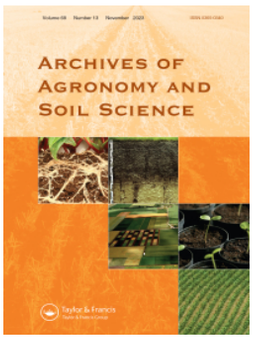

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Genetic variability, character association and path analysis in sugarcane genotypes

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ABSTRACT

The study, conducted at Tana-Beles Sugarcane plantation in Ethiopia from May 2022 to October 2023, used a partially balanced lattice design with two replications to assess variability and trait associations among 196 sugarcane genotypes collected from 14 countries. Highly significant ($p < 0.0001$) variability was observed for all traits; especially genotypes with fuzz exhibited wider variation for cane (20.97–135.31 t/ha) and sugar yield (1.83–20.42 t/ha), highlighting their potential for improvement. Except for single cane weight, brix, and purity, all traits displayed moderate to high heritability (H^2 : 31–79%) and genetic advance (GAM: 10.69–53.14%), indicating potential for improvement through phenotypic selection being controlled by additive gene actions. The number of millable stalks, stalk length, stalk diameter, brix and cane yield showed significant positive genotypic correlations ($r = 0.49$, $r = 0.55$, $r = 0.41$, $r = 0.65$, and $r = 0.98$, respectively) and strong direct positive effects (0.33, 0.47, 0.75, 0.51 and 0.83, respectively) on sugar yield. Thus, Sugar yield, along with these traits, can serve as selection criteria for identifying high-sugar-yielding sugarcane genotypes. Consequently, the top three sugarcane genotypes for multi-traits, namely B552–11, FG04–466, and B707–1, could be evaluated across seasons for commercial use at Tana-Beles.

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Introduction

Blessed with remarkable sucrose accumulation capabilities and the highest potential for biomass production among plant species, sugarcane (*Saccharum* spp.) stands out as one of nature's most efficient converters of solar energy into sugar (Gianotto et al. 2011; Hoang et al. 2015; Mirajkar et al. 2019). As a member of the Gramineae family, sugarcane has been cultivated across the world on all inhabited continents for centuries, primarily for the production of sugar and, more recently, for the manufacturing of bioethanol. In Ethiopia, the cultivation of sugarcane holds a rich historical significance, tracing its roots back to the 16th century, when it found a place in local households and farmers' fields (Tena et al. 2018).

Since the establishment of commercial sugarcane production in 1951, this crop has not only catered to the demand for sugar in domestic and industrial sectors but has also generated valuable by-products such as molasses and bagasse, opening up abundant employment opportunities for the local population; and making a substantial contribution to the national economy (Teklemariam 1991; Tena et al. 2016).

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Ethiopia's diverse climatic and soil conditions have proven highly favourable for sugarcane cultivation and yield (Anonymous 2014; Semiea et al. 2019). Despite these advantageous conditions, Ethiopia faces challenges in meeting its domestic sugar demand. Moreover, sugar production per hectare has shown a concerning downward trend in major sugar estates over the years. Specifically, between 1998 and 2019, sugar production per hectare declined from 166 to 84 tons at Finchaa, from 140 to 101 tons at Wonji, and from 165 to 157 tons at Metahara sugar estates (Tolera et al. 2023). This decline in productivity is primarily attributed to the lack of high-yielding, improved sugarcane cultivars well-adapted to the diverse agro-ecologies of Ethiopian sugarcane plantations (Kebede et al. 2013; Tena et al. 2016).

In the pursuit of creating superior sugarcane cultivars, delving into the depths of genetic variation is an essential undertaking. This exploration uncovers the hidden riches of traits that await enhancement, empowering breeders to create cultivars that can meet the demands of future agriculture. Genetic variability, which lies at the core of plant breeding, acts as a guiding force, leading breeders through the labyrinth of traits and enabling them to identify and harness the untapped genetic potential residing within the diverse germplasm of sugarcane. By expanding the range of trait variation within the pool of germplasm, we broaden the horizons of possibility, establishing fertile ground for selective breeding to thrive. This expansion of the genetic landscape opens pathways to innovation, facilitating the introduction of novel traits that empower sugarcane to prosper in the face of evolving challenges.

The effective development of breeding strategies, particularly for perennial crops like sugarcane, requires a deep comprehension of how traits are inherited and the anticipated genetic advancements. This necessitates a thorough examination of both heritable and non-heritable components of observed variability, aiming to unravel the complex interactions among genes that govern trait expression and the reliability of phenotypic predictions in determining breeding value (Ullah et al. 2012). Although high heritability is often considered desirable, it does not guarantee substantial genetic progress (Amin et al. 2004).

To achieve successful trait improvement and accurate estimation of expected genetic advancements, high heritability values must be accompanied by significant genetic gains (Johnson et al. 1955; Udeh and Ogbu 2011).

Besides a clear understanding of the heritable proportion of variation, knowledge of the predicted yield improvement that can be achieved through selection is imperative for effective planning of breeding experiments and successful development of improved sugarcane varieties (Kumar et al. 2018). Variance component analysis is a valuable technique for estimating the extent of heritable variation and anticipated genetic gains in desirable traits, guiding the selection of superior genotypes as parents for hybridization and industrial use. For single-trait selection, genotypes should be selected based on traits with moderate to high heritable variation and genetic advance. For multi-trait selection, genotypes should be selected based on moderate to high heritability and genetic advance values, as well as strong positive and highly significant genotypic correlation with and a high direct positive effect on the main yield component: sugar yield (Borém et al. 2016). Correlation analysis is useful to identify the relative degree of association between the economic trait; sugar yield and its contributing characters, while path analysis further partitions the correlation coefficients to point out the relative contribution of the associated characters to the main yield component. Studies on the variability, heritability, and predicted genetic progress (Tadesse et al. 2014; Tena et al. 2016; Tesfaye et al. 2020) as well as character association (Tadesse et al. 2014; Tena et al. 2016; Mebrahtom et al. 2016) among the agro-morphological and biochemical traits of sugarcane have been carried out in Ethiopia. However, the type of genetic material, the trait being measured, and the environmental conditions to which the material is exposed determine the extent of variability and heritability (Burton and DeVane 1953; Singh and Chaudhary 1999), while association between traits is influenced by the test material, the test environment, and their interactions (Pires and Da Costa 1980).

