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Genetic Analysis of Agronomic Traits in Sorghum Parents and Hybrids Across Diverse Male Sterile Cytoplasms and Varying Soil Moisture Conditions

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ABSTRACT

The predominance of A_1 cytoplasm in sorghum hybrid breeding has limited the exploitation of alternative cytoplasmic male sterility (CMS) sources such as A_2, A_3 and A_4. This study evaluated the combining ability and heterosis of hybrids derived from diverse CMS backgrounds (A_1, A_2, A_3 and A_4) under both drought and irrigated conditions. A total of 241 F_1 hybrids, 35 parents and 4 checks were assessed for yield and related traits across two seasons and moisture regimes. Significant genotype × environment interactions were observed, highlighting the need for environment-specific recommendations. Notably, A_1 (ICSA 38, ICSA 55 and ICSA 502), A_2 (ICSA 724) and A_4 (ICSA 758) CMS lines exhibited strong general combining ability (GCA) for grain yield under drought, while several A_1 and A_2 lines performed well under irrigation. Restorer lines Parbhani Shakti and ICSR 13038 produced high-yielding hybrids across environments, with ICSV 15014 and ICSR 13009 showing universal fertility restoration. Specific combining ability (SCA) and heterosis analyses identified ICSA 675 × ICSR 13038 (A_1) and ICSA 724 × ICSV 15014 (A_2) as top performers under drought, and ICSA 735 × ICSR 13038 (A_2) under irrigation. Mean versus stability analysis revealed G151 and G229 as highly stable hybrids. The results confirm the competitive potential of A_2 CMS as an alternative to A_1, supporting cytoplasmic diversification for enhanced yield stability and resilience in sorghum breeding programmes.

1 | Introduction

Sorghum (*Sorghum bicolor* L. Moench) is widely cultivated as a staple commodity for both human consumption and animal feed in several countries around the world. As a resilient crop, sorghum plays a critical role in food security, bio-energy production and livestock feed, particularly in arid and semi-arid regions. However, improving its productivity under varying moisture regimes remains a significant challenge for breeders. Since the crop is primarily grown in semi-arid environments, drought stress is the most consequential abiotic factor affecting sorghum production. This stress considerably undermines productivity, posing threats to food and nutritional security for communities dependent on sorghum (Eggen et al. 2019). The global demand for food is estimated to double by 2050 (Tilman et al. 2011), yet increasing water scarcity poses a major hazard

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to food production systems, concerns that are projected to intensify as climate change accelerates (Rabara et al. 2018; IPCC 2014).

Stephens and Holland (1954) identified the first source of cytoplasmic male sterility (CMS) in sorghum. Following the deployment of the CMS in commercial hybrid production first released hybrid, CSH1 in 1961 in India, numerous sorghum hybrids have been developed and commercialized for global cultivation. Most of these hybrids are derived from the A_1 cytoplasmic source (Praveen et al. 2015; Prasad et al. 2017; Reddy et al. 2010), which has become the choice for hybrid breeding because of the paucity of restorers for other CMS systems (Moran and Rooney 2003). Over the decades, the adoption of hybrids has significantly enhanced grain and fodder yields, contributing to increased production of the crop wherever the technology reached. In many countries, sorghum plays a pivotal role for food security and supports livestock production. It provides a stable crop option for smallholder farmers, particularly in areas prone to drought and other environmental stresses. Despite the success of A_1-based hybrids, there remains untapped potential in exploring alternative cytoplasmic sources, such as A_2, A_3, A_4, 9E and A_6 (Stephens and Holland 1954; Quinby 1970; Jebril et al. 2021; Reddy et al. 2008). The use of these alternative sources may strengthen hybrid breeding programmes, offering improved resilience and performance under a wider range of growing conditions. The utilization of diverse cytoplasmic sources has the potential to broaden the genetic base, improve adaptability and enhance tolerance to biotic stresses such as disease, pest and abiotic stresses, such as drought. Diversifying CMS cytoplasm can help prevent disease outbreaks by increasing genetic diversity, as large-scale cultivation of crops with a single, narrow CMS source can create vulnerability to pests and diseases. For example, in maize, the widespread use of a specific T-type cytoplasm for hybrid production led to genetic vulnerability, creating susceptibility to diseases. The development of high-yielding hybrid requires comprehensive insights on combining ability and the nature of gene action, and diversity or parental lines including the use of diverse cytoplasmic backgrounds. Evaluation of available sorghum germplasm for agronomic performance under drought stress conditions can help breeders identify tolerant genotypes that can be used as parents for developing hybrids with improved drought tolerance.

Sorghum hybrid technology is a powerful tool for increasing production. For hybrid technology to be successful, it is essential that suitable and stable pollen parental lines on diverse cytoplasmic sources be identified so that developing viable hybrid combinations becomes easy and rapid. Identifying stable restorer lines with significant GCA effects for yield has profound implications for enhancing crop productivity. These lines are valuable genetic resources for developing high-yielding hybrids, thereby contributing to food security. Understanding the genetic factors contributing to high yield allows breeders to target specific genotypes for further exploration and utilization in hybridization, which facilitates the development of superior hybrids with optimized yield performance. Considering these critical factors, the present research aimed to identify promising parental lines and hybrids across diverse cytoplasmic backgrounds, with a particular emphasis on performance under drought stress conditions. The primary objective was to develop and harness high-yielding sorghum hybrids that combine drought resilience with cytoplasmic diversity, thereby facilitating their potential for commercial cultivation in drought-prone regions.

2 | Material and Methods

2.1 | Parental Materials and Establishment of L×T Crosses

Twenty-three CMS seed parents, representing four diverse cytoplasmic backgrounds A_1, A_2, A_3 and A_4 (which includes 15 CMS lines from the A_1 cytoplasmic source, three from A_2, three from A_3 and two from A_4) and 12 testers from the ICRISAT sorghum breeding programme were used in this study. The selected parental lines were crossed using the Line×Tester mating design as outlined by Kempthorne (1957) during the Rabi 2020 season. A total of 276 successful crosses were generated through hand pollination. Fertility restoration ability was assessed for all 12 testers, with all identified as effective restorers on A_1 and A_2 cytoplasmic sources, and five showing restoration ability on A3 and A_4 cytoplasmic backgrounds based on their respective F_1 hybrids. Out of the 276 hybrids, only 241 F_{1s} that exhibited complete seed set under bagging conditions during the 2021 rainy season evaluation were selected for yield trials. The agronomic performance trial was conducted during the post-rainy 2021 and summer 2022 seasons under irrigated and drought stress (two cropping seasons×two irrigation regimes) evaluating a total of 280 genotypes (comprising 241 F_1 hybrids, 35 parents and 4 checks).

2.2 | Phenotypic Data Collection and Statistical Analysis

Depending on the intended attributes, the hybrid F_{1s} were phenotyped either per plant or per plot basis. In each plot, five healthy plants were randomly selected to measure plant height (PH), number of leaves per plant (NL), panicle length (PL) and panicle width (PWI). The mean values of these measurements were used for subsequent statistical analysis. On a plot basis, the following metrics were recorded: days to 50% flowering (DFF), days to maturity (DM), hundred seed weight (HSW), panicle weight per hectare (PWt) and grain yield per hectare (PY). Just 1 week before harvest, the average height of five plants in the elementary plot was taken using a 5-m telescopic rod (5-m grade rod aluminium) that was vertically laid on the ground. Five panicles were randomly selected from each genotype to measure the length from the base of the panicle to the tip of the topmost spikelet, and the average length was expressed in centimetres. Plants in the experimental plot were hand-harvested at grain maturity; the panicles were weighed, and the grain yield was calculated. At the widest point, the panicle's width was measured in centimetres. PWI and length measurements were followed by threshing to calculate grain yield. After thoroughly drying the seeds at a moisture level of 12%, the weight of 100 well-filled grains from each plant was counted and recorded in grams.

