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Research Article

Elucidation of gene action and combining ability for grain and fodder yield and contributing traits in sorghum [*Sorghum bicolor* (L.) Moench]

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Abstract

The present investigation was undertaken to achieve information on gene action and combining ability in sorghum [*Sorghum bicolor* (L.) Moench]. The experimental material consisted of eleven parents and their 28 Line \times Tester crosses. The evaluation was carried out during *Kharif*, 2020 at Sorghum Research Station, S. D. Agricultural University, Deesa. The ratio of σ^2_D/σ^2_H being more than unity was found for days to flowering, which suggested a more significant role of additive genetic variance in the inheritance of this trait. In contrast, the rest of the yield and its component traits showed non-additive genetic variance. The *gca* effects indicated that parents, SR 3019, CSV 31 and GJ 43 were found as good general combiners for grain yield per plant. While, parents DS 156, CSV 31 and SPV 2682 were good general combiners for dry fodder yield per plant and its contributing traits. Based on estimates of *sca* effects, the most promising hybrids for grain yield per plant were *viz.*, SR 2980 \times CSV 31, SR 3019 \times SPV 2573 and DSF 117 \times SPV 2682, whereas for dry fodder yield per plant were *viz.*, SR 3048 \times CSV 31, GJ 43 \times SPV 2573 and DSF 168 \times SPV 2573. The good general combiners for yield and contributing traits can be utilized in intensive crossing programme and select transgressive segregants for desired characters in segregating generations to develop superior lines.

Keywords: L \times T analysis, Gene action, combining ability, Grain yield, Dry fodder yield

INTRODUCTION

Sorghum [*Sorghum bicolor* (L.) Moench] is an often cross-pollinated, diploid ($2n = 2x = 20$) crop with a genome, about 25 per cent the size of maize or sugarcane. It is a C_4 plant with higher photosynthetic efficiency and higher abiotic stress tolerance (Nagy *et al.*, 1995; Reddy *et al.*, 2009). Sorghum is the fifth most important cereal crop globally and is the dietary staple of more than 500 million people in 30 countries (Goswami *et al.*, 2020., Gami *et al.*, 2021). It is grown on 40 million hectares in 105 countries of Africa, Asia, Oceania and America. Africa and India account for the largest share (> 70 %) of the global sorghum area, while the U.S.A., India, Mexico, Nigeria, Sudan and Ethiopia are the major

sorghum producers (Kumar *et al.*, 2011). It is the third most important food grain crop in India, next to rice and wheat. In India, sorghum is mainly used as food, feed and forage crop. Besides this, it also provides raw materials for the production of starch, fiber, dextrose, syrup, bio-fuels, vinegar, alcohol and other products.

In a hybridization programme, selecting the right type of parents is a crucial step for a breeder. Combining ability is a relative ability of an inbred or a clone when crossed to another inbred or clone to transmit desirable traits or a specific trait to its progeny. The concept of combining ability as a measure of gene action was proposed

by Sprague and Tatum (1942). It is a powerful tool to discriminate between good and poor combiners and select appropriate parental material. It also provides information on the nature of gene action involved in the inheritance of various traits. Thus, it helps plant breeders to develop improved hybrids, high yielding varieties and also helps to identify the best combiner in the breeding procedure. The Line \times Tester analysis technique suggested by Kempthorne (1957) has been extensively used to compare with the other methods because it provides a more systematic approach to assess the combining ability of parents and crosses for different quantitative characters and contributing characters. Besides, it gives an overall genetic picture of the materials under investigation in a single generation.

MATERIALS AND METHODS

The experimental material comprises seven females (DSF 117, DSF 168, DS 156, GJ 43, SR 2980, SR 3048 and SR 3019), four males (CSV 31, CSV 17, SPV 2682 and SPV 2573) and 28 F_1 hybrids. Parents were crossed in a Line \times Tester fashion during summer 2020. Hybridization was carried out through hand emasculation and hand pollination. Simultaneously parental genotypes were also maintained through selfing to get pure seeds of parents for the experiment. The experimental materials consisted of 39 entries comprising 28 crosses and 11 parents evaluated in Randomized Block Design with three replications during *Kharif, 2020* at Sorghum Research Station, SDAU, Deesa. Each genotype was sown in two rows of two-meter length. The distance between rows and within rows was 45 cm and 15 cm, respectively. The observations were recorded both as visual assessment for days to flowering, while measurement on randomly selected five competitive individual plants for total plant height (cm), the number of leaves per plant, stem girth (mm), leaf length of the blade (cm), leaf width of the blade (cm), panicle length (cm), grain yield per plant (g), dry fodder yield per plant (g), grain protein content (%), fodder protein content (%), Brix content (%) and HCN content (ppm). The replication-wise mean values for all the characters were subjected to statistical analysis. The analysis of variance was carried out as per the procedure suggested by Panse and Sukhatme (1985). The mean value of 39 entries (Parents and their F_1 hybrids) were entered in the computer and combining ability analysis was carried out according to the procedure given by Kempthorne (1957).

