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Predominance of duplicate epistasis on inheritance of important yield attributing traits in ridge gourd (*Luffa acutangula* (L.) Roxb.)

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Abstract

An experiment was conducted on ridge gourd in six generations *i.e.,* P_1, P_2, F_1, F_2, BC_1 and BC_2 of VRG-24 x VRG-13 and Swarna Manjari x Arka Prasan in Randomized Block Design with three replications. The main aim of the study was to investigate the genetic mechanisms controlling yield and quality traits through generation mean analysis. Epistatic gene effects were found to play a crucial role in regulating most of the traits studied, except for days to male flowering, days to female flowering, node of first female flower, average fruit weight, and rind thickness in various crosses. Duplicate epistasis was particularly prominent across the majority of traits, suggesting that these traits could be effectively exploited through heterosis breeding and reciprocal recurrent selection strategies. Additionally, complementary epistasis was observed in the cross VRG-24 x VRG-13 for traits such as node of first female flower, number of female flowers per vine, and number of fruits per vine. This highlights the potential of the VRG-24 x VRG-13 cross to produce desirable transgressive segregants with enhanced trait combinations.

Key words: Duplicate, complementary, transgressive, epistasis, ridge gourd

Introduction

Luffa acutangula (L.) Roxb commonly known as ridge gourd belongs to family cucurbitaceae is an annual herb found in parts of India, especially along the coastal lines (Swetha and Muthukumar, 2016). The whole plant is also used for the treatment of ulcers and sores (Arunachalam *et al.,* 2012). In a nutritional point of view, *Luffa acutangula* seeds are an excellent agricultural product and its kernel have been found potentially rich in protein and fat (39 and 44 %) which are higher than those contained in many plant seeds. The fruit contains carbohydrates, carotene, fat, protein, phytin, amino acids, alanine, arginine, cystine, glutamic acid, glycine, hydroxyproline, leucine, serine, tryptophan and pipecolic acid. Its leaves and flowers contain flavonoids (Schilling and Heiser, 1981) and herb contains saponins and acutosides (Nagao *et al.*, 1991). The seeds are also found to be a good source of certain amino acids, phosphorous, iron, and magnesium (Kamel and Bernice, 1982). Despite the presence of several valuable medicinal and nutritional attribute, the productivity of ridge gourd remain unsatisfactory to a large extent and are attributable to the limited research effort concentrated in this crop.

Ridge gourd is a vine which produce pale yellow flowers. Anthesis starts in the evening by 5.00 PM and continues up to 8.00 PM. Pollen grains are fertile from the time of dehiscence till two to three days in winter and one to five days in rainy season. The stigma is reported to be receptive from six hours before anthesis and continues to be receptive till 84 hours after anthesis (Hari, 2006). Ridge gourd being a monoecious and cross-pollinated crop, exhibits considerable heterozygosity resulting in natural variability in the population.

The primary breeding objective of ridge gourd is to improve the yield and quality of the fruit. The yield trait is a complex character and governed by polygenic which have small and cumulative effect and expression of which is continuous in nature. Therefore, to attain the actual yield potential, the fundamental understanding of the genetics and inheritance that underlies the yield and its component characters are urgently required. Hence, adopting appropriate breeding and selection strategies for targeted trait improvement largely depends on the knowledge of gene action and effects operating in a particular breeding population. In this regard, generation mean analysis (Mather and Jinks, 1982), scaling and joint scaling tests were used. It provides information not only about the presence or absence of heterosis or inbreeding depression but also provides information on the additive, dominance and epistasis effect of a gene for any type of complex trait. These information can be used by a breeder to adopt an appropriate breeding or selection method for the genetic improvement of ridge gourd. Only a few preliminary studies have been reported in ridge gourd for understanding the genetics of yield and yield attributing characters (Varmoda, 2006; Dhumal, 2018).

Hence, the present investigation aims to elucidate the gene action involved in the inheritance of yield components in ridge gourd through generation mean analysis.

