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Gene Effects for Agronomic Traits in Safflower (Carthamus tinctorius L.) under Drought Stress

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Abstract

The mode of agronomic traits inheritance was investigated in safflower ($Carthamus\ tinctorius\ L.$) in drought stress as a new report. Five generation including P_1 , P_2 , F_1 , F_2 and F_3 that derived from the cross of IL.111 (drought sensitive) ×Mex.22-191 (drought tolerance) were used in a Completely Randomized Block Design with two replications. Generation mean analysis was used to estimate genetic parameters. The additive model [d] was fitted for seed-weight, dry weight/plant and number of seeds/plant. The simple additive-dominance model [d, h] was fitted for number of seeds/capsule. Additive-dominance model was not adequate for plant height, number of branches per plant and number of capsules per plant. Hence, dominance× dominance epistasis [l] was added to fit the model as [d, h, l] for these traits. So, the genetic control of mentioned traits was under additive, dominance and dominance× dominance gene effects. Obtained results could be suitable for designing of breeding strategies to improve seed yield of safflower in drought stress. The highest value for broad-sense (0.94) and narrow-sense (0.9) heritability were denoted to seeds/capsule.

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Introduction

Drought stress is considered as a major limiting factor for plant production in arid and semi-arid regions (Munns., 2002). Development of drought tolerance cultivars that could be adapted to arid climates is an important aim in crops breeding (Blum., 1988).

Safflower (Carthamus tinctorius L.) is an important oil seed crop that has been grown as a source for vegetable oil for human and industrial consumptions (Knowles., 1985; Dajue & Mundel., 1996 and Singh., 2007). Historically, it was used for fabric dyes, food coloring and medicinal purposes (Weiss., 2000). Safflower is grown commercially in Iran, as one of its cultivation centers in the old world (Golkar et al., 2010) The mode of inheritance detection and gene action of seed yield and its components, are very helpful for safflower breeding (Mirsa et al., 1994). Information on genetic components (additive & dominance) plays an important role for understanding traits gene action in stress environment (Singh & Pawar., 2005). Besides to additive-dominance

models, epistatic or non-allelic interactions could have an important role in genetic control of studied traits (Singh & Pawar., 2005). Epistatic effects could contribute in heterosis expression for specific hybrid (Kearsey & Pooni., 1996). To have an efficient breeding program for drought tolerance genotypes of safflower, it is necessary to find the mode of inheritance and magnitude of gene effects. Genetic models have been deployed for estimation of different genetic effects (Kearsey & Pooni., 1996). Generation Mean Analysis (GMA) is a simple and useful technique for estimating genetic effects of additive, dominance and epistatic (non-allelic) interactions of a quantitative trait (Mather & Jinks., 1982; Singh & Singh., 1992 and Singh & Pawar., 2005). Toledo et al. (1991) suggested that the fiveparameter model was good as the back cross studies for estimation of gene effects, and gives satisfactory results.

There are some reports about the estimation of genetic effects for agronomic traits of safflower in

normal conditions, but it seems that there isn't any information about genetic control of agronomic traits of safflower in drought condition.

Genetic control of salt tolerance has been reported in reproductive stage (Nakaei et al., 2014). In drought conditions, the additive model [d] was fitted for branches/plant, seeds/capsule and seed yield/plant. Also, the simple additive-dominance model [d, h] was fitted for number of seeds/plant.

The identification of gene action in drought tension, could be an effective way breed strategies for production of drought-tolerance genotypes in safflower. The objectives of this novel study were:

- 1) To estimate genetic parameters, heritability and dominance ratio of studied traits using :P₁, P₂, F₁, F₂ and F₃ in drought stress.
- To test the accuracy of different genetic models for studied traits in drought stress.

