

GENETIC TOOLS AND PROXY PLANT CHARACTERISTICS TO EXPEDITE GRAIN YIELD IMPROVEMENT IN SORGHUM HYBRIDS FROM DIVERSE MALE STERILITY CYTOPLASM'S

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ABSTRACT

Correlation, path analytics, and genetic variability were investigated in this work, for yield and yield component traits in 280 sorghum F1 hybrids during *Rabi* 2021 and *Summer* 2022 seasons. Considerable amount of genetic variation was observed for all the traits studied, confirming the scope for further selection for superior and desirable hybrids. The broad sense heritability was high for all traits evaluated, and the correlation between genotypic coefficient of variation (GCV) and phenotypic coefficient of variation (PCV) was almost perfect ($r=0.99$, $p<0.001$) and their means comparable (sample estimates mean difference = 1.3), implying the low level of the environmental effect, and a high level additive genetic factors effects on the measured traits. There was a high positive correlation between days to 50 % flowering (DFF) and days to maturity (MAT), MAT and number of leaves per plant (NLP), plant height (PH) and hundred seed weight (HSW), panicle width (PW) and panicle weight per hectare (PWT), PWT and yield (YLD). The correlation coefficients between YLD and the rest of the traits evaluated were low except for PL, PW, and PWT that showed medium, medium, and high positive correlation, respectively. PL, PW, and PWT should therefore be considered in the indirect selection process to identify superior sorghum genotypes with higher grain yield potential. Since the three traits were favorably correlated with grain yield, selection can simultaneously improve all traits by tandem selection, or indirect selection and index selection. The direct and indirect effects of PWT as revealed by path analytics were instrumental to the observed correlation between YLD and PL, PW and PWT. PWT was therefore the sole trait able to determine YLD along with the major component traits in this work. These findings are expected to expedite and enhance genetic gains in sorghum breeding.

KEYWORDS: Grain sorghum hybrids, genetic variability, path analyses, additive gene action, grain yield proxy traits

Sorghum [*Sorghum bicolor* (L.) Moench] also known as the “King of Millets” is a multifunctional crop that is cultivated for food, feed, fuel, and fodder; it is a staple crop for hundreds of millions of semi-arid people in Asia and Africa (Mwamahonje *et al.* 2021). Sorghum is a C4 plant with increased photosynthetic and resource use efficiency (RUE), and a strong abiotic and biotic stress tolerance. Its capacity to survive in dry and hot environments, coupled with genetic variability in photoperiod response, explains its extensive and sustainable cultivation under rainfed conditions of India and other world's drylands, and across the earth's latitudes (Habyarimana *et al.*, 2021). Sorghum is resurging under higher latitudes for feed, biofuel, the manufacture of specialty health-promoting foods rich in antioxidants, and for use as a substitute for climate change susceptible crops (e.g., maize), traditional grains diet, and for meeting gluten-free needs

(Habyarimana *et al.*, 2019). Cytogenetically, sorghum is a diploid crop species with $2n = 2x = 20$, where $2n$, n , $2x$, and 20 , respectively, the somatic chromosome number, the gametic chromosome number, two complete sets ($2x$) of chromosomes, and the total chromosome number of a sorghum cell. Sorghum's small genome (730 Mb) makes it an excellent test bed for the functional genomics studies of C4 grasses and other crop species (Habyarimana *et al.*, 2020). The *S. bicolor* genome sequence was first released in 2009 (Paterson *et al.*, 2009) and the current version is 3.1.1 released in 2018 reports more than 34,000 annotated genes several of which can be harnessed in genetic introgressions to improve yields and quality plant characteristics (McCormick *et al.*, 2018). Sorghum is the fifth-most significant cereal crop in the world, with Africa and India accounting for the largest share (> 70%) of the world's sorghum area; the top producing nations

are the United States, India, Mexico, Nigeria, Sudan, and Ethiopia (source: <https://www.fao.org/faostat/en/#data/QCL>). During the period between 1960 and 2020, sorghum productivity in India increased by more than 175% wherever hybrids were grown, highlighting the importance of heterosis for grain yield in this crop. In sorghum, the superiority of the F₁, or hybrid vigour, depends on the environment and the genotypes used (Mindaye, *et al.*, 2016). Sorghum hybrids have been grown by farmers in developed countries since the late 1950s driven by the discovery of the cytoplasmic male sterility system, allowing cost-effective hybrid production, and are increasingly being adopted in the developing world (Mindaye *et al.*, 2016,). For instance, the technology for sorghum hybrid cultivar development is well advanced in Asia, while in Africa open-pollinated varieties are the prevalent products.