Despite favorable conditions, Ethiopian sugarcane production faces declining yields due to the lack of high-yielding and adapted cultivars. Additionally, Tana-Beles is a new sugar development project, and there is no information on how the sugarcane genotypes used in this study will perform in this new environment. Furthermore, determining the variability among these genotypes and studying the genetic parameters will help to expand the available germplasm genetic base for further crop improvement. Therefore, the aim of this study was to identify traits with moderate to high heritability and genetic advance values, as well as strong positive genotypic correlation with and a high direct positive effect on sugar yield. This will help to identify superior sugarcane genotypes for commercialization, pinpoint the most important traits for selection, identify potential parents for hybridization to develop improved sugarcane varieties for multiple traits, and achieve increased genetic gain.

Materials and methods

Experimental site

The study took place at the Tana-Beles Sugarcane plantation in Ethiopia from May 2021 to October 2023. It was conducted across two main seasons: the summer or rainy season (June to August) and the off-season or dry season, which was irrigated using furrow irrigation (October to May). The Tana-Beles is located at 11°30′latitude and 36°41′ longitude, at an altitude of 1110 meters above sea level. It has an average annual rainfall of 1447 mm, and average low and high temperatures of 16.4°C and 32.5°C, respectively.

Plant materials

This study included 196 sugarcane genotypes, of which 98 (50%) were from Barbados (83 F_1 genotypes germinated from recently introduced three-way crosses, 14 old collections and one standard check variety). The remaining 98 genotypes included 26 local collections from Ethiopia, 21 from France, and 11 from the USA. The rest of the experimental materials (40) were obtained from India (7), Brazil (7), Mauritius (5), South Africa (4), the Philippines (4), Demerara (4), Thailand (3), Mexico (3), Cuba (2), and Puerto Rico (1). Supplementary Tables 1 and 2 present detailed descriptions of the test materials used in the study.

Experimental design and cultural practices

The experiment was set up in a partially balanced lattice design with two replications. The plots were spaced 1.5 m apart, and the incomplete blocks were spaced 2.9 m apart. The border spacing was 5 m. Each plot was 21.75 m^2, equivalent to three furrows of 5 m in length and 1.45 m in width. The experimental materials were seven-month-old cane, cut into three bud setts and planted in an end-to-end pattern on Luvisol type. Estate recommended agronomic management practices, including fertilization with DAP at 250 kg ha^{-1} during planting, furrow irrigation, earthing-up at three months after planting and manual weeding, were consistently followed throughout the growth period.

Data collection

Agro-morphological traits

The study adopted the descriptors from (GRIN 2004) for qualitative agro-morphological and bio-chemical traits of *Saccharum* species. A total of 16 quantitative traits were assessed at relevant plant growth stages, comprising 11 agro-morphological traits and 5 biochemical traits.

For traits like stalk length in meters (SL), stalk diameter in centimetres (SD), single cane weight in kilograms (SCW), number of internodes (NI), and internode length in centimetres (IL),

10 plants were randomly selected from the middle row of each genotype for individual measurements. Whereas data for sprouted bud numbers (SPN45), tiller numbers at three (TL3MAP), four (TL4MAP), and five (TL5MAP) months after planting, and number of millable stalks (NMS), were collected on a plot basis and converted to per-hectare values. Cane yield (CY) was determined by multiplying the number of millable stalks (NMS) by the single cane weight (SCW).

Biochemical traits

Response variables for brix (%), pol (%), and purity (%) of the juice were measured from a composite juice sample of 10 sugarcane stalk samples taken from the middle furrow at 18 months after planting.

Brix content in juice: At Tana-Beles Research Station, Jeffco cane crusher was used to crush and extract the juice from the sugarcane stalks. Then, the method described by Meade and Chen (1977) was followed to measure the brix content of the juice. The brix content is a measure of the total amount of dissolved solids in the juice. To measure the brix content, 150 ml sample of the extracted juice was taken and filtered using Whatman No. 91 filter paper and filter aid. Then, precision refractometer was set at 20°C to measure the refractive index of the juice. The refractive index is a measure of how much light is bent when it passes through the juice. The brix percentage of the juice can be determined directly by measuring the refractive index of the juice with a refractometer.

Pol percent in juice: The concentration of pol in juice was determined using Horne's dry lead acetate method described by Meade and Chen (1977). The composite juice sample of 300 ml was mixed with lead acetate (1 g/100 mL) before being allowed to flocculate for around 30 seconds. The flocculated sample is filtered via filter paper from which 200 ml clear juice was polarized at 20°C in order to obtain the pol reading using a precision polarimeter. Then, the Polarimeter reading was multiplied by the corresponding brix and pol reading values from Table.

Purity percent in juice: The purity percent of sugarcane juice is calculated by dividing the pol percent by the brix percent. The purity (%) is a measure of the proportion of sucrose in the total dissolved solids in the juice.

Recoverable sucrose percent (RS): It is calculated using the Winter Carp formula described by Hundito (2010) as

$$\mathrm{RS}(\%) = ((\mathrm{Pol}\% - (\mathrm{Brix}\% - \mathit{Pol}\%)) \times 0.7)) \times 0.75. \quad (1)$$

Where 0.75 represents the correction factor between theoretical yields of molasses mixed juice as established by milling test, and 0.7 designates the quantity of sucrose lost in the final processing. Sugar yield (SY): The sugar yield is calculated by multiplying the cane yield (CY) by the recoverable sucrose percent (RS).

Statistical analysis

Variance analysis

The analysis of variance for 11 agro-morphological and five biochemical traits was performed following the procedure for partially balanced lattice design using R computer program version 4.2.3 with the Agricolae and MASS packages (R Core Team 2023).

The mean square values of traits for the experimental genotypes by their countries of introduction were compared to the pooled mean squares of the experimental genotypes within countries. The pooled mean squares for genotypes within countries of introduction and the mean squares of genotypes within each country were compared to the pooled within-country error mean square values. For each country of introduction and for the entire data set, the mean, range, and percent coefficient of variation for all the traits were calculated using the method described by Pecetti et al (Pecetti et al. 1992) andPecetti and Damania (1996).