Materials and methods

The experiment was carried out during summer 2020 at College of Horticulture, Venkataramannagudem, Dr. Y.S.R. Horticultural University, West Godavari, Andhra Pradesh using available breeding material. Experimental parents were selected based on their higher yield, earliness and yield attributing traits. The experimental material used in the experiment are presented in Table 1.

Table 1. Details of P_1, P_2, F_1, F_2, BC_1 and BC_2 populations

Cross 1	
P_1	VRG-24
P_2	VRG-13
F_1	VRG-24 x VRG-13
F_2	VRG-24 x VRG-13
BC_1	(VRG-24 x VRG-13) x VRG-24
BC_2	(VRG-24 x VRG-13) x VRG-13
Cross 2	
P_1	Swarna Manjari
P_2	Arka Prasan
F_1	Swarna Manjari x Arka Prasan
F_2	Swarna Manjari x Arka Prasan
BC_1	(Swarna Manjari x Arka Prasan) x Swarna Manjari
BC_2	(Swarna Manjari x Arka Prasan) x Arka Prasan

Six basic generations (P_1, P_2, F_1, F_2, BC_1 and BC_2) of two crosses *viz.,* VRG-24 x VRG-13 and Swarna Manjari x Arka Prasan were grown in Randomized block design with three replications in *summer*, 2020 at College of Horticulture, Venkataramannagudem. The data was recorded from six generations for 18 characters *viz.,* days to male flowering, days to female flowering, node of first male flower, node of first female flower, number of male flowers per vine, number of female flowers per vine, sex ratio, fruit set percentage, fruit length (cm), fruit girth (cm), number of fruits per vine, average fruit weight (g), rind thickness (mm), flesh thickness (mm), number of seeds per fruit, fruit yield per vine (kg), fibre content (g/100g), TSS (^{0}Brix).

Generation mean analysis was followed to estimate the gene effects for six parameter model (Hayman, 1958). To detect the presence of non allelic interactions ABCD scaling tests were performed suggested by Hayman and Mather (1955). The student 't' test was used to test the significance of the scales. In addition to scaling test, data was further subjected to joint scaling test because sometimes scaling test remain inadequate to fully explain the additive-dominance model (Deb and Khaleque, 2009). In instance, where scaling test is inadequate, six-parameter model or digenic interaction model (Hayman 1958) was used to estimate the gene effects.

Six parameters in joint scaling test represent mean effect [*m*], genetic effects including additive [*d*] and dominance [*h*] and gene interaction effects comprising additive × additive [*i*], additive × dominance [*j*] and dominance × dominance [*l*]. The square roots of respective variances were used for the computation of standard error which were used to calculate the 't' values for testing significance of the corresponding gene effects. The type of epistasis was determined only when dominance (*h*) and dominance × dominance (*l*) effects were significant. The same sign of '*d*' and '*l*' effects indicated complementary epistasis while different signs indicated duplicate epistasis (Kearsey and Pooni, 1996). Statistical analysis for generation mean analysis was carried out using OP Stat software (Sheoran *et al.,* 1998).

Results and discussion

The computation of generation mean analysis was done to devise the magnitude of gene action for yield and its attributing traits using recorded data of six generations (P_1, P_2, F_1, F_2, BC_1 and BC_2). The results of the mean performance of six generations derived from both crosses were presented in Table 2.

The generation F_1 showed inferiority for the characters *viz.,* average fruit weight (265.998) and TSS (3.240) in cross VRG-24 x VRG-13; fruit length (27.612), fruit girth (14.198), rind thickness (5.242), number of seeds per fruit (121.868) and fibre content (0.260) in cross Swarna Manjari x Arka Prasan and node of first male flower in both crosses (1.998, 1.868) than their parents. It is suggesting that the lower magnitude of hybrid vigour in respect of these traits. This is apparently indicated the influence of inbreeding depression. Angadi (2015) and Rao (2017) obtained similar results of inbreeding depression in certain traits of bitter gourd.

