

INDUCED GENETIC VARIABILITY, HERITABILITY AND TRAIT ASSOCIATIONS IN YELLOW-PERICARP SORGHUM [SORGHUM BICOLOR (L.) MOENCH] MUTANTS

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ABSTRACT

Yellow-pericarp sorghum possesses nutritional and industrial value owing to its carotenoid content, low condensed-tannin concentration and high starch recovery. However, such landraces in peninsular India remain largely unimproved with limited genetic diversity available for conventional breeding. The present study explored genetic variability and trait associations in 60 M4 derived mutant lines from the yellow-pericarp sorghum landrace “Udgir Piwali” through gamma irradiation (100–500 Gy), ethyl methanesulphonate (EMS; 0.1–0.3%) and their combined treatments. Sixty-four entries, including three released checks and the parental control were evaluated for 19 morphological, yield and physiological traits in a randomized block design with two replications during post rainy season of 2024–25 at Parbhani, Maharashtra, India. Analysis of variance revealed significant differences among entries for all traits, with the greatest variation observed for fodder yield and panicle-related traits. Phenotypic coefficients of variation exceeded genotypic coefficients for all traits. Panicle weight and fodder yield showed high heritability (80 and 88%, respectively) coupled with high genetic advance as per cent of mean (37.72 and 37.27%), indicating substantial scope for selection. Grain yield per plant exhibited moderate heritability (55%) and genetic advance (15.59%). Genotypic correlation analysis showed strong positive associations of grain yield with panicle length ($r_g = 0.910$), panicle weight (0.855), panicle width (0.687) and stem diameter (0.592). Path analysis identified positive direct effects of internodal length, panicle length and days to maturity, whereas flag leaf area and plant height exhibited negative direct effects. The study identified 400Gy-2, 400Gy-4, 500Gy-3, 300Gy-5 and 0.2% EMS-4 as promising mutant lines for further evaluation. These lines may serve as useful genetic resources for improving productivity in yellow-pericarp sorghum.

KEYWORDS: Sorghum bicolor; yellow pericarp; induced mutagenesis; heritability; path coefficient analysis

INTRODUCTION

Sorghum [*Sorghum bicolor* (L.) Moench] is the fifth most important cereal of the world and the principal dry land staple of the semi-arid tropics of Asia and Africa. It is cultivated on approximately 40.50 million hectares globally, with a production of 62.47 million tones and an average productivity of 1542 kg ha⁻¹, while India accounts for 4.15 million hectares and 4.40 million tones at a productivity of 1060 kg ha⁻¹ [1]. Within India, Maharashtra and Karnataka together contribute nearly 59 per cent of national production, followed by Madhya Pradesh (11.5 per cent), Tamil Nadu (9 per cent), Rajasthan (6.5 per cent) and Andhra Pradesh (6 per cent) [2]. The crop owes its resilience to C4 photosynthetic efficiency, a deep and fibrous root system, effective osmotic adjustment and the capacity to enter quiescence under moisture deficit, all of which allow it to produce grain and fodder on residual soil moisture where other cereals fail. Sorghum grain supplies about 11.6 per cent protein, 72.6 per cent starch, 1.6 per cent minerals and 1.6 per cent crude fiber, and its Stover provides more than 50 per cent total digestible nutrients with about 8 per cent protein, so that the same crop simultaneously underpins food, feed and fodder economies in the rabi tracts of peninsular India.

Pericarp color within the species is far more than a descriptive character. Yellow-pericarp genotypes accumulate carotenoids and xanthophylls in the pericarp and mesocarp, contain lower concentrations of condensed tannins than brown-pericarp types, and yield a substantially higher proportion of extractable starch, of the order of 80.5

per cent compared with 68–75 per cent in white and dark grain [3]. These attributes have direct commercial consequences: yellow-grain sorghum can replace up to three-quarters of the maize component in broiler rations without depressing bird performance, and the reduced tannin content improves protein digestibility for human food uses. Despite this potential, yellow-pericarp sorghum in peninsular India persists mainly as farmer-maintained rabi landraces such as Udgir Piwali of the Marathwada region. Such landraces are tall, late and photoperiod-sensitive, with a low harvest index and grain yields of only 18–20 q ha⁻¹, and they have never been subjected to systematic recombination breeding because the yellow-pericarp gene pool is too narrow to sustain a conventional hybridization program.

Induced mutagenesis offers a direct route past this constraint. Because mutational events do not depend on pre-existing allelic diversity, they can create novel variation inside an otherwise closed genetic background while retaining the adaptive and quality attributes of the parental landrace [4]. Gamma irradiation and alkylating agents such as EMS have been used successfully in sorghum to reduce plant height, advance flowering, increase seed size and modify drought-related physiological traits [5] [6] [7]. The mere appearance of variants, however, does not by itself constitute breeding progress. Two questions must be answered before a mutagenized population can be used efficiently. The first concerns the heritable fraction of the induced variation, which requires partitioning of phenotypic variance into genotypic and environmental components and estimation of heritability and expected genetic advance, since only that portion of the observed variability which is transmitted to the next generation can be captured by selection [8] [9] [10]. The second concerns the interrelationships among traits, because breeders necessarily select on components rather than on yield alone, and indirect selection is efficient only when correlations have been resolved into direct and indirect causal contributions by path coefficient analysis [11] [12]. Although both classes of parameter have been estimated repeatedly in sorghum, the published work is dominated by conventional germplasm, hybrid parents and forage types, and studies conducted on mutagenized populations of colored-pericarp landraces remain scarce. Yellow-pericarp material in particular has been almost entirely neglected, so that breeders working on this nutritionally valuable group have no quantitative guidance on which traits will respond to selection or on how grain yield is causally assembled in a mutant background. The present investigation was therefore undertaken with two specific objectives: (i) to study the extent of genetic variability, heritability and expected genetic advance for nineteen quantitative traits in the M4 generation of yellow-pericarp sorghum mutants derived from the landrace Udgir Piwali; and (ii) to study character association and path analysis among grain yield and its attributing traits in the same generation, so as to define an efficient selection strategy for this material.