Analysis of genetic variation, heritability, and genetic advance

The phenotypic variability among the test genotypes was estimated using range, mean, standard error, phenotypic variance, genotypic variance, and coefficients of variation. These components of variance were then used to calculate phenotypic and genotypic variability, heritability in a broad sense (H^2), genetic advance in absolute units (GA), and genetic advance as a percentage of the mean (GAM).

Then, the method suggested by Burton and DeVane (1953) was used to estimate the genotypic and phenotypic variances of the traits. The genotypic variance (σ^2g) and phenotypic variance (σ^2p) were calculated using the formula:

$$\sigma^2\mathrm{g} = (\sigma^2\mathrm{t} - \sigma^2 e), \textit{and } \sigma^2\mathrm{p} = \sigma^2\mathrm{g} + \sigma^2 e, \textit{respectively}. \quad (2)$$

Where σ^2t is the mean square of the particular trait, σ^2e is the mean square of error (environmental variance) and r is the number of replications.

The phenotypic coefficient of variation (PCV), genotypic coefficient of variation (GCV), and environmental coefficient of variation (ECV) were calculated using the formula described by Singh and Chaudhary (1999) as:

$$GCV(\%) = \left(\frac{\sqrt{\sigma^2 g}}{X}\right) \times 100, \mathrm{PCV}(\%) = \left(\frac{\sqrt{\sigma^2 p}}{X}\right) \times 100 \text{ and } \mathrm{ECV}(\%) = \left(\frac{\sqrt{\sigma^2 e}}{X}\right) \times 100. \quad (3)$$

Where X is the grand mean of the trait.

Heritability in a broad sense (H^2) was calculated for each trait using the formula illustrated by Allard (Allard 1960), as

$$H^2 = \left(\sigma^2\mathrm{g}/\sigma^2\mathrm{p}\right) \times 100. \quad (4)$$

The expected genetic advance in absolute units (GA) and the genetic advance as the percent of the mean were computed following the formula described by Johnson et al. (1955). Accordingly,

$$GA = \mathrm{k} \times \sigma \times \mathrm{H2}, \text{and } \mathrm{GAM} = (\mathrm{GA}/\mathrm{X}) \times 100. \quad (5)$$

Where k is the standardized selection differential at 5% selection intensity (2.063) and σ is the phenotypic standard deviation.

Genotypic correlation, path and path index analysis

The genotypic correlation coefficient was computed using the standard procedure described by Singh and Chaudhary (1999), while genotypic path coefficient analysis was carried out following the method suggested by Lynch and Walsh (1998) using the variability package in R statistical software version 4.2.3 (R Core Team 2023). Finally, path index analysis was carried out based on the results of genotypic path coefficients using R for Windows or RindSel version 3.0 (Pacheco et al. 2016).

Results and discussion

Agromorphological and biochemical traits variability

The analysis of variance revealed highly significant ($p < 0.001$) variations in agro-morphological and biochemical traits among 196 genotypes collected from 14 different countries (Supplemental Table S3). This indicates the genotypes had significant agro-morphological and biochemical trait variations. Similar findings have been reported in other studies, where sugarcane has shown significant variability in agro-morphological and biochemical traits (Khan et al. 2004; Perera et al. 2012; Tadesse et al. 2014; Gowda et al. 2016; Tena et al. 2018; Tolera et al. 2023).

Further partitioning of the mean square values by country of origin revealed higher values within countries compared to pooled values across countries, suggesting variation between genotypes

within a nation exceeds variation among genotypes from different nations. Notably, the Barbados genotypes displayed significant variability for all examined traits. However, the level of country-specific trait variability was variable.

Greater variability for NMS was observed for the genotypes from Mexico and U.S.A.. The NI (Mexico), SL (Ethiopia, France, Mexico, and U.S.A.), IL (Ethiopia, France, and Mexico), SD (Ethiopia and France), SCW (Demerara, France, and U.S.A.), and CY (Ethiopia, France, and U.S.A.) were; however, only significantly variable for genotypes of specific nations. The variation in brix (France, India, and U.S.A.), pol (Ethiopia, India, Mexico, and U.S.A.), purity (Ethiopia, U.S.A.), RS (Ethiopia, India, and U.S.A.), and SY (Ethiopia, France, and U.S.A.), were also particular. The genotypes of sugarcane from the different nations exhibit trait-specific variability, pointing to significant sources of variation for traits that could be targeted for improvement. Esayas et al (Tena et al. 2018) found the existence of high variation in CY and SY among sugarcane genotypes from the Tigray region of Ethiopia (Tena et al. 2018).

To effectively compare the relative variability of different traits measured in different units, the coefficient of variation (CV) proves invaluable. This metric, expressed as a percentage, compares the standard deviation to the overall mean. It allows for comparisons of the same characteristic across populations with varying sizes, means, and variances. It also enables comparisons of distinct traits within different populations (Tena et al. 2018).

This study revealed large coefficients of variation (CVs) for both agro-morphological and bio-chemical traits, both across different countries and within populations from the same country. However, Cuba and Puerto Rico exhibited zero CVs, which could be attributed to the small number of genotypes from these two nations (Supplemental Table S4).

The CV for SPN45 varied from 9.23 for Mexican genotypes to 45.71 for Barbadian. For TL3MAP, the CV values ranged from 6.87 (Philippines) to 40.77 (Mexico). Similarly, the CV for NMS ranged from 1.51 (Mexico) to 32.19 (U.S.A.), while the CV for NI ranged from 3.19 (Mexico) to 27 (Philippines). Additionally, the CV for SL ranged from 5.87 (Mexico) to 21.2 (India), and for IL it varied from 1.62 (Mexico) to 23.3 (South Africa). The CV for SD ranged from 1.19 (Demerara) to 9.92 (Philippines). Similarly, CV for SCW varied from 2.21 (Thailand) to 38.68 (U.S.A.). Demerara genotypes displayed the lowest CY CV (10.94), while the U.S.A. had the highest (40.23). Furthermore, the CV for brix ranged from 1.5 (Philippines) to 11.23 (Demerara.) Pol levels varied from 0.38 (Mexico) to 10.57 (Brazil). Purity spanned from 0.74 (Thailand) to 6.42 (South Africa). The CV for RS varied from 1.38 (South Africa) to 11.60 (Brazil). Finally, SY values varied from 10.83 (Brazil) to 38.52 (U.S.A.).

