



Genetic variance and predicted response for three types of recurrent selection procedures in forage sorghum [*Sorghum bicolor* (L.) Moench]

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Abstract

The present investigation was undertaken in the Forage and Millet Section, Department of Plant Breeding and Genetics, Punjab Agricultural University, Ludhiana to study the genetic variance and predicted response to selection for fodder yield and its components, hydrocyanic acid (HCN), water use efficiency (WUE) and quality traits over two environments viz., normal environment (Env-N) and water stress environment (Env-S) in forage sorghum [*Sorghum bicolor* (L.) Moench]. In this experiment, 100 families of each type viz. full sib, half sib and S_1 were evaluated. The trend for mean fodder yield and yield contributing traits viz., plant height, number of leaves per plant, leaf area index and HCN content showed that the mean of full sib families exceeded the mean of half sib and S_1 families. This indicated that heterosis and inbreeding depression were important for these traits in this population. More contribution of additive gene effects than dominance effects for genetic control of green fodder yield and other important characters was found in both the environments. For HCN content, the ratio of $\sigma^2_A/\sigma^2_{A+D}$ was less than 0.5 in Env-N and greater than 0.5 in Env-S which suggested that dominance and/or epistasis were more influential in controlling HCN content under Env-N. Additive genetic variation estimates appeared to be sufficiently great to permit substantial progress by any of the three family systems of selection, but S_1 family selection seems to be the most promising, particularly for improving green fodder yield, yield components, HCN content and WUE traits.

Keywords: Forage sorghum, Genetic analysis, HCN, WUE, Yield, Quality traits

Introduction

Sorghum [*Sorghum bicolor* (L.) Moench], although classified as often cross pollinated, was bred traditionally as a self pollinated crop. Large number of male sterile (A) lines were developed after the discovery of cytoplasmic

male sterility (Stephons and Holland, 1954) and F_1 hybrid production became practical breeding approach. Thus the use of cytoplasmic male sterility and harvesting only the male sterile plants from each generation made possible large scale production of new genetic recombinations and conversion of a normally self fertilizing population into a cross fertilizing one. This in turn permitted the introduction of recurrent selection schemes in sorghum (Doggett and Eberhart, 1968; Ross *et al.*, 1971; Doggett, 1972). Recurrent selection methods are most suitable for the improvement of those traits that are inherited in a quantitative manner. The essential features of these methods are the improvement of the mean performance of the population by increasing the frequency of the genes that affect traits under selection, appearance of new combination of genotypes that never existed in the base population and maintenance of genetic variability by recombination of superior genotypes for further and continuous improvement.

The three types of recurrent selection methods viz., half-sib, full-sib and selfed (S_1) progeny selections are normally used by breeders with success. Half-sib selection requires two generations per cycle since it involves progeny testing. This method of selection is known as 'Half-sib family selection' because the unit of selection is half-sib families and a breeder has control over only one of the parents, i.e., male-sterile plants (females). Full-sib families can be developed by crossing selected male-fertile plants to selected male-sterile plants. In this scheme of selection, the unit of selection is full-sib families and the breeder has the control over both the parents unlike in half-sib family selection. It is one of the most effective selection schemes for sorghum (Gardner, 1972). S_1 family selection requires three generations per cycle. The basic concept behind selfed progeny selection is to expose deleterious recessive genes to facilitate their elimination during evaluation and to increase additive genetic variation. Jan-orn *et al.* (1976)

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studied a sorghum population and predicted that S_1 family testing and selection offers the greatest promise for improvement, whether calculated on a cycle or on an annual basis. Scanty reports are available on the inheritance of physiological traits affecting water use efficiency (WUE) and quality traits in forage sorghum. Therefore, the present study was performed to ascertain the relative improvement expected under different selection systems and the inheritance of various traits in sorghum populations viz., half sib, full sib and S_1 families having diverse genetic make-up.

