Euphytica (2025) 221:145
https://doi.org/10.1007/s10681-025-03598-1

RESEARCH

Estimation of seasonal, additive and non-additive genetic components in diploid banana (*Musa* spp.)

Violet Akech · Stanley John Bayo · Therése Bengtsson · Rodomiro Ortiz · Rony Swennen · Salvador Gezan · Marnik Vuylsteke · Allan Brown

Received: 30 June 2025 / Accepted: 4 August 2025

Abstract This study focuses on improving the efficiency of breeding diploid bananas for important traits such as yield, fruit size and weight. Partitioning genetic variance into additive and non-additive components is crucial. This is challenging in most commonly available family structures in banana breeding due to reduced fertility and ploidy complications. However, the availability of replicated clones of full-sib progeny allows greater insight into the genetics of perennial diploid bananas. Clones of nine full-sib families, generated through a factorial mating design consisting of six diploid parthenocarpic female and two wild diploid male banana (*Musa* spp.) parents, were evaluated at the International Institute of Tropical Agriculture in Arusha. Data were collected over two harvests (plant crop and first ratoon) to provide a better understanding of the genetic architecture of key traits and their seasonal influence. Pedigree-based models were fitted to the data to estimate additive, dominance, epistatic variance components, and seasonal effects. Additive variance was the major source of genetic variance for most traits. Dominance and epistatic variances were non-significant for most traits, with a few exceptions. Broad-sense and narrow-sense heritability estimates were high for most traits. A significant positive correlation was found between yield traits and between the plant and first ratoon crops for yield traits, which will help accelerate selection and improve genetic gains. These results enhance our understanding of the genetic architecture of quantitative traits in bananas and lay a foundation for further study in this almost recalcitrant to cross-breeding but important crop.

Keywords Additive · BLUP · Clonal model · Heritability · *Musa* · Non-additive

Abbreviations
BLUP Best linear unbiased prediction

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s10681-025-03598-1.

V. Akech (✉) · R. Swennen
International Institute of Tropical Agriculture, Ibadan, Uganda
e-mail: V.Akech@cgiar.org; violet.akech@slu.se

V. Akech · T. Bengtsson · R. Ortiz
Swedish University of Agricultural Sciences, Alnarp, Sweden

S. J. Bayo · A. Brown
International Institute of Tropical Agriculture, Arusha, Tanzania

R. Swennen
Department of Biosystems, KU Leuven, Willem De Croylaan 42, B 3001 Heverlee, Belgium

S. Gezan
VSN International, Hamel Hempstead, UK

M. Vuylsteke
Gnomixx B.V., Melle, Belgium

Published online: 21 August 2025

Introduction

Production of bananas (including cooking and dessert types) in Africa remains low at about 31 t ha^{-1} $year^{-1}$ compared to 70 t ha^{-1} $year^{-1}$ in Asia (FAO 2022). Tanzania, second leading producer after Uganda, accounts for 23.4% of production (Lescot 2020), yet its average yield remains low at about 8.8 million t ha^{-1} $year^{-1}$ (FAO 2020) due to abiotic and biotic stresses. Around 70–95% of Tanzanian households grow bananas for food and income (Kilimo Trust 2012; Nkuba et al. 2003). Predominant cultivars are East African Highland Bananas (EAHB), mainly triploid Matooke (AAA) and diploid Mchare (AA), followed by brewing, dessert, and plantain cultivars (Evers 1992; De Langhe et al. 2001; Kalyebara et al. 2007; Madalla et al. 2023; Maruo 2007). Mchare are edible parthenocarpic diploids (AA) grown in the north-central region and southern highlands of Tanzania, valued for their unique texture (Brown et al. 2017; De Langhe et al. 2001; Onyango et al. 2009; Perrier et al. 2019).

Mchare is phenotypically diverse yet has a narrow genetic base (Kitavi et al. 2016; Nyine et al. 2017; Ortiz 1997; Perrier et al. 2011), with all genotypes considered the same clone set (Onyango et al. 2009). As a diploid, Mchare better aids understanding genetic architecture than triploid bananas. Mchare breeding focuses on improving yield, disease resistance, especially Fusarium, and desirable consumer traits (Brown et al. 2017; Madalla et al. 2023). Current schemes cross diploid (2×) female cultivars with diploid (2×) male accessions as resistance donors (Bayo et al. 2024). Progeny are evaluated over at least two crop cycles (mother plant referred to as plant crop or cycle 1 and first ratoon referred to as cycle 2). Efficient breeding requires comprehensive knowledge of trait genetics and identifying parent genotypes that, when combined, produce superior offspring. Understanding genetic variances, covariances, and parameters like trait heritability is essential for effective selection strategies (Milligan et al. 1990).

Combining ability and heritability are key statistics to studying crop trait genetics (Sprague and Tatum 1942). General combining ability (GCA) helps to identify parents with superior genetic merit based on offspring performance, while specific combining ability (SCA) identifies the best cross combinations based on cross performance (Fasahat et al. 2016; Viana and Matta 2003). The relative importance of GCA and SCA, which respectively represent the additive and non-additive genetic components is critical for partitioning genetic variance and choosing best breeding strategy in diploid bananas. Knowing the heritability of key traits helps Mchare breeders estimate improvement potential, as higher-heritable traits generally are easier to improve by crossbreeding (Bernado 2014; Falconer and Mackay 1996; Holland et al. 2003; Schmidt et al. 2019a).

Breeding and evaluating banana hybrids is challenging due to low fertility in cultivated germplasm, causing failed pollinations and poor seed germination (Batte et al. 2019; Brown et al. 2017; Ortiz 2013; Swennen and Vuylsteke 1993). This limits offspring production, causes staggered planting, and complicates establishing balanced, well-replicated field trials.

Banana is a perennial ratoon crop requiring up to three years to complete two fruiting cycles (Brown et al. 2017; Karamura et al. 2011; Swennen and Ortiz 1997). Flowering and harvest are unsynchronized, resulting in plants at various developmental stages simultaneously (Tixier et al. 2004; Nayar 2010; Lescot 2020). This asynchrony introduces environmental heterogeneity across seasons, making it essential to estimate seasonal effects and genotype-by-season interactions for accurate breeding value predictions. Overlapping generations of individuals, known as production cycles (hereafter cycles), benefit farmers but complicate hybrid evaluations. These cycles vary by season among genotypes and plants of the same genotype, necessitating consideration of environmental factors like planting season and flowering time on trait variation.

Lack of synchronization in growth and data collection leads to unbalanced datasets with heterogeneous variances and covariances of adjusted means (Schmidt et al. 2019b). The best linear unbiased prediction (BLUP) method improves estimation of genetic effects in such cases. The method is widely used for evaluating and selecting crops, including clonally propagated species such as potatoes (Ortiz et al. 2021; Slater et al. 2014; Ticona-Benavente and Silva Filho 2015), acai berry (Teixeira et al. 2012), sugarcane (Mbuma et al. 2020; Shanthi et al. 2008; Zeni Neto et al. 2013), trees (Chen et al. 2020; Isik et al. 2003; Weng et al. 2008) and passion fruit (Santos et al. 2015). Pedigree-based BLUP further

improves estimates and selection accuracy by borrowing information from related individuals (Bernardo 2020; Piepho et al. 2008). From these BLUPs, greater accuracy is attained in selecting superior individuals, estimating heritability, and determining parental GCA and SCA of the crosses. In sugarcane, family selection for sugar yield has improved selection efficiency, increased heritability estimates, yielded more accurate breeding values and better resource use than individual selection (Mbuma et al. 2020; Shanthi et al. 2008; Stringer et al. 2011).

The full clonal model (Chen et al. 2020; Muñoz et al. 2014; Pisaroglo de Carvalho et al. 2014), a modification of the animal model, is commonly used for clonally replicated individuals with pedigree information. It applies here due to the diploid nature of the Mchare breeding population, enabling estimation of parental and clonal GCA, clonal values of offspring, and SCA of crosses. This is vital in parental improvement, allowing selection of high-GCA parents and high-genetic-value clones to design superior crosses for backward and forward selection and hybrid evaluations for advancement and release. When both parents are known, pedigree information in the full clonal model partitions genetic variance into additive and non-additive components, allowing estimation of broad- and narrow-sense heritability and dominance and epistatic ratios.

This study aimed to optimize the Mchare breeding pipeline by improving selection accuracy and genetic gains. Objectives were to (1) quantify genetic variation for key traits and partition additive and non-additive effects using the full clonal model, (2) assess seasonal environmental effects, and (3) determine genetic correlations among key traits and cycles. To our knowledge, this is the first use of the clonal model for estimating genetic parameters and their partitioning in banana breeding.

Materials and methods

Hybrid production

Six diploid female Mchare cultivars were hand-pollinated with pollen from two wild diploid males according to an incomplete factorial design (Bayo et al. 2024), resulting in nine full-sib families (Table 1). Seeds were then collected from ripe fruits and subjected to embryo rescue as described by Luyiga et al. (2024). The progeny's ploidy was checked by flow cytometry (Dolezel 1997; Loureiro et al. 2021) following a standard protocol adopted by the International Institute of Tropical Agriculture (IITA) (Akech et al. 2024a). The tissue culture-derived plantlets were hardened off for 2–3 months in a screen-house and then transplanted into the field from 2018 to 2021 following a protocol described by Akech et al. (2024b). Planting was staggered according to the availability of the plantlets. The population consisted of 45 progenies from nine families. (Supplementary Table S1).