2. MATERIALS AND METHODS

2.1 Plant material and mutagenic treatments

The experimental material originated from the yellow-pericarp rabi sorghum landrace Udgir Piwali, collected from Udgir tahsil of Latur district, Maharashtra, India. The landrace is tall (mean plant height 227 cm), flowers in 72 days, matures in 118 days, records a 100-seed weight of 2.62 g and yields 18–20 q ha⁻¹ of grain together with 96–98 q ha⁻¹ of fodder. Genetically uniform seed of the landrace was treated at the Nuclear Agriculture and Biotechnology Division, Bhabha Atomic Research Centre, Mumbai, with five doses of gamma radiation (100, 200, 300, 400 and 500 Gy), three concentrations of ethyl methanesulphonate (0.1, 0.2 and 0.3 per cent) and four combination treatments (100 Gy + 0.1 per cent EMS, 100 Gy + 0.2 per cent EMS, 200 Gy + 0.1 per cent EMS and 200 Gy + 0.2 per cent EMS). Untreated seed of the same landrace was maintained throughout as a control. The mutagenised populations were advanced by single-plant progeny selection through the M1, M2 and M3 generations, and phenotypically distinct, agronomically desirable and cytologically stable progenies were carried forward to constitute the M4 material evaluated here.

2.2 Experimental site, design and management

Sixty selected M4 mutant lines were evaluated together with three released checks (CSV-29R, Parbhani Moti and Parbhani Super Moti) and the control of Udgir Piwali, giving a total of 64 entries. The trial was conducted in a randomized block design with two replications during rabi 2024–25 at research farm of department of Genetics & Plant Breeding, Vasantrao Naik Marathwada Krishi Vidyapeeth, Parbhani (19°16' N latitude, 76°47' E longitude, 409 m above mean sea level). The site is characterized by shallow to medium black calcareous soil and a mean annual rainfall of 865.3 mm, of which the greater part is received during the south-west monsoon, so that the rabi crop is grown largely on stored soil moisture. Each entry was sown in a plot of 0.9 m × 4.0 m at a spacing of 45 cm between rows and 15 cm between plants within a row. A fertilizer dose of 80:40:40 kg N:P₂O₅:K₂O ha⁻¹ was applied, and all other agronomic operations and plant-protection measures followed the recommended package of practices for rabi sorghum in the region.

2.3 Observations recorded

Observations were recorded on five randomly selected competitive plants per entry in each replication for nineteen traits, namely days to 50 per cent flowering, plant height (cm), inter nodal length (cm), stem diameter (cm), days to maturity, number of primaries per panicle, number of grains per primary, panicle length (cm), panicle width (cm), panicle weight (g), 100-seed weight (g), fodder yield per plant (g), grain yield per plant (g), relative water content (per cent), SPAD chlorophyll content, number of leaves per plant, leaf length (cm), leaf breadth (cm) and flag leaf area (cm²). Flag leaf area was computed as length × breadth × 0.75 following the linear-measurement method of Kemp [13]. Relative water content was determined gravimetrically from the fresh, fully turgid and

oven-dry weights of leaf discs sampled at flowering, and chlorophyll content was recorded non-destructively on the flag leaf using a SPAD-502 chlorophyll meter.

2.4 Statistical analysis

Data were subjected to analysis of variance for a randomized block design following Panse and Sukhatme [14], and the significance of genotypic differences was tested against the error mean square. Genotypic variance was estimated as $\sigma^2_g = (MS_g - MSe)/r$ and phenotypic variance as $\sigma^2_p = \sigma^2_g + MSe$, where MS_g and MSe are the genotypic and error mean squares and r is the number of replications. Genotypic and phenotypic coefficients of variation were calculated after Burton and DeVane [8] and classified as low (below 10 per cent), moderate (10–20 per cent) and high (above 20 per cent) following Sivasubramanian and Madhavamenon [15]. Broad-sense heritability was estimated as the ratio of genotypic to phenotypic variance according to Hanson et al. [9] and classified as low (below 30 per cent), moderate (31–60 per cent) and high (above 60 per cent) after Johnson et al. [10]. Expected genetic advance was computed as $GA = K \times \sigma_p \times h^2_{bs}$, where $K = 2.06$ is the standardized selection differential corresponding to five per cent selection intensity [16], and was expressed as a percentage of the trait mean to give genetic advance as per cent of mean.

Genotypic and phenotypic correlation coefficients between all pairs of traits were estimated from the corresponding variance and covariance components following Al-Jibouri et al. [17], and their significance was tested against tabulated values of the correlation coefficient at $n - 2$ degrees of freedom. Path coefficient analysis was carried out by partitioning the genotypic correlations into direct and indirect effects following Wright [11] as elaborated by Dewey and Lu [12], taking grain yield per plant as the resultant variable and the remaining eighteen traits as causal variables. The residual effect, which measures the contribution of factors not included in the analysis, was obtained as $\sqrt{1 - \sum p_{iri}}$. All computations were performed using standard biometrical procedures implemented in R and INDOSTAT.

3. RESULTS AND DISCUSSION

3.1 Analysis of variance and the discriminating power of the trial

Analysis of variance for the M4 generation (Table 1) established that mutagenic treatment of Udgir Piwali had generated statistically detectable genetic differences for the entire set of nineteen traits. Nineteen traits showed statistically significant differences among the genotypes at the 1% level of significance ($P \leq 0.01$). Replication effects were non-significant for all traits, confirming the adequacy of blocking and the homogeneity of the experimental field. The magnitude of discrimination nevertheless varied greatly among characters, and this gradient carries the first practical message of the study. Fodder yield per plant recorded by far the widest separation of genotypic from error mean squares, with a variance ratio of 15.57, followed by panicle weight (8.84), number of primaries per panicle (5.61), plant height (4.45), panicle length (4.17) and grain yield per plant (3.47). At the opposite extreme, days to maturity and SPAD chlorophyll content (1.54 each), stem diameter (1.55), number of leaves per plant (1.57) and relative water content (1.61) barely exceeded the critical ratio, so that although differences among entries were statistically significant, the genotypic signal in these traits was small relative to experimental error. Figure 1 displays this ranking alongside the corresponding partitioning of phenotypic variance and shows that mutagenesis released substantially more exploitable variation in biomass and panicle architecture than in phenological or leaf-physiological characters. Comparable spectra of induced variation, with biomass and panicle traits responding most strongly to gamma rays and EMS, have been reported in sorghum by Kalpande et al. [4], Surashe et al. [5], Patel et al. [6] and Suthakar et al. [18].

