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Combining ability and gene action in relation to alloplasmic isonuclear lines in pearl millet [*Pennisetum glaucum*(L.) R. Br.]

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Abstract
The Line × Tester analysis involving two CMS lines with diverse (A_1, A_4 and A_5) cytoplasmic sources and six testers (males) of pearl millet was carried out at JAU, Jamnagar (Gujarat) during Kharif 2018 to identify crosses and good combiners for developing new hybrids to achieve higher yield. The variance due to GCA and SCA showed that the non-additive components were pre-dominant for the expression of days to 50% flowering, plant height (cm), number of effective tillers per plant (no.), ear head diameter (cm), grain yield per plant (g) and Fe and Zn content (ppm) Whereas, additive components were predominant for the expression of days to maturity and ear head diameter (cm). Among the female parents ICMB 96222 were identified as good general combiner for grain yield per plant and some other component traits. Among the male parents J-2597, J-2598 and J-2603 was good general combiner for most of the characters. Among the 36 hybrids, five crosses (ICMA$_5$ 95222 x J-2597, ICMA$_4$ 95222 x J-2597 ICMA$_5$ 96222 x J-2596, ICMA$_4$ 96222 x J-2584 and ICMA$_1$ 96222 x J-2597) were identified as good specific combiners based on significant and positive sca effect for grain yield per plant.

Keywords: Combinig ability, gene action, alloplasmic isonuclear lines, pearl millet

Introduction
Pearl millet [*Pennisetum glaucum* (L.) R. Br.] belongs to family Poaceae and genus *Pennisetum*. Pearl millet is the sixth most important and widely grown potential cereal crop in the world and is the fourth in India, after rice, wheat and maize. Pearl millet is diploid (2n=14) in nature and commonly known as bajra, cat tail millet, and bulrush millet in different parts of the world, which is believed to be originated Africa. C4 species, it is endowed with a very high photosynthetic efficiency and more ability for dry matter production. It is a highly cross-pollinated crop with protogynous flowering and wind borne pollination mechanism, which fulfill one of the essential biological requirements for hybrid development.

Pearl millet is an important coarse cereal crop and serves as stable diet for the millions of people thriving under hunger. The better nutritive value of pearl millet grains appear from its protein, fat and mineral matters contents. It is also rich in vitamin A, vitamin B, thiamin as well as riboflavin contents and imparts substantial energy to the body with easy digestibility (Pal *et al.*, 1996) [10].

The information on the magnitude and nature of prevalent genetic variation is essentially needed to infer about genetic potential of a particular population. Combining ability studies are regarded useful to select best combining parents, which upon crossing would produce more desirable segregants. Such studies also elucidate the nature and magnitude of gene action involved in the inheritance of grain yield and its components, which will decide the breeding programme to be followed in segregating generations. There are several techniques for evaluating the varieties or lines in terms of their combining ability and genetic makeup. Among these, line × tester analysis as proposed by Kempthorne (1957) [5] has been extensively used to assess the combining ability of parent and crosses of different quantitative characters.

Materials and Methods
The experimental material for present investigation comprised of two CMS line with diverse cytoplasm each having three sources of cytoplasm (A_1, A_4 and A_5) ICMA$_1$ 95222, ICMA$_4$ 95222, ICMA$_5$ 95222, ICMA$_1$ 96222, ICMA$_4$ 96222, ICMA$_5$ 96222 and six testers (males)

developed at JAU, Jamnagar *viz*., J-2584, J-2591, J-2596, J-2597, J-2598 and J-2603. The selected 6 lines were crossed with 6 testers in Line × Tester (L x T) mating design to generate 36 crosses. The generated 36 hybrids are divided in two groups based on genetic background of female parent i.e. ICMA 95222 and ICMA 96222 and it is designated group 1 and group 2 hybrids, respectively. The checks included in this experiment were GHB-732 and HHB-299. The experimental materials comprised of single cross hybrids, parents and checks were evaluated during *Kharif*, 2018 at JAU, Jamnagar.
Five competitive plants from each experimental plot of each replication were selected randomly for recording observations on component characters *viz*., Days to 50% flowering, days to maturity, plant height, number of effective tillers per plant, ear head length, ear head diameter, grain yield per plant, test weight, Fe content and Zn content. The combining ability analysis was carried out using line x tester mating design as per the procedure suggested by Kempthorn (1957).

