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Nature of gene action and genetic parameters for yield and its components in chickpea

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To determine the gene action and genetic parameters of agro-morphological traits in chickpea, five genotypes of chickpea as a half diallel crossed with each other in 2008, five parents and 10 progenies were planted as randomized complete block design with three replications and some traits including days to flowering and maturity were recorded on row basis when 50% plants flowered or matured. Plant height, biomass, harvest index, number of primary branches, number of pods per plant, number of seeds per plant, 100-seed weight and seed yield were recorded for each plant (10 observation). Based on analysis of variance, variance due to additive gene effects showed significant differences for plant height and number of primary branches per plant. Both additive and dominance genetic effects were significant for days to flowering, days to maturity, biomass, 100-seed weight, harvest index, number of pods, seeds and seed yield per plant. Higher values (>1) of the average of dominance (H1/D)^{1/2}, a measure of over dominance, were observed in this study except for plant height and harvest index. Higher values of narrow-sense heritability was also observed for harvest index (67%), 100-seed weight (56%) and plant height (42%) indicating that huge genetic gain could be achieved for these traits.

Key words: Additive, chickpea, diallel, dominance, heritability.

INTRODUCTION

According to Upadhyaya et al. (2001), chickpea (*Cicer* arietinum L.) is a major food legume and an important source of protein in many countries in Asia. However, chickpea production in these countries is still low (0.78 t ha^{-1}) and limited by biotic and abiotic stress factors (Saxena, 1993; Upadhyaya et al., 2001). Genetic improvement of yield in these environments has been recognized to be difficult for plant breeders as compared to favourable environments. Seed yield is a complex character controlled by several genetic and environ-mental factors and also depends on interaction of many other characters. Breeders always look for genetic variation among

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traits to select desirable types. Some of these characters are highly associated with seed yield. As in all cultivated plants, the main objective of chickpea breeding is to improve cultivars having high yield and quality. Since genotypic and environmental factors are the main components for determining yield and quality in plants, the primary aim should be the determination of effects of genotypic factors for selection.

Plant breeders and geneticists often use diallel mating designs to obtain genetic information for an interest trait from a fixed or randomly chosen set of parental lines. The diallel mating design and its modifications has been used by several chickpea breeders to evaluate the potential of populations for intra population improvement and the usefulness of parents in inter population breeding programs, and to select inbred lines in hybrid breeding programs. The estimation of additive and non-additive gene action through this technique could be useful in determining the possibility of commercial exploitation of heterosis and isolation of pure lines among the progenies of the good hybrids (Stuber, 1994). The diallel cross has

Abbreviations: DF, Days to 50% flowering; DM, days to maturity; 100-SW, 100-seed weight; HI, harvest index; No. PB, number of primary branches; No. P/p, number of pods per plant; No. S/p, number of seeds per plant; PHT, plant height; SY/p, seed yield per plant.

Table 1. Analysis of variance of a 5 x 5 half-diallel cross set for quantitative characters in chickpea (according to Walters and Morton, 1978).

Source	Df	DF	DM	PHT (cm)	No. PB	No. P/p	No. S/p	Biomas	100-SW (g)	SY/p (g)	Н
rep	2	4.01 ^{ns}	0.67 ^{ns}	82.7**	0.19*	812.5*	980.9*	331.6*	4.7 ns	94.3**	30.5ns
а	4	124.9**	128.9**	152.23**	0.44**	2490.3**	2876.5**	565.9**	19.8**	206.2**	408.7**
b	10	120.6**	120.8**	25.14 ^{ns}	0.09 ^{ns}	593.9**	846.11**	183.13*	17.6**	74.7**	168.6**
b1	1	39.34**	8.4 ns	8.5 ^{ns}	0.23*	100.02 ^{ns}	658.9 ^{ns}	82.4ns	58.4**	98.4**	531.9**
b2	4	139.8**	156.7**	37.4*	0.17*	1351.1**	1365.01**	364.6**	5.4 ^{ns}	68.3*	36.04**
b3	5	121.5**	114.5**	18.7ns	-0.01 ^{ns}	86.9 ^{ns}	468.5 ^{ns}	58.10 ^{ns}	19.2**	74.9**	201.9*
Error	24	4.54	3.02	11.7	0.04	168.5	188.9	64.3	2.03	14.7	12.4

*, **Significant at the 0.05 and 0.01 probability levels, respectively. a, Additive effect; b, dominance effect; b1, mean dominance deviation; b2, dominance deviation due to each parent; b3, dominance deviation due to each crossing combination. DF, Days to 50% flowering; DM, days to maturity; PHT, plant height; No. PB, number of primary branches; No. P/p, number of pods per plant; 100–SW, 100-seed weight; No. S/p, number of seeds per plant; SY/p, seed yield per plant; HI, harvest index.

been defined as the group of all possible crosses among several genotypes (Griffing, 1956). Diallel analysis has been used in chickpea to provide important information on general and specific combining ability, determining genetic variances, estimating heritability and maternal effects (Singh et al., 1999; Hovav et al., 2003; Şakar and Biçer, 2004; Anbessa et al., 2006).