Table 1 Factorial-crossing scheme used to obtain the progeny

Female	Borneo (wild)	Calcutta 4 (wild)	Sub-total
Akondro mainty	–	2	2
Huti-White	4	19	23
Ijihu Inkundu	1	2	3
Kahuti	2	–	2
Mchare laini	2	11	13
Nshonowa	–	2	2
Sub-total:	9	36	45

Trial site and design

This research was conducted at IITA banana farms in Arusha, Tengeru, situated at the Nelson Mandela African Institution of Science and Technology, in Tanzania. The geographical coordinates of the experimental site were approximately 3°24′03''S latitude and 36°47′34''E longitude, with an altitude of 1200 m above sea level.

The location experiences a tropical highland climate with a moderately cool thermal zone (Nicholson 2017). The climatic conditions are influenced by a bimodal rainfall pattern, consisting of a long rainy season from late March to early June (locally referred to as 'Masika') and a short rainy season from October to December (locally referred to as 'Vuli'). However, it is important to note that annual rainfall can vary with averages between 900 and 1400 mm year^{-1} (Grieser et al. 2006; Kabanda 2018; Meya et al. 2020; Stevens et al. 2020). Throughout the experiment, the total precipitation received was approximately 903 mm per year. It is noteworthy that this

falls below the optimal range for banana production (1100–2650 mm per year). The distribution of rainfall exhibited uneven patterns, including dry spells lasting more than two months. The season, locally referred to as 'Kiangazi', lasting from January to late February, has high temperatures (average of 28 °C) and low relative humidity, 'Kipupwe' lasting from July to August, has low temperatures (average of 13 °C) and no rainfall; and 'Demani' lasting from late August to September, has high temperatures and high relative humidity. Consequently, the suboptimal precipitation levels necessitated supplementary irrigation (van Asten et al. 2011; Varma and Bebber 2019).

The experimental layout followed a randomized complete block design with three blocks and three plants (clones) per plot. Parental lines were represented by multiple plants (6–20) per block. Two lines of Matooke were planted around the experimental trial as a border effect (field layout in Supplementary Table S2). Supplemental water was provided through drip irrigation (rate of 4 L hr^{-1}) for two hours per day, three days a week to ensure each mat received at least 60 L per week. Manure and inorganic fertilizers were applied twice a year, with each mat (group of banana plants that grow from a corm) receiving nitrogen, phosphorus, and potassium (NPK): 92 g urea, 100 g triple super phosphate (TSP) and 300 g muriate of potash (MOP), respectively. After the flowering of the plant crop, only three plants per mat were maintained: plant crop (mother) to represent cycle 1, first ratoon (daughter) to represent cycle 2 and second ratoon (granddaughter) to represent cycle 3 of production.

Data collection

The yield-related traits scored included: bunch weight at full maturity in kg (BW), number of hands (cluster) (NH), fruit length in cm (FL), fruit circumference in cm (FC), and fruit finger weight in grams (FW). Ten random fingers were measured for FL, FC and FW. The vegetative (growth) traits included: number of standing functional leaves at flowering (NFL) (count of leaves that have 50% or more of their surface as green, healthy and photosynthetic active tissue at flowering), plant height at flowering in cm (PH), plant girth at 100 cm from the soil surface (PG), plant stature (PS) which was calculated as PG/PH, and the total number of suckers at flowering (NS). Yield per year (YLD) was calculated using the following formulae:

$$\mathrm{YLD} = \frac{\text{Total bunch weight harvested across the two cycles} \times 365}{\text{Number of days between planting and harvest of first ratoon crop}}$$

The cycling traits included: days to flowering (DPF, days between planting to flowering of the plant crop), days to fruit maturity (DFH, days between flowering and harvesting) and cycling time defined as the number of days between the flowering of the plant crop (cycle 1) to the flowering of the first ratoon crop (cycle 2). Total number of suckers (NS) and DPF were recorded for cycle 1 only. All other traits were recorded for both the plant crop (cycle 1) and the first ratoon crop (cycle 2). A detailed description of the traits analysed in this study is given in Supplementary Table S3. The dates of planting and flowering for each plant were recorded and later provided information of year and season of planting (YP and SP, respectively), and year and season of flowering (YF and SF, respectively).

Data analysis

All genetic analyses were carried out using the software ASReml-R v. 4.2 (Butler et al. 2023) obtained by a copyright license, which fits linear mixed models (LMM) with complex data sets using sparse matrix models. ASReml-R is equipped with the residual maximum likelihood (REML) for variance component estimation using the average information algorithm (Butler et al. 2023). Other analyses were performed using R v4.0 (R Development Core Team 2019).

Table 2 Overview of fixed and random effects as part of the linear mixed model fitted to each trait group

Trait group	Block*	Cycle*	Add^{g,p}	Add:Cycle^{g,p}	Fam^{g,p}	Clonal^{g,p}	Plot^{p}	YP:SP^{p}	YF:SF^{p}	Cycle:YF:SF^{p}	Cycle:Plot^{p}	Residual^{p}
1	✓		✓		✓	✓	✓	✓	✓			✓
2	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓		✓
3	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓
4	✓		✓		✓	✓	✓	✓	✓			✓

Trait group 1 = days to flowering (DPF), total number of suckers at flowering (NS),

Trait group 2 = bunch weight at full maturity (kg) (BW), number of hands (NH), number of standing functional leaves at flowering (NSFL), plant height at flowering (cm) (PH), plant girth at 100 cm from soil surface (cm) (PG), plant stature (PS), days to fruit maturity (DFM)

Trait group 3 = fruit length (mm) (FL), fruit circumference (mm) (FC), fruit finger weight (grams) (FW)

Trait group 4 = yield/year/plant (kg) (YLD), cycling time (days) (CT)

*indicates fixed effects

^{g}indicates the corresponding variance component contributing to the genotypic variance of the heritability calculation

^{p}indicates the corresponding variance component contributing to the total phenotypic variance of the heritability calculation

Estimation of variance components and genetic parameters

After inspecting the data for inconsistencies, outliers and normality, specific linear mixed models (LMMs) were fitted to each trait group, and variance components, BLUPs, and predicted means were calculated. Specific LMMs were used according to the terms applicable to a trait group as indicated in Table 2. An example for trait group 2 is illustrated by Eq. 1. Phenotypic observations obtained for two cycles (trait groups 2 and 3 (Table 2)), were analysed as repeated measurements. The pedigree information was used to compute the additive pedigree-based relationship matrix using standard methods (Mrode 2005; Walsh and Lynch 2018). This matrix was constructed using the '*ainverse*' function in ASReml-R.

Trait group 2: traits with data collected over two cycles

$$\begin{aligned} Trait_{abcdefjpq} = {} & Block_b + Cycle_c + Add : \\ & Cycle_{ac} + Fam_d + Clonal_e \\ & + Plot_j + YF : SF_{fs} + YP : SP_{ps} \\ & + YF : SF : Cycle_{fsc} + \epsilon_{abcdefjpq} \end{aligned} \quad (1)$$

where the trait has been measured on the qth plant in plot j at cycle c, planted in season s of the year p and flowering in season s of the year f. Block and Cycle are the only fixed terms in the model accounting for the variation between the three blocks and the two cycles, respectively. All other terms are random: Add, Fam and Clonal accounts for the additive, family and clonal variance, respectively; Plot accounts for the plot-to-plot variation; YP:SP and YF:SF account for the variation due to seasonal fluctuations across year during planting and flowering, respectively; YF:SF:Cycle accounts for the cycle specific seasonal fluctuations across year in flowering; finally, ϵ accounts for the random noise. The LMM fitted to trait group 3 data has the additional random term Cycle:Plot, accounting for the 10 measurements on the same plant (modelling pseudo-replications).

The additive (V_A), dominance (V_D) and epistatic (V_I) variances were calculated according to Walsh and Lynch (2018) using their variance component estimators (σ^2), as follows:

$$V_A = \sigma^2_{add}$$

$$V_D = 4\sigma^2_{Fam}$$

$$V_I = \sigma^2_{Clonal} - 3\sigma^2_{Fam}$$

where the sum V_A, V_D and V_I is the total genetic variance,V_g with $\sigma^2_{add}, \sigma^2_{Fam}$, and$\sigma^2_{Clonal}$ representing the additive, dominance and interaction variance components.

Heritability

In addition to the calculation of the broad-sense heritability, the decomposition of the genetic component into additive and non-additive variances allowed for the calculation of the narrow-sense heritability (h^2). Broad-sense heritability (H^2), calculated by dividing the total genetic variance component by the total phenotypic variance; the narrow-sense heritability (h^2), was calculated by dividing the additive genetic variance component by the total phenotypic variance. The total phenotypic variance is the sum of all variance components contributed by all terms indicated 'p', in Table 2. The residual variance was divided by 3 because of the three blocks (replicates) in the experimental design, and therefore, their definition is about the mean clonal response.

Correlations

The genetic correlation analysis between a pair of traits in each cycle was based on a bivariate model which estimated the covariance between the two traits. Correlations between cycles for each trait was estimated as a variance component between cycle 1 and cycle 2 for each trait, considering cycles as repeated measurements. The correlations were modelled using the uniform heterogeneous (corh) variance structure in ASReml-R 4.2. The correlations were then tested for significance by fitting a reduced model having the diagonal variance structure, using likelihood ratio tests (LRT).

BLUPs

Breeding values (BVs), a type of BLUPs, were generated for parental lines, progeny and crosses. Breeding values for the parental lines could be interpreted as twice the GCA and used to select the best parental lines; other BLUP values are used to select the best crosses using the sum of the SCA of the cross, the GCA of the male, and GCA of the female parent in that cross. BLUPs for the individuals could be used to select the best individual to serve as good parents in future crosses or as hybrids for further evaluation or release.

