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Selection of parents in a population hybrid breeding scheme for sweetpotato in Uganda

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Abstract

Sweetpotato (*Ipomoea batatas* [L.] Lam. [$2n = 6x = 90$]) is a highly heterozygous, clonally propagated crop for which population hybrid breeding is expected to result in yield jumps and large genetic gain increases. The main objective of this study was to select parents for a heterosis exploiting breeding scheme in Uganda using general combining ability and index selection aggregating yield and biotic stress traits. Two large and very diverse breeding populations established in Uganda (UGA A, 50 parents; UGA B, 80 parents) were recombined for this study into a hybrid population comprising 8097 genotypes from 1097 interpopulation families. Parents and offspring clones were evaluated in unreplicated trials across five environments during 2018/2019, together with two commercial checks (Ejumula and NASPOT 8). Using mixed model analysis, breeding values (BVs) were estimated across traits (i.e., storage root yield, commercial roots per plant, foliage yield, and resistance to sweetpotato virus disease [SPVD] and Alternaria blight). For storage root yield, the BVs ranged from 3.5 to 10 t ha^{-1} and from 2 to 12 t ha^{-1} for parents in UGA A and B, respectively. For SPVD resistance, scored one month before harvest, the BVs ranged from 3.3 to 4.3 and from 3.1 to 4.7 for parents in UGA A and B, respectively. Out of 130 parental candidates, 40 parents were selected (20 for each parental group). The plan is to use in the future GCA values combined by a modified Pesek-Baker index using standardized desired genetic gains to select parents together with other information such as flesh color of parental material.

KEYWORDS
desired genetic gains, heterosis, hybrids, Pesek-Baker index, sweetpotato

Abbreviations: ALT, *Alternaria* blight; BLUP, best linear unbiased prediction; BV, breeding value; CIP, International Potato Center; EA, East Africa; FYTHA, foliage yield in t ha^{-1}; GCA, general combining ability; GS, genomic selection; G×E, genotype by environment interaction; HEBS, heterosis exploiting breeding scheme; NCRPP, number of commercial roots per plant; SCA, specific combining ability; SPVD, Sweetpotato Virus Disease, RYTHA, storage root yield in t ha^{-1}; VIR1, SPVD evaluated 8 weeks after planting; VIR2, SPVD evaluated 1 month before harvesting.

1 | INTRODUCTION

Sweetpotato (*Ipomoea batatas* [L.] Lam. [$2n = 6x = 90$]) is a highly heterozygous, clonally propagated hybrid. Breeding for superior hybrid clones is possible in clonally propagated crops using a heterosis exploiting breeding scheme (HEBS) with separated gene-pools (Grüneberg et al., 2022). Polycross breeding using one gene-pool has been the backbone of sweetpotato breeding in past decades (Grüneberg et al., 2015), but it does not systematically exploit the phenomenon of heterosis. The HEBS concept as known in grain crops such as maize needs to be adjusted to be applicable to sweetpotato. Up to date homozygous lines cannot be developed in sweetpotato because the crop is usually self-incompatible and progress toward inbreeding is much slower in hexaploids compared to diploids (Gallais, 2003).

The HEBS concept in sweetpotato has been previously described (David et al., 2018; Diaz et al., 2021; Grüneberg et al., 2015): heterosis increments can be determined by comparing (a) the parental mean with the mean across the segregating offspring clones (Diaz et al., 2021; Grüneberg et al., 2022), and/or (b) comparing the mean estimates of intra- and inter-gene pool crosses. The latter approach was used in the fundamental maize study by Moll et al. (1965), where homozygous inbreed lines were still too weak to be used in hybrid breeding. The subdivision of sweetpotato parental material into gene pools is an initial step in a HEBS using population hybrid breeding and has been conducted using molecular markers for the breeding platforms in Uganda and Peru (David et al., 2018; Diaz et al., 2021). Reciprocal recurrent selection for superior hybrid breeding populations derived from the recombination of two mutually heterotic gene-pools has been shown to lead to large yield jumps and genetic gains (Grüneberg et al., 2022). Moreover, this procedure allows for more efficient selection for traits for which inbreeding is needed, such as resistance to sweetpotato virus disease (SPVD), by recombination of related genotypes within gene-pools. Heterosis in crops is linked to nonadditive genetic effects (dominance, over-dominance, and epistatis) (Ceballos et al., 2015). However, when selecting new parents, it is the genetic additive variance that determines the medium- and long-term response to selection because only gametes are passed from one generation to the next, as is outlined in textbooks on selection in plants (Hallauer et al., 2010; Wricke & Weber, 1986), and it is an antecedent for auto-polyploid sweetpotato breeding in the medium and long terms, as highlighted by Gemenet and Khan (2017). Nevertheless, due to the presence of dominance in gametes of autoploids, the genetic gain in one cycle of selection overestimates genetic gain in the medium and long terms (Gallais, 2003).

The International Potato Center (CIP) sweetpotato breeding platform in Uganda, which serves the East Africa (EA) subregion, uses the product profile approach to focus breeding activities on key traits necessary to replace older varieties, and thereby achieves high adoption rates (Ragot et al., 2018). EA is the most important target area of CIP's sweetpotato breeding efforts because the crop—especially pro-vitamin-A orange-fleshed varieties—has become a common part of the daily diet in the subregion (Mwanga et al., 2021). Storage root yield is a priority trait in sweetpotato, but biotic and abiotic stress factors can even be ranked higher where drought or diseases commonly result in low yields. Resistance to SPVD, a co-infection of sweet potato chlorotic stunt virus and other viruses such as sweet potato feathery mottle virus, is crucial for any variety to be successful in EA (Gibson & Kreuze, 2015). In Uganda, potential varieties are routinely screened for SPVD and *Alternaria* blight (ALT) resistance (Mwanga et al., 2009). Vine production is another key trait in a sweetpotato product profile because this root crop is propagated by vine cuttings, and farmers need sufficient planting material for the next growing season. All successful varieties adopted at scale by farmers in EA are easy to propagate and have strong vines.

The goal of hybrid breeding in sweetpotato is the improvement of breeding populations with respect to mean and genetic variation, not commercial hybrid seed production for varieties, as is the case in many grain crops (Grüneberg et al., 2022). Selection of improved varieties is conducted via elite crosses in which parents with high general combining ability (GCA) are crossed on a large scale (large numbers of genotypes per cross). These elite crosses, done in isolations (ISOs), include repeated cross combinations as well as crosses that never have been done before. A critical challenge for clonally propagated crop breeders is to identify suitable parents to obtain high genetic gains and selection responses, respectively, in subsequent breeding cycles across all key traits. In sweetpotato, as in other root and tuber crops and bananas, farmer acceptance and adoption depend on many traits. One trait that is below the lowest value demanded by farmers or consumers can result in farmers switching back to old varieties or farmer varieties. In population improvement, breeders

Core Ideas

- High SPVD pressure environments might not be appropriate to estimate genetic parameters for yield traits.
- The determination of GCA appears to be extremely important for the selection of sweetpotato parents.
- The proposed modified Pesek-Baker index resulted in satisfactory prediction of responses across all key traits.

need to avoid undesired gains due to negative trait associations, including negative responses in one or more traits. This so called "multi-trait selection problem" can render entire breeding populations useless for varietal selection (Yan & Wallace, 1995).

