

Breeding for Rust Resistance and Generation Mean Analysis of Cowpea *Vigna unguiculata* (L.) Walp.

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Abstract

Cowpea is an important multipurpose grain legume. The lack of high yielding rust resistance lines is one of the constraints in this crop. Based on this objective, the components of gene effects for yield and yield attributing characters were studied following five parameters model of Hayman. Utilizing the means of five basic populations (P_1 , P_2 , F_1 , F_2 and F_3) derived after crossing two diverse parents TCM-77-4 resistance to rust and HC-98-66 susceptibility to rust. By considering generation means, heterosis, inbreeding depression, variability, gene effects and inheritance pattern of rust resistance indicating that for seed yield non-additive gene action was more involved, as compared to other type of gene action. In F_1 , non-additive gene action of over-dominance was observed for days to maturity, plant height, primary branches and 100 seed weight. Partial degree of dominance was observed for days to 50% flowering, secondary branches, pods per plant, pod length and seed yield, while complete dominance was observed for flower initiation. Variability studies indicate that high GCV was recorded for primary branches per plant and secondary branches per plant in both F_2 and F_3 generations. The estimate of broad sense heritability was high for most of the characters except number of seeds per pod and test weight, which showed medium heritability in F_2 . In F_3 high heritability was noticed for most of the characters except for days to flower initiation, plant height and secondary branches per plant. Whereas high genetic advance was noticed for primary branches per plant, secondary branches per plant, number of pods per plant and number of seeds per pod in both the generations. While in F_2 and F_3 high heritability and genetic advance was noticed for primary branches per plant, number of pods per plant and number of seeds per pod in both the generations. For seed yield, dominance \times dominance gene action was more involved, followed by additive gene action even for characters that usually show association with plant height, secondary branches, pod length and seeds per pod ; additive and / or additive \times additive gene effects were significant in gene action. Hence the selection can be carried in further advanced generation for superior segregant rust resistance lines.

Key words : Cowpea, Rust resistance, Generation mean analysis.

Cowpea *Vigna unguiculata* (L.) Walp is one of the rich sources of human protein, and has most likely been used as poor men meat since, neolithic times. It is mainly cultivated in arid dry zone. The yield of cowpea is low 600 kg/ha. One of the major reasons for low productivity is non-availability of high yielding and rust resistance varieties in cowpea. This is due to lack of basic genetic studies to breed varieties in cowpea to tolerant to diseases. The plant breeding methodology for upgrading the yield potential largely depends on the availability of reliable information on the nature and magnitude of gene effects parents in the population. Generation mean analysis, which provides the estimates of the main gene action (additive \times dominance) and their digenic interaction

(additive \times additive, additive \times dominance, and dominance \times dominance) helps in understanding the performance of the parent used in the cross and potential of the cross to be used either through exploitation of heterosis or selection. Inheritance pattern of rust resistance reveals the genetics working in cowpea, it assists in the breeding of high yielding rust resistance lines.

Methods

Two diverse parents namely TCM-77-4 and HC-98-66 (Table 1) were selected for crossing program. The five basic generations of the cross, viz., two parents (P_1 , P_2) their F_1 , F_2 and F_3 were grown in

Table 1. Salient features of parent lines of cowpea *Vigna unguiculata* (L.) Walp.

	Variety	Pedigree/ origin	Yield (kg/ha)	Plant habit	Leaf shape	Pod type	Dura- tion (days)	Other features
1	TCM-77-4	Trombay (BARC)	1200	Prostrate	Triangular	Slightly curved pods	88—90	Resistant to rust
2	HC-98-66	Hissar	1000	Erect	Triangular	Medium short pods	90—92	Susceptible to rust

randomized complete block design with three replications. Generations were randomized within cross. The spacing maintained between rows were 45 cm and between plants were 30 cms. Data on five randomly selected plants in each of the parents and F_1 's and 160 plants of F_2 's and 12 to 13 F_3 families generation were selected for recording observation viz., days to first flower initiation, days to 50% flowering, days to maturity, plant height (cm), primary branches per plant, secondary branches per plant, number of pods per plant, pod length (cm), number of seeds per pod, seed yield (g/plant) and hundred seed weight (g).