Results and Discussion

The analysis of variance for combining ability for all the characters was carried-out according to the line × tester analysis proposed by Kempthorne (1957) [5]. The mean squares due to lines, tester and lines × tester were first tested against the error mean squares. If, line × tester interaction component found significant, the mean squares due to lines and testers were further tested against their respective interaction mean squares. The results obtained from the present study in respect to analysis of variance for combining ability are presented in Table 1. Partitioning of variances due to the crosses under investigation showed that the mean squares due to female (lines) were significant for days to maturity and test weight. Whereas, the mean squares due to male (testers) were found significant for two characters *i.e.* days to maturity and test weight. The mean squares due to line x testers were found significant for all characters except plant height, ear head length and ear head diameter. The mean squares due to female (lines) were found significant for days to maturity and test weight when tested against mean square due to lines x testers interaction. Similarly the mean squares due to male (testers) were also found significant for days to maturity and test weight when tested against mean square due to lines x testers interaction.

The estimated variances due to females (lines) (σ^2l) were higher than the corresponding variances due to males (testers) (σ^2t) for all the characters except days to maturity, plant height and test weight. The estimates of σ^2sca were higher than the corresponding σ^2gca for all characters except days to maturity and ear head length.

The greater than one unity ratio of σ^2gca:σ^2sca were only for days to maturity and ear head length indicated that this character was governed by additive type of gene action. Similar results were also reported by Sushir (2002) [11], Valu (2006) [12], Mungra *et al*. (2015) [8], Nandaniya *et al*. (2016) [9], Bagra, *et al*. (2017) [2] and Ladumor *et al*.(2018) [6]. Whereas, less than one unity ratio of σ^2gca:σ^2sca were for days to 50% flowering, plant height, number of effective tillers per plant, ear head diameter, grain yield per plant, test weight, Fe and Zn content suggested that these characters were predominately under the control of non-additive gene action. Similar results were also reported by Arulselvi *et al*. (2009) [1], Govindaraj (2011), Lakshmana *et al*. (2011) [7], Bhadalia *et al.*, (2014) [3], Kanatti *et al*. (2014) [4], Mungra *et al*., (2015) [8], Nandaniya *et al*. (2016) [9], Bagra, *et al.*, (2017) [2] and Ladumor *et al.* (2018) [6]. The results of the analysis of the variance for combing ability were also confirmed from the additive (σ^2A) and dominance (σ^2D) components ofvariance.

The estimate of gca effects showed a wide range of variability among the parents in both the conditions (Table 2). None of the parents was consistently good general combiner for all the characters.

Female ICMB 95222 was good general combiner for days to 50% flowering, days to maturity and Fe content whereas female ICMB 96222 was good general combiner for number of effective tillers per plant, grain yield per plant, test weight and Zn content. The male parent J-2584 was good general combiner for days to 50% flowering and days to maturity. The male parent J-2597was good general combiner for number of effective tillers per plant and test weight. The male parent J-2598 was good combiner for number of effective tillers per plant, grain yield per plant and Zn content. The parent J-2603 was good general combiner for grain yield per plant and Fe content.

The estimates of sca effects for group 1 and group 2 (Table 3) revealed that none of the cross was significant for all the characters. Three crosses exhibited significant negative sca effect for days to flowering in group 1. The maximum sca effect was observed for the A_1 cytoplasm based cross $ICMA_1$ 95222 x J-2598 followed A_4 and A_5 cytoplasm based crosses $ICMA_4$ 95222 x J-2596 and $ICMA_5$ 95222 x J-2584, respectively. In group 2, total three crosses showed significant sca effect in desirable direction. The maximum sca effect was observed forthe A_1 cytoplasm based cross $ICMA_4$ 96222 x J-2596 in within group as well as between group followed by A_1 and A_5 cytoplasm based crosses $ICMA_1$ 96222 x J-2591 and $ICMA_5$ 96222 x J-2597, respectively.

In group 1, for days to maturity only one hybrid based on A_1 cytoplasm $ICMA_1$ 95222 x J-2603 showed significant sca effect in desirable direction. In group 2, only one cross based on A_4 cytoplasm $ICMA_4$ 96222 x J-2596 showed highest significant sca effect in desirable direction in within group as well as between groups.