Materials and Methods

Experimental site and design: Experiment was carried out at Forage and Millet Research Farm, Punjab Agricultural University, Ludhiana located at 30° 91' N, 75° 85' E and 256 m above sea level in the Punjab state, India. The experimental material consisted of four diverse low HCN content populations viz., HC 308, RSSV 9, Ramkel and SSG 59-3, bulk crossed to three low HCN CMS lines viz., ICM 94003A, ICM 94012A and NSS 1005A. The crossed seed was bulked and subjected to random mating in an isolated plot to generate population having diverse genotypes with new recombinants. The newly generated population was sown in an isolated block and one hundred open pollinated male sterile plants selected at random were taken to obtain seeds for half sib families; one hundred random male sterile plants were crossed to fertile plants selected at random to obtain seeds for full sib families; and one hundred male fertile plants selected at random were self pollinated to obtain seeds for S_1 families. A total of 100 families of each type viz., full sib, half sib and S_1 were sown and evaluated in a randomized block design with two replications over two environments viz., normal (N) and water stress (S). The environments were created by applying normal five irrigations in one environment (Env-N) i.e. normal environment and by skipping the second and fourth irrigation in the other environment (Env-S) i.e. water stress environment. The fertilization was done by applying fertilizer @ 50 kg of N (110 kg urea) and 20 kg P_2O_5 (125 kg single superphosphate) per ha. All the entries were planted in a plot size of 3 m x 1.25 m (3 meter row length and 0.25 meter distance between the rows) with 5 rows of each.

Observations and analysis: The observations were recorded on ten random plants in both the environments from each replication for 13 morpho-physiological traits viz., early vigour, days to 50% flowering, plant height (cm), leaf stem ratio (LSR), green fodder yield (kg/plot), dry

fodder yield (kg/plot), regeneration ability, number of leaves/plant, relative leaf water content (RWC; %), leaf area index (LAI), photosynthetic efficiency (SPAD reading), specific leaf weight (SLW), proline content (n moles/g of dry sample) and four quality and anti-quality traits viz., total soluble solids (TSS) content (%), hydrocyanic acid (HCN) content (ppm), crude protein (%) and *in vitro* dry matter digestibility (IVDMD; %) as standard procedure given by Tilley and Terry (1963). The HCN content (ppm) was determined by picrate paper method. Relative leaf water content was calculated as $RWC = [(Fresh\ weight - Dry\ weight) / (Saturated\ weight - Dry\ weight)] \times 100$ (Weatherley, 1950). Leaf area index (LAI) was measured using canopy analyzer (Sunscan-type SS1) in each row of all lines in a plot, under field condition. Photosynthetic capacity in terms of chlorophyll content was recorded by soil plant analytical development (SPAD) chlorophyll meter in five intact plants per plot (using third/fourth leaf from top of the plant) in each replication from all genotypes. Specific leaf weight (SLW) was measured as the ratio of dry matter of leaves per plant (g) divided by leaf area per plant. Proline content was estimated as per procedure by Bates *et al.* (1973). The statistical analysis was carried out according to Jan-orn *et al.* (1976).

Results and Discussion

Genetic analysis: Population improvement by recurrent selection is an important component of breeding programmes with naturally cross-fertilizing plants, whether the aim is open-pollinated, synthetic or hybrid cultivars. The need for broadening the germplasm base in breeding populations to avoid genetic vulnerability and the availability of the genetic male-sterile genes prompted the development of random-mating grain sorghum populations and the use of recurrent selection systems to improve those populations. With characters of low heritability, improvement is faster with family selection than with single plant selection because replicated trials allow the effects of environmental and genotype x environmental interaction variation to be reduced (Bradshaw, 1983). In plant species, such as sorghum which can be easily selfed by the breeder, S_1 family selection is possible. Therefore, the relative improvement expected under different selection systems i.e. predicted response to selection for three types of families viz., full sib, half sib and S_1 using the estimated genetic variances were obtained under different environments.

Analysis of variance: The perusal of results for analysis of variance for individual environment (data not given)

revealed that the progenies of full sib, half sib and S_1 families differed significantly for all the characters under both the environments except for regeneration ability in Env-N. With respect to regeneration ability, the variability among half sib and S_1 progenies was not present under Env-N as indicated by their non-significant mean squares.

Mean performance of families: The mean for different characters under study in individual environments were recorded (Table 1). The mean for early vigour, plant height, green fodder yield, dry fodder yield, regeneration ability, number of leaves per plant, relative water content, leaf area index, photosynthetic capacity and crude protein were higher in Env-N than in Env-S for all three types of families. But dry fodder production decreased and water use efficiency increased under water stress condition in sorghum (Niyazi, 2018). However, mean days to 50 per cent flowering, specific leaf weight and HCN content were higher under Env-S than in Env-N. Similar trend for days to flowering and plant height was reported by Somegowda *et al.* (2019). For protein and HCN content, the findings were in agreement with Nejad *et al.* (2014) who revealed that percentage of protein decreased under water stress conditions but the toxic prussic acid responsible for HCN content increased. Similar trend for HCN content was also reported by Neilson *et al.* (2015) and Gleadow *et al.* (2016) in sorghum. No trend was observed for leaf stem ratio, TSS per cent and *in vitro* dry matter digestibility for all three families, though

Somegowda *et al.* (2019) observed decrease in *in vitro* dry matter digestibility due to water stress. The proline content was estimated only in Env-S as it plays a role of osmo-protectant and has importance in Env-S.