Heterosis was calculated as the percentage increase or decrease of mean F_1 performance by standard methods (1, 2). Inbreeding was computed as the per cent increase or decrease from F_1 to F_2 and F_2 to F_3 generation considering the over all means of F_1 , F_2 and F_3 generations for the characters. Joint scaling test (3, 4) was carried out to estimate gene effects and simultaneously the adequacy of additive-dominance three parameters viz., m, d and h were determined. For the characters, three parameter model was found inadequate, the following five gene effects were estimated by the following the method standard (5).

Table 2. Means, standard errors and variances for yield and agro-morphological characters in cowpea cross TCM-77-4 × HC-98-66. SE—Standard error.

Generations	Days to flower initiation		Days to 50% flowering		Days to maturity		Plant height (cm)	
	Mean ± SE	Variance	Mean ± SE	Variance	Mean ± SE	Variance	Mean ± SE	Variance
P_1	64.57 ± 0.71	5.04	68.33 ± 0.72	5.18	88.27 ± 0.12	0.14	22.73 ± 0.13	0.17
P_2	56.47 ± 0.49	2.40	60.83 ± 0.34	1.14	90.63 ± 0.58	3.36	53.67 ± 0.54	2.9
F_1	56.47 ± 0.53	2.89	60.87 ± 0.34	1.14	87.87 ± 0.37	1.36	18.57 ± 0.57	3.24
F_2	55.90 ± 0.49	14.40	63.23 ± 0.34	6.84	85.20 ± 0.47	13.23	24.97 ± 0.97	56.43
F_3	57.23 ± 0.52	10.81	60.77 ± 0.26	2.70	84.83 ± 0.29	3.36	28.63 ± 0.55	12.09
Generations	Primary branches/plant		Secondary branches/plant		No. of pods/plant		Pod length (cm)	
	Mean ± SE	Variance	Mean ± SE	Variance	Mean ± SE	Variance	Mean ± SE	Variance
P_1	4.73 ± 0.38	1.44	10.27 ± 0.58	3.36	14.40 ± 0.40	1.6	17.93 ± 0.38	1.44
P_2	4.83 ± 0.38	1.44	7.17 ± 0.34	1.14	13.30 ± 0.45	2.02	13.83 ± 0.20	0.40
F_1	4.93 ± 0.38	1.44	8.73 ± 0.09	0.80	13.47 ± 0.67	4.48	13.53 ± 0.13	0.16
F_2	5.97 ± 0.41	10.08	10.67 ± 0.33	6.51	16.10 ± 0.36	7.7	12.83 ± 0.30	5.40
F_3	7.13 ± 0.61	14.88	11.30 ± 0.50	10.00	17.60 ± 0.68	18.49	14.47 ± 0.34	4.62
Generations	No. of Seeds/pod		Seed yield / plant (g)		100 seed weight (g)			
	Mean ± SE	Variance	Mean ± SE	Variance	Mean±SE	Variance		
P_1	13.87 ± 0.41	1.68	12.77 ± 0.26	0.68	9.20 ± 0.06	0.036		
P_2	11.30 ± 0.55	3.02	9.17 ± 0.37	0.76	6.73 ± 0.12	0.144		
F_1	11.00 ± 0.55	3.02	12.20 ± 0.25	0.62	9.33 ± 0.15	0.224		
F_2	11.13 ± 0.32	6.12	10.97 ± 0.30	5.40	9.50 ± 0.06	0.216		
F_3	12.20 ± 0.55	12.09	12.43 ± 0.35	4.89	9.70 ± 0.06	0.144		

Table 3. Estimates of heterosis and inbreeding depression for yield and morphological characters in the cowpea cross TCM-77-4 × HC-98-66. *-Significance at 0.05 probability level, **-Significance at 0.01 probability level.