The level of genetic variability in a population is crucial to the success of plant breeding efforts, including the development of sorghum hybrid cultivars. The list of key genetic parameters that are used to measure genetic variability includes the coefficient of variation (CV), broad-sense heritability (H), correlation coefficient, and path analytics, which are some of the key tools breeders use for successful crop improvement (Tiwari *et al.*, 2019, Immanuel *et al.*, 2011, and Xu *et al.*, 2017). The correlation coefficients inform the breeder about the magnitude and direction of the relationships that existed between traits; a favorably correlated trait can be used as a surrogate for a corresponding complex trait if it is relatively cheap, has high heritability, and it is easily phenotyped, so it can expedite breeding and enhance genetic gain. The path analytic method extends the correlation analysis as it dissects and better explains the correlation coefficients (Khandelwal *et al.*, 2015; Khadakbhavi *et al.*, 2017). Path analysis is used by the breeding community as a decision-support tool to quantify the direct and indirect contributions of proxy traits to the targeted effect or outcome variable and to determine the path model that best fits the pattern of correlations found in the datasets.

The above breeding tools were extensively studied in sorghum (for a review refer to the following references-Habyarimana *et al.*, 2018, Momo *et al.*, 2023, and Patil *et al.*, 2023). For instance, some researchers have used these methods to identify the essential characteristics for increasing yield, such as

days to 50% flowering, panicle width, panicle weight, leaf number, and hundred seed weight, as the main determinants of yield (Verma *et al.*, 2019, Momo *et al.*, 2023, and Patil *et al.*, 2023), thereby allowing for direct selection of these traits. Most of the available scientific literature concentrated on OPVs and hybrids derived mainly from the *Milo* cytoplasm *i.e.*, A₁ (Reddy *et al.*, 2010, Praveen *et al.*, 2015 and Prasad *et al.*, 2017). The present work was therefore undertaken to close this gap by deriving the breeding parameters and tools from a diverse pool of sorghum F₁ hybrids produced from crosses involving A₁, A₂, A₃, and A₄ cytoplasm (for a review refer to the following references -Stephens and Holland 1954, Quinby 1970, Reddy *et al.*, 2008 and Jebil *et al.*, 2021). The importance of cytoplasmic and nuclear genetic diversity of male-sterile (A) and restorer (R) lines in sorghum cannot be overemphasized. Particularly, the diversity in A cytoplasm can avoid the disease outbreak that happened in the 1970s for southern corn leaf blight of corn hybrids possessing a uniform Texas (T) cytoplasm (Tatum, 1971).

In view of the aforementioned, this study was conducted to identify the genetic variability and heritability, as well as the characteristics associated with yield enhancements in complex pool sorghum hybrids derived from diverse seed parent cytoplasm and restorer backgrounds.

MATERIAL AND METHODS

We carried out this investigation using 280 genotypes, of which 241 were F₁ hybrids, 35 parental lines and 4 standard checks, under 4 environments (2 seasons × 2 irrigation regimes) *i.e.*, during post rainy 2021 and summer 2022 under irrigation and post flowering drought stress. Seed parents included A₁, A₂, A₃, and A₄ cytoplasm. The experimental design was alpha lattice design with 2 replications. The elementary plot consisted of two rows 2 m long with spacing of 60 cm and 15 cm between and within rows, respectively. All the recommended agronomic practices were followed to raise a good crop. For each genotype, plant height (PH), number of leaves per plant (NLP), panicle length (PL), and panicle width (PW), were determined on randomly selected five healthy plants. On a full plot basis, days to 50% flowering (DFF), days to maturity (MAT), hundred seed weight (HSW), panicle weight per hectare (PWt), and yield per hectare (YLD) were

recorded. Mean data of each character was subjected to analysis. Burton (1952) and Shafique, *et al.*, 2016 approach was used to quantify the genotypic (GCV) and phenotypic (PCV) coefficients of variation. The genetic advance (GA) was determined using Johnson *et al.*, (1955) method, while broad sense heritability (H) was estimated as suggested by Lush (1940). Correlation between different traits was assessed by the Pearson correlation coefficient Wright (1921) and path analysis as described by Wright (1934). The R software was used for statistical analyses.