Results

Variance components and heritability estimates

Genetic and non-genetic variance components as obtained by fitting the LMM for the different traits are given in Table 3. Figure 1 illustrates the additive, dominance and epistasis variance components as calculated from the additive, family and clonal variance components, and seasonal variance components, for the yield traits. The analysis revealed significant ($p \leq 0.05$) and highly significant ($p \leq 0.001$) additive effects for all traits except for the NS, NFL and DFH. All traits had estimates of the dominance and epistatic variance components close to zero, except for NS and PS for which the strongest and significant genetic component was the dominance variance component. Some of the genetic variance was allocated to epistatic variance for BW and PG, albeit not statistically significant. Seasonal variations were very small and non-significant for yield-related traits. The variance components associated with seasonal variation in planting time (YP:SP) were highly significant ($p < 0.001$) for agronomic traits except for PG, and non-significant for cycling traits except for DPF. Seasonal variation in flowering time (YF:SF) was significant ($p < 0.001$) for only NS and NFL among the agronomic traits and for DPF and CT among the cycling traits. The cycle:year:season component of flowering was a significant ($p < 0.01$) source of variation for BW, NH and FC, among the yield-related traits, and for PG ($p < 0.001$) and PS ($p < 0.05$) among the agronomic traits. The additive variance component for all yield-related traits except BW and NH was the highest in proportion to the total variation (Fig. 1).

Broad-sense heritability (H^2) and narrow-sense heritability (h^2) estimates varied from 0.68 for FC, to zero for DPF and CT (Table 4).

Table 3 Variance components, their standard errors and likelihood ratio test results for the investigated traits

Trait		Dominance	Epistatic	Additive	YP:SP	YF:SF	Cycle:YF:SF	Plot	Cycle:Plot	Residual
Yield	BW	0	4.24 ± 4.10***	11.10 ± 5.70***	0.49 ± 0.55	0.37 ± 0.71	0.46 ± 0.67**	4.00 ± 1.20	–	14.00 ± 1.10
	NH	0	0	0.99 ± 0.27***	0.01 ± 0.09	0	0.09 ± 0.06*	0	–	1.80 ± 0.13
	FC	0	0	4.70 ± 1.05***	0.03 ± 0.05	0.01 ± 0.10	0.05 ± 0.05**	0	2.03 ± 0.14***	0.35 ± 0.00
	FL	0	0.02 ± 0.07	17.13 ± 3.90***	0.18 ± 0.29	0	0.42 ± 0.35	0	10.00 ± 0.67***	1.94 ± 0.04
	FW	0	2.28 ± 6.00	1057.40 ± 250.36***	1.80 ± 12.60	0	7.80 ± 13.23	0	725.00 ± 47.50***	65.90 ± 1.32
	YLD	0	0	20.57 ± 7.68***	0.51 ± 1.04	0	0	12.82 ± 4.55	–	8.74 ± 1.24
Agronomic	NS	8.41 ± 7.80	0	0	1.46 ± 1.17***	1.09 ± 0.82**	–	1.41 ± 0.81	–	6.69 ± 0.67
	NFL	0	0	3.28 ± 1.17	1.91 ± 1.34***	1.97 ± 0.97***	0	0.01 ± 0.01	–	14.49 ± 0.96
	PH	0	0	1554.10 ± 352.82***	133.10 ± 102.90**	10.47 ± 32.41	0	0	–	1710.03 ± 116.32
	PG	0	9.59 ± 5.85	11.79 ± 7.24**	1.89 ± 2.07	1.27 ± 4.00	7.18 ± 4.82***	0.01 ± 0.05	–	54.58 ± 3.72
	PS	0.81 ± 0.86	0	0.41 ± 0.25**	0.16 ± 0.16**	0.03 ± 0.20	0.26 ± 0.24*	0	–	4.75 ± 0.31
Cycling	DPF	964.64 ± 1123.90	0	157.82 ± 313.08***	41,092.89 ± 18,762.38***	52,150.00 ± 21,614.52	–	0	–	1364.26 ± 124.98
	DFH	452.68 ± 781.17	0	82.01 ± 278.56	10.38 ± 781.17	102.20 ± 334.76	202.50 ± 238.10	1.32 ± 7.42	–	6980.16 ± 474.93
	CT	0	2.00 ± 5.00	962.16 ± 363.47*	0	81,899.10 ± 35,148.56	–	0	–	938.78 ± 120.57

YP year of planting, *YF* year of flowering, *SP* season of planting, *SF* season of flowering, *BW* bunch weight at full maturity (kg), *NH* number of hands, *FL* fruit length (mm), *FC* fruit circumference (mm), *FW* fruit finger weight (grams), *YLD* yield/year/plant (kg), *NFL* number of standing functional leaves at flowering, *PH* plant height at flowering (cm), *PG* plant girth at 100 cm from soil surface (cm), *PS* plant stature, *NS* total number of suckers at flowering, *DPF* days to flowering, *DFH* days to fruit maturity, *CT* cycling time (days)

"–" means the term was not included in the model, standard errors of dominance or epistatic genetic variances were not estimated due to zero or near zero estimates. *, **, *** indicate significant at $p \leq 0.05$, $p \leq 0.01$ and $p \leq 0.001$, respectively

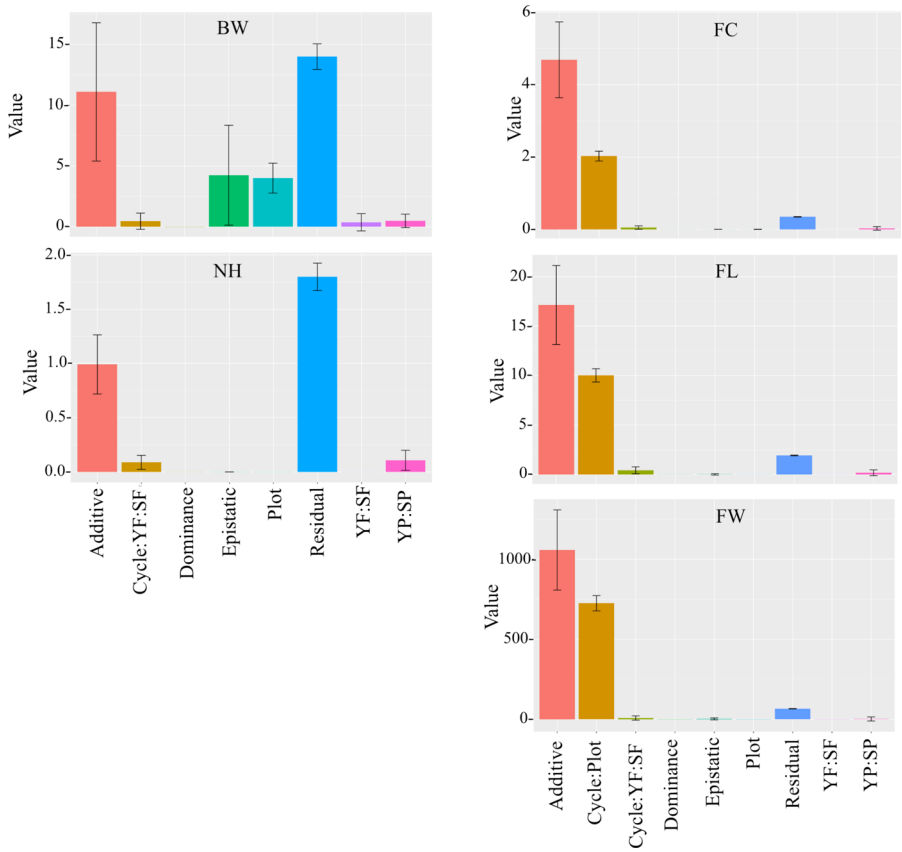


Fig. 1 Plot of variance components for the five yield traits. *BW* bunch weight at full maturity (kg), *NH* number of hands, *FL* fruit length (mm), *FC* fruit circumference (mm), *FW* fruit finger weight (grams)

For all yield-related traits, both H^2 and h^2 estimates were above 0.5, except h^2 for BW. Only PH, among the agronomic traits, had an H^2 above 0.5. There was a low H^2 and h^2 for all cycling traits. Interestingly, except BW, H^2 and h^2 estimates were similar for all yield-related traits, NFL and PH, while h^2 was smaller than H^2 for all other traits.

Genetic correlations

The estimates of additive genetic correlation between the evaluated traits ranged from 0.01 to 0.99 in cycle 1 (Table 5) and from 0.05 to 0.99 in cycle 2 (Table 6). The highest positive correlations were observed among the yield-related traits ($0.84 < r < 0.99$, $p \leq 0.001$). A positive and significant correlation was observed between BW and all fruit traits (FC, FL, FW) except NH in cycle 1, which were similarly significant and positively correlated to each other. Yield per year was significant and positively correlated with all yield-related traits except NH. The number of hands had a significant positive correlation with PH, and PG, but had non-significant negative correlations of low magnitude with the cycling traits DPF, DFH and CT. There were significant and positive correlations of high magnitude ($0.80 < r < 0.94$, $p \leq 0.001$; Table 4) for all yield traits between cycle one (plant crop) and cycle two (first ratoon crop). Plant height and PG, also had a positive significant correlation of high magnitude ($r > 0.60$) between cycle one and cycle two (Table 4). The model failed to estimate the correlation coefficients across cycles for PS and DFH.

