Environment and Ecology 40 (3C) : 1670—1679, July—September 2022 ISSN 0970-0420

Study of Gene Effects for Ethanol Yield and its Component Traits in Sweet Sorghum [Sorghum bicolor (L.) Moench] using Generation Mean Analysis

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Received 6 May 2022, Accepted 23 June 2022, Published on 26 August 2022

ABSTRACT

Generation mean analysis was carried out to estimate the nature and magnitude of gene effects for sugar yield and its component traits in sweet sorghum (*Sor-ghum bicolor* (L.) Moench). Six basic generations,

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S.K. Naffez Umar Assistant Professor, Department of Statistics and Computer Applications, Agricultural College, Bapatla, India Email : kavya.pati@gmail.com *Corresponding author namely P₁, P₂, F₁, F₂, BC₁P₁, BC₁P₂ of cross ICSB 14029 × ICSV 15006 were evaluated in summer, 2019. The mean performance of the F_1 in all the crosses indicated role of non-additive gene action which includes both dominance as well as epistatic interactions. The scaling tests as well as chi square test from joint scaling test were highly significant for 11 characters excluding stem girth and 1000 grain weight, indicating inadequacy of simple additive-dominance model. The six generation mean analysis carried out for 13 quantitative characters indicated significance of dominance gene effects for days to flowering, plant height, fresh stalk weight, juice yield, grain yield and ethanol yield. Based on the signs of [h[^]] and [l[^]] gene effects, complementary gene interaction was evident in the inheritance of days to 50% flowering, days to maturity, juice yield, ethanol yield, while, duplicate gene interaction in the inheritance was evident for plant height, number of nodes per plant, stem girth, panicle weight, 1000 grain weight, fresh stalk weight, brix %, total sugars estimation, grain yield indicating predominantly dispersed alleles at the interacting loci. Days to 50% flowering, Juice yield and ethanol yield expressed complementary epistasis along with dominance × dominance interaction. Due to presence of duplicate epistasis in the present crosses it minimizes the manifestation of heterosis. Hence, selection for high ethanol yielding genotypes would be effective if dominance and epistatic effects were first reduced by few generations of selfing.

Keywords Sweet sorghum, Gene effects, Additive effects. Dominance effects, Heterosis.

INTRODUCTION

Sorghum Sorghum bicolor (L.) Moench is a C_4 crop belonging to family Poaceae with chromosome number 2n=20, possessing different range of products like grain sorghum, forage sorghum, sweet sorghum which is native to semiarid tropics and subtropics. In India and Africa, it is used as food crop while in Europe and United states it is used as feed for livestock. Profuse alternative use of sorghum is not only as food and feed but also as a bioenergy crop which has rich amounts of sugars in stalks (10–20%) as in sugarcane (Hunter and Anderson 1997) terming it as sweet sorghum.

The dependency on fossil fuels is very high and they are depleting day by day, where there is need for other alternate sources like biofuels from plant-based products like Sugarcane, Corn, Sweet sorghum (Reddy *et al.* 2005) Sweet potato (Lareo *et al.* 2013) and sugar beet (Duraisam *et al.* 2017). The above-mentioned crops are food crops, which may hinder the food security if used for biofuels, but there are few crops for biofuel purpose like Sweet sorghum. In south American countries like Brazil, it is grown as a source crop for ethanol production (Doggett 1988). Currently, the ethanol blending with gasoline in Brazil is 18 to 27.5% (Lopes *et al.* 2016.).

The present commercial ethanol production in India is only through sugarcane, where the by-product from sugar refineries i.e., molasses which is utilized for the ethanol production. When compared to sugarcane, the juice from sweet sorghum is possessing high amounts of reducing sugars which aids in the efficient fermentation, producing clear and potable ethanol with low aldehydes (Ratnavathi *et al.* 2003).