RESULTS AND DISCUSSION

Genetic variation among test plant materials is the precondition for efficient breeding and selecting desirable superior candidates. On the other hand, assessing the correlation and the path analytic models between the proxy traits and the outcome dependent variable e.g., the economic trait such as grain yield (Shedge *et al.*, 2019), is critical for the successful deployment of the best selection criteria. Since grain yield is a polygenic and complex trait that is influenced by a huge range of other factors, direct selection based solely on an association pattern between two variables may occasionally mislead the breeder; therefore, direct and indirect effects should be differentiated for effective selection (Awol and Alise fikre,

2018), and it is here that path analytics comes in (Swetha *et al.*, 2019). In addition to evaluating the potential for the simultaneous enhancement of two or more traits, path analytics will help in understanding the desirable and unwanted interaction of plant characteristics (Shanmugam and Kalaimagal, 2019). The heritability of the plant characteristics helps gauge the relative importance of the genetic factors relative to the noise from the environment in order to avoid disturbing breeding surprises when a bred-for trait gets lost at the farmer's level.

Analysis of variance for experimental designs

The analysis of variance for the nine quantitative traits using the four environments and entire data set revealed highly significant differences between genotypes for all the traits studied. A significant genotype $\times$ environment interaction was also observed. It can be inferred therefore that genetic variability among the genotypes studied was supported by statistical inference and the performance of the genotypes varied with varying environmental conditions (Table 1). Under such circumstances, techniques such as biplot models e.g., AMMI biplot = the additive main effects and multiplicative interaction and GGE biplot = genotype+ genotype $\times$ environment analyses will be useful to determine the environmental and the genotypic behaviors allowing targeted breeding recommendations.

Table 1. ANOVA for yield and its attributing parameters in sorghum

S.No.	Characters	Mean sum of squares					
		Replications	Genotypes	Environment	Genotype: Env	Rep:Block	Residuals
		(D.f. = 1)	(D.f. =279)	(D.f. =3)	D.f=837	D.f=68	D.f=1051
1	DFF	26.29	88.08***	29330.65***	24.28***	5.14	3.99
2	MAT	174.15	107.72***	35159.6***	28.39***	6.57	4.86
3	NLP	7.46	5.31***	2355.04***	1.86***	2.05	0.89
4	PH (cm)	277.68	9237.27***	542736.05***	557.7***	235.5	148.03
5	PL (cm)	0.062	34.48***	1178.35***	3.61***	1.37	1.77
6	PW (cm)	4.92	1.03***	90.62***	0.25***	0.24	0.19
7	HSW (g)	1.51	0.76***	84.65***	0.12***	0.07	0.06
8	PWt (kg/ha)	0.02	3.31***	52.6***	0.97***	0.42	0.38
9	YLD (kg/ha)	0.002	2.11***	52.13***	0.76***	0.2	0.25

*** Significant at 0.001 per cent level,

DFF: Days to 50% flowering, MAT: Days to maturity, PH: Plant Height, NLP: Number of leaves per plant, PL: Panicle length, PW: Panicle width, PWt: Panicle weight per hectare, HSW: 100 seed weight, YLD: Yield per hectare.