None of cross registered positive and significant sca effect in group 1 for plant height. In group 2, only two crosses showed significant and positive sca effect, the highest being expressed by the A_1 cytoplasm based cross $ICMA_1$ 96222 x J-2597 followed by $ICMA_1$ 96222 x J-2597.

Three crosses showed significant sca effect in desirable direction for number of effective tillers per plant in group 1. The highest sca effect was exhibited by A_5 cytoplasm based cross $ICMA_5$ 95222 x J-2597 followed A_4 and A_1 cytoplasm based crosses $ICMA_4$ 95222 x J-2598 and $ICMA_1$ 95222 x J-2584, respectively. In group 2, total three crosses showed significant sca effect in desirable direction the highest positive sca effect was exhibited by the A_4 cytoplasm based cross $ICMA_4$ 96222 x J-2597 followed A_5 and A_1 cytoplasm based crosses $ICMA_5$ 96222 x J-2596 and $ICMA_1$ 96222 x J-2597, respectively.

Among all crosses, none of cross showed significant and positive sca effect for ear head length and ear head diameter

In group 1, total two crosses based on A_5 and A_4 sources of cytoplasm $ICMA_5$ 95222 x J-2597 and $ICMA_4$ 95222 x J-2597 showed significant sca effect in desirable direction for grain yield per plant. In group 2 total three crosses showed significant sca effect in desirable direction. Among them the highest positive sca effect was exhibited by the A_5 cytoplasm based cross $ICMA_5$ 96222 x J-2596 in within group as well as between groups followed A_4 and A_1 cytoplasm based crosses $ICMA_4$ 96222 x J-2584 and $ICMA_1$ 96222 x J-2597, respectively.

Four crosses showed significant positive sca effect in group 1 for test weight. Among them the highest and positive sca effect was exhibited byA_1 cytoplasm based crosses ICMA$_1$ 95222 x J-2596 and ICMA$_1$ 95222 x J-2598 followed A_5 and A_4 cytoplasm based crosses ICMA$_5$ 95222 x J-2591 and ICMA$_4$ 96222 x J-2603, respectively. In group 2, total six crosses showed significant sca effect in desirable direction. Out of these, the highest positive sca effect was exhibited by the A_4 cytoplasm based crosses ICMA$_4$ 96222 x J-2597 in within group as well as between groups followed A_1 and A_5 cytoplasm based crosses ICMA$_1$ 95222 x J-2597, ICMA$_1$ 96222 x J-2591 andICMA$_5$ 96222 x J-2597, respectively.

In group 1 only one cross based on A_5 cytoplasm based cross ICMA$_5$ 95222 x J-2603 showed significant sca effect in desirable direction while in group 2 cross ICMA$_5$ 96222 x J-2591 showed highest significant sca effect in desirable directionin within group as well as between groups for Fe content.

Only one cross based on A_4 cytoplasm ICMA$_4$ 95222 x J-2584 showed significant sca effect in desirable direction in group 1 for Zn content. In group 2, the highest positive sca effect was exhibited by the A_5 cytoplasm based cross ICMA$_5$ 96222 x J-2596 in within group as well as between groups followed by A_4 cytoplasm based cross ICMA$_4$ 96222 x J-2591 showed significant sca effect in desirable direction.

From the present findings it can be concluded that sufficient variation was present in the material for grain yield and its components. Both additive and non-additive genetic variances were found important in the expression of all the traits. The additive gene action was more important for the two characters such as days to maturity and ear head length. Thus, it would be possible to improve these traits through pedigree breeding method. The preponderance of non- additive genetic variance was observed in the inheritance for eight characters such as days to 50% flowering, plant height, number of effective tillers per plant, ear head diameter, grain yield per plant, test weight and Fe and Zn content. This suggested that heterosis breeding or bi-parental mating would be more suitable for the improvement of these traits in pearl millet. The female ICMB 96222 and the males J-2598 and J-2603 displayed high gca effect and for grain yield per plant and some desirable traits like number of effective tillers per plant, Fe and Zn content. Therefore, these parents were identified as good general combiners and could be preferred in breeding programme as these parents upon crossing, are expected to give desirable segregants in the succeedinggenerations.