The characters such as of sex ratio (9.934), fruit length (33.892), number of seeds per fruit (185.802) and fibre content (0.336) in cross VRG-24 x VRG-13; days to male flowering (26.936), node of first female flower (11.268), average fruit weight (292.332) and flesh thickness (40.002) in Swarna Manjari x Arka Prasan and days to female flowering in both the crosses (35.002, 35.800) showed partial dominance *i.e.,* F_1 means are intermediate of the means of their parents. It was found that there is a little inbreeding depression as well as hybrid vigour for these traits. These results are in line with those reported by Odedara *et al.* (2020) in bottle gourd.

The performance of F_1's were superior than their parents was recorded for the characters *viz.,* fruit girth (18.136), rind thickness (7.1922) and flesh thickness (50.576) in the cross VRG-24 x VRG-13; sex ratio (9.934, 10.708) and TSS (3.240, 3.254) in the cross Swarna Manjari x Arka Prasan and number of male flowers per vine and number of female flowers per vine in both the crosses. It indicated the overdominance which means these traits could be exploited through heterosis breeding due to hybrid vigour. Similar findings were observed in Co-1 x Jaipur long of ridge gourd by Varmoda (2006), Mohan *et al.* (2012) in ash gourd and Konkan Harita x Arka Sujat of ridge gourd by Dhumal. (2018).

The transgressive segregants were observed in F_2 which were superior in performance than F_1's in days to male flowering (27.399) of the cross Swarna Manjari x Arka Prasan indicating delayed male flowering in F_2 population and also observed in days to female flowering (36.767, 37.083), node of first male flower (4.283, 3.766), node of first female flower (15.433, 11.767), sex ratio (10.4621, 10.915), rind thickness (7.192, 8.761) and fibre content (1.614, 0.975) in both the crosses. Similar results were obtained by Mishra *et al.* (2015) in bitter gourd and Dhumal (2018) in ridge gourd whereas inbreeding depression was observed in which the performance of F_2 progenies was inferior to F_1's for the traits such as number of male flowers per vine (228.500), fruit girth (14.793), fruit length (27.688), flesh thickness (39.199) and number of seeds per fruit (146.217) of the

Table 2. Generation mean for different traits in the ridge gourd cross VRG-24 x VRG-13 and Swarna Manjari x Arka Prasan

Trait	VRG-24 x VRG-13						Swarna Manjari x Arka Prasan					
	P_1	P_2	F_1	F_2	B_1	B_2	P_1	P_2	F_1	F_2	B_1	B_2
Days to male flowering	28.466	29.334	26.934	26.899	27.834	29.150	28.402	26.402	26.936	27.399	27.717	25.817
Days to female flowering	34.934	37.868	35.002	36.767	33.084	36.784	35.934	35.470	35.800	37.083	36.550	37.400
Node of first male flower	2.332	2.266	1.998	4.283	3.650	2.766	3.532	2.068	1.868	3.766	3.301	3.783
Node of first female flower	14.266	10.798	10.266	15.433	15.167	12.667	14.864	10.934	11.268	11.767	12.484	13.800
Number of male flowers per vine	234.200	252.266	311.666	228.500	208.500	183.400	221.266	249.932	250.534	286.750	185.900	187.528
Number of female flowers per vine	25.130	24.936	31.536	22.216	24.700	19.700	22.734	25.336	27.470	26.734	21.000	20.100
Sex ratio	9.378	10.174	9.934	10.461	8.570	9.495	9.686	9.416	10.708	10.915	9.110	9.637
Fruit set percentage	49.642	52.128	56.844	53.328	49.908	48.964	48.298	52.098	55.788	50.806	50.793	50.253
Fruit length (cm)	27.360	34.940	33.892	27.688	22.915	26.284	34.068	31.232	27.612	27.681	26.775	21.825
Fruit girth (cm)	14.032	13.696	18.136	14.793	14.767	18.275	16.032	19.950	14.198	15.574	16.791	18.402
Number of fruits per vine	12.468	13.000	17.934	11.550	12.234	9.617	11.002	13.200	15.334	13.300	10.650	10.100
Average fruit weight (g)	290.668	363.668	265.998	293.833	269.185	320.519	335.668	290.668	292.332	270.567	267.055	291.000
Rind thickness (mm)	5.704	6.384	7.1922	7.192	5.727	7.691	6.562	6.712	5.242	8.761	6.408	8.186
Flesh thickness (mm)	38.992	37.584	50.576	39.199	41.251	49.811	44.514	56.838	40.002	40.836	47.084	50.424
Number of seeds per fruit	134.002	202.934	185.802	146.217	141.450	202.333	147.732	254.066	121.868	141.267	187.732	198.515
Fruit yield per vine (kg)	3.644	4.696	4.794	3.411	3.279	3.188	3.672	3.874	4.448	3.611	2.860	2.985
Fibre content (g/100g)	1.346	0.262	0.336	1.614	0.595	0.631	2.122	0.174	0.260	0.975	0.171	0.152
TSS (^{o}Brix)	3.880	3.240	3.240	3.085	2.644	2.535	1.980	2.320	3.254	1.932	2.690	2.599

