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Evaluation of fodder yield and fodder quality in sorghum and its interaction with grain yield under different water availability regimes

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ABSTRACT

Sorghum is widely grown as a failsafe crop in semi-arid regions particularly in post rainy season. Though the effect of drought on crop performance is studied widely there are few studies illustrating the association of fodder quality and agronomic traits under drought. To study the interactions we evaluated a set of 24 cultivars under drought for three years in post rainy season. The effect of drought was evident in delayed flowering (by 2 days) and reduce plant height (by 0.98 cm) compared to control. The fodder digestibility traits were reduced (*in vitro* organic matter digestibility by 2.25 times) under drought. All the plant growth and yield parameters recorded higher heritability compared to fodder quality parameters (<0.75) in most of the season in both control and stress environments. The scatter plot showed best (ICSV700-P10, N13, PB15881-3, SP 2417-P3) and poor (296B, ICSB377-P1, ICSV1, IS9830) performing entries in control and stress plots. The agronomic and the fodder quality traits have shown no significant relationship between them, hence independent association can be utilized to breed for desirable traits. Identification of contrasting lines could be the key to identify genes controlling the fodder quality traits under drought.

1. Introduction

Sorghum is the fifth most important grain crop in the world, and a major food crop in the Asian and African continents. In India, sorghum is cultivated in an area of 5.7 m ha, and a production of 3 m tonnes is recorded (PDFSR database). Sorghum plays an important role as fodder, in the health and nutrition of a large livestock population in India, having 20 % livestock population of the world [1]. Livestock in semi-arid and tropics are underproductive and weak, due to the unavailability of feed and competition for land with other crops. Marginal farmers may have limited opportunities to cultivate, particularly during the lean season, where owning livestock is an alternate income generator. These farmers use crop residues for livestock feeding, which are reported to be low in nutritional quality. This indirectly affects the productivity of livestock and thus in turn affecting farmers' livelihood and income. To address this issue, in the last decade, crop improvement has shifted the focus on the development of dual-purpose cultivars. Dual-purpose crop has been of keen interest to improve both grain yield and biomass quality. This increases the chances of smallholder farmers running a mixed livestock-crop system. These dual-purpose crops not only increase the feed quality but also reduce the land and water competition.

Sorghum is one such dual-purpose crop where all the plant parts have economic use due to whole plant utilization. It is a potential candidate for yield in terms of grain and biomass (feed) with optimal inputs during crop cultivation and or under adverse climatic conditions. The innate drought resistance nature of the crop has opened wide suitability for cultivation in the drier agro-ecologies. It competes with corn in the area where water is a scarcer resource, predominantly in semi-arid and tropics. Sorghum not only proved to be high yielding than maize under conditions of limited water supply [2] but also showed fodder quality on par with that of maize [3]. It is mostly cultivated in post rainy (*rabi*) season in India, and most of the cultivation is taken in *vertisols* as they have high water retention capability [4]. During the plant life cycle

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in post rainy, it encounters terminal drought stress, major pests and disease which reduce yield and quality. Farmers run into a huge loss as grain yield is reduced and the quality of biomass is declined. This has a high financial and economic impact because a difference of 5% units in *in vitro* matter digestibility (IVOMD) – a key fodder nutritional trait, which is highly correlated with stover pricing – is associated with a price premium of 20 % and higher [5]. To assess the quality of the fodder produced, near-infrared spectroscopy (NIRS) has been standardised by (ILRI-India); although it invloves destructive sampling, this method has been optimized using the wet lab data for all the traits under study.

Several factors influence biomass quantity and quality, major reasons are biotic (pest and disease) or abiotic stress (drought, salinity, and nutrition), followed by genotype-dependent variations, stage of crop harvest (flowering, dough grain or maturity) and environmental effects during growth. Major pest like shoot fly incidence at early crop growth stage is known to reduce yield (both biomass and grain), in the post rainy season under highly irrigated conditions [6]. Drought effect on plant invariably causes a delay in flowering, decreases biomass quantity and quality, and increases lignin accumulation [6,7]. Stage of crop harvest and environmental factors are known to have high influence on the forage quality [9]. Interaction between drought and stalk rot has shown that the well-irrigated plants have a lesser incidence of disease than plants under stress [10]. Relation among fodder quantity and quality studies will help to breed for traits without any forfeiture [11, 12]. Additionally, a broad genetic base for higher genetic gain is the path for sustainable sorghum production as the diversified lines ensure resilience in the crop improvement program. Released cultivars with stress tolerance can be a good source to tap the cryptic gene combinations for higher yields. Genotypes in multi-year trials are highly influenced by environmental factors which show confounding effects on trait heritability or stability. Assessment of the trait performance across the year is crucial accounting the G × E interactions and biplots are suggested as the best method to dissect the effect of G × E [13].

Drought experiments are more focused on plant behavior, grain and biomass yield and only limited experiments have been performed for drought response on fodder quality particularly for terminal drought in *vertisols*. Dual-purpose crop improvement can be accelerated along with the information derived on laboratory traits. The dual-purpose sorghum cultivars are promising and have been identified and validated using simple laboratory traits that can be used for phenotyping the entries for higher digestibility [14]. It has been stated repeatedly that sorghum fodder is marginally rich in nutrients, produces an optimal level of yield and thus can be used as potential fodder in scarce rainfall areas [3]. In this study, we examined the effect of drought and controlled conditions in the field for three years to genrate agronomic data and NIRS data was generated for respective biomass samples by scanning. These along with GBS data was used to identify the best contrasting parents for two prime traits i.e. dry stalk weight and IVOMD.

2. Materials and methods

2.1. Genetic material

The test entries comprise 24 accessions, these entries were used for developing recombinant inbred lines (RIL) populations. The accessions, in pairs, segregated for several traits important for sorghum production and were used for development of RIL populations (Table 1). The traits for which these accessions segregate include important, biotic and abiotic stresses, agronomic and yield parameters, and few novel traits such as Biological Nitrification Inhibition (BNI). This diversity was the primary reason for exploring the genetic variability (magnitude) for fodder quality in sorghum. This study will help to find a suitable RIL parent amongst the available set to start dissecting fodder quality further.

Table 1
The list of germplasm used as parents of the RIL population evaluated in the current study.

S. No.	Germplasm name	# Traits	DFF (days) *	PH (cm) *
1	296B	SFR, SBR, APH,GMR, BNI, Zn-Fe	80	111.11
2	BTx623	ST, SWT	71	131.39
3	Bulk Y-P1	GMR	67	122.12
4	E 36-1	STG, SHL	73	157.91
5	ICSB370-2-9-P2	GMR	72	156.42
6	ICSB377-P1	GMR	76	158.04
7	ICSR93024	ST, SWT	80	246.54
8	ICSV1	SFR, SBR	70	151.15
9	ICSV700-P10	SFR, SBR	73	229.60
10	ICSV745	SBR	74	159.41
11	ICSV93046-P1	ST	75	221.34
12	IS18551	SFR, SBR, APH	76	222.00
13	IS41397-3-P6	GMR	75	152.40
14	IS8219-P1	GMR	71	159.04
15	IS9830	STG, SHL	61	186.06
16	M 35-1	OPV	72	221.28
17	N13	STG, SHL	68	183.82
18	Parbhani Moti	OPV	75	226.78
19	PB15220-1	SBR	70	133.43
20	PB15881-3	SBR	76	133.23
21	PVK 801-P23	GMR, BNI, Zn-Fe	80	156.60
22	S35	ST, SWT	75	167.71
23	SP 2417-P3	GMR	83	117.30
24	SP 39105-P7	ST	72	217.00

DFF-Days to fifty percent flowering; PH-plant height (cm); *- Trait mean values derived from across years and water regimes.# Parents segregating for target trait for which bi-parental mapping population developed; Shoot Fly Resistance-SFR; Stem Borer Resistance-SBR; Stay-green expression-STG; Aphids resistance-APH; Grain Mold Resistance-GMR; Salinity tolerance-ST; Stem Sweetness and related traits-SWT; Biological Nitrification Inhibition-BNI; Zn and Fe grain density/micronutrient bio-fortification- Zn-Fe; Striga resistance-SHL, OPV-Popular OPV cultivated in post rainy season in India.