Characters	Heterosis (%)		Inbreeding depression	
	Mid parent	Better parent	F ₁ -F ₂	F ₂ -F ₃
1. Days to first flower initiation	-6.69	00.00	1.01	-2.38
2. Days to 50% flowering	-5.32**	1.035	-3.8**	3.89
3. Days to maturity	-1.76*	-0.453	3.03**	0.43
4. Plant height	-51.38**	-18.34**	-34.64**	-14.65
5. Primary branches/plant	3.13	4.14	-20.89	-19.43**
6. Secondary branches / plant	0.23	14.89*	-22.10**	-5.904
7. Number of pods / plant	-2.74	-6.45	-19.52**	-9.31
8. Pod length (cm)	-14.80**	-24.53**	5.17*	-12.78**
9. Number of seeds per pod	-12.55**	-20.69**	-1.18	-9.61*
10. Seed yield	11.21**	-4.46**	11.18**	-9.6**
11. Test weight	17.21**	1.41	-1.82	-2.10**

PCV and GCV were worked out (6). Heritability (7) and genetic gain were predicted using the formula $GA = h^2 \times pxk$ (8, 9).

Results and Discussion

Means, standard errors of the means, variance of parents and three generations (F₁, F₂ and F₃) of the cross of cowpea for different characters are presented in Table 2. HC-98-66 was found to be earliest in flower initiation than TCM-77-4 by nine days. Both F₁ and

F₂ took 56 days for flower initiation ; whereas F₃ took one day extra (57 days) with high variance for this trait. HC-98-66 took 60 days for 50% flowering whereas TCM-77-4 took 68 days. F₁ and F₃ were early for 50% flowering compared to F₂ by two days. Among the segregating populations F₂ showed high variance. TCM-77-4 was early to mature than HC-98-66 by 3 days. However, the F₁ took more or less same number of days to maturity as of parent TCM-77-4 (88 days). But segregating generations F₂ and F₃ matured two and three days earlier than TCM-77-4 respectively.

Table 4. Genetic variability parameters for yield and yield attributing traits in cowpea cross of TCM-77-4 × HC-98-66.

Genetic parameters	Days to first flowering		Days to 50% flowering		Days to maturity		Plant height (cm)		Primary branches/plant		Secondary branches/plant	
	F ₂	F ₃	F ₂	F ₃	F ₂	F ₃	F ₂	F ₃	F ₂	F ₃	F ₂	F ₃
Mean	55.90	57.23	63.23	60.77	85.20	84.43	24.97	28.63	5.97	7.13	10.67	11.30
PCV (%)	6.69	5.74	4.14	5.98	4.26	2.16	30.08	12.14	53.18	54.10	23.91	27.98
GCV (%)	5.91	4.84	3.59	1.84	3.71	1.81	26.20	10.22	46.31	45.54	20.81	23.55
Heritability (%)	88.19	41.17	67.25	81.8	91.30	62.50	96.27	55.55	92.85	71.42	78.6	54.54
GA as % mean	12.14	4.86	5.73	10.07	8.01	2.78	59.65	13.89	101.72	79.59	35.88	31.43
Genetic parameters	Pods per plant		Pod length (cm)		Seeds per pod		Seed yield (g)		Hundred seed weight (g)			
	F ₂	F ₃	F ₂	F ₃	F ₂	F ₃	F ₂	F ₃	F ₂	F ₃		
Mean	16.10	17.60	12.83	14.47	11.13	12.20	10.97	12.43	9.50	9.70		
PCV (%)	17.23	24.43	18.11	14.85	22.22	28.50	6.30	17.79	4.80	3.91		
GCV (%)	14.99	20.56	15.77	12.50	19.35	23.99	5.49	14.97	4.26	3.29		
Heritability (%)	64.93	83.33	87.65	60.00	57.95	62.50	87.20	62.50	49.04	60.00		
GA as % mean	23.04	41.94	32.70	18.35	26.52	36.69	11.32	23.16	4.84	4.83		

Table 5. Gene effects on yield and agro-morphological characters in the cowpea cross of TCM-77-4 × HC-98-66. *-Significance at 0.05 probability level, **-Significance at 0.01 probability, D-Duplicate or dominant epistasis, C- Complementary / recessive gene interaction, (1) N indicates no effect is significant, (2) If only one effect is mentioned, it means that the other effects in the desirable direction are not significant.

