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Genetic analysis of seed growth rate and progress towards flowering in chickpea (*Cicer arietinum* L.)

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Abstract

Genetic analysis of seed growth rate (SGR) and progress towards flowering (RPF) along with yield components was carried out in chickpea using Hayman's and Griffing's diallel procedures. Estimates of genetic parameters showed significant additive and non-additive gene effects in the inheritance of the traits studied. The additive component was predominant for RPF, SGR and seed weight, and the non-additive component was predominant for pods per plant, seeds per plant, seeds per pod and seed yield. Estimate of the narrow-sense heritability was high (90%) for RPF, SGR and seed weight, and low for the remaining traits. The close association observed between SGR and seed weight makes it possible to select for higher SGR through selection for larger seed size. SGR and seed weight could be used as selection criteria for yield improvement.

Key words : Chickpea, combining ability, genetic analysis, heritability

Introduction

In most plant species, the rate of progress towards flowering (RPF) relates more closely to the underlying biological events, which lead to flowering besides having several other advantages such as linear response to photoperiod as well as temperature [1]. It allows rational genetic analysis by separating the confounding effects of the genes conferring photoperiod sensitivity from those conferring temperature sensitivity [2-3]. This information helps plant breeders to match phenology of cultivars with resources and constraints of the target environment. Another physiological process of breeders interest is the rate of dry matter accumulation in seeds or seed growth rate (SGR) for maximization of yield. In chickpea, both the traits exhibited genetic variability and provide the possibility for genetic manipulation. However, phenotypic selection for RPF and SGR could be effective and meaningful only if their heritability and correlation with seed yield are high. Genetic studies reported so far in chickpea had largely focussed on yield and yield components [4-15]. Keeping in view the inadequate information on the genetics of physiological traits and inconsistent reports on yield components, the study was undertaken to determine gene actions involved in the inheritance of RPF and SGR along with yield and its components, and discuss the possibility of using them as selection criteria for yield improvement.

Materials and methods

On the basis of yield potential, seed weight and crop duration, six genotypes comprising four desi viz., Harigantas, ICCV91501, WR315 and C235, and two kabuli viz., ICCV2 and C104 were crossed in all possible combinations. The parents and their 15 F_1 hybrids were evaluated in a randomized complete block design with three replications at the International Crop Research Institute for the Semi-Arid Tropics (ICRISAT) in post-rainy seasons, 1991/92 and 1992/93. The plot size was a 3-m long row with a distance of 30 cm between rows and 10 cm within row. Observation on days to first flower was recorded on every plant to measure the rate of progress towards flowering (RPF), i.e. the reciprocal of the time taken from sowing to flowering. Seed growth rate (SGR) was determined by monitoring dry weight of 100 seeds from the tagged pods at weekly interval till plants reached physiological maturity. One hundred seeds removed from the harvested pods were dried at 60°C for 36 hours to take dry weights and finally averaged to calculate seed growth rate on daily basis. Observations on seed yield and its components were recorded on ten randomly selected plants. The validity of assumptions for diallel analysis were determined by analysis of variance of (Wr-Vr) and (Wr + Vr), and joint regression analysis of Wr/Vr as described by Mather and Jinks [16]. Once the basic assumptions of diallel analysis were fulfilled, the data were subjected to genetic analyses following Hayman [17, 18] and Jinks [19]. Combining ability was analyzed following the fixed-effect model of Griffing [20].

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Results and discussion

Analysis of variance revealed significant variation among the parents (P) and their hybrids (F_1) for the traits studied (Table 1). The hybrids as a group were significantly different from the parents (P vs F_1) with regard to RPF, SGR, pods per plant, seeds per plant and seed yield, indicating heterotic response for them. Overall mean of the hybrids was less than that of the parents for RPF, SGR, seeds per pod and seed weight.