The trend for mean fodder yield and yield contributing traits viz., plant height, number of leaves per plant and leaf area index showed that the mean of full sib families exceeds the mean of half sib families which in turn exceeds the mean of S_1 families. The mean HCN content among three families also followed the same trend. This indicated that the heterosis and inbreeding depression were important for fodder yield, yield contributing traits and for HCN content. Similar trend for yield was reported by Jan-orn *et al.* (1976) and Deshmukh *et al.* (2011) in sorghum.

Estimates of family components of variance

Estimates of family components of variance for different characters in three types of families under Env-N and Env-S were made (Table 2).

Yield and morpho-physiological traits: For early vigour under Env-N, the half sib variance was highest, whereas under Env-S, the full sib family variance was greater than half-sib and S_1 variances. Therefore, the two environments showed different trend for the three types of family variances. For days to 50 per cent flowering, the variances followed the same trend with half sib variances

Table 1. Mean of full sib (FS), half sib (HS) and self (S_1) families for different traits under Env-N and Env-S

Characters	Environment Family type	Env-S			Env-N		
		FS	HS	S_1	FS	HS	S_1
Early vigour		2.51	2.39	2.23	3.10	2.74	2.62
Days to 50% flowering (days)		55.54	58.08	55.82	51.99	54.43	52.15
Plant height (cm)		189.60	186.73	178.53	216.30	210.45	206.10
Leaf stem Ratio		0.57	0.44	0.50	0.56	0.45	0.49
Green fodder yield (kg/plot)		8.02	7.80	6.92	10.37	9.55	9.09
Dry fodder yield (kg/plot)		2.10	2.02	1.77	2.71	2.53	2.30
Regeneration ability		3.31	3.48	3.51	3.55	3.72	3.75
No. of leaves/plant		8.39	8.07	7.46	10.32	10.09	9.50
Relative water content (%)		74.12	77.67	75.92	78.22	80.49	79.29
Leaf area index		2.11	1.90	1.79	2.86	2.69	2.53
Photosynthetic capacity (SPAD reading)		27.13	30.48	28.65	38.70	40.05	39.61
Specific leaf weight (mg/cm ²)		4.93	5.55	5.32	4.61	5.25	5.00
Proline (n mol/g)		185.70	206.50	196.21	-	-	-
TSS (%)		7.63	6.90	6.16	7.44	7.29	6.95
Crude protein (%)		7.37	7.46	7.48	8.08	8.46	8.35
HCN (ppm)		12.10	10.30	10.50	10.90	7.50	7.70
IVDMD (%)		57.20	57.20	58.50	56.00	57.10	58.90

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Table 2. Estimates of family components of variance of full sib (FS), half sib (HS) and self (S_1) families for different traits under Env-N and Env-S

Characters	Environment	Env-S			Env-N		
	Family components of variance	$\sigma^2_{(FS)}$	$\sigma^2_{(HS)}$	$\sigma^2_{(S1)}$	$\sigma^2_{(FS)}$	$\sigma^2_{(HS)}$	$\sigma^2_{(S1)}$
Early vigour		0.09	0.07	0.06	0.07	0.12	0.10
Days to 50% flowering (days)		3.28	14.92	12.45	3.57	14.06	11.92
Plant height (cm)		373.89	337.75	435.43	324.14	189.00	539.78
Leaf stem Ratio		0.03	0.03	0.03	0.04	0.06	0.05
Green fodder yield (kg/plot)		6.28	7.27	7.88	6.41	5.00	7.09
Dry fodder yield (kg/plot)		0.39	0.47	0.46	0.45	0.37	0.52
Regeneration ability		0.21	0.35	0.43	0.09	0.02	0.11
No. of leaves/plant		1.21	0.84	1.31	1.30	1.08	1.74
Relative water content (%)		40.40	29.30	35.41	29.03	32.17	32.20
Leaf area index		0.19	0.26	0.23	0.10	0.14	0.11
Photosynthetic capacity (SPAD reading)		13.88	17.63	16.38	28.08	35.68	31.69
Specific leaf weight (mg/cm ²)		2.77	2.38	2.61	3.12	2.29	2.77
Proline (n mol/g)		9952.80	10179.79	11636.93	-	-	-
TSS (%)		1.65	1.07	0.51	0.79	1.04	0.06
Crude protein (%)		0.10	0.39	0.23	0.12	0.51	0.30
HCN (ppm)		2.06	0.51	2.22	3.23	1.42	3.08
IVDMD (%)		5.21	1.82	2.43	3.99	1.57	2.48