Grain yield is a quantitative trait which is controlled by several genes. Knowledge of genetic components of multi genetic traits and environmental effects is important for choosing suitable breeding methods, size of populations and intensity of selection (Biçer and Şakar, 2008). With this view, the present study was undertaken to understand the genetics of agro-morphological traits in chickpea using 5×5 half-diallel cross in order to select suitable parent and crosses to evolve them in chickpea breeding programs.

MATERIALS AND METHODS

The experiment was conducted at the experimental farm of the Sara-Rood Dry Land Research Station in Kermanshah (west of Iran) during the spring of 2008. Five genotypes (Arman, Hashem, ILC588, ICCV₂ and ILC3979) of Kabuli chickpea were chosen. The choice of the genotypes was based on their differences for many agronomic characters. The experimental materials comprised of F₁ (obtained generation from two genotypes hybridization) populations from a 5 x 5 half-diallel cross and five parents.

Agronomic practices

The experimental materials were sown by hand during early spring of 2008 in a randomized complete block design with three replications. Each replication comprised of 5 parents and 10 F_{1s} . The number of seeds per row was 20. Weeds were removed by hand.

Studied traits

To eliminate marginal effects, observations were recorded only on 10 plants located in middle of the rows. Mature plants were individually harvested. Days to flowering and maturity were recorded on row basis when 50% plants flowered or matured. Plant height, biomass, harvest index, number of primary branches, number of pods per plant, number of seeds per plant, 100-seed weight and seed yield were recorded for each plant.

Statistical analysis

Analysis of variance (ANOVA) in the half-diallel set was performed based on the method described by Walters and Morton (1978) using the microcomputer program "DIALL win 98" developed by Ukai (1989) and estimated genetic parameters analysis using D_2 program.

RESULTS AND DISCUSSION

Gene effects

Analysis of variance (ANOVA) of half-diallel according to Walters and Morton (1978) is given in Table 1. The significant a and b effects shows genetic variations due to additive and dominance gene effects, respectively. The b_1 effect is the average indication of heterosis that was significant for days to flowering, 100-seed weight, harvest index, number of primary branches and seed yield per plant; the b_2 parameter is specific heterosis relative to each parent and indicates different dominance and recessive gene frequencies in parents for all traits except 100-seed weight. The b_3 parameter that is mainly an indication of dominant part and is similar to specific combining ability (SCA) in Griffing method, was significant for days to flowering, maturity, 100-seed weight, harvest index and seed yield per plant (Table 1).

ANOVA analysis showed that only additive gene effects were found to be significant for plant height and number of primary branches. In addition, additive gene effects were also significant for days to flowering, maturity, biomass, 100-seed weight, harvest index, number of seeds, pods and seed yield per plant. The magnitude of the additive gene effects was much higher than dominant effects. These findings show the possibility of early generation selection for some characters in this study (Table 1). According to Malhotra and Singh (1989), Singh et al. (19992, 1993), Sakar and Bicer (2004) and Bicer