Table 1. Analysis of variance for nineteen quantitative traits in 64 M4 yellow-pericarp sorghum entries evaluated in a randomized block design during rabi 2024–25

Trait	Replications (df = 1)	Genotypes (df = 63)	Error (df = 63)	Variance ratio
Days to 50% flowering	15.82	35.159**	15.38	2.29
Plant height (cm)	242.55	704.290**	158.26	4.45
Inter nodal length (cm)	19.38	14.212**	5.38	2.64
Stem diameter (cm)	0.21	0.388**	0.25	1.55
Days to maturity	79.70	51.989**	33.76	1.54
Number of primaries per panicle	4.96	61.258**	10.91	5.61
Number of grains per primary	0.61	11.094**	3.87	2.87
Panicle length (cm)	0.00	7.964**	1.91	4.17

Trait	Replications (df = 1)	Genotypes (df = 63)	Error (df = 63)	Variance ratio
Panicle width (cm)	1.00	1.183**	0.50	2.37
Panicle weight (g)	47.90	386.580**	43.73	8.84
100-seed weight (g)	0.13	0.123**	0.04	3.08
Fodder yield per plant (g)	22.61	701.500**	45.05	15.57
Relative water content (%)	101.98	62.227**	38.74	1.61
SPAD chlorophyll content	2.80	31.977**	20.75	1.54
Number of leaves per plant	2.48	1.065**	0.68	1.57
Leaf length (cm)	2.42	27.224**	14.34	1.90
Leaf breadth (cm)	0.11	0.714**	0.24	2.98
Flag leaf area (cm ²)	159.30	752.360**	270.19	2.78
Grain yield per plant (g)	26.39	68.209**	19.66	3.47

Values are mean squares. * Significant at $P \leq 0.05$; ** Significant at $P \leq 0.01$.

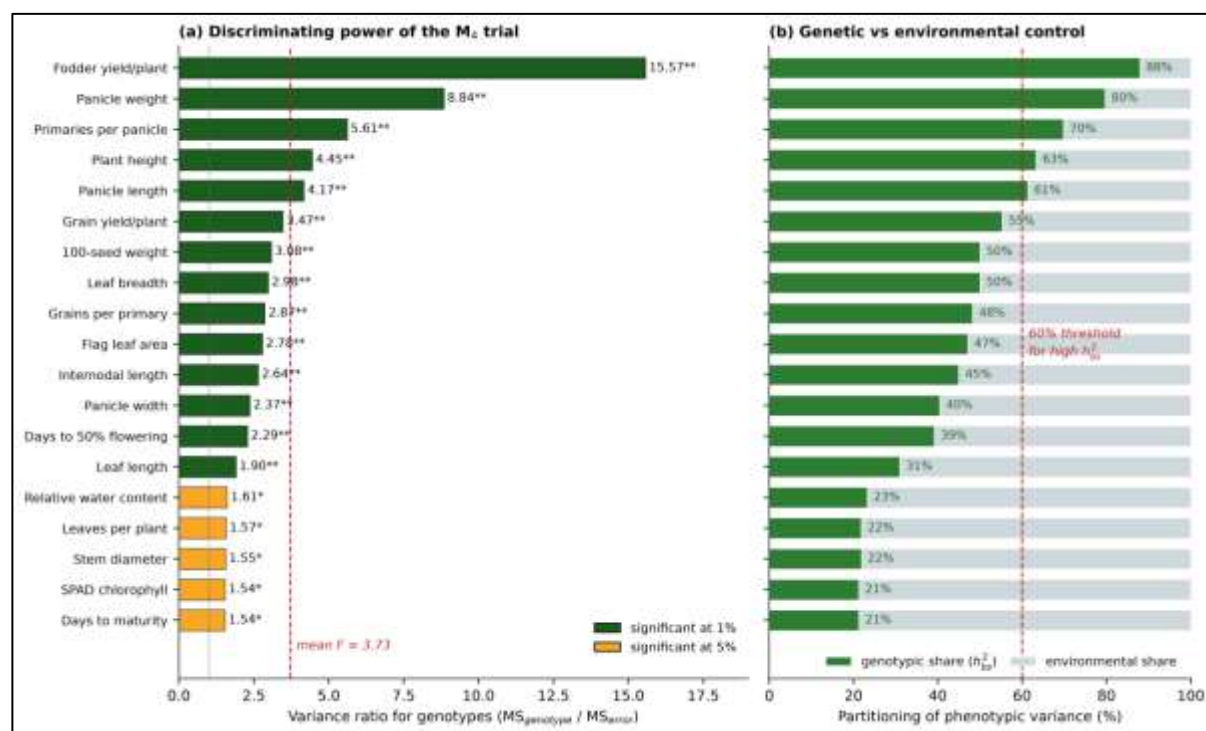


Figure 1. Discriminating power of the M₄ trial and partitioning of phenotypic variance. Panel.

(a) ranks the nineteen traits by the variance ratio of genotypic to error mean squares, with the trait-averaged ratio of 3.73 indicated as a reference; panel (b) resolves the phenotypic variance of each trait into its genotypic (heritable) and environmental fractions, the vertical line marking the 60 per cent threshold conventionally used to define high heritability.

3.2 Mean performance and the spectrum of induced variation

Mean performance confirmed that the statistically significant variation was also agronomically meaningful, since for most traits the mutant population spanned a range extending well on both sides of the parental phenotype (Table 2). Days to 50 per cent flowering varied from 64 to 82 days about a mean of 74.76 days, and days to maturity from 108 to 126 days about a mean of 115.46 days, so that progenies flowering ten days earlier and maturing seven days earlier than the population mean were recovered. Plant height ranged from 192.60 to 260.50 cm about a mean of 235.16 cm, and inter nodal length from 14.40 to 24.00 cm, indicating that both dwarfing and elongation mutations were induced. For the yield complex the ranges were even wider in relative terms: panicle weight varied from 27.59 to 100.58 g about a mean of 63.82 g, fodder yield per plant from 62.25 to 146.40 g about

a mean of 93.91 g, number of primaries per panicle from 33.30 to 63.90, panicle length from 9.92 to 17.91 cm and grain yield per plant from 39.09 to 59.51 g about a mean of 48.39 g. Physiological traits varied over narrower relative ranges, relative water content from 58.17 to 80.51 per cent and SPAD chlorophyll content from 46.90 to 64.38 units.

The recovery of progenies that flower earlier and stand shorter than the parental landrace is of direct agronomic importance in rabi sorghum, where terminal moisture stress penalizes late genotypes and excessive height predisposes the crop to lodging. That such shifts occurred in both directions is characteristic of physical and chemical mutagenesis, which generates a largely random spectrum of changes from which the breeder must select, and is consistent with the induced variation reported in sorghum by Thange et al. [19], Anisiyah and Indriatama [20] and Shivaprasad et al. [7].