cross VRG-24 x VRG-13; average fruit weight (270.567) and TSS (1.932) of the cross Swarna Manjari x Arka Prasan and number of fruits per vine (11.550, 13.300), fruit set percentage (53.328, 50.806) and fruit yield per vine (3.411, 3.611) of both the crosses. These results are in conformity with results of Pitchaimuthu and Sirohi (1997) in bottle gourd and Varmoda (2006) in ridge gourd.

None of the scaling tests were significant in respect of days to female flowering and average fruit weight of both the crosses (VRG-24 x VRG-13 and Swarna Manjari x Arka Prasan) and days to male flowering of the cross Swarna Manjari x Arka Prasan indicating the absence of digenic non-allelic interaction (epistasis). In such cases additive-dominance model is fit to explain the inheritance of these traits which could be improved through pedigree or bulk selection. These results are in accordance with performance of CHRG-1 x CHRG-2 in ridge gourd Varmoda (2006), Rathod *et al.* (2021) and Bhoi *et al.* (2021) in bitter gourd. The performance of backcross generations (BC_1 and BC_2) were near to their respective parents, indicated that these traits were quantitatively inherited. Similar results were reported by Rathod *et al.* (2021) and Bhoi *et al.* (2021) in bitter gourd.

Genetic studies using generation mean analysis: In the present study, scaling test was found to be significant for most of the traits. This indicates the presence of inter-allelic interaction in majority of the traits so additive-dominance alone will not be sufficient to exploit such traits. Hence, six-parameter model was employed to estimate six components of genetic variation, *viz., m, d, h, i, j* and *l* which was given by Jinks and Jone (1958). The significant and positive '*d* ' was observed for node to first male flower, node to first female flower and number of male flowers per vine in the cross VRG-24×VRG-13, while fruit length and days to male flowering showed significant in cross Swarna Manjari x Arka Prasan which indicates that additive effect of the genes is predominant and selection of these traits could be more effective in later generations instead of early generations F_2 or F_3.

Highly significant and positive values of '*h*' was recorded for fruit girth and flesh thickness in the cross VRG-24 x VRG-13 while TSS showed significant positive values in the cross Swarna Manjari x Arka Prasan indicates the predominance of dominant gene effect. The traits such as node to first male flower, node to first female flower, number of male flowers per vine, fruit length, days to male flowering, fruit girth, flesh thickness and TSS in respective crosses mentioned in Tables 3 and 4 with high magnitude of dominance and additive gene effect which could be improved by pedigree or bulk methods.

Among the interaction effects, additive x additive (*i*) gene effect was found to be significant and in desired direction for days to first male flower appearance, fruit girth and flesh thickness in the cross VRG-24 x VRG-13 while node to first female flower, number of male flowers per vine, flesh thickness, number of seeds per fruit were significant in the cross Swarna Manjari x Arka Prasan. The additive x additive (*i*) gene effect values are higher than dominance (*h*) gene effect in Swarna Manjari x Arka Prasan indicates predominance of additive x additive gene interactions. Hence, simple selection procedure can be adopted for improvement of these traits.