2.2. Experiment details

The set of 24 entries were planted during short days of photoperiod season of post rainy which normalized the photoperiod response. The experiment was laid out in an alpha lattice design with 3 replications each under control (irrigated) and stress (irrigation withheld). The trial was conducted for three years - 2012, 2013, and 2015 in post rainy season in *vertisols* (black soil). Year-wise weather parameters for all three years during the crop growth period from October to March are furnished (Fig. 1).

2.2.1. Agronomic practices and drought induction

Sowing was performed on tractor mounted 4 cone planter (John Deer, 7100 US model) with a spacing of 60 cm between rows and 10 cm between plants. A basal dose of ammonium phosphate @150 Kg/ha and no other form of fertilizer was applied. All entries were sown in 2 rows of 6 m length out of which central 4 m was harvested to record observations. All practices of plant protection were applied similarly for both control and stress plots except irrigation. Irrigation was withheld in the stress field before initiation of booting, at 50 Days After Sowing (DAS) and continued further until maturity, whereas in control plots irrigation was provided whenever required. Further to avoid water seepage from control to stress plots, buffer rows (8) of bulk sorghum were sown between two treatment plots.

2.3. Phenotyping for agronomic traits

The parameters mentioned below were considered to collect data regarding the response of agronomic traits and yield parameters with fodder quality traits. Days to fifty percent flowering (anthesis in half of panicle and half of plot population), plant height (plant basis-from base

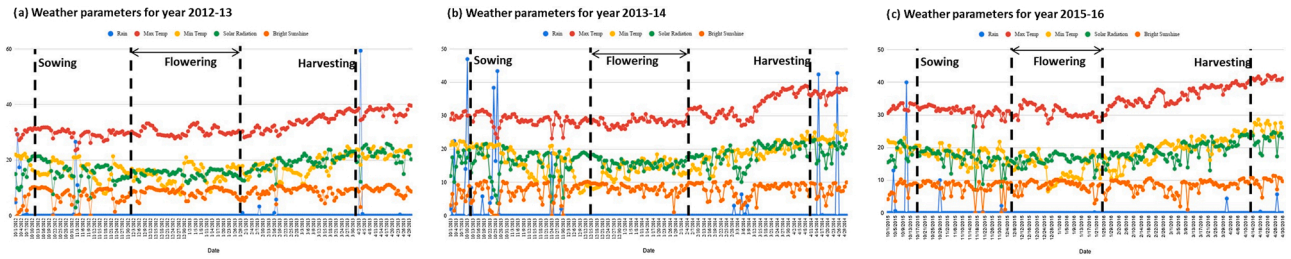


Fig. 1. Weather parameters during the period of conducting trial indicating from time from sowing to flowering up to harvesting time for the year (1a) 2012-13, (1b) 2013-14 and (1c) 2015-16.

of plant the to tip of panicle-cm), grain yield (weight from per plot-Kg), stalk yield (fresh and dry per plot- Kg), and test weight (100 seed weight-g).

2.4. Phenotyping for fodder quality traits

Post recording of agronomic traits the biomass was dried, chopped, and ground to allow the powdered fodder pass through a 1 mm sieve). Following fodder quality traits were recorded: nitrogen (N%, dry matter basis), NDF (neutral detergent fiber-%), ADF (acid detergent fiber-%) and *in vitro* organic matter digestibility (IVOMD-%) were determined by Near-Infrared Spectroscopy (NIRS) calibrated against conventional wet laboratory analyses. The NIRS instrument used was a FOSS Forage Analyzer 5000 (FOSS XDS RCA, Win ISI IV, Denmark) with software package Win ISI II. Few outliers were observed and samples were rescanned to capture proper data points. A basal NIRS calibration was developed and validated by conventional laboratory analysis for sorghum using calibration and validation set with a Global H value of 1 [15]. The basal NIRS equation was developed and validated by conventional laboratory analysis and updated by analysing 10 % of the new stover sample submission [15].

2.5. Statistical analysis

Combined analysis of variance across years and treatments were performed using the Restricted Maximum Likelihood (ReML) procedure of GenStat 17 edition for Windows (VSN International, Hemel Hempstead, UK, 2015) considering year, treatment and replication as fixed, block and entry as random factor. BLUP's (best linear unbiased prediction-random effect terms) and BLUE's (best linear unbiased estimation-fixed effect terms) were estimated from the combined analysis of variance. Broad sense heritability was performed for combined and individual environments. The site regression model (commonly known as GGE Biplot) [16] was used to visualize the GEI patterns and to understand the interrelationships among various test genotypes and across years. Pearson's correlation was performed to establish a relationship between all agronomic and NIRS traits under both the treatments.

2.6. Genotyping and phylogenetic analysis

Out of the 24 parents used in the study due to poor germination only 22 entries were sequenced. DNA was isolated from leaves of each accession at 4- to 6-leaf stage using the modified hexadecyltrimethyl ammonium bromide (CTAB) protocol [17] from 12-day-old seedlings and genotyping done following the GBS (genotyping by sequencing) approach [18] with ApeKI restriction enzyme used for complexity reduction. SNPs were called using TASSEL v5.2 GBS pipeline against sorghum assembly v3.1. The SNP calling was performed on TASSEL 5.2 with default parameters, followed by filtering for minimum allelic frequency (MAF) of 0.01, recording a final SNP count of 55,136 after filtering. Phylogenetic analysis was performed using the unweighted pair-group method with arithmetic mean (UPGMA) algorithm implemented in TASSEL v5.2.58 [12,19]. The hierarchical population structure was estimated by using the ADMIXTURE program, a model-based estimation of ancestry in unrelated individuals using the maximum-likelihood method [20]. ADMIXTURE implements a cross-validation (CV) feature that allows, together with the number of iterations to convergence, to determine the number of subpopulations (k values) that best fits the data. An analysis of molecular variance (AMOVA) to estimate population differentiation among populations with 1000 permutations was performed using Arlequin version 3.5.2.2 deriving the population level differentiation statistics (FST) [21]. Gowers distance matrix was performed on R version 3.6.2 using the cluster package and daisy function and respective phylogeny tree for different years and pooled was constructed in Darwin 6.0.21 using hierarchically clustering in UPGMA (unweighted pair group method with arithmetic mean).

