yield, adaptability, and stability to develop cultivars that are well adapted to growing regions. Tables 5, 6, and 7 summarize the three BLUP-based indices HMGV, RPGV, and HMRPGV for selecting genotypes with high mean performance, stability, and adaptability. Coincidence in genotype ranking was observed for all indices, indicating the possibility of making reliable genetic value predictions using a single selection criterion that encompasses yield, stability, and adaptability. N23 had the greatest yield associated with adaptability and stability across all sites (Table 5). This hybrid outperformed the overall mean of all genotypes tested in Tanzania and Uganda by 34.2%, resulting in an HMRPGV × μ value of 22.5 t·ha⁻¹ per year. Despite producing the greatest yield (37.8 t·ha⁻¹) during 3 years of advanced yield trials in Uganda, this hybrid was not advanced for release as a new cultivar (Tushemereirwe et al. 2015). It was instead reserved for multilocation participatory trials in Tanzania and Uganda to find clones that combine BLS resistance with stable high yield and other desirable quality traits by farmers (Kubiriba et al. 2016; Lorenzen et al. 2010; Tushemereirwe et al. 2015). N23 was developed through a series of interploidy crosses between the female fertile EAHB 'Kazirakwe' and the 'Matooke' improved diploid '7197-2'. As a result, its exceptional performance is most likely a result of its parent 'Kazirakwe', which is known for its high yield and adaptability.

The hybrid N17 was ranked second overall, and similarly in Uganda, outperforming the overall average yield by 29.5% (Tables 5 and 7). It was also preferred by Ugandan farmers for its culinary qualities, and it won first place in sensory testing (data not shown). As a result, it is a candidate for release in Uganda. N27, N18, N13, and N4 were ranked third, fourth, fifth, and sixth across all sites, respectively, in terms of yield, stability, and adaptability, implying they are also the most stable and adapted. In Tanzania, the top five for yield, stability, and adaptability were N23, N27, N7, N18, and N4, whereas in Uganda, the top five were N23, N17, N18, N2, and N8. N23 and N18 genotypes are thus shared among the top five in both countries, whereas the rest are specific to Tanzania and Uganda. Others that performed well but did not make the top five were

Table 6. Best linear unbiased predictions (BLUPs) for yield potential [YLD (tonnes/hectare/year)] of 24 banana genotypes evaluated for yield and stability in three Tanzania sites, along with the stability of their genotypic values [harmonic mean of the genotypic values (HMGV)], adaptability of genotypic values [relative performance of the genotypic values (RPGV)], genotypic values capitalized by the interaction (RPGV × μ_T), stability and adaptability of genotypic values [harmonic mean of relative performance of genotypic values (HMRPGV)], and mean genotypic values (HMRPGV × μ_T).

Genotype code	Genotype[i]	YLD$_{BLUPs}$	HMGV	RPGV	RPGV × μ_T	HMRPGV	HMRPGV × μ_T
N23	NARITA 23	21.20	18.90	1.56	20.50	1.54	20.30
N27	NARITA 27	16.60	15.40	1.28	16.80	1.27	16.70
N7	NARITA 7	20.30	17.20	1.26	16.60	1.26	16.50
N18	NARITA 18	16.60	14.50	1.22	16.00	1.22	16.00
N4	NARITA 4	16.20	14.40	1.20	15.80	1.20	15.70
N12	NARITA 12	15.20	14.00	1.17	15.40	1.17	15.40
N13	NARITA 13	15.70	14.00	1.17	15.40	1.17	15.30
N8	NARITA 8	14.60	13.00	1.09	14.40	1.09	14.30
N9	NARITA 9	11.00	10.70	1.08	14.20	1.07	14.10
N25	NARITA 25	14.50	13.20	1.09	14.30	1.07	14.10
Eny	Enyoya	10.30	10.00	1.02	13.50	1.02	13.50
N10	NARITA 10	13.00	12.10	1.02	13.30	1.01	13.30
N26	NARITA 26	13.00	11.90	1.01	13.20	1.00	13.20
N2	NARITA 2	13.60	11.90	0.99	13.00	0.99	13.00
N21	NARITA 21	12.20	11.20	0.94	12.40	0.94	12.40
N20	NARITA 20	11.50	10.40	0.88	11.60	0.88	11.60
N11	NARITA 11	12.40	9.87	0.91	12.00	0.86	11.40
N6	NARITA 6	11.40	9.86	0.86	11.20	0.85	11.10
Wil	Williams	11.20	9.72	0.84	11.10	0.84	11.00
Mbwaz	Mbwazirume	12.00	9.39	0.82	10.70	0.81	10.60
N14	NARITA 14	8.08	7.76	0.68	8.89	0.67	8.80
NdizUg	Ndizi Uganda	9.65	8.52	0.68	8.88	0.67	8.75
N15	NARITA 15	7.73	6.32	0.59	7.73	0.56	7.34
N19	NARITA 19	6.12	4.63	0.48	6.24	0.42	5.52

[i] NARITA are primary and secondary triploid 'Matooke' hybrids. 'Mbwazirume' is a standard local cultivar planted in five sites, excluding Sendusu. Site-specific local cultivar Ndizi Uganda was planted in Lyamungo and Mitalula, and 'Enyoya' in Maruku. 'Williams' is a giant Cavendish and a black leaf streak–susceptible cultivar.

N12, N13, N8, N9, and N25 in Tanzania, and N13, N12, N4, N24, and N11 in Uganda. N27 was denied for advancement in Tanzania because of a lack of sensory characteristics, whereas N24 was among the top performers in Uganda in terms of sensory characteristics (Marimo et al. 2020). N8 and N13, on the other hand, performed well, but because they are of a juice banana type, they cannot be recommended to farmers for food use. However, one juice banana in Tanzania (N13) and two in Uganda (N13 and N8) tended to be among the best for yield, stability, and adaptability, thus indicating an additional source of income for farmers as a means of sustaining their livelihood.