Progeny performance and parental combining ability for yield traits

The additive best linear unbiased predictor (BLUP) values were used to assess the performance of the parents and the progeny in both cycles (Supplementary Tables S4 and S5). The additive BLUP estimates for BW among the female parents ranged from −1.4 (Kahuti) to 2.4 (Akondro mainty), and for yield per year, from −2.4 (Ijihu Inkundu) to

Table 4 Broad-sense (H^2), narrow-sense (h^2) heritability estimates for all traits and correlation of traits between cycle 1 (plant crop) and cycle 2 (first ratoon crop)

Trait category	Trait	H^2	h^2	correlation
Yield	BW	0.61 ± 0.07	0.44 ± 0.18	0.80**
	NH	0.55 ± 0.08	0.55 ± 0.08	0.86***
	FC	0.68 ± 0.05	0.68 ± 0.05	0.93***
	FL	0.60 ± 0.06	0.60 ± 0.06	0.93***
	FW	0.58 ± 0.06	0.58 ± 0.06	0.94***
	YLD	0.56 ± 0.12	0.56 ± 0.12	
Agronomic	NS	0.46 ± 0.11	0.16 ± 0.16	
	NFSL	0.27 ± 0.08	0.27 ± 0.08	−0.40
	PH	0.68 ± 0.06	0.68 ± 0.06	0.61***
	PG	0.43 ± 0.08	0.24 ± 0.13	0.68***
	PS	0.30 ± 0.08	0.14 ± 0.08	–
Cycling	DPF	0	0	
	DFM	0.16 ± 0.14	0.03 ± 0.09	–
	CT	0	0	

BW bunch weight at full maturity (kg), *NH* number of hands, *FL* fruit length (mm), *FC* fruit circumference (mm), *FW* fruit finger weight (grams), *YLD* yield/year/plant (kg), *NFL* number of standing functional leaves at flowering, *PH* plant height at flowering (cm), *PG* plant girth at 100 cm from soil surface (cm), *PS* plant stature, *NS* total number of suckers at flowering, *DPF* days to flowering, *DFH* days to fruit maturity, *CT* cycling time (days)

*, **, *** indicate significant at $p \leq 0.05$, $p \leq 0.01$ and $p \leq 0.001$, respectively. '–' indicates correlations not estimable by the model

2.3 (Huti-White). Four and two female parents had negative BLUP values for BW and yield per year, respectively. The progeny had a higher range of additive BLUP values than their female parents for BW (−2.6 to 3.8) and yield per year (−3.0 to 8.7). Of the ten best-performing genotypes according to their additive BLUPs for BW, nine were progeny and one parent (Supplementary Table S4 and Fig. 2a) while nine (all among the top performers for BW) were progeny and one parent for yield per year (Supplementary Table S4). The trend described above for BW is for the plant crop (cycle one) but a similar trend was observed in the first ratoon crop (cycle two) (Fig. 2b). Since breeding value (BV) is twice the GCA, the trend for GCA of parents is similar to the trend of the described above.

Discussion

Variance components and combining ability

The results from this study show that the strongest genetic variance component for most traits especially yield-related characteristics in this breeding population, is primarily the additive variance component. This has been observed previously by Tenkouano et al. (2012), who reported the predominant role of additive genetic effects on the expression of bunch weight, fruit filling time and fruit length in triploid plantain half-sib families from crosses between the tetraploid plantain-banana hybrids and improved diploid germplasm (either plantain-banana derived hybrids or improved banana germplasm). Dominance was detected only for cycling traits DPF and DFH, and epistatic variance only for BW and PG though non-significant. The relatedness among the female parents since they belong to the same clonal set (Onyango et al. 2009) could have led to reduced heterozygosity in the progeny and hence less opportunity for detecting dominance and epistatic effects, and inflated estimates of additive variance because dominance and epistatic effects may be confounded with additivity. The significance and magnitude of the additive genetic effects for all traits except for the number of suckers, number of functional leaves and days from flowering to harvest, indicate that breeding progress for these traits in diploid banana breeding is feasible. Similar observations of significant GCA and non-significant SCA for yield traits have been reported in plantain-banana hybrids (Oselebe and Tenkouano 2008; Tenkouano et al. 1998). This would suggest that differences in additive effects of the parents are the main reasons for the differences among the offspring and that exploring intra- and inter-locus interaction is of less importance in the improvement of this population. For maximum genetic gain, the breeding strategy for Mchare diploid banana breeding should similarly focus on the development and selection of cultivars, by the accumulation of favourable alleles as suggested for the 4x – 2× and/or 3x – 2× breeding scheme in the generation of elite diploid and tetraploids hybrids to be used as parents and secondary triploids (Ortiz 2013; Ortiz and Swennen 2014).

The non-significant YP:SP and YF:SF for yield traits could be because the experimental station

Table 5 Additive correlation coefficients between traits in cycle 1

	BW	NH	FC	FL	FW	YLD	NS	NFL	PH	PG	PS	DPF	DFH
BW													
NH	0.07 ns												
FC	0.88***	−0.17											
FL	0.84***	0.07	0.94***										
FW	–	−0.09	0.99***	0.99***									
YLD	0.99***	0.04	0.90***	0.86***	0.99***								
NS	−0.24	0.09	0.17	−0.55	–	0.37							
NFL	0.04	−0.13	–	0.30*	0.27	0.06	0.38*						
PH	0.44*	0.77***	0.22	0.39*	0.01	0.46*	–	0.44					
PG	0.49	0.58**	0.23	0.45	0.34	−0.09	0.16	0.30	0.93***				
PS	0.28	–	0.25	0.26**	0.49	0.03	−0.06	−0.12	–	0.47			
DPF	0.53	−0.14	0.61***	0.56**	−0.12	0.40	–	0.33	−0.19	0.05	–		
DFH	0.19	−0.05	0.16	0.10	−0.04	–	–	0.15	0.31	–	–	−0.12	
CT	−0.33	0.12	0.15	−0.59	−0.23	0.39	0.37	–	−0.22	–	–	–	–

BW bunch weight at full maturity (kg), *NH* number of hands, *FL* fruit length (mm), *FC* fruit circumference (mm), *FW* fruit finger weight (grams), *YLD* yield/year/plant (kg), *NFL* number of standing functional leaves at flowering, *PH* plant height at flowering (cm), *PG* plant girth at 100 cm from soil surface (cm), *PS* plant stature, *NS* total number of suckers at flowering, *DPF* days to flowering, *DFH* days to fruit maturity, *CT* cycling time (days)

*, **, *** indicate significant correlation at $p \leq 0.05$, $p \leq 0.01$ and $p \leq 0.001$, respectively. '–' indicates correlations not estimable by the model

Table 6 Additive correlation coefficients between traits in cycle 2

	BW	NH	FC	FL	FW	NFL	PH	PG	PS
BW									
NH	0.49*								
FC	0.98***	0.18							
FL	0.85***	0.28	–						
FW	0.89***	0.28	–	–					
NFL	−0.24	0.39	−0.15	−0.40	−0.11				
PH	0.72***	0.99***	0.51**	0.70***	0.34	0.15			
PG	–	0.87**	0.75***	0.67	0.89***	0.30	–		
PS	–	–	0.33	–	–	–	–	–	
DFH	−0.15	−0.22	−0.05	−0.23	−0.57	0.65	–	–	–

'–' indicates correlations not estimable by the model

BW bunch weight at full maturity (kg), *NH* number of hands, *FL* fruit length (mm), *FC* fruit circumference (mm), *FW* fruit finger weight (grams), *NFL* number of standing functional leaves at flowering, *PH* plant height at flowering (cm), *PG* plant girth at 100 cm from soil surface (cm), *PS* plant stature, *DFH* days to fruit maturity

*, **, *** indicate significant correlation at $p \leq 0.05$, $p \leq 0.01$ and $p \leq$ $p \leq 0.001$, respectively

where this trial was conducted had access to year-round irrigation, which may have reduced the impact of seasonal variation during planting, flowering, and fruit development, hence a non-significant variation for yield traits. Further research should evaluate the impact of seasonal variation in farmers' fields where the plantations are primarily rain-fed as this is important for later on-farm trials of selected hybrids. The significant Cycle:Year:Season of flowering effect identifies an important source of variation for yield

traits, plant height and plant stature, thereby suggesting that flowering season and different seasons between years and cycles affect these traits. This is because cycle number (whether a particular plant is the first ratoon (cycle 2) or the second ratoon crop (cycle 3) is determined when that plant or ratoon is flowering (when the inflorescence containing the female and male flowers appears at the top of the plant), so this makes cycle dependent on when flowering occurs. Most variance components in this study had high standard errors. This is expected as there was a limited number of progenies used in the trial. The small family size with related parents, and few offspring per family may also have led to the difficulty in capturing all the genetic variance and confounding of variance components of the target traits, making it difficult to partition them accurately. This is a challenge also faced in tree breeding (Baltunis et al. 2009; Chen et al. 2020; Isik et al. 2003). Thus, there is a need to establish the optimal family size required to capture the maximum genetic gain possible. The use of deeper pedigree records, if available, and appropriate statistical models such as genomic and or hybrid best linear unbiased predictions (GBLUP, HBLUP models) is recommended to correct for such relatedness effects (Crossa et al. 2017; Jiang and Reif 2015; Munoz et al. 2014). In addition, the parent genotypes were not randomly sampled from the population. Calcutta 4 and Borneo were selected as males for their host plant resistance to pathogens (particularly to *Fusarium oxysporum* f. sp. *cubense* causing wilt) and abundant production of pollen despite their undesirable bunch characteristics (Calcutta 4 and Borneo) (Bayo et al. 2024; Ortiz 2015; Pillay et al. 2012), while the females referred to generally as 'Mchare' are farmer-preferred landraces that belong to the same clone set (Onyango et al. 2009). This may not strictly follow the assumptions that 'there is no selection among parents or progeny' and that 'the reference population is a non-inbred random mating population', which might affect the genetic variance components (Lynch and Walsh 1998).