Moreover, variance component analysis helps identify traits that exhibit significant heritable variation and anticipate genetic improvement through phenotypic selection. This analysis enables the selection of superior genotypes of these traits as potential parents for hybridization and industrial use.

Table 1 summarizes the pooled mean performance values, range, heritability, and genetic advance for 16 phenotypic traits of 196 test genotypes. In addition, individual genotype means for each trait are presented in Supplemental Table S5.

With a mean of 10,071 and a difference of 22,529 sprouts per hectare, SPN45 ranged from 1,839 for the genotype CP02–926 from U.S.A. to 24,368 for the genotype B549–30 from Barbados. The mean of TL3MAP was 29,671, with a range of 8,966 (H784605, U.S.A.) to 55,172 (Tafach Ageda, Ethiopian landrace), and a difference of 46,206 tillers per hectare. Similarly, the mean of TL4MAP was 24,544, ranging from 5,977 (B47419, Barbados) to 46,897 (B527–1, Barbados), a difference of 40,920 tillers per hectare.

With a mean of 31,144 and a difference of 51,007 tillers per hectare, TL5MAP ranged from 9,223 (CP02–926, U.S.A.) to 60,230 (B549–11, Barbados). The wide range unit values in the number of sprouted buds and tillers indicate greater variability among the test genotypes for these traits, suggests promising potential for developing sugarcane cultivars with superior tillering. In addition, the greater mean values for TL4MAP and TL5MAP for the sugarcane genotypes derived from the three-way hybrid genotypes of fuzz indicate the greater tillering potential of fuzz-derived genotypes

Table 1. Variability, broad sense heritability and genetic advance estimates for 16 phenotypic traits of 196 genotypes of sugarcane obtained from 14 countries.

Traits	Range	Range unit	Mean ± SE	σ^2e	σ^2g	σ^2p	ECV	GCV	PCV	H^2	GA	GAM
SPN45	1,839–24,368	22,529	10,071 ± 1.66	25.86	25.35	51.21	23.34	23.11	32.85	0.50	7.30	33.50
TL3MAP	8,966–55,172	46,206	29,671 ± 3.21	96.72	353.62	450.34	15.22	29.11	32.85	0.79	34.33	53.14
TL4MAP	5,977–46,897	40,920	24,544 ± 4.42	183.77	235.93	419.71	25.35	28.72	38.31	0.56	23.72	44.36
TL5MAP	9,223–60,230	51007	31,114 ± 5.38	277.59	244.08	521.67	24.60	23.07	33.73	0.47	22.01	32.51
NMS	9,655–50,345	40,690	27,758 ± 4.76	213.24	136.13	349.37	24.15	19.30	30.91	0.39	15.00	24.81
SL (m)	0.75–2.25	1.50	1.55 ± 0.19	0.07	0.04	0.10	16.91	12.27	20.89	0.35	0.23	14.85
NI	11.0–33.4	22.40	20.78 ± 3.15	19.85	8.84	28.69	21.44	14.31	25.78	0.31	3.40	16.36
IL (cm)	0.046–0.136	0.0897	0.08 ± 0.01	0.00	0.00	0.00	18.70	12.92	22.38	0.33	0.01	15.37
SD (cm)	2.027–3.485	1.458	2.58 ± 0.16	0.05	0.06	0.11	8.65	9.33	12.72	0.54	0.36	14.09
SCW (kg)	0.398–1.60	1.202	0.86 ± 0.16	0.05	0.02	0.07	26.96	16.45	31.58	0.27	0.15	17.65
CY (t ha^{-1})	20.97–135.31	114.34	70.56 ± 13.42	360.10	275.47	635.58	26.89	23.52	35.73	0.43	22.51	31.90
Brix (%)	16.37–23.5	7.13	20.04 ± 0.96	1.84	1.13	2.97	6.77	5.30	8.60	0.38	1.35	6.73
Pol (%)	11.63–20.87	9.24	17.19 ± 1.02	2.09	1.75	3.84	8.41	7.69	11.39	0.46	1.84	10.69
Purity (%)	68.82–94.58	25.76	85.73 ± 2.50	12.46	8.48	20.94	4.12	3.40	5.34	0.41	3.82	4.46
RS (%)	6.25–14.47	8.22	11.41±0.90	1.63	1.34	2.97	11.18	10.15	15.10	0.45	1.60	14.06
SY (t ha^{-1})	1.829–20.422	18.59	8.12±1.58	5.01	5.88	10.90	27.59	29.88	40.67	0.54	3.67	45.22

Notes: σ2g: genotypic variance; σ^2e: environmental variance; σ2p: phenotypic variance; ECV (%): environmental coefficient of variance; GCV (%): genotypic coefficient of variance; PCV (%): phenotypic coefficient of variance; H^2 (%): broad sense heritability, GA: genetic advance, GAM (%): genetic advance as percentage of the mean. SPN45: the number of sprouted buds per plot 45 days after planting; TL3MAP, TL4MAP and TL5MAP: number of tillers per plot three, four and five months after planting, respectively; NMS: the number of millable stalks per plot; SL: stalk length in meters; NI: number of internodes per stalk in centimetres; IL: internodal length in centimetres; SD: stalk diameter in centimetres; SCW: single cane weight in kilograms; CY: cane yield in tons per hectare; RS: recoverable sucrose percent; and SY: sugar yield in tons per hectare.

and highlight the potential of selection and hybridization in improving this trait. However, the mean, range and range unit values obtained in our findings differ from the previous reports of Esayas et al (Tena et al. 2018). These discrepancies likely stem from differences in the genotypes' genetic potential, the test environment and their interactions.

The number of millable stalks (NMS) ranged from 9,655 (B685–1, Barbados) to 50,345 (B658–10, Barbados), with a remarkable difference of 40,690 stalks per hectare. The mean values for stalk length (SL) varied from 0.75 (B4789–11, Barbados) to 2.25 (145-Z, Ethiopian landrace), with a difference of 1.50 and an overall average of 1.55. The mean performance values for internode length (IL) ranged from 0.046 (FG06–119, France) to 1.36 (DB414–66, Demerara), with a mean value of 0.08 and a difference of 0.0897. The number of internodes per stalk (NI) ranged from 11.0 (B3172, Barbados) to 33.40 (FG06–695, France), with a difference of 22.40 and a mean of 20.78. The wide range of variations in means performance in NMS, SL, IL, and NI across the sugarcane genotypes of the respective countries indicates substantial variation and greater potential for improvement in these traits. Previous studies (Gowda et al. 2016; Tena et al. 2018; Kumar et al. 2019) have also reported wide variations in the number of millable stalks, SL, and IL, which aligns with our findings.