Four of the top 10 genotypes have been released in the past 6 years: the N23, N18, and N4 genotypes in Tanzania, and the N7 genotype in both Tanzania and Uganda. These cultivar releases illustrate the current success that is being experienced by banana breeding in East Africa. 'Mbwazirume', a comparison local check, was in 23rd place out of 30 genotypes tested across sites, 20th out of 24 genotypes tested in Tanzania, and 16th out of 22 genotypes tested in Uganda. Despite being one of the best EAHBs in terms of farmers' preferred sensory attributes, the poor yield performance of 'Mbwazirume' is unsurprising, as noted in previous research results (Erima et al. 2016; Ssali et al. 2010). Not only did the local checks perform poorly, also several hybrids fared poorly and were ranked among the last. N15 and N19, for example, were the two genotypes that ranked among the last across all sites. N15 and N19 were the last two in Tanzania, whereas N16 and 'Kisansa' were the last two in Uganda. These

findings suggest that high-yielding, stable genotypes are not always the result of banana crossbreeding.

RELATIONSHIP BETWEEN YIELD AND BLS RESISTANCE. A variety of pathogens and pests damage crop plants, resulting in significant yield loss. Resistance has been defined as the "inherent capacity of a plant to prevent or restrict the entry or subsequent activities of a pathogenic agent when the plant is exposed, under suitable environmental conditions, to sufficient inoculum of a pathogen to cause disease" (Bhargava and Srivastava 2019). In addition, any resistance breeding effort attempts to develop superior high-yielding genotypes that are resistant for a long time (Craenen and Ortiz 2003; Tushemereirwe 1996). The regression analysis results revealed that INSL had no significant effect ($P >$ 0.05) on hybrid yield, stability, and adaptability (Table 8). Indeed, INSL accounts for only 0.43% yield variance across sites, 0.07% in Tanzania, and 3.36% in Uganda.

GENOTYPE, ENVIRONMENT, AND THEIR INTERACTION EFFECTS ON YIELD. The ability of a plant breeding program to provide farmers with genotypes with guaranteed superior performance for yield or quality across a range of environments is critical to its success. Understanding the factors that lead to a good phenotype is necessary to achieve this goal (Malosetti et al. 2013). The genotypes with high yield potential and stability, as well as the testing environment relationships were visualized using AMMI biplots. Principal component 1 (PC1) and principal component 2 (PC2) accounted for 100% of the variation in yield in Tanzania and 100% of the variation in Uganda (Fig. 1A–D). In Tanzania, PC1

Table 7. Best linear unbiased predictions (BLUPs) for yield potential [YLD (tonnes/hectare/year)] of 22 banana genotypes evaluated for yield and stability in three Uganda sites, along with the stability of their genotypic values [harmonic mean of the genotypic values (HMGV)], adaptability of genotypic values [relative performance of the genotypic values (RPGV)], genotypic values capitalized by the interaction (RPGV × μ_g), stability and adaptability of genotypic values [harmonic mean of relative performance of genotypic values (HMRPGV)], and mean genotypic values (HMRPGV × μ_g).

Genotype code	Genotype[i]	YLD$_{BLUPs}$	HMGV	RPGV	RPGV × μ_g	HMRPGV	HMRPGV × μ_g
N23	NARITA 23	25.60	22.70	1.40	24.20	1.40	24.20
N17	NARITA 17	26.10	22.40	1.40	24.20	1.39	24.10
N18	NARITA 18	20.70	18.90	1.16	20.10	1.16	20.10
N2	NARITA 2	19.60	18.00	1.11	19.20	1.10	19.20
N8	NARITA 8	18.30	17.30	1.06	18.30	1.05	18.30
N13	NARITA 13	19.90	17.60	1.05	18.20	1.05	18.10
N12	NARITA 12	17.80	17.10	1.04	18.10	1.04	18.00
N4	NARITA 4	18.00	17.00	1.04	18.00	1.04	18.00
N24	NARITA 24	17.60	17.00	1.04	18.00	1.03	17.90
N11	NARITA 11	19.20	17.80	1.02	17.70	1.02	17.60
N21	NARITA 21	16.60	16.10	0.99	17.10	0.98	17.00
N9	NARITA 9	16.90	15.50	0.92	15.90	0.92	15.90
Wil	Williams	12.60	12.70	0.91	15.80	0.91	15.80
N7	NARITA 7	15.00	15.10	0.92	15.90	0.91	15.80
N6	NARITA 6	16.70	15.10	0.91	15.80	0.90	15.70
Mbwaz	Mbwazirume	11.60	11.80	0.85	14.70	0.85	14.70
N14	NARITA 14	15.50	14.30	0.85	14.70	0.84	14.60
Mpolo	Mpologoma	18.90	20.30	0.84	14.50	0.84	14.50
N10	NARITA 10	13.60	13.70	0.85	14.80	0.83	14.40
Nak	Nakitembe	10.60	10.90	0.78	13.60	0.78	13.60
N16	NARITA 16	12.70	13.00	0.75	13.00	0.75	13.00
Kisa	Kisansa	9.59	10.10	0.73	12.60	0.73	12.60

[i] NARITA are primary and secondary triploid 'Matooke' hybrids. 'Mbwazirume' is a standard local cultivar planted in five sites, excluding Sendusu. Site-specific local cultivars Kisansa and Nakitembe were planted in Kawanda and Mbarara and 'Mpologoma' in Sendusu. 'Williams' is a giant Cavendish and a black leaf streak–susceptible cultivar.

explained 76.56% of the genotype and GEI (GGE) variance in yield, whereas PC2 explained 23.44%. PC1 accounted for 88% of the GGE variance for yield in Uganda, whereas PC2 accounted for 11%. Given that a model's variability must be at least 70% to be deemed reasonably reliable (Gauch 2013), the combined variability of PC1 and PC2 was adequate. The AMMI1 model, with yield on the abscissa and PC1 scores for genotypes and environments on the ordinate, is depicted in Fig. 1A and C. The larger the IPCA scores, either negative or positive, the more

specifically adapted a genotype is to a certain environment; the smaller the IPCA scores, the more stable the genotype is over all environments investigated (Crossa et al. 1990; Gauch 2006).