Multi-trait selection indices were originally developed by Smith (1936) in plant breeding and Hazel (1943) in animal breeding. Many index selection procedures have been developed to take into account heritability, interrelationships of traits using genetic and phenotypic correlations, and economic weight of traits—for an overview see Wricke and Weber (1986) and Baker (1986). The so-called "index of desired gains" or "Pesek-Baker index" (Pesek & Baker, 1969) has been reported to be the most efficient selection index in sugarcane breeding (de Azeredo et al., 2017) and is recommended as the most appropriate tool for sweetpotato population improvement (Grüneberg et al., 2015). The Pesek-Baker index is based on the desired gain for each trait of interest to be set by the breeder using the genetic variance–covariance matrix estimates. The desired genetic gain for each trait corresponds to economic weights in other indices. If the breeder uses realistic and/or appropriate desired genetic gains, this index can be efficient; however, in cases in which the desired genetic gains are not realistic and/or appropriate (e.g., when the desired genetic gains are set more than twice as large as the square root of the genetic variance), the Pesek-Baker index can lead to disappointing selection decisions and a very low selection response for overall traits.

In this study, we present a selection of parents for a sweetpotato population hybrid breeding program in Uganda using a modified Pesek-Baker index. The desired genetic gains in the Pesek-Baker index were chosen in standardized units relative to the square root of the genetic variance estimates in order to avoid unrealistic desired genetic gains—in other words, to choose appropriate desired genetic gains within the range of ±2 multiplied with the square root of the genetic variance estimates of traits. This procedure has previously been used in sweetpotato (Grüneberg et al., 2022) but has only been described as supplemental information; the multi-trait selection approach in this study might have contributed to the large genetic gains observed.

There were three objectives in this study: (i) to estimate best linear unbiased predictions (BLUPS) for parents and offspring, GCA and SCA values, family predictions and breeding values (BVs) for each parent; (ii) to determine Pesek-Baker index scores with appropriate desired genetic gains to facilitate selection decisions among parents to be used for intra-gene pool recombination for the next breeding cycle; and (iii) to predict the response to selection by selecting parents for population improvement.

2 | MATERIALS AND METHODS

This study used two genetically distinct and diverse sweetpotato populations created as the foundation for implementing HEBS in Uganda. Population UGA A, with 50 genotypes, and population UGA B, with 80 genotypes, were established in Uganda on the basis of SSR markers (David et al., 2018). Controlled manual crosses between UGA B as the female and UGA A as the male pool resulted in the development of 1097 interpopulation families. All trials with this hybrid population were conducted at the NARO research station in Namulonge, Uganda (0°31′22″N, 32°38′09″E, 1137 m above sea level) in 2018 and 2019, comprising five environments (Table 1), under high SPVD pressure. The full set of 130 parents and 8095 offspring clones was evaluated in the first trial in 2018 season A, but the number of offspring clones decreased to 5031 in the subsequent trials due to the loss of weak material. The parental clones were replicated four times in 2019 but unreplicated in the trials in 2018. Season A corresponded to the main rainy season, and the second season B corresponded to the less reliable minor rainy season. Standard agricultural practices such as appropriate fertilization N/P/K rates, regular weeding, and rotation with other crops were used.

Trials were planted using a design, as described by Westcott (1981), in which the 130 parents and the unreplicated offspring clones were completely randomized, whereas two checkclones were planted in a grid, with the check clones alternating within and between the grid rows which occur at both sides of each 10 test plot rows. The checks were "Ejumula," an SPVD-susceptible variety, and "NASPOT 8," an SPVD-resistant variety, both of which have orange-fleshed roots. Plot size was a 1 m row, with 0.3 m between plants within rows and 1 m between rows. Recorded traits were as follows: noncommercial (<100 g) and commercial roots (≥100 g) with the number of commercial roots per plant (NCRPP), total storage root yield (RYTHA) in t ha^{-1}, foliage yield (FYTHA) in t ha^{-1}, SPVD evaluated 8 weeks after planting (VIR1) and evaluated 1 month before harvesting (VIR2), scored on a scale of 1–9 with 1 indicating no symptoms and 9 indicating severe symptoms, and ALT evaluated 1 month before harvesting on a scale of 1–9, with 1 indicating no symptoms and 9 indicating severe symptoms. The phenotyping traits are described in detail by Grüneberg et al. (2019).

Statistical analysis was conducted by linear mixed models with R (R Core Team, 2019) and the asremlR package (Butler, 2020). Ordinal traits are treated as continuous variables in the analysis not to overcomplicate the statistics. This is a reasonable assumption since all ordinal traits have at least nine levels. Each trial was curated with the R function "check.data" and adjusted values for RYTHA, NCRPP and FYTHA were calculated with the R function

TABLE 1 Description of trial sites used in this study (numbers 1 and 2 in the trial code are labeling different trials during the same season with different planting and harvest dates at the same experimental station).

Trial	Season	Site	Number of progeny	Number of family	Progeny per family	Progeny per female	Progeny per male	Planting date	Harvest date
2018A	2018A	1	8095	1097	1 to 24	6 to 288	5 to 310	25/03/2018	13/12/2018
2018B1	2018B	1	5031	1034	1 to 23	2 to 237	3 to 194	01/11/2018	09/06/2019
2018B2	2018B	2	5018	1033	1 to 23	2 to 237	3 to 194	15/11/2018	23/06/2019
2019A1	2019A	1	5031	1034	1 to 23	2 to 237	3 to 194	02/05/2019	17/10/2019
2019A2	2019A	2	5031	1034	1 to 23	2 to 237	3 to 194	21/05/2019	20/11/2019

"aj.w," both described in the R package "st4gi" (Eyzaguirre, 2022). Curation included the detection of data inconsistencies (out of range or out of scale values and identification of incongruencies like plants or roots with zero weight) and detection of outliers based on the interquartile range and analysis of residuals for the fitted model. The grid of check clones captured the spatial differences and trends: the mean values of all checks were used for the adjustment with a higher weight for the checks closer to the plot.

BLUPs were fitted using a linear mixed model chosen by Akaike's information criterion and took the following form: $Y_{ijkl} = \mu + G_{ki} + T_j + E_k + TE_{jk} + \varepsilon_{ijkl}$, where the response variable Y_{ijkl} is the adjusted value (by the grid of checks) of the lth observation of the ith genotype of type j in the kth environment, μ is the fixed intercept, T_j is the fixed effect for type of genotype (check, parent, progeny), E_k is the fixed effect for environment, TE_{jk} is the fixed environment-by-type interaction effect, G_{ki} is the random environment-specific genetic effect of the ith genotype in the kth environment with $G_i = (G_{1i}, \cdots, G_{5i})^T \sim N(0, \mathbf{\Sigma_G})$ multivariate normally distributed, and $\varepsilon_{ijkl} \sim N(0, \sigma^2_\varepsilon)$ are normally distributed and independent random residual error terms. The variance–covariance matrix $\mathbf{\Sigma_G}$ of the random genetic effect G_i was parametrized by an order 2 factor analytic model to accommodate the heterogeneity of genetic variances and genetic covariances across environments in a parsimonious manner (Piepho, 1998). Broad-sense heritabilities (H^2) were estimated as proposed by Cullis et al. (2006) accounting for unbalanced data and correlated genetic effects. The formula is as follows:

$$H^2 = 1 - \frac{\bar{v}_\Delta^{\text{BLUP}}}{2\sigma_g^2},$$

where σ_g^2 is the genetic variance and $\bar{v}_\Delta^{\text{BLUP}}$ is the average variance of the difference of two genotypic BLUPs.