With a mean of 2.58 cm and a difference of 1.48 cm, SD values varied from 2.0 (B4789, Barbados) to 3.48 (B519–1, Barbados).

Abdul et al (Neil et al. 2009) classified sugarcane genotypes with stalk diameter values ranging from 2.0–3.48 as medium thick. Stalk diameter (SD) a heritable and stable trait across environments (Khan et al. 2016). With a difference of 1.20 kg and mean value of 0.86 kg, single cane weight (SCW) values exhibited notable variability, ranging from 0.40 (FG06–725, France) to 1.60 (FG05–695, France). Similarly, cane yield (CY) varied markedly, ranging from 20.96(B564–11, Barbados) to 135.31 (B552–11, Barbados) with a mean of 70.56 and a difference of 114.34, both from three-way hybrid genotypes, highlighting the presence of substantial variability and potential of the hybrid materials to develop high cane yielding sugarcane cultivars. This aligns with previous reports by (Gowda et al. 2016; Tena et al. 2018; Kumar et al. 2019) who also documented significant variability in cane yield within sugarcane populations.

Brix percent values ranged from 16.37 (DB386–60, Demerara) to 23.50 (vmc96–89, Philippines), with an average of 20.04 and a difference of 7.13. The pol percent values ranged from 11.63 (B549–

30, Barbados) to 20.87 (vmc96–89, Philippines), with a mean of 17.19 and a difference of 9.24. With an average of 85.73% and a difference of 25.76%, purity percent ranged from 68.82 (B549–30, Barbados) to 94.58 (B154–6). Recoverable sucrose percent (RS) varied from 6.25 (B549–30, Barbados) to 14.47 (CP701321, U.S.A.), with a mean of 11.41 and a difference of 8.22. Sugar yield (SY) exhibited a mean of 8.12 (t/ha), with a notable difference of 18.59, and range of 1.83 (B572–11, Barbados) to 20.42 (B552–11, Barbados). The range of mean performance variations for these the biochemical traits indicates the presence of variation among the test genotypes for these traits. Wider range of variation in sugar yield trait was reported (Gowda et al. 2016; Tena et al. 2018; Kumar et al. 2019), which align with this result.

The current study has elucidated the existence of substantial phenotypic variability among the test genotypes, as demonstrated by their wide range of mean performance values. Notably, genotypes from three-way hybrid crosses displayed higher numbers of sprouted buds, tillers, millable stalks, stalk diameter, cane yield, purity, and sugar yield. These superior hybrids also exhibited greater variation within themselves for millable stalk number, cane yield, purity, and sugar yield, indicating further potential for selection and hybridization, highlighting the promise of the three-way hybrid genotypes for enhancing sugarcane quality and yield due to their inherent diversity and superior average performance.

Furthermore, estimation of genotypic coefficients of variation (GCV), environmental coefficients of variation (ECV), phenotypic coefficients of variation (PCV); and heritability in broad sense (H^2), genetic advance in absolute units (GA) and genetic advance as percent of the mean (GAM) is imperative to determine trait responses to selection. Hence, the variance of the evaluated phenotypic traits should be dissected into its components.

Phenotypic and genotypic coefficients of variation

The genotypic coefficient of variation (GCV) quantifies the variation attributed to genetic factors, while the phenotypic coefficient of variation (PCV) encompasses the total variation in a trait, influenced by both genetic and environmental factors. GCV serves as a valuable measure for evaluating the extent of variability among test genotypes and is classified as low (<10%), moderate (10–20%), and high (>20%) (Shivasubramanian and Menon 1973; Deshmukh et al. 2012).

This study examined a variety of sugarcane traits and observed different levels of GCV (3.40–29.88) values (Table 1). Purity, brix, pol, and SD showed low GCV (3.40–9.33), indicating limited genetic variation, while RS, SL, IL, NI, SCW, and NMS displayed moderate GCVs (10.15 to 19.30), suggesting some genetic diversity. However, TL3MAP, TL4MAP, TL5MAP, SPN45, CY and SY displayed high GCV values (23.07–29.88), signifying substantial genetic variation within the population.

The combined utilization of GCV and heritability (H^2) provides valuable insights into the heritable component of the variation (Johnson et al. 1955) and allows for predicting the potential genetic advance achievable through phenotypic selection (Burton and DeVane 1953).

Heritability and genetic advance

Heritability (H^2) estimates the proportion of heritable variation and is categorized as high (>60%), medium (30–60%), and low (0–30%) (Burton and DeVane 1953). In addition to GCV and H^2, considering the genetic advance as percent of a mean (GAM) is crucial for reliably predicting the progress attainable after one generation of selection (Wright 1921). GAM is categorized as low (0–10%), medium (10–20%), and high (>20%) (Johnson et al. 1955).

This study investigated H^2 (%) and GAM (%) of various sugarcane traits (Table 1). Heritability (H^2) values ranged from low (27%) for SCW to high (79%) for TL3MAP). However, all the remaining traits considered showed moderate H^2 (31–56%). Similarly, GAM (%) was low for purity (4.46) and brix (6.73), indicating limited potential for improvement through selection in these traits. The GAM (%) was moderate for pol (10.69), RS (14.06), SD (14.09), SL (14.85), IL

(15.37), NI (16.36) and SCW (17.65), suggests some potential for improvement in these traits. However, high GAM (%) values were observed for NMS (24.81), CY (31.90), TL5MAP (32.51), SPN45 (33.5), TL4MAP (44.36), SY (45.22) and TL3MAP (53.14). These traits exhibited the greatest potential for improvement through breeding programs due to their high heritability and genetic advance.