The best genotypes for wide adaptation are those with a high mean yield and stability. They are close to the biplot's center and above the grand mean of main effect yield. As banana breeders are frequently drawn to genotypes that are high yielding and relatively more stable, N2, N4, N8, N12, N13, N18, N25, and N27 in Tanzania, and N2, N4, N8, N12, N18, N13, N24, and 'Mpologama' in Uganda were deemed the best. Stable genotypes, according to Yan and Kang (2003), ensure consistent yields with little variation year after year. With average stability, the top-yielding genotypes were N7 and N23 in Tanzania, and N17 and N23 in Uganda. These hybrids are also advantageous because they are more closely related to stable genotypes, and breeders routinely select genotypes with a high mean yield and moderate stability that perform well in specific environments for specific adaptation. Denis and Gower (1996) suggested that plant breeders should consider GEI to avoid missing a cultivar whose average performance was poor but performed well when grown in specific environments or selecting a cultivar whose average performance was good but performed poorly when grown in a specific environment. N19, N15, and 'Ndizi Uganda' in Tanzania, as well as 'Kisansa', 'Nakitembe', and 'Mbwazirume' in Uganda, had the lowest yield and stability. These results demonstrate that most farmers' cultivars used as checks had low and unstable yield, which may be attributed to their limited ability to withstand unpredictable climatic conditions combined with greater pathogen impacts. The biplot also revealed that the

Table 8. Regression analysis for yield potential (tonnes/hectare/year) of 30 banana genotypes evaluated for yield and stability in six Tanzanian and Ugandan sites, with 24 genotypes evaluated in three Tanzanian sites and 22 genotypes evaluated in three Ugandan sites in relation to host plant resistance to the black leaf streak pathogen measured by the percentage index of non-spotted leaves.

Location	Model	df	F value	R^2 (%)
Across sites	Regression model	1	0.12[NS]	0.43
	Error	28	3.49	
	Total	29	—	
Tanzania sites	Regression model	1	0.01[NS]	0.07
	Error	22	3.39	
	Total	23	—	
Uganda sites	Regression model	1	0.69[NS]	3.36
	Error	20	3.11	
	Total	21	—	

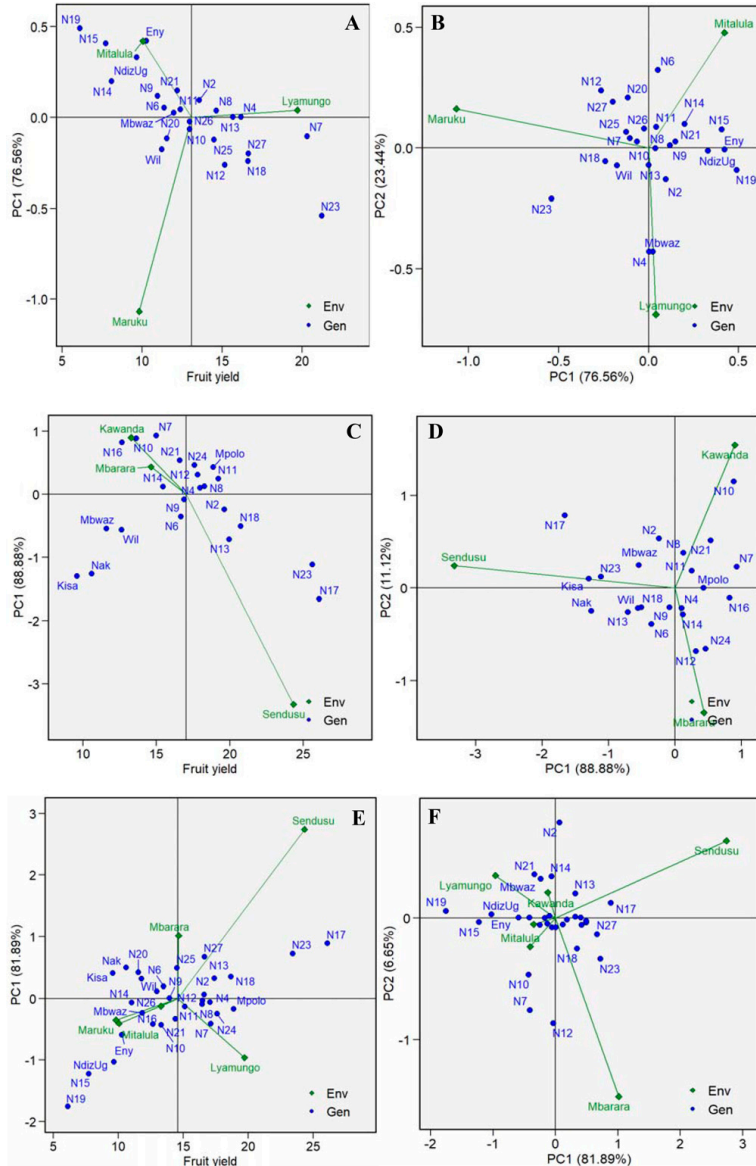R^2 = coefficient of determination.
NS indicates nonsignificant at $P > 0.05$.