In India, ethanol is used in three different ways. Of the total available ethanol produced, potable liquor occupies the major share (45%), the next 40% is used in the chemical industry as a solvent in synthesis of other organic chemicals and the rest is used for blending with petrol and other purposes. The growth of user industries and use of ethanol has been continually increasing year by year which is creating a huge demand, but the production and availability of ethanol has largely lagged behind. The countries viz., Brazil, The United States of America (USA) and China are the top ethanol producing countries respectively, while India stands in 4th position producing around 2000 million liters of ethanol, primarily from sugarcane molasses (Prasad *et al.* 2018).

The World ethanol production has increased from 13.6 billion gallons in 2007 to 22.3 billion gallons by 2012 (Satyanarayana and Rameshchandra 2014). India has produced 530.09 million gallons of ethanol in 2019 (www.staista.com). In order to reduce carbon monoxide emission through automobiles, Indian government has mandated for blending of five per cent ethanol with petrol and diesel and could save nearly 80 million liter of petrol annually, if petrol is blended with ethanol by 10% (GAIN report 2013). The current ethanol production raw material is through sugarcane molasses which is lagging in production and the most of the distilleries (ethanol based) work only for 180 days i.e., during the peak period of sugarcane harvesting stage. The government has no stringent regulations for blending ethanol in petrol (gasoline) due to truncated production of sugarcane crop and it's by product in the past decade. The sweet sorghum can be a best alternative for ethanol production to meet up the demand of the country, by providing year the round operations to molasses-based ethanol distilleries and provide an assured income to the farmers. Generation mean analysis provides information on the relative importance of average effects of the genes (additive effects), dominance deviations and effects due to nonallelic genetic interactions, yet it is a simple, but useful technique for estimating gene effects for a polygenic trait, its greatest merit lying in the ability to estimate epistatic gene effects such as additive •additive, dominance •dominance and additive •dominance effects (Ganapati et al. 2020).

MATERIALS AND METHODS

The experiment was carried out to estimate the nature and magnitude of gene effects for sugar yield and its component traits in sweet sorghum *Sorghum bicolor* (L.) Moench. Six basic generations, namely P_1 , P_2 , F_1 , F_2 , BC_1P_1 , BC_1P_2 of cross ICSB 14029 × ICSV 15006