Characters	Gene effects						Chi square value	Type of epistasis	Order of magnitude of gene effects
	(m)	(d)	(h)	(i)	(l)				
1. Days to 1st flowering	55.90**	4.05**	-3.17	8.97**	8.62	11.37**	D	N	
2. Days to 50% flowering	63.23**	4.05**	5.0**	16.51**	-19.46**	92.75**	D	l	
3. Days to maturity	85.20**	-1.18	2.75*	1.97*	5.15	100.70**	C	N	
4. Plant height	24.96**	-15.46**	-14.04**	-25.34**	2.48	128.23**	D	D	
5. Primary branches	5.96**	-0.049	-3.80*	-4.05*	3.46	15.33**	D	N	
6. Secondary branches	10.66**	1.55**	-2.97*	0.10	-1.77	31.67**	C	D	
7. No. of pods/plant	16.10**	0.55	-0.57**	-4.27*	0.97	33.39**	C	N	
8. Pod length	12.83**	2.05**	-3.88**	2.56**	10.57**	38.96**	D	l > i > d	
9. No. of seeds/pod	11.13**	1.28**	-2.93	-	-	2.1	-	D	
10. Seed yield/plant	10.96**	1.80**	-3.08**	-0.72	11.11**	11.37**	D	l.>d	
11. Test weight	9.5**	1.23**	-0.64**	0.45*	0.62	75.00**	D	d.>i	

TCM-77-4 was dwarf parent (22.73 cm) compared that of HC-98-66 (53.67 cm) with a low variability. Mean plant height of F₁ (18.57 cm) lower than the height of TCM-77-4. There was an increase in plant height in F₂ and F₃ with a high variance in both segregating generations. Primary branches per plant were minimum in TCM-77-4 (4.73) and HC-98-66 (4.83). There was increase in variance for primary branches per plant in F₂ and F₃ compared to non-segregating generation TCM-77-4 possessed more number of secondary branches (10.27) than HC-98-66 (7.17). F₁ was intermediate in producing secondary branches (8.73). Mean number of secondary branches increased in segregating populations F₂ and F₃. F₃ displayed higher magnitude of variance among the segregating generations for this trait. Mean number of pods per plant in F₁ (13.47) was intermediate between the two parents TCM-77-4 (14.40) and HC-98-66 (13.30). There were high variability between F₂ (16.10 pods per

plant) and F₃ (17.60 pods per plant) compared to parents and F₁. Highest pod length was observed in TCM-77-4 (17.93 cm) and lowest in HC-98-66 (13.83 cm). F₁ mean was less than that of both the parents. The magnitude of variation was low in F₂ (12.83 cm) compared to F₃ (14.47 cm). The better parent TCM-77-4 exhibited highest mean number of seeds per pod (13.87) compare to other parent HC-98-66 (11.30). There was decrease in number of seeds per pod in F₁ (11.00). The variation for number of seeds per pod in F₃ (12.20) was more compared to F₂ (11.13). Among the five populations, the mean seed yield per plant was highest for TCM-77-4 (12.77 g) compared to other generations. The mean seed yield per plant was intermediate between F₁ (12.20 g) compared to both the parents. There was increase of variability for seed yield per plant from F₂ (10.97 g) to F₃ (12.43 g) population. The mean of 100 seed weight in F₁ (9.33 gm) surpassed both parents. In segregating generations

Table 6. Phenotypic segregation of reaction to rust in F₁ and F₂ generation of cowpea cross (TCM-7-4 × HC-98-66).