Table 1. Analysis of variance for seed yield and its components in chickpea

Source of variation	Mean Squares							
	d.f.	RPF	SGR	Pods/ plant	Seeds/ plant	Seeds/ pod	Seed weight	Seed yield
Replications	2	0.01	0.02	24.0	1231	0.02	128.1	1.9
Genotypes	20	0.47**	2.58**	11391**	21340**	0.08**	7341.0**	613.7**
Parents (P)	5	1.05**	4.50**	10806**	28882**	0.09**	11656.4**	322.1*
F_1	14	0.25**	2.05**	5994*	10408*	0.08**	6320.3**	433.7**
P Vs F_1	1	0.60**	0.42**	89880**	136690**	0.00	55.2	4632.7**
Residual	40	0.01	0.05	2361	3277	0.021	123.8	111.1

*,**Significant at 5% and 1% levels of probability

The validity of inference drawn from the results of diallel analysis depends on the fulfillment of six assumptions i.e., diploid segregation, homozygous parents, absence of maternal effect, no multiple allelism, no epistasis and independent distribution of genes among parents. The nature of the crop (diploid segregation) and parents (homozyhous) fulfilled the first two assumptions whereas five combinations, ICCV2 × C235, Harigantas × WR315, C104 × C235, C104 × WR315, and C104 × ICC91501 which were tested for reciprocal differences showed absence of maternal effects for the traits. Homogenity of (Wr-Vr) over arrays and nonsignificant deviation of regression coefficient from unity (Table 2) indicated fulfillment of the last three assumptions.

Table 2. Tests of hypotheses for seed yield and its components in chickpea

Character	F test of heterogeneity of (d.f. 5, 12)		T test of b on the null hypothesis (d.f. 4)	
	Wr-Vr	Wr+Vr	b = 0	b = 1
RPF	1.58	5.10**	6.70**	1.13
SGR	0.49	3.57**	8.55**	0.02
Pods/plant	1.16	4.13*	3.17*	0.69
Seeds/plant	0.95	2.67(8%)	3.72*	2.03
Seeds/pod	0.51	0.82	1.89	0.57
Seed weight	1.15	4.01*	4.15**	0.95
Seed yield	2.45	5.76**	2.39	1.36

*, **Significant at 5% and 1% levels of probability

The additive (D) and dominance (H_1) components of genetic variance, were significant for the traits studied except for seed yield for which only dominance component was significant (Table 3). The other dominance components, H_2 and h^2 were also significant for all the traits except h^2 for SGR, seeds per pod and seed weight. The additive gene action was, however, predominant for RPF, SGR and seed weight, and the dominance component for pods per plant, seeds per plant, seeds per pod and seed yield. A high estimate of narrow-sense heritability for RPF, SGR and seed weight, and a low estimate for the remaining traits supported the above results. Average degree of dominance as indicated by the $(H_1/D)^{1/2}$ ratio suggested partial dominance for RPF, SGR and seed weight, complete dominance for seeds per plant and seeds per pod, and apparent over-dominance for pods per plant and seed yield. For all the traits studied, gene symmetry was evidenced from the non-significant F values, and distribution of unequal gene frequencies in the parents by lower than 0.25 value of the $H_2/4H_1$ ratio. The $[(4DH_1)^{1/2} + F]/[(4DH_1)^{1/2} - F]$ ratio was significantly greater than unity (2.04) for RPF, pods per plant (1.85) and seeds per plant (1.57), suggesting more dominant than the recessive alleles in the parents and their level of dominance remained almost constant over loci as shown by high estimates (near unity) of the $0.5/[D(H_1-H_2)]^{1/2}$ ratio i.e. 0.71 for RPF, 0.73 for pods per plant and 0.67 for seeds per plant. A close correspondence between parental means and their array means ($r > 0.85^{**}$) for RPF, SGR, seed weight, seeds per pod and seeds per plant indicated high prepotency of the parents in transmitting these traits to their off-springs. Distribution of genes for RPF, pods per plant, seeds per plant, and seed yield showed concentration of dominant alleles in the late parents (WR315, C104 and C235) and recessive alleles in the early parents (ICCV91501, Harigantas and ICCV2). For SGR and seed weight, most of the dominant alleles

Tale 3. Estimates of genetic parameters for seed yield and its components in chickpea