Selection was then exercised trait by trait against the population mean, and the resulting inventory of promising mutants is presented in Table 3. Ten lines exceeded the population mean for grain yield per plant, namely 200Gy-1, 200Gy-3, 300Gy-2, 300Gy-4, 300Gy-5, 400Gy-2, 400Gy-4, 500Gy-3, 0.2 per cent EMS-4 and 200Gy + 0.2 per cent EMS-1. A number of lines recurred across several trait categories: 400Gy-2 was identified as promising for eleven of the nineteen traits, while 400Gy-4, 500Gy-5, 300Gy-1, 300Gy-5 and 0.2 per cent EMS-4 each appeared in four or more categories. This multi-trait convergence, summarized graphically in Figure 2, indicates that a limited number of mutational events reorganized the source–sink balance of the landrace as a whole rather than altering single characters in isolation, and it identifies these lines as the most valuable products of the mutagenesis programme and as candidate donors for subsequent recombination breeding.

Table 2. Mean, range and variability classification of nineteen traits in the M4 generation of yellow-pericarp sorghum mutants

Trait	Mean	Minimum	Maximum	Range as % of mean
Days to 50% flowering	74.76	64.00	82.00	24.1
Plant height (cm)	235.16	192.60	260.50	28.9
Inter nodal length (cm)	19.83	14.40	24.00	48.4
Stem diameter (cm)	3.66	2.92	5.28	64.5
Days to maturity	115.46	108.00	126.00	15.6
Number of primaries per panicle	50.99	33.30	63.90	60.0
Number of grains per primary	23.84	18.40	28.50	42.4
Panicle length (cm)	13.53	9.92	17.91	59.0
Panicle width (cm)	5.39	3.96	7.29	61.8
Panicle weight (g)	63.82	27.59	100.58	114.4
100-seed weight (g)	3.03	2.39	3.84	47.9
Fodder yield per plant (g)	93.91	62.25	146.40	89.6
Relative water content (%)	67.90	58.17	80.51	32.9
SPAD chlorophyll content	54.20	46.90	64.38	32.2
Number of leaves per plant	8.87	7.00	10.50	39.5
Leaf length (cm)	54.74	45.70	64.60	34.5
Leaf breadth (cm)	5.50	4.08	7.02	53.5
Flag leaf area (cm ²)	229.86	181.27	259.55	34.1
Grain yield per plant (g)	48.39	39.09	59.51	42.2

Range as per cent of mean is computed as $(\text{maximum} - \text{minimum}) \times 100 / \text{mean}$ and expresses the breadth of induced variation on a comparable scale across traits.

Table 3. Promising M4 mutant lines identified for individual traits on the basis of mean performance superior to the population mean

Trait	Promising mutant lines
Earliness (days to 50% flowering)	100Gy-3, 100Gy-4, 200Gy-5, 0.1% EMS-2, 0.2% EMS-1, 200Gy+0.1% EMS-1, 200Gy+0.1% EMS-4, 200Gy+0.2% EMS-3
Plant height (dwarfness)	100Gy-1, 300Gy-5, 400Gy-1, 400Gy-2, 400Gy-5, 500Gy-2, 500Gy-5, 0.2% EMS-1, 100Gy+0.1% EMS-2
Inter nodal length	400Gy-5, 500Gy-2, 500Gy-3, 0.2% EMS-5, 0.3% EMS-3, 100Gy+0.1% EMS-1, 100Gy+0.2% EMS-1
Stem diameter	300Gy-1, 300Gy-5, 400Gy-1, 400Gy-2, 0.3% EMS-1
Days to maturity	100Gy-3, 400Gy-1, 400Gy-2, 400Gy-4, 500Gy-3
Number of primaries per panicle	100Gy-1, 300Gy-2, 300Gy-4, 400Gy-2, 0.2% EMS-4
Number of grains per primary	300Gy-2, 400Gy-2, 0.2% EMS-3, 200Gy+0.2% EMS-4, 200Gy+0.2% EMS-5
Panicle length	200Gy-1, 200Gy-3, 300Gy-5, 400Gy-2, 400Gy-4, 500Gy-5
Panicle width	200Gy-3, 300Gy-2, 300Gy-3, 0.1% EMS-5, 0.2% EMS-3, 0.2% EMS-4
Panicle weight	200Gy-3, 300Gy-5, 400Gy-4, 500Gy-3, 500Gy-5, 0.3% EMS-2
100-seed weight	100Gy-2, 200Gy-4, 400Gy-4, 500Gy-5, 0.3% EMS-2
Fodder yield per plant	300Gy-1, 400Gy-1, 400Gy-2, 500Gy-5, 0.2% EMS-1
Relative water content	200Gy-3, 400Gy-1, 400Gy-2, 0.3% EMS-1, 0.3% EMS-2
SPAD chlorophyll content	100Gy-1, 300Gy-5, 400Gy-4, 500Gy-5, 0.3% EMS-2
Number of leaves per plant	300Gy-1, 300Gy-4, 400Gy-2, 0.2% EMS-4
Leaf length	200Gy-5, 0.3% EMS-3, 100Gy+0.1% EMS-3
Leaf breadth	100Gy-1, 300Gy-1, 0.2% EMS-4
Flag leaf area	300Gy-3, 500Gy-5, 0.1% EMS-4, 0.2% EMS-1
Grain yield per plant	200Gy-1, 200Gy-3, 300Gy-2, 300Gy-4, 300Gy-5, 400Gy-2, 400Gy-4, 500Gy-3, 0.2% EMS-4, 200Gy+0.2% EMS-1