P ₁ (TCM- 77-4)	P ₂ (HC- 98-66)	F ₁	Character	Frequ- ency	Segregating generation characters		χ ²	P
Resistant	Susceptible	Resistant	Reaction to disease (3 : 1 ratio)	Obs Exp	Resistant 137 140	Susceptible 49 46	0.26	0.7-0.5

Table 7. Breeding behavior of reaction to rust (3 : 1) in F_3 families for different characters in cross (TCM-77-4 \times HC-98-66).

Expected ratio (1 : 2 : 1)	B. T. for		B. T. for		χ^2	P
	asynchronous flowering	Segregation into 3 : 1	synchro-erous	synchro-erous		
Observed	12	19	9		0.55	0.8-0.7
Expected	10	20	10			

mean 100-seed weight was 9.50 g in F_2 and 9.70 g in F_3 .

Heterosis of the F_1 over the mid-parent as well as over the better parent and inbreeding depression from the F_1 to F_2 , F_2 to F_3 were presented character wise for TCM-77-4 \times HC-98-66 (Table 3). Non-significant negative midparent heterosis and negative inbreeding depression from F_2 to F_3 was observed for days to flower initiation. Significant negative heterosis over mid parent and significant negative inbreeding was observed from F_1 to F_2 in favor of days to 50% flowering. Significant negative midparent heterosis and significant positive inbreeding depression was observed for days to maturity. Significant negative heterosis for midparent and better parent, significant negative inbreeding depression was observed from F_1 to F_2 for plant height. Positive heterosis was observed for midparent and better parent, negative inbreeding depression from F_2 to F_3 was observed for primary branches per plant. Significant negative better parent heterosis and significant inbreeding depression from F_1 to F_2 was observed for secondary branches per plant. Heterosis expressed by the hybrids over midparent and better parent were negative, significant negative inbreeding depression was observed for number of pods per plant. Significant negative midparent and better parent heterosis, significant negative inbreeding depression was observed for pod length. Significant midparent and better parent heterosis, significant negative inbreeding depression was observed for number of seeds per pod. The significant positive midparent heterosis and significant negative better parent heterosis, significant posi-

tive inbreeding depression from F_1 to F_2 and significant negative inbreeding depression from F_2 to F_3 were observed for seed yield. Significant positive midparent heterosis and significant negative inbreeding depression from F_2 to F_3 were observed for hundred seed weight. Over-dominance was observed for days to maturity, plant height, primary branches and seed weight. Partial degree of dominance was observed for days to 50% flowering, secondary branches, pods per plant, pod length and seed yield, while complete dominance was observed for flower initiation.

The genetic parameters viz., variability, heritability and genetic advance in F_2 and F_3 generations were estimated and are given in Table 4. The Phenotypic Coefficient of Variation (PCV) was higher than the respective Genotypic Coefficient of Variation (GCV) in both F_2 and F_3 generations for all characters studied. The GCV ranged from 3.59% for days to 50% flowering to 46.31% for primary branches per plant in F_2 , while in F_3 range was 1.81% (days to maturity) to 45.54% (primary branches per plant). High GCV was recorded for primary branches per plant and secondary branches per plant in both F_2 and F_3 generations. Low GCV was observed for days to flower initiation, days to 50% flowering, days to maturity and 100 seed weight. Same trend was noticed for PCV. There was narrow difference between PCV and GCV for all characters.

The estimate of broad sense heritability was high for most of the characters except number of seeds per pod and test weight, which showed medium heritability in F_2 . Whereas in F_3 high heritability was noticed for most of the characters except for days to flower initiation, plant height and secondary branches per plant. The genetic advance as per cent of mean varied from 5.73% (days to 50% flowering) to 101.72% (primary branches per plant) in F_2 while in F_3 it was ranged from 2.78% (days to maturity) to 79.59% (primary branches per plant). Low genetic advance was noticed for days to maturity and 100 seed weight in both F_2 and F_3 generations. Whereas high genetic advance was noticed for primary branches per plant, secondary branches per plant, number of pods per plant and number of seeds per pod in both the generations.