Among the principal aims considered in most crop breeding programs is the identification and selection of the best-performing lines (clones in the case of bananas) for commercial release and use as parents in future crossing schemes (Oakey et al. 2006). The genetic combination of identified parents determines the genetic variability among progeny populations, which eventually is exploited during selection (Balzarini 2000). Hence, parent evaluation is critical in any plant breeding program. Making crosses with complementary genotypes is expected to increase genetic gains in populations because of a higher accumulation of additive genes (Stringer et al. 2011; Zhou and Mokwele 2016). Through conducting mating designs such as factorial or diallel, the genetic influences of these parental genotypes can be partitioned into additive and non-additive components (Topal et al. 2004).

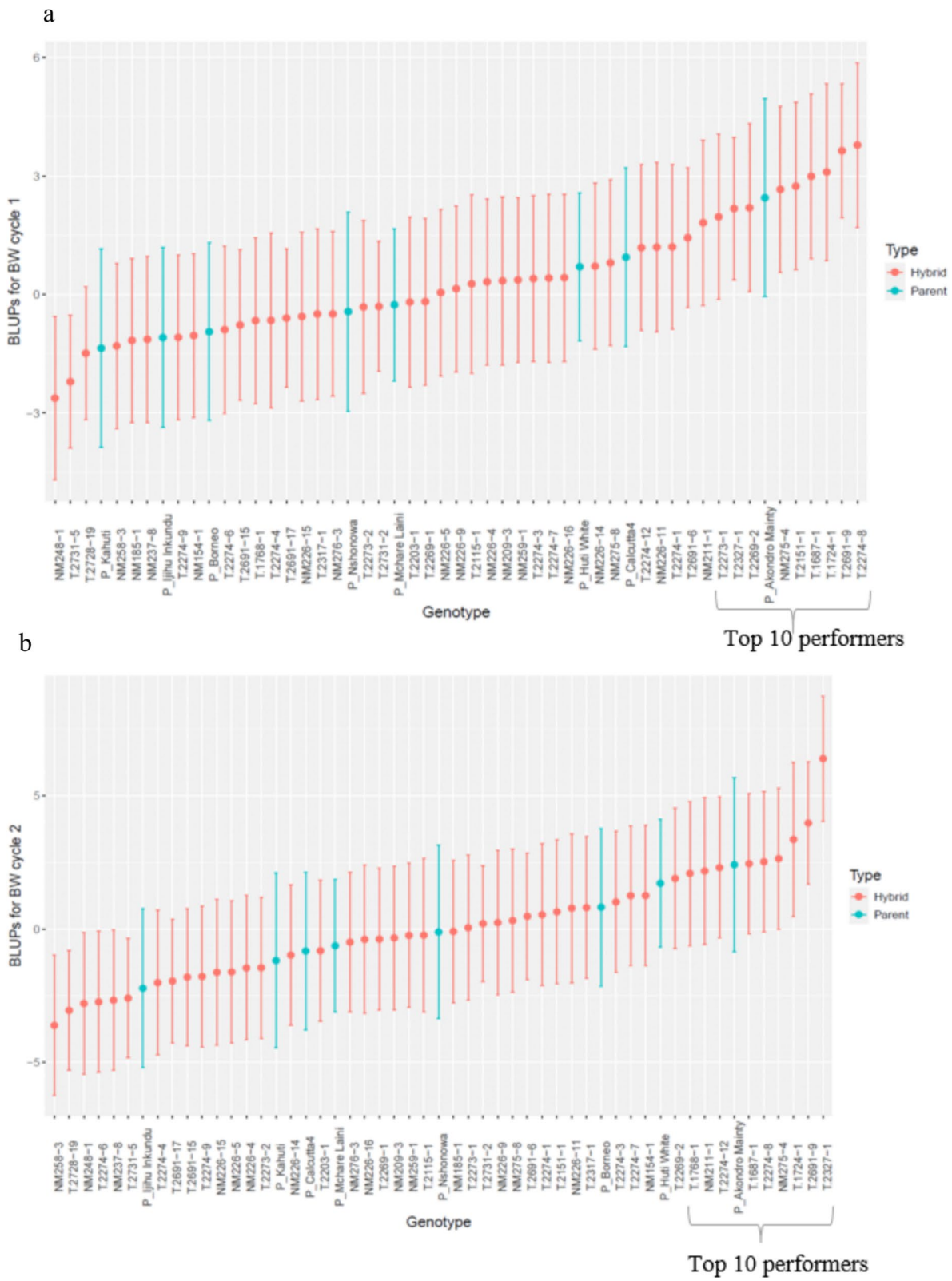
The analysis from the clonal model indicated that additive effects were highly significant; however, the GCA values of the parents were not significant, and differences in GCA among female parents in this study did not relate to their performance in their offspring. This shows that parental performance may not be an accurate indicator of breeding value because most banana accessions are genetically heterozygous. The inconsistent performance of the parents could also be due to the limited number of progenies per cross.

Heritability

The high H^2 of yield-related traits indicates sufficient genetic variation, making improvement feasible. The h^2 was high and similar to H^2 for yield-related traits, which confirms that these traits are under the control of additive gene action. General combining ability effects represent the fixable and heritable component of genetic variance and have a direct association with narrow-sense heritability and homozygosity (Fasahat et al. 2016). The highly significant additive variance for yield traits reported in this study and high h^2 further indicate the predominance of additive gene action for these traits and the recommendation for recurrent selection as the trait improvement-breeding scheme. The response to selection is defined by the equation:

$$R = h^2 S.$$

where R is the response to selection, S is the selection differential and h^2 is the narrow-sense heritability (Falconer and Mackay 1996; Piepho and MöHring 2007). Hence, the high h^2 for yield traits reported in this research will increase the response to selection leading to increased genetic gain. The H^2 and h^2 for


a
BLUPs for BW cycle 1
6
3
0
−3
Type
Hybrid
Parent
NM248−1
T.2731−5
T.2728−19
P_Kahuti
NM258−3
NM185−1
NM237−8
P_Ijihu Inkundu
T.2274−9
NM154−1
P_Borneo
T.2274−6
T.2691−15
T.1768−1
T.2274−4
T.2691−17
NM226−15
T.2317−1
NM276−3
P_Nshonowa
T.2273−2
T.2731−2
P_Mchare Laini
T.2203−1
T.2269−1
NM226−5
NM226−9
T.2115−1
NM226−4
NM209−3
NM259−1
T.2274−3
T.2274−7
NM226−16
P_Huti White
NM226−14
NM275−8
P_Calcutta4
T.2274−12
NM226−11
T.2274−1
T.2691−6
NM211−1
T.2273−1
T.2327−1
T.2269−2
P_Akondro Mainty
NM275−4
T.2151−1
T.1687−1
T.1724−1
T.2691−9
T.2274−8
Genotype
Top 10 performers
b
BLUPs for BW cycle 2
5
0
−5
Type
Hybrid
Parent
NM258−3
T.2728−19
NM248−1
T.2274−6
NM237−8
T.2731−5
P_Ijihu Inkundu
T.2274−4
T.2691−17
T.2691−15
T.2274−9
NM226−15
NM226−5
NM226−4
T.2273−2
P_Kahuti
NM226−14
P_Calcutta4
T.2203−1
P_Mchare Laini
NM276−3
NM226−16
T.2269−1
NM209−3
NM259−1
T.2115−1
P_Nshonowa
NM185−1
T.2273−1
T.2731−2
NM226−9
NM275−8
T.2691−6
T.2274−1
T.2151−1
NM226−11
T.2317−1
P_Borneo
T.2274−3
T.2274−7
NM154−1
P_Huti White
T.2269−2
T.1768−1
NM211−1
T.2274−12
P_Akondro Mainty
T.1687−1
T.2274−8
NM275−4
T.1724−1
T.2691−9
T.2327−1
Genotype
Top 10 performers

◂**Fig. 2** Ranking of genotypes according to their Best Linear Unbiased Predictor (BLUP) values for bunch weight in the plant crop (**A**) and bunch weight in the first ratoon crop (**B**)

yield-related traits found in our study are lower than those previously reported by Nyine et al. (2018), Batte et al. (2020), and Toniutti et al. (2022) in triploid banana populations, and those summarized by James et al. (2012) in *Musa*. This is because heritability estimates are known to vary with different study populations, environments, and methods of computation (Acquaah 2007; Umar et al. 2014) and because their definitions are not consistent across studies. For example, Nyine et al. (2018) used genomic BLUP (GBLUP), while Batte et al. (2020) applied a formula that accounted for three cycles and three years of experiments to calculate H^2 in large Matooke populations.

Both methods of computation differ from our approach, as described in Sect. 2.4.2, as well as in study population, sample size and ploidy levels (triploid vs diploid levels).