Fig. 1. Biplots showing principal components (PCs) for 24, 22, and 30 banana genotypes (Gen) after their testing in six sites (Env) in Tanzania (**A**, **B**), Uganda (**C**, **D**), and across countries (**E**, **F**), respectively, evaluated for yield potential and stability. The scores were calculated by fitting the singular value decomposition of the double-centered best linear unbiased prediction interaction effects matrix derived from a linear mixed model with symmetric singular value decomposition ($\alpha = 12$). The axes are equally scaled. Cultivar codes are given in Table 1.

greatest yielding sites were Lyamungo in Tanzania and Sendusu in Uganda, whereas Maruku in Tanzania and Kawanda in Uganda were the lowest yielding sites (Fig. 1A and C).

Mitalula in Tanzania, as well as Kawanda and Mbarara in Uganda, contributed little to GEIs because of poor genotype discrimination ability (Fig. 1A and C). The vectors were significantly longer at the Tanzanian sites of Maruku and Lyamungo, as well as Sendusu in Uganda, thereby contributing significantly to the GEI. As a result, they provided the ideal environment for cultivar genetic differentiation. Frutos et al. (2014) emphasized

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that the ideal test environments are both discriminating (informative) and representative of the target environment, whereas Ortiz and de Cauwer (1998) suggested that the ideal environment for breeders' selections would be one that maximizes phenotypic differences among genotypes—in other words, one in which breeders can do effective visual selection. The ability to discriminate among genotypes for yield performance was highly correlated at the Ugandan sites of Mbarara and Kawanda, particularly for N7. Sendusu forms an obtuse angle with Kawanda and Mbarara, thereby indicating that it is distinct from the others and may have influenced its high yield. N7 and N21 were adapted to Kawanda and Mbarara, respectively, whereas N17 and N23 were adapted solely to Sendusu. The vectors for Lyamungo and Maruku had a maximum angle of less than 90°. This suggests that genotypes are classified similarly at these two sites. N23 has been adapted to both Maruku and Lyamungo, whereas N4 has been adapted to Lyamungo, and N12 and N18 have been adapted to Maruku. Mitalula and Lyamungo form an obtuse angle, thus indicating that these two sites are distinct. N6, N15, and N19 were the best adapted to Mitalula (Fig. 1A and C).

The level of adaptation of the hybrids and local cultivars, as well as the effects of different environments on their yield, are shown in Fig. 1B and D. The biplots reveal that most of them were relatively close to the mean (stable), with the exception of the top-yielding hybrids, which retained their average stability and adaptability to a specific location. In Tanzania, for example, N23 continues to be adapted to the Lyamungo and Maruku sites, whereas N4 and 'Mbwazirume' are only adapted to the Lyamungo site. Most of the low-yielding hybrids, such as N6, N11, and N20, were adapted to Mitalula or Maruku, thereby confirming the findings revealed by Fig. 1A and C (i.e., these are low-yielding sites in Tanzania). In Uganda, N17 as well as N10 and N12 were the most unstable, contributing significantly to GEIs. N17 was adapted for the high-yielding site in Sendusu, whereas N10 and N12 were adapted to Kawanda and Mbarara, respectively. Similar to Tanzania, most genotypes in Uganda are near the center, thereby indicating that they are stable.

The biplots from six Tanzanian and Ugandan sites are shown in Fig. 1E and F. For the first two IPCAs, the cumulative variance was 88.5%. PC1 was responsible for 81.9% of the GGE variance in yield, whereas PC2 was responsible for 6.7% (Fig. 1E and F). The results of the biplots across sites confirm the findings of the individual country analysis, indicating that high-yielding genotypes such as N23 and N17 remain suited to the Lyamungo and Sendusu sites, respectively (Fig. 1E). The majority of genotypes that were stable in the individual country analysis remained stable, with N12, N8, N4, N18, N24, and 'Mpologoma' retaining a high level of stability (Fig. 1E). The genotypes with lower yields, such as N19, N15, 'Ndizi Uganda', 'Enyoya', 'Kisansa', N16, 'Nakitembe', and N14, have held their position as low-yielding genotypes in the cross-site analysis. Similarly, Mitalula, Maruku, and Kawanda have remained low-yielding sites. Figure 1F reveals the level of adaptation across sites, with N17 adapting to Sendusu in Uganda, N23 adapting to Mbarara and Sendusu in Uganda, and 'Mbwazirume', N21, and N2 adapting to Lyamungo in Tanzania. Most genotypes, including N18, N4, and N13, were near the biplot origin and above the grand mean, thus indicating high yield and stability (Fig. 1E). Sendusu and Mbarara in Uganda, as well as Lyamungo in Tanzania,

provide an optimal setting for cultivar genetic differentiation (i.e., discrimination ability) (Fig. 1F).

The hybrids N23, N7, N4, N27, and N18 in Tanzania, and N18, N4, N12, N24, N17, N2, and N23 in Uganda are recommended for cultivar release and 'Matooke' banana production in the target population of environments in the East African region from where the testing sites were drawn. These hybrids combine high yield, stability, and adaptability. The three BLUP-based indices ranked these hybrids similarly, thus confirming their unique performance. These hybrids have high host BLS resistance, as indicated by the nonsignificant effect of INSL scores on yield, stability, and adaptability. As a result, they are reliable to be introduced into areas where BLS has a severe impact and threatens farmers' livelihoods.

Lyamungo in Tanzania and Sendusu in Uganda provide the greatest mean productivity combined with good discrimination ability, making them ideal for future breeding evaluation. Furthermore, the six sites were found to be diverse, and their clustering suggests individual groups that could be used as separate zones for cultivar evaluation and regional cultivar deployment. The findings of this study also reveal that, after more than 20 years of breeding, a reasonable genetic progress for yield trait was achieved. However, enhancing genetic gains in banana breeding programs and its realization in farmers' fields calls for an integration of multiple aspects including germplasm resources, genomics, breeding, and agronomic practices together with improved seed delivery systems. Cultivar evaluation in the presence of unpredictable GEIs is a persistent problem in banana breeding. There appears to be no easier way to select superior banana cultivars than to test widely and select for both average yield and stability.