Complementary type of epistasis was recorded for node of first female flower, number of female flowers per vine and number of fruits per vine in the cross VRG-24 x VRG-13. The complementary epistasis indicated that the parents selected for crossing were diverse for that particular trait *i.e.,* improvement through pedigree method and early selection would be beneficial. Hence, it is possible to realize enhanced genetic gain in the breeding programme. These results are in accordance with the findings of Konkan Harita x Arka Sujat in ridge gourd by Dhumal. (2018), Odedara *et al.* (2020) in bottle gourd and Bhoi *et al.* (2021) in bitter gourd.

Duplicate type of epistasis was observed for number of male flowers per vine, sex ratio, fruit length, fruit girth, flesh thickness, fruit yield per vine, fibre content and TSS in both the crosses (VRG-24 x VRG-13 and Swarna Manjari x Arka Prasan); days to male flowering, days to female flowering, node of first male flower and fruit set percentage in cross VRG-24 x VRG-13 and node of first female flower, number of female flowers per vine, number of fruits per vine and number of seeds per fruit in cross Swarna Manjari x Arka Prasan. Hence, it would be better to exploit these characters by heterosis breeding, reciprocal recurrent

Table 3. Generation mean for different traits in the ridge gourd cross VRG-24 x VRG-13

Trait	A	B	C	D	*m*	*d*	*h*	*i*	*j*	*l*	
DMF	-0.267	-2.032	4.072	-3.186*	26.899**	-1.316	4.405	6.371*	-1.765	-8.670	Duplicate
DFF	3.769	-0.697	-4.262	3.667	36.767**	-3.700**	-8.733*	-7.334	-4.466	10.406	Duplicate
NMF	-2.970**	-1.268*	-8.538**	2.150*	4.283**	0.884*	-4.601**	-4.300**	1.702	0.062	Duplicate
NFF	-5.802**	-4.269**	-16.136**	3.033	15.433**	2.501**	-8.331*	-6.065	1.533	-4.006	
MFV	128.867**	197.132**	195.798**	65.100**	228.500**	25.100**	-61.768	-130.201**	68.265**	456.200**	Duplicate
FFV	7.266**	17.072**	24.276**	0.031	22.216**	5.000	6.441	-0.062	9.806**	24.400**	
SR	2.172	1.119	-2.422	2.856**	10.461**	-0.924	-5.555**	-5.713**	-1.053	9.004**	Duplicate
F.S.	6.671*	11.044**	2.148	7.783	53.328**	0.943	-9.608	-15.567	4.373	33.282**	Duplicate
F.L.	15.415**	16.265**	19.332**	6.174	27.688**	-3.365	-9.606	-12.348	0.850	44.028**	Duplicate
F.G.	2.635	-4.717	4.830	-3.456*	14.793**	-3.508**	11.184**	6.912*	-7.352**	-8.994	Duplicate
N.F.V	5.935**	11.699**	15.138**	1.248	11.550**	2.616**	2.704	-2.496	5.764**	20.130**	
A.F.W	18.297	-11.372	11.000	-2.037	293.833**	-51.335	-57.095	4.075	-29.669	2.850	-
R.T.	1.442	-1.805	-5.176	2.407	7.912**	-1.964**	-3.665	-4.813	-3.247**	4.450	-
F.T.	7.066	-11.462	20.934	-12.665*	39.199**	-8.560**	37.618**	25.330*	-18.528**	-29.726	Duplicate
N.S.F	36.904	-15.930	123.674*	-51.350	146.217**	-60.883**	120.034	102.700	-52.834	-81.726	-
F.Y	1.880*	3.114**	4.284*	0.355	3.411**	0.091	-0.086	- 0.710	1.234	5.704*	Duplicate
F.C	0.492	-0.663*	-4.174**	2.002**	1.614**	-0.036	-4.471**	-4.003**	-1.155*	3.832**	Duplicate
TSS	1.659*	1.236*	0.912	0.991*	3.085**	0.109	-2.477*	-1.983*	-0.423	4.878**	Duplicate

Table 4. Generation mean for different traits in the ridge gourd cross Swarna Manjari x Arka Prasan