			Comonatio			
Character	P ₁	P ₂	Generatio F ₁	F ₂	BC ₁	BC ₂
	1	1 2	1	1 2	B01	<i>BC</i> ₂
1 Days to 50%	flowering (days)					
Range	72.00- 75.00	83.00 - 85.00	76.00 -80.00	72.00 -79.00	70.00 - 74.00	72.00 - 85.00
Mean + SE	73.40 ± 0.33	83.75 ± 0.32	79.00 ± 0.580	73.25 ± 0.47	72.46 ±0.43	77.39 ± 1.79
Variance	0.568	0.51	1.684	3.556	1.29	22.470
2 Days to matu	irity (days)					
Range	115.00 -117.00	121.00 - 124.00	119 - 127	115.00 - 117.00	115.00 - 118.00	114.00 - 125.00
Mean + SE	116.50 ± 0.271	122.60 ± 0.468	121.70 ± 1.171	115.18 ± 0.40	117.07 ± 0.30	118.50 ± 1.40
Variance	0.368	1.095	6.853	2.663	0.661	13.889
3 Plant height (cm)					
Range	180.80-210.60	243.60 - 323.50	197.40 -304.30	172.60 -254.60	140.80 - 224.30	187.65 - 323.50
Mean + SE	195.47 ± 3.233	295.285 ± 8.364	$233.560 \pm \! 12.818$	207.69 ± 5.45	214.57 ± 11.55	237.29 ± 15.91
Variance	195.479	295.285	233.560	207.694	214.579	237.29
4 Number of no						
Range	9.00 - 11.00	14.00 - 16.00	12.00 -15.00	10 - 14	9-15	11.00 - 15.00
Mean + SE	10.55 ± 0.27	15.05 ± 0.27	14.30 ± 0.38	12.51 ± 0.40	12.28 ±0.76	13.78 ± 0.47
Variance	0.366	0.366	0.747	2.571	4.138	1.58
5 Stem girth (c	· · · · · · · · · · · · · · · · · · ·					
Range	2.30 - 3.20	3.00 - 3.60	1.90 - 3.40	1.80 - 2.50	1.40 -3.20	1.80 - 3.60
Mean + SE	2.85 ± 0.123	3.23 ± 0.071	2.635 ± 0.197	2.700 ± 0.105	2.750 ± 0.159	2.85 ± 0.16
Variance	0.075	0.025	0.194	0.175	0.177	0.180
6 Panicle weig						
Range	42.60 - 53.70	38.60 - 50.70	37.67 - 55.21	21.50 - 49.53	25.45- 52.40	22.70 - 55.60
Mean + SE	47.62 ± 1.286	44.74 ± 3.594	48.31 ± 1.983	37.33 ± 1.900	45.15 ± 2.249	44.69 ± 2.94
Variance	8.265	64.579	19.653	57.780	35.400	60.546
7 1000 grain w	eight (g)					
Range	20.80 - 27.70	16.20 - 29.80	17.70 - 35.85	14.35 - 32.76	17.20 - 35.85	10.40 - 31.45
Mean + SE	24.12 ± 0.930	22.79 ± 1.492	25.28 ± 2.262	23.91 ± 1.109	23.676 ± 1.470	22.123 ± 1.368
Variance	4.323	11.316	25.59	19.68	15.11	13.09
8 Fresh stalk w						
Range	42.28 - 56.53	56.13 - 75.94	29.75 - 58.73	29.82 - 50.71	21.75 - 48.73	22.82 -75.94
Mean + SE	51.14 ± 1.938	62.42 ± 2.120	58.095 ± 3.431	44.943 ± 1.858	47.702 ± 3.338	48.559 ± 4.225
Variance	1.938	2.120	3.431	1.858	3.338	4.255
9 Juice yield (t	· ·					
Range	11170.36	14992.58	16562.95	6755.55 -	8562.95 -	9567.0 -
	-13511.10	-19970.35	-23392.57	21051.83	19229.61	20874.05
Mean + SE	12466.65 ± 362.96	17151.83 ± 605.435	19876.28±895.31	14101.14±921.59		$17104.74 \pm$
	<pre>/ ***</pre>		1000000.0		1087.53	1358.02
Variance	658700.25	1832755.99	4007930.43	13589411.60	8279165.82	12.9538.71
10 Brix%						
Range	16-17	14-16	15 - 17	14 - 20	14 -16	14 -17
Mean + SE	16.70	15.60	15.75	16.31	14.64	15.60
Variance	0.221	0.358	0.408	2.726	0.460	0.840
11 Total soluble	0					
Range	14.15 - 15.02	7.15 – 9.15	13.27 - 15.02	12.40 - 15.02	12.40 -14.15	12.40 -15.02
Mean + SE	14.75 ± 0.183	13.80 ± 0.235	13.929 ± 0.250	13.765 ± 0.252	13.679 ± 0.435	13.929 ± 0.344
Variance	0.167	0.276	0.314	1.015	1.328	0.828
12 Ethanol yie						
Range	841.22 - 1080.41	1062.77 - 1503.93				737.19–1669.18
Mean + SE	979.47 ± 30.92	1260.219 ± 52.38	1472.61 ± 67.21	1055.78 ± 71.42	1001.53 ± 75.18	1273.93±112.28
Variance	4780.42	13722.97	22589.77	81620.23	39571.00	88255.74

Table 1. Range, mean with their standard error and variance of six generations of the sorghum *[Sorghum bicolor (L.) Moench]* cross'ICSB 14029 × ICSV 15006' in respect of 13 quantitative characters.

Table 1. Continued.