Materials and Methods

The experimental materials consisted of three homogenous generations including: $[P_1 \ (IL.111): an Iranian genotype; P_2 \ (Mex.22-191): a Mexican genotype and <math>F_1]$ and two heterogenous generations: F_2 and F_3 families. Parental genotypes of P_1 and P_2 were selected as drought-sensitive and drought-tolerance, respectively. This study was conducted at Research Farm of Shahid Bahonar University of Kerman $(56^{\circ}58')$ longitude and $30^{\circ}15'$, 2044 m asl, with an arid and semi-arid climate) in 2011. The pH of soil experiment was 7.8 with Clay loamy texture. Fertilizer was applied before sowing (100 kg/ha P2O5) and 25 kg/ha Zn) and at stem elongation (50 kg/ha N).

The experiment was conducted based on five generations of P_1 , P_2 , F_1 , F_2 and F_3 , based on a Completely Randomized Block Design (CRBD) with two replications. Each block consisted of 100 rows of F_3 families, 6 rows for each generation of P_1 , P_2 , F_1 and 3 rows for F_2 generation that spaced 50 cm and 5 cm between and within rows, respectively. Drought stress was applied at 10% of flowering stage of genotypes. After this period, the stress experiment received water once 80 ± 5 mm evaporation had occurred from pan class A, according to Ashkani et al. (2007). So, this drought condition could have an effect on seed yield and its components seriously.

Five randomly plant was selected in each row of different generations (F_1 , F_2 and F_3) for trait measurement. Different agronomic traits were measured after the complete maturity stage at each plant. The traits included: plant height, number of branches per plant, number of capsules per plant, total dry weight per each plant, seed yield per plant, 1000-seed weight, number of seeds per plant and number of seeds per capsule. Each plant harvested and then the seed yield and its components were calculated.

• Statistical models

The joint scaling test (Mather & Jinks., 1982) was employed to estimate the mean (m), additive effect (d), dominance effect (h), additive ×additive (i), additive ×dominance (j) and dominance × dominance (l) parameters according to following formulae:

$$Y=m+\alpha[d]+\beta[h]+\alpha^2[i]+2\alpha\beta[j]+\beta^2[l]$$

In this equation, α , β , α^2 , $2\alpha\beta$ and β^2 are the coefficient for genetic parameters of [d], [h], [i], [j] and [l], respectively. The best model was selected by using non-significant Chi-square test (χ^2) (Mather & Jinks., 1982). Genetic variance details (D and H) and environmental effects variance (E₁ and E₂) were calculated by using four normal equations based on least square method (Mather & Jinks., 1982).

$$V_{F2} = \frac{1}{2}D + \frac{1}{4}H + E_1,$$

$$V_{\overline{F_3}} = \frac{1}{2}D + \frac{1}{16}H + E_2$$

$$\overline{V}_{F3} = \frac{1}{4}D + \frac{1}{8}H + E_1$$

$$W_{F2.F3} = \frac{1}{4}D + \frac{1}{2}H + E_1$$

 $W_{F2.F3=} = \frac{1}{4}D + \frac{1}{8}H + E_1$ The significance of parameters [m, d, h, i, j and l] were tested with t-test at 1% and 5% of probabilities (Steel & Torrie., 1980). Broad-sense (h_b^2) and Narrow-sense (h_n^2) heritability was estimated by Following formulae:

$$h_{b=}^2 \qquad \frac{V_{F2} - \sqrt{V_{p1} \times V_{p2}}}{V_{F2}}$$
 (Mahmud & &

Keramer., 1951)

$$h^{2}_{n} = \frac{1/2D}{V_{F2}}$$
 (Mather & Jinks., 1982).

Homogeneity of variance and Generation Mean Analysis (GMA) was carried out by SAS.9.1.

Results

The mean comparison for studied traits in different generations is shown in Table 1. The IL.111 (P_1) mean was greater than Mex. 22-191 (P_2) mean for 1000-seed weight and the number of seeds per capsule (Table 1). The F_1 mean was greater than the mean of both parents, only for seed yield per plant and the number of seeds per plant. This result implied that heterotic effects could be effective for improvement of these traits. The means of F_2 generation for studied traits were in the range of parent means, except for seed yield (Table 2). Mean comparison showed that P_1 and P_2 have significant differences for most of the traits.