maximum and full sib variances minimum under both the environments. S_1 family variances were in between full sib and half sib family variances under both the environments. For plant height under both the environments, S_1 variance exceeds full sib and half sib family variance. Therefore, the environments did not have any effects on the trend of three types of family variances. For leaf stem ratio under Env-N, half sib variance tend to exceed both S_1 and full sib variances, the later having an equal magnitude, whereas in Env-S, change in trend was observed *i.e.* S_1 variance was greater than both half sib and full sib variances. In both the environments, S_1 variance was maximum followed by full sib and half sib families with respect to green fodder yield. However, half sib variance was more than full sib variance under Env-S, whereas under Env-N full sib variance was greater than half sib for this character. For dry fodder yield, under Env-N, half sib variance was least with S_1 variance being maximum, whereas in water stress environment *i.e.* Env-S, half sib variance was maximum followed by S_1 and full sib. In case of regeneration ability under Env-N, the full sib variance was maximum, but the S_1 and half sib family variance was non-significant, whereas under Env-S the S_1 variance was maximum followed by half sib and full sib variances.

Physiological traits: In case of number of leave per plant under both the environments, S_1 variance was maximum followed by full sib and half sib family variances. For

relative water content under Env-N, S_1 variance exceeded both half sib and full sib variances, whereas in Env-S, full sib variance was greater than half sib and half sib variance was greater than S_1 . For leaf area index and photosynthetic capacity, same trend was followed with half sib variance being maximum followed by S_1 and full sib under both the environments. In case of specific leaf weight, full sib variance was maximum followed by S_1 and half sib under both the environments. For proline content under Env-S, the S_1 variance was maximum followed by half sib and full sib.

Quality and anti-quality traits: For total soluble solids under Env-N, half sib variance was higher than full sib variance followed by S_1 , whereas under Env-S, full sib variance was higher than half sib and S_1 . For crude protein under both the environments, same trend was followed with half sib variance being maximum followed by S_1 and full sib. In case of hydrocyanic acid content in Env-N, full sib variance was more than S_1 which was in turn more than half sib, whereas under Env-S, S_1 variance was maximum followed by full sib and half sib. For *in vitro* dry matter digestibility, full sib variance was higher than S_1 and half sib under both the environments.

Comparison among the family variances of three types of families for different traits revealed that the trend with respect to the relative magnitude of these variances change with the shift in the environment for the traits *viz.*,

early vigour, leaf stem ratio, green fodder yield, dry fodder yield, regeneration ability, relative water content, total soluble solids and hydrocyanic acid. Therefore, for these traits, trend in the variances among the three families get altered by the change in environment, whereas, for traits like days to 50 per cent flowering, plant height, number of leaves per plant, leaf area index, photosynthetic capacity, specific leaf weight, proline content, crude protein and *in vitro* dry matter digestibility did not show any change in the trend by the change in environment. The family variance among S_1 families tends to exceed that of full-sib or half-sib families for fodder yield and yield contributing traits *viz.*, plant height and number of leaves per plant under both the environments. This was consistent with genetic theory. These results were in agreement with Jan-orn *et al.* (1976) who also revealed that the family variance among S_1 families tends to exceed that of full-sib or half-sib families for fodder yield and yield contributing traits.

Estimates of additive (σ^2_A), dominance (σ^2_D) and the additive genetic variance due to average effects of gene substitution in S_1 families ($\sigma^2_{A^*}$): Genetic components of variance estimated for each of the three types of families have a genetic interpretation. In the absence of epistasis, they have some expectation according to which additive genetic variance (σ^2_A), dominance variance (σ^2_D) and the additive genetic variance due to average effects of gene substitution in S_1 families ($\sigma^2_{A^*}$) were estimated. In view of the expectations of the three family components of variance, some conclusions concerning the kind of gene action for different traits was drawn.

In both the environments, σ^2_A (additive variance) was more than σ^2_D (dominance variance) for all the characters under study (Table 3), which were in accordance with the findings of Bittinger *et al.* (1981) who revealed that additive variance was more than dominance variance for all the traits studied except yield. The dominance variances estimated, according to the predictions, were all found to be negative for all the characters except for hydrocyanic acid and *in vitro* dry matter digestibility in both the environments, and for regeneration ability, in Env-N. Ratios of estimated dominance variances to additive genetic variances were also recorded (Table 4). For all the traits except hydrocyanic acid and *in vitro* dry matter digestibility these ratios were negative because of negative dominance variance estimates. Therefore, these ratios made the meaningful interpretations difficult. These negative dominance variances could either be due to sampling error or assortative mating. If these

negative values were assumed to be zero or very small positive values then the interpretation, of additive variance playing an important role in controlling these traits could be drawn. These results were in agreement with the findings of Deshmukh *et al.* (2011). In Env-S for hydrocyanic acid, σ^2_D variance was greater than σ^2_A indicating the importance of dominance of genes controlling this trait. The ratio of σ^2_D/σ^2_A was greater than one *i.e.* 2.04 for hydrocyanic acid in Env-S. But in Env-N, the ratio was less than one, indicating the preponderant role of additive genes in controlling this trait.