	Generation							
Character	\mathbf{P}_{1}	\mathbf{P}_2	F ₁	F_2	BC_1	BC_2		
13 Grain yiel	d (t ha ⁻¹)							
Range	4.39 - 5.44	3.73 - 5.60	3.96 - 6.01	1.44 - 5.36	1.85 - 5.29	1.66 - 5.51		
Mean + SE	4.13 ± 0.131	4.630 ± 0.219	4.84 ± 0.244	$3.66 {\pm} 0.2676$	4.531 ± 0.287	4.00 ± 0.333		
Variance	0.086	0.240	0.297	1.222	0.575	0.778		

were evaluated in summer, 2019. The experiment was conducted in a Randomized Block Design with four replications. Each entry of parents and F_1 was raised in two rows of 4 m length with 45 × 15 cm spacing. F_2 was raised in 10 rows of 4 m length with 45 × 15 cm and backcrosses seed with 4 rows of 4 m length with 45 × 15 cm. The data was recorded on following parameters : Days to 50% flowering, Days to maturity, Plant height, Number of nodes per plant, Stem girth, Panicle weight, 1000 grain weight, Fresh stalk weight, Juice yield, Brix %, Total Soluble Sugars, Computed ethanol yield, Grain yield.

RESULTS AND DISCUSSION

The choice of an efficient breeding program depends

to a large extent on knowledge of the type of gene action involved in the expression of the character. The knowledge on nature of gene action for ethanol yield and its component traits like Brix % and Juice content in the breeding material can provide useful information for selecting proper breeding procedure for future genetic enhancement. Genetic enhancement for increased ethanol yield and its attributing traits is very important to make sweet sorghum more profitable to the farmers and the industry, while sustaining grain yield and other important components. In the present study only single cross has been studied for 6 parameter model.

Per se performance : The mean performance of $P_1, P_2, F_1, F_2, BC_1P_1$ and BC_1P_2 families of the cross

Table 2. Scaling tests for 13 characters in the cross 'ICSB 14029 x ICSV 15006' of Sorghum *[Sorghum bicolor* (L.) Moench] (Mather, 1949). Note: * and ** Significance at P = 0.05 and 0.01 respectively.

Sl. No.	Character	А	Scaling test B	С	D
1	Days to 50% flow-				
	ering (days)	7.471 ± 0.546 **	$7.964 \pm 1.822 **$	22.150 ±1.131 **	-3.357 ± 1.035
2	Days to maturity				
	(days)	$4.057 \pm 0.675 **$	$7.300 \pm 1.543 **$	$21.750 \pm 1.452 **$	-5.196 ± 0.828
3	Plant height (cm)	-0.118 ± 13.313	$54.259 \pm 17.662 **$	$127.109 \pm 17.417 **$	-36.484 ± 11.246
4	Number of nodes				
	per plant	0.279 ± 0.804	$1.779 \pm 0.531 **$	4.138 ±0.910**	-1.040 ± 0.604
5	Stem girth (cm)	-0.010 ± 0.197	0.151 ± 0.786	0.555 ± 0.296	-0.207 ± 0.154
6	Panicle weight (g)	$5.641 \pm 2.540*$	3.681 ± 3.586	$39.672 \pm 4.692 **$	-15.175 ± 2.653
7	1000 seed weight (g)	2.061 ± 1.078	3.791 ± 1.969	1.785 ± 0.543	2.034 ± 1.360
8	Fresh stalk yield				
	(T ha-1)	-0.164 ± 3.876	9.397 ± 4.709	$45.983 \pm 5.258 **$	-18.375 ± 3.281
9	Juice yield (1 ha-1)	$3901.686 \pm 1.189.987^{**}$	2818.629 ± 1461.59	11766.470 ± 2079.30 **	-2523.076 ± 1267.311
10	Brix %	3.164 ±0.312 **	0.136 ± 0.398	-1.450 ± 0.890	$2.375 \pm 0.466 **$
11	Total soluble sugars				
	(%)	$1.329 \pm 0.462 **$	-0.131 ± 0.384	$1.335 \pm 0.582 **$	-0.079 ± 0.375
12	Ethanol yield (1 ha-1)	449.028 ± 83.794 **	184.958 ± 120.098	961.777 ± 160.774 **	-163.895 ± 98.318
13	Grain yield (T ha-1)	0.615 ± 0.318	$1.462 \pm 0.371 **$	4.511 ± 0.617 **	-1.217 ± 0.353