RESULTS AND DISCUSSION

The analysis of variance for combining ability and estimates of variance components are given in **Table 1**. The analysis of variance for combining ability partitioning the total genetic variance into general combining ability, representing the additive type of gene action and specific combining ability as a measure of the non-additive type of gene action was carried out for thirteen characters. The mean sum of squares due to female (lines) and male

(testers) were highly significant for all the traits except panicle length. The mean sum of squares due to males was higher in magnitude for days to flowering, stem girth, leaf length of the blade, leaf width of the blade, panicle length, dry fodder yield per plant, grain protein content and brix content than the female indicated the more outstanding contribution of male towards these traits, while in rest of traits showed more contribution of female. The mean sum of squares due to the Line \times Tester interaction was significant for all traits except panicle length. It signified the contribution of hybrids for specific combining ability variance components.

The ratio of σ^2_D/σ^2_H being more than unity was found for days to flowering, suggesting a greater role of additive genetic variance in the inheritance of this trait. This trait can be improved further as a source of favourable genes for earliness by selecting desired transgressive segregants from segregating generations. The predominant role of additive gene action was observed in days to flowering is analogous with results reported earlier by Hariprasanna *et al.* (2012), Soujanya *et al.* (2017), Sen *et al.* (2018) and Rathod *et al.* (2019) in sorghum.

The magnitude of specific combining ability variance was higher than general combining ability variance for rest of the traits *viz.*, total plant height, the number of leaves per plant, stem girth, leaf length of the blade, leaf width of the blade, panicle length, grain yield per plant, dry fodder yield per plant, grain protein content, fodder protein content, brix content and HCN content which indicated the importance of non-additive gene effects in the inheritance of these traits, which suggesting exploitation of these traits for improvement of yield through heterosis breeding. The above results were in accordance with the findings of Patel *et al.* (2018), Parmar *et al.* (2019), Rathod *et al.* (2019), Patel *et al.* (2021) for total plant height; Sen *et al.* (2018), Parmar *et al.* (2019), Rathod *et al.* (2019), Patel *et al.* (2021) for number of leaves per plant; Patel *et al.* (2018), Sen *et al.* (2018), Parmar *et al.* (2019), Patel *et al.* (2021) for stem girth; Kumari *et al.* (2018), Parmar *et al.* (2019), Rathod *et al.* (2019), Patel *et al.* (2021) for leaf length of blade; Kumari *et al.* (2018), Patel *et al.* (2018), Sen *et al.* (2018), Patel *et al.* (2021) for leaf width of blade; Hariprasanna *et al.* (2012), Kumar and Chand (2015), Ingle *et al.* (2018), Patel *et al.* (2018) for panicle length; Jadhav and Deshmukh (2017), Ingle *et al.* (2018), Rathod *et al.* (2019), Patel *et al.* (2021) for grain yield per plant; Soujanya *et al.* (2018), Parmar *et al.* (2019), Rathod *et al.* (2019), Patel *et al.* (2021) for dry fodder yield per plant; Chaudhari *et al.* (2017), Vekariya *et al.* (2017), Rathod *et al.* (2019), Patel *et al.* (2021) for fodder protein content; Dehinwal *et al.* (2017), Soujanya *et al.* (2018), Parmar *et al.* (2019), Patel *et al.* (2021) for Brix content; Kumar *et al.* (2013), Padmashree *et al.* (2014), Chaudhari *et al.* (2017), Dehiwal *et al.* (2017) for HCN content in sorghum.