The crosses in based on A_5 cytoplasm ICMA$_5$ 96222 x J-2596 and ICMA5 95222 x J-2597 followed by A_4 and A_1 cytoplasm based crosses ICMA$_4$ 96222 x J-2584,ICMA4 95222 x J-2597 and ICMA$_1$ 96222 x J-2597 displayed high sca effect for grain yield per plant. The high sca status of the hybrids indicated that substantial role was also played by dominance and epistatic interaction. Such crosses could be exploited through heterosis breeding.

Table 1: Analysis of variance for combining ability and variance components for different characters in pearl millet.

Source	d. f.	Days to 50% Flowering	Days to maturity	Plant height (cm)	Number of effective tillers per plant	Ear head length (cm)	Ear head diameter (cm)	Grain yield per plant (g)	Test weight (g)	Fe content (ppm)	Zn content (ppm)
		1	2	3	4	5	6	7	8	9	10
Replications	2	34.95**	47.28**	602.46	0.02	19.58	0.02	45.62	0.19	7.84	273.17*
Lines (Females)	5	6.03	7.325*+	400.15	0.25	16.46	0.04	479.21	5.89*+	388.08	176.49
Tester (males)	5	2.77	14.25**++	897.41	0.29	10.32	0.07	388.88	7.34*+	242.25	151.27
Females x Males	25	3.16**	2.294**	699.93	0.13**	8.37	0.11	221.97**	2.21**	183.34**	96.05**
Error	70	0.47	0.8775	425.63	0.02	7.34	0.07	31.20	0.14	88.27	39.17
Variance components											
σ^2l (female)		0.30	0.35	-1.41	0.01	0.50	-0.001	24.88	0.31	16.65	7.62
σ^2t (male)		0.12	0.74	26.20	0.01	0.16	0.0001	19.87	0.40	8.554	6.22
σ^2lt		0.89	0.47	91.43	0.03	0.33	0.013	63.59	0.69	31.69	18.96
σ^2gca		0.21	0.55	12.39	0.01	0.33	-0.0009	22.38	0.35	12.60	6.92
σ^2sca		0.89	0.47	91.43	0.03	0.33	0.013	63.59	0.69	31.69	18.96
σ^2gca/σ^2sca		0.24	1.16	0.13	0.38	1.00	-0.065	0.35	0.51	0.39	0.36

*, ** Significant at 5 and 1% levels, respectively.

+, ++ Significant at 5 and 1% levels, respectively against lines x testers interaction

Table 2: Estimation of general combining ability (gca) effect for different character in pearl millet

Sr. No.	Parents	Days to 50% flowering	Days to maturity	Plant height (cm)	Number of effective tillers of plant	Ear head length (cm)	Ear head diameter (cm)	Grain yield per plant (g)	Test Weight (g)	Fe Content (ppm)	Zn Content (ppm)
		1	2	3	4	5	6	7	8	9	10
	Lines (Females)										
1	ICMB 95222	-1.31**(G)	-1.50**(G)	-0.003 (A)	-0.20** (P)	-0.21* (P)	-0.03 (A)	-4.15** (P)	-0.02** (P)	1.49**(G)	-2.86** (P)
2	ICMB 96222	1.38** (P)	1.50** (P)	0.004 (A)	0.20**(**G**)	0.21 (A)	0.03 (A)	4.15**(G)	0.02**(G)	-1.50*(P)	2.86**(G)
	SE(gi)	0.16	0.22	4.86	0.03	0.63	0.06	1.31	0.08	2.21	1.47
	SE(gi-gj)	0.23	0.31	6.87	0.05	0.90	0.09	1.86	0.12	3.13	2.08
	Testers (Males)										
1	J-2584	-0.75**(G)	-1.24**(G)	1.39 (A)	-0.02 (A)	0.17 (A)	0.03 (A)	-0.60 (A)	0.03 (A)	1.85 (A)	1.76 (A)
2	J-2591	0.24 (A)	-0.07 (A)	3.04 (A)	-0.14** (P)	-0.12 (A)	0.07 (A)	2.13 (A)	-1.03** (P)	-1.92 (A)	-1.73 (A)
3	J-2596	0.01 (A)	-0.29 (A)	-2.36 (A)	0.03 (A)	-0.20 (A)	-0.10 (A)	-7.62** (P)	-0.01 (A)	-3.48 (A)	-2.28 (A)
4	J-2597	0.35* (P)	1.48** (P)	1.79 (A)	0.16**(G)	0.04 (A)	-0.01 (A)	-2.56 (A)	0.98**(G)	-1.14 (A)	-3.00* (P)
5	J-2598	0.07 (A)	0.31 (A)	8.59 (A)	0.10*(G)	1.23 (A)	0.04 (A)	3.60**(G)	-0.009 (A)	-1.87 (A)	4.60**(G)