Sl. No.	Character	М	D	Н	χ^2
	Days to 50% flowering (days)	77.946 **	5.393 **	-2.802	449.51**
	Days to maturity (days)	119.121 **	2.628	-2.862	271.1**
	Plant height (cm)	240.510 **	45.31**	-37.870	62.41**
	Number of nodes per plant	12.678 **	2.201 **	1.122 **	27.1**
;	Stem girth (cm)	3.033**	0.186 **	-0.504	4.31*
5	Panicle weight (g)	43.492 **	-3.247	1.349	74.68**
	1000 seed weight (g)	23.185**	-0.914	0.856	4.49**
	Fresh stalk yield (t ha-1)	55.270 **	5.094 **	-19.598 **	86.48**
)	Juice yield (1 ha ⁻¹)	14597.896 **	2275.706**	3791.579 **	38.09**
0	Brix %	16.033**	-0.323	-0.793	116.61**
1	Total soluble sugars (%)	14.232**	-0.448	-0.467	12.94**
2	Ethanol yield (1 ha-1)	1098.085 **	138.720 **	240.940 **	54.55**
3	Grain yield (t ha ⁻¹)	4.596 **	-0.183	-0.201	60.59**

Table 3. Joint scaling test for 13 characters in 'ICSB 14029 × ICSV 15006' cross of Sorghum (*Sorghum bicolor* L. Moench) (Cavalli, 1952). Note: * and ** Significance at P = 0.05 and 0.01 respectively.

ICSB 14029 × ICSB 15006 are shown in Table 1. The mean performance of the two parental lines were different from each other for all the thirteen characters viz., days to 50% flowering, days to maturity, plant height, number of nodes pr plant, stem girth, panicle weight,1000 grain weight, fresh stalk weight, Brix %, total soluble sugars, juice yield, ethanol yield. Also the mean performances of F_1 and F_2 for the above said characters were different from those of both the parents and they tended towards their respective female parents (P_2) except for number of nodes per plant, stem girth, panicle weight, 1000 grain weight, juice yield, ethanol yield, grain yield.

The F_1 means were greater than the respective mid-parent mean values for all the given characters indicating dominance except plant height, stem girth,1000 grain weight, brix % which recorded lower mid parental values. The BC₁P₁ and BC₁P₂ family means were tended towards their respective parents and overlapped with each other which indicate gene interactions for characters fresh stalk weight and total soluble sugars.

Scaling tests and joint scaling tests

The mean and variance of six generations viz., P_1 , P_2 , F_1 , F_2 , BC_1P_1 and BC_2P_2 of the cross 'ICSB 14029 ×ICSV 15006' in respect of 13 traits were subjected to scaling tests as per the method of Mather (1949) and

Joint scaling test as per the method of Cavalli (1952) to test the presence or absence of gene interaction in the inheritance of these traits. The significance of any one of these scales is taken to indicate the presence of non-allelic interactions, which can be noted as : The significance of A and B scales indicates the presence of all the three types of non-allelic interactions viz., additive \times additive [i^], additive \times dominance [j^] and dominance \times dominance [1[^]]. The significance of C scale suggests dominance \times dominance $[1^{n}]$ type of interaction. D scales provide a test of [i[^]], type of interaction (additive x additive) (Singh and Chaudhary, 1977). Joint scaling test revealed that both additive and dominance gene effects were highly significant for all the traits except in days to maturity, panicle weight, 1000 seed weight, brix %, total soluble sugars, grain yield were nonsignificant. The results of scaling tests, joint scaling test and gene effects in respect of 13 traits have been tabulated in Tables 2–4, respectively and presented trait wise below.

Days to 50 % flowering (days)

The tests 'A' 'B' and 'C' are highly significant indicating inadequacy of additive-dominance model, which was further asserted by significance of additive component as well as high level of significance of chi-square value in joint scaling test indicating role of non-allelic interactions in the genetic control of the trait.