2.3 | Design, Layout of the Experiment, Experimental Site and Soil Topography

Seed parents, pollen parents and their F_1 hybrids were grown in two seasons, i.e., post-rainy 2021 and summer 2022, each under irrigation and drought stress conditions using alpha lattice design with two replications at the International Crops Research Institute for the Semi-Arid Tropics, Patancheru, Hyderabad, Telangana, India (latitude 20°42′10.59″ N and longitude 76°59′57.97″ E), at 285 m above mean sea level. The soil was medium black with clay, properly levelled with uniform topography and a precise drainage system. Plants in both the water regimes were raised under the same field conditions till 65 days after sowing (DAS), ensuring that the crop does not face water stress. To simulate drought-stressed condition and to stress the plants at flowering, irrigation was stopped at 65 DAS (10 days prior to anthesis) (Upadhyaya et al. 2017). Care was taken to avoid seepage entry of water by planting five border rows along the water stressed field.

2.4 | Statistical Analyses and Software Used

For each measurement, the mean values from all replicates were computed. 'R' software version 4.2.3 was used for all statistical analysis, including the computation of analysis of variance (ANOVA) for the two moisture regimes. The effects of genotype on the yield components and yield were partitioned into parent, hybrid and environment effects to assess the significance of combining ability of the parental lines and hybrids under different environments. The hybrid effects were further subdivided into three components: CMS line × restorer interaction effects, restorer line and CMS line. They represent the specific combining ability (SCA) effects, the general combining ability (GCA) effects for restorer line and the GCA effects for CMS line, respectively. The GCA and SCA effects were tested for significance using a *t*-test. Correlation between different traits was assessed by the Pearson correlation coefficient.

2.5 | Estimation of Heterosis

The heterosis effects, expressed as percentage increase or decrease relative to the parents or standard check (useful heterosis), were calculated according to the established procedure (Shull 1914).

2.5.1 | Mid-Parent Heterosis (MPH)

MPH is determined by the difference between the mean of the F_1 hybrid and the mean of its parental lines, calculated as follows:

$$\mathrm{MPH}\,(\%) = \frac{\overline{\mathrm{F}}_1 - \overline{\mathrm{MP}}}{\overline{\mathrm{MP}}} \times 100$$

where $\overline{\mathrm{MP}} = \frac{\overline{\mathrm{P}}_1 + \overline{\mathrm{P}}_2}{2}$ (mid-parent value), $\overline{\mathrm{P}}_1$ = mean performance of first parent, $\overline{\mathrm{P}}_2$ = mean performance of second parent and $\overline{\mathrm{F}}_1$ = mean performance F_1 hybrid.

2.5.2 | Better-Parent Heterosis (BPH; Heterobeltiosis)

The formula utilized to calculate heterosis over the better parent (BP) is as follows:

$$\text{Heterobeltiosis}\,(\%) = \frac{\overline{\mathrm{F}}_1 - \overline{\mathrm{BP}}}{\overline{\mathrm{BP}}} \times 100$$

where BP = mean performance of better parent in desired direction, and $\overline{\mathrm{F}}_1$ = mean performance F_1 hybrid.

2.5.3 | Percent Heterosis Over Standard Check (Standard Heterosis)

$$\text{Standard heterosis} = \frac{\overline{\mathrm{F}}_1 - \overline{\mathrm{sc}}}{\overline{\mathrm{sc}}} \times 100$$

$\overline{\mathrm{F}}_1$ = mean performance of F_1 hybrid, and SC = mean of standard check.

The significance of heterosis was evaluated using the 't' test. The computed 't' value was compared to the tabulated 't' value at the degrees of freedom from ANOVA, which included parents, checks and F_1's, at significance levels of $p = 0.05$ and $p = 0.01$.

2.6 | Seed Producibility

The seed producibility of maintainer lines was evaluated by bagging the panicles at flowering. After maturity, the seed set under bagging was recorded and expressed as a percentage, ranging from 0% (no seed set) to 100% (complete seed set).

3 | Results

3.1 | ANOVA for Yield and Its Attributing Parameters

The ANOVA for yield and yield-related traits revealed highly significant ($p < 0.001$) differences among genotypes, environments and their interaction effects across all traits studied (Table 1). The presence of significant genotype × environment interactions indicates substantial genetic variability among the genotypes, with performance strongly influenced by environmental conditions. These findings highlight the importance of environment-specific recommendation of genotypes to enhance breeding efficiency.

3.2 | Correlation of Yield and Yield Associated Traits

The magnitude and direction of correlations among plant traits were interpreted following the classification of Gomez and Gomez (1984), wherein correlation values of 0–0.1, 0.1–0.5, 0.5–0.8 and 0.8–1.0 are categorized as zero, low, medium and high, respectively, while a value of 1.0 denotes a perfect correlation. A high positive correlation was observed between PWt and PY across both environments, i.e., drought (Figure 1A)

TABLE 1 | ANOVA for yield and its attributing parameters in sorghum.

Source of variation	df	Mean sum of squares								
		DFF	DM	NL	PHT (cm)	PL (cm)	PWI (cm)	HSW (g)	PWt (t/ha)	PY (t/ha)
Environment	3	29330.65***	35159.6***	2355.04***	542736.05***	1178.35***	90.62***	84.65***	52.6***	52.13***
Genotypes	279	88.08***	107.72***	5.31***	9237.27***	34.48***	1.03***	0.76***	3.31***	2.11***
Replications	1	26.29	174.15	7.46	277.68	0.062	4.92	1.51	0.02	0.002
Genotype × Env	837	24.28***	28.39***	1.86***	557.7***	3.61***	0.25***	0.12***	0.97***	0.76***
Rep × Block	68	5.14	6.57	2.05	235.5	1.37	0.24	0.07	0.42	0.2
Residuals	1051	3.99	4.86	0.89	148.03	1.77	0.19	0.06	0.38	0.25

Abbreviations: DFF, days to 50% flowering; DM, days to maturity; HSW, 100 seed weight; NL, number of leaves per plant; PHT, plant height; PL, panicle length; PWI, panicle width; PWt, panicle weight per hectare; PY, yield per hectare.

***Significant at 0.001% level.

and irrigated (Figure 1B), as well as in the pooled analysis (Figure 1C). Similarly, medium positive values of correlation were recorded between PWI and PY under all environments. Low positive correlations were noted between yield and PH, NL, PL and HSW. Conversely, low but negative and significant correlations were observed between yield and both DFF and DM under the irrigated environment.

3.3 | ANOVA for Combining Ability

The ANOVA was used to determine different sources of variations related to combining ability of the nine characteristics investigated in both irrigated and drought environments. ANOVA for yield and yield-related traits have revealed significant ($p < 0.01$ and $p < 0.05$) differences between lines, testers, line × tester, environments and their interaction components for all the plant characteristics studied under drought stress (Table 2) and irrigated environments (Table 3). The significant effects of lines, testers, line × tester, line × environment, tester × environment and line × tester × environment interaction under both the environments, i.e., irrigated and drought environments of the traits under investigation, justifies the selection of genotypes through combining ability estimates in order to determine the environmental and the genotypic behaviours allowing targeted breeding recommendations to expedite the hybrid development process, making downstream testing more efficient for different moisture regimes.

3.4 | Combining Ability Variances and Gene Action for Drought Stress and Irrigated Environments

The analysis revealed that the degree of dominance exceeded unity for PH and PL in both drought stress (Table 4) and irrigated conditions (Table 5), indicating the presence of additive gene action. The NL displayed additive gene action specifically in the irrigated environment. PH inheritance was mainly influenced by the GCA variance of the restorer lines, whereas PL inheritance was primarily determined by the GCA variances of both CMS lines and restorer lines.