Genetic correlations

The positive and significant genetic correlation observed between BW and all fruit traits (FC, FL, and FW), along with their high heritability estimates, suggests that these traits can be improved simultaneously. Selecting for large fruits is likely to also result in heavier bunches. Similarly, yield components can serve as indirect selection criteria for yield improvement in Mchare breeding populations, as previously suggested for plantain germplasm in Nigeria (Tenkouano et al. 2002). Previous studies have reported that fruit number, fruit weight, fruit length, finger circumference and the number of hands are key traits contributing to bunch weight and, ultimately, yield in bananas (Baiyeri et al. 2000; Batte et al. 2021; Tenkouano et al. 2002). Early-cycle phenotyping can be reduced by initially selecting for bunch weight, followed by selection for component traits of yield such as fruit dimensions. This would save labour, resources and time. The significant, positive and high genetic correlations among yield traits observed in this study align with findings by Uwimana et al. (2020) and Nyine et al. (2017). The positive and significant genetic correlation between the number of hands with plant height and plant girth suggest that increasing the number of hands will result in taller and sturdier plants capable of supporting the larger bunches until harvest. A similar trend was observed in the plant crop (cycle 1) of irrigated diploid and triploid banana genotypes in Tanzania (Uwimana et al. 2020). The genetic correlation between plant height and bunch weight in cycle one is of low magnitude. This suggests that the selection of dwarf Mchare hybrids with heavy bunches may be possible. A similar significant but low genetic correlation ($r=0.37$, $n=307$; and $r=0.41$, $n=36$, significant at $p\leq0.05$) between plant height and bunch weight has been reported in triploid *Musa* hybrids (Nyine et al. 2017; Tenkouano et al. 2002). However, Ortiz (1997) reported higher genetic correlations between these two traits in tetraploid-plantain ($r=0.78$, $n=33$ significant at $p\leq0.001$) and diploid-plantain hybrids ($r=0.56$, significant at $p\leq0.001$), as observed in cycle two in our study.

In bananas, maximal yields are typically achieved in their first ratoon or later. Traditionally, practice has been to select high-yielding progeny once data of the ratoon crop 1 and even of ratoon crop 2 are available (Batte et al. 2019; Madalla et al. 2022; Tushemereirwe et al. 2015). However, our results show that selection of the highest yielding hybrids can be made already when the plant crop is harvested, given the strong and significant genetic correlations (above 0.79) observed between the plant crop and first ratoon crop for all yield-related traits. This means that if a hybrid performed well in the plant crop (cycle 1) for BW, NH, FC, FL and FW, traits that are proxies of yield, it continued to perform as well or even better in the first ratoon crop (Fig. 2a, Fig. 2b). The observation for bunch weight with a genetic correlation of 0.56 (significant at $p\leq0.001$) between the plant crop and first ratoon crop was first reported in *Musa* cv. AAB False Horn plantain in Nigeria (Swennen and De Langhe 1985). This is an important observation for banana breeding as it indicates that the selection of hybrids for these traits can be done in the plant crop (cycle 1) instead of waiting for the second fruit cycle (ratoon crop). Selecting in cycle one instead of selecting after two harvests saves at least two years enabling faster breeding decisions and greater genetic gain. The failure of the model to estimate the correlation

coefficients between cycle one and cycle two for PS and DFH is likely due to very low additive variance estimates in one cycle compared to the other cycle for these traits (see Supplementary Table S6).

Using the equation of Moose and Mumm (2008),

$$\Delta G = \frac{h^2 \sigma_p i}{L}$$

where ΔG is the genetic gain, h^2 is the heritability, σ_p is the phenotypic variability in the population, i is selection intensity and L is the length of the selection cycle; our work shows that the large narrow-sense heritability and restriction to only data from one cycle contributes to increasing genetic gain in bananas, by increasing the numerator (h^2) and reducing the denominator (L), the latter with at least two years. This will increase genetic gain for yield traits.

Conclusion

The clonal model using the pedigree-based BLUP method identified highly significant additive genetic variation for most traits evaluated. The partitioning of the genetic variation into additive and non-additive effects led to an improved estimation of narrow-sense heritability (h^2). The strong, significant and positive genetic correlations for yield traits between the plant crop and the first ratoon crop demonstrate the potential to improve selection efficiency in a diploid breeding population by reducing the length of the selection cycle. These results improve our current understanding of the genetic control and architecture of quantitative traits that should be considered when developing breeding strategies for the diploid Mchare banana improvement program.

Author contributions All authors contributed to the study's conception and design. Material preparation and data collection were performed by SB, data analysis was performed by VA and MV. Data analysis interpretation was done by all authors. The first draft of the manuscript was written by VA and all authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.

Funding Open access funding provided by Swedish University of Agricultural Sciences. Open-access funding was provided by the Swedish University of Agricultural Sciences. This work was supported, in whole, by the Gates Foundation [INV-002979 (formally OPP1213871)]. The conclusions and opinions expressed in this work are those of the authors alone and shall not be attributed to the Foundation. Under the grant conditions of the Foundation, a Creative Commons Attribution 4.0 License has already been assigned to the Author Accepted Manuscript version that might arise from this submission.

Data availability The list of all plant entries, raw datasets and datasets generated during and or analysed during the current study and supplementary materials are publicly available in: Figshare: Estimation of Seasonal, Additive and Non-additive Genetic Components in Diploid Banana (*Musa* spp.). [(https:/doi.org/https://doi.org/10.6084/m9.figshare.28787240) The dataset has a CC-BY 4.0 license applied.

Declarations

Conflict of interest Author Dr Marnik Vuylsteke was employed by Gnomixx B.V. The remaining authors declare no competing interests to declare that are relevant to the content of this article.

References

Acquaah G (2007) Principles of plant genetics and breeding. Wiley-Blackwell, Oxford

Akech V, Oparok T, Nyanzi N, Simba R, Nasuuna C, Nabukenya C, Arinaitwe IK, Uwimana B (2024a) Standard operating procedure (SOP) for ploidy analysis in banana. Int Inst Trop Agric. https://doi.org/10.25502/TS4M-WN43/D

Akech V, Swennen R, Brown A (2024b) Standard operating procedure (SOP) for field establishment of banana crosses. Int Inst of Trop Agric. https://doi.org/10.25502/5F71-6Z84/D

Baiyeri K, Mbah B, Tenkouano A (2000) Yield components of triploid and tetraploid *Musa* genotypes in Nigeria. HortScience 35:1338–1343. https://doi.org/10.21273/hortsci.35.7.1338

Baltunis BS, Wu HX, Dungey HS, Mullin TJT, Brawner JT (2009) Comparisons of genetic parameters and clonal

value predictions from clonal trials and seedling base population trials of radiata pine. Tree Genet Genomes 5:269–278. https://doi.org/10.1007/s11295-008-0172-y

Balzarini MG (2000) Biometrical models for predicting future performance in plant breeding. Louisiana State University, Baton Rouge. https://doi.org/10.31390/gradschool_disstheses.7178

Batte M, Swennen R, Uwimana B, Akech V, Brown A, Tumuhimbise R, Hovmalm HP, Geleta M, Ortiz R (2019) Crossbreeding East African highland bananas: lessons learnt relevant to the botany of the crop after 21 years of genetic enhancement. Front Plant Sci 10:81. https://doi.org/10.3389/fpls.2019.00081

Batte M, Nyine M, Uwimana B, Swennen R, Akech V, Brown A, Hovmalm HP, Geleta M, Ortiz R (2020) Significant progressive heterobeltiosis in banana crossbreeding. BMC Plant Biol 20:489. https://doi.org/10.1186/s12870-020-02667-y

Batte M, Swennen R, Uwimana B, Akech V, Brown A, Geleta M, Ortiz R (2021) Traits that define yield and genetic gain in East African highland banana breeding. Euphytica 217:193. https://doi.org/10.1007/s10681-021-02920-x

Bayo SJ, Massawe V, Ndakidemi PA, Venkataramana P, Mlaki A, Mduma H, Jomanga K, Swennen R, Brown A (2024) Pollen amount and viability in Mchare and selected wild (AA) banana (*Musa acuminata*) genotypes: Prospects for Breeding. American Society for Horticultural Science 59:632–638. https://doi.org/10.21273/hortsci17608-23

Bernardo R (2014) Essentials of plant breeding. Stemma Press, Woodbury, NJ

Bernardo R (2020) Breeding for Quantitative Traits in Plants, 3rd edn. Stemma Press, Woodbury, NJ

Brown A, Tumuhimbise R, Amah D, Uwimana B, Nyine M, Mduma H, Talengera D, Karamura D, Kuriba J, Swennen R (2017) Bananas and plantains (*Musa* spp.). Genetic improvement of tropical crops. Springer, Cham, pp 219–240

Butler DG, Cullis BR, Gilmour AR, Gogel BG, Thompson R (2023) ASReml-R reference manual version 4.2. VSN International Ltd., Hemel Hempstead, HP2 4TP, UK

Chen Z-Q, Hai HNT, Helmersson A, Liziniewicz M, Hallingbäck HR, Fries A, Berlin M, Wu HX (2020) Advantage of clonal deployment in Norway spruce (*Picea abies* (L.) H. Karst). Ann for Sci 77:1–15. https://doi.org/10.1007/s13595-020-0920-1

Crossa J, Pérez-Rodríguez P, Cuevas J, Montesinos-López O, Jarquín D, de los Campos G, Burgueño J, González-Camacho JM, Pérez-Elizalde S, Beyene Y, Dreisigacker S, Singh R, Zhang X, Gowda M, Roorkiwal M, Rutkoski J, Varshney RK (2017) Genomic selection in plant breeding: methods, models, and perspectives. Trends Plant Sci 22(11):961–975. https://doi.org/10.1016/j.tplants.2017.08.011

De Langhe E, Karamura D, Mbwana A (2001) Tanzania *Musa* expedition 2001. International Network for the Improvement of Banana and Plantain, Montpellier, France.