Genetic parameters: variability, heritability, and genetic advance

The estimates of genetic parameters which include heritability in broad sense, phenotypic (PCV) and genotypic (GCV) coefficients of variation, and genetic advance are presented in Table 2. The PCV was statistically higher than GCV for all the characters studied with $t = 3.2879$, $p < 0.05$, 95 percent confidence interval = 0.3915608 – 2.2306614, indicating the existence environmental effects on the observed phenotypic data. However, the correlation between GCV and PCV was almost perfect ($r = 0.99$, $p < 0.001$), and their means comparable (sample estimates mean difference = 1.3) implying the low level of the environmental noise, and a high level of genetic factors effects on the measured traits. This was also confirmed by the high values of the broad sense heritability. The latter ranged from 66% to 94% for grain yield and plant height, respectively. The PCV and GCV ranged from 3.6% (NLP) to 20.9% (YLD) and from 2.9 (NLP, MAT)

(2013), Karpe *et al.*, (2023), Dev *et al.*, (2019), and Toor (2020). For PW and PL, PCV and GCV were low, while GA was moderate (10-20%) and heritability high, which is in agreement with Arunkumar *et al.*, (2022) and Vinodhini *et al.*, (2022). For PH, PWt, HSW and YLD, PCV and GCV were low, while heritability and GA values were high as reported by Hamidou *et al.*, (2018), Nikiema (2023), Gebregergs and Mekbib (2020) and Kalpande *et al.*, (2019). From the high broad sense heritability and the comparable GCV and PCV it can be inferred the existence of low level of the environmental noise, and a high level additive genetic factors effects on the measured traits.

Correlation analysis

The magnitude and direction of the correlation between plant characteristics was interpreted according to Gomez and Gomez (1984) as follows: 0–0.1, 0.1–0.5, 0.5–0.8, and 0.8–1, 1, interpreted as, zero, low, medium, high, and perfect, respectively. There was a high or perfect positive correlation between DFF and

Table 2. Heritability, coefficient of variation and genetic advance for yield and its component traits in sorghum hybrids.

S.No.	Trait	PCV (%)	GCV (%)	Heritability in broad sense (H) (%)	Genetic Advance as % mean
1	DFF	4.2	3.6	73.0	6.4
2	MAT	3.8	2.9	74.0	5.1
3	NLP	16.5	16.0	94.1	31.9
4	PH (cm)	3.6	2.9	68.7	5.1
5	PL (cm)	9.1	8.6	89.6	16.9
6	PW (cm)	7.9	6.9	76.8	12.4
7	HSW (g)	17.3	14.7	72.0	25.7
8	PWt (kg/ha)	12.1	11.1	83.6	20.9
9	YLD (kg/ha)	20.9	16.9	65.8	28.4

DFF: Days to 50% flowering, MAT: Days to maturity, PH: Plant Height, NLP: Number of leaves per plant, PL: Panicle length, PW: Panicle width, PWt: Panicle weight per hectare, HSW: 100 seed weight, YLD: Yield per hectare.

to 16.9% (YLD), respectively. Genetic advance was low (0-10%) for DFF, MAT and NLP, moderate (10-20%) for PL and PW, and high ($>20\%$) for PH, HSW, PWt and YLD (kg ha^{-1}). The results obtained in this study are in agreement with previous research works. Low GCV, PCV and GA, and high heritability were reported for the DFF, MAT and NLP by Arunkumar *et al.*, (2013), Khandelwal *et al.*, (2015), Nirosh *et al.*,

MAT, MAT and NLP, PH and HSW, PW and PWt, and PWt and YLD (Figure 1). Medium positive values of Pearson correlation were observed between DFF and NLP, PH and PW, PL and YLD, PW and HSW, PW and YLD, PWt and HSW. The correlation between PH and NLP, PH and PWt, PH and YLD, NLP and PW, NLP and PWt, NLP and HSW, NLP and YLD, and PL and PW, and YLD and HSW was low and

positive, while low and negative correlation was observed between DFF and PWt, DFF and HSW, DFF and YLD, MAT and PWt, MAT and HSW, and MAT and YLD. Similar findings were presented by Khandelwal *et al.*, (2015), Vinodhini *et al.*, (2022), Arunkumar *et al.*, (2020), and Khadakabhavi *et al.*, (2017).