The GCA to SCA variance ratio was found to be less than one, suggesting that nonadditive gene action played a dominant role in most traits, including DFF, PWI, PWt, HSW and PY, across both irrigated and drought stress conditions. Inheritance of these traits was largely driven by SCA variance, emphasizing the importance of nonadditive gene action in their genetic determination.

3.5 | GCA Effects Estimates of Diverse Male Sterile Lines and Universal Restorer Parents

The GCA effects of the CMS line and pollen parents for all measured traits were evaluated under drought stress (Table S5) and irrigated environment (Table S6). Negative GCA was critical for DFF, PH and DM, whereas positive GCA was a prerequisite for other traits examined in the study. None of the CMS lines consistently functioned as good general combiners for all traits across environments, indicating specificity in their

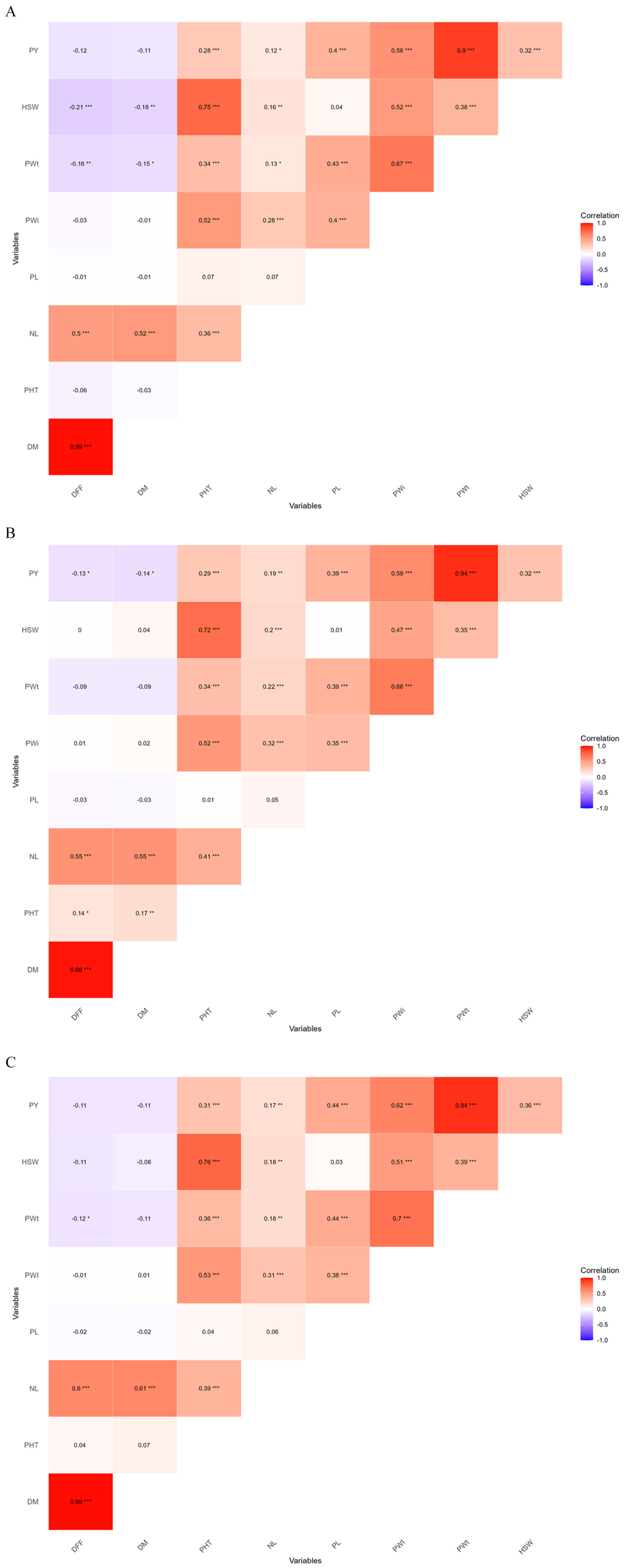

FIGURE 1 | Legend on next page.

FIGURE 1 | Heatmap visualizing the correlation of yield and yield parameters in sorghum under drought environment (1A), irrigated environment (1B) and pooled environments (1C).

performance. Notably, CMS lines ICSA 38, ICSA 55 and ICSA 502 from the A_1 cytoplasmic background, along with ICSA 724 from A_2 and ICSA 758 from A_4, showed positive and significant GCA effects for yield under drought conditions. In contrast, under irrigated conditions, CMS lines such as ICSA 37, ICSA 56, ICSA 57, ICSA 433, ICSA 502, ICSA 675 and ICSA 29005 from A_1, as well as ICSA 724 from A_2, exhibited similar positive effects for yield. Similarly, among the testers in terms of grain yield under irrigated conditions, the stable restorers ICSV 15014 and ICSR 13009 exhibited positive and significant GCA effects, with Parbhani Shakti and ICSR 13038 also showing strong performance across both environments. This highlights their potential as key genetic contributors for improving sorghum grain yield.

3.6 | SCA Effects Estimates of Diverse Cytoplasmic-Based Hybrids

The SCA effects for the nine traits in both irrigated and drought environments are detailed in Tables S1 and S2. Among the traits evaluated, PH exhibited the widest range of SCA effects, with a greater number of hybrids showing significant SCA values ($p < 0.05$) compared to the other traits. For DFF, DM and PH, negative SCA effects were desirable, reflecting a preference for shorter crop duration and reduced plant stature. In contrast, positive SCA effects were favourable for yield-related traits and other productivity-associated attributes. Some hybrids displayed negative and significant SCA effects for DFF, DM and PH traits, while others showed positive and significant SCA effects for yield and productivity-related traits. For example, the hybrid ICSA 675 × ICSR 13038 (A_1 cytoplasmic background) demonstrated the highest positive and significant SCA effect for grain yield, identifying it as the most promising hybrid under drought conditions. Similarly, hybrids ICSA 724 × ICSV 15014 (A_2 background), as well as ICSA 52 × Giddi Maldandi, ICSA 627 × ICSR 17008 and ICSA 502 × SPV 1411 (all from the A_1 background), also exhibited substantial positive and significant SCA effects for grain yield, placing them among the top performers. For irrigated environments, the optimal heterotic hybrids were ICSA 735 × ICSR 13038, ICSA 724 × ICSR 13041 and ICSA 712 × Parbhani Shakti from A_2, along with ICSA 56 × Giddi Maldandi and ICSA 29005 × Giddi Maldandi from A_1. These hybrids exhibited the highest positive and significant SCA effects for grain yield, establishing them as the leading choices for high productivity in irrigated conditions.

3.7 | Heterosis Analysis

3.7.1 | MPH and BPH of Hybrids Under Drought and Irrigated Environments

MPH and BPH were evaluated by comparing hybrids with their respective parents in experiments conducted under both drought stress and irrigated conditions. The sorghum hybrids displayed significant MPH and BPH, with notable variation in the heterosis observed across different traits (Tables S3 and S4). The BPH range for PWt, HSW and plot yield under drought stress conditions was as follows: −12.0% to 145.4%, −22.9% to 44.4% and −34.9% to 208.8%, while under irrigated conditions, the BPH values for these traits ranged from −22.3% to 102.63%, −27.8% to 44.3% and −37.1% to 174.1%, respectively. All hybrids exhibited favourable MPH across all nine traits, highlighting the potential of these hybrids for improving key agronomic traits in both environments.