51. No.	Character	М	D	Н	Ι	j	1	Type of epistasis
1	Days to 50% flow-	73.250	-4.929	7.139	6.714	0.493	8.721	Complimentary
	ering (days)	±0.236 **	± 0.921	$\pm 2.093 **$	± 2.070 **	± 1.857	$\pm 2.262 **$	
2	Days to maturity	115.188	-1.429	12.543	10.393	3.243	0.964	Complimentary
	(days)	± 0.204 **	±0.721	± 1.762	$\pm 1.657 **$	$\pm 1.467 **$	± 3.229	
3	Plant height (cm)	207.694	-22.714	61.146	72.968	54.377	-18.827	Duplicate
		±2.727 **	± 9.835	± 23.494	$\pm 22.491*$	* ± 20.175*	* ± 43.023	-
1	Number of nodes	12.516	-1.500	3.580	2.080	1.500	-0.023	Duplicate
	per plant	± 0.200	± 0.452	$\pm 1.227 **$	± 1.208	± 0.924	± 2.024	*
5	Stem girth (cm)	2.700	-0.017	0.007	-	-	-	-
		± 0.052 **	± 0.113	± 0.325				
5	Panicle weight	37.334	0.458	32.482	30.350	-1.960	-21.029	Duplicate
	(g)	$\pm 0.950 **$	± 1.851	± 5.481	$\pm 5.306**$	± 4.165	± 8.766	•
,	1000 seed wei-	23.917	1.553	-2.215	-	-	-	-
	ght (g)	$\pm 0.555 **$	± 1.547	± 3.228				
3	Fresh stalk	38.943	-0.856	24.062	36.750	9.562	-27.516	Duplicate
	yield (T ha ⁻¹)	$\pm 0.929 **$	± 2.704	± 6.821 **	$\pm 6.562 **$	± 5.596	± 12.027	-
)	Juice yield	14401.140	-2884.11	7 10113.19	0 5046.152	2 -1083.055	51 1674.172	
	(1 ha ⁻¹)	±460.798	± 869.908	± 579.893	± 2534.6	22 ±1775.2	255 ± 4053.559	Complimentary
		**	**	**	**			
0	Brix %	16.313	-0.964	-5.510	-4.750	-3.029	8.050	Duplicate
		$\pm 0.206 **$	± 0.215	± 0.946	± 0.931	± 0.463	$\pm 1.239 **$	
11	Total soluble	13.765	-0.250	-0.193	0.157	-1.461	1.041	
	sugars (%)	$\pm 0.126 **$	± 0.277	± 0.763	± 0.749	± 0.574	± 0.831	Duplicate
2	Ethanol yield	1055.787	-272.405	680.556	327.797	264.070	306.195	-
	(1 ha ⁻¹)	$\pm 35.712 **$	± 67.567	± 200.067	$\pm 196.63**$	* ±138.514	± 314.471	Complimentary
3	Grain yield	3.660	0.525	2.548	2.433	0.847	-0.356	Duplicate
	$(T ha^{-1})$	± 0.138 **	$\pm 0.220 **$	± 0.720 **	±0.706 **	± 0.458	± 1.074	*

Table 4. Gene effects for 13 characters in the cross 'ICSB 14029 × ICSV 15006' of Sorghum [Sorghum bicolor (L.) Moench]. Note :* and ** Significance at P = 0.05 and 0.01 respectively.

Days to maturity (days)

The inadequacy of simple additive-dominance model and presence of digenic or still higher order epistasis in the inheritance of this trait is confirmed by the presence of highly significant scaling tests 'A' 'B' and 'C', which was further confirmed by high level of significance of chi-square value obtained in Joint scaling test.

Plant height (cm)

'B' and 'C' tests are highly significant while 'A' and 'D' are nonsignificant negative. Additive component as well as chi-square values were also highly significant specifying inadequacy of simple additive-dominance model and presence of gene interaction in the genetic control of this trait.