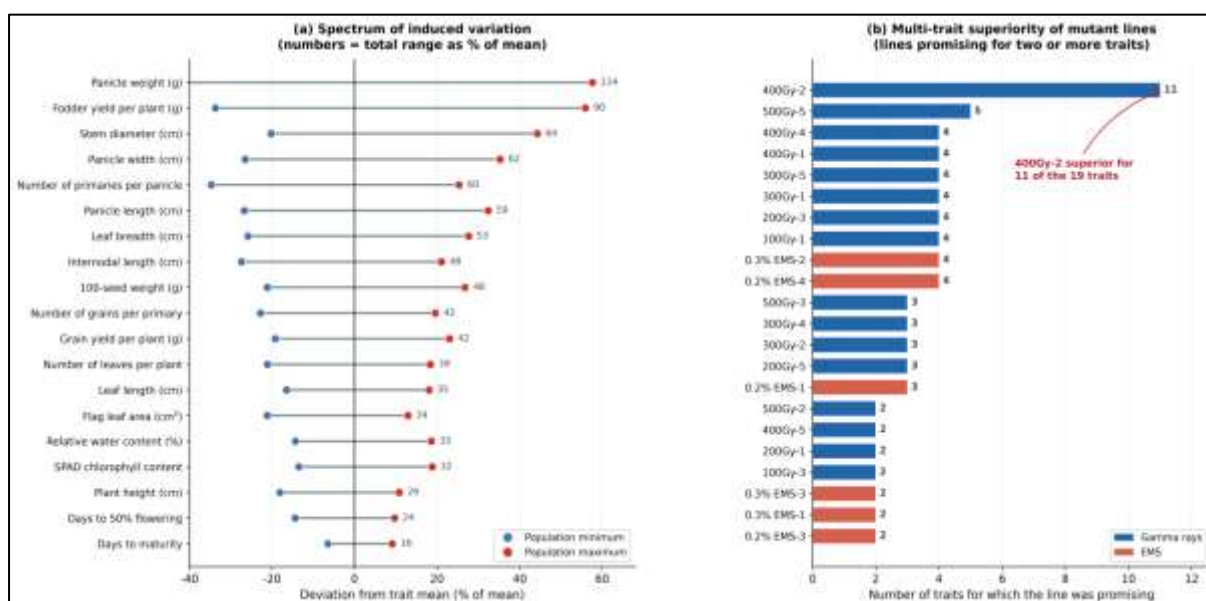


Figure 2. Spectrum of induced variation and multi-trait performance of mutant lines.

Panel (a) presents the mean and range of each trait as deviations expressed in per cent of the trait mean, so that the breadth of induced variation can be compared directly across characters of different scale; panel (b) ranks the mutant lines by the number of traits for which they were identified as promising and indicates the mutagen class of each line.

3.3 Genetic variability, heritability and expected genetic advance

Partitioning of the phenotypic variance (Table 4) clarified how much of the observed variation was heritable and therefore available to selection. Phenotypic coefficients of variation exceeded their genotypic counterparts for every trait, as is inevitable, but the magnitude of the gap proved highly informative. Panicle weight (GCV 20.52 per cent, PCV 22.98 per cent) and fodder yield per plant (GCV 19.29 per cent, PCV 20.57 per cent) showed gaps of only 2.5 and 1.3 percentage points respectively, indicating that their phenotypic expression was governed predominantly by genotype. In contrast, stem diameter (7.15 against 15.45 per cent), relative water content (5.05 against 10.46 per cent), SPAD chlorophyll content (4.37 against 9.47 per cent) and number of leaves per plant (4.92 against 10.54 per cent) showed gaps of 5.4 to 8.3 percentage points, betraying strong environmental modulation of the phenotype. Figure 3a visualizes this contrast as a dumbbell array in which the length of each connector is a direct measure of environmental interference.

By the classification of Sivasubramanian and Madhavamenon [15], high genotypic variability (GCV above 20 per cent) was confined to panicle weight, and moderate variability (10–20 per cent) was recorded for fodder yield per plant, panicle length, panicle width, inter nodal length and grain yield per plant. All remaining traits, including all four physiological characters, fell in the low class. The practical consequence is that the mutagenesis program has furnished ample heritable variation for panicle architecture and biomass but comparatively little for phenology and leaf physiology, and selection objectives should be framed accordingly.

Table 4. Genetic variability parameters for nineteen traits in the M4 generation of yellow-pericarp sorghum mutants

Trait	σ^2_g	σ^2_p	GCV (%)	PCV (%)	h^2_{bs} (%)	GA	GAM (%)
Days to 50% flowering	9.89	25.27	4.21	6.72	39	4.05	5.42
Plant height (cm)	273.01	431.28	7.03	8.83	63	27.08	11.52
Inter nodal length (cm)	4.41	9.80	10.59	15.78	45	2.90	14.65
Stem diameter (cm)	0.07	0.32	7.15	15.45	21	0.25	6.81
Days to maturity	9.12	42.87	2.61	5.67	21	2.87	2.48
Number of primaries per panicle	25.18	36.08	9.84	11.78	70	8.63	16.93
Number of grains per primary	3.61	7.48	7.97	11.47	48	2.72	11.42
Panicle length (cm)	3.03	4.94	12.86	16.42	61	2.80	20.73
Panicle width (cm)	0.34	0.84	10.84	17.04	41	0.77	14.22
Panicle weight (g)	171.42	215.16	20.52	22.98	80	24.07	37.72
100-seed weight (g)	0.04	0.08	6.68	9.45	50	0.30	9.73
Fodder yield per plant (g)	328.23	373.28	19.29	20.57	88	35.00	37.27
Relative water content (%)	11.74	50.48	5.05	10.46	23	3.41	5.02
SPAD chlorophyll content	5.61	26.37	4.37	9.47	21	2.25	4.15
Number of leaves per plant	0.19	0.87	4.92	10.54	22	0.42	4.73
Leaf length (cm)	6.44	20.78	4.64	8.33	31	2.91	5.32
Leaf breadth (cm)	0.24	0.48	8.81	12.58	49	0.70	12.72
Flag leaf area (cm ²)	241.08	511.28	6.76	9.84	47	21.96	9.56
Grain yield per plant (g)	24.27	43.93	10.18	13.70	55	7.54	15.59

σ^2_g = genotypic variance; σ^2_p = phenotypic variance; GCV = genotypic coefficient of variation; PCV = phenotypic coefficient of variation; h^2_{bs} = broad-sense heritability; GA = expected genetic advance at 5 per cent selection intensity; GAM = genetic advance as per cent of mean.