3.7.2 | Selection of Hybrids Based on Standard Heterosis of Hybrids Under Drought and Irrigated Environments

The evaluation of hybrids under irrigated and drought stress conditions revealed significant heterotic responses for yield. Across the environments, the direction and magnitude of heterosis varied, highlighting the influence of environment in shaping hybrid performance. For grain yield, the hybrid ICSA 735 × ICSR 13038 (A_2) exhibited the highest and most consistent heterotic advantage, with a 65.70% increase under irrigated environment. Similarly, under drought, ICSA 675 × ICSR 13038 (A_1) recorded a 42.64% yield increase over check, reinforcing the strong combining ability of ICSR 13038 as a restorer in enhancing yield resilience. The other hybrids also displayed substantial heterosis, indicating their potential utility in hybrid breeding programmes aimed at enhancing productivity under irrigated and drought conditions.

3.8 | Parents and Hybrid Stability Across Environments

The upset style plot visualizing the stable GCA of seed parents (Figure 2A) and pollen parents (Figure 2B) across environments highlighted several stable GCA parental lines. The pollen parental lines, such as ICSR 13038, Parbhani Shakti and M35-1-19, displayed stable GCA performance across all four environments (E1, E2, E3 and E4). Seed parental lines, notably, ICSA 724 ranks as high stability of GCA in both E1 and E4, while ICSA 57 (E2 and E3) and ICSA 88001 (E3) display more environmental specificity. ICSA 38 displayed high stability of GCA in three environments (E1, E2 and E3).

The GGE biplot mean vs. stability represents the mean yield versus stability view for all tested genotypes, with PC1 and PC2 explaining 41.24% and 23.75% of the variation, respectively (Figure 3). The genotypes are distributed throughout the plot, with most clustering between mean yields of 2.0 and 3.2. Notably, a few genotypes such as G229 (ICSA 735 × ICSR 13038) and G151 (ICSA 675 × ICSR 13038) exhibit exceptionally high mean yields, above 4.0, and also display considerable stability values.

TABLE 2 | Analysis of variance for L×T mating design for nine quantitative traits under drought stress in sorghum.

Components of variance	DF	DFF	DM	PHT	NL	PL	PWI	PWt	HSW	PY
Environments	1	12116.8**	10696.6**	3959.74**	956.12**	741.07**	534.65**	124.74**	304.93**	215.16**
Replications	2	26.72**	43.7**	1.78	1.11	5.81	2.16	14.89**	7.36	12.33
Treatments	279	15.88**	16.26**	43.22**	4.03**	11.51**	3.31**	5.29**	6.02**	5.32**
Hybrids	240	15.42**	15.57**	19.08**	3.38**	6.87**	1.61**	4.1**	3.34**	4.75**
Line	22	36.03**	37.29**	19.5**	4.81**	26.97**	2.09*	4.18**	6.94**	3.46**
Tester	11	135.21**	143.04**	253.38**	17.1**	50.63**	4.58**	10.37**	21.91**	11.57**
Line × Tester	207	6.88**	6.54**	5.27**	2.35**	2.32**	1.39*	3.72**	1.89**	4.49**
Parent	34	19.8**	21.49**	61.36**	5.91**	16.67**	1.93**	0.85	9.64**	1.49
Parent-Lines	22	11.92**	13.46**	6.14**	3.36**	6.26**	2.32	0.75	2.36	1.53
Parent-Testers	11	34.1**	35.62**	36.91**	4.14**	10.79**	0.86	1.09	4.15**	1.42
Parent-Lines vs. Testers	1	36.06**	42.6**	1507.46**	79.23**	314.65**	5.07	0.47	233.05**	1.92
Check	3	12.61**	15.41**	28.99**	0.03	46.69**	5.55	2.17	3.72	3.40
Hybids vs. Parents vs. Checks	2	6.83**	2.62	2383.07**	52.63**	402.03**	227.15**	222.34**	264.09**	132.95**
Env × Treatment	279	7.99**	7.5**	6.78**	2.25**	2.75**	1.53**	3.2**	2.14**	3.55**
Env × Hybrid	240	7.75**	7.31**	5.03**	2.15**	2.22**	1.25	3.47**	2.07**	3.85**
Env × Line	22	6.36**	7.02**	3.43**	2.68**	4.2**	1.55	2.92**	3.52**	5.39**
Env × Tester	11	32.92**	23.09**	17.87**	3.65**	4.64**	1.27	8.55**	2.75	7.05**
Env × Line × Tester	207	6.55**	6.53**	4.35**	2.05**	1.88**	1.20	3.26**	1.83**	3.5**
Env × Parent	34	9.86**	8.97**	11.18**	2.21**	4.54**	2.51	0.92	2.25**	1.07
Env × Parent_Line	11	11.17**	12.15**	1.42	1.71	3.31	2.53	0.65	1.51	0.89
Env × Parent_Tester	11	6.74**	3.69**	9.2**	2.74	4.95**	2.1	0.75	1.30	0.69
Env × Parent-Line vs Tester	1	36.06**	42.6**	1507.46**	79.23**	314.65**	5.07	0.47	233.05**	1.92
Env × Check	3	2.36	3.43**	22.03**	2.85*	9.22**	2.59	8.32**	2.51	7.65**
Env × (P vs. H vs. C)	2	13.27**	9.83**	95.47**	10.89**	28.79**	14.68**	1.39	5.39	3.82

*Significant at the 5% level.
**Significant at the 1% level.

TABLE 3 | Analysis of variance for L×T mating design for nine quantitative traits under irrigated environment in sorghum.

Components of variance	DF	DFF	DM	PHT	NL	PL	PWI	PWt	HSW	PY
Environments	1	6441.98**	7101.92**	2718.67**	2638.88**	864.82**	92.19**	34.95**	1527.77**	3.20
Replications	2	6.53	7.87*	7.04**	1.52	3.68*	26.88**	11.21**	4.72*	17.80*
Treatments	279	12.99**	12.57**	46.94**	3.20**	10.59**	3.66**	7.07**	8.51**	7.19**
Hybrids	240	11.77**	11.19**	18.75**	2.66**	6.64**	1.88**	4.87**	5.29**	5.64**
Line	22	26.46**	23.65**	22.79	5.87**	24.83**	2.43*	5.97**	11.64**	7.64**
Tester	11	90.12**	91.09**	289.83**	15.20**	59.38**	7.13**	22.06**	23.98**	25.54**
Line×Tester	207	5.74**	5.42**	3.50**	1.55**	1.86**	1.54**	3.8**	3.59**	4.31**
Parent	34	21.66**	22.50**	77.37**	4.84**	19.47**	2.46**	1.61*	14.58**	1.39
Parent-Lines	22	8.70**	9.63**	10.21**	2.61**	11.33**	2.17**	1.30	4.13**	1.59*
Parent-Testers	11	30.15**	29.01**	30.82**	3.53**	11.24**	1.42	2.35*	3.65**	1.04
Parent-Lines vs. Testers	1	211.22**	233.08**	2025.29**	67.83**	289.88**	20.37**	0.00	365.77**	0.10
Check	3	5.77*	6.25*	35.85**	1.07**	50.69**	6.58*	4.15*	1.21	6.27*
Hybids vs. Parents vs. Checks	2	1.87	5.15*	2559.28**	39.92**	272.61**	233.63*	352.31**	302.76**	289.09**
Env×Treatment	279	6.39**	6.23**	5.10**	1.90**	2.10**	1.36*	2.68**	1.92**	2.9**
Env×Hybrid	240	6.14**	5.93**	3.90**	1.82**	1.87**	1.26*	2.89**	1.88**	3.13**
Env×Line	22	9.26**	11.25**	3.82**	2.30**	2.98**	0.87	3.98**	5.72**	3.87**
Env×Tester	11	16.08**	13.92**	29.06**	8.34**	2.86*	2.07*	6.76**	3.02*	7.27**
Env×Line×Tester	207	5.24**	4.89**	2.49**	1.45*	1.67**	1.26*	2.56**	1.31*	2.84**
Env×Parent	34	7.26**	7.7**	8.00**	1.88*	3.09**	1.73*	1.41*	2.32*	1.23
Env×Parent_Line	22	8.67**	9.49**	1.70	2.02*	3.65**	1.91*	1.29	2.14*	1.28
Env×Parent_Tester	11	5.69**	4.45**	7.15**	2.72*	1.60	1.66	2.03*	1.16	1.55
Env×Parent-Line vs Tester	1	211.22**	233.08**	2025.29**	67.83*	289.88**	20.37**	0.00	365.77**	0.10
Env×Check	3	13.75**	13.38**	8.25**	1.69	1.40	0.45	1.14	1.19	3.68*
Env×(P vs. H vs. C)	2	18.35**	15.96**	73.87**	8.43**	14.83***	5.97*	0.39	2.35	4.05*

*Significant at the 5% level.
**Significant at the 1% level.
***Significant at the 0.1% level.