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J. Amer. Soc. Hort. Sci. 147(6):334–348. 2022.

III

TARIBAN1, TARIBAN2, TARIBAN3, and TARIBAN4 'Matooke' Cooking Banana Cultivars for the Great Lakes Region of Africa

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Bananas and plantains (*Musa* sp.) are important staple and income-generating fruit crops for millions of people worldwide (Robinson and Saúco 2010; Ssebuliba et al. 2005). They are edible and vegetatively propagated parthenocarpic species (Ortiz 1997; Simmonds 1962). East African highland bananas (EAHBs) are a distinct group of cultivars found only in the highland of African Great Lakes region, where the "greatest mass of bananas in the world" are found (Simmonds 1966). Bananas are important in the food economy of millions of people in this region, with annual per capita consumption estimated to be between 250 and 600 kg (Karamura et al. 2012). These triploid ($2n = 3x = 33$ chromosomes) cultivars are known locally as Matooke. When fully ripe, they can be eaten raw like dessert bananas; however, because their pulp is insipid, they are mostly eaten after cooking. Shepherd (1957) referred to them as the 'Lujugira-Mutika' subgroup of the AAA genome group. They are also known by its acronym (EAHBs) because they thrive on the East African plateau at altitudes ranging from 900 to 1800 m above sea level (Davies 1995). A small group of these EAHBs are processed into a beverage, and called beer or 'Mbidde' bananas.

The major threats to the future sustainability of EAHB production across the region are pests such as banana weevils *Cosmopolites sordidus*, burrowing nematode *Radopholus similis*, black leaf streak (BLS) pathogen *Pseudocercospora fijiensis*, *Fusarium* wilt *oxysporum* f. sp. cubense, and banana bacterial wilt *Xanthomonas campestris* pv. *musacearum* (Tushemereirwe et al. 2015). EAHBs are susceptible to the airborne fungal pathogen *P. fijiensis*, which causes BLS and was previously known as black Sigatoka. The pathogen causes necrotic leaf lesions on the photosynthetic area of the host plant, resulting in fruit yield losses (up to 50%) and poor fruit quality (Craenen and Ortiz 1998; Mobambo et al. 1993; Swennen and Vuylsteke 1991; Swennen et al. 1989; Vuylsteke et al. 1993). Long-term host plant resistance is thought to be the best option for BLS disease control because fungicide-based control is expensive and could be hazardous to human health and the environment (Churchill 2011). Furthermore, large banana plantations elsewhere spend up to US\$1000·ha^{-1} on disease control each year, accounting for up to 30% of total production costs (Alakonya et al. 2018; Churchill 2011).

In 1994, the International Institute of Tropical Agriculture (IITA) and Uganda's National Agricultural Research Organization (NARO) together began to breed EAHBs (Tushemereirwe et al. 2015). Several interploidy crosses between triploid 'Matooke' and the diploid ($2n = 2x = 22$) wild nonparthenocarpic banana 'Calcutta-4' (AA), a donor of BLS resistance, were used to produce primary tetraploid ($2n = 4x = 44$) hybrids; thereafter, they were included in crossing blocks with improved diploid bananas to obtain secondary triploid and tetraploid hybrids (Tushemereirwe et al. 2015). The best EAHB hybrids developed by NARO and IITA were called NARITAs; they were selected based on

their bunch weight, host plant resistance to *P. fijiensis*, and fruit quality traits. These were evaluated at five sites over three cropping cycles (mother plant and at least two ratoons) in Tanzania and Uganda. The best four hybrids were released in Tanzania in 2021, as TARIBAN1 ('NARITA 4'), TARIBAN2 ('NARITA 7'), TARIBAN3 ('NARITA 18'), and TARIBAN4 ('NARITA 23'). They were registered on Tanzania's national cultivar list, thus becoming available for farmer multiplication and distribution. In Tanzania, their mean yield potential could reach 20.3 t·ha^{-1} per year, with their bunches weighing up to 51.0 kg.

Origin. The secondary triploid banana hybrids 'TARIBAN1', 'TARIBAN2', and 'TARIBAN3', and the primary triploid 'TARIBAN4', ensued. The parents of the primary tetraploid hybrids (female parents of secondary triploid hybrids) are EAHBs and 'Calcutta 4' (C4). C4 (*M. acuminata* ssp. *burmannica*) is an inedible wild diploid banana accession from Myanmar (De Langhe and Devreux 1960) with resistance to BLS (Tushemereirwe et al. 2015) and some nematode species, such as *R. similis* (burrowing nematode) and *P. coffeae* (banana root nematode) (Dochez et al. 2009; Viaene et al. 2000), whereas the EAHBs are farmer cultivars that dominate the African Great Lakes Region, where they are endemic (Karamura 1998; Pillay et al. 2001). TARIBAN1 is a secondary triploid derived from crossing the primary tetraploid '660K-1' ('Enzirabahima' × 'Calcutta 4') and the IITA's bred-diploid 'TMB2 × 9128-3' (Pillay et al. 2012; Tenkouano et al. 2003). 'TARIBAN2' is a secondary triploid that resulted from crossing the primary tetraploid '1201K-1' ('Nakawere' × 'Calcutta 4') and an improved diploid 'SH3217', which was bred by the Fundación Hondureña de Investigación Agrícola in La Lima (Honduras). 'TARIBAN3' is a secondary triploid offspring derived from crossing the primary tetraploids '365K-1' ('Kabucuragye' × 'Calcutta 4') and '660K-1' ('Enzirabahima' × 'Calcutta 4'). TARIBAN4 is a primary triploid derived from crossing the EAHB cultivar Kazirakwe and the IITA's diploid male parent 'TMB2 × 7197-2' (Tushemereirwe et al. 2015).