GCA and SCA were estimated using the following model: $\mu_{ijkl} = \mu + F_i + M_j + C_k + E_l + \varepsilon_{ijkl}$, where μ is a fixed intercept, E_l is the fixed environment effect, and $F_i \sim N(0, \mathbf{\Sigma_F})$, $M_j \sim N(0, \mathbf{\Sigma_M})$, $C_k \sim N(0, \mathbf{\Sigma_C})$, and $\varepsilon_{ijkl} \sim N(0, \sigma^2_\varepsilon)$ are normally distributed and independent random effects for female, male, cross, and residual error, respectively. The variance–covariance matrices $\mathbf{\Sigma_F}$, $\mathbf{\Sigma_M}$, and $\mathbf{\Sigma_C}$ of the random effects F_i, M_j, and C_k were parametrized by order 2 factor analytic models to accommodate heterogeneity of genetic variances and genetic covariances across environments. Family predictions and BVs were extracted from the GCA and SCA estimations:

$$\text{Family predictions} = \text{SCA} + \text{GCA}_{\text{female}} + \text{GCA}_{\text{male}},$$

$$\text{BVs parental population A} = \mu + 2\text{GCA}_{\text{male}},$$

$$\text{BVs parental population A} = \mu + 2\text{GCA}_{\text{female}}.$$

The Pesek-Baker index (Pesek & Baker, 1969) was calculated following the notation of Wricke and Weber (1986). The genotypic (G) and phenotypic (P) variance–covariance matrices were estimated on the BVs of each parent (N = 130) across five environments. The vector of desired genetic gains k was determined by the square root of the genetic variance of trait i (σ_{gi}) multiplied by the desired genetic gain in standardized units (k_s) of each trait, within the range of ±2, to be chosen by the breeder. This ensures the determination of "appropriate" desired genetic gains by $k = \sigma_{gi} k_s$. The k_s of each trait in this study were set by breeders: 2, 2, 1, −2, −2, and 0 for RYTHA, NCRPP, FYTHA, VIR1, VIR2, and ALT, respectively.

The vector b, of weights for phenotypic observed traits to calculate index scores, was obtained by $b = G^{-1}k$. The index scores aggregating six traits were calculated for each parent by parental groups (A and B), and parents were sorted by the index in descending order.

The correlation coefficient between the index and trait i was calculated by $\sigma_{Ii} = \Sigma_{bi}\sigma_{gij}$. The standard error of the index was calculated as follows: $\sigma_I = \sqrt{b'Pb}$. The predicted selection response for each trait i was determined by: $R_i = t\frac{\sigma_{Ii}}{\sigma_I}$ with t the selection intensity, which was set to 1.755 and corresponds to a selection fraction of 10% (e.g., of these response calculations, see Wricke & Weber, 1986).

The best 15 parents were selected based on the highest Pesek-Baker index scores. An additional five orange-fleshed parents with the highest Pesek-Baker index among orange-fleshed parents were added to each parental group (A and B) in order to ensure a balanced selection in each group with respect to pro-vitamin-A-rich parents.

3 | RESULTS

The mean BLUP predictions for RYTHA, NCRPP, FYTHA, VIR1, VIR2, and ALT are presented for parents (n = 130) and off-spring clones (n = 8095 in trial 2018A, n = 5031 in other trials) determined across five trials (Table 2). Yield traits exhibited very high performance in the first environment (2018A) but decreased rapidly in subsequent environments, with consistent high environment specific heritabilities for all trials. Parents usually outperformed the offspring in all traits reported, with the exception of 10 offspring clones that exhibited higher RYTHA than the highest yielding parent, while 333 offspring clones had lower RYTHA than the lowest yielding parent. Negative heritability values were set to zero (ALT in 2018A, NCRPP in 2019, VIR1, VIR2 in 2019, and ALT in 2019A2), which was the case when the average standard error of the genotypic BLUPS was larger than the genetic variance multiplied by two.

The frequency of family predictions (on the basis of SCA and GCA) was plotted in a histogram for each trait (i.e., RYTHA, NCRPP, FYTHA, VIR1, VIR2, and ALT), together with boxplots of the BVs (based on GCA) for both parental groups (UGA A and B) and the boxplot of the BLUP per se performance of all parents (Figure 1). RYTHA ranged from 2 to 15 t ha^{-1} among family predictions (histogram) and among BVs (boxplots 1 and 2), while the per se performance of parents ranged from 0 to 40 t ha^{-1} (boxplot 3). Across all traits, the range in BVs was greater for parental group UGA B than parental group UGA A, due to a difference in population size. For the yield-related traits, the range in BLUPs performance of the parents was double that of the family predictions. In 21% of the families, RYTHA predictions were observed to be larger than the mid-parental value.

For the top 5 and bottom 5 ranked parents for RYTHA BVs (top 5 [low rank]: KRE691, ARA209, RAK865, MLE194, HMA496; bottom 5 [high rank]: Resisto, Kyabafuruki, Huarmayano, PAL134, IGA998), the ranking positions of remaining traits (i.e., NCRPP, FYTHA, VIR1, VIR2 and ALT) underwent an extreme change (Figure 2). Only one parent (KRE691) in the top 5 remains within the top 30 for all traits (130 rank positions for 130 parents). On the other hand, for the bottom 5 parents for RYTHA (high rank position), a better (lower) rank position was observed for the disease scores (i.e., VIR1, VIR2, and ALT).

Yield and yield-related traits (i.e., RYTHA, NCRPP, and FYTHA) were positively correlated (Table 3), with the highest correlation found between RYTHA and NCRPP exhibiting a genotypic correlation of $r = 0.896$ and a phenotypic correlation of $r = 0.862$. Yield and yield-related traits were negatively correlated with disease traits (i.e., VIR1, VIR2, and ALT), exhibiting the strongest negative association between FYTHA and VIR2 with a genotypic correlation of $r = -0.795$ and a phenotypic correlation of $r = -0.701$.

The Pesek-Baker index was used to determine weights for each key trait (b_i) in the linear index so that gains are positive (k_s within the range of >0 up to 2) for the yield traits (i.e., RYTHA, NCRPP, and FYTHA), whereas gains were negative for the SPVD scores (i.e., VIR1 and VIR2), which indicates improvement (k_s within the range of <0 to −2), and gains were zero for ALT (Table 4). No improvement was desired for the trait ALT due to genetic correlations with other traits (i.e., RYTHA, NCRPP, FYTHA, VIR1, and VIR2) (Table 3). The genetic and phenotypic variance components, estimated from the BVs of the parents across five environments, resulted in a standard error of 3.42 for the index. The weights b_i (1.42, 3.75, −0.22, −10, −3, and 0.44 for RYTHA, NCRPP, FYTHA, VIR1, VIR2, and ALT, respectively) in the index for observed phenotypic value in key traits resulted in a predicted selection response of 1.38 t ha^{-1}, 0.13, 2.66 t ha^{-1}, −0.13, −0.28, and 0 for RYTHA, NCRPP, FYTHA, VIR1, VIR2, and ALT, respectively (Table 4).