3. Results

3.1. Treatment (drought) effect

Treatment effect (drought-irrigation withheld at 50 DAS) showed low values of mean, range, $\sigma^2 g$ and heritability for all agronomic traits, except for days to fifty percent flowering (Table 2). A similar trend was observed for fodder quality traits except for fiber fractions where mean, range, $\sigma^2 g$, $\sigma^2 g \times y$ were high under stress. However, heritability was still high in control than under stress for fiber fractions as well. Stress plots on average have a delayed flowering by 2 days. Plant height was 10 cm less in stressed plants compared to control plants. The reduction in grain yield by 322 g plot^{-1}, fresh weight by 3948 g plot^{-1}, dry weight by 29 g plot^{-1}, test weight by 0.5 g, IVOMD by 2.25 % was observed. The nitrogen content was recorded higher range under control conditions (0.80–1.00 %) than in stress (0.75−0.95%). Whereas fiber fractions were accumulated more under stress conditions (NDF 60 % and ADF was 42.71 % in stress) than under control, (NDF-56.51 % and ADF-40.30 % under control). The IVOMD has a significant difference in trait heritability under stress (32) compared to control (82).

3.2. Year-wise effects

Significant variations were observed for all traits recorded in different years under two treatments. The variation across year is high and does not follow a definite pattern, indicating the role of unpredictable environmental conditions. Year-wise mean, range, genotypic variance (standard error) and heritability for agronomic and fodder quality traits under both treatments are presented in Table 2.

3.2.1. Agronomic traits

Average duration observed for flowering was high in 2013 (85 days) in 2012 (72 days) and 2015 (61 days) under control whereas under stress 71, 88 and 65 days respectively in 2012, 2013 and 2015. Plant height was low in 2012 (159 cm) and was similar in 2013 and 2015 (185 and 186 cm) under control while in stress the 153, 173 and 172 cm in 2012, 2013 and 2015, respectively. Grain weight was low in 2013 (1522

Table 2
Year-wise mean, range, genotypic variance and broad-sense heritability for agronomic and fodder quality traits under both treatments.

Trait	Treatment	Control				Stress			
	Year	Mean	Range	σ^2g (±SE)	h^2	Mean	Range	σ^2g (SE) (±SE)	h^2
	2012	72	55.51–85.44	59.82** (±17.81)	99	71	54.64–85.04	53.287** (±15.83)	99
DFF	2013	85	66.77–100.15	61.12** (±18.34)	99	88	68.14–102.06	47.09** (±14.41)	98
	2015	61	56.30–68.98	9.57* (±6)	75	65	59.59–74.79	39.21* (±16.23)	84
	2012	159.02	113.85–246.89	1188.95** (±355.5)	99	153.45	95.42–229.86	1430.96**(±426.09)	99
PHT	2013	185.74	115.47–259.72	2001.98 **(±596.57)	99	173.31	109.91–239.63	1674.85** (±498.97)	99
	2015	186.20	120.11–286.49	2475.04 **(±736.35)	99	172.69	111.00–240.96	1736.39 **(±515.52)	99
	2012	1707.09	1172.3–2114.1	70,144** (±29475)	75	1512.35	881.03–2043.84	123238 **(±42404)	90
GW	2013	1522.04	861.25–2186.91	68633** (±22021)	95	1126.94	430.43–1844.04	82477 **(±25938)	96
	2015	1812.17	1087.30–2346.62	113444** (±39415)	91	1434.99	887.92–1838.75	92332* (±30301)	94
	2012	7295.46	4257.34–14854.35	5711192** (±1750709)	97	2465.24	794.34–6051.67	2088376 **(±654615)	95
FSW	2013	6536.31	3006.57–11722.56	4113809** (±1241217)	99	4156.00	1449.81–6995.91	2593230** (±786884)	98
	2015	7243.85	2731.24–13685.22	7963244** (±2408451)	98	2611.56	1143.52–7916.20	2523839 **(±751278)	99
	2012	404.6	244.02–508.45	6681 **(±2275)	88	363.56	281.62–526.22	5033** (±1927)	79
DSW	2013	353.18	259.65–466.8	4668** (±1645)	91	337.17	219.10–456.88	3559** (±1262)	90
	2015	483.54	392.06–580.54	1742** (±988)	77	372.71	273.99–464.66	1923* (±1021)	78
	2012	2.81	1.84–4.22	0.29388** (±0.08)	96	2.10	1.35–3.47	0.28668** (±0.086)	97
TW	2013	3.13	2.08–4.78	0.4978** (±0.16)	94	2.87	1.59–4.60	0.5797** (±0.18)	97
	2015	2.90	1.94–4.49	0.56692 ** (±0.17)	98	2.40	1.53–3.73	0.39787* (±0.11)	99
	2012	0.85	0.76–0.98	0.005* (±0.002)	80	0.84	0.75–0.97	0.003226* (±0.001)	79
NDM	2013	0.83	0.76–0.97	0.001* (±0.002)	43	0.74	0.65–0.89	0.004188* (±0.001)	80
	2015	0.96	0.85–1.06	0.003* (±0.001)	76	0.87	0.79–0.99	0.001834 (±0.0009)	73
	2012	57.25	53.97–60.06	3.447* (±1.48)	68	62.78	59.03–65.83	4.773** (±1.84)	81
NDF	2013	55.96	52.4–58.29	2.99 (±1.441)	76	56.60	53.19–59.75	6.65 (±2.63)	80
	2015	56.31	53.45–58.07	1.238 (±0.94)	60	60.72	57.73–64.40	3.178 (±1.33)	79
	2012	40.25	37.08–42.38	2.245*(± 0.90)	61	44.03	41.26–46.65	3.466* (±1.45)	79
ADF	2013	39.99	37.14–42.07	1.633 (±1.03)	68	41.23	38.04–44.2	5.224 (±2.09)	80
	2015	40.67	37.99–42.46	1.896 (±0.88)	75	42.88	38.85–45.23	4.4393** (±1.65)	81
	2012	50.77	48.56–53.64	2.201 *(±0.97)	66	46.46	44.29–49.52	2.329* (±0.96)	79
IVOMD	2013	48.84	46.74–51.74	1.676 (±0.99)	70	48.24	45.79–51.31	5.081* (±1.96)	80
	2015	47.33	45.33–49.93	1.829* (±0.76)	78	45.50	43.28–49.42	3.515** (±1.25)	82

(DFF: days to fifty percent flowering-days; PHT: plant height-cm; GW: grain weight- g; FSW: fresh stalk weight- Kg plot^{-1}; DSW: dry stalk weight- Kg plot^{-1}; TW: test weight- g; NDM: nitrogen dry matter basis-%; NDF-neutral detergent fiber-%; ADF-acid detergent fiber-% ;IVOMD: *in vitro* organic matter digestibility-%; σ^2g-genotypic variances; SE: standard error; h^2: broad sense heritability), significance -**@1% P, *@5%P.

g), and had similar yield in 2012 (1707 g) and 2015 (1812 g) in control treatment whereas under stress 1512, 1126 and 1434 g in 2012, 2013 and 2015, respectively. Similarly, fresh weight (g/plot) was 7295 in 2012, 6536 in 2013 and 7243 in 2015 under control and stress 2465 in 2012, 4156 in 2013 and 2611 in 2015. The dry weight (g/plot) in 2012 was 404.6, 2013 was 353.18 and in 2015 were 483.54 under control then under stress the dry weight was 363.56, 337.17 and 372.71 in 2012, 2013 and 2015, respectively. Test weight was high in 2013 (3.13 g) then 2015 (2.90 g) and 2012 (2.81 g) under control and stress had a similar pattern of 2013 (2.87 g), 2015 (2.40 g) and 2012 (2.10 g).