Dolezel J (1997) Application of flow cytometry for the study of plant genomes. J Appl Genet 38:285–302

Evers G (1992) Banana cultivar diversity in the area of Morogoro, Tanzania. Fruits-Paris 47:377–377

Falconer DS, Mackay TFC (1996) Introduction to Quantitative Genetics. Longman London, United Kingdom.

FAO (2020) Statistical database. Food and agricultural Organization of the United Nations, Rome, Italy http://www.fao.org/faostat/en/#data/QC/visualize [Accessed March 28, 2024].

FAO (2022) Statistical database. Food and agricultural Organization of the United Nations, Rome, Italy. Available at: http://faostat.fao.org/ [Accessed April 20, 2024].

Fasahat P, Rajabi A, Rad JM, Derera J (2016) Principles and utilization of combining ability in plant breeding. Biomet Biostat Int J 4:1–24. https://doi.org/10.15406/bbij.2016.04.00085

Grieser J, Gommes R, Bernardi M (2006) New locclim–the local climate estimator of FAO. Geophys Res Abstr 8:08305

Holland JB, Nyquist WE, Cervantes-Martínez CT, Janick J (2003) Estimating and interpreting heritability for plant breeding: an update. Plant Breed Rev 22:9–112. https://doi.org/10.1002/9780470650202.ch2

Isik F, Li B, Frampton J (2003) Estimates of additive, dominance and epistatic genetic variances from a clonally replicated test of loblolly pine. For Sci 49:77–88. https://doi.org/10.1093/forestscience/49.1.77

James A, Ortiz R, Miller R (2012) Map-based cloning in *Musa* spp. In: Pillay M, Ude G, Kole C (eds) Genetics, Genomics, and Breeding of Bananas. CRC Press, Boca Raton, FL, pp 124–155. https://doi.org/10.1201/b11776-9

Jiang Y, Reif JC (2015) Modeling epistasis in genomic selection. Genetics 201(2):759–768. https://doi.org/10.1534/genetics.115.177907

Kabanda T (2018) Long-term rainfall trends over the Tanzania coast. Atmosphere 9:155. https://doi.org/10.3390/atmos9040155

Karamura D, Karamura E, Blomme G (2011) General plant morphology of *Musa*. In: Pillay M, Tenkouano A (eds) Banana breeding: progress and challenges, 2nd edn. CRC Press, Boca Raton, FL, pp 1–20. https://doi.org/10.1201/b10514-2

Kalyebara R, Nkuba JM, Ramadhan MS, Byabachwezi EMK, Edmeades S (2007) Overview of the banana economy in the Lake Victoria regions of Uganda and Tanzania. In: Smale M, Tushemereirwe WK (eds) An economic assessment of banana genetic improvement and innovation in the Lake Victoria region of Uganda and Tanzania. International Food Policy Research Institute, Washington D.C., USA, pp 25–25. https://doi.org/10.2499/9780896291645rr155

Kilimo Trust (2012) Analysis of the banana value chains in Tanzania and Uganda. consumption, productivity and challenges. VCA report in improving the banana value chain in the EAC Region.

Kimunye J, Jomanga K, Tazuba AF, Were E, Viljoen A, Swennen R, Mahuku G (2021) Genotype X Environment response of 'Matooke' hybrids (Naritas) to *Pseudocercospora fijiensis*, the cause of black Sigatoka in banana. Agronomy 11:1145. https://doi.org/10.3390/agronomy11061145

Kitavi M, Downing T, Lorenzen J, Karamura D, Onyango M, Nyine M, Ferguson M, Spillane C (2016) The triploid East African Highland banana (EAHB) genepool is

genetically uniform arising from a single ancestral clone that underwent population expansion by vegetative propagation. Theor Appl Genet 129:547–561. https://doi.org/10.1007/s00122-015-2647-1

Lescot T (2020) Banana genetic diversity. Close-Up Fruitrop 269:98–102. https://www.fruitrop.com/en/Articles-by-subject/Varieties/2020/Banana-genetic-diversity [Accessed May 4, 2024].

Loureiro J, Kron P, Temsch EM, Koutecký P, Lopes S, Castro M, Castro S (2021) Isolation of plant nuclei for estimation of nuclear DNA content: overview and best practices. Cytometry A 99:318–327. https://doi.org/10.1002/cyto.a.24331

Luyiga J, Bamisaye B, Kiurugo M, Serebe C, Tumushabe J, Ademulegun T, Amah D (2024) Standard operating procedure (SOP) for banana embryo culture. Int Inst Trop Agric. https://doi.org/10.25502/8DZC-RC18/D

Lynch M, Walsh B (1998) Genetics and analysis of quantitative traits. Sinauer Sunderland, Minnesota.

Madalla NA, Swennen R, Brown AF, Massawe C, Shimwela M, Mbongo D, Kindimba G, Kubiriba J, Tumuhimbise R, Okurut AW, Carpentier S, Van den Bergh I, Crichton R, Machida L, Weltzien E, Ortiz R (2022) Yield stability of East African highland cooking banana 'Matooke' hybrids. J Am Soc Hortic Sci 147:334–348. https://doi.org/10.21273/jashs05246-22

Madalla NA, Swennen R, Brown A, Carpentier S, Van den Bergh I, Crichton R, Marimo P, Weltzien E, Massawe C, Shimwela M (2023) Farmers' preferences for East African highland cooking banana "Matooke" hybrids and local cultivars. Agric Food Secur 12:1–20. https://doi.org/10.1186/s40066-023-00407-7

Maruo S (2007) Development of the plantain-based culture of the Nyakyusa of Southern Tanzania. Afr Study Monogr 34:21–38

Mbuma NW, Zhou MM, van der Merwe R (2020) Estimating breeding values of genotypes for sugarcane yield using data from unselected progeny populations. Euphytica 216:2. https://doi.org/10.1007/s10681-019-2540-0

Meya IA, Ndakidemi AP, Mtei KM, Swennen R, Merckx R (2020) Optimizing soil fertility management strategies to enhance banana production in volcanic soils of the Northern highlands. Tanzania Agronomy 10:289. https://doi.org/10.3390/agronomy10020289

Milligan S, Gravois KA, Bischoff KP, Martin F (1990) Crop effects on broad-sense heritabilities and genetic variances of sugarcane yield components. Crop Sci 30:344–349. https://doi.org/10.2135/cropsci1990.0011183x003000020020x

Moose SP, Mumm RH (2008) Molecular plant breeding as the foundation for 21st century crop improvement. Plant Physiol 147:969–977. https://doi.org/10.1104/pp.108.118232

Mrode RA (2005) Linear models for the prediction of animal breeding values, CABI, Wallingford, Oxon, United Kingdom. pp 311–316. https://doi.org/10.1079/9780851990002.0311.

Muñoz PR, Resende MF Jr, Gezan SA, Resende MDV, de Los CG, Kirst M, Huber D, Peter GF (2014) Unraveling additive from nonadditive effects using genomic relationship matrices. Genetics 198:1759–1768. https://doi.org/10.1534/genetics.114.171322

Nayar N (2010) The bananas: botany, origin, dispersal. Hortic Rev 36:117–164. https://doi.org/10.1002/9780470527238.ch2

Nicholson SE (2017) Climate and climatic variability of rainfall over eastern Africa. Rev Geophys 55:590–635. https://doi.org/10.1002/2016rg000544

Nkuba JM, Mgenzi SRB, Ishika M, Mushongi C (2003) Evaluating the marketing opportunities for banana and its products in the principle banana growing countries of ASARECA. Case study of Tanzania. Maruku Agricultural Research and Development Institute, Bukoba, Tanzania

Nyine M, Uwimana B, Swennen R, Batte M, Brown A, Christelová P, Hribová E, Lorenzen J, Doleziel J (2017) Trait variation and genetic diversity in a banana genomic selection training population. PLoS ONE 12:6. https://doi.org/10.1371/journal.pone.0178734

Nyine M, Uwimana B, Blavet N, Hřibová E, Vanrespaille H, Batte M, Akech V, Brown A, Lorenzen J, Swennen R (2018) Genomic prediction in a multiploid crop: genotype by environment interaction and allele dosage effects on predictive ability in banana. The Plant Genome 11:2. https://doi.org/10.3835/plantgenome2017.10.0090

Oakey H, Verbyla A, Pitchford W, Cullis B, Kuchel H (2006) Joint modeling of additive and non-additive genetic line effects in single field trials. Theor Appl Genet 113:809–819. https://doi.org/10.1007/s00122-006-0333-z

Onyango M, Karamura D, Keeley S, Manshardt R, Haymer D (2009) Morphological characterisation of East African AAB and AA dessert bananas (*Musa* spp.). V International Symposium on Banana: ISHS-ProMusa Symposium on Global Perspectives on Asian Challenges. Acta Horticultura 897:95–105. https://doi.org/10.17660/actahortic.2011.897.