To obtain a comprehensive understanding of the potential for selection and improvement, it is advisable to consider GCV, H^2, and GAM together (Allard 1960). Traits that display significant genetic variation, with a substantial genetic influence, and have a high potential for improvement through selection, can be effectively enhanced by selecting individuals with superior trait performances (Johnson et al. 1955).

In line with this principle, the present study identified TL3MAP exhibited high GCV, H^2, and GAM, indicating a promising opportunity to improve this trait through selection breeding. Likewise, SPN45, TL4MAP, TL5MAP, CY and SY displayed high GCV and GAM alongside moderate H^2. This indicates the existence of substantial heritable variation with significant genetic gain for these traits among the test genotypes, presenting encouraging prospects for selection and hybridization to improve these traits. High GCV for the number of sprouted buds (Chaudhary 2001; Tolera et al. 2023), tillers, and cane yield were reported (Tena et al. 2016; Tesfaye et al. 2020), which aligns with the current study.

However, SL, NI, IL and RS showed moderate GCV, H^2 and GAM, indicating the presence of a medium level of genetic variability and genetic advance, with a significant influence of both genetic and environmental factors on the trait. This implies the possibility to achieve moderate improvement to these traits via phenotypic selection.

The number of millable stalks (NMS) had low GCV, moderate H^2 and high GAM. The limited genetic variation in this trait indicates limited possibility to improve this trait via phenotypic selection. Stalk diameter (SD) and pol had low GCV coupled with moderate H^2 and GAM; SCW had low H^2 along with moderate GCV and GAM, while brix and purity showed moderate H^2 along with low GCV and GAM. Though the moderate H^2 and GAM indicate that these traits are controlled by additive gene action, the low GCV indicates limited inherent genetic variation for these traits within the population.

The moderate GCV and GAM along with low H^2 in SCW; and low GCV and GAM coupled with moderate H^2 in brix and purity indicates that the phenotypic expression of these three traits were regulated by non-additive (dominance and epistatic) gene actions. This implies that such traits could be improved through improved management practices and heterosis breeding than selection.

Consequently, these trait: number of sprouted buds, tillers, number of internodes, internode length, stalk length, cane yield, recoverable sucrose percent, and sugar yield have substantial genetic variability, strongly influenced by genetics, and expected to respond favorably to selection, presents an excellent target for improvement. Thus, the top 5% of the sugarcane genotypes with superior performance values of these traits are presented in Supplemental Table S7. Besides using the selected sugarcane genotypes for superior sugar yield as parents for hybridization, these sugarcane genotypes: B552–11, FG04–466, V- 106, B707–1, FG05–771, FG05–696, B491–18, B658–11, B528–30 and MTP97–203 could also be tested over seasons for industrial use at Tana – Beles.

Generally, the studied genotypes had substantial phenotypic variation and hence rich genetic material for improvement. The three-way hybrid genotypes exhibited higher mean number of sprouted buds, tillers, stalk number, stalk diameter, cane yield, purity and sugar yield. Additionally, these superior hybrids also displayed even greater variation within themselves for stalk number, cane yield, purity, and sugar yield, suggesting even further potential for selection and breeding, highlighting the promise of three-way hybrid genotypes for enhancing sugarcane quality and yield due to their inherent diversity and superior average performance.

Selection based only on single trait could inadvertently affect other desirable traits as might have potential correlations with other agronomically important traits. Thus, careful assessment of potential trade-offs via association analysis, and simultaneously consideration of multi-trait selection

indices to account for their interrelationships and relative importance is imperative. Therefore, it is worthwhile to carefully identify and select the traits with high genotypic correlation coefficients with and high positive direct effect on sugar yield.

Correlation analysis

Correlation analysis is a statistical measure used to determine the direction and magnitude of association between traits and the practical viability of indirect selection, which, in some cases, may lead to more rapid progress than direct selection (Cruz et al. 2006; Ferreira et al. 2007; Barbosa et al. 2017). Correlations can be of a phenotypic, genotypic, or environmental nature. Phenotypic correlations have genetic and environmental causes, but only genetic causes are heritable and used in breeding programmes (Cruz et al. 2006; Esposito et al. 2011). Genotypic correlations among traits affecting the economic trait explain the true association as they exclude any environmental influences (Aman et al. 2020).

Results of genotypic correlation coefficient analysis revealed that except for SPN45, all the traits studied depicted highly significant and positive genotypic association with SY (Table 2). This indicates that improvement in these traits could lead to SY improvement. Sugar yield (SY) had the highest degree of association with CY (0.98**), followed by SCW (0.67**), pol and RS (0.61**), brix (0.57**), SL (0.55**), MSN and purity (0.49**), TL3MAP, TL4MAP and TL5MAP (0.46**), SD (0.41**), NI (0.26**) and IL (0.19**). The highly significant and positive association between SY and these traits indicates that improvement in these traits enhances sugar yield. In agreement with the current study result, a highly significant and positive genotypic correlation was reported between SY and the major agro-morphological traits: NMS, SCW, and CY trait (Masri 2015; Masri et al. 2022).

However, correlation analysis does not account for cause-and-effect relationships between a set of variables. To address this limitation, Wright (Wright 1921) introduced path-coefficient analysis.

Path analysis

Path analysis partitions correlation coefficients of predictor variables into their direct and indirect impacts on the dependent variable, which in this case is sugar yield. It identifies traits that have a significant positive direct effect on the economic trait, thus indicating which traits should be targeted for indirect selection to improve the overall economic trait. This process ultimately aids in identifying the most influential trait for selection, thereby enhancing the efficiency of the selection process.

It is important to note that studies of this nature are necessary, as associations between traits can vary based on factors such as population structures, test environments, and management strategies. Therefore, considering these variables is essential when interpreting the results of path analysis and determining the most effective selection strategies.

Lenka and Mishra (1973) categorized path coefficient values as follows: negligible (less than 0.1), weak (0.11–0.19), medium (0.2–0.29), strong (0.3–0.9), and very strong (≥1). Accordingly, Table 3 presents the direct and indirect effects of all the examined traits on SY, excluding NI, pol, and purity due to their severe multicollinearity issues.

The genotypic path coefficient analysis findings revealed that the direct and indirect effects of SPN45 on SY were largely negligible. This suggests that enhancing SPN45 has a minimal impact on SY and, consequently, holds little significance for SY improvement. Mebrahtom et al (2016) also reported negligible direct and indirect effects of SPN45 on SY, aligning well with the current results.