Table 3
Mean, range, genotypic variance, genotypic and year variances and broad-sense heritability for agronomic and fodder quality traits to evaluate effect under different water regimes.

Treatment	Control					Stress				
Traits	Mean (±SE)	Range	σ^2g (±SE)	$\sigma^2g \times y$ (±SE)	h^2	Mean (±SE)	Range	σ^2g (±SE)	$\sigma^2g \times y$ (±SE)	h^2
DFF	72 (±0.83)	60.39–82.03	15.32* (±8.47)	31.02** (±7.52)	57	74.55 (±0.87)	61.6–83.46	22.32 (±9.96)	23.42** (±6.95)	67
PHT	176.98 (±3.12)	116.77–264.36	1672.24 ** (±515.72)	207.86 ** (±47.5)	96	166.48 (±2.84)	105.45–228.7	1536.1** (±462.13)	78.13* (±19.32)	98
GW	1680.43 (±27.91)	1040.28–1960.07	29574 (±16179)	51167** (±14650)	57	1358.09 (±26.96)	744.56–1659.61	17876 (±15329)	77034** (±18565)	38
FSW	7025.25 (±167.50)	4228.27–12573.9	3830504* (±1354835)	2036942 ** (±461273)	84	3077.59122.68)	1432.68–6987.92	1573930 ** (±55964)	857593** (±194545)	84
DSW	400 (±7.37)	309.13–491.11	2998 *(±1156)	1458* (±5590)	78	371.27 (±6.03)	281.71–460.96	1941 (±859)	1434* (±587)	68
TW	2.94 (±0.04)	2.03–4.38	0.36864* (±0.11)	0.06861 (±0.01)	92	2.46 (±0.05)	1.58–3.84	0.32842** (±0.10)	0.06499* (±0.01)	92
NDM	0.88 (±0.01)	0.8–1	0.002* (±0.001)	0.001* (±0.0008)	66	0.82 (±0.01)	0.75–0.95	0.002* (±0.0008)	0.0006 (±0.0004)	78
NDF	56.51 (±0.19)	53.87–58.27	1.716 (±0.759)	0.668 (±0.543)	68	60.00(±0.27)	57.27–62.95	1.879 (±1.046)	2.812 ** (±0.962)	56
ADF	40.30 (±0.15)	37.8–41.88	1.313 (±0.56)	0.52 (±0.36)	70	42.71 (±0.21)	40.71–45.11	1.076 (±0.869)	3.382 ** (±1.023)	40
IVOMD	48.98 (±0.18)	47.17–51.48	1.68 **(±0.61)	0.09* (±0.26)	82	46.73 (±0.19)	44.73–48.54	0.63 (±0.65)	3.01 ** (±0.86)	32

TRT: Treatment; DFF: days to fifty percent flowering-days; PHT: plant height-cm; GW: grain weight- Kg plot^{-1}; FSW: fresh stalk weight- Kg plot^{-1}; DSW: dry stalk weight- Kg plot^{-1}; TW: test weight- g; NDM: nitrogen dry matter basis-%; NDF-neutral detergent fiber-%; ADF-acid detergent fiber-%; IVOMD: *in vitro* organic matter digestibility-%; σ^2g: genotypic variances; $\sigma^2g \times y$: genotypic and year variances; h^2: broad sense heritability; SE: standard error), significance -**@1% P, *@5%P.

3.2.2. Fodder quality traits

Fodder quality traits obtained from NIRS analysis for three years have shown considerable variations (Table 2). Nitrogen on dry matter basis was high in 2015 (0.96 %) followed by 2012 (0.85 %) and least in 2013 (0.83 %) under control conditions. Under stress condition it was high in 2015 (0.87 %) then 2012 (0.84 %) and in 2013 (0.74 %). The NDF (%) recorded was 57.25, 55.96 and 56.31 under control and 62.78, 56.6 and 60.72 under stress in 2012, 2013 and 2015, respectively. The ADF (%) recorded was 40.25, 39.99, and 40.67 under control and under stress 44.03, 41.23, 42.88, in year 2012, 2013 and 2015, respectively. The IVOMD recorded 50.77 in 2012, 48.84 in 2013 and 47.33 in 2015 under control and stress 46.46 in 2012, 48.24 in 2013 and 45.50 in 2015.

3.3. Genotypic variances (σ^2g) and G × Y interactions ($\sigma^2g \times y$)

Genotypic and G × Y interactions variance for agronomic and fodder quality traits is significantly high for three years. The year-wise σ^2g is presented in Table 2 whereas σ^2g and $\sigma^2g \times y$ for different water regimes are presented in Table 3.

3.3.1. Agronomic traits

The σ^2g is higher for all traits in control plots than in stress plots except for flowering (15 in control plot and 22 in stress plot). The $\sigma^2g \times y$ for grain weight was 51167 in control and 77034 in stress plot. Plant height, fresh weight, dry weight and test weight had higher σ^2g than $\sigma^2g \times y$ interaction variance under control conditions. The $\sigma^2g \times y$ is higher than σ^2g for all traits both under control and stress plots, except test weight.

3.3.2. Fodder quality traits

Year-wise σ^2g shows considerable variation for all fodder quality traits predicted using NIRS. IVOMD has higher genetic variances than other traits under stress and control for three years of evaluation. But all the σ^2g across years is higher under stress conditions than control conditions, except for nitrogen content on dry matter basis which is marginally high in control (0.003) than stress (0.002) for three years. The comparison of σ^2g, for nitrogen (0.002) under both the treatments was the same, but the $\sigma^2g \times y$ was higher under stress (0.0006) conditions than control (0.001). No definite trend was observed for fiber fractions in the current experiment.

3.4. Heritability

The broad-sense heritability both year-wise (Table 2) and two different water regimes (Tables 2 and 4) have been analysed, and discussed below. Across three years no definite pattern is observed but across treatments, the heritability is high in control than under stress, except for plant height, fresh stalk weight and test weight.

3.4.1. Agronomic traits

Days to fifty percent flowering showed high heritability in 2012 and 2013 than in 2015. Plant height recorded 99 % heritability under both treatments in all the three years of experiment. Grain weight recorded 75, 95 and 91 under control and stress 90, 96 and 94 %, in 2012, 2013 and 2015, respectively. Fresh weight showed higher heritability ranges over dry weight for all three years under both treatments. Test weight has shown above 90 % heritability for all years under different treatments. Comparing performance in control and stress plots for plant height (96 and 98 %), fresh weight (84 under both treatments) and test weight (92 under both treatments) recorded high heritability. On the other hand, days to fifty percent flowering (57 and 67), grain weight (57 and 38) and dry weight (78 and 68) under control and stress respectively.

3.4.2. Fodder quality traits

Fodder quality traits showed moderate heritability for all traits. The nitrogen content had shown moderate heritability under control (66%) and shown higher heritability under stress (78%) than under control for analysis performed across treatment and years. For fiber fractions and IVOMD, the year-wise data shows higher heritability under control than under stress. Heritability for fiber fractions was high under control (NDF and ADF -68 and 70%) than stress (NDF and ADF -56 and 40%, respectively). Assessment of heritability under treatments has shown that nitrogen was highly heritable in stress (78%) than in control (66%). The digestibility traits on the other hand, have recorded higher heritability in control (IVOMD-82%) and low heritability in stress plots (IVOMD-32%).