The GCA estimates for parents were only slightly associated with the parental BLUP per se performance ($r < 0.5$,

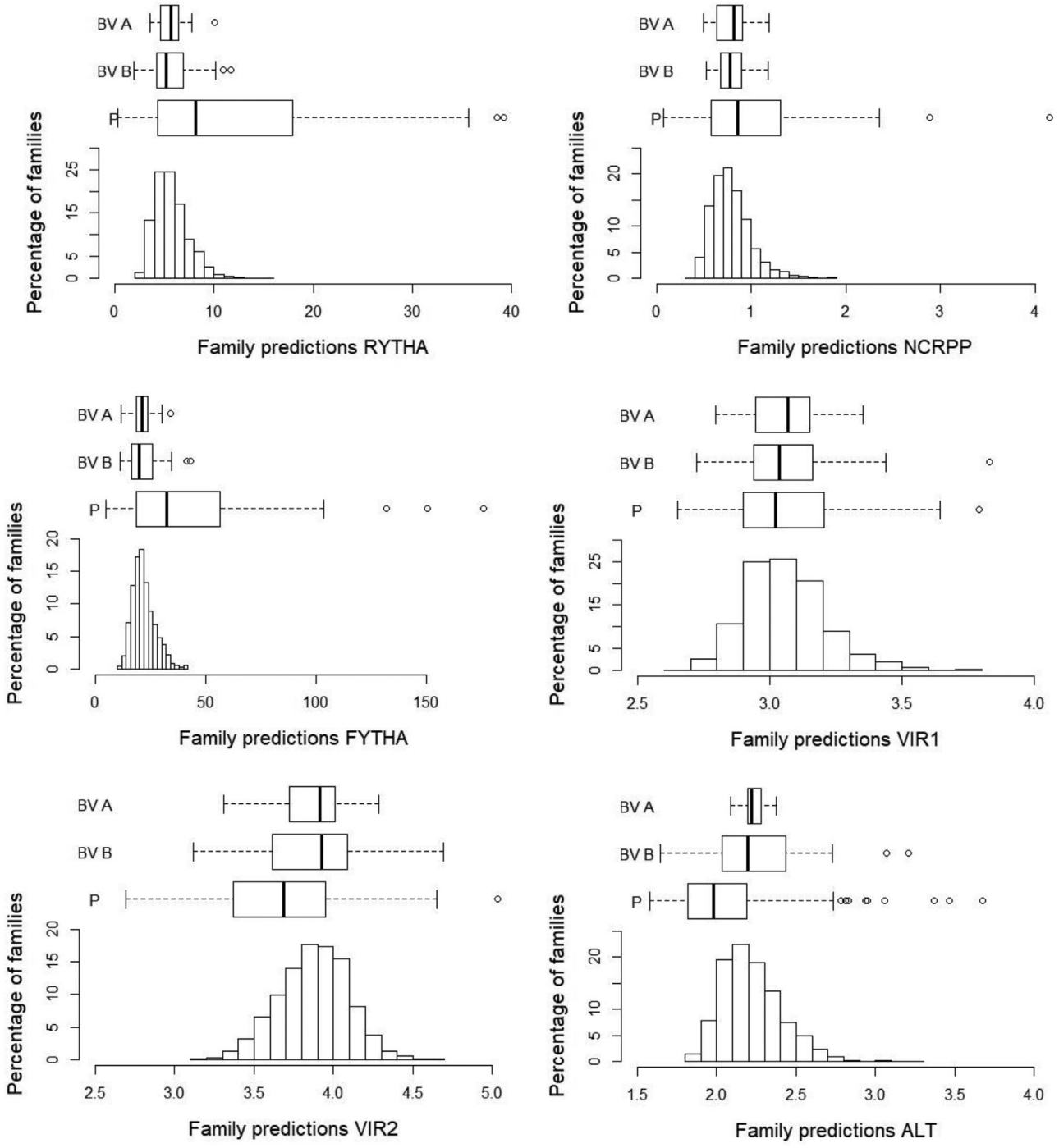

FIGURE 1 Frequency distribution of family predictions (SCA + Caf_{etal} + GCA_{male}) for observed traits; families in histogram N = 1097, boxplots of breeding values (BV based on general combining ability [GCA]) for female parents (B, $n = 80$) and male parents (A, $n = 50$), and BLUP per se performance of all parents (P); RYTHA, storage root yield in t ha^{-1}; NCRPP, number of commercial roots per plant; FYTHA, foliage yield in t ha^{-1}; VIR1 and VIR2, SPVD evaluated 8 weeks after planting and 1 month before harvesting, respectively, scored on a scale from 1 to 9 with 1 indicating no symptoms and 9 indicating severe symptoms; ALT, *Alternaria* blight evaluated 1 month before harvesting on a scale from 1 to 9 with 1 indicating no symptoms and 9 severe symptoms.

TABLE 2 BLUP prediction, genetic variance component, and heritability estimates of parents ($n = 130$) and progeny ($n = 8095$ in trial 2018A; $n = 5034$ in other trials) by environment for observed traits.

Trial		RYTHA	NCRPP	FYTHA	VIR1	VIR2	ALT
2018A	Parents	33.45	2.37	81.99	3.44	3.43	2.15
	Progeny	10.79	1.96	31.70	2.78	3.30	2.01
	σ^2_G	399.3	5.67	2898	1.20	0.66	0.23
	H^2	0.995	0.947	0.997	0.854	0.583	0.000
2018B1	Parents	6.57	0.62	21.68	3.28	4.77	2.74
	Progeny	6.47	0.69	15.86	3.57	5.05	2.99
	σ^2_G	101.2	0.63	232.9	0.28	0.55	1.56
	H^2	0.980	0.525	0.969	0.368	0.494	0.823
2018B2	Parents	9.07	0.97	31.42	3.41	4.38	2.33
	Progeny	6.95	0.75	21.82	3.17	4.84	2.72
	σ^2_G	110.3	0.62	626.8	0.32	0.60	1.11
	H^2	0.982	0.517	0.988	0.447	0.541	0.753
2019A1	Parents	4.31	0.57	32.57	2.23	2.72	1.60
	Progeny	1.55	0.27	16.38	2.80	3.17	1.75
	σ^2_G	22.50	0.18	994.2	0.00	0.22	0.31
	H^2	0.912	0.000	0.993	0.000	0.000	0.122
2019A2	Parents	3.47	0.42	34.09	2.93	3.05	1.53
	Progeny	2.24	0.33	20.37	3.08	3.12	1.64
	σ^2_G	47.91	0.29	973.3	0.00	0.14	0.23
	H^2	0.959	0.000	0.993	0.000	0.000	0.000
$\bar{v}^{BLUP}_{\Delta}$		3.959	0.597	14.50	0.349	0.553	0.551
σ^2_{Error}		8.915	0.161	192.8	0.856	0.843	0.416

Note: σ^2_G, variance component estimations due to genotypes; H^2, Cullis broad-sense heritability; $\bar{v}^{BLUP}_{\Delta}$, average standard error of the genotypic BLUPS; and σ^2_{Error}, variance component estimations due to error.

Abbreviations: ALT, Alternaria blight evaluated 1 month before harvesting on a scale from 1 to 9 with 1 indicating no symptoms and 9 sever symptoms; FYTHA, foliage yield in t ha^{-1}; NCRPP, number of commercial roots per plant; RYTHA, storage root yield in t ha^{-1}; VIR1 and VIR2, SPVD evaluated 8 weeks after planting and 1 month before harvesting, respectively, scored on a scale from 1 to 9 with 1 indicating no symptoms and 9 indicating severe symptoms.

TABLE 3 Genotypic and phenotypic (in brackets) correlations (r values) for observed traits.

	NCRPP	FYTHA	VIR1	VIR2	ALT
RYTHA	0.896 (0.862)	0.799 (0.772)	−0.353 (−0.208)	−0.624 (−0.527)	−0.413 (−0.346)
NCRPP		0.586 (0.585)	−0.386 (−0.215)	−0.518 (−0.420)	−0.120 (−0.105)
FYTHA			−0.481 (−0.409)	−0.795 (−0.701)	−0.602 (−0.514)
VIR1				0.925 (0.791)	−0.270 (−0.327)
VIR2					0.571 (0.586)

Abbreviations: ALT, Alternaria blight evaluated 1 month before harvesting on a scale from 1 to 9 with 1 indicating no symptoms and 9 sever symptoms; FYTHA, foliage yield in t ha^{-1}; NCRPP, number of commercial roots per plant; RYTHA, storage root yield in t ha^{-1}; VIR1 and VIR2, SPVD evaluated 8 weeks after planting and 1 month before harvesting, respectively, scored on a scale from 1 to 9 with 1 indicating no symptoms and 9 indicating severe symptoms.