Table 1. Analysis of variance (mean square) for combining ability, estimates of components of variance and their ratio for various characters in sorghum

Sources of variation	d.f.	Days to flowering	Total plant height	Number of leaves per plant	Stem girth	Leaf length of blade	Leaf width of blade	Panicle length
Replications	2	5.91	171.50	0.005	0.53	10.35	0.54	5.98
Hybrids (Crosses)	27	70.46**	5561.24**	10.15**	37.82**	149.59**	2.24**	18.17
Female in hybrid	6	33.26**	13231.40**	20.18**	43.09**	68.50**	1.25**	11.56
Male in hybrid	3	342.90**	3339.55**	11.38**	78.06**	112.98**	1.93**	23.83
Females × Males (L × T)	18	37.45**	3374.80**	6.60**	29.36**	182.72**	2.62**	19.44
Error	76	2.15	201.82	0.43	5.08	15.08	0.22	11.95
Components of variance:								
σ^2 Females		-0.35	821.38	1.13	1.14	-9.52	-0.11	-0.66
σ^2 Males		14.55	-1.68	0.23	2.32	-3.32	-0.03	0.21
σ^2_D		18.26	595.23	1.11	3.78	-11.15	-0.12	-0.21
σ^2_H		11.77	1057.66	2.05	8.09	55.88	0.80	2.49
σ^2_D / σ^2_H		1.55	0.56	0.54	0.47	-0.20	-0.16	-0.08

Sources of variation	d.f.	Grain yield per plant	Dry fodder yield per plant	Grain protein content	Fodder protein content	Brix content	HCN content
Replications	2	0.72	847.43	0.88	0.10	2.39	1.11
Hybrids (Crosses)	27	151.07**	15385.91**	2.43**	2.93**	5.22**	428.32**
Female in hybrid	6	347.95**	15725.43**	1.56**	1.37**	2.77**	804.44**
Male in hybrid	3	133.08**	30654.76**	2.36**	1.30**	3.64**	241.00**
Females × Males (L × T)	18	492.11**	58694.59**	2.73**	3.73**	6.31**	334.17**
Error	76	8.05	563.71	0.35	0.04	0.77	5.50
Components of variance:							
σ^2 Females		21.63	249.80	-0.10	-0.20	-0.29	39.19
σ^2 Males		2.13	853.66	-0.02	-0.12	-0.13	-4.44
σ^2_D		18.43	1268.14	-0.09	-0.29	-0.38	22.85
σ^2_H		26.80	4054.74	0.79	1.23	1.85	109.56
σ^2_D / σ^2_H		0.69	0.31	-0.12	-0.24	-0.20	0.02

** P ≤ 0.01.

 $\sigma^2_{D=}$ Additive genetic variance; $\sigma^2_{H=}$ Dominance genetic variance

The general combining ability effects of eleven parents for thirteen traits are depicted in **Table 2**. Parents' *gca* effects explicated that none of the parents consistently good general combiner for all the traits under study. The female parent GJ 43 was a good general combiner for days to flowering, total plant height, number of leaves per plant, grain yield per plant, fodder protein content and HCN content; DS 156 was a good general combiner for total plant height, number of leaves per plant, dry fodder yield per plant, fodder protein content and HCN content; SR 3048 was good general combiner for total

plant height, the number of leaves per plant, stem girth and brix content; SR 3019 was good general combiner for leaf length of the blade, leaf width of the blade and grain yield per plant; SR 2980 was good general combiner for leaf width of blade and HCN content. The *gca* effects of males indicated that the parent CSV 31 was a good general combiner for days to flowering, total plant height, the number of leaves per plant, leaf length of the blade, leaf width of the blade, grain yield per plant and dry fodder yield per plant; SPV 2682 was good general combiner for total plant height, the number of leaves per plant, dry

Table 2. The estimates of general combining ability (*gca*) effects of the parents for various characters in sorghum