The magnitude of the S_1 family component of variance relative to additive genetic variance (σ^2_A) calculated from half-sib families and the comparison of $\sigma^2_{A^*}$ with σ^2_A were of considerable interest. When dominance and epistasis were absent, $\sigma^2_{S_1} = 4\sigma^2_{HS}$ and $\sigma^2_{A^*} = \sigma^2_A$, except for random errors of sampling. For all traits, $\sigma^2_{S_1} < 4\sigma^2_{HS}$; and for most traits, $\sigma^2_{S_1}$ was only 20 per cent to 70 per cent of $4\sigma^2_{HS}$. Likewise for all traits studied, the ratios of $\sigma^2_{A^*}/\sigma^2_A$ were less than one. This showed that dominance and epistasis were present for all the traits under study. Ratio of $\sigma^2_{A^*}$ to σ^2_A being less than 1.0 for all the traits in both the environments, suggested that σ^2_A was greater than $\sigma^2_{A^*}$. These ratios were highest for plant height (0.79) and lowest for *in vitro* dry matter digestibility (0.26) in Env-N, whereas these ratios were highest for regeneration ability (0.66) and lowest for total soluble solids (0.23) in Env-S.

Recurrent selection of superior individuals or families and their recombination to form an improved population should increase the frequencies of favourable alleles and thus increase the chances of extracting new superior genetic combination for use as cultivars or in hybrids. Whereas, continued sampling from the original population without recombination would be relatively ineffective (Jan-orn *et al.*, 1976). Estimates of $\sigma^2_{A^*}$ relative to σ^2_A suggested that frequencies of favourable alleles might be less than 0.5, in that case improvement should be possible with no loss in genetic variance. As pointed out in the results, $\sigma^2_{A^*}$ tends to be consistently smaller than σ^2_A , and the ratio $\sigma^2_{A^*}/\sigma^2_A$ tends to be near 0.5 for most traits in both the environments. This could occur due to dominance with frequencies of favourable alleles less than 0.5. It could also occur due to bias in estimates of σ^2_A resulting from relatively few males pollinating each male-sterile plant on which seed for the half-sib family was produced. No information is available concerning the randomness of pollen fertilizing the male-sterile plants. If no bias occurred, it can be concluded that traits having $\sigma^2_{A^*}/\sigma^2_A$ greater than 0.5 were largely controlled by additive effects of genes.

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Table 3. Estimated genetic variances of full sib (FS), half sib (HS) and self (S_1) families for different traits under Env-N and Env-S

Characters	Environment	Env-S			Env-N		
		σ^2_A	σ^2_D	$\sigma^2_{A^*}$	σ^2_A	σ^2_D	$\sigma^2_{A^*}$
Early vigour	Estimated genetic variance	0.28	-0.20	0.11	0.48	-0.68	0.27
Days to 50% flowering (days)		59.68	-106.24	39.01	56.24	-98.20	36.47
Plant height (cm)		1351.00	-1206.44	737.04	756.00	-215.44	593.64
Leaf stem Ratio		0.13	-0.14	0.07	0.24	-0.31	0.12
Green fodder yield (kg/plot)		29.08	-33.04	16.14	20.00	-14.36	10.68
Dry fodder yield (kg/plot)		1.88	-2.20	1.01	1.48	-1.16	0.81
Regeneration ability		1.40	-1.96	0.92	0.08	0.20	0.06
No. of leaves/plant		3.36	-1.88	1.78	4.32	-3.44	2.60
Relative water content (%)		117.20	-72.80	53.61	128.68	-141.24	67.51
Leaf area index		1.04	-1.32	0.56	0.56	-0.72	0.29
Photosynthetic capacity (SPAD reading)		70.52	-85.52	37.76	142.72	-173.12	74.97
Specific leaf weight (mg/cm ²)		9.52	-7.96	4.60	9.16	-5.84	4.23
Proline (n mol/g)		40719.16	-41627.12	22043.71	-	-	-
TSS (%)		4.28	-1.96	1.00	4.16	-5.16	1.35
Crude protein (%)		1.56	-2.72	0.91	2.04	-3.60	1.20
HCN (ppm)		2.04	4.16	1.18	5.68	1.56	2.69
IVDMD (%)		7.28	6.31	0.85	6.28	3.40	1.63

