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

Noel A. Madalla
The Alliance of Bioversity International and CIAT, P.O. Box 2704, Arusha, Tanzania; and Swedish University of Agricultural Sciences, Department of Plant Breeding, P.O. Box 190, SE 23422, Lomma, Sweden

Rony Swennen
International Institute of Tropical Agriculture, P.O. Box 7878, Kampala, Uganda; and KU Leuven, Department of Biosystems, W. De Croylaan 42, 3001 Heverlee, Belgium

Allan F. Brown
International Institute of Tropical Agriculture c/o The Nelson Mandela African Institution of Science and Technology, P.O. Box 447, Arusha, Tanzania

Cornel Massawe, Mpoki Shimwela, Daud Mbongo, and Grace Kindimba
Tanzania Agricultural Research Institute, P.O. Box 1571, Dodoma, Tanzania

Jerome Kubiriba, Robooni Tumuhimbise, and Asher W. Okurut
National Agricultural Research Laboratories, P.O. Box 7065, Kampala, Uganda

Sebastien Carpentier and Inge Van den Bergh
The Alliance of Bioversity International and CIAT, Willem De Croylaan 42, 3001 Heverlee, Belgium

Rhiannon Crichton
Bioversity International, Parc Scientifique Agropolis II, 34397 Montpellier Cedex 5, France

Lewis Machida
The Alliance of Bioversity International and CIAT c/o National Agricultural Research Laboratories–Kawanda, P.O. Box 24384, Kampala, Uganda

Eva Weltzien
Department of Agronomy, University of Wisconsin-Madison, 1575 Linden Drive, Madison, WI 53706, USA

Rodomiro Ortiz
Swedish University of Agricultural Sciences, Department of Plant Breeding, P.O. Box 190, SE 23422 Lomma, Sweden

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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.

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

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Current address for N.A.M.: Swedish University of Agricultural Sciences, Department of Plant Breeding, PO Box 190, SE 23422 Lomma, Sweden.
N.A.M. is the corresponding author. E-mail: n.madalla@cgiar.org.

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

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		Altitude	Rainfall	Temp (°C)			Soil type	YLD	H^2
		Lat.	Long.	(m)	(mm·year^{-1})	Min.	Max.	Avg.		(t·ha^{-1}·year^{-1})	
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

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

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

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

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

$$\mathbf{y} = \mathbf{Xb} + \mathbf{Zu} + \mathbf{e},$$

where $\mathbf{y}$ 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 ($i = 1, 2, \ldots, g$; $j = 1, 2, \ldots, e$; $k = 1,2, \ldots, b$), $\mathbf{b}$ is an $eb \times 1$ vector of fixed effects, $\mathbf{u}$ is an $m\ [= g + ge] \times 1$ vector of random effects, $\mathbf{X}$ is an $n \times eb$ design matrix relating $\mathbf{y}$ to $\mathbf{b}$, $\mathbf{Z}$ is an $n \times m$ design matrix relating $\mathbf{y}$ to $\mathbf{u}$, and $\mathbf{e}$ is an $n \times 1$ vector of within-group errors (Olivoto and Lúcio 2020; Yang 2007). The vectors $\mathbf{b}$ and $\mathbf{u}$ were estimated using the well-known mixed model equation (Henderson 1975)

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

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

$$\mathrm{BLUP}_i = \mu + \hat{g}_i.$$

The effect of the ith genotype in the jth environment $(\hat{g}_{ij})$ 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 $h_g^2 = \left(\hat{\sigma}_{\alpha t}^2 + e\hat{\sigma}_{\alpha}^2\right)/\left(\hat{\sigma}_{\alpha t}^2 + \hat{\sigma}_{\delta}^2 + e\hat{\sigma}_{\alpha}^2\right)$, and $h_{ge}^2 = \hat{\sigma}_{\alpha\tau}^2/\left(\hat{\sigma}_{\alpha\tau}^2 + \hat{\sigma}_{\varepsilon}^2\right)$ 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

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

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 $\left(\hat{\sigma}_{\alpha}^2\right)$, variance of GEIs $\left(\hat{\sigma}_{\alpha\tau}^2\right)$, residual variance $\left(\sigma_{\varepsilon}^2\right)$, phenotypic variance $\left(\sigma_p^2\right)$, broad-sense heritability (H^2), coefficient of determination for the genotype-vs.-environment interaction effects $\left(r_i^2\right)$, heritability of the genotypic mean $\left(H_m^2\right)$, accuracy of genotype selection (As), correlation between genotypic values across environments (r_{gei}), genotypic coefficient of variation ($\mathrm{CV_g}$, measured as a percentage), and residual coefficient of variation ($\mathrm{CV_r}$, 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

$$\mathrm{HMGV}_i = \frac{n}{\sum_{j=1}^{n} \frac{1}{\mathrm{GV}_{ij}}},$$

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 × μ). The RPGV was

$$\mathrm{RPGV}_i = \frac{1}{n}\frac{\sum_{j=1}^{n}\mathrm{GV}_{ij}}{M_j},$$

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 × μ) penalized for instability and capitalized for GEIs. The HMRPGV was calculated according to Resende (2004) as

$$\mathrm{HMRPGV}_i = \frac{n}{\sum_{j=1}^{n} \frac{1}{\mathrm{RPGV}_{ij}}}.$$

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 ($\alpha = 1/2$).