Joint scaling test of five generation means pertaining to the gene effects due to additive, dominance and epistatic effects such as additive \times additive, domi-

nance \times dominance were estimated for yield and agromorphological characters (Table 5). The significant of chi-square value indicated the inadequacy of simple additive-dominance 3 parameters model in the expression of days to flower initiation. The magnitude of additive effect was found to be significant over the dominance effect. However, the magnitude of additive \times additive interaction effect was significant over the dominance \times dominance interaction effect with duplicate type of gene action governing this trait. For days to 50% flowering highly significant chi-square value indicated the inadequacy of simple additive-dominance 3 parameters model. All the five parameters viz., m, d, h, i and l were significant with duplicate type of epistasis. However, additive and additive \times additive gene interaction magnitude were significant and positive. Failure of additive-dominance model was evident from the significance of chi-square test indicating that digenic interaction effect was governing days to maturity. The magnitude of dominance effect was found to be higher when compared to that of additive effect. However, the magnitude of additive \times additive interaction effect was significant over dominance \times dominance effect with complementary gene action governing this trait. It was clear that additive dominance model was inadequate in explaining the inheritance of plant height, as indicated by significance of chi-square value. Additive, dominance and additive \times additive gene interaction were significant but it was in negative direction. The genes controlling this trait were found to interact each other in a duplicate manner. The dominance model was inadequate in explaining the inheritance of primary branches per plant, as indicated by the significance of chi-square value. Dominance and additive \times additive gene interactions were significant but in negative direction and duplicate gene interaction acting on this character. It was that additive-dominance model was inadequate in explaining the inheritance of secondary branches, as indicated by the significance of chi-square value. The trait was governed by digenic interaction of additive genes, which were positively significant, whereas dominance was significant but in negative direction. The genes controlling this trait were found to interact each other in a complementary manner. For number of pods per plant, the magnitude of dominance effect was found to be significant, but in negative direction

over the additive effect. However, the magnitude of additive \times additive interaction effect was also in negative direction but significant over the dominance \times dominance interaction with complementary epistasis. Variations for pod length were not explained adequately by three-parameter model. Therefore, the model was extended to include additive \times additive (i) and dominance \times dominance (l) epistatic effects. All the parameters were significantly positive, except dominance gene effect, which was showing negative effect. A duplicate type of gene interaction was found to govern this trait. A three-parameter model was found to be sufficient to explain all the variations among generation means for number of seeds per pod because of non-significant chi-square test. Only additive effect was found to be significant. A full five-parameter model was necessary to explain the inheritance of seed yield per plant. Significant variation was found for all gene actions except additive \times additive gene effect with duplicate type of epistasis. Both dominance and additive \times additive gene effects were in negative direction, whereas dominance \times dominance gene interaction was in positive direction. As observed additive-dominance model was not sufficient to explain the expression of hundred seed weight/test weight. All the gene effects were found to be significant except the dominance \times dominance gene interaction. Duplicate type of gene interaction was found to be governing this trait.

Reaction to Rust Disease

The TCM-77-4 a resistant parent and HC-98-66 a susceptible to rust disease. The F_1 was resistant and F_2 was segregating at a ratio 3 : 1, indicating rust resistance governed by a dominant gene (Tables 6 and 7). Previous study indicates complementary gene action governing this character (10).

Just as in the present study non-additive gene action was found operating to a greater extent than additive gene action for days to flower initiation, days to 50% flowering, days to maturity, secondary branches, number of pods per plant, seed yield and hundred seed weight. Early studies indicate preponderance of additive gene action over non non-additive gene action, such contradictory results were possible depending on genetic material used in different studies (10, 11).

For plant height, primary branches, pod length and seeds per pod, preponderance of additive gene action over non-additive gene action was reported by earlier workers (12—16). Whereas, in certain studies for the same characters non-additive gene action was found more important than additive gene action (17—19).

In this cross, even for characters that usually show correlation with yield (20) viz., plant height, secondary branches, pod length and seeds per pod : additive and / or additive \times additive gene effects were significant. Hence, selection can be continued in further advanced generation to finally obtain a higher yielding and rust resistance genotypes in homozygous condition.

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