Figure 3). Parents with high BLUP per se performance for RYTHA exhibited GCA estimates around zero, and low performing parents were observed with high GCA estimates. Negative GCA estimates for FYTHA were found across the entire range of parents' BLUP per se performance for FYTHA. Regression lines were estimated for both parental groups together. VIR1 had a medium r value of the correlation between BLUP per se prediction and GCA estimates ($r = 0.474$). This value is much higher than the association of VIR1 BLUP per se prediction and GCA estimates ($r = 0.142$).

In each of the parental populations (UGA A and B), 20 parents were selected (Tables 5 and 6). The 20 selected clones for intra-gene pool recombination in parental population UGA

TABLE 4 Parameters for multi-trait selection using the Pesek-Baker index based on the breeding values of parents across five environments (σ^2_G, genetic variance; σ^2_P, phenotypic variance; k_s, desired genetic gain in standardized units; b_i, $\mathbf{G}^{-1}k$ where $\mathbf{G}$ is the genotypic variance-covariance matrix and $k_i = \sigma_{gi}k_s$; σ_{Ii}, correlation coefficient between the index and trait i; R_i, predicted selection response: $1.755\frac{\sigma_{Ii}}{\sigma_I}$ with the standard error of the index $\sigma_{Ii} = 3.42$).

Trait	σ^2_G	σ^2_P	k_s	σ_{Ii}	b_i	R_i
RYTHA	1.80	3.35	2	2.68	1.42	1.38
NCRPP	0.015	0.026	2	0.245	3.75	0.13
FYTHA	26.8	38.0	1	5.18	–0.22	2.66
VIR1	0.015	0.026	–2	–0.247	–10.07	–0.13
VIR2	0.076	0.085	–2	–0.553	–3.00	–0.28
ALT	0.046	0.054	0	0	0.43	0

Abbreviations: ALT, Alternaria blight evaluated 1 month before harvesting on a scale from 1 to 9 with 1 indicating no symptoms and 9 sever symptoms; FYTHA, foliage yield in t ha^{-1}; NCRPP, number of commercial roots per plant; RYTHA, storage root yield in t ha^{-1}; VIR1 and VIR2, SPVD evaluated 8 weeks after planting and 1 month before harvesting, respectively, scored on a scale from 1 to 9 with 1 indicating no symptoms and 9 indicating severe symptoms.

TABLE 5 Estimated breeding values and rank based on the Pesek-Baker index (with $k_s = 2$ for RYTHA and NCRPP, $k_s = 1$ for FYTHA, $k_s = -2$ for VIR1 and VIR2, and $k_s = 0$ for ALT) for the 20 selected parents in population A.

Selected parent		RYTHA	NCRPP	FYTHA	VIR1	VIR2	ALT	Pesek-Baker index rank
MLE194	A50	10.05	1.08	34.23	2.83	3.31	2.20	1
NK318L	A49	7.12	1.01	26.21	2.86	3.46	2.24	2
KML872	A32	6.36	1.08	22.52	2.79	3.70	2.26	3
NASPOT 7	A30	7.80	0.89	26.80	3.00	3.66	2.24	4
RAK808	A25	5.69	0.75	19.63	2.85	3.57	2.21	5
NASPOT 9 O[a]	A22	6.39	0.93	22.31	2.91	3.73	2.20	6
Tororo3	A23	6.65	0.85	30.00	2.85	3.57	2.18	7
MPG1128	A11	6.13	0.99	24.78	2.93	3.65	2.35	8
LUW1274	A28	6.12	0.91	22.34	2.93	3.74	2.27	10
NASPOT 10 O[a]	A31	7.10	0.92	19.61	3.19	3.84	2.27	14
Carrot C[a]	A01	7.16	1.03	21.33	3.17	4.00	2.24	15
KMI61	A06	6.21	0.82	29.01	2.90	3.62	2.22	16
KBL648	A14	6.10	0.93	20.93	3.07	3.91	2.12	18
Oguroiwe	A35	6.03	0.90	19.62	3.09	3.90	2.20	19
APA323	A39	5.89	0.78	21.43	3.07	3.72	2.22	21
Mayai[a]	A03	7.02	1.01	25.52	3.14	4.05	2.18	22
Ejumula[a]	A02	7.57	1.19	23.82	3.35	4.02	2.15	23
RAK819	A18	5.32	0.76	22.99	2.95	3.96	2.34	26
RAK835	A46	6.22	0.87	20.95	3.16	3.99	2.15	27
Otada	A40	5.98	0.74	29.93	3.00	3.72	2.09	32
Mean of selected parents		6.646	0.922	24.198	3.003	3.756	2.217	
Mean of all parents in population A ($n = 50$)		5.634	0.792	21.440	3.055	3.875	2.234	
Difference between selection and all parents		1.012	0.130	2.758	–0.052	–0.119	–0.017	

[a]Orange-fleshed parents.

Abbreviations: ALT, Alternaria blight evaluated 1 month before harvesting on a scale from 1 to 9 with 1 indicating no symptoms and 9 sever symptoms; FYTHA, foliage yield in t ha^{-1}; NCRPP, number of commercial roots per plant; RYTHA, storage root yield in t ha^{-1}; VIR1 and VIR2, SPVD evaluated 8 weeks after planting and 1 month before harvesting, respectively, scored on a scale from 1 to 9 with 1 indicating no symptoms and 9 indicating severe symptoms.