Genetic parameter	RPF	SGR	Pods/ plant	Seeds/ plant	Seeds/ pod	Seed weight	Seed yield
D	0.346**± 0.017	1.48**±0.031	2852.25**±744.78	8567.30**±1178.76	0.022**±0.005	3844.11**±175.87	72.05±53.73
H_1	0.158**±0.042	0.39**±0.078	11733.92**±1890.69	14840.47**±2992.38	0.035*±0.012	1325.66**±446.46	488.64**±136.40
H_2	0.122**±0.037	0.27**±0.070	9755.40**±1689.00	13193.79**±2673.17	0.029*±0.011	915.83*±398.83	421.95**±121.85
h^2	0.126**±0.025	0.08±0.047	18939.35**±1136.81	28854.65**±1799.22	−0.005±0.007	14.49±268.44	978.33**±82.01
F	0.160**±0.040	−0.03±0.075	3447.81±1819.49	4995.27±2879.70	−0.008±0.012	−462.22±429.65	−28.93±131.26
E	0.005±0.006	0.02±0.012	749.87**±281.50	1059.9*±455.53	0.007**±0.002	41.34±66.47	35.31±20.31
$(H_1D)^{1/2}$	0.675	0.51	2.03	1.32	1.26	0.59	2.6
$H_2/4H_1$	0.193	0.18	0.21	0.22	0.21	0.17	0.22
h^2/H_2	1.036	0.29	1.94	2.19	−0.16	−0.02	2.32
Heritability (ns)	0.76	0.91	0.18	0.37	0.56	0.90	0.37
Heritability (bs)	0.97	0.98	0.81	0.85	0.78	0.98	0.84

*, **Significant at 5% and 1% levels of probability

were concentrated in kabuli parents (C104 and ICCV2). Significant negative correlation between the order of dominance of the parents (Wr+Vr) and parental mean (Yr) for pods per plant (−0.84**), seeds per pod (−0.84**) and seed yield (−0.95**) suggested dominance in positive direction for most of the genes involved. However, this correlation was positive for RPF (0.95**) suggesting dominance in negative direction.

Analysis of variance for combining ability (Table 4) showed significant variance for general (gca) as well as specific (sca) combining abilities for all the traits studied. The results obtained from combining ability analysis were in good accordance with the conclusions drawn from the component analysis of Hayman's method. Combining ability effects (Table 5) suggest C104 as a good general combiner for yield. For other traits, good general combiners were Harigantas and ICCV2 for RPF; C104 and ICCV2 for SGR; WR315 for pods per plant; WR315 and C 235 for seeds per plant; ICCV91501 and C235 for seeds per pod; C104 and ICCV2 for seed weight. A positive relationship was observed between performance of a parent *per se* and its gca effect for all the traits except pods per plant. A cross between Harigantas and C104 appears to be a good combination as it exhibited significantly positive sca for SGR, pods per plant, seeds per plant, seed weight and seed yield. The crosses with significant sca effects for seed yield per plant were Harigantas × C 104, ICCV2 × C235, ICCV2 × C104, ICCV91501 × W315 and ICCV2 × W315. This might have resulted from simultaneous significance of sca effects for related component traits such as pods and/or seeds per plant.

Since selection to improve one trait may change another trait, correlation of RPF and SGR with other yield components and seed yield was studied (Table 6). RPF exhibited significantly negative correlation with seed yield indicating detrimental effect of higher RPF on yield. The observation that SGR correlated positively with seed weight but negatively with seed number shows that variation in dry matter accumulation causes variation in seed size. The same relationship was obtained between seed weight and traits of sink capacity, e.g., pods per plant (−0.217), seeds per plant (−0.586) and seeds per pod (−0.840). The significant positive correlation of SGR (0.412) and seed weight (0.462) with seed yield suggests that yield in chickpea is limited by inherent low SGR as selection for higher SGR would inversely affect seed number in consequent lines. Significantly positive correlation was observed among pods per plant, seeds per plant and seed yield.