According to Table 2, the dominance-additive model [d and h] was adequate for the number of seeds per capsule in drought stress, but the contribution of

additive gene action was more than dominance in drought stress (Table 2).

The additive model [d] was fitted for dry weight/plant and the number of seeds per plant (Table 2). This result implied on the importance of selection for improvement of these traits. Also, additive gene action was found for genetic control of seed yield/plant and 1000-seed weight (Table 2). Simple additive-dominance model was insufficient to explain the differences among generation means for plant height, branches/plant and capsule/plant that implied on the importance of epistasis on genetic control of these traits (Table 2).

Variance analysis was carried out to obtain different variance components in different generations (Table 3). Different variance estimates (D, H, E_1 and E_2) are presented in Table 3 according to Mather and Jinks method (1982). The sum of F_2 plants variance (V_{F2}),

 F_3 progeny variances average (\overline{V}_{F3}), F_3 progeny average variance ($V_{\overline{F3}}$) is calculated. The additive variance component (D) was higher than the (H) for plant height, capsule/ plant, seed yield and seeds/capsule.

Heritability (broad and narrow) of studied traits is presented in Table 4. Broad-sense heritability ranged from 58% (number of capsules per plant) to 99% (number of seeds per plant). Narrow-sense heritability ranged from 26% (number of seeds/plant) to 90% (seeds/capsule). The highest value (90%) of narrow-sense heritability was devoted to the number of seeds per capsule (Table 4).

The average of dominance ratio $(\sqrt{H/D})$ was more

than unity for number of branches per plant, dry weight of each plant, 1000-seed weight and the number of seeds per plant.

Table 1. Mean and standard errors of safflower generations in drought stress condition.

Character	P_1	P_2	F_1	F_2	F_3
Plant height	85.16± 9.23	144± 12.83	95±5.44	86.22±11.44	92.68±13.62
Branches/ plant	1.33± 1.75	10.83 ± 4.35	8.50±1.35	5.77±2.68	8.08±2.87
Capsules/ plant	12.33± 7.94	27.16± 8.28	22.50±6.77	15±7.50	18.66±9.86
Dry weight/ plant	52.9± 10.3	98.66± 30.34	92.16±21.94	64.37±35.86	78.19±38.95
Seed yield /plant	13.16± 8.82	18.43 ± 8.96	20.76±6.49	12.88±7.49	16.54±10.26
1000-seed weight	43.10± 6.03	32.50±4.35	40.70±7.88	36.14±3.66	38.19±16.65
Seeds/ plant	313.33± 87.89	454.50±201.49	525.66±177.37	351.22±181	440.23±264.15
Seeds/ capsule	30.10± 11.55	19.32±3.36	23.24±2.69	24.35±6.20	24.92±9.50

Table 2. Estimation of gene effects and their standard error for different traits in generations of IL.111×Mex.22-191 cross

Character	[m]	[d]	[h]	[i]	[1]	χ^2	Non-allelic interaction
Plant height	11.57±2.98**	-14.73±3.20**	-40.58±15.04**	-	34.84±12.54**	0.64	Duplicate
Branches /plant	9.93±0.87**	-2.38±0.92**	-9.56±0.92**	-	8.03±3.60*	3.24	Duplicate
Capsules/ plant	20.99±2.13**	-7.46±2.34*	-13.53±10.81*	-	14.46±9.26**	1.68	Duplicate
Dry weight /plant	78.09±6.31**	-24.71±6.40**	-5.66±32.55 ^{ns}	-	18.28±29.21 ^{ns}	1.87	-
Seed yield/ plant	16.93±1.80**	-3.56±1.83*	-3.90±9.19 ^{ns}	-	7.01 ± 8.36^{ns}	2.91	-
1000-seed weight	38.76±1.37**	5.60±1.50*	-5.96±7.30 ^{ns}	-	6.45 ± 7.66^{ns}	2.23	-
Seeds/ plant	453.74±42.28**	-132.63±43.64**	-108.92±217.5 ^{ns}	-	159.77±204.5 ^{ns}	2.62	-
Seeds / capsule	25.47±0.63**	-2.23±1.54*	-2.23±1.54*	-	-	0.00001	-

ns, * and ** , non significant and significant at 5% and 1% level of probability, respectively.