The indirect effects of the TL3MAP (0.44), TL4MAP (0.42), and TL5MAP (0.47) on SY mediated through CY were strongly positive. This implies that improving the number of tillers indirectly enhances SY by increasing CY. However, the indirect effects of TL5MAP on SY via SD were strongly negative (0.39), while their indirect effects via NMS (0.28) and SCW (0.15) were positive.

The negative effects via SD could be counterbalanced by the positive effects via NMS and SCW. The indirect influence of NMS on SY, mediated through SD, was markedly negative (0.6). However, its direct effect (0.33) and indirect effects exerted through SCW (0.37) and CY (0.49) on SY were positive.

Table 2. Genotypic correlation coefficients between eleven-agromorphological and five biochemical traits of 196 sugarcane genotypes gathered from 14 different countries.

Traits	SPN45	TL3MAP	TL4MAP	TL5MAP	MSN	NI	SL (m)	IL (cm)	SD (cm)	SCW (kg)	CY (t ha^{-1})	Brix (%)	Pol (%)	Purity (%)	RS (%)	SY (tha^{-1})
SPN45		0.45**	0.43**	0.41**	0.23**	-0.06^{NS}	−0.24**	-0.13^{NS}	-0.04^{NS}	-0.11^{NS}	0.05^{NS}	-0.06^{NS}	-0.05^{NS}	-0.01^{NS}	-0.04^{NS}	0.03^{NS}
TL3MAP			0.82**	0.84**	0.51**	0.25**	0.25**	-0.07^{NS}	−0.14*	0.14^{NS}	0.52**	0.08^{NS}	0.07^{NS}	0.07^{NS}	0.07^{NS}	0.46**
TL4MAP				0.90**	0.54**	0.27**	0.21**	-0.09^{NS}	−0.2**	-0.03^{NS}	0.52**	0.04^{NS}	0.07^{NS}	0.09^{NS}	0.07^{NS}	0.46**
TL5MAP					0.86**	0.07^{NS}	0.18*	0.05^{NS}	−0.52**	−0.28**	0.58**	-0.03^{NS}	-0.03^{NS}	-0.04^{NS}	-0.04^{NS}	0.46**
MSN						-0.09^{NS}	-0.02^{NS}	0.05^{NS}	−0.80**	−0.7 **	0.59**	-0.09^{NS}	-0.06^{NS}	-0.003^{NS}	-0.05^{NS}	0.49**
NI							0.38**	−0.63**	−0.15*	0.12^{NS}	0.26**	0.03^{NS}	0.16*	0.37**	0.23**	0.26**
SL (m)								0.47**	−0.15*	0.42**	0.68**	0.10^{NS}	0.09^{NS}	0.03^{NS}	0.09^{NS}	0.55**
IL (cm)									0.04^{NS}	0.22**	0.28**	0.05^{NS}	-0.07^{NS}	−0.30**	-0.13^{NS}	0.19**
SD (cm)										0.79**	0.07^{NS}	0.14^{NS}	0.09^{NS}	0.026^{NS}	0.08^{NS}	0.41**
SCW (kg)											0.70**	0.34**	0.29**	0.13^{NS}	0.27**	0.67**
CY(t ha^{-1})												0.22**	0.23 **	0.178*	0.23**	0.98**
Brix (%)													0.97 **	0.65**	0.93**	0.57**
Pol (%)														0.85**	0.99**	0.61**
Purity (%)															0.93**	0.49**
RS (%)																0.61**
SY (tha^{-1})																

Note: SPN45: sprouted bud numbers per hectare at 45 days after planting; TL3MAP, TL4MAP and TL5MAP: tiller numbers per hectare at three, four and five months after planting, respectively; NMS: millable stalk numbers per hectare; SL: mean length of stalk in meters; NI: internodal numbers per stalk; IL: length of internodes in centimetres; SD: stalk girth or diameter in centimetres; SCW: single stalk or cane weight in kilograms; CY: cane yield in tons per hectare; RS: recoverable sucrose percent; and SY: sugar yield in tons per hectare. Alpha = 5%. '**' = $p < 0.001$; '*' = $p < 0.01$ and 'ns'= $p > 0.05$.

Table 3. Genotypic path coefficients between sugar yield and ten-agromorphological and two biochemical traits of 196 sugarcane genotypes obtained from 14 different countries.

	Indirect effects												
Traits	SPN45	TL3MAP	TL4MAP	TL5MAP	MSN	SL (m)	IL (cm)	SD (cm)	SCW (kg)	CY (t ha^{-1})	Brix (%)	RS (%)	Direct effects
SPN45		−0.06	−0.07	0.05	0.08	−0.11	0.04	−0.02	0.06	0.04	−0.03	0.00	0.07
TL3MAP	0.03		−0.14	0.11	0.17	0.12	0.02	−0.10	−0.07	0.44	0.04	0.00	−0.14
TL4MAP	0.03	−0.11		0.12	0.17	0.10	0.03	−0.16	0.02	0.42	0.02	0.00	−0.18
TL5MAP	0.03	−0.12	−0.16		0.28	0.08	−0.02	−0.39	0.15	0.47	−0.02	0.00	0.13
MSN	0.02	−0.07	−0.09	0.11		−0.01	−0.01	−0.60	0.37	0.49	−0.05	0.00	**0.33**
SL (m)	−0.02	−0.04	−0.04	0.02	−0.01		−0.13	−0.12	−0.22	0.57	0.05	0.00	**0.47**
IL (cm)	−0.01	0.01	0.02	0.01	0.02	0.21		0.03	−0.11	0.24	0.06	0.00	−0.28
SD (cm)	0.00	0.02	0.04	−0.07	−0.26	−0.07	−0.01		−0.41	0.07	0.08	0.00	**0.75**
SCW (kg)	−0.01	−0.02	0.01	−0.04	−0.23	0.20	−0.06	0.59		0.59	0.18	0.00	−0.52
CY (t ha^{-1})	0.00	−0.07	−0.09	0.07	0.19	0.32	−0.08	0.06	−0.37		0.11	0.00	**0.83**
Brix (%)	0.00	−0.01	−0.01	0.00	−0.03	0.04	−0.03	0.11	−0.18	0.18		−0.01	**0.51**
RS (%)	0.00	−0.01	−0.01	−0.01	−0.02	0.04	0.03	0.07	−0.14	0.20	0.48		−0.01
Residual: 0.117													

Note; number of internodes per stalk, pol percent and purity percent were excluded from path coefficient analysis due to their severe multicollinearity problem.