Parameter	DF	DM	PHT(cm)	No. PB	No. P/p	No. S/p	BIOMAS	100-SW(gr)	SY/p(gr)	HI
ß-1	$0.005 \pm 0.14^*$	0.29± 0.13*	1.12 ±0.19 ^{ns}	0.76 ± 0.27 ^{ns}	0.30±.29*	0.47 ±0.29 ^{ns}	0.21±0.23*	0.69 ± 0.18^{ns}	0.47 ± 0.25 ns	0.79 ±0.1 ^{ns}
D±S.E.(D)	37.9 ± 15 *	42.05±16.9*	46 ±4.3*	0.16 ±0.021*	727.02 ±145.2*	849.6 ±145*	148.5±44*	6.08 ±0.89*	58.03 ±10.5*	131.7 ±6.3*
H2±S.E. (H2	150.1* ±36.7	1604±1.5*	25.3±10.6*	0.11±0.052*	1147.6± 255.7*	1218.9 ±354.7*	325.2±108*	2.2*±7.4	78.5 ±25.6*	69.12 ±15.4*
F±S.E. (F))	54± 37.4 ^{ns}	67.5±42.3 ^{ns}	30.8±10.8*	0.16± 0.054*	959.6 ± 362.7*	929.03 ±261.8*	213.5±110 ^{ns}	-1.3 ±2.25 ^{ns}	40.7 ±26.12 ns	19.6± 15.7 ^{ns}
h2 ± S.E.(h2)	12.8±24.8 ^{ns}	2.3± 28 ^{ns}	5.7 ±7.2 ^{ns}	0.06 ±0.04 ^{ns}	5.6± 240.2 ^{ns}	156.2 ±239.5 ^{ns}	12.1± 72.6 ^{ns}	14.3 ± 1.5*	23.6± 17.3 ns	130.4 ± 10.4*
E ± S.E.(E)	4.5±6.2 ^{ns}	3.02± 7 ^{ns}	11.7±1.8*	0.044±0.009*	168.5 ±59.3*	188.9 ±59.13*	64.5± 18*	1.85 ±0.37*	14.7 ± 4.2*	12.4 ± 2.6*
(H1/D)1/2	2.23	2.19	0.88	1.011	1.47	1.39	1.7	1.24	1.32	0.77
H2/4H1	0.199	0.19	0.18	0.174	0.182	0.183	0.19	0.198	0.195	0.22
KD/KR	1.93	2.16	2.2	2.9	2.62	2.3	2.43	0.85	1.72	1.22
К	0.1	0.015	0.2	0.5	0.0048	0.1	0.037	1.9	0.3	1.9
R(Yr, Wr+Vr)	-0.73	-0.41	0.76	-0.25	0.00	-0.32	-0.34	-0.75	-0.75	-0.97
h2NS	0.21	0.19	0.42	0.26	0.18	0.27	0.15	0.56	0.37	0.67
h2BS	0.91	0.94	0.62	0.55	0.70	0.72	0.62	0.78	0.73	0.86

Table 2. Genetic parameters of quantitative traits in chickpea.

*, **Significant at the 0.05 and 0.01 probability levels, respectively. DF, Days to 50% flowering; DM, days to maturity; PHT, plant height; No. PB, number of primary branches; No. P/p, number of pods per plant; 100–SW, 100-seed weight; No. S/p, number of seeds per plant; SY/p, seed yield per plant; HI, harvest index.

and Sakar (2008), plant height, days to maturity and 100-seed weight could be selected by breeders in early generations but it is not possible for days to flowering, number of pods and seeds per plant. Days to flowering and maturity are very important traits for drought escape in terminal drought environments (Toker et al., 2007). These charac-ters cannot be used in early generation selection because they are regulated by additive and dominance gene actions. Bicer and Sakar (2008) reported similar findings for days to maturity. Breeding for plant height is very important for machinery harvesting and chickpea cultivation development in the world. Fortunately, because of the essential role of additive gene effects in plant height heritability, it seems early generation selection is effective (Table 1). Malhotra and Singh (1989), Singh et al. (1992, 1993), Sakar and Bicer (2004) and Bicer and Sakar (2008) reported similar findings for plant height but biomass was controlled by additive and dominance gene effects, however the additive

component had higher value. Additive gene effects contributed to the variation in number of primary branches (Table 1); indicating that genetic gain in selection for this trait could be possible. Both additive and dominance gene effects were significant for 100-seed weight, harvest index, seeds and seed yield per plant.

However, additive gene effects were higher than dominance gene effects. According to Singh et al. (1982), Upadhyaya et al. (2006), Dhaiwal and Gill (1973), Şakar and Biçer (2004) and Biçer and Şakar (2008) both additive and dominance gene effects play role in the heritance of 100-seed weight, harvest index, number of seeds and seed yield per plant but number of pods and seeds per plant play a role only in additive gene effects.