Number of nodes per plant

'B' and 'C' tests were highly significant. The additivedominance components as well as chi-square value of joint scaling test were also highly significant, which clearly stipulates the major role of gene interaction in the inheritance of this trait.

Stem girth (cm)

None of the tests were significant for stem girth which indicates the adequacy of simple additive –dominance model. The dominance component of joint scaling test were also non-significant, which indicates absence of gene interaction of this trait.

Panicle weight (g)

The tests 'A' and 'C' are significant at 5% and 1% re-

spectively, confirming the absence of additive-dominance model, significance of chi-square value in joint scaling test indicating role of gene interaction in the genetic control of the trait.

1000 grain weight (g)

Absence of significant values in 'A', 'B' 'C' and 'D' test indicates the absence of non-allelic interactions. Non significance of additive and dominance components were also highly significant indicating adequacy of simple additive-dominance.

Fresh stalk yield (t ha⁻¹)

'A', 'B' are non-significant but 'C' test was highly significant. In joint scaling, the additive dominance components as well as chi-square value were also highly significant, which clearly stipulating major role of gene interaction in the inheritance of this trait.

Juice yield (l ha⁻¹)

Out of the four tests viz., A and C are highly significant and positive except D test which is negative. The additive dominance components and chi-square value of joint scaling test were also highly significant suggesting failure of additive-dominance model to explain the inheritance and presence of epistasis in the genetic control of this trait.

Stem girth (cm)

None of the tests were significant for stem girth which indicates the adequacy of simple additive –dominance model. Baskheti and Bhatt (2005) indicated additive, dominance and epistatic interactions which is deviating from the current reported results.

Panicle weight (g)

It is evident from six parameter model that only additive × additive [i²] component (30.35) is significant and others are nonsignificant. Operation of duplicate type of epistasis was evidenced from the estimates of [h²] and [l²], which had opposite signs.

1000 grain weight (g)

Absence of significant values in 'A', 'B' 'C' and 'D' test indicates the absence of non-allelic interactions.

Fresh stalk yield (t ha⁻¹)

As per the model, only $[h^{2}]$ component (24.062) is highly significant and positive while $[d^{2}]$ component (-0.856) is negative non-significant. Among, the three type of gene interaction, only $[i^{2}]$ type is highly significant in positive direction. The opposite signs of $[h^{2}]$ and $[l^{2}]$ components indicated the presence of duplicate type of epistasis in the genetic control of the trait. Audilakshmi *et al.* (2010) reported similar result for highly significant dominance component.

Juice yield (l ha⁻¹)

In the given model, only $[h^2]$ component (10113.190) is highly significant and positive while $[d^2]$ component (-2884.117) is negative non-significant. Among, the three type of gene interaction, only $[i^2]$ type (5046.152) is highly significant in positive direction. The same signs of $[h^2]$ and $[l^2]$ components indicated the presence of complementary type of epistasis in the genetic control of the trait. Similar results were reported by Audilakshmi *et al.* (2010) and Kumar *et al.* (2011).

Brix %

The additive (-0.964), dominance component (-5.510) were noticed nonsignificant and negative and only [1[°]] component (8.050) is positive significant. However, joint scaling test also indicated non significance of both additive and dominance gene effects. Duplicate epistasis was operating in the cross as evidenced from the estimates of [h[°]] and [1[°]] which had opposite signs. The additive and dominance components results quoted by Premalatha *et al.* (2006), Audilakshmi *et al.* (2010), Kumar *et al.* (2011) were significant for this trait which is deviating from the current result.

Total soluble sugars (%)

Both $[d^{\uparrow}]$ (-0.250) and $[h^{\uparrow}]$ (-0.193) gene effects are

nonsignificant in negative direction. The dominance \times dominance [l] (1.041) type of interaction is significant and positive. The estimates of [h[^]] and [l[^]] components with opposite signs indicating the duplicate nature of epistasis for the trait. Sanjanareddy *et al.* (2011) reported both additive and dominant genes controlled overall sugar yield.