S. No.	Parents	Days to flowering	Total plant height	Number of leaves per plant	Stem girth	Leaf length of blade	Leaf width of blade	Panicle length	Grain yield per plant	Dry fodder yield per plant	Grain protein content	Fodder protein content	Brix content	HCN content
FEMALE PARENTS (Lines):														
1	DSF 168	-0.24	-23.26**	-1.01**	-0.10	-1.12	-0.25	-0.55	-1.00	3.03	0.30	-0.55**	0.06	-0.82
2	DSF 117	-2.49**	-32.14**	-1.30**	-1.47*	-2.00	0.05	-1.12	-2.62**	-35.25**	0.01	0.02	0.08	17.06**
3	SR 2980	-0.24	-16.35**	0.03	0.91	-0.19	0.44**	0.05	1.24	12.30	0.07	-0.18**	0.29	-4.21**
4	SR 3048	2.85**	16.38**	0.51**	-2.68**	0.36	-0.43**	-0.59	-4.68**	-31.92**	0.06	-0.09	0.65*	0.58
5	SR 3019	0.43	-29.66**	-1.26**	-0.88	4.85**	0.39**	0.67	10.59**	-26.16**	0.09	0.09	-0.05	0.37
6	GJ 43	-1.15**	40.17**	2.20**	1.19	-2.28*	-0.03	-0.29	1.71*	9.73	0.26**	0.14*	-0.11	-8.50**
7	DS 156	0.85	44.86**	0.84**	3.03**	0.38	-0.16	1.83	-5.24**	68.27**	-0.78	0.56**	-0.92**	-4.47**
	S.Em. \pm	0.42	4.10	0.19	0.65	1.12	0.14	1.00	0.82	6.85	0.17	0.06	0.25	0.68
MALE PARENTS (Testers):														
1	CSV 31	-1.30**	11.81**	0.44**	2.59**	2.06*	0.29**	0.67	3.70**	29.02**	0.25	-0.23**	-0.30	4.84**
2	CSV 17	-5.11**	-14.62**	-0.86**	-0.63	1.91*	0.21*	0.38	-0.61	-43.68**	-0.36**	-0.17**	0.22	-0.19
3	SPV 2682	3.80**	9.15**	0.76**	0.04	-2.43**	-0.37**	0.54	-1.23	34.91**	-0.20	0.08	0.47*	-2.02**
4	SPV 2573	2.61**	-6.33*	-0.33*	-2.00**	-1.53	-0.13	-1.59*	-1.86**	-20.25**	0.32*	0.32**	-0.40*	-2.63**
	S.Em. \pm	0.32	3.10	0.14	0.49	0.84	0.10	0.75	0.62	5.18	0.13	0.04	0.19	0.51

* $P \leq 0.05$, ** $P \leq 0.01$.

fodder yield per plant, brix content and HCN content; SPV 2573 was good general combiner for stem girth, grain protein content, fodder protein content and HCN content; CSV 17 was good general combiner for days to flowering, leaf length of the blade and leaf width of the blade.

The results based on specific combining ability effects of hybrids revealed that none of the hybrids was consistently superior for all the characters (**Table 3**). Considering the performance of the *sca* effects, eight hybrids for grain yield per plant and nine hybrids for dry fodder yield per plant manifested desirable and significant *sca* effects. In the case of other component traits, seven hybrids for days to flowering, nine hybrids for total plant height, six hybrids for the number of leaves per plant, six hybrids for stem girth, five hybrids for leaf length of the blade, seven hybrids for leaf width of the blade, one hybrid for panicle length, six hybrids for brix content, seven hybrids for grain protein content, twelve hybrids for fodder protein content and nine hybrids for HCN content manifested significant and desirable *sca* effects. Based on estimates of *sca* effects, the most promising hybrids for grain yield per plant were viz., SR 2980 \times CSV 31, SR 3019 \times SPV 2573 and DSF 117 \times SPV 2682 based on significant positive *sca* effects and for dry fodder yield per plant were viz., SR 3048 \times CSV 31, GJ 43 \times SPV 2573 and DSF 168 \times SPV 2573. These crosses also exhibited positive

significant *sca* effects for other contributing traits viz., total plant height, the number of leaves per plant, leaf length of the blade, leaf width of the blade, panicle length, grain protein content, fodder protein and brix content. So, these hybrids showing significant *sca* effect can be directly used for hybrid breeding programmes.