TABLE 4 | Estimates of GCA and SCA variances, proportionate gene action and contribution of lines, testers and line × tester interaction on the performance of sorghum hybrids for the characters under study in drought stress.

		Variances of		Degree of dominance		Contributions of		
S. no.	**Trait**	**σ^2GCA**	**σ^2SCA**	**σ^2GCA/σ^2SCA**	**Nature of gene action**	**Line**	**Tester**	**Line × tester**
1	**DFF**	4.10	5.35	0.77	Nonadditive	21.40	40.15	38.45
2	**DM**	4.95	5.74	0.86	Nonadditive	21.89	41.99	36.12
3	**PHT**	196.83	112.13	1.76	Additive	9.96	64.71	25.33
4	**NL**	0.002	0.006	0.33	Nonadditive	13.56	24.10	62.34
5	**PL**	0.77	0.49	1.58	Additive	36.39	34.16	29.45
6	**PWI**	0.00	0.01	0.29	Nonadditive	11.97	13.12	74.91
7	**PWt**	0.02	0.23	0.08	Nonadditive	9.42	11.69	78.89
8	**HSW**	0.01	0.01	0.77	Nonadditive	19.45	30.71	49.84
9	**PY**	0.01	0.20	0.05	Nonadditive	6.72	11.23	82.05

TABLE 5 | Estimates of GCA and SCA variances, nature of gene action and contribution of lines, testers and line × tester interaction on the performance of sorghum hybrids for the characters under study in irrigated environment.

		Variances of		Degree of dominance		Contributions of		
S. No	**Trait**	**σ^2GCA**	**σ^2SCA**	**σ^2GCA/σ^2SCA**	**Nature of gene action**	**Line**	**Tester**	**Line × tester**
1	**DFF**	2.60	4.11	0.63	Nonadditive	21.08	35.90	43.02
2	**DM**	3.34	4.97	0.67	Nonadditive	19.68	37.89	42.43
3	**PHT**	217.07	62.15	3.49	Additive	11.36	72.23	16.41
4	**NL**	0.003	0.003	1.07	Additive	20.92	27.09	51.98
5	**PL**	1.04	0.39	2.67	Additive	34.48	41.22	24.30
6	**PWI**	0.01	0.03	0.35	Nonadditive	11.86	17.40	70.74
7	**PWt**	0.05	0.22	0.21	Nonadditive	11.32	20.91	67.78
8	**HSW**	0.01	0.04	0.33	Nonadditive	20.28	20.89	58.84
9	**PY**	0.04	0.19	0.21	Nonadditive	12.53	20.95	66.52

3.9 | Parental Lines Seed Producibility Under Drought and Irrigated Environments

Depending on a variety of parameters, such as the producibility of the female parent, the synchronization of female and male flowering, the lack of processing losses and the presence of acceptable seed quality characteristics, each hybrid parent had a unique degree of producibility. The yield potential is a genetically determined ability of parents/genotypes to generate optimal yield in specific environments. The results (Figure 4) clearly indicate that the yield potential is largely a genetically determined ability of parental lines to perform optimally in specific environments. Under drought conditions, ICSB-735 (A_2) recorded the highest seed producibility (97.0%), followed by ICSB-502 (94.3%), ICSB-37 (93.3%), ICSB-52 (93.3%) and ICSB-56 (93.3%) also maintained high stability. In contrast, ICSB-57 showed the lowest seed producibility (78.3%) under drought stress. Under irrigated conditions, the seed parental lines ICSB-724 (97.5%) (A_2) and ICSB-712 (96.5%) (A_2) performed the best, followed closely by ICSB-758 (96.5%). The seed parental lines, ICSB-502 and ICSB-88001 (A_1), also showed strong performance, each recording 96%. Across environments, B-lines associated with the A_2 conversion stream exhibited higher seed producibility than those associated with the A_1 stream. Because these evaluations were conducted on maintainer lines, the observed differences reflect the genetic backgrounds of the B-lines and should not be interpreted as cytoplasm (A_1 vs. A_2) effects. The consistently higher seed producibility observed among A_2 stream maintainer lines across environments underscores the value of their nuclear genetic backgrounds and, operationally, the A_2 CMS system's capacity owing to fewer restorers to broaden and diversify the female pool, including drought-tolerant lines.