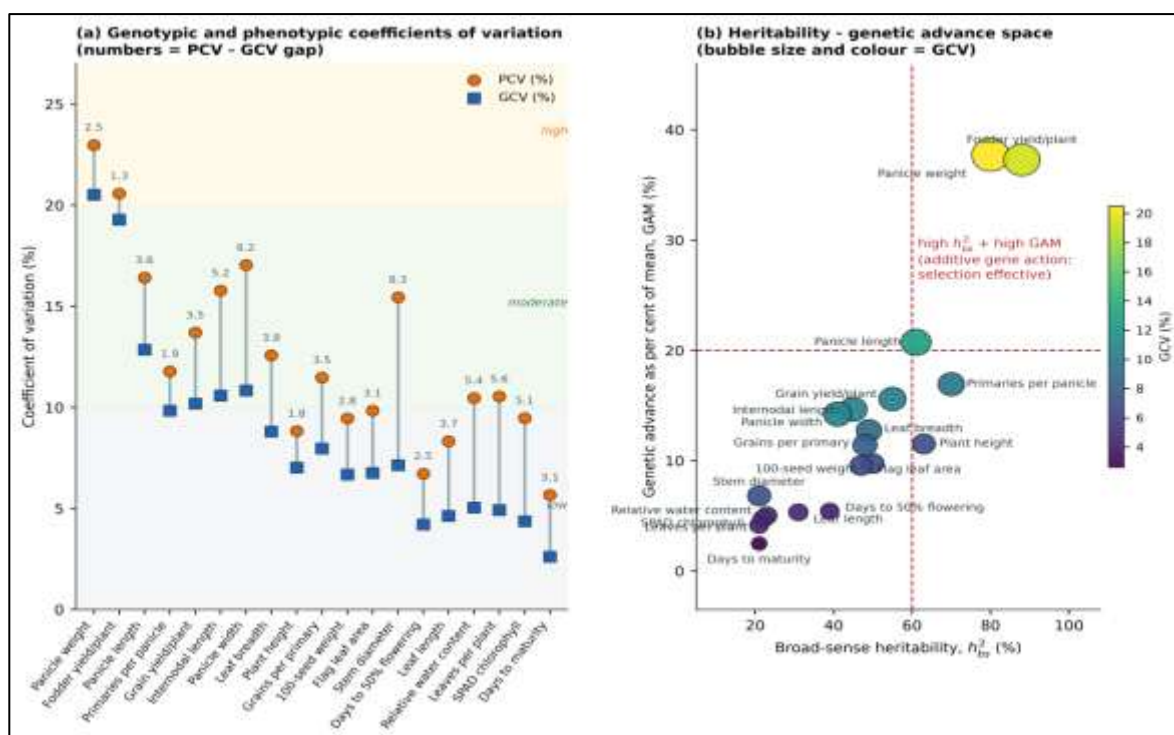


Figure 3. Genetic variability, heritability and expected genetic advance in the M4 generation.

Panel (a) contrasts genotypic and phenotypic coefficients of variation for each trait, the annotated value being the PCV–GCV gap and the shaded bands the conventional low, moderate and high classes; panel (b) locates each trait in heritability–genetic advance space, bubble size and colour representing GCV, so that the upper-right quadrant identifies the traits for which simple phenotypic selection will be most rewarding.

Broad-sense heritability ranged from 21 per cent for stem diameter and days to maturity to 88 per cent for fodder yield per plant. High heritability, above 60 per cent by the classification of Johnson et al. [10], was recorded for fodder yield per plant (88 per cent), panicle weight (80 per cent), number of primaries per panicle (70 per cent), plant height (63 per cent) and panicle length (61 per cent). Moderate heritability was observed for grain yield per plant (55 per cent), 100-seed weight (50 per cent), leaf breadth (49 per cent), number of grains per primary (48 per cent), flag leaf area (47 per cent), inter nodal length (45 per cent), panicle width (41 per cent), days to 50 per cent flowering (39 per cent) and leaf length (31 per cent), while low heritability characterized relative water content (23 per cent), number of leaves per plant (22 per cent), SPAD chlorophyll content (21 per cent), days to maturity (21 per cent) and stem diameter (21 per cent).

Because heritability alone can be misleading when the additive component is small, it must be interpreted jointly with expected genetic advance. The combination of high heritability with high genetic advance as per cent of mean, which is the signature of predominantly additive gene action and therefore of straightforward response to phenotypic selection, was observed for panicle weight (h^2_{bs} 80 per cent, GAM 37.72 per cent), fodder yield per plant (88 per cent, 37.27 per cent), panicle length (61 per cent, 20.73 per cent) and number of primaries per panicle (70 per cent, 16.93 per cent). Grain yield per plant occupied an intermediate position, with moderate heritability (55 per cent) and a GAM of 15.59 per cent, which accords with its status as a composite character influenced by non-additive gene action and environmental buffering. Traits such as days to maturity (21 per cent, 2.48 per cent), SPAD chlorophyll content (21 per cent, 4.15 per cent), relative water content (23 per cent, 5.02 per cent) and number of leaves per plant (22 per cent, 4.73 per cent) combined low heritability with negligible expected advance and should not be used as primary selection criteria in early generations, however attractive they may appear on physiological grounds; improvement in these characters will require replicated evaluation over seasons rather than single-plant selection. Figure 3b maps these relationships and delineates the selection-priority quadrant.

These estimates correspond closely with published values for comparable sorghum material. High heritability coupled with high genetic advance for panicle weight and fodder yield was reported in sorghum mutants by Shivaprasad et al. [7] and Anisayah and Indriatama [20], in coloured-pericarp rabi sorghum by Karpe et al. [21], and in diverse germplasm by Santhiya et al. [22], Behera et al. [23] and Khandelwal et al. [24]. Equally, the low heritability of phenological and leaf-physiological traits observed here parallels the findings of Deepalakshmi and Ganesamurthy [25], More et al. [26] and Tesfamichael et al. [27], who attributed the discrepancy between phenotypic and genotypic coefficients of variation in such traits to their high sensitivity to soil moisture and temperature during the rabi season.

3.4 Character association: the correlation structure of grain yield

Genotypic correlation coefficients of the eighteen component traits with grain yield per plant (Table 5) produced an unambiguous hierarchy. Panicle length ($r_g = 0.910$), panicle weight (0.855), panicle width (0.687) and stem diameter (0.592) were very strongly and positively associated with grain yield, followed by days to maturity (0.422), number of grains per primary (0.390), 100-seed weight (0.371) and fodder yield per plant (0.335), all significant at the one per cent level. Number of leaves per plant (0.319) and plant height (0.250) were significant at five per cent. Relative water content (0.223), inter nodal length (0.110), number of primaries per panicle (0.082) and flag leaf area (0.077) were positive but non-significant, while SPAD chlorophyll content (-0.015), leaf length (-0.032), leaf breadth (-0.047) and days to 50 per cent flowering (-0.195) were weakly negative. Genotypic correlations exceeded their phenotypic counterparts in magnitude for most trait pairs, indicating that the associations have a genetic rather than merely environmental basis and can therefore be exploited in selection. The negative association of days to 50 per cent flowering with grain yield is of particular value in rabi sorghum, because it indicates that selection for earliness, which is essential for escaping terminal moisture stress, need not be purchased at the cost of productivity. Conversely, the strong positive correlation of fodder yield per plant with grain yield (0.335) shows that grain and fodder improvement are compatible objectives in this material, an important consideration in the Marathwada region where Stover is a major component of farm income.