The analysis of variance for combining ability revealed that the mean sum of squares due to female (lines) and male (testers) was highly significant for all the traits except panicle length. The ratio of σ^2_D/σ^2_H being more than unity was found for days to flowering, suggesting a more significant role of additive genetic variance in inheriting this trait. Parents' *gca* effects explicated that the parents SR 3019, CSV 31 and GJ 43 were found good general combiners for grain yield per plant. While, parents DS 156, CSV 31 and SPV 2682 were good general combiners for dry fodder yield per plant and its contributing traits. These good general combiners for yield and contributing traits can be utilized in intensive crossing programmes and select transgressive segregants for desired characters in segregating generations to develop superior lines. The most promising hybrids for grain yield per plant were viz., SR 2980 \times CSV 31, SR 3019 \times SPV 2573 and DSF 117 \times SPV 2682 based on significant positive *sca* effect and for dry fodder yield per plant were viz., SR 3048 \times CSV 31, GJ 43 \times SPV 2573 and DSF 168 \times SPV 2573.

Table 3. The estimates of specific combining ability (sca) effects of the hybrids for various characters in sorghum

S.No.	Hybrids	Days to flowering	Total plant height	Number of leaves per plant	Stem girth	Leaf length of blade	Leaf width of blade	Panicle length
1	DSF 168 × CSV 31	0.38	-7.81	2.48**	-0.25	-1.49	-0.11	0.76
2	DSF 168 × CSV 17	0.19	23.04**	0.45	1.56	-0.32	0.80**	0.77
3	DSF 168 × SPV 2682	0.29	-18.57*	-3.43**	-2.92*	1.54	-0.21	-1.84
4	DSF 168 × SPV 2573	-0.86	3.34	0.50	1.60	0.27	-0.49	0.31
5	DSF 117 × CSV 31	-1.70*	1.40	-0.84*	-0.25	11.79**	1.10**	-1.07
6	DSF 117 × CSV 17	1.77*	19.25*	-0.64	0.77	-14.52**	-1.80**	-0.78
7	DSF 117 × SPV 2682	-7.46**	-11.94	1.52**	3.12*	0.95	0.32	6.90**
8	DSF 117 × SPV 2573	7.39**	-8.71	-0.05	-3.63**	1.78	0.38	-5.05*
9	SR 2980 × CSV 31	-1.62	-7.97	-0.98*	-1.29	-10.69**	-1.75**	-0.08
10	SR 2980 × CSV 17	-1.14	7.79	-0.51	-3.43*	1.79	0.63*	-1.56
11	SR 2980 × SPV 2682	0.95	-2.73	0.86*	1.51	3.30	0.74**	-1.04
12	SR 2980 × SPV 2573	1.81*	2.92	0.63	3.22*	5.60*	0.39	2.68
13	SR 3048 × CSV 31	-3.37**	55.63**	0.13	3.86**	9.41**	0.83**	1.25
14	SR 3048 × CSV 17	0.11	-28.44**	0.09	-0.75	1.45	0.46	1.00
15	SR 3048 × SPV 2682	6.20**	5.20	1.64**	0.82	-2.81	-0.21	0.16
16	SR 3048 × SPV 2573	-2.94**	-32.39**	-1.85**	-3.93**	-8.04**	-1.08**	-2.41
17	SR 3019 × CSV 31	1.05	-3.49	-0.69	3.83**	5.38*	-0.11	-1.18
18	SR 3019 × CSV 17	0.19	18.85*	0.53	2.70*	0.09	-0.49	0.39
19	SR 3019 × SPV 2682	0.62	-33.59**	-1.34**	-4.62**	-6.30**	-0.63*	-0.65
20	SR 3019 × SPV 2573	-1.86*	18.23*	1.50**	-1.91	0.83	1.22**	1.44
21	GJ 43 × CSV 31	0.96	32.09**	0.60	-2.73*	-2.40	0.12	-0.61
22	GJ 43 × CSV 17	-1.56	-50.65**	0.40	-1.57	-1.02	0.19	-0.34
23	GJ 43 × SPV 2682	1.20	33.99**	-0.80*	1.46*	-0.01	-0.66*	-1.35
24	GJ 43 × SPV 2573	-0.61	-15.44	-0.21	2.84*	3.42	0.35	2.31
25	DS 156 × CSV 31	4.30**	-69.85**	-0.71	-3.17	-11.99**	-0.08	0.92
26	DS 156 × CSV 17	0.44	10.16	-0.32	0.73	12.53**	0.20	0.53
27	DS 156 × SPV 2682	-1.80*	27.64**	1.55**	0.63	3.33	0.65*	-2.18
28	DS 156 × SPV 2573	-2.94**	32.04**	-0.52	1.81	-3.87	-0.77**	0.72
SEm (±)		0.84	8.20	0.38	1.30	2.24	0.84	8.20
Range	Minimum	-7.46	-69.85	-3.43	-4.62	-14.52	-1.80	-5.05
	Maximum	7.39	55.63	2.48	3.86	12.53	1.22	6.9
Number of +ve significant		5	9	6	7	5	7	1
Number of -ve significant		7	6	6	6	5	6	1

* P ≤ 0.05, ** P ≤ 0.01.