Table 4. Analysis of variance for combining ability for seed yield and its components in chickpea

Source	df	Mean squares						
		RPF	SGR	Pods/ plant	Seeds/ plant	Seeds/ pod	Seed weight	Seed yield
gca	5	0.50**	3.16**	3321.30**	12295.10**	0.07**	8873.60**	289.02**
sca	15	0.04**	0.10**	3955.74**	5388.19**	0.01	304.82**	177.32**
Error	40	0.01	0.02	786.95	1092.37	0.01	41.28	37.04

*, **Significant at 5% and 1% levels of probability

Table 5. General and specific combining ability effects for seed yield and its components in chickpea

Characters	RPF	SGR	Pods/ plant	Seeds/ plant	Seeds/ pod	Seed weight	Seed yield
Parents							
1. Harigantas	0.29**	−0.36**	−8.75	−9.23	0.04	−19.1**	−5.41*
2. ICCV 2	0.21**	0.58**	−19.92	−45.08**	−0.09*	29.62**	−0.42
3. ICCV 91501	0.08*	−0.38**	−12.22	4.73	0.08*	−22.6**	−5.88*
4. WR 315	0.02	−0.38**	35.50*	42.42*	−0.02	−14.95**	2.11
5. C 235	−0.27**	−0.45**	12.14	46.68**	0.11*	−26.51**	−0.95
6. C 104	−0.32**	1.00**	−6.75	−39.53*	−0.12*	53.54**	10.55**
SE of G (I)	0.022	0.043	9.05	10.67	0.03	2.07	1.96
Crosses							
1 × 2	−0.082	−0.588**	48.01*	100.32**	0.24**	−36.16**	6.43
1 × 3	−0.345**	0.102	31.05	29.68	−0.08	−1.09	2.23
1 × 4	−0.132*	0.002	25.26	29.39	−0.05	−0.28	2.44
1 × 5	−0.117*	0.202*	15.39	0.2	−0.12	2.3	−1.31
1 × 6	−0.194**	0.364**	92.75**	84.14**	−0.12	23.47**	25.09**
2 × 3	0.305**	−0.015	−25.96	−33.17	−0.01	8.98	0.08
2 × 4	−0.049	−0.311**	65.39**	65.25*	−0.02	−18.90**	9.57*
2 × 5	−0.154**	−0.102	39.45	53.22*	0.02	−3.53	12.44*
2 × 6	−0.088	0.020	55.97*	38.36	−0.09	5.64	10.99*
3 × 4	−0.166**	−0.094	69.9**	87.53**	−0.03	−2.18	9.95*
3 × 5	−0.059	−0.481**	−33.92	−5.03	0.19**	−15.13**	−8.27
3 × 6	−0.112*	−0.085	11.85	29.35	0.05	−1.17	6.95
4 × 5	0.094	0.006	22.93	30.05	−0.01	7.38	5.83
4 × 6	0.029	0.305**	−36.84	−60.04*	−0.05	25.98**	−1.64
5 × 6	0.145*	−0.096	−22.88	−7.34	0.09	−4.2	0.59
SE of S (I, J)	0.050	0.096	20.53	24.19	0.06	4.70	4.46
Mean performance of the trait	1.84	3.38mg	276.5	346.44	1.31	17.11g	56.40g

*, **Significant at 5% and 1% levels of probability

The inference that the additive gene effects were more important for seed weight is in close agreement with earlier studies [4-11]. The importance of both additive and non-additive gene effects for pods per plant, seeds per plant, seeds per pod and seed yield are in conformity with earlier reports [8-13]. However, the results differed from the findings of earlier reports [5, 6, 11, 15] where non-additive gene effects were of major importance for these characters. Predominance of additive gene action in the genetic control of SGR as found in this study was earlier reported for cowpea [21] and rice [22]. The apparent over-dominance of genes for pods per plant, seeds per plant and seed yield may be attributed to the nonrandom gene distribution among the parents thus transforming partial dominance into apparent over-dominance [23]. Therefore, further studies are needed for the genetic analysis of pods per plant, seeds per plant and seed yield involving large number of parents in diallel crosses.

For incorporating high yield in chickpea, C104 seems to be a good combiner. Since high yield in C104 resulted from accumulation of positive alleles, it would be easy to identify segregants having positive alleles at all the loci. The fact that seed weight and SGR are found to be controlled mainly by additive gene action and that the estimate of narrow-sense heritability was high, large genetic gains can be made through simple selection scheme such as pedigree method. However, direct selection for SGR would be very difficult due to the complicated procedure involved in measuring the trait. The close association observed between SGR and seed weight makes it possible to select for higher SGR through selection for larger seed size in chickpea improvement programmes.

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