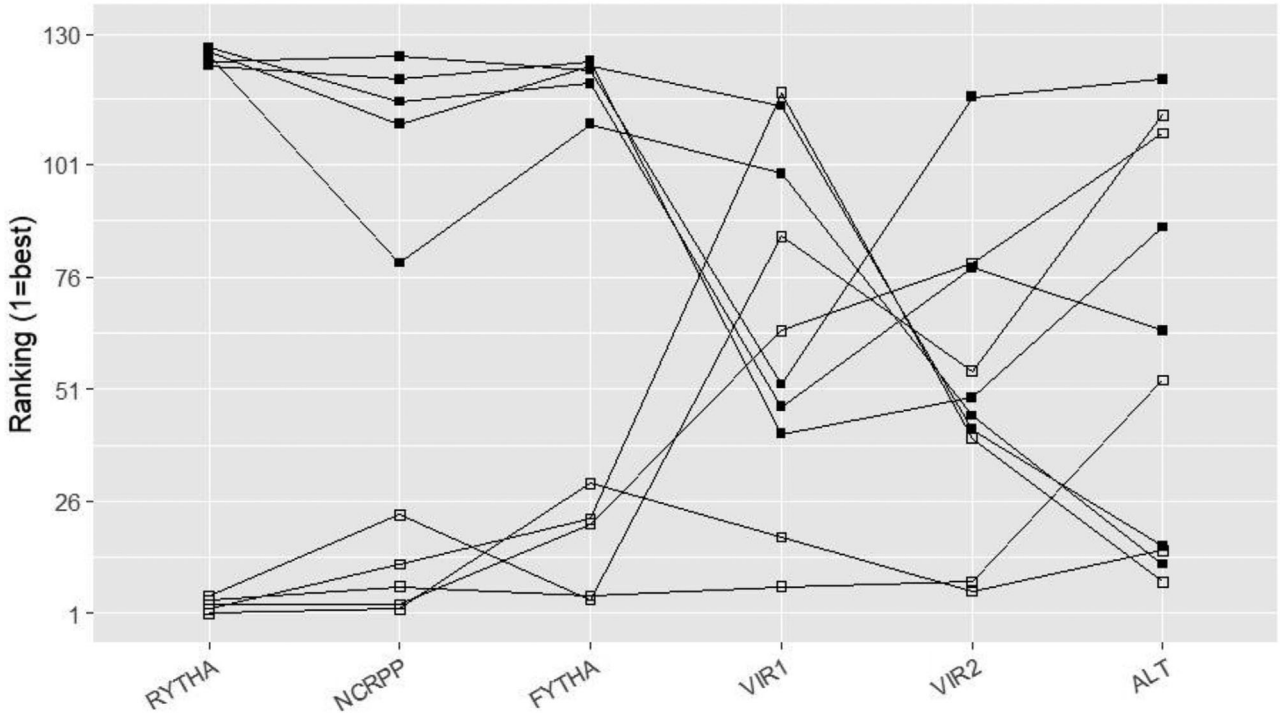

FIGURE 2 Breeding value (BV) of parents ranking for observed traits presented for the top 5 (open squares) and bottom 5 (solid squares) ranked parents for storage root yield; RYTHA, storage root yield in t ha^{-1}; NCRPP, number of commercial roots per plant; FYTHA, foliage yield in t ha^{-1}; VIR1 and VIR2, SPVD evaluated 8 weeks after planting and 1 month before harvesting, respectively, scored on a scale from 1 to 9 with 1 indicating no symptoms and 9 indicating severe symptoms; ALT, *Alternaria* blight evaluated 1 month before harvesting on a scale from 1 to 9 with 1 indicating no symptoms and 9 severe symptoms.

A (Table 5) included five orange-fleshed clones (i.e., Carrot C, Ejumula, Mayai, NASPOT 9 O, and NASPOT 10 O) with a maximum Pesek-Baker index rank of 23. Four other parents (i.e., APA323, RAK819, RAK835, and Otada) were also included in the selection despite their Pesek-Baker index values of 21, 26, 27, and 32, respectively (reason: selection decisions were already made after two seasons of evaluation and not three). The breeding value mean differences between selected fraction and all parents were positive for the yield traits (1.01 t ha^{-1} RYTHA, 0.13 NCRPP, and 2.76 t ha^{-1} FYTHA) and negative for the disease traits (−0.05 VIR1, −0.12 VIR2, and −0.02 ALT).

The 20 selected parents in parental population UGA B (Table 6), including five orange-fleshed clones (i.e., CIP199062.1, Jewel, Resisto, Raihna and SPK004), had a maximum Pesek-Baker index rank of 68. Two released varieties (Sowola and NASPOT 11) and two other parents (i.e., SRT43 and RAK848) were also included in the selection, despite their Pesek-Baker index rank values of 26, 31, 28, and 30, respectively (reason was the same as for parental population A). The breeding value mean differences between selected fraction and all parents were positive for the yield traits (1.28 t ha^{-1} RYTHA, 0.06 NCRPP, 2.07 t ha^{-1} FYTHA) and negative for the disease traits (−0.08 VIR1, −0.25 VIR2, and −0.09 ALT).

4 | DISCUSSION

Developing an applied sweetpotato breeding population for genetic studies is challenging because of (i) incompatibility among parents, (ii) unbalanced true seed production, (iii) different rates of growth in offspring, and (iv) biotic stresses (Grüneberg et al., 2015). A complex sporophytic self- and cross-incompatibility system favors outcrossing; however, many cross combinations provide no true seed (Mwanga et al., 2017). For example, only 27% of the handcrossings in this study (80 female parents × 50 male parents) were successful. The first field evaluation started with 8095 progeny from 1097 families. However, many weak clones were lost in the subsequent season (number of offspring clones decreased to 5031), but with respect to families the decrease was small (number of families decreased to 1034). The population used in this study is unique to EA and was used to investigate the potential for implementing HEBS in this region.

Owing to very unequal SPVD pressure in and across fields (Mwanga et al., 2013), several seasons are needed to determine whether a clone is moderately to highly resistant to SPVD. To minimize the number of genotypes that could avoid SPVD infection, planting material from the previous season and trial was used in subsequent seasons to facilitate the transmission of viruses. Heritability was calculated following the