σ^2_A and σ^2_D are the additive genetic and dominance variances, respectively, in the random mating population, $\sigma^2_{A^*}$ is the variance due to the average effect of gene substitution in S_1 families of the random mating population

Table 4. Estimates of ratios of genetic variances in full sib (FS), half sib (HS) and self (S_1) families for different traits under Env-N and Env-S

Characters	Ratios of genetic variances Environment	σ^2_D/σ^2_A		$\sigma^2_{A^*}/\sigma^2_A$	
		Env-S	Env-N	Env-S	Env-N
Early vigour		-0.71	-1.42	0.39	0.56
Days to 50% flowering (days)		-1.78	-1.75	0.65	0.65
Plant height (cm)		-0.89	-0.28	0.55	0.79
Leaf stem Ratio		-1.06	-1.26	0.53	0.50
Green fodder yield (kg/plot)		-1.14	-0.72	0.56	0.53
Dry fodder yield (kg/plot)		-1.17	-0.78	0.54	0.55
Regeneration ability		-1.40	2.50	0.66	0.75
No. of leaves/plant		-0.56	-0.80	0.53	0.60
Relative water content (%)		-0.62	-1.10	0.46	0.52
Leaf area index		-1.27	-1.29	0.54	0.52
Photosynthetic capacity (SPAD reading)		-1.21	-1.21	0.54	0.53
Specific leaf weight (mg/cm ²)		-0.84	-0.64	0.48	0.46
Proline (n mol/g)		-1.02	-	0.54	-
TSS (%)		-0.46	-1.24	0.23	0.32
Crude protein (%)		-1.74	-1.76	0.58	0.59
HCN (ppm)		2.04	0.27	0.58	0.47
IVDMD (%)		0.87	0.54	0.12	0.26

Negative values were assumed to be either zero or very small positive values; however, negative ratios were indicated where they existed

The green fodder yield and dry fodder yield had σ^2_A/σ^2_P greater than 0.5 in both the environments suggesting that yield was controlled much more by additive gene action than by dominance in this sorghum population and that the frequencies of favourable genes may be less than 0.5 in both the environments. In Env-S, the ratio of σ^2_A/σ^2_P were less than 0.5 for early vigour (0.39), relative water content (0.46), specific leaf weight (0.48), total soluble solids (0.23) and *in vitro* dry matter digestibility (0.27), suggested the role of dominance and epistasis in controlling these traits in the population. All other traits viz., days to 50 per cent flowering, plant height, leaf stem ratio, green fodder yield, dry fodder yield, regeneration ability, number of leaves per plant, leaf area index, photosynthetic capacity, proline content, crude protein and hydrocyanic acid had values greater than 0.5 indicating less dominance of genes controlling these traits. Whereas, in Env-N only specific leaf weight, total soluble solids, hydrocyanic acid and *in vitro* dry matter digestibility showed σ^2_A/σ^2_P less than 0.5 suggested that dominance and/or epistasis were more influential in controlling these traits.

Predicted response to single trait selection for three types of families: Predicted response to selection for individual traits assuming that 10 per cent out of a large number of individuals or families were selected under the different recurrent selection systems was calculated

using formulas of Empig *et al.* (1972). In the numerator of the prediction equations for family selection, $(1/4)\sigma^2_A$, $(1/2)\sigma^2_A$ and σ^2_A were used for half-sib, full-sib and S_1 family selection, respectively. If $\sigma^2_{A^*}$ or $\sigma^2_{S_1}$ from our data were used in place of σ^2_A for S_1 families, predicted response to S_1 family selection was lower. Predicted response to selection for three types of families under Env-N and Env-S was also recorded (Table 5).

Predicted responses in fodder yield from selection of the highest yielding 10 per cent of the families indicated that S_1 family selection offers the greatest promise for population improvement. Similar results were reported by Jan-orn *et al.* (1976), Zaveri *et al.* (1989), Dutt and Nirania (2005) and Ajala *et al.* (2009). On the other hand, estimates of genetic advance (GA expressed as per cent of mean) by Singh *et al.* (2014) showed that full-sib progenies had higher GA for most of the traits studied and revealed that full-sib progeny selection yielded significantly more superior progenies (18%) than did half-sib progeny selection (7.7%). The differential response to selection for different characters studied under two different environments could be expected as some characters could respond better to the stress environment than the others. Such change in genetic advance with the change in environment was also reported by Bittinger *et al.* (1981).