Table 5. Genotypic correlation coefficients of component traits with grain yield per plant and their direct effects from path coefficient analysis in the M4 generation

Trait	r_g with grain yield	Direct effect	Largest positive indirect effect (via)	Largest negative indirect effect (via)
Panicle length (cm)	0.910**	2.253	0.663 (days to maturity)	-0.847 (inter nodal length)
Panicle weight (g)	0.855**	-0.630	0.837 (panicle length)	-0.630 (self-compensating)
Panicle width (cm)	0.687**	0.271	0.663 (panicle length)	-0.382 (inter nodal length)
Stem diameter (cm)	0.592**	0.528	1.847 (panicle length)	-1.844 (inter nodal length)
Days to maturity	0.422**	0.968	1.612 (panicle length)	-1.681 (inter nodal length)
Number of grains per primary	0.390**	-0.840	1.164 (panicle length)	-0.945 (inter nodal length)
100-seed weight (g)	0.371**	0.510	0.888 (flag leaf area)	-2.660 (stem diameter)
Fodder yield per plant (g)	0.335**	-0.080	1.124 (panicle length)	-0.773 (inter nodal length)
Number of leaves per plant	0.319*	0.213	0.715 (leaf length)	-0.532 (days to 50% flowering)
Plant height (cm)	0.250*	-1.597	1.211 (panicle length)	-3.430 (inter nodal length)
Relative water content (%)	0.223	-0.368	1.281 (panicle length)	-2.611 (inter nodal length)
Inter nodal length (cm)	0.110	3.430	0.564 (panicle length)	-0.564 (plant height)
Number of primaries per panicle	0.082	-0.945	0.612 (panicle length)	-0.640 (inter nodal length)
Flag leaf area (cm ²)	0.077	-2.866	0.825 (inter nodal length)	-0.170 (leaf breadth)
SPAD chlorophyll content	-0.015	-0.279	0.862 (flag leaf area)	-1.457 (inter nodal length)
Leaf length (cm)	-0.032	-0.598	1.512 (inter nodal length)	-0.401 (primaries per panicle)

Trait	rg with grain yield	Direct effect	Largest positive indirect effect (via)	Largest negative indirect effect (via)
Leaf breadth (cm)	-0.047	0.662	0.736 (flag leaf area)	-0.204 (SPAD chlorophyll)
Days to 50% flowering	-0.195	0.821	0.612 (days to maturity)	-2.047 (inter nodal length)

* Significant at $P \leq 0.05$; ** significant at $P \leq 0.01$. Residual effect of the path analysis = 0.148

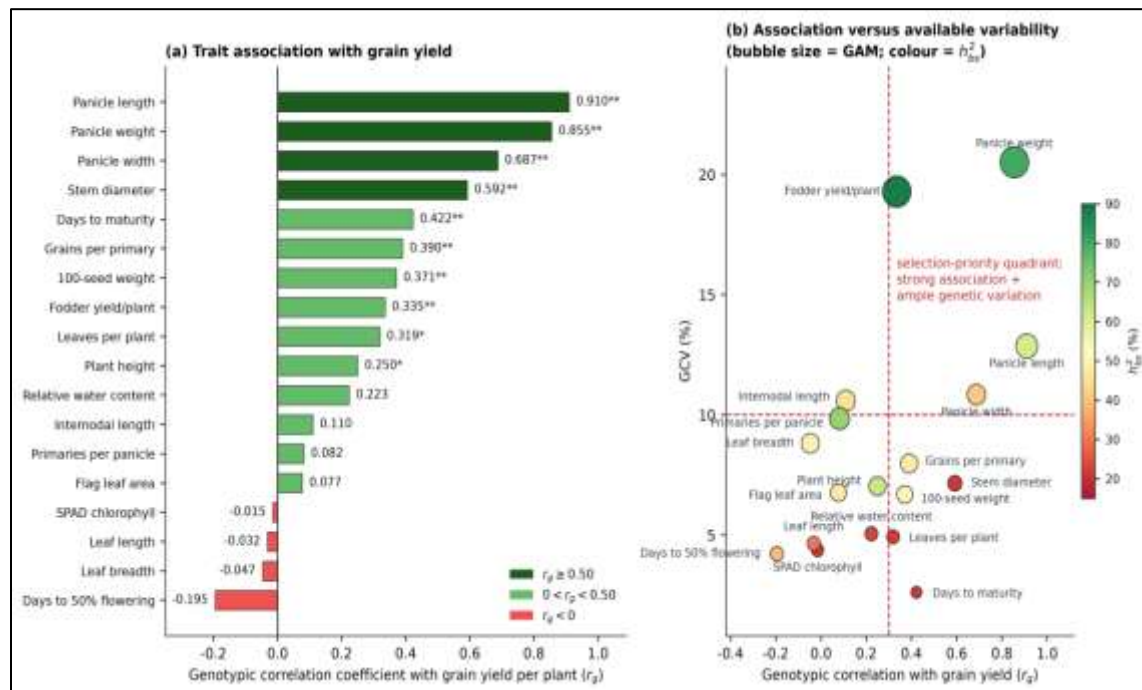


Figure 4. Genotypic association of component traits with grain yield per plant in the M4 generation.

Panel (a) ranks traits by the magnitude and sign of their genotypic correlation with grain yield; panel (b) plots the same correlations against the genotypic coefficient of variation, with bubble size representing genetic advance as per cent of mean and color representing broad-sense heritability, thereby separating traits that combine strong association with ample heritable variation from those that are strongly associated but genetically nearly invariant.

Beyond the yield column, the correlation matrix disclosed a coherent developmental syndrome within the mutant population. Days to 50 per cent flowering was strongly and positively correlated with relative water content (0.833), stem diameter (0.657) and days to maturity (0.633), but negatively with inter nodal length (-0.596) and number of leaves per plant (-0.648); inter nodal length was in turn negatively correlated with relative water content (-0.761) and leaf breadth (-0.634), and positively with plant height (0.537). Within the panicle, length was tightly associated with weight (0.815) and width (0.738), and number of primaries per panicle with number of grains per primary (0.542). Leaf breadth was strongly correlated with SPAD chlorophyll content (0.731), and stem diameter with fodder yield per plant (0.538). Taken together, these relationships indicate that mutagenesis separated the population into a late-flowering, thick-stemmed, water-retentive phenotype with short internodes and a broader leaf canopy on the one hand, and an early, elongated-internode phenotype with reduced water retention on the other. Comparable correlation structures in sorghum have been documented by Patil et al. [28], Chavhan et al. [29], Goswami et al. [30], Begum et al. [31] and Iyanar et al. [32].

3.5 Path coefficient analysis: distinguishing cause from association

The correlation coefficient conflates the direct influence of a trait with influences transmitted through other traits. Therefore, genotypic correlations were partitioned into direct and indirect path coefficients with grain yield per plant as the resultant variable (Table 5 and Figure 5). The residual effect of 0.148 indicates that the eighteen causal traits jointly accounted for 85.2 per cent of the variation in grain yield, so the trait set was adequate for a causal interpretation and few important determinants were omitted.