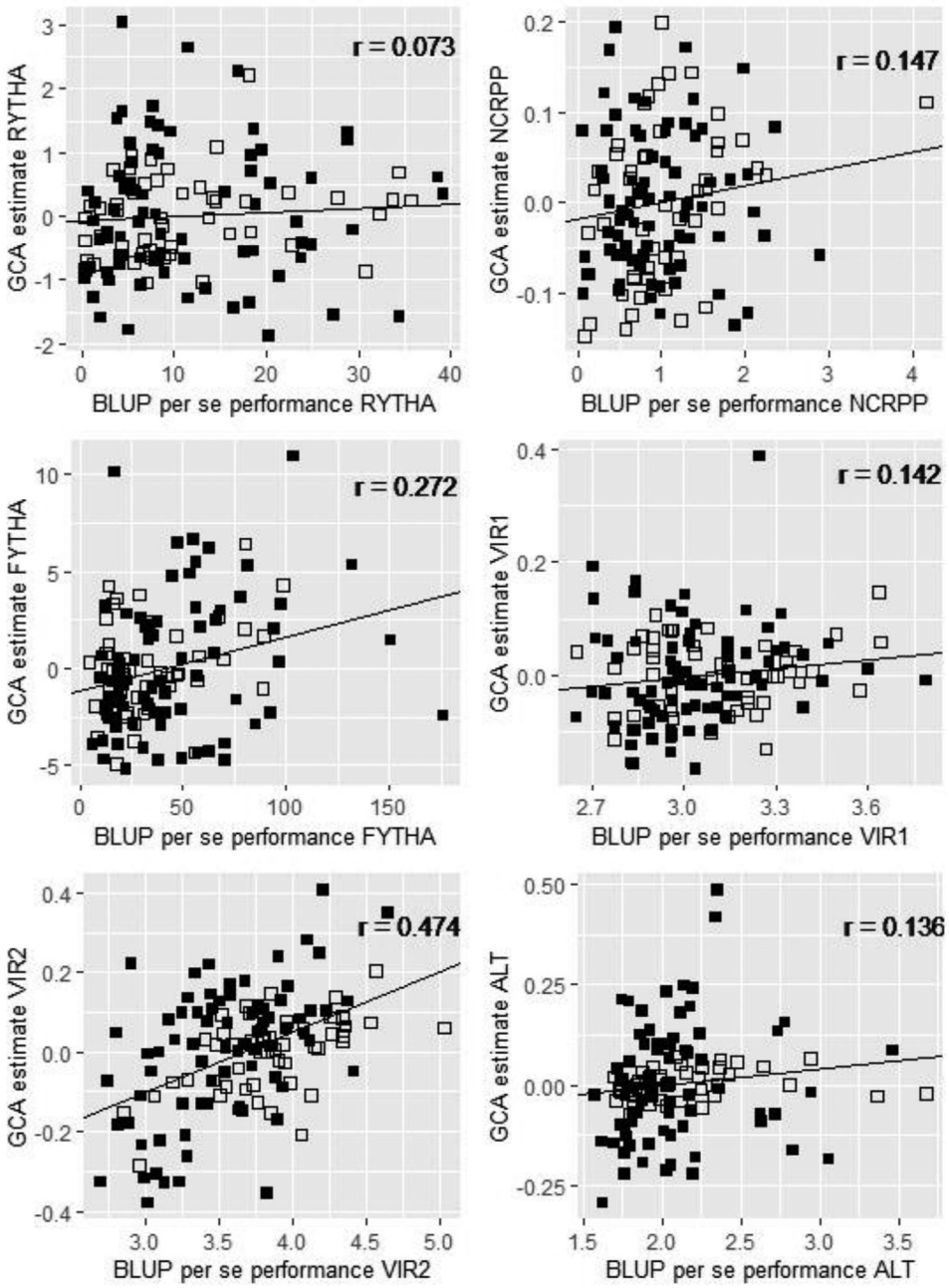

FIGURE 3 Parental BLUP per se performance plotted against the general combining ability (GCA) estimates for population A (open squares) and population B (solid squares) for observed traits; RYTHA, storage root yield in t ha^{-1}; NCRPP, number of commercial roots per plant; FYTHA, foliage yield in t ha^{-1}; VIR1 and VIR2, SPVD evaluated 8 weeks after planting and 1 month before harvesting, respectively, scored on a scale from 1 to 9 with 1 indicating no symptoms and 9 indicating severe symptoms; ALT, *Alternaria* blight evaluated 1 month before harvesting on a scale from 1 to 9 with 1 indicating no symptoms and 9 severe symptoms.

method suggested by Cullis et al. (2006) for situations in which data are unbalanced (different number of repetitions per genotype). Note that heritabilities can be estimated negative because of the approximation of nongenetic variation on the basis of the standard error of genetic estimates across environments. In contrast to this study, most studies in sweetpotato have reported variance components in later breeding stages based on advanced clones tested in multiple environments. These include the studies across Kenya and Uganda (Grüneberg et al., 2004), across diverse environment of Peru (Grüneberg et al., 2005), in Uganda (Tumwegamire et al., 2016), Ethiopia (Gurmu et al., 2017), and Ghana (Swanckaert et al., 2020).

The success of plant breeding depends to a large extent on the knowledge of the genetic structure of the populations used and efficiency in achieving genetic gains. The probability of

TABLE 6 Estimated breeding values and rank based on the Pesek-Baker index (with $k_s = 2$ for RYTHA and NCRPP, $k_s = 1$ for FYTHA, $k_s = -2$ for VIR1 and VIR2, and $k_s = 0$ for ALT) for the 20 selected parents in population B.

Selected parent		RYTHA	NCRPP	FYTHA	VIR1	VIR2	ALT	Pesek-Baker index rank
KRE691	B16	11.70	1.18	25.66	2.89	3.24	1.98	1
APA356	B28	8.36	0.86	30.93	2.74	3.22	1.93	2
MBR536	B17	8.28	0.95	32.30	2.78	3.11	1.94	3
MKN121	B29	7.93	0.75	27.70	2.84	3.26	2.05	5
ARA29	B02	10.92	1.02	27.02	3.27	3.74	1.87	6
MLE199	B08	7.59	0.88	18.95	3.03	3.60	1.79	7
MSK194	B51	6.30	0.70	20.06	2.81	3.69	2.41	9
NASPOT 5	B30	6.68	0.95	26.60	2.91	3.41	2.08	10
LUW1257	B15	6.89	1.03	22.46	3.03	3.65	2.09	13
MLE179	B19	8.46	0.80	24.77	3.16	3.61	2.32	16
CIP199062.1[a]	B78	6.67	1.09	20.19	2.99	4.07	2.27	17
KML942	B10	6.83	0.66	28.05	2.95	3.22	2.03	19
SRT43	B06	7.71	0.77	17.78	3.17	4.04	2.21	26
Sowola	B26	6.49	1.01	18.50	3.15	3.77	1.89	28
NASPOT 11	B54	4.54	0.72	20.58	2.87	3.52	2.18	30
RAK848	B47	5.48	0.89	41.62	2.72	3.17	1.91	31
Jewel[a]	B69	5.07	0.78	19.65	2.94	3.88	2.44	32
Resisto[a]	B71	4.99	0.82	16.22	3.08	4.21	2.60	43
Raihna[a]	B76	3.87	0.59	17.60	2.93	4.02	2.70	51
SPK004[a]	B33	3.48	0.65	13.57	3.20	4.13	2.15	68
Mean of selected parents		6.912	0.856	23.511	2.973	3.628	2.142	
Mean of all parents in population B ($n = 80$)		5.634	0.792	21.44	3.055	3.875	2.234	
Difference between selection and all parents		1.278	0.064	2.071	–0.082	–0.247	–0.092	

[a]Orange-fleshed parents.

Abbreviations: ALT, Alternaria blight evaluated 1 month before harvesting on a scale from 1 to 9 with 1 indicating no symptoms and 9 sever symptoms; FYTHA, foliage yield in t ha^{-1}; NCRPP, number of commercial roots per plant; RYTHA, storage root yield in t ha^{-1}; VIR1 and VIR2, SPVD evaluated 8 weeks after planting and 1 month before harvesting, respectively, scored on a scale from 1 to 9 with 1 indicating no symptoms and 9 indicating severe symptoms.

finding superior offspring clones in a breeding population can be increased through improvement of the population means while maintaining the genetic variances (Wricke & Weber, 1986). Selection reduces genetic variance, depending on the selection intensity and accuracy, but the lost genetic variance can be restored through recombination between breeding cycles (Rutkoski, 2019). We found low hybrid vigor in the inter-pool offspring clones. However, it is expected that after one reciprocal recurrent cycle of recombination and selection, hybrid vigor will become more pronounced (Hallauer et al., 2010). The hybrid vigor estimates in our study were, to a large extent, confounded by SPVD effects, which is indicated by the observed negative correlation of RYTHA and SPVD scores ($r = -0.594$). The hybrid breeding population in this study was exposed to pronounced SPVD pressure for three seasons, which affected the segregating offspring more (SPVD resistance is a recessive trait; Mwanga, Yencho, et al., 2002; Mwanga, Kriegner, et al., 2002) than the parents, which were the results of intensive preselection for SPVD resistance for a long time prior to their inclusion in crossing blocks.

Grüneberg et al. (2015), who studied contrasting sweetpotato clones, reported for RYTHA a mid-parent mid-offspring correlation of $r = 0.705$, but in this study, the mid-parent value of two parents exhibited a surprisingly low association with the family mean. To obtain precise mid-parent mid-offspring associations, field plots must be balanced. This study was not designed to compare parents and offspring clones, as each parent was grown in an unreplicated 1 m row plot, whereas the area covered by the offspring of each family was much larger (several 1 m row plots, depending on the number of genotypes per family) than those of parents (two 1 m row plots for each family). Mid-parent mid-offspring correlations in sweetpotato are expected to be lower than in diploids (Grüneberg et al., 2015), and correlations around 0.3

were subsequently observed (Diaz et al., 2021; Grüneberg et al., 2022). The strikingly low mid-parent mid-offspring association in the EA breeding platform observed in this study might underline the importance of determining the breeding value of parents on the basis of offspring performance and the selection of parents using their combining ability.