Table 5. Predicted response from single trait selection using different intra population recurrent selection systems in random mating sorghum population under Env-N and Env-S

Characters	Environment	Env-S			Env-N		
	Family type	FS	HS	S ₁	FS	HS	S ₁
Early vigour		0.61	0.23	1.14	1.18	0.36	1.90
Days to 50% flowering (days)		13.64	5.67	24.19	11.77	5.32	21.16
Plant height (cm)		54.41	27.72	100.74	31.62	19.12	47.12
Leaf stem Ratio		0.57	0.28	1.18	0.94	0.41	1.90
Green fodder yield (kg/plot)		9.54	4.34	17.40	6.58	3.35	10.72
Dry fodder yield (kg/plot)		2.30	1.07	4.45	1.65	0.86	3.15
Regeneration ability		1.89	0.82	3.02	0.13	0.24	0.24
No. of leaves/plant		2.00	1.01	3.81	2.39	1.26	4.32
Relative water content (%)		15.28	8.81	32.01	17.91	9.22	35.50
Leaf area index		1.68	0.76	3.15	0.99	0.50	2.09
Photosynthetic capacity (SPAD reading)		13.93	5.81	22.63	20.33	10.06	39.70
Specific leaf weight (mg/cm ²)		4.92	2.64	10.09	4.48	2.61	9.49
Proline (n mol/g)		338.00	161.48	636.33	-	-	-
TSS (%)		2.46	1.31	5.65	3.14	1.30	5.53
Crude protein (%)		1.89	0.92	3.88	1.90	0.97	4.32
HCN (ppm)		1.15	0.64	1.78	2.40	1.45	4.78
IVDMD (%)		2.09	1.38	5.74	1.33	1.14	4.63

Response to selection of top 10% of a family ($k = 1.755$). $GA = (1.755 * \sigma^2_A) / \sigma_P$, where k is the standardized selection differential (1.755); σ^2_A is the estimated additive genetic variance and σ_P is the estimated phenotypic standard deviation of family progeny mean

Recurrent selection procedures in sorghum

Our investigations revealed that maximum predicted response to selection could be achieved through S_1 family selection. Full-sib family testing and selection appeared to be the second best method after S_1 progeny selection system. Similar trend was reported by Amaral Jr. *et al.* (2016) who observed higher predicted gains for both full-sib families and S_1 as compared to possible gains with the selection among half sib families. For all the traits, with few exceptions, S_1 family selection offered the greatest expected gains. But these exceptions included three quality characters namely total soluble solids, crude protein and *in vitro* dry matter digestibility in Env-S. For total soluble solids and *in vitro* dry matter digestibility, full sib family selection appeared to have maximum genetic advance whereas for crude protein, half sib family selection offered highest genetic gain under Env-S. Predicted response to selection increased in Env-S than in Env-N for traits namely days of 50 per cent flowering, plant height, green fodder yield, dry fodder yield, regeneration ability, leaf area index, specific leaf weight and *in vitro* dry matter digestibility for each type of families. However, for the traits viz., early vigour, leaf stem ratio, number of leaves per plant, relative water content, photosynthetic capacity, specific leaf weight and hydrocyanic acid content, response to selection was more in Env-N and less in Env-S. In case of crude protein, response to full sib family selection increased but decreased under half sib and S_1 family selection in Env-S than in Env-N. In case of total soluble solids, response to full sib family selection decreased but increased under half sib and S_1 family selection in Env-S than in Env-N.

Conclusion

From the present investigation, it was concluded that additive genetic variation estimates appeared to be sufficiently large to permit substantial progress by any of the three family systems of selection, but S_1 family testing and selection appeared to be the most promising, particularly for improving green fodder yield and yield components, HCN content and WUE traits.