3.5. Correlation and association study

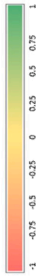
The correlation and association between traits were studies using Pearson's correlation, 'which-won-where' plots were plotted for the important traits (DSW and IVOMD) and Genotype × Trait association was plotted as the combination of Genotype (Combination of Year & Entries) × Trait (Combination of Treatment & Traits).

3.6. Correlation

Correlation between agronomic and fodder quality traits performed for two treatments have been presented in Table 4. Plant height has shown a positive (significantly) correlation with fresh and dry weight across treatments: 0.79 and 0.84 under stress and 0.79 and 0.90 under control. The nitrogen and fiber fractions are significantly negatively correlated to digestibility across both treatments. The nitrogen content has a negative correlation with test weight (-0.42 at P = 5%).

Table 4
Correlation between the agronomic and fodder quality traits between control and stress environments.

Treatment	S_DFF	S_PHT	S_GW	S_FSW	S_DSW	S_TW	S_NDM	S_NDF	S_ADF	S_IVOMD
C_DFF	**0.93****	-0.06	0.26	0.22	0.16	-0.18	0.08	-0.24	-0.15	0.16
C_PHT	-0.02	**0.99****	0.21	**0.79****	**0.84****	0.07	-0.29	0.12	0.05	0.05
C_GW	0.43	0.18	**0.92****	0.21	0.41	-0.27	-0.13	0.06	0.07	0.19
C_FSW	0.33	**0.79****	0.28	**0.91****	**0.76****	0.12	-0.31	-0.10	-0.10	0.18
C_DSW	0.15	**0.90****	0.33	**0.79****	**0.93****	0.19	-0.18	-0.05	-0.07	0.15
C_TW	-0.16	0.11	-0.09	0.09	0.20	**1.00****	-0.36	-0.18	-0.25	0.21
C_NDM	0.14	-0.31	-0.20	-0.01	-0.31	**-0.42***	**0.93****	-0.25	-0.06	-0.36
C_NDF	-0.12	0.27	0.23	-0.01	0.25	-0.13	0.08	**0.73****	**0.66****	**-0.69****
C_ADF	-0.03	0.16	0.15	-0.03	0.18	-0.21	0.25	**0.65****	**0.71****	**-0.79****
C_IVOMD	0.07	-0.04	0.12	-0.02	0.01	0.18	**-0.50***	**-0.48****	**-0.56****	**0.86****



(DFF: days to fifty percent flowering-days; PHT: plant height-cm; GW: grain weight- Kg plot-1; FSW: fresh stalk weight- Kg plot-1; DSW: dry stalk weight- Kg plot-1; TW: test weight- g; NDM: nitrogen dry matter basis-%; NDF-neutral detergent fiber-%; ADF-acid detergent fiber-%; IVOMD: in vitro organic matter digestibility-%; P@ 5% (P value>0.40*) and 1% (P value>0.52**); C: Control; S: Stress), the colour density from red to green is directly proportional to coefficient values from negative (red) to positive (green) as indicated in color indent on right hand bar.

3.7. 'Which-won-where'

The 'Which-won-where' plots were drawn for dry stalk weight (Fig. 2a) and IVOMD (Fig. 2b). In the dry stalk weight scatter plot the clustering for treatment in two years is prominent, but not in 2015. Year-wise clustering is very strong for dry stalk yield except for 2013. Germplasm 16 and 9 is performing well in 2015 year in control and stress, 24 and 11 in 2013 control and 18 in 2013 stress and finally 12 in 2012 for both treatments. All other germplasm entries are performing poor for dry stalk yield. Genotypes like 23, 20, 17, 19, 22, 5, 18, 2 and 24 have highest mean yield, while, 4, 15 and 10 have yield close to grand mean and, the rest of the entries have yielded lower than average yield. In the IVOMD plot discrimination of treatments is well shown between the control and stress plots, except for the stress 2013. Germplasm 9 (ICSV700-P10) is performing well in 2013 stress, 17 (N13), 20 (PB15881-3) and 24 (SP 2417-P3) is performing well in 2012 and 2015 stress. Germplasm 16 is performing well in control (M 35-1). Entries like 1 (296B), 6 (ICSB377-P1), 8 (ICSV1), 15 (IS9830) and 19 (PB15220-1) are performing poor.

3.8. Genotype × Trait association

In the Genotype × Trait association (Fig. 3) plot the treatment had not much effect on the association of traits, as all control and stress vectors are next to each other (only acute angles). However, for nitrogen and fiber fractions the stress form one group and control forms a tighter group, whereas the IVOMD falls in a different group altogether. The agronomic traits like grain weight, dry stalk weight and plant height are highly associated with each other across treatments (forming an acute angle). Amongst fodder quality traits, nitrogen and fiber fractions are negatively associated with IVOMD under both treatments. The dry stalk weight under both treatments forms an acute angle (positive association) IVOMD under control conditions whereas right angle (no association) IVOMD under stress.

3.9. Diversity analysis using GBS SNPs and Cluster analysis using Gowers' distance matrix

The SNPs identified from GBS analysis were used for constructing a phylogenetic tree showing the diversity of the parents. Phylogenetic

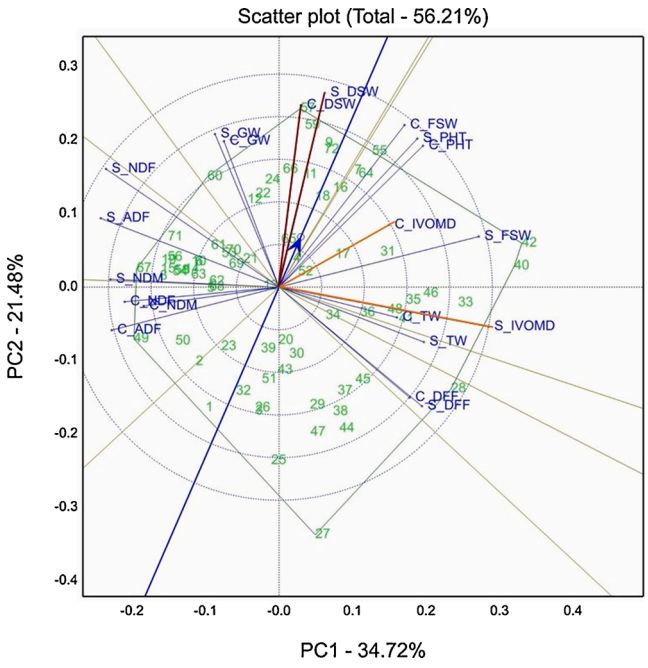


Fig. 3. Genotype × Trait plot showing the association between agronomic and fodder quality traits under two treatments.

diversity analysis on 22 parents showed three major groups further sub-dividing into other groups (Fig. 4a). The three clusters (C1, C2 and C3) formed on basis of pooled data using the unweighted pair-group method with arithmetic mean (UPGMA). Five accession *viz*., BTx623, ICSB377-P1, ICSB370-2-9-P2, IS8219-P1, SP 39105-P7 constituted cluster C1 and seven accessions *viz*., E 36-1, IS41397-3-P6, S35, ICSV 1, PVK 801, PB15220, IS9830 formed cluster 3 and rest form yet another distinct cluster. The hierarchical population structure was determined using the model-based ADMIXTURE program assuming k = 1–18 population was estimated. The effective group number was estimated by calculating Δk by estimating CV values k = 1 to k = 7 (Fig. 4b) and k = 3 was found to be appropriate with least CV error value for plotting population structure (Fig. 4c).