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:

$$\mathrm{WAASB}_i = \sum_{k=1}^{p} |\mathrm{IPCA}_{ik} \times \mathrm{EP}_k| / \sum_{k=1}^{p} \mathrm{EP}_k,$$

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

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

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 multigeneration 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 $t \cdot ha^{-1}$ per year. Despite producing the greatest yield (37.8 $t \cdot ha^{-1}$) 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).

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 $P > 0.05$.

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

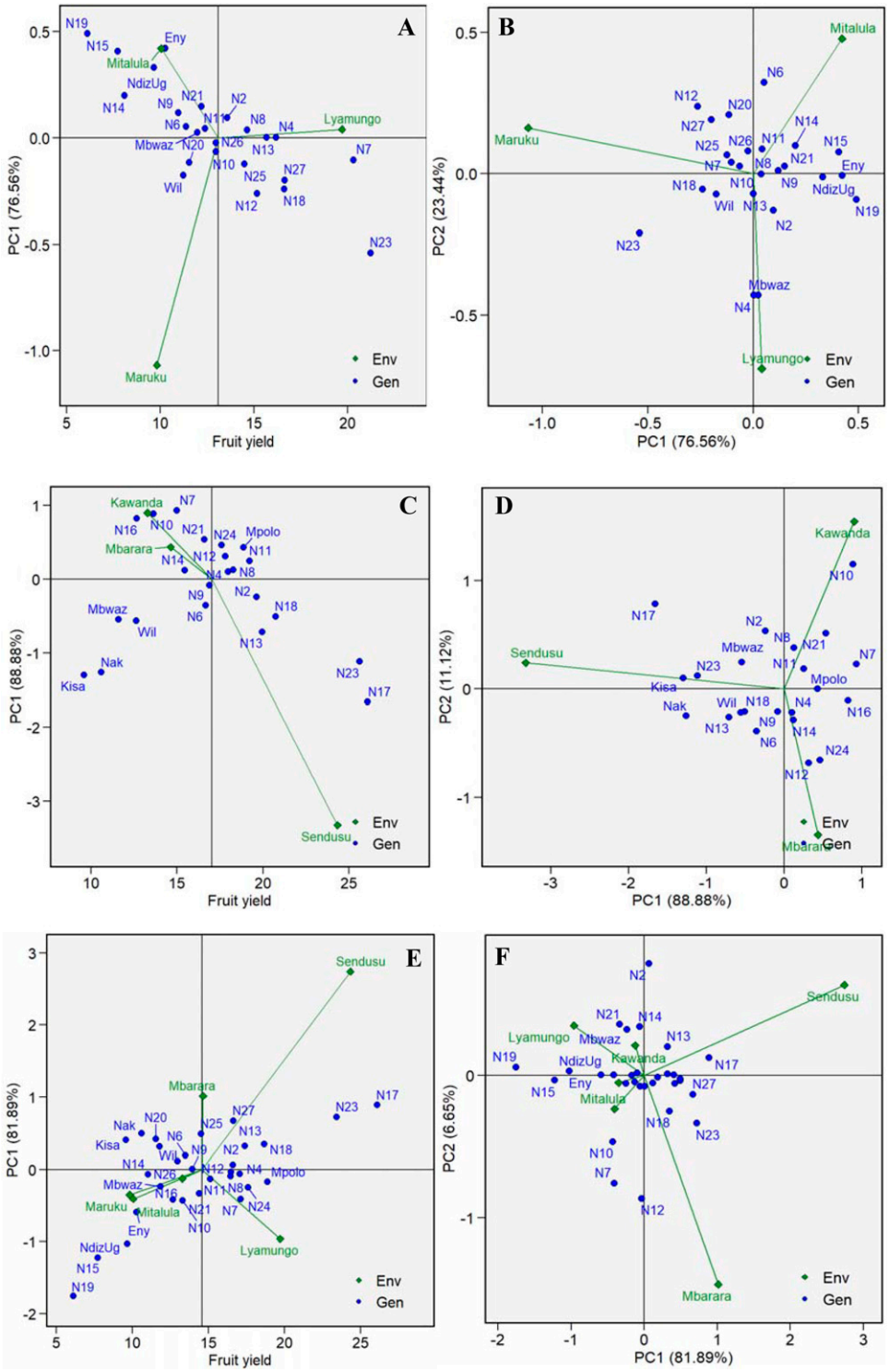

Fig. 1. Biplots showing principal components (PCs) for 24, 22, and 30 banana genotypes (Gen) after their testing in six sites (Env) in Tanzania (**A**, **B**), Uganda (**C**, **D**), and across countries (**E**, **F**), respectively, evaluated for yield potential and stability. The scores were calculated 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

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 to 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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