df = 1 α =0.01 χ^2 =6.63 and df = 1 α =0.05 χ^2 =3.84

[[]m]: mean, [d]:additive, [h]:dominance, [i]:additive ×additive, [j]: additive× dominance, [l]: dominance× dominance.

Table 3. Estimation of additive (D), dominance (H) and Environment variances (E₁ and E₂) for different traits of safflower

Characters	D	Н	V_{F3}^-	$ar{ar{V}}_{F3}$	E_I	E_2
Plant height	61.63	38.10	72.33	20.71	31	204.79
Branches /plant	4.35	11.24	7.78	2.49	2.81	3.57
Capsules/ plant	101.41	95.56	95	37.37	20.41	58.29
Dry weight /plant	1592.10	2235.77	1597.84	678.78	242.85	770.9
Seed yield/ plant	137.22	0.0001	102.65	34.26	34.30	53.96
1000-seed weight	394.52	1303.13	558.56	250.59	8.55	30.66
Seeds/ plant	37890.6	131564.22	70998.4	25952.09	19162.11	33655.64
Seeds / capsule	170.19	0.21	94.24	43	8.46	45.94

Table 4. Estimation of broad-sense and narrow-sense heritability of studied traits in IL.111×Mex.22-191 cross in safflower

character	Broad-sense h ² (%)	Narrow-sense h ² (%)	$\sqrt{H/D}$	
Plant height	61	43	0.76	
Branches /plant	84	27	1.61	
Capsules/ plant	58	53	0.96	
Dry weight /plant	99	49	1.18	
Seed yield/ plant	73	66	0.08	
1000-seed weight	97	35	1.81	
Seeds/ plant	99	26	1.84	
Seeds / capsule	94	90	0.015	

Discussion

Generation mean analysis fitted different genetic models for studied traits of safflower under drought stress. Obtained results of this study were similar to the reports of Mandal and Banerjee (1997), Singh et al. (2005) and Golkar et al. (2012) and for genetic control of number of seeds per capsule in normal condition. Literature reviews showed that there isn't any reports about the genetic control of dry weight/ plant and the number of seeds per plant in normal or stress condition. So, these novel finding could be important for improvement of these traits in safflower breeding. This result confirms the results of Shahbazi and Saeidi (2007) about genetic control of seed yield/plant. Other reports pointed at predominance role of dominance gene action in genetic control of seed yield/plant (Mandal & Banerjee., 1997; Gupta & Singh., 1988; Singh et al., 2005) that was different to our results. This discrepancy could be related to different genotypes and environmental conditions. The differences in gene action of a trait in different environments could be compromised from the significant effect of that stress condition on gene activity (Blum., 1988). Environmental factors (such as drought and salinity) also induce changes in gene expression. Plant responses to different stresses are

highly complex and involve changes at the gene expression, transcriptome, cellular, and physiological levels (Atkinson & Urwin., 2012). The importance of additive gene action in genetic control of 1000-seed weight was previously reported by Golkar et al. (2012) and Shahbazi and Saeidi (2007) in normal condition. Kotecha and Zimmerman (1978) reported the partial or over dominance for seed weight in different crosses of safflower. The efficiency of any selection program is mainly dependent on additive genetic variance which is due to the breeding value of the genotype (Falconer & Mackay., 1996). Therefore, selection through selfing will be effective for mentioned traits improvement. For plant height, number of branches per plant and number of capsules per plant, the additive (d), dominance (h) and dominance × dominance (1) effects played an important role in genetic control of these traits. In these traits, the sign of [h] and [l] is opposite; hence duplicate epistasis is involved (Mater & Jinks., 1982). Hence, there is a problem in selection as well as complex nature of inheritance for improvement of these traits. This type of epistasis makes it difficult to fix the increased level of a character because the positive effect of one parameter would be cancelled out by the negative effect of another.