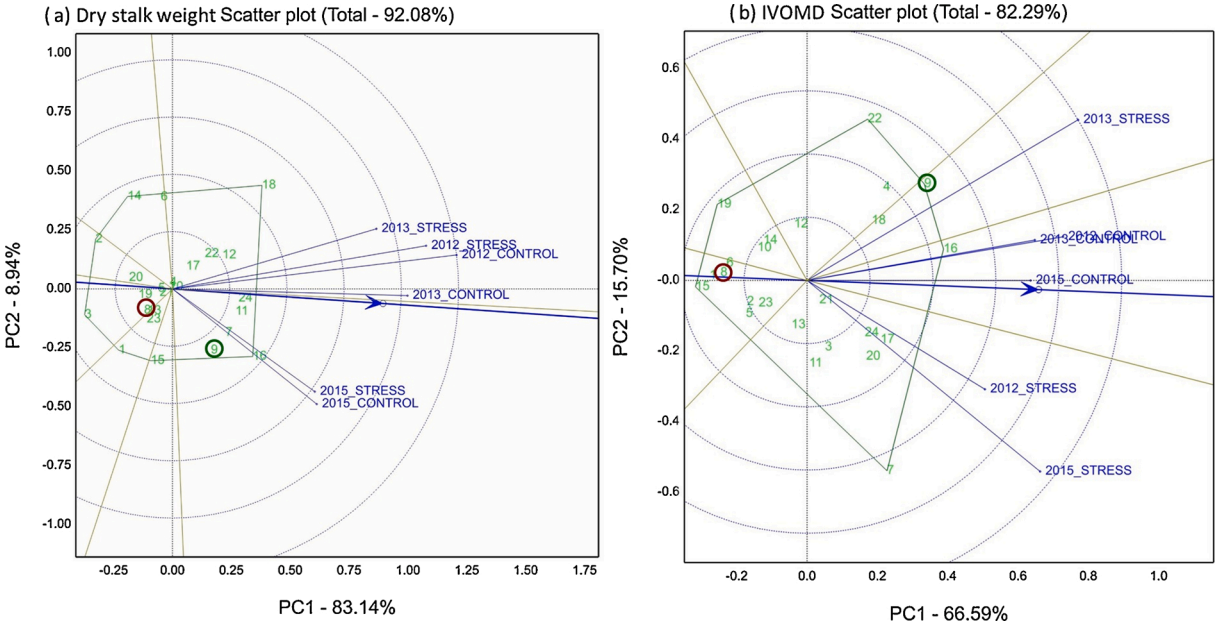


Fig. 2. 'Which-won-where' scatter plot for (2a) Dry stalk and (2b) IVOMD across years and treatments.

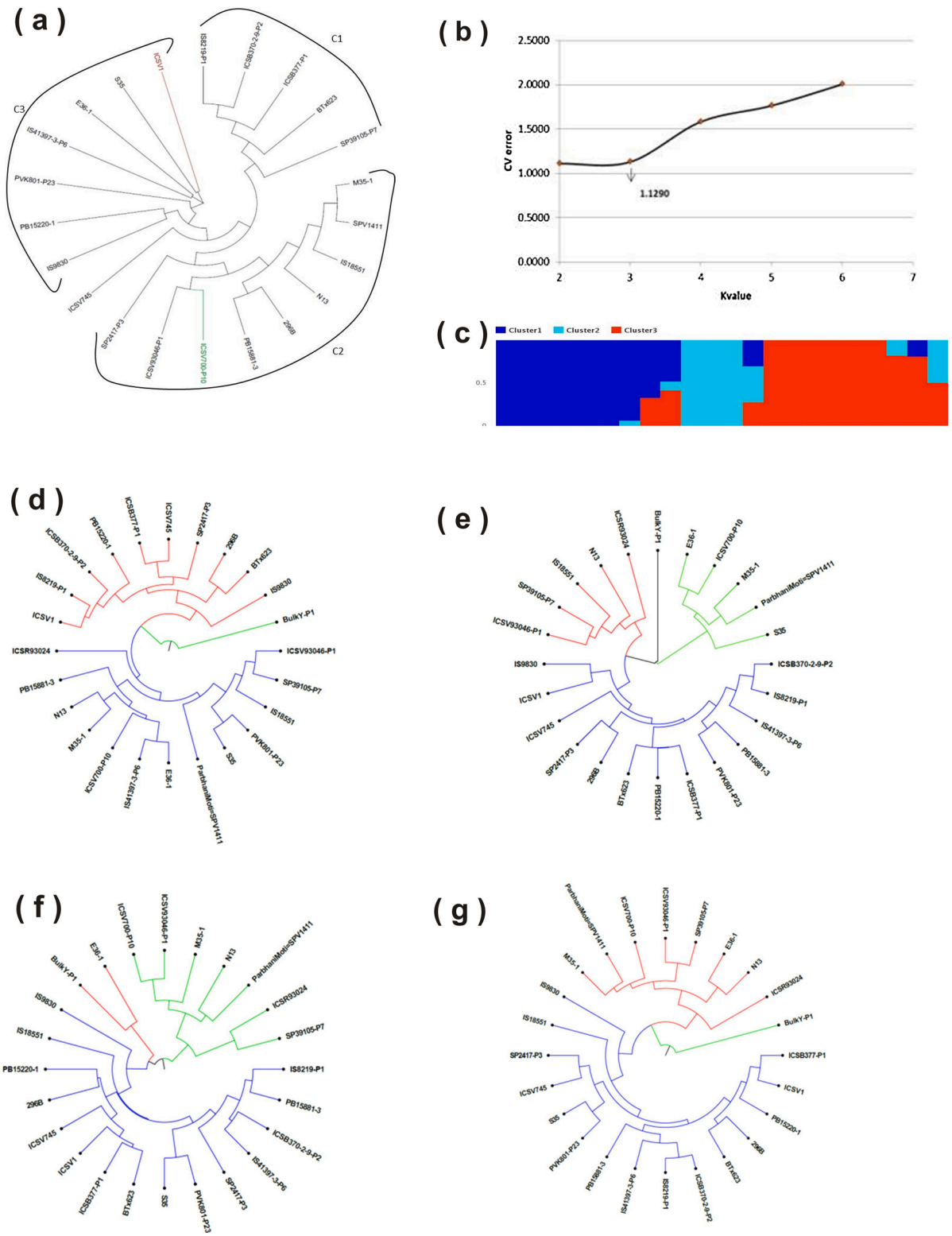


Fig. 4. Genetic diversity of 22 (out of 24 parents). (4a) unweighted pair-group method with arithmetic mean (UPGMA) (4b) the graph to identify minimum k value (k = 3: 1.1290) (4c) Phylogenetic analysis implemented in TASSEL v5.2.58. Phylogeny tree generated using Darwin for the year (4d) 2012 (4e) 2013 and (4f) 2015 and (4 g) pooled.