Trait	A	B	C	D	*m*	*d*	*h*	*i*	*j*	*l*	
DMF	-0.095	1.705	-0.918	1.264	27.399**	1.900**	-2.994	-2.528	1.800	4.138	-
DFF	-1.366	-3.530	-5.328	0.216	37.083**	-0.850	-0.334	-0.432	-2.164	-4.464	-
NMF	-1.201	-3.630**	-5.728**	0.449	3.766**	-0.483	-1.829	-0.897	-2.429**	-3.934	-
NFF	1.165	-5.398	1.268	-2.750	11.767**	-1.317	3.870	5.501*	-6.563**	-9.734*	Duplicate
MFV	100.00**	125.411**	-174.734**	200.073**	286.750**	-1.628	-385.210*	400.145**	25.411	625.556**	Duplicate
FFV	8.204**	12.606**	-3.924	12.367**	26.734**	0.900	-21.299**	-24.734**	4.402**	45.544*	Duplicate
SR	2.173*	0.850	-3.142	3.083**	10.915**	-0.527	-5.008**	-6.165**	-1.323	9.188**	Duplicate
F.S.	2.501	7.374**	8.742	0.566	50.806**	0.540	4.460	-1.133	4.873	11.008	-
F.L.	8.130*	15.194**	9.802	6.761	27.681**	4.950*	-18.560*	-13.522	7.064	36.846**	Duplicate
F.G.	-3.352*	-2.655	2.082	-4.045	15.574**	-1.611	4.296	8.089*	0.697	-14.096*	Duplicate
N.F.V	5.036**	8.334**	1.672	5.849**	13.300**	0.550	-8.465**	-11.698**	3.298**	25.068**	Duplicate
A.F.W	93.890	1.001	128.732	-16.921	270.567**	-23.945	-23.945	33.841	-92.889	61.050	-
R.T.	-1.011	-4.418**	-11.286**	2.929	8.761**	-1.778**	-7.252	-5.857	-3.407**	0.428	-
F.T.	-9.651*	-4.007	18.012	-15.835**	40.836**	-3.340	20.996	31.670**	5.644	-45.328*	Duplicate
N.S.F	-105.864**	-21.096	80.468	-103.714**	141.267**	-10.783	128.397	207.428**	84.768*	-334.388**	Duplicate
F.Y	2.400**	2.352**	1.998	1.377*	3.611**	-0.125	-2.079	-2.754*	-2.754	7.506**	Duplicate
F.C	2.040**	0.670**	-0.546	1.628**	0.975**	0.019	-4.414**	-3.256**	-1.370**	5.966**	Duplicate
TSS	-0.146	0.377	3.082	-1.426	1.932**	0.092	3.955*	2.851	0.523	-2.620	Duplicate

selection and full sib selection. These results are similar to the findings of Kumari *et al.* (2015) in bitter gourd, Ganesh (2017) in ridge gourd, Odedara *et al.* (2020) in bottle gourd and Panigrahi *et al.* (2023) in bitter gourd.

From the results of the present study, it can be concluded that the mean performance of F_1 exceeded the parents for number of male flowers per vine and number of female flowers per vine in both the crosses indicating that these traits can be exploited through heterosis breeding. The reduction in mean performance of F_2 population than F_1 for number of fruits per vine, fruit set percentage and fruit yield per vine in both crosses was observed which apparently indicated influence of inbreeding depression. Significance of one or more scaling tests, *i.e.* A, B, C and D in most of the traits revealed the presence of epistasis in both the crosses except for days to female flowering and average fruit weight where additive gene action was predominant. The characters such as node of first female flower, number of female flowers per vine and number of fruits per vine in the cross VRG-24 x VRG-13 showed complimentary epistasis have the possibility of considerable amount of heterosis. Majority of the characters were showed duplicate epistasis in the present study, hence these traits could be improved through heterosis, reciprocal recurrent selection or full sib selection. These findings signified that the breeding of high-yielding ridge gourd genotypes can be undertaken by combining the breeding approaches based on hybridization followed by selection.

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