Path coefficient analysis

Identification of breeding parameters and tools to maximize grain yield in sorghum hybrids was the major objective in this work. As in other crops, the efficiency of sorghum breeding program depends on the direction and the magnitude of the correlation among the economic (grain yield) outcome and the different component traits and the breeder's ability to account for the relative direct and indirect importance of each component trait. In this work, the correlation coefficients between grain yield and the rest of the traits evaluated were low except for PL, PW, and PWt that showed medium, medium, and high positive correlation with grain yield, respectively (Figure 1). The latter three plant characteristics should therefore be considered in the selection process to isolate superior sorghum genotypes with higher grain yield potential. Plant breeders routinely select on multiple traits, but progress can be complicated by genetic correlations. As per our findings, since the three traits were favorably correlated with grain yield, selection can simultaneously improve all traits by tandem selection, or indirect selection and index selection. The importance of panicle length on grain yield was also reported by Senbetay *et al.* (2020), whereas the importance of panicle length and panicle weight was reported by Khandelwal *et al.* (2015). The direct and indirect effects of PWt were instrumental to the observed correlation between grain yield and PL, PW and PWt. Panicle weight was therefore the sole trait able to determine the grain yield along with the major component traits in this work. This finding is particularly important in situations of shuttle breeding, or when two planting seasons are closely in tandem (e.g., *kharif* vs. *rabi* season in Asia) and there is not enough time and resources to thresh entire plots and/or weigh grains from vast breeding pipelines. Here, panicles can be harvested from entire plots, weighed for selection purposes, but only part of them threshed to get seeds to plant selected lines in the following season. Threshing the remnant panicles and/or

weighing the seed can be postponed to a more convenient time or forgone altogether to save resources, depending upon the breeder's instructions.

The direct effects are described as partial regression coefficients, which quantify the influence of one variable on another while accounting for influencing variables. For instance, a change in one standard deviation of PWt in Table 3 showed nearly as much as tenfold the impact on grain yield than a one standard deviation change in the PH. On the other hand, in a path model, the magnitude of indirect effects is determined by the product of the path coefficients along the pathway between the two causally-related variables (Habyarimana *et al.*, 2018 and Khadakabhavi *et al.*, 2017).

We observed discrepancies in the direction and/or the magnitude between the direct effects of DFF and MAT, and the correlation between these traits and grain yield. The discrepancy in terms of magnitude between the DFF direct effect and the correlation with grain yield was mainly dependent on the increased MAT indirect effect, while the discrepancy in terms of both magnitude and direction of the MAT direct effect vs. correlation with grain yield was dependent on DFF to a great extent, and on NLP and PWt to a lesser extent. The discrepancy between the HSW direct effect and the correlation with grain yield was mainly influenced by the indirect effect exerted by DFF, MAT and PWt.

CONCLUSION

Grain yield is a complex quantitative trait governed by several genetic factors mostly with minor effects, and showing important interaction with the environment. In several crops, proxy traits were identified for indirect selection for grain yield. In this work, the correlation coefficients between grain yield and the rest of the traits evaluated were low except for PL, PW, and PWt that showed medium, medium, and high positive correlation with grain yield, respectively; these traits should therefore be considered in the selection process to isolate superior sorghum genotypes with higher grain yield potential. Since the three traits were favorably correlated with grain yield, selection can simultaneously improve all traits by tandem selection, or indirect selection and index selection. On the other hand, we were able to identify panicle weight as the

Table 3. Phenotypic (P) path coefficients of yield and its component traits in sorghum

S. No.	Trait	DFF	MAT	PH	NLP	PL	PW	PWt	HSW	YLD
1	^a DFF	-3.65	<u>3.35</u>	0.005	<u>0.30</u>	-0.001	0.0	<u>-0.14</u>	0.02	-0.11
2	MAT	<u>-3.65</u>	3.35	0.010	<u>0.30</u>	-0.003	-0.01	<u>-0.13</u>	0.02	-0.11
3	NLP	<u>-0.18</u>	<u>0.30</u>	0.11	<u>0.16</u>	0.003	<u>-0.34</u>	<u>0.54</u>	<u>-0.18</u>	0.41**
4	PH (cm)	<u>-2.88</u>	<u>2.68</u>	0.04	0.38	0.009	<u>-0.23</u>	<u>0.36</u>	-0.06	0.3**
5	PL (cm)	0.03	-0.06	0.002	0.02	0.16	-0.20	<u>0.60</u>	-0.01	0.54**
6	PW (cm)	0	0.06	0.07	<u>0.17</u>	0.06	-0.51	<u>1.0</u>	<u>-0.13</u>	0.75**
7	HSW (g)	<u>0.43</u>	<u>-0.36</u>	0.05	<u>0.11</u>	0.08	<u>-0.44</u>	1.20	<u>-0.11</u>	0.97**
8	PWt (kg/ha)	<u>0.51</u>	<u>-0.33</u>	0.09	<u>0.11</u>	0.008	<u>-0.33</u>	<u>0.62</u>	-0.21	0.48**