Table 3 Continued...

S.No.	Hybrids	Grain yield per plant	Dry fodder yield per plant	Grain protein content	Fodder protein content	Brix content	HCN content
1	DSF 168 × CSV 31	4.70**	4.90	0.93**	-0.68**	-0.83	-4.93**
2	DSF 168 × CSV 17	-2.32	-1.69	-1.06**	0.89**	0.41	2.11
3	DSF 168 × SPV 2682	-0.48	-84.12**	0.70*	0.11	-0.89	-4.61**
4	DSF 168 × SPV 2573	-1.90	80.91**	-0.57	-0.32**	1.31*	7.43**
5	DSF 117 × CSV 31	-3.02	-20.58	0.10	0.29*	1.19*	22.22**
6	DSF 117 × CSV 17	0.78	31.72*	1.01**	0.77**	0.11	1.51
7	DSF 117 × SPV 2682	5.48**	68.43**	-0.46	-1.31**	0.18	-17.62**
8	DSF 117 × SPV 2573	-3.25	-79.57**	-0.65	0.26*	-1.49**	-6.11**
9	SR 2980 × CSV 31	10.05**	4.81	-1.54**	-0.20	-1.43**	-12.89**
10	SR 2980 × CSV 17	-5.43**	-45.21**	0.25	-0.05	-1.04*	-3.50*
11	SR 2980 × SPV 2682	-4.54**	42.23**	0.33	0.12	2.58**	10.37**
12	SR 2980 × SPV 2573	-0.08	-1.83	0.96**	0.14	-0.11	6.01**
13	SR 3048 × CSV 31	3.48*	111.62**	0.34	0.02	1.29*	1.95
14	SR 3048 × CSV 17	2.86	-45.10**	0.59	0.63**	0.97	-2.25
15	SR 3048 × SPV 2682	-0.89	14.63	-0.48	0.04	-3.48**	-6.18**
16	SR 3048 × SPV 2573	-5.45**	-81.15**	-0.44	-0.68**	1.22*	6.48**
17	SR 3019 × CSV 31	-5.79**	-33.84*	0.64	1.31**	-0.59	-2.61
18	SR 3019 × CSV 17	4.70**	33.90*	-1.16**	-1.55**	-0.27	-1.80
19	SR 3019 × SPV 2682	-6.86**	-42.38**	-1.00**	-1.06**	0.49	1.07
20	SR 3019 × SPV 2573	7.95**	42.32**	1.53**	1.30**	0.37	3.33*
21	GJ 43 × CSV 31	-3.73*	-89.74**	-0.44	-1.15**	0.80	-6.64**
22	GJ 43 × CSV 17	-1.58	30.40*	-0.43	-1.48**	-0.50	0.87
23	GJ 43 × SPV 2682	3.27*	-22.96	0.91**	1.80**	-0.13	3.75**
24	GJ 43 × SPV 2573	2.04	82.30**	-0.05	0.83**	-0.17	2.03
25	DS 156 × CSV 31	-5.69**	22.84	-0.03	0.42**	-0.44	2.90*
26	DS 156 × CSV 17	0.99	-4.02	0.81*	0.80**	0.33	3.06*
27	DS 156 × SPV 2682	4.02*	24.18	0.01	0.31**	1.24*	13.21**
28	DS 156 × SPV 2573	0.69	-42.99**	-0.78*	-1.52**	-1.12*	-19.17**
SEm (±)		1.64	13.71	2.24	0.34	0.12	0.51
Range	Minimum	-6.86	-89.74	-1.54	-1.55	-3.48	-19.17
	Maximum	10.05	111.62	1.53	1.80	2.58	22.22
Number of +ve significant		8	9	7	12	6	10
Number of -ve significant		7	9	5	9	5	9

* P ≤ 0.05, ** P ≤ 0.01.

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