Genetic parameters estimated

Estimates of genetic components were calculated for each trait using D_2 program. These results are

based on Hayman's (1954) method of deviation of regression coefficient from one (slope) and are given in Table 2. Significant values were observed for days to flowering, maturity, biomass and number of pods per plant (Table 2). The other method was based on Hayman's (1954) method of analysis of variance for Wr-Vr values. The Wrshown here) was significant for days to flowering and maturity, demonstrating additive-dominance model inadequacy. Hence, in addition to additive and dominance gene effects, epistasis gene effects were effective for controlling days to flowering and maturity. These epistatic effects can cause bias in the estimates of the additive and dominance components. For other characters, additive-dominance model appears to be adequate. This result shows that breeding for most important traits in chickpea could be simplified because of the absence of epistatic effects in the control of these traits. Similar results have been published by different researchers (Kidambi, 1988; Malhotra and Singh, 1989; Singh et al., 1992; Anbessa et al., 2006). Analysis of variance Wr+Vr value was significant for days to flowering, maturity and harvest index (not shown here). These results show the presence of dominance gene effects for these traits. Additive variance was significant for all characters in this assay. According to Zafar and Abdullah (1971), Singh et al. (1992) and Biçer and Şakar (2008) reports, both additive and dominance variance are the main components for most agronomic characters such as days to flowering, maturity, plant height, basal pod height, number of branches, pods and seeds per plant, seed yield, 100-seed weight and seed size.

Environmental variance was found to be significant for all traits except for days to flowering and maturity that indicated high level of environmental pressure. The average degree of dominance (H1/D)^{1/2} for all characters, except for plant height and harvest index was higher than unity, indicating over dominance for most traits studied in this research. However, the degree of dominance value for plant height and harvest index was less than unity, indicating the presence of partial dominance for these traits. Biçer and Şakar (2008) reported occurrence of partial dominance for most characters but Muhelbauer and Singh (1987) reported that number of branches, pods and seeds per plant show over dominance.

Dhaiwal and Gill (1973) reported that number of pods per plant and grain yield exhibited positive over dominance but 100-seed weight showed no dominance effect. The proportion of positive and negative genes (H2/4H1) was unequal, showing different distribution of genes among parents. The (H2/4H1) component ranged from 0.17 for numbers of primary branches to 0.23 for harvest index, indicating that negative genes are more frequent. Proportion of dominant and recessive genes in the parents (KD/KR) indicated that parents carry more dominant than recessive genes for most characters but 100-seed weight (KD/KR) value was lower than the one showed by parents that carry more recessive than dominant genes for this trait (Table 2). Greater ratio of dominant to recessive genes (KD/KR) with positive value (F) indicates that dominant genes except for 100-seed weight are more numerous for most studied traits (Table 2). Days to flowering and maturity were controlled by at least one group of genes (k = 0.1). Kumar and Van Rheenen (2000), Or et al. (1999) and Cho et al. (2002) reported that days to flowering was determined by one major gene, but Bicer and Sakar (2008) and Anbessa et al. (2006) reported that days to flowering was governed by three and two major genes, respectively. 100-seed weight and harvest index were controlled by at least two genes (K=1.9, 1.5, 1.9), respectively (Table 2).

These finding are in agreement with results of Biçer and Şakar (2008) and Upadhaya et al. (2006). Other characters studied in this research were controlled by at least one group of gene (Table 2). The sign of correlation coefficient (R) between averages of joint parent for each row (Yr) and (Wr+Vr) value indicated dominance direction (Table 2). The coefficient of correlation between (Yr) and (Wr+Vr) was negative and high, for days to flowering, maturity, biomass, 100-seed weight, harvest index, number of primary branches, seeds and seed yield per plant. Hence, for these traits, amplifier alleles were dominance but as for plant height and number of pods, with positive and high (R), reducer alleles were dominant. These results correspond to previous findings in this research. The highest and lowest narrow-sense heritability was obtained for harvest index (0.67) and biomass (015), respectively. The narrow-sense heritability was relatively high for plant height (42%), 100-seed weight (56%), seed yield per plant (37%) and harvest index (67%), indicating that great genetic gain could be achieved for these traits in chickpea breeding. Bicer and Sakar (2008) reported higher values of narrow-sense heritability for 100-seed weight (96%), days to flowering (84%), seeds (78%) and pods per plant (74%).

The narrow - sense heritability was low for days to flowering (20%) and maturity (19%), these results must be considered by breeders who want to create drought tolerance lines with early maturity in chickpea. The broadsense heritability was found to be more than narrowsense heritability for all traits, ranging from 55 to 94% (Table 2). This indicate that both additive and non additive components of genetic variances are involved in governing the inheritance of almost all the quantitative traits in chickpea, as dominance component appeared to be high in magnitude. Tambal et al. (2000) reported that broad-sense heritability ranged from 11 to 87% and seed yield and plant height had the lowest heritability values. Hence, early generation selection could not be used for most characters in chickpea. However, Joshi et al. (2004) reported that both additive (fixable) and non-additive (non-fixable) components of genetic variances are involved in governing the inheritance of all quantitative and qualitative traits in wheat

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