We further used Gowers' distance matrix derived from individual and across season (Fig. 4d, 4e, 4f, and 4 g, respectively) analysis for drawing the cluster trees (using Darwin) and it revealed three distinct clusters with BulkY –P1 forming unique cluster in 2012 and pooled while the 2013 and 2015 three distinct clusters were observed (Fig. 4d, e, f, and g). In all seasons and pooled analysis ICSV1 and ICSV700-P10 were agrouped in different clusters indicating consistent diversity between two parents. From AMOVA, results substantially showed more genetic variation within populations (45 %) than within individuals (29 %) and least variations were observed among populations (26 %)

Table 5
Analysis of molecular variance (AMOVA) and Wright's fixation indices. F_{IS}: inbreeding coefficient; F_{ST}: measure of population substructure; F_{IT}: overall inbreeding coefficient.

Source of variation	Sum of squares	Variance components	Percentage variation	Fixation Indices	
Among populations	72139.61	2365.43	25.92	F_{IS}	0.61
Among individuals within populations	168843.8	4140.22	45.37	F_{ST}	0.26
Within individuals	49721.5	2620.46	28.71	F_{IT}	0.71
Total	290704.9	9126.11			

(Table 5). The Gowers' distance ranged from 0.06 to 0.61 and the distance between ICSV1 (8) and ICSV700-P10 (9) was observed at 0.47 (Table 6, indicated in grey highlighted cell for entry no. 8 and entry no.9).

4. Discussion

Breeding for forage cultivars with drought tolerance have been of prime importance and adapting molecular technologies will provide the swift in breeding and identifying the genes in regulating the plant responses under stress [22]. The experiment was conducted (i) to evaluate the effect of drought on fodder yield and quality, (ii) to study the correlation between fodder yield and quality using diverse lines and (iii) identify diverse parents that can be utilized for candidate gene identification using population. The effect of drought is vital but considering the importance of the variation across years by the environment, genotype, genotype × year wise interaction variances and trait heritability has also been discussed below.

4.1. Drought and environmental factors affect the biomass yield and quality

The drought is known to affect biomass accumulation and quality [23–25]. The quality in terms of fiber fractions (cellulose and hemicellulose) and lignin were reduced significantly by water deficit conditions [25]. The year-wise environmental variation (Fig. 1) could be due to factors involved directly or indirectly during the plant cultivation [26]. The rainfall received has wide variations during crop growth stages from the month of October and November. The cumulative rainfall during October to April during crop growth period for the year 2012−13 was 183.5 mm, in 2013−14 was 326.1 mm and in 2015−16 the rainfall was least 76.8 mm. However, during first two months of growth the variation in rainfall for 2012, 2013 and 2015 was 100.8, 207.2 and 63.9 mm, respectively. Variability in rainfall alone can be the single greatest cause of differences in forage production for a given location which was assessed using the agronomic traits [22,27]. Although, the soil moisture level is recharged after the rains, particularly in *vertisols* and *entisol*, towards the end of the crop cycle the moisture level in the soil profile goes down gradually [4], which again affects the yield and quality of the fodder.

4.2. Cultivar dependent variations for biomass yield and quality

The genotypic variance is always higher in control plots than in stress except for flowering and grain yield (for which days to flowering is an attributed trait). Genotypic variance was high than genotype × year interaction variances under control conditions, *vice versa* under stress conditions [26]. The genotypic variations are the cause for significant differences in the fodder yield and quality attributed traits [28,12], which increases the nutritional quality of sorghum forages above the current levels through varietal improvement [12]. The agronomic trait (plant height) and fiber fractions are extremely genotypic dependent [25]. The significant genotypic variances ($\sigma^2 g$) and genotype × year interaction variance indicate the existence of substantial variability for a particular trait and directional selection may be effective for those traits [29,12]. The natural genetic variations should be exploited to increase productivity by developing high yielding varieties and hybrids [30,31] along with resistance to biotic and abiotic resistance. Although genotypic variability can be utilized to achieve higher genetic gain further in crop improvement towards fodder quality [12], the variations from widely available genetic resources are not utilized to maximum potential. Hence, it is essential to evaluate a diverse set of germplasm in various locations and across different years [26].

4.3. Biomass yield and quality are complex traits

Broad sense of heritability was moderate to high for all the traits (except for nitrogen) indicating that traits are controlled by additive genes and therefore had a minimum influence of environmental conditions [32]. Estimation of heritability provides information on trait architecture and improves selection efficiency and optimizes resource use [33]. The biomass accumulations through structural fiber accumulation have also been reported with moderate heritability [34]. Fodder quality traits have shown low heritability for most important digestibility factor (IVOMD) under stress, but it is high in control conditions, indicating that fodder quality is reduced by drought [25]. Therefore, biomass yield and quality (fiber fractions) with low to moderate heritability are suggested to be complex traits and indirect selection from yield attributed traits could be more efficient [35].

4.4. Biomass yield and quality can be improved simultaneously

Correlation and association studies help to direct the selection towards compatible traits leading to improvement of two traits that have positive or no association. Days to fifty percent flowering is non-significantly but negatively correlated to grain yield, results are in confirmation with [30]. Plant height is positively correlated with fresh weight and dry weight [36,37]. Positive relation between plant height, fresh weight and dry weight were reported in studies by [38,39]. Fodder yield can be improved by selection of positively associated yield attributed traits [32]. Grain weight was not associated and showed no dependency with fresh and or dry weight [29,40]. Desirable fodder quality traits had shown no significant association with agronomic traits in current experiment, across treatments. Nitrogen is negatively, though non-significant, associated with plant height and fresh stalk weight. Significant negative associations were observed between fiber, lignin fractions and IVOMD whereas, significant positive associations were observed amongst the fiber fractions themselves. Since none of the agronomic traits or the fodder quality traits are significantly associated simultaneous crop development for yield and quality can be performed. Results are contrary to the reports [11] where the nitrogen and the digestibility traits have (significantly) negative association with the grain yield. The nitrogen is reported to be marginally rich in sorghum in many studies and recently was reported by [41]. The fiber fractions are reportedly low in the entries selected for present study, compared to study reported by [41] the NDF was in the range of 70.13–82.19 %, ADF in the range of 47.87–78.86 %. This could maximize the opportunity to select the entries with optimum fiber fractions and higher digestibility for further studies. The Genotype × Trait association and correlation between traits show that there is no strong relation (neither positive nor negative) between dry stalk yield and IVOMD across treatments (Table 4 and Fig. 3). Similar results were inferred by [42,43] when they reported no link of lignin and digestibility to biomass yield and therefore suggested simultaneous improvement.