^aThe pathways are read horizontally, with each row representing a distinct path from one characteristic (exogenous variable) in the first column to the resulting plot yield (PY) via intermediate variables. Direct and indirect effects are represented by diagonal and off-diagonal values in a row respectively. To make the table easier to read, we highlighted the indirect effects (Gomez and Gomez, 1976) that were larger than or equal to 0.10. The right-most column represents the Pearson's correlation coefficient between respective exogenous variable and the outcome variable, and each coefficient was decomposed into the corresponding direct and indirect effects (Habyarimana et al., 2018). Traits in the first column from top to bottom: DFF: Days to 50% flowering, MAT: Days to maturity, PH: Plant Height, NLP: Number of leaves per plant, PL: Panicle length, PW: Panicle width, PWt: Panicle weight per hectare, HSW: 100 seed weight, YLD: Yield per hectare. Phenotypic Residual effect = 0.040, * Significant at the 5 per cent and **1 percent probability levels, respectively.

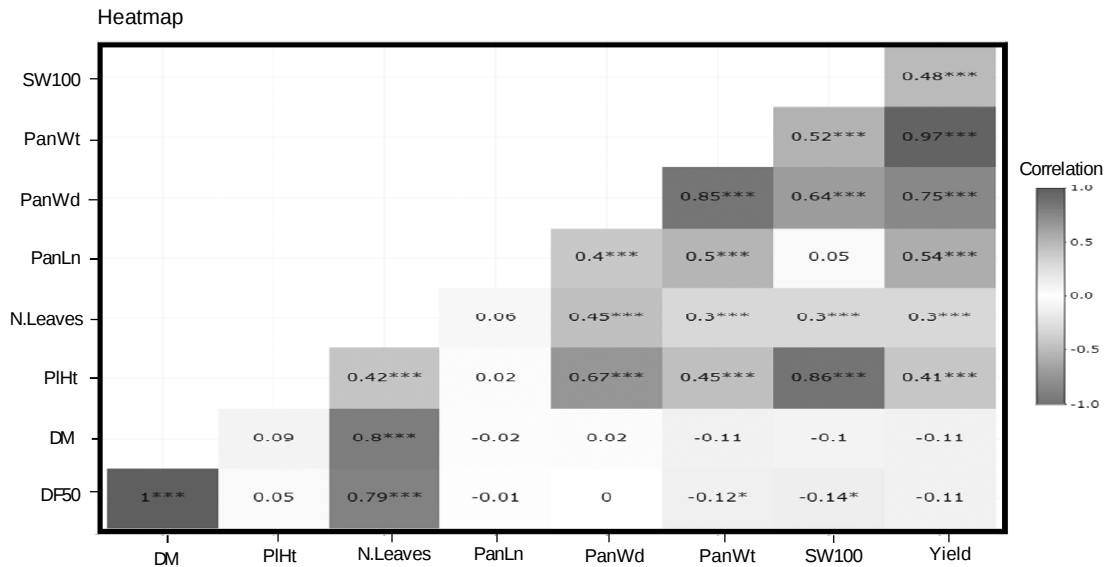


Fig.1: Heatmap visualizing the correlation of yield and its attributing traits in sorghum

The pathways are read horizontally, with each row representing a traits association with corresponding trait falling in that particular column. Traits in the Y-axis from bottom to top: DFF: Days to 50% flowering, MAT: Days to maturity, PH: Plant Height, NLP: Number of leaves per plant, PL: Panicle length, PW: Panicle width, PWt: Panicle weight per hectare, HSW: 100 seed weight, YLD: Yield per hectare.

sole trait to predict the grain yield along with the major component traits with high to very high accuracy, and can therefore be used as a standalone plant characteristic proxy for grain yield in sorghum.

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