In this situation reciprocal recurrent selection is likely useful for effective utilization of both types of additive and non-additive gene effects simultaneously. Negative sign of [h] for plant height, number of branches per plant, number of capsules per plant and the number of seeds per capsule showed that reductive alleles were involved in dominant phenotype (Mater & Jinks., 1982).

Degree of dominance ratio ($\sqrt{H/D}\,$) which explains

the ratio of additive to dominance gene effects is compromised from [D] and [H] components of variance generation analysis (Mater & Jinks., 1982). The inconsistency between genetic effects for genetic parameters could be resulted from gene dispersion and two directional effects (Mather & Jinks., 1982). Shahbazi & Saeidi (2007) reported that dominance ratio was less than unity of 100-seed weight and number of branches/plant that was different to our results. This discrepancy could be related to different genetic backgrounds and environments (normal condition).

Additive gene effect might be little because of gene dispersion and also dominance gene effect can be little because of two directional dominant (Mather & Jinks., 1982). Genetic variances are mean squares of each locus effects and are not affected by gene dispersion and dominance effect. Thus, the data of generation variances can be used to complete genetic information (Khodambashi et al., 2012). The predominace role of additive gene action for the number of seeds per capsule, was reported by Mandal and Banerjee (1997), Singh et al. (2005) and Golkar et al. (2012) in normal conditions.

The selection efficiency is related to the magnitude of heritability (Kearsey & Pooni., 1996). High percents of broad-sense heritability (>70%) suggested that environmental effects constitute a major portion of the total phenotypic variation of included traits. Golkar et al. (2012) reported a high value for broadsense heritability of the number of seeds/capsule (99%) that was similar to our results. Pahlavani et al. reported medium low narrow-sense heritability for capsules/ plant (9%) that was similar to our results. Singh et al. (2008) reported high broad-sense heritability for 100-seed weight in normal condition. This value could be related to other gene actions such as epistasis that involved in genetic control of the number of capsule/plant (Shahbazi & Saeidi., 2007). The high value for broad-sense heritability for the number of branches/plant (84%) in our study was different with the reports of Camas and Esendal (2006). Results of narrow-sense heritability indicated that selection for number of seeds per capsule could be successful, because of the high proportion of additive component in total genetic variance. Other studied traits had medium narrowsense heritability that implied on most of the genetic variances, is due to dominance gene action. The discrepancy in estimation of heritabilities for a trait is

mostly caused by the heritability is not a property of a trait itself, but it is related to the population, environmental conditions, method of evaluation of genotype and parameter estimation (Falconer & Mackay., 1996). This study gives novel findings about the genetic control of Seed yield and its components in drought environment. Selection in early generations for 1000-seed weight, the number of seeds per capsule and the number of seeds per plant could be desirable for seed yield improvement in drought stress. On the other hand, those characters which were mostly controlled by additive effects and have high narrow-sense heritability can be improved by selection and inbred lines could be used as commercial cultivars. But for those traits that are mainly controlled by dominance interaction effects, heterosis breeding might be effective development of superior hybrid cultivars (Singh & Singh., 1992). For improving those traits that both additive and non-additive effects of genes were contributed in their inheritance, the reciprocal recurrent selection might be suggested, since this breeding procedure will concentrate additive effects of genes, but will not allow dissipating non-additive gene effects (Iqbal & Nadeem., 2003). This finding could propose that early selection in IL.111×Mex. 22-191 could be applied as the best strategy for improvement of seed yield of safflower in drought stress, without considering its components.

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