Ethanol yield (t ha-1)

Negative and non-significant additive gene effect $[d^{2}]$ (-272.405) and positive significant is noticed for dominant $[h^{2}]$ component (680.58). However none of the epistatic components are highly significant. Complementary type of epistasis was found operating in the inheritance of biomass as evidenced by same signs of $[h^{2}]$ and $[l^{2}]$ components. Vinaykumar (2009) reported dominant gene effects for this trait.

Grain yield (t ha-1)

The [d^{$^{-}$}] (0.525) & [h^{$^{-}$}] (2.548) component is highly significant and positive. Among interaction components, additive × additive [i^{$^{-}$}] component (2.433) is highly significant and positive. Duplicate gene interaction based on the significance of opposite signs of [h^{$^{-}$}] and [l^{$^{-}$}] components was noticed in the genetic control of this trait. Shivani and Sreelakshmi (2013), Iraddi *et al.* (2014), Karande and Lad (2015), Gaddimeedi *et al.* (2018) and Lad *et al.* (2019).

The mean performance of 6 generations indicated that the F_2 means were lesser than the F_1 means except for brix % and stem girth and between mid-parental values in respect of all the traits except panicle weight, grain yield indicating high degree of inbreeding depression. These results depict the predominant role of non-additive gene action which includes both dominance as well as epistatic interactions.

The F_1 means were greater than the respective mid-parent mean values for all the given characters, indicating dominance for important traits like juice yield, ethanol yield and grain yield conforming the re-

port Kumar *et al.* (2011). The BC_1P_1 and BC_1P_2 family means were tended towards their respective parents and overlapped with each other which indicate gene interactions. Chi-square significance of joint scaling test indicated the inadequacy of additive-dominance model which in turn indicated the presence of non-allelic interactions.

The scaling tests as well as chi-square test from joint scaling test were highly significant in the cross ICSB 14029 x ICSV 15006 cross for 11 characters excluding stem girth and 1000 grain weight, indicating inadequacy of simple additive-dominance model and justifying the use of six parameter model for the detection of gene interactions.

The six generation mean analysis carried out for 13 quantitative characters indicated significance of dominance gene effects for days to flowering, plant height, Fresh stalk yield, juice yield, grain yield and ethanol yield. Significance of one or more interaction types is observed (additive \times additive or additive \times dominance or dominance × dominance) in all the 13 traits except nodes per plant, stem girth, 1000 grain weight, total sugars estimation and ethanol yield. Based on the signs of [h[^]] and [l[^]] gene effects, complementary gene interaction was evident in the inheritance of days to 50% flowering, days to maturity, juice yield, ethanol yield, while, duplicate gene interaction in the inheritance was evident for plant height, number of nodes per plant, panicle weight, fresh stalk yield, brix %, total sugars estimation, grain yield indicating predominantly dispersed alleles at the interacting loci (Jinks and Jones 1958).

CONCLUSION

The present study of 13 characters for generation mean analysis suggested that dual gene effects (additive and dominance) were important, but dominance gene effect had more profound effect. When gene interactions are significant i.e., additive \times additive, simple selfing in early generations will yield desired genotypes. If additive x dominance or dominance x dominance gene interactions are present, heterosis breeding will be useful, as in hybrids, heterozygous condition is fixed (Audilakshmi et al. 2010).

Higher magnitude of dominance gene effects and dominance gene interactions could not be exploited for heterosis breeding due to presence of duplicate epistasis in the present crosses as it minimizes the manifestation of heterosis (Kearsey and Pooni 1996). Hence, selection for high ethanol yielding genotypes would be effective if dominance and epistatic effects were first reduced by few generations of selfing. Then biparental mating followed by internating of selected progeny and selection in subsequent segregating generation or population improvement methods may possibly serve the purpose. Days to 50% flowering, Juice yield and ethanol yield expressed complementary epistasis along with dominance × dominance interaction. Usually, characters with non-additive gene action coupled with duplicate type of gene interaction, can be improved through recurrent selection or diallel selective mating.

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