6	J-2603	0.07 (A)	-0.18 (A)	-12.46* (P)	-0.13** (P)	-1.12 (A)	-0.02 (A)	5.04**(G)	0.03 (A)	6.57**(G)	0.65 (A)
	SE(gj)	0.16	0.22	4.86	0.03	0.63	0.06	1.31	0.08	2.21	1.47
	SE(gi-gj)	0.23	0.31	6.87	0.05	0.90	0.09	1.86	0.12	3.13	2.08

*, ** Significant at 5% and 1% levels, respectively.
(G) = Good combiner (A) = Average combiner (P) = Poor combiner

Table 3: Specific combining ability effects of crosses for different characters in pearl millet

Sr. No.	Crosses of group 1	Days to 50% flowering	Days to maturity	Plant height (cm)	Number of effective tillers per plant	Ear head length (cm)	Ear head diameter (cm)	Grain yield per plant (g)	Test weight (g)	Fe content (ppm)	Zn content (ppm)
		1	2	3	4	5	6	7	8	9	10
1	ICMA$_1$ 95222 x J-2584	-0.51	-0.48	8.75	0.20*	0.22	0.26	-3.67	-0.42	10.25	0.62
2	ICMA$_1$ 95222 x J-2591	0.14	0.01	-1.10	-0.49**	-1.74	-0.14	-7.13*	-0.09	0.70	-1.21
3	ICMA$_1$ 95222 x J-2596	1.37**	1.57**	21.97	-0.18	1.80	0.27	2.03	1.05**	-9.07	-6.99
4	ICMA$_1$ 95222 x J-2597	1.03*	1.13*	-4.38	-0.18	0.45	-0.19	-2.25	-1.38**	2.92	-2.60
5	ICMA$_1$ 95222 x J-2598	-1.35**	-1.03	-10.38	0.02	0.13	-0.13	6.35	0.75**	2.98	5.12
6	ICMA$_1$ 95222 x J-2603	-0.68	-1.20*	-14.85	0.12	-0.87	-0.07	4.66	0.09	-7.79	5.06
7	ICMA$_4$ 95222 x J-2584	-0.13	-0.14	2.14	-0.15	0.76	-0.11	4.06	0.26	9.31	7.50*
8	ICMA$_4$ 95222 x J-2591	0.87*	0.68	-11.71	0.03	-0.53	-0.07	-1.08	0.31	6.75	-5.99
9	ICMA$_4$ 95222 x J-2596	-1.24**	-0.75	3.03	-0.08	0.47	0.08	-9.98**	0.34	1.31	6.23
10	ICMA$_4$ 95222 x J-2597	-0.24	0.13	0.80	-0.14	-0.10	-0.05	7.12*	-1.22**	-3.35	2.28
11	ICMA$_4$ 95222 x J-2598	0.03	-0.37	0.003	0.25**	-0.79	-0.11	0.02	-0.27	-5.96	-5.32
12	ICMA$_4$ 95222 x J-2603	0.70	0.46	5.73	0.09	0.19	0.27	-0.13	0.57*	-8.07	-4.71
13	ICMA$_5$ 95222 x J-2584	-0.96*	-0.53	7.17	-0.06	1.95	0.16	6.26	0.43	-8.90	-4.26
14	ICMA$_5$ 95222 x J-2591	0.03	-1.03	-12.48	-0.002	-1.32	-0.08	4.31	0.71**	-7.79	2.56
15	ICMA$_5$ 95222 x J-2596	0.25	0.85	16.39	-0.11	2.89	0.06	-7.21*	-0.64**	5.09	4.45
16	ICMA$_5$ 95222 x J-2597	1.25**	0.40	7.04	0.28**	-1.28	0.12	10.44**	-0.46*	6.09	1.50
17	ICMA$_5$ 95222 x J-2598	-0.13	0.57	8.43	0.11	0.09	-0.10	-8.17*	0.38	-5.51	-3.10
18	ICMA$_5$ 95222 x J-2603	-0.46	-0.25	-26.56*	-0.21*	-2.32	-0.16	-5.63	-0.42	11.03*	-1.15

*, ** Significant at 5% and 1%levels, respectively.