Inter nodal length exerted the largest positive direct effect (3.430), followed by panicle length (2.253), days to maturity (0.968), days to 50 per cent flowering (0.821), leaf breadth (0.662), stem diameter (0.528), 100-seed weight (0.510), panicle width (0.271) and number of leaves per plant (0.213). The apparent paradox that inter nodal length showed a near-zero total correlation with grain yield (0.110) despite the largest direct effect is

resolved by its strong negative indirect effect through plant height (-0.564) and the reciprocal cancellation between the two traits: a plant attains height either by producing more internodes or by elongating existing ones, and only the second route contributes positively to grain yield once height itself is held constant. Flag leaf area displayed the largest negative direct effect (-2.866) and plant height the second largest (-1.597), yet both retained slightly positive total correlations because of strong positive indirect routes through panicle length (0.825 and 1.211 respectively). Panicle weight provides the clearest instance of a purely indirect contributor: its very high total correlation (0.855) arises almost entirely from a positive indirect effect via panicle length (0.837), its own direct effect being negative (-0.630), which is biologically sensible because at a given panicle length a heavier panicle reflects greater rachis and glume mass rather than greater grain mass.

The practical implication of this analysis is that selection indices for yellow-pericarp sorghum should be constructed primarily on panicle length, panicle width, stem diameter and 100-seed weight, since these four traits combine significant positive genotypic correlations with positive direct effects and therefore respond to selection in the intended direction without hidden compensation. Panicle weight and fodder yield per plant are best treated as confirmatory rather than primary criteria, because their apparent contribution is mediated through panicle length; selecting on them directly risks accumulating rachis mass rather than grain. Simultaneous selection for excessive plant height and very large flag leaf area should be avoided, since both act as negative direct drains on grain yield, most plausibly through competition for assimilates during grain filling in a crop growing on a finite store of soil moisture. Days to maturity, though possessing a favorable positive direct effect (0.968), should be handled cautiously because its low heritability (21 per cent) and negligible expected advance (2.48 per cent of the mean) limit the reliability of single-plant selection for this character.

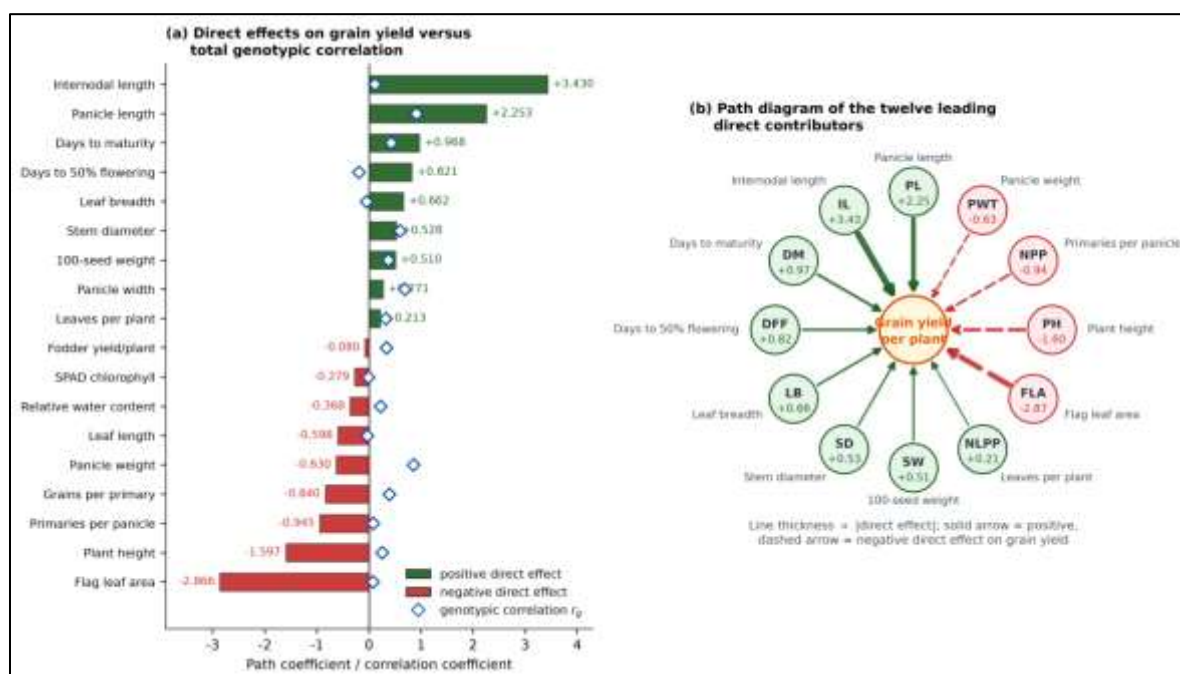


Figure 5. Genotypic path analysis of grain yield per plant in the M4 generation.

Panel (a) compares the direct path coefficient of each trait with its total genotypic correlation, allowing traits whose association is largely indirect to be distinguished from true causal contributors; panel (b) presents the twelve leading direct contributors as a path diagram in which arrow thickness is proportional to the absolute direct effect and line style denotes its sign.

These conclusions accord with the path analyses reported for sorghum by Zinzala et al. [33], Khadakbhabhi et al. [34], Warkad et al. [35], Veerabadhiran and Kennedy [36], Sunku et al. [37] and Nimbalkar et al. [38], all of whom identified panicle dimensions and seed weight as the principal causal determinants of grain yield, and with the observation of Lenka and Mishra [39] that traits with high total correlations but negative direct effects must be interpreted through their indirect pathways rather than used naively as selection criteria.

4. CONCLUSIONS

The study demonstrated that induced mutagenesis generated substantial phenotypic variation in the yellow-pericarp rabi sorghum landrace Udgir Piwali. Significant variation was observed for all 19 traits, with panicle weight and fodder yield showing high genetic variability, heritability and expected genetic advance, indicating good prospects for selection. Grain yield was positively associated with several panicle, stem and yield-component traits, supporting their potential use as selection criteria; however, the reported path coefficients and residual effects require verification before establishing a definitive selection index. Based on overall performance, six mutants (400Gy-2, 400Gy-4, 500Gy-3, 300Gy-5, 500Gy-5 and 0.2% EMS-4) were identified as promising. Given the single-season, single-location evaluation, these lines should be considered candidates for further validation.

Multi-environment trials are required to assess stability and genotype $\times$ environment interactions. Further characterization of nutritional quality traits and molecular profiling will help confirm their genetic distinctness and identify genomic regions underlying desirable phenotypes.

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