References

- Ajala, S. O., C. E. Ago and G. Olaoye. 2009. Comparison of predicted responses to three types of recurrent selection procedures for the improvement of maize (*Zea mays* L.). *Journal of Plant Breed and Crop Science* 1: 284-292.
- Amaral Jr, A.T. Do., I. L. deJ. Freitas, A G. Guimarães, C. Maldonado, O. Arriagada and F. Mora. 2016. Bayesian analysis of quantitative traits in popcorn (*Zea mays* L.) through four cycles of recurrent selection. *Plant Production Science* 19: 574-578.
- Bates, L., R. P. Waldren and I. D. Teare. 1973. Rapid determination of free proline for water-stress studies. *Plant and Soil* 39: 205-207.
- Bittinger, T. S., R. P. Cantrell, J. D. Axtell and W. E. Nyquist. 1981. Analysis of quantitative traits in PP9 random mating sorghum population. *Crop Science* 21: 664-669.
- Bradshaw, J. E. 1983. Estimating the predicted response to S_1 family selection. *Heredity* 51: 415-418.
- Deshmukh, M. P., R. B. Deshmukh and P. B. Ghopade. 2011. Quantitative genetic analysis in relation to population improvement in sorghum [*Sorghum bicolor* (L.) Moench]. *Ecology, Environment and Conservation* 17: 507-606.
- Doggett, H. 1972. Recurrent selection in sorghum populations. *Heredity* 28: 9-29.
- Doggett, H. and S. A. Eberhart. 1968. Recurrent selection in sorghum. *Crop Science* 8: 119-121.
- Dutt, Y. and K. S. Nirania. 2005. Efficiency of half-sib, full-sib and S_1 progeny recurrent selection methods for improvement in grain and dry fodder yield in pearl millet [*Pennisetum glaucum* (L.) R Br]. *Indian Journal of Genetics and Plant Breeding* 65: 257-260.
- Empig, L. T., C. O. Gardner and W. A. Compton. 1972. *Theoretical gains for different population improvement procedures*: Bulletin No. 26 (revised), Nebraska Agricultural Experiment Station.
- Gardner, C. O. 1972. Development of superior population of sorghum and their role in breeding programs. In: N. G. P. Rao and L. R. House (eds). *Sorghum in Seventies*. Oxford and IBH Publishing Co, New Delhi. pp. 180-96.
- Gleadow, R., M. J. Ottman, B. Kimball, G. Wall, P. Pinter and R. LaMorte. 2016. Drought-induced changes in nitrogen partitioning between cyanide and nitrate in leaves and stems of sorghum grown at elevated CO_2 are age dependent. *Field Crops Research* 185: 97-102.
- Jan-orn, J., C. O. Gardner and W. M. Ross. 1976. Quantitative genetic studies of the np3r random-mating grain sorghum population. *Crop Science* 16: 489-496.
- Neilson, E. H., A. Edwards, C. Blomstedt, B. Berger, B. L. Møller, and R. Gleadow. 2015. Utilization of a high-throughput shoot imaging system to examine the dynamic phenotypic responses of a C_4 cereal crop plant to nitrogen and water deficiency over time. *Journal of Experimental Botany* 66: 1817-1832.

- Nejad, M. M., T. S. Nejad and A. R. Shokohfar. 2014. The effect of auxin foliar spray on qualitative traits of forage sorghum var. speed-feed under water deficit stress. *Journal of Biodiversity and Environmental Sciences* 4: 178-184.
- Niyazi, B. A. M. 2018. Forage production and water use efficiency (WUE) of sorghum (*Sorghum bicolor* L.) under drought stress as affected by silicon (Si) treatments. *International Journal of Engineering Research and Technology* 7: 32-38.
- Ross, W. M., C. O. Gardner and P. T. Nordquist. 1971. Population breeding in sorghum. *Proceedings of 7th Biennial Grain Sorghum Research Utilization Conference*. Lubbock, Texas. pp 93-98.
- Singh, V. V., Maharaj Singh, J. S. Chauhan, Dhiraj Singh and M. L. Meena. 2014. Comparison of half-sib and full-sib progeny selection methods in Indian mustard (*Brassica juncea* L.) under rainfed conditions. *SABRAO Journal of Breeding and Genetics* 46: 81-88.
- Somegowda, V.K., K.V.S.V. Prasad, R. Devulapalli, A. Vemula, A. Rathore, M. Blümmel and S. P. Deshpande. 2019. Evaluation of sorghum fodder yield and quality under water stressed condition. International Livestock Research Institute, Patancheru, Hyderabad, India. <https://hdl.handle.net/10568/100283>.
- Stephens, J. C. and R. H. Holland. 1954. Cytoplasmic male sterility for hybrid seed production. *Agronomy Journal* 46: 20-23.
- Tilley, J. M. A. and R. A. Terry. 1963. A two stage technique for *in vitro* digestion of forage crops. *Journal of British Grassland Society* 18: 104-111.
- Weatherley, P. E. 1950. Studies in the water relations of the cotton plant. I. The field measurement of water deficits in leaves. *New Phytologist* 49: 81-87.
- Zaveri, P. P., P. S. Phul and B. S. Dhillon. 1989. Observed and predicted genetic gains from single and multi-trait selections using three mating designs in pearl millet. *Plant Breeding* 103: 270-277.