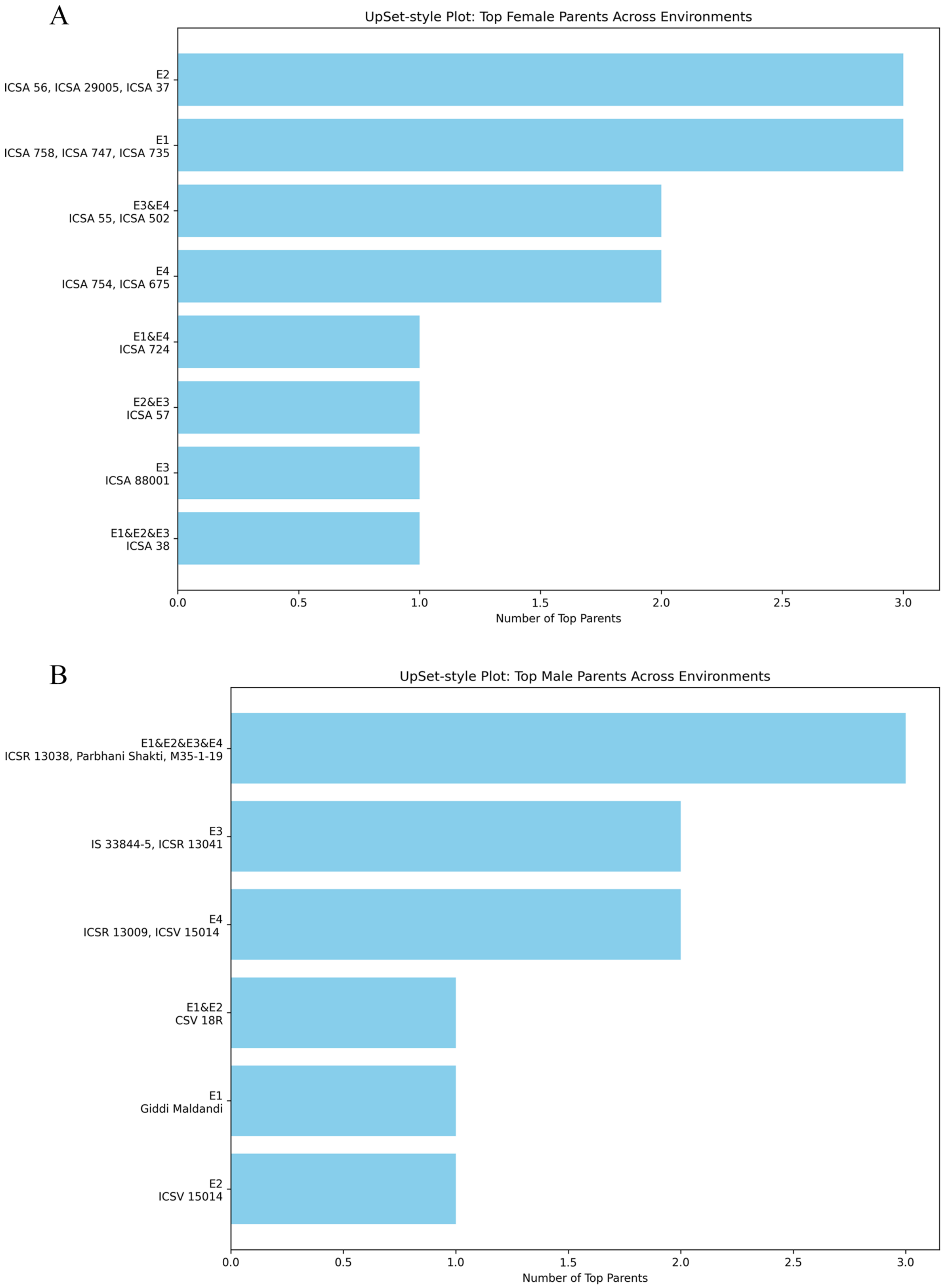

FIGURE 2 | Legend on next page.

FIGURE 2 | Upset style plot visualizing the top-performing seed parent (Figure 2A) and pollen parent (Figure 2B) among the environments studied. (E1: 2021 post-rainy—drought, E2:2021 post rainy—irrigated, E3:2022 summer—drought, E4: 2022 summer—irrigated).

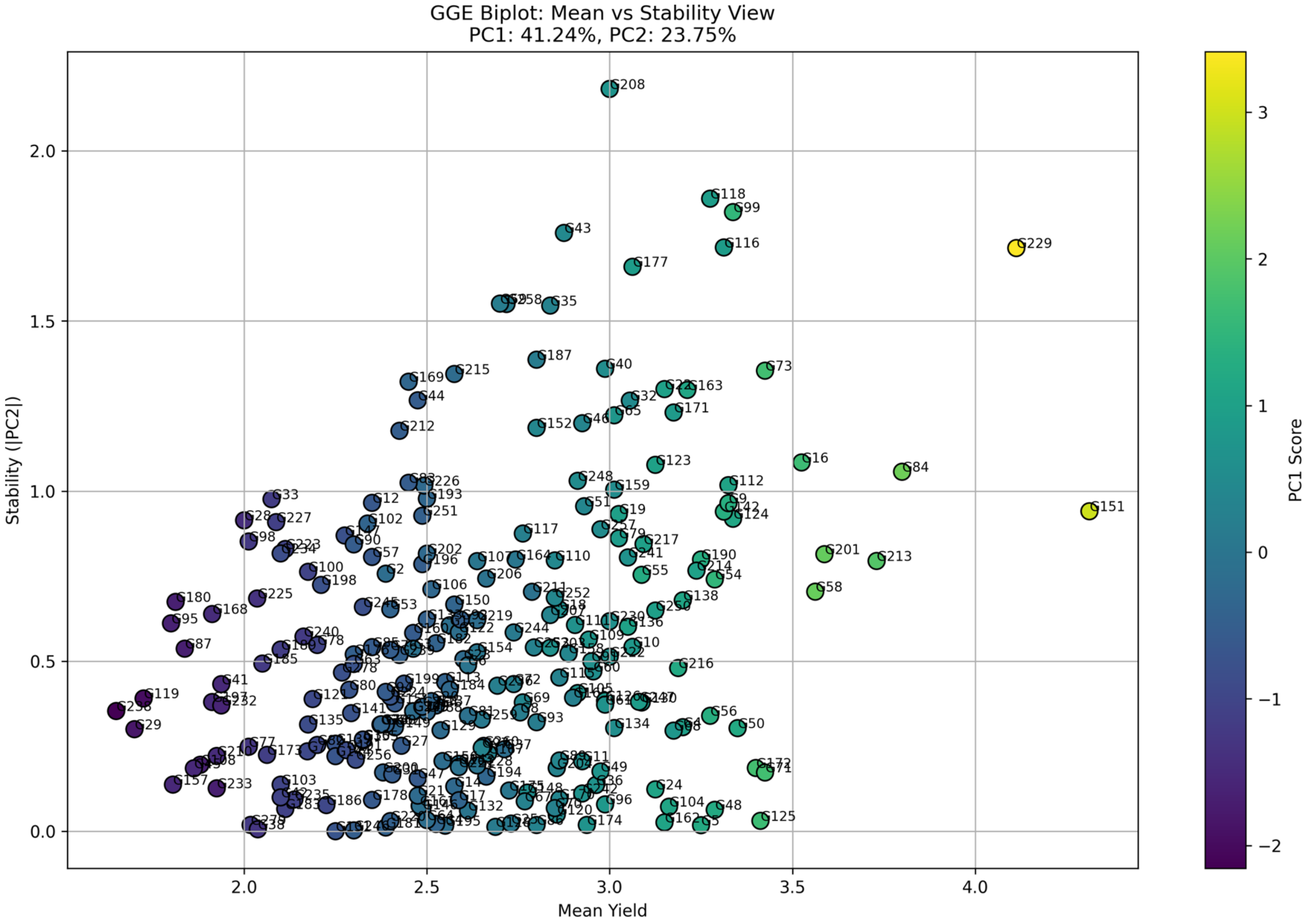

FIGURE 3 | GGE biplot: mean vs. stability showing the relationship between mean performance and stability of genotypes evaluated across four environments.

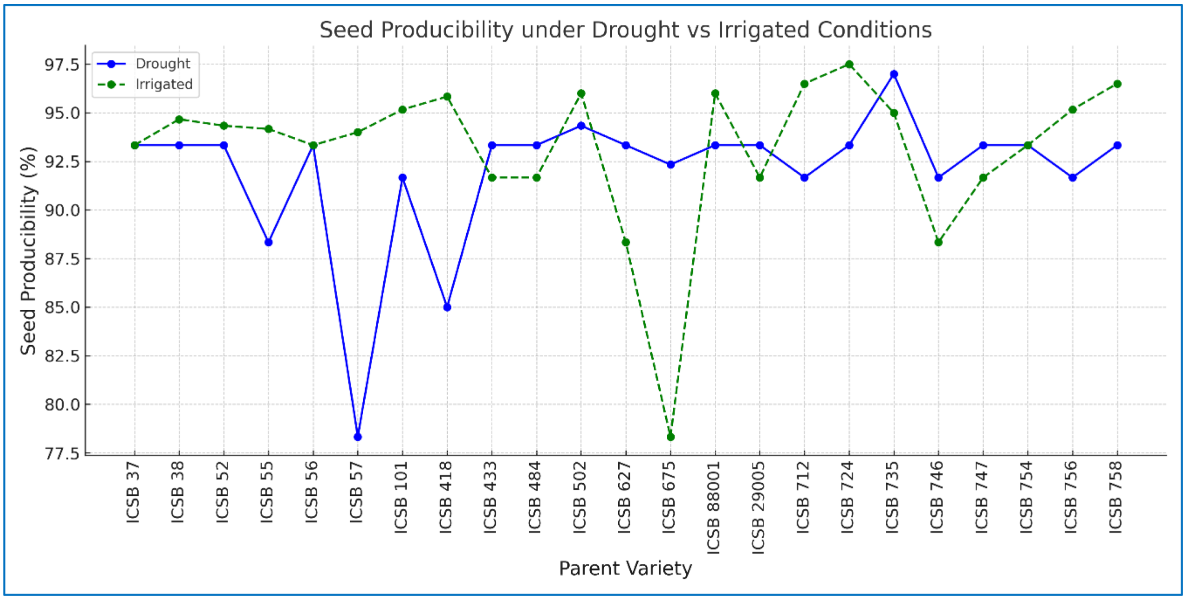

FIGURE 4 | Seed producibility of parental lines under drought and irrigated conditions.