Table 3: (Contd…)

Sr. No.	Crosses of group 2	Days to 50% flowering	Days to maturity	Plant height (cm)	Number of effective tillers per plant	Ear head length (cm)	Ear head diameter (cm)	Grain yield per plant (g)	Test weight (g)	Fe content (ppm)	Zn content (ppm)
		1	2	3	4	5	6	7	8	9	10
19	ICMA$_1$ 96222 x J-2584	-0.29	-0.37	-15.36	-0.21*	-2.00	-0.13	-6.79*	-1.04**	-8.46	3.17
20	ICMA$_1$ 96222 x J-2591	-1.63**	-0.53	0.30	-0.09	0.95	-0.009	-2.60	0.77**	-5.68	-5.99
21	ICMA$_1$ 96222 x J-2596	1.25**	0.68	-28.74*	0.02	-3.73*	0.16	2.69	0.01	2.20	-6.10
22	ICMA$_1$ 96222 x J-2597	-0.40	-0.42	25.09*	0.25**	2.29	-0.09	8.49*	1.04**	0.87	3.95
23	ICMA$_1$ 96222 x J-2598	0.87*	0.40	-6.10	-0.007	0.50	0.06	2.06	0.40	8.59	0.67
24	ICMA$_1$ 96222 x J-2603	0.20	0.24	24.81*	0.03	1.99	0.006	-3.86	-1.18**	2.48	4.28
25	ICMA$_4$ 96222 x J-2584	0.92*	0.68	-8.30	0.13	-1.12	-0.04	13.06**	0.05	-4.57	-0.76
26	ICMA$_4$ 96222 x J-2591	0.92*	0.85	12.10	-0.10	0.50	0.05	6.09	-0.46*	-8.13	8.06*
27	ICMA$_4$ 96222 x J-2596	-2.18**	-1.92**	-2.01	0.08	0.45	-0.05	-5.72	-0.62**	0.09	-5.71
28	ICMA$_4$ 96222 x J-2597	-0.51	-0.70	-9.03	0.28**	-0.52	0.16	-11.51**	1.31**	0.09	-4.99
29	ICMA$_4$ 96222 x J-2598	0.42	0.46	2.35	-0.21*	0.18	0.05	-4.69	-0.96**	5.14	-0.93
30	ICMA$_4$ 96222 x J-2603	0.42	0.63	4.88	-0.18	0.50	-0.17	2.77	0.68**	7.37	4.34
31	ICMA$_5$ 96222 x J-2584	0.98*	0.85	5.60	0.09	0.17	-0.13	-12.92**	0.72**	2.37	-6.26
32	ICMA$_5$ 96222 x J-2591	-0.35	0.01	12.88	0.15	2.14	0.26	0.41	-1.25**	14.14*	2.56
33	ICMA$_5$ 96222 x J-2596	0.53	-0.42	-10.64	0.27**	-1.88	-0.52**	18.19**	-0.13	0.37	8.12*
34	ICMA$_5$ 96222 x J-2597	-1.13**	-0.53	-19.53	0.004	-1.74	0.04	-12.29**	0.70**	-6.63	-0.15
35	ICMA$_5$ 96222 x J-2598	0.14	-0.03	5.69	-0.16	-0.11	0.23	4.42	-0.30	-5.24	3.56
36	ICMA$_5$ 96222 x J-2603	-0.18	0.13	5.99	0.14	0.50	0.12	2.19	0.25	-5.01	-7.82*
	SE(Sij)	0.39	0.54	11.91	0.09	1.56	0.15	3.22	0.21	5.42	3.61
	SE(Sij-Skl)	0.56	0.76	16.84	0.13	2.21	0.22	4.56	0.30	7.67	5.11

*, ** Significant at 5% and 1% levels, respectively.

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