Crossing and preliminary field trials were conducted at an IITA breeding site in central Uganda (Sendusu 0°31′N, 32°36′E, 1140 m above sea level). This site soil is an isoperthemic Rhodic Kandiudalf/Rhodic Nitisol (United States Department of Agriculture taxonomy/World Referennce Base) with a 4% slope and pH ranging from 5.4 to 6.4 in the upper 20 cm. Sendusu receives 1200 mm of rain each year, which is distributed bimodally. The crossbreeding effort began with

the identification of seed-producing 'Matooke cultivars in NARO and IITA banana germplasm collections in Kawanda and Sendusu, respectively (Batte 2019). Twelve triploid Matooke cultivars were selected, propagated in vitro, planted in the field, and pollinated by hand with C4; primary tetraploid hybrids were produced. These primary tetraploids had residual seed fertility, thus causing low fruit quality because of seed set; therefore, it is unsuitable for eating. This problem was resolved by crossing the primary tetraploids with improved diploids, resulting in seedsterile secondary triploid hybrids that were selected for their productivity and host plant resistance to BLS (Tushemereirwe et al. 2015). Planting materials from the selected triploid hybrids were multiplied, and the superiority of each hybrid in terms of bunch yield, fruit taste, and response to BLS was evaluated in a series of field trials (Tushemereirwe et al. 2015). The promising secondary and primary triploid hybrids were evaluated and selected for their performance in unreplicated early evaluation trials, then in replicated preliminary yield trials, and finally in advanced yield trials over three cropping cycles in Sendusu and Kawanda. Kawanda lies at an altitude of 1210 m above sea level and at 00°25′N, 00°32′E. It has a bimodal type of rainfall, with the "short" rains beginning in March/April to June, and the "long" rains beginning in August to November/December (Barekye 2009).

The aim of the different stages of evaluation was to identify promising hybrids that could be advanced for cultivar release. From more than 1000 hybrid seeds, 28 hybrid clones were selected and tested during preliminary yield trials, and 18 were selected and tested during advanced yield trials. The 18 crossbred hybrids selected during the advanced yield trials were advanced to multisite testing and on-farm trials for further evaluation and selection in comparison with a local 'Matooke' EAHB check known as 'Mbwazirume'. After several years of intensive testing, 27 superior 'Matooke' hybrids were chosen for testing by farmers in a variety of target end-user environments.

Multisite trials involving the Matooke and other banana cultivars were performed in Tanzania from 2016 to 2019, with the aim of selecting breeding clones that combine BLS resistance with steady high production and other desirable traits and that have the potential for adoption by farmers and consumers. The sites were Mitalula, Maruku, and Lyamungo in the northeastern and southern highlands of Tanzania, and the trials were performed by the Tanzania Agriculture Research Institute in collaboration with Bioversity International and IITA. 'TARIBAN2', one of the 24 hybrids included in the multisite testing as a hybrid check, was already released by NARO in Uganda under the name 'Kiwangaazi' (syn. 'KABANA 6H') (Nowakunda et al. 2015). It was released as a new banana cultivar for Tanzania in June 2021, after 3 years of testing.

Four replications of 2 to 3-month-old tissue culture plants were planted in deep holes (≈100 cm deep and 100 cm wide) spaced 3 m apart, resulting in a plant population density of 1152 plants/ha. There were 12 plants per testing clone in each plot, thus having a total of 48 plants for each clone per site. Each hole received 10 kg of well-decomposed organic manure at the time of planting. The design that was used was a randomized complete block design. The testing breeding clones were planted alongside Mbwazirume (EAHB subgroup, AAA genome), a local Matooke cultivar, to compare performance. During the dry season, irrigation was used in Lyamungo and Mitalula, and mulching was used at the Maruku site every year to keep the soil moist. Other management practices aligned with effective crop husbandry practices used by farmers. No chemical or biological pesticides were used.

The youngest leaf spotted (YLS) described by Viljoen et al. (2017) was used to determine host plant resistance to *P. fijiensis* in the field. 'Williams', a BLS-susceptible Cavendish dessert banana cultivar, served as the control. Increased YLS readings indicated that the plant had more healthy leaves and, thus, was more resistant to BLS. During flowering, the number of standing leaves and the YLS were recorded. The severity of BLS was determined visually by estimating the leaf area with symptoms for each standing leaf, with 0 indicating no visible symptoms, 1 indicating less than 1% of the leaf area infected, 2 indicating 1% to 5% of the leaf area infected, 3 indicating 6% to 15% of the leaf area infected, 4 indicating 16% to 33% of the leaf area infected, 5 indicating 34% to 50% of the leaf area infected, and 6 indicating 51% to 100% of the leaf area infected (Fig. 1) (Gauhl 1994). To account for genetic differences in the number of standing leaves, the index of nonspotted leaves (INSL) was calculated as follows:

$$INSL = \left[(YLS - 1)/NSL \right] \times 100$$

where YLS and NSL indicate the youngest leaf spotted and the number of standing leaves, respectively. YLS=NSL+1 when the YLS was 0. The INSL represents the proportion of standing leaves that do not exhibit severe BLS symptoms (Craenen and Ortiz 1998).