4 | Discussion

Estimates of GCA indicate the prevalence of favourable alleles with additive effects in parental lines. Assessing the GCA of each parent is essential for the development of superior hybrid genotypes as it provides information for breeders to assess the genetic potential of breeding material for various desired traits (Medraoui et al. 2023). Conversely, SCA effects offer valuable insights into hybrid performance (Cruz et al. 2012). The magnitude of the GCA/SCA ratio is strongly influenced by the genetic divergence between female and male pools. In our opinion, however, the establishment of heterotic pools does not necessarily increase the GCA effects in sorghum; rather, it utilizes and identifies desirable GCA effects within distinct germplasm groups to efficiently develop superior hybrids. According to Singh and Gupta (2019), establishing heterotic pools allows for the improvement of GCA within the pools and, consequently, for the increase of SCA between them. By grouping genetically dissimilar individuals into distinct heterotic pools, breeders can maximize heterosis in crosses between these pools, leading to superior hybrid performance and higher yields. This understanding is crucial for breeding programmes, as knowledge of combining ability components is vital for selecting genetically diverse parents for cross-breeding initiatives. This is crucial for identifying promising hybrids or developing superior lines from them (Allard 1956).

The correlation coefficients between grain yield (PY) and most of the evaluated traits were generally low, except for panicle weight (PWt), which exhibited a consistently high positive correlation both within individual environments and across environments. Panicle weight was therefore identified as the sole trait capable of reliably determining grain yield, in conjunction with the major component traits examined in this study. This finding is particularly valuable in the context of shuttle breeding or when cropping seasons occur in close succession (e.g., *kharif* and *rabi* in Asia), where limited time and resources constrain the ability to thresh entire plots or record grain weight across extensive breeding pipelines. Under such conditions, panicles can be harvested from whole plots and weighed for selection purposes, while only a portion may be threshed to obtain seed for advancing selected lines to the next season. Threshing of the remaining panicles and/or weighing of the seed can be deferred to a more convenient time or omitted altogether, depending on the breeder's requirements, thereby optimizing both efficiency and resource use. Therefore, selecting for panicle weight can significantly speed up sorghum breeding because it allows breeders to select for high-yield potential before threshing and individual grain calibration, which are labour-intensive post-harvest processes. High panicle weight is linked to desirable traits like large panicles, good grain filling and a high grain-setting rate, making it an effective indirect selection criterion for increasing yield.

The predominance of GCA effects for several traits highlights the role of additive gene action, particularly for PL and PH, where GCA/SCA variance ratios exceeded unity, indicating strong heritability and scope for early selection. These results corroborate earlier reports that additive effects largely determine the inheritance of morphological traits in sorghum (Sarker et al. 2003; Hill and Mackay 2004). In contrast, significant SCA effects for grain yield, panicle weight and HSW underscore the contribution of nonadditive gene action, including dominance and overdominance, which are critical for identifying superior hybrids (Zhou et al. 2017; Alam et al. 2007). Such patterns reflect the complexity of genetic control in sorghum and the importance of exploiting both additive and nonadditive effects in hybrid development. Among CMS lines, ICSA 38 and ICSA 502 (A_1), ICSA 724 (A_2) and ICSA 758 (A_4) showed desirable GCA effects for grain yield and panicle weight, while exhibiting negative effects for DFF, maturity and PH, making them ideal for breeding medium-height, high-yielding hybrids under drought conditions. Under irrigated environments, lines such as ICSA 37, ICSA 56, ICSA 57, ICSA 433, ICSA 502, ICSA 627, ICSA 675 and ICSA 29005 (A_1), along with ICSA 724 (A_2), emerged as effective combiners for multiple traits.

Under drought conditions, the restorer lines Parbhani Shakti and ICSR 13038, effective on both A_1 and A_2 cytoplasmic backgrounds, exhibited strong GCA for PWt, grain yield, early flowering, early maturity and medium PH. In irrigated environments, ICSV 15014, Parbhani Shakti, ICSR 13009 and ICSR 13038 were identified as good general combiners for DFF, DM, panicle weight and grain yield, with ICSV 15014 and ICSR 13009 further demonstrating stability as universal restorers across A_1, A_2, A_3 and A_4 cytoplasmic backgrounds (Kasanaboina et al. 2024). Collectively, these results highlight the availability of restorer lines with both drought tolerance and broad adaptability across environments and cytoplasmic sources. Notably, Parbhani Shakti and ICSR 13038 showed desired GCA effects for grain yield and associated traits, making them exceptional candidates for restorer parents on A_1 and A_2 backgrounds. Incorporation of such stable and universal restorers into breeding pipelines will not only sustain hybrid seed production but also diversify hybrid development, thereby enhancing resilience to climate variability and contributing to sustainable food production. The hybrid ICSA 675 × ICSR 13038 (A_1) exhibited the highest significant SCA effects for grain yield under drought conditions, while ICSA 735 × ICSR 13038 (A_2) had the highest SCA effects for grain yield under irrigated conditions. The significance of SCA effects in determining hybrid performance has been highlighted in numerous studies. Various studies, Sayed and Said (2016), Mengistu et al. 2020, Kenga et al. 2004, Jain and Patel (2014), Aruna et al. 2010 and Akata et al. (2017), have reported that SCA effects play a more dominant role than GCA effects in influencing grain yield and its related traits in sorghum.

For hybrid breeding programme to be successful, it is essential to maintain an acceptable amount of heterosis for grain yield and associated attributes. Thus, the distinct genetic makeup of the germplasm collection governs the degree of heterosis. Grain yield heterosis varied from 39% to 80% (Quinby 1967), whereas Wagaw and Tadesse (2020) reported heterosis ranging from 52.1% to 123.5%. Our research demonstrated that key agronomic characteristics of sorghum hybrids exhibited significant MPH and BPH. In the irrigated environment, the maximum MPH of PY was 220.4%, whereas in a drought environment, it was 231.5%. The maximum BPH for PY was 174.1% in an irrigated environment and 208.8% in a drought environment. Since the majority of breeding initiatives prioritize increasing grain yield (Blum et al. 1990), we identified grain yield as a key performance indicator for hybrids since no F1 sorghum hybrids exhibited strong, desirable SCA and high heterosis impacts across all the combination traits we evaluated.