Ortiz R (1997) Secondary polyploids, heterosis, and evolutionary crop breeding for further improvement of the plantain and banana (*Musa* spp. L) genome. Theor Appl Genet 94:1113–1120. https://doi.org/10.1007/s001220050524

Ortiz R (2013) Conventional banana and plantain breeding. VII international symposium on banana: ISHS-ProMusa symposium on bananas and plantains: Towards Sustainable Global Production. Acta Horticultura 986:177–194. https://doi.org/10.17660/actahortic.2013.986

Ortiz R (2015) Plant breeding in the omics era. Springer International Publishing, New York. https://doi.org/10.1007/978-3-319-20532-8

Ortiz R, Swennen R (2014) From crossbreeding to biotechnology-facilitated improvement of banana and plantain. Biotechnol Adv 32:158–169. https://doi.org/10.1016/j.biotechadv.2013.09.010

Ortiz R, Reslow F, Crossa J, Cuevas J (2021) Heritable variation, genetic and phenotypic correlations for tuber traits and host plant resistance to late blight for potato breeding in Scandinavian testing sites. Agriculture (Basel) 11:1287. https://doi.org/10.3390/agriculture11121287

Oselebe H, Tenkouano A (2008) Combining ability for important agronomic traits in *Musa* L. diploid populations. J Agric Biotechnol Ecol 1:93–104

Perrier X, De Langhe E, Donohue M, Lentfer C, Vrydaghs L, Bakry F, Carreel F, Hippolyte I, Horry J-P, Jenny C (2011) Multidisciplinary perspectives on banana (*Musa* spp.) domestication. Proc Natl Acad Sci U S A 108:11311–11318. https://doi.org/10.1073/pnas.1102001108

Perrier X, Jenny C, Bakry F, Karamura D, Kitavi M, Dubois C, Hervouet C, Philippson G, De Langhe E (2019) East African diploid and triploid bananas: a genetic complex transported from South-East Asia. Ann Bot 123:19–36. https://doi.org/10.1093/aob/mcy156

Piepho H-P, MöHring J (2007) Computing heritability and selection response from unbalanced plant breeding trials. Genetics 177:1881–1888. https://doi.org/10.1534/genetics.107.074229

Piepho HP, Möhring J, Melchinger AE, Büchse A (2008) BLUP for phenotypic selection in plant breeding and variety testing. Euphytica 161:209–228. https://doi.org/10.1007/s10681-007-9449-8

Pillay M, Elayabalan S, Ashokkumar K, Jabekumar S, Kirubarkaran P (2012) Functional genomics and transcriptomics in Musa. In: Pillay M, Ude G, Kole C (eds) Genetics, genomics, and breeding of bananas. CRC Press, New York, NY, USA, pp 157–180

Pisaroglo de Carvalho M, Gezan SA, Peternelli LA, Barbosa MHP (2014) Estimation of additive and nonadditive genetic components of sugarcane families using multitrait analysis. Agron J 106:800–808. https://doi.org/10.2134/agronj2013.0247

R Development Core Team (2019) R: A Language and environment for statistical computing. The R Foundation for Statistical Computing, Vienna, Austria.

Santos EA, Viana AP, de Oliveira Freitas JC, Rodrigues DL, Tavares RF, Paiva CL, Souza MM (2015) Genotype selection by REML/BLUP methodology in a segregating population from an interspecific *Passiflora* spp. crossing. Euphytica 204:1–11. https://doi.org/10.1007/s10681-015-1367-6

Schmidt P, Hartung J, Bennewitz J, Piepho H-P (2019a) Heritability in plant breeding on a genotype-difference basis. Genetics 212:991–1008. https://doi.org/10.1534/genetics.119.302134

Schmidt P, Hartung J, Rath J, Piepho H-P (2019b) Estimating broad-sense heritability with unbalanced data from agricultural cultivar trials. Crop Sci 59:525–536. https://doi.org/10.2135/cropsci2018.06.0376

Shanthi R, Bhagyalakshmi K, Hemaprabha G, Alarmelu S, Nagarajan R (2008) Relative performance of the sugarcane families in early selection stages. Sugar Tech 10:114–118. https://doi.org/10.1007/s12355-008-0019-8

Slater AT, Wilson GM, Cogan NO, Forster JW, Hayes BJ (2014) Improving the analysis of low heritability complex traits for enhanced genetic gain in potato. Theor Appl Genet 127:809–820. https://doi.org/10.1007/s00122-013-2258-7

Sprague GF, Tatum LA (1942) General vs. specific combining ability in single crosses of corn. Agronomy 34:923–932. https://doi.org/10.2134/agronj1942.00021962003400100008x

Stevens B, Diels J, Vanuytrecht E, Brown A, Bayo S, Rujweka A, Richard E, Ndakidemi PA, Swennen R (2020) Canopy cover evolution, diurnal patterns and leaf area index relationships in a Mchare and Cavendish banana cultivar under different soil moisture regimes. Sci Hortic 272:109328. https://doi.org/10.1016/j.scienta.2020.109328

Stringer J, Cox M, Atkin F, Wei X, Hogarth D (2011) Family selection improves the efficiency and effectiveness of selecting original seedlings and parents. Sugar Tech 13:36–41. https://doi.org/10.1007/s12355-011-0073-5

Swennen R, De Langhe E (1985) Growth parameters of yield of plantain (*Musa* cv. AAB). Ann Bot 56:197–204

Swennen R, Ortiz R (1997) Morphology and growth of plantain and banana: IITA Research Guide 66. International Institute of Tropical Agriculture, Ibadan, Nigeria.

Swennen R, Vuylsteke D (1993) Breeding black sigatoka resistant plantains with a wild banana. Trop Agric 70:74–77

Teixeira DHL, Oliveira MdSPd, Gonçalves FMA, Nunes JAR (2012) Índices de seleção no aprimoramento simultâneo dos componentes da produção de frutos em açaizeiro. Pesqui Agropec Bras 47:237–243. https://doi.org/10.1590/s0100-204x2012000200012

Tenkouano A, Crouch J, Crouch H, Ortiz R (1998) Genetic diversity, hybrid performance, and combining ability for yield in *Musa* germplasm. Euphytica 102:281–288

Tenkouano A, Ortiz R, Baiyeri K (2002) Phenotypic and genetic correlations in *Musa* populations in Nigeria. Afr Crop Sci J 10:121–132. https://doi.org/10.4314/acsj.v10i2.27544

Tenkouano A, Ortiz R, Vuylsteke D (2012) Estimating genetic effects in maternal and paternal half-sibs from tetraploid-diploid crosses in *Musa* spp. Euphytica 185:295–301. https://doi.org/10.1007/s10681-011-0583-y

Ticona-Benavente CA, Silva Filho DFd (2015) Comparison of BLUE and BLUP/REML in the selection of clones and families of potato (*Solanum tuberosum*). Genet Mol Res 14:18421–18430. https://doi.org/10.4238/2015.december.23.30

Tixier P, Malezieux E, Dorel M (2004) SIMBA-POP: a cohort population model for long-term simulation of banana crop harvest. Ecol Modell 180:407–417. https://doi.org/10.1016/j.ecolmodel.2004.04.028

Toniutti L, Rio S, Martin G, Hoarau J-Y, Salmon F (2022) Variation of morphological and yield traits in a banana (*Musa acuminata*) breeding program of triploid populations: lessons for selection procedures and criteria. Acta Hort 1362:539–546. https://doi.org/10.17660/actahortic.2023.1362.72

Topal A, Aydın C, Akgün N, Babaoglu M (2004) Diallel cross analysis in durum wheat (*Triticum durum* Desf.): identification of best parents for some kernel physical features. Field Crops Res 87:1–12. https://doi.org/10.1016/j.fcr.2003.08.015

Tushemereirwe W, Batte M, Nyine M, Tumuhimbise R, Barekye A, Ssali T, Talengera D, Kubiriba J, Lorenzen J, Swennen R (2015) Performance of NARITA banana hybrids in the preliminary yield trial for three cycles in Uganda. Available at https://www.researchgate.net/publication/320628821.

Umar U, Ado S, Aba D, Bugaje S (2014) Estimates of combining ability and gene action in maize (*Zea mays* L.)

under water stress and non-stress conditions. J Biol Agric Healthc 4:247–253

Uwimana B, Zorrilla-Fontanesi Y, van Wesemael J, Mduma H, Brown A, Carpentier S, Swennen R (2020) Effect of seasonal drought on the agronomic performance of four banana genotypes (*Musa* spp.) in the East African Highlands. Agronomy 11:4. https://doi.org/10.3390/agronomy11010004

van Asten PJ, Fermont A, Taulya G (2011) Drought is a major yield loss factor for rainfed East African highland banana. Agric Water Manage 98:541–552. https://doi.org/10.1016/j.agwat.2010.10.005

Varma V, Bebber DP (2019) Climate change impacts on banana yields around the world. Nat Clim Change 9:752–757. https://doi.org/10.1038/s41558-019-0559-9

Viana JMS, Matta FdP (2003) Analysis of general and specific combining abilities of popcorn populations, including selfed parents. Genet Mol Biol 26:465–471. https://doi.org/10.1590/s1415-47572003000400010

Walsh B, Lynch M (2018) Family-Based Selection Evolution and selection of quantitative traits. Oxford University Press, Oxford. https://doi.org/10.1093/oso/9780198830870.001.0001

Weng YH, Park YS, Krasowski MJ, Tosh KJ, Adams G (2008) Partitioning of genetic variance and selection efficiency for alternative vegetative deployment strategies for white spruce in Eastern Canada. Tree Genet Genomes 4:809–819. https://doi.org/10.1007/s11295-008-0154-0

Zeni Neto H, Daros E, Bespalhok Filho JC, Scapim CA, Vidigal MCG, Vidigal Filho PS (2013) Selection of families and parents of sugarcane (*Saccharum* spp.) through mixed models by joint analysis of two harvests. Euphytica 193:391–408. https://doi.org/10.1007/s10681-013-0947-6

Zhou M, Mokwele A (2016) Family versus individual plant selection for stem borer (*Eldana saccharina*) resistance in early stages of sugarcane breeding in South Africa. S Afr J Plant Soil 33:89–96. https://doi.org/10.1080/02571862.2015.1084546