We used the protocols of Swennen and De Langhe (1985) to evaluate growth and yield characteristics throughout the crop cycle. The yield potential (tonnes/hectare per year) was calculated using data from the first two crop cycles as follows:

$$YLD = BW \times 365 \times PD/(DH \times 1000)$$

where BW and DH are bunch weight per plant and days to harvest, respectively, and 365 and PD are days per year and plant density per hectare, respectively (Ortiz 1997; Swennen and De Langhe 1985; Tenkouano et al. 2019). The weight of the bunch was determined using a hanging spring scale with a
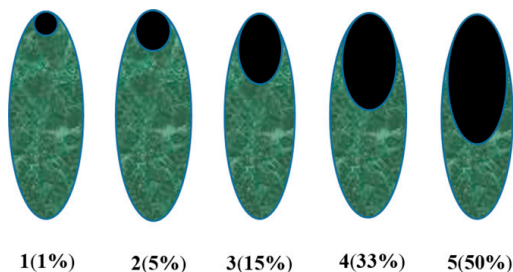
1(1%)   2(5%)   3(15%)   4(33%)   5(50%)

Fig. 1. Black leaf streak (BLS) severity scoring to estimate the infection caused by *P. fijiensis* on a single banana plant (Viljoen et al. 2017). The percentage of banana leaf area infected by BLS is shown in black. The remaining uninfected leaf area is shown in green.

genotypes, as determined by the percentage of INSL (Table 1). The INSL of TARIBAN3 was lower than that of Mbwazirume, but it exceeded the 70% threshold required for a banana cultivar to be considered resistant. Furthermore, when compared with 'Mbwazirume', 'TARIBAN' hybrids may gain at least one extra leaf without BLS spotting (Table 1). The host response to BLS in the selected germplasm is characterized by slow or delayed disease development, which entails a long incubation period (time between infection and symptom emergence), as well as effective suppression of symptom progression and spread.

The 'TARIBAN' hybrids resemble their female parents in terms of phenotype, with a

Table 1. Mean performance of the four 'Matooke' cooking banana cultivars 'TARIBAN' released in Tanzania averaged over the first two crop cycles.

Cultivar	Parents	Bunch wt (kg/plant)	Yield potential (tonnes/hectare per yr)	Plant ht (cm)	Plant girth (at 100 cm)	Functional leaves at flowering	Youngest leaf spotted (YLS) at flowering	Index of nonspotted leaf (INSL) at flowering
'TARIBAN1'	660K-1 × 9128-3	26.9	15.7	277.0	51.1	9.6	10.8	99.7
'TARIBAN2'	1201K-1 × SH3217	34.2	16.5	382.0	54.0	11.0	10.7	86.8
'TARIBAN3'	365K-1 × 660K-1	26.5	16.0	259.0	51.7	10.0	9.7	73.2
'TARIBAN4'	'Kazirakwe' × 7197-2	32.7	20.3	277.0	57.5	9.9	11.1	89.1
'Mbwazirume'	East African cultivar	15.8	10.6	243.0	51.2	8.8	8.9	75.6
Multisite mean		27.2	15.8	287.6	53.1	9.9	10.2	84.9
SE of differences[i]		6.5	5.2	20.6	7.5	0.7	0.8	3.6
ANOVA F probability[ii]		0.001	0.01	<0.001	0.01	0.001	<0.001	<0.001
Coefficient of variation		43.0	54.1	16.1	21.3	35.1	39.5	22.6

[i] *SE* of differences as estimated using the mean square error of the analysis of variance (ANOVA).
[ii] Probability of the F-test from the ANOVA.

capacity of 300 kg suspended on a tripod stand.

A panel of more than 300 banana farmers from three Tanzanian sites completed the consumer acceptability tests of the cooked hybrid by scoring it using a scale of 1 to 5, with 1 indicating extreme dislike (i.e., very bad) and 5 indicating extreme liking (i.e., very good) based on the sensory attributes of taste, aroma, mouth feel (or texture in the mouth), color, texture in hand, and overall acceptability (Marimo et al. 2020; Nowakunda and Tushemereirwe 2004). Tanzanian farmers evaluated boiled fruit as the main product. Farmers at Lyamungo also evaluated the fruit as machalari (i.e., chopped bananas boiled with meat and other ingredients) and mtori (i.e., boiled banana mixed with meat and smashed after cooking to make a thick porridge). The final selection of prospective 'Matooke' hybrids was guided by a product profile that includes host plant resistance to BLS, culinary acceptability, and bunch weight significantly higher than the standard local check 'Mbwazirume'.

Description and performance. The average bunch weight of four triploid hybrids across sites ranged from 26.5 to 34.2 kg, with potential yields ranging from 16.0 to 20.3 t·ha^{-1} per year. 'TARIBAN2' had the largest bunch weight (34.2 kg) of the four hybrids, followed by 'TARIBAN4', 'TARIBAN1', and 'TARIBAN3' (Table 1). The bunch weight of the check cultivar, Mbwazirume, was 15.8 kg, thereby demonstrating that the 'TARIBAN' hybrids have a heavier bunch weight. Cultivars with a huge bunch are

preferred by banana growers, traders, and domestic users because they command a high market price and, hence, boost family income (Dadzie and Orchard 1997; Ssemwanga et al. 2000). The four hybrids have a pendulous compact bunch with more fruit per bunch, as well as heavy and large fruit. With the exception of 'TARIBAN3', which produces few suckers and takes a long time to sprout, all four hybrids have good suckering potential.

The assessment of the YLS at flowering in the three Tanzanian sites revealed that three of the four 'TARIBAN' hybrids had higher levels of BLS resistance than their susceptible EAHB parents and their reference

medium to tall plant size, rapid cycling (with the exception of 'TARIBAN3', which has a longer growth cycle), and higher fruit productivity, all of which are highly desirable traits for banana production by farmers. Additionally, they produce parthenocapic fruit with an erect curved fruit orientation (Fig. 2). Three of the four 'TARIBAN' hybrids have a height shorter than 350 cm (Table 1), which is the maximum indicated in 'Matooke' product profiles. 'TARIBAN1' and 'TARIBAN4' have the shortest plant height (277 cm) of the four triploid hybrids, whereas 'TARIBAN2' is the tallest, surpassing the product profile threshold by 32 cm. 'TARIBAN2' is also
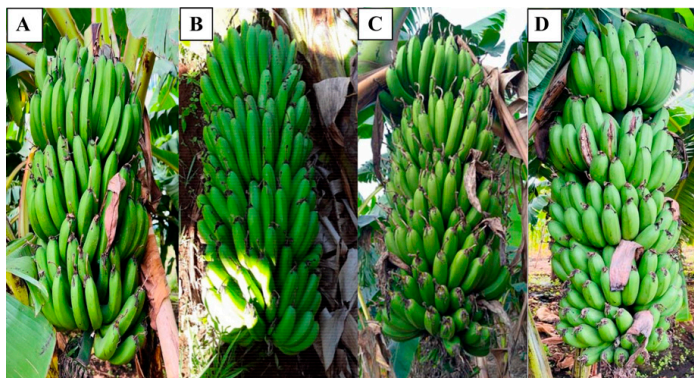