Table 6
Gower's genetic distance among 24 parents used in the current study.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24
1	0	0.13	0.4	0.37	0.17	0.16	0.45	0.15	0.48	0.24	0.36	0.31	0.23	0.17	0.29	0.55	0.42	0.48	0.21	0.24	0.24	0.35	0.19	0.37
2		0	0.38	0.35	0.14	0.14	0.43	0.14	0.45	0.2	0.34	0.27	0.24	0.15	0.26	0.51	0.38	0.46	0.17	0.25	0.26	0.33	0.23	0.32
3			0	0.32	0.42	0.51	0.61	0.47	0.48	0.51	0.47	0.57	0.37	0.4	0.55	0.44	0.42	0.48	0.53	0.36	0.44	0.47	0.48	0.52
4				0	0.26	0.34	0.3	0.37	0.19	0.34	0.25	0.34	0.21	0.28	0.47	0.2	0.14	0.25	0.42	0.17	0.26	0.22	0.35	0.23
5					0	0.1	0.39	0.13	0.35	0.15	0.24	0.24	0.14	0.06	0.28	0.42	0.28	0.36	0.17	0.19	0.2	0.23	0.2	0.24
6						0	0.42	0.09	0.41	0.11	0.29	0.19	0.19	0.14	0.25	0.48	0.36	0.41	0.13	0.24	0.2	0.27	0.16	0.29
7							0	0.47	0.28	0.45	0.26	0.31	0.39	0.39	0.51	0.35	0.23	0.32	0.46	0.31	0.38	0.34	0.46	0.22
8								0	0.47	0.17	0.37	0.24	0.23	0.16	0.2	0.54	0.39	0.48	0.15	0.29	0.28	0.35	0.23	0.34
9									0	0.34	0.19	0.33	0.29	0.36	0.55	0.14	0.19	0.18	0.46	0.26	0.27	0.19	0.37	0.19
10										0	0.25	0.17	0.21	0.17	0.29	0.43	0.35	0.34	0.19	0.27	0.13	0.19	0.13	0.28
11											0	0.19	0.22	0.26	0.44	0.21	0.22	0.14	0.4	0.24	0.2	0.16	0.3	0.11
12												0	0.25	0.25	0.31	0.37	0.31	0.3	0.3	0.29	0.24	0.25	0.25	0.18
13													0	0.12	0.38	0.36	0.24	0.29	0.24	0.15	0.15	0.19	0.19	0.27
14														0	0.3	0.43	0.27	0.37	0.17	0.17	0.21	0.24	0.21	0.26
15															0	0.61	0.39	0.56	0.23	0.43	0.39	0.45	0.35	0.45
16																0	0.23	0.14	0.57	0.33	0.36	0.28	0.47	0.21
17																	0	0.25	0.37	0.21	0.27	0.21	0.38	0.18
18																		0	0.49	0.28	0.25	0.17	0.38	0.17
19																			0	0.29	0.28	0.34	0.24	0.38
20																				0	0.19	0.19	0.23	0.23
21																					0	0.11	0.14	0.25
22																						0	0.24	0.17
23																							0	0.35
24																								0

1 = 296B, 2=BTx623, 3=BulkY-P1, 4=E36-1, 5=ICSB370-2-9-P2, 6=ICSB377-P1, 7 = ICSR93024, 8 = ICSV1, 9=ICSV700-P10, 10 = ICSV745, 11=ICSV93046-P1, 12 = IS18551, 13=IS41397-3-P6, 14=IS8219-P1, 15 = IS9830, 16 = M35, 17 = N13, 18=Parbhani Moti = SPV1411, 19=PB15220-1, 20=PB15881-3, 21=PVK801-P23, 22 = S35, 23=SP2417-P3, 24=SP39105-P7.

4.5. Identification of contrasting parents

The genetic mapping and genetic dissection of complex traits such as fodder quality needs very systematic selection of accessions for formulation of genetic populations such as RILs. The selection of most contrasting accessions, to serve as parents, for a given target trait usually is not the best way to develop the genetic population. The biological/phenological and breeding context of the trait has the major role in trait expression, phenotyping and genetic dissection. So it's imperative that there is a balanced selection criterion used for identifying contrasting parents, not only from their genetic diversity/distance vie point but also with appropriate selection weight for trait stability. The set of 24 accessions involved in this study are known to segregate for several biotic (including insect-pest), abiotic (including drought and salinity), economic traits (grain yield, *Rf* genes) and also novel traits (such as BNI). The GBS SNP based diversity analysis helps to identify the contrasting parents on the basis of the genetic distance between lines. Moreover, contrasting parents can be chosen from the field evaluation conducted for the target fodder quality traits in the current study. The performance of these lines across three years using 'which-won-where' plot and diversity analysis further helped short list most contrasting accessions. The biplot helped to identify the diverse set of entries based on two most important traits from fodder quality view point *viz.*, dry weight and IVOMD of fodder. The two accessions selected were ICSV1 and ICSV700-P10, had considerable difference for these traits. Nevertheless, based on biomass quantity- mainly DSW, these two genotypes may not be the superior entries, yet they had significant difference for IVOMD. Furthermore, the population structure and phylogenetic distance based clusters provide criterion for selecting candidate entries with optimal genetic diversity [44,45], which is essential for ensuring enough recombination frequency for genetic mapping. The test entries in current study are limited but are a diverse set of parents which were used to develop recombinant inbred populations (RILs) segregating for biotic, abiotic resistance and/or yield associated traits. The phylogeny analysis revealed that the 22 parents are distributed across three clusters based on genetic diversity. Broader genetic base and exploiting existing variability in a population base is crucial for crop improvement [12]. The two accessions *viz.*, ICSV1 and ICSV700-P10 (Fig. 3) grouped in two different clusters. The F_{ST} value of 0.259 was obtained across all parents also indicated relatively large variation considering small population size. The phylogeny tree generated using the phenotypic data based Gowers' distance matrices also showed three clusters, and the ICSV1 and ICSV700-P10 were grouped in different cluster in each year and in pooled data as well. This combined approach of identifying the contrasting parents by – evaluating the trait performance across years and environments (stress treatments) for their stability and genetic performance; and also scanning genomes of these candidate accessions to estimate molecular markers based genetic diversity helped to identify the more stable and optimally diverse accessions. The identified accessions *viz.*, ICSV1 and ICSV700-P10 will serve as parents for RIL population for dissection of genes responsible for higher fodder quality under drought conditions.

5. Conclusion

Considerable variations exist for agronomic and fodder quality traits which can be exploited by breeders for developing superior cultivars without compromising for fodder quality traits. Association between agronomic and fodder quality traits indicates an independent association for superior traits without trade- off. In our study two main traits of interest are biomass quantity and quality, assessed by dry stalk weight and IVOMD, respectively. The three years of field evaluation, both in control and stress environments clearly indicated the role of availability of water in fodder quality traits. Also the biplot analysis clearly indicated that agronomic traits of economic importance such grin yield and biomass traits including fodder quality are quiet independent. So as

observed in previous studies, simultaneous improvement of both the grain and fodder traits is possible. The evaluation of the set of 24 accessions for the field trait performance across years and environments, and estimating the genetic diversity by employing GBS SNPs has helped to identify phenotypically contrasting and optimally genetically diverse accessions *viz*., ICSV1 and ICSV700-P10. This combined approach will further streamline the trait discovery research for fodder quality traits in sorghum. These studies in long term will help farmers to secure economic returns even under water stress period with sustainable grain production and improved fodder quality.

Credit author statement

Vinutha K Somegowda: performed the experiments, analysed and interpreted data; wrote the paper; Anilkumar Vemula: performed statistical analysis; Jalaja Naravula: guidance; Gandham Prasad: SNP calling; Laavanya Rayaprolu: Darwin and cluster analysis; Abhishek Rathore: guidance; Michael Blümmel: guidance; Santosh P Deshpande: conceived and designed the experiments, guidance and review for writing.

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Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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