SPN45: sprouted bud numbers per hectare at 45 days after planting; TL3MAP, TL4MAP and TL5MAP: tiller numbers per hectare at three, four and five months after planting, respectively; NMS: millable stalk numbers per hectare; SL: mean length of stalk in meters; NI: internodal numbers per stalk; IL: length of internodes in centimetres; SD: stalk girth or diameter in centimetres; SCW: single stalk or cane weight in kilograms; CY: cane yield in tons per hectare; RS: recoverable sucrose percent; and SY: sugar yield in tons per hectare.

This suggests that enhancing NMS has a substantially greater positive impact on SY than its indirect negative effect mediated through SD. Notably, a high positive direct effect of NMS on SY was reported (Masri 2015), aligning with the present findings. Despite a moderately adverse impact on SY through SCW (−0.22), SL exerted a strong positive influence directly (0.47) and indirectly through CY (0.57). While the direct effect of IL on SY was moderately negative (−0.28), it indirectly contributed positively to SY through CY (0.24) and SL (0.21).

The direct effect of SD on SY was strong positive (0.74); however, its indirect effects through the NMS (0.26) and SCW (−0.41) were negative. The direct effects of SCW on SY were strongly negative (−0.52), but its indirect effects through SD (0.59) and CY (0.59) were strongly positive. The fact that the positive impacts of SL and IL, as well as SD and SCW, on SY outweigh their negative impacts suggests that improving these characteristics is crucial for increasing SY. A strong positive indirect effect of SL on SY (Mebrahtom et al. 2016); a strong positive direct effect of SCW on SY; and a strong positive indirect effect of SD on SY through SCW (Al-Sayed et al. 2012), aligns with this finding.

Cane yield (CY) exerts a substantial positive direct effect on SY (0.83), complemented by an indirect positive effect mediated by SL (0.32). However, this positive influence is partially counterbalanced by a strong negative indirect effect through SCW (−0.37). These findings corroborate previous reports of a strong positive direct effect of CY on SY (Kumar et al. 2018; Tesfaye et al. 2020), emphasizing the crucial role of CY in enhancing SY. Additionally, both the direct effect of brix (0.51) and the indirect effect of RS mediated by brix (0.48) are strongly positive, implying that improvements in these traits contribute to increase SY. Conversely, a negligible and negative direct effect of brix on SY was reported (Al-Sayed et al. 2012; Mebrahtom et al. 2016; Masri et al. 2022). The difference could be due to the variation in the test materials, environment and their interactions.

Notably, SCW (−0.52) exhibited a significant negative direct effect on SY. This indicates that increase in stalk thickness leads to reduction in sugar yield. This study also revealed that CY exerted the most substantial positive direct effect on SY (0.83), followed by SD (0.75), brix (0.51), SL (0.47), and NMS (0.33). Besides their high direct positive effect on SY, the variability analysis of CY, SD, SL, and NMS elucidated that the phenotypic expression of these traits was regulated by additive gene actions and thus respond well to selection.

Therefore, using these traits as selection criteria, the Smith-Hazel selection index method described by Pacheco et al. (2016) was employed to point out the sugarcane genotypes with superior performance for these traits. The result of Smith – Hazel selection index for the top 5% the sugarcane genotypes evaluated is presented in Supplemental Table S7.

Accordingly, the top 5% s sugarcane genotypes selected for multi-trait improvement were B552–11, FG04–466, B707–1, FG05 771, B491–18, DB386/60, B658–11, B528–30, CP70/321 and B517–40. Among these, B552–11, FG04–466, B707–1, FG05–771, B491–18, B658–11, and B528–30, were previously been selected for their high sugar yield based on variance component analysis and were chosen once more for their greater multi-trait performances. Therefore, besides their suitability as parents for hybridization, these sugarcane genotypes could be evaluated over seasons for industrial use at the Tana-Beles.

Conclusions and future perspectives

This study revealed that the GCV, PCV, H2, and GAM values ranged from 3.40 to 29.88, 5.34 to 32.85, 27 to 79, and 4.46 to 53.14, respectively. Notably, the number of sprouted buds, tillers, internodes, internode length, cane yield, recoverable sucrose, and sugar yield exhibited moderate to high values across all four variance components. This indicates significant heritable variation with substantial genetic gains, implying promising opportunities for trait improvement. However, focusing solely on a single trait during selection can inadvertently affect other valuable correlated traits. Therefore, it is beneficial to identify traits that exhibit a high genotypic correlation with and a strong direct positive effect on sugar yield. This approach enhances selection efficiency and facilitates the development of improved sugarcane varieties with increased genetic gains across multiple traits. Sugar yield had highly significant positive correlation with the number of tillers, millable stalks, internodes, stalk and internode length, stalk diameter, single cane weight, cane yield, brix, pol, purity, and recoverable sucrose. Of these, the number of millable stalks, stalk length, stalk diameter, cane yield, and brix exhibited strong positive direct effects on sugar yield. Consequently, the top 5% genotypes with higher sugar yield, including B552–11, FG04–466, V-106, B707–1, FG05–771, FG05–696, B491–18, B658–11, B528–30, and MTP97–203, could be tested for commercial use and as potential parents for sugar yield improvement. Notably, 70% of these genotypes (B552–11, FG04–466, B707–1, FG05–771, B491–18, B658–11, and B528–30) were previously selected for their high sugar yield based on variance component analysis and have been chosen once again for their superior multi-trait performances. Hence, these genotypes can serve as potential parents for multi-trait improvement. In conclusion, sugarcane breeding programs could focus on traits exhibiting heritable genetic variation with substantial genetic gains, significant positive correlations, and strong direct positive effects on sugar yield. Selecting promising genotypes based on these traits will lead to the creation of superior sugarcane varieties with greater sugar yield and other desirable traits.

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Disclosure statement

No potential conflict of interest was reported by the author(s).

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Data availability statement

Data related to this study can be found from the corresponding author on releasable request.

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