Fig. 2. Bunches of the four new Matooke cooking banana cultivars released by the Tanzania Agriculture Research Institute (TARI) in June 2021: (**A**) 'TARIBAN1'; (**B**) 'TARIBAN2'; (**C**) 'TARIBAN3'; and (**D**) 'TARIBAN4'.

Table 2. Morphological characteristics distinguishing four Matooke cooking banana cultivars (TARIBAN) released in Tanzania.

Descriptor	Cultivar			
	'TARIBAN1'	'TARIBAN2'	'TARIBAN3'	'TARIBAN4'
Fruit shape	Straight (or slightly curved)	Straight (slightly curved)	Straight (slightly curved)	Straight (or slightly curved)
Fruit apex	Pointed	Blunt-tipped	Blunt-tipped and remains of flower relicts	Blunt-tipped
Rachis position	Falling vertically	With a curve	With a curve	Falling vertically
Rachis appearance	Male flowers/bracts above the male bud	Neutral/flowers and presence of withered bracts	Male flowers/bracts above the male bud	Neutral
Pseudostem color (with sheath)	Medium green	Green	Dark green	Black green
Pigmentation of the underlying pseudostem	Pink-purple	Purple	Red-purple	purple-brown
Blotches at the petiole base	Large blotches	Large blotches	Large blotches	Extensive pigmentation
Male bud peduncle color	Dark green	Green	Green	Dark green
Male bud shape	Intermediate	Ovoid	Intermediate	Ovoid
Bract apex shape	Obtuse	Slightly pointed	Slightly pointed	Obtuse

Table 3. Sensory attributes and mean performance of Matooke cooking banana cultivars (TARIBAN) released in Tanzania.

Cultivar	Fruit sensory attributes[i]					
	Color	Aroma	Taste	Mouthfeel	Texture	Overall acceptability
'TARIBAN1'	3.86	3.81	3.56	3.26	3.29	3.58
'TARIBAN2'	3.60	3.70	3.54	3.50	3.43	3.57
'TARIBAN3'	3.73	3.86	3.86	3.87	3.83	3.91
'TARIBAN4'	3.14	3.41	3.21	3.05	3.03	3.27
'Mbwazirume'	4.21	4.02	4.03	3.96	3.90	4.15
Multisite mean	3.71	3.76	3.64	3.53	3.49	3.70
SE of differences[ii]	0.19	0.11	0.19	0.23	0.23	0.19
ANOVA F probability[iii]	<0.001	<0.001	<0.01	<0.01	< 0.01	< 0.01
Coefficient of variation	11.20	6.34	9.50	12.00	11.60	9.85

[i] Hedonic scale of 1 to 5, where 1 = very bad, 2 = bad, 3 = fair, 4 = good, and 5 = very good.
[ii] SE of differences estimated from the mean square error of the analysis of variance (ANOVA).
[iii] Probability of the F-test from the ANOVA.

known for its larger girth (54 cm). Nowakunda et al. (2015) reported comparable results with the official release of Kiwangaazi in Uganda (TARIBAN2 in Tanzania), claiming it is a tall cultivar with a plant height of more than 3 m. Tall banana plants are normally vulnerable to windbreak, but 'TARIBAN2' is protected by its larger girth of more than 50 cm at a height of 1 m. The 'TARIBAN' cultivars have regulated suckering behavior, with only a few suckers escaping apical dominance and developing into the ratoon crop. Table 2 lists the key characteristics that distinguish them based on the International Plant Genetic Resources Institute (1996) standard descriptor list for bananas.

To meet end-user demand, hybrids must show a balance among high yield, host plant resistance to pests and pathogens, and desired culinary quality (Nowakunda and Tushemereirwe 2004). The sensory characteristics of the hybrids were closest to those of 'Mbwazirume' for color, aroma, taste, mouthfeel, texture, and overall acceptability (Table 3). Mbwazirume is one of the most popular consumer-preferred Matooke cooking banana cultivars because of the high-quality attributes of its cooked food.

Availability. 'TARIBAN1', 'TARIBAN2', 'TARIBAN3', and 'TARIBAN4' are available from TARI at its subcenters of Horti-Tengeru, Maruku, and Mitalula in Tanzania. Additionally, tissue culture plantlets are

available from designated private tissue culture laboratories in Tanzania. The National Banana Research Program of NARO in Kawanda, Uganda, is responsible for maintaining the 'TARIBAN' (or 'KABANA') in Uganda at on-station fields and in vitro. They are accessible through NARO and specific domestic private tissue culture enterprises.

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East African highland bananas (EAHBs or *Musa* AAA-EA), which include cooking and brewing types ('Matooke' and 'Mbidde'), dominate production in the region and contribute 3 to 22% of daily calorie intake, which is estimated to be 147 kilocal/person. Several pathogens and pests threaten the long-term viability of EAHB production across East Africa. To overcome these challenges, breeders should employ all available technologies to increase yield. This thesis investigated the crucial factors that should be considered when evaluating and releasing improved 'Matooke' banana cultivars. The study was able to identify adapted, stable, high-yielding, pathogen and pest resistant and farmers' preferred 'Matooke' hybrids.

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