Without prior knowledge of the usefulness of a cross, the number of crosses has to be maximized, and the number of genotypes per cross has to be minimized to reduce the risk of raising no good crosses, as discussed in detail by Wricke and Weber (1986). This principle was aggressively applied in sweetpotato polycross breeding, with breeding nurseries of up to 150 parents (Grüneberg et al., 2015). It is worth noting that each sweetpotato seed capsule contains a maximum of only four seeds, which makes the crop extremely different from potato or tomato in which one successful pollination results in more than 100 true seeds. Large numbers of true seed and genotypes are needed from polycrosses or by controlled handcrosses to achieve high selection intensities in sweetpotato, which are required to combine high-yield and biotic stress resistance, as Mwanga et al. (2017) pointed out in a discussion of polycross breeding versus handcross breeding. In cases where not many handcross true seeds are produced (our assumption: less than 400 successful cross combinations with 5–20 true seeds per cross combination), it is still favorable to conduct polycrosses. However, in cases in which there is information about the value of a cross, resulting from offspring evaluations, it is more efficient to have fewer, better crosses and to raise large numbers of genotypes per cross (Wricke & Weber, 1986). This principle has been applied to rice with great success in increasing breeding efficiency (Witcombe et al., 2013).

Sweetpotato breeders at CIP in Peru and Uganda have started to follow this principle with the establishment of elite crosses, or "ISOs," in which a few parents with high GCA are recombined and disseminated elite true seed from ISOs to Bangladesh, China (W. J. Grüneberg, personal communication, 28 June 2022 at African Potato Association conference 2022 in Lilongwe, Malawi), Ethiopia, Rwanda, and Tanzania (R. Ssali, personal communication, 28 June 2022 at African Potato Association conference 2022 in Lilongwe, Malawi). Our study is the first in EA in applied breeding to provide information on the value of a cross using offspring information. The best parents, those which have proven to be good "family makers" (high GCA), were chosen for improving the two sweetpotato gene pools in Uganda. This is additionally linked to elite cross combinations in "ISOs" to exploit high SCA and to produce true seed on a very large scale—thousands of true seeds and new genotypes—without laborious hand crossings. Using such elite populations from "ISOs," a breeding hub can truly serve an entire region by disseminating large numbers of improved true seed with high population means for the selection of new varieties by National Agricultural Research Institutes (NARIs). This has so far only been partially achieved though polycross breeding at breeding hubs, as NARIs have occasionally complained about the poor performance of true seed obtained from polycross breeding hubs. It is hypothesized that this new approach to sweetpotato population improvement will result in a large impact in EA through yield increases and greater frequency of SPVD resistance in elite material.

Genetic analysis in polyploid crops such as sweetpotato is complicated by the presence of multiple alleles at a given locus. The autopolyploid segregation ratios of sweetpotato are usually very complex. Our study clearly shows that the per se performance of parents is poorly correlated with the GCA estimates of parents (Figure 3)—often close to zero, especially for RYTHA. Hence, parent/offspring evaluations appear to be absolutely vital for sweetpotato population improvement, and this might hold true for other clonally propagated crops. However, it takes at least two extra years to make interpopulation crosses in population hybrid breeding, to multiply enough planting material, and to conduct field evaluations of the offspring. It has been argued that genomic selection (GS) could speed up the process of selecting new parents by estimating the BVs of the genotypes (Budhlakoti et al., 2022). Friedmann et al. (2018) and Crossa et al. (2017) elaborated on the use of GS for parent selection in the crops of focus of the CGIAR Research Programs on Roots, Tubers and Bananas (RTB). The GS models developed for seed-propagated crops may be suitable for variety development in clonally propagated crops because early selection stages show no segregating generations in variety extraction and evaluations can be conducted at a very large number of environments to obtain data to train GS models. However, for population improvement and parental selection additive, dominance and epistatic effects play an important role with different magnitudes for individual traits, as demonstrated by Ceballos et al. (2015) for cassava, and populations derived from a large number of parents are often evaluated in a very limited number of environments. Elite crossing might be very well suited to train GS models and to test GS for adequate selection among offspring clones, but from the breeder's perspective, GS for parental selection remains challenging and requires careful validation with respect to the genetic gains achievable across traits. Variety extraction and the early breeding stages might be the "low-hanging fruit" to apply GS successfully in sweetpotato before embarking on the cumbersome and extremely critical selection of new parents, which determines breeding progress in the medium and long term, and which holds a risk of errors that can destroy an entire breeding population. Admittedly, this is a conservative approach, but it would reduce the risk of failure in population improvement. However, there are other opinions that GS should be straightforwardly applied for selection of parents (Gemenet & Khan, 2017).

Certainly, a crucial point in population improvement is the appropriate improvement over yield and yield-related traits, without risking that too many genotypes fall below the lowest acceptable value (threshold level) in the subsequent breeding cycle(s) for any quality or resistance key trait. These considerations have had tremendous impact, such as on structuring plant breeding into a variety development and selection component (targeting the best genotype) linked but clearly separated from a population improvement strategy (targeting the best set of parents) (Gallais, 2003). Our study focused on a sweetpotato hybrid breeding scheme for population improvement that features recombination of the best parents in which a new set of parents is selected by discarding bad parents or bad family makers. Our target was to discard 60%–75% of the parental material of the previous polycross breeding program (130 parents grouped into two gene pools) on the basis of offspring information using the interpopulation offspring performance. However, many key traits determine the value of a parent, and in contrast to variety development and selection, where wrong decisions are recognizable within a few selection stages, it takes a generation for a wrong choice of parents to become visible, and there is a considerable risk that such errors can lead to useless breeding populations and programs that do not make progress for a long time. This is why multi-trait selection of parents might be the most difficult part of breeding. It appears that our proposed multi-trait selection procedure is promising (Table 4) because for traits where the desired response is positive it predicts a positive response in standardized units, for those traits where the desired response is negative it predicts a negative response in standardized units (SPVD), and for those traits where no change is a desired response it predicts a zero response in standardized units (ALT), although there is a pronounced negative association between yield and yield-related trait with SPVD, especially VIR2 ($r < -0.500$).

The modified Pesek-Baker index resulted in a preliminary set of selected parents. A final set of selected parents was composed by considering additional information of flesh color and adding outstanding clones of the NASPOT varieties (Mwanga et al., 2009). The orange-fleshed parents mostly fell out of the top 20 in each gene-pool but were partially included in the final selected set of parents due to the importance of having beta-carotene alleles in breeding populations. Careful consideration of additional information is necessary to interpret responses of parental material to multi-trait selection. This is different from genetic gain in which repeated selection cycles result in a linear genetic trend. A rough estimate of expected genetic gains (Table 4)—although it considers only the short term—is already very useful to obtain information about the potential medium- and long-term progress within a breeding program, but in cases in which additional information is used in the multi-trait selection procedure (Tables 5 and 6), the effect should be monitored to determine whether the selection decisions will lead to genetic gain over time.

In conclusion, areas that experience high virus pressure might not be the most appropriate environments for sweetpotato heterosis studies because the effects of SPVD can easily be confounded with breeding results for yield and yield-related traits. The determination of GCA appears to be extremely important for the selection of sweetpotato parents because the per se performance of parents provides only very limited information about their value as parents. This is much more pronounced in hexaploid crops than in diploid crops. For the first time in EA, our study used GCA across traits in a sweetpotato population hybrid breeding program. The proposed method to determine desired genetic gains using a modified Pesek-Baker index resulted in satisfactory prediction of means across all key traits in the selected fraction of parents. Thus, this approach should be used in future studies.

AUTHOR CONTRIBUTIONS

Jolien Swanckaert wrote the manuscript with contributions from other authors. Reuben Ssali supported the data collection in the field. Robert Mwanga gave his input during the final selection of parents. Maria Andrade gave her input as an experienced sweetpotato breeder. Bert De Boeck and Raul Eyzaguirre supported the data analysis. Hugo Campos is the PI of the SweetGAINS project and reviewed before final submission. Wolfgang J. Grüneberg suggested the modification of the index selection procedure, mentored, and supervised the first author in shaping the manuscript.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

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