Upon comparison of heterosis across water regimes, PY heterosis tended to be more pronounced under irrigated conditions. For instance, the cross ICSA 735 × ICSR 13038 (A_2) recorded the highest yield heterosis (65.7%) under irrigation, whereas the best-performing cross under drought (ICSA 675 × ICSR 13038 [A_1]) showed comparatively lower heterosis (42.6%). This pattern suggests that favourable growing conditions allow fuller expression of dominance and overdominance effects, resulting in higher yield heterosis under irrigated conditions. Under drought, heterosis levels were relatively subdued, possibly due to stress-induced constraints on resource allocation and reduced expression of genetic potential. The next best cross under irrigation, ICSA 56 × Giddi Maldandi, expressed 37.41% heterosis for yield, which was slightly lower than the top-performing cross but still substantial. In contrast, under drought, ICSA 724 × ICSV 15014 recorded 30.23% yield heterosis, representing the next best after ICSA 675 × ICSR 13038. This again shows that yield heterosis values are generally higher under irrigation than drought. The reduction in heterosis under drought may be explained by the physiological and metabolic limitations imposed by water deficit, which restricts the full expression of hybrid vigour. Similarly, the PWt exhibited substantial positive heterosis in both regimes, though higher values were again observed under irrigation (ICSA 735 × ICSR 13038, 46.18%) compared to drought (ICSA 675 × ICSR 13038, 30.65%). This suggests that panicle weight remains a stable and reliable contributor to yield even under stress, but its full potential is maximized under irrigated conditions. In nature, drought stress exacerbates the productivity challenges of sorghum, making the enhanced performance of hybrids crucial for developing resilient and high-yielding varieties, as heterosis breeding is a key strategy for achieving drought tolerance in sorghum hybrids. Studies have shown that hybrids can demonstrate better water use efficiency, root traits and photosynthetic performance under drought conditions, resulting in higher final productivity and yield (Dai et al. 2024).

The mean versus stability analysis identified the hybrids ICSA 675 × ICSR 13038 (G151) and ICSA 735 × ICSR 13038 (G229) as highly stable across environments. Both genotypes demonstrated superior mean yields in combination with consistent performance, indicating their suitability for cultivation across diverse moisture regimes. Such stable hybrids are valuable targets in breeding programmes aimed at developing varieties with reliable productivity under variable conditions.

PH is a critical trait influencing both agronomic performance and harvestability. In modern mechanized systems, particularly in the United States, Europe and Australia, grain sorghum hybrids exceeding 200 cm are considered impractical for combine harvesting due to increased risks of lodging, header losses and reduced harvesting efficiency. In these systems, hybrids are typically bred to a stature of 1.1–1.4 m, with well-exerted panicles and sturdy stalks that facilitate efficient machine operations (Hu et al. 2018). In contrast, the production environment in India presents a different context. Sorghum in many regions is still cultivated under traditional or subsistence systems where harvesting is carried out manually or with tractor-operated reaper-windrowers (Nalawade et al. 2009). In such situations, hybrids with PH around 180–200 cm can still be agronomically and commercially viable, particularly when they combine early maturity, drought resilience and high grain yield. Our results illustrate this trade-off. Hybrids such as ICSA 675 × ICSR 13038 (~200 cm) achieved a 42% yield increase over the best-performing check, alongside early flowering, early maturity and superior grain and panicle weight, indicating strong adaptability under drought. Similarly, ICSA 55 × ICSR 13038 and ICSA 433 × ICSR 13038 (A_1 cytoplasm) also outperformed checks by 3.38% and 7.88%, respectively, despite their ~200-cm stature.

Encouragingly, some high-yielding hybrids exhibited more moderate PH closer to the ideal for mechanization. For instance, ICSA 724 × ICSV 15014 (A_2 cytoplasm) combined a 30.23% yield advantage with ~180-cm stature, early maturity and high panicle and grain weight, making it a promising candidate under drought. Likewise, ICSA 52 × Giddi Maldandi (A_1 cytoplasm; ~180 cm) yielded 10.85% more than the check, striking a balance between productivity and reduced height. These findings suggest that while tall hybrids (~200 cm) with high-yield potential may remain relevant under hand-harvested or semi-mechanized systems in India, the development of shorter, high-yielding and drought-tolerant hybrids (~170–180 cm) will be increasingly important to align with evolving mechanization trends. The contrasting performance of hybrids also underscores the importance of parental lines from cytoplasmic backgrounds and restorer parents such as ICSR 13038 and Parbhani Shakti, both of which displayed strong GCA in shaping plant stature and harvest suitability.

The present study highlights the contrasting performance of sorghum parental lines under drought and irrigated environments. Among the evaluated parental lines, ICSB-735 (A_2) achieved the highest producibility under drought (97.0%), while ICSB-724 (97.5%) (A_2) and ICSB-712 (96.5%) demonstrated superior performance under irrigation. Lines such as ICSB-502, ICSB-37, ICSB-52 and ICSB-56 maintained high producibility (> 93%) (A_1) across both environments, with ICSB-502 and ICSB-88001 achieving 96% under irrigation. Our findings highlight a breeding programme opportunity rather than a cytoplasmic effect. Because we scored maintainer (B) lines, we did not evaluate pollen-sterile A-lines and therefore cannot attribute differences to A_1 vs. A_2 cytoplasm. Future work directly comparing A-lines in A_1 and A_2 cytoplasms under identical nuclear backgrounds is necessary to quantify cytoplasm effects on seed producibility. In sorghum, A_2 typically has fewer restorers than A_1, which can expand the usable female parent pool: Drought-tolerant or otherwise elite backgrounds that would be restored under A_1 can remain nonrestored under A_2, facilitating their deployment as female seed parents. Thus, our data were generated on B-lines (nuclear genetic background), and they support the strategic use of the A_2 CMS system to diversify and strengthen the female pool for hybrid seed production under both stress and optimal conditions.

5 | Conclusion

This research underscores the pivotal role of cytoplasmic diversification in advancing sorghum hybrid breeding, with an emphasis on the strategic incorporation of A_2 CMS lines alongside the widely adopted A_1 system. Both A_1 and A_2 parental lines demonstrated robust GCA, while their respective hybrids exhibited pronounced SCA and marked heterosis, particularly under drought conditions. The identification of stable parental lines and hybrids that consistently perform across varying moisture regimes highlights their suitability for deployment in environments with unpredictable water availability. Importantly, PWt emerged as a dependable indirect selection criterion for grain yield, thereby streamlining the breeding process and enhancing selection efficiency. The expansion of the female parent pool through the inclusion of A_2-based lines facilitates the integration of drought-tolerant germplasm, directly addressing critical challenges in sorghum improvement. These findings advocate for the targeted integration of diverse cytoplasmic sources to broaden genetic variability, reinforce yield stability and bolster resilience in sorghum hybrids. Increasing the representation of A_2 cytoplasm within breeding programmes is strongly recommended to expedite the development of high-yielding, stress-resilient cultivars. Overall, this study offers practical guidance for breeders seeking to enhance sorghum productivity and sustainability, especially in the context of shifting climatic patterns and the growing need for reliable, adaptable crop varieties.

Author Contributions

Krishna Kasanaboina: writing – original draft, investigation, formal analysis. **B. V. Vara Prasad:** writing – review and editing. **C. V. Sameer Kumar:** writing – review and editing. **D. Saida Naik:** writing – review and editing. **D. Srinivasa Chary:** writing – review and editing. **Sonal Chavan:** writing – review and editing. **Vinod Kumar Reddy Yaram:** writing – review and editing. **Sunita Gorthy:** writing – review and editing. **Jayakumar Jaganathan:** writing – review and editing. **Ephrem Habyarimana:** writing – review and editing, supervision, methodology, conceptualization.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

Data will be made available on request.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section. **Table S1:** Estimates of specific combining ability (SCA) effects of hybrids for grain yield and yield-contributing traits under drought conditions. **Table S2:** Estimates of specific combining ability (SCA) effects of hybrids for grain yield and yield-contributing traits under irrigated conditions. **Table S3:** Estimates of mid-parent heterosis, better-parent heterosis and standard heterosis of hybrids for grain yield and yield-contributing traits under drought conditions. **Table S4:** Estimates of mid-parent heterosis, better-parent heterosis and standard heterosis of hybrids for grain yield and yield-contributing traits under irrigated conditions. **Table S5:** Estimates of general combining ability (GCA) effects of lines and testers for grain yield and yield-contributing traits under drought stress in sorghum. **Table S6:** Estimates of general combining ability (GCA) effects of lines and testers for grain yield and yield-contributing traits under irrigated conditions in sorghum.