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Generation mean analysis to determine genetic components of drought tolerance in safflower (*Carthamus tinctorius* L.)

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Abstract

Safflower (*Carthamus tinctorius* L.) is one of the important oilseed crops grown commercially in Iran. The production of cultivars with high seed yield and oil content is the most important purpose of safflower breeding. Study of genes action to improve morphological traits especially under drought stress condition is very important. For this purpose, an experiment was conducted in 2013-2015 in the researching farm in Isfahan, Iran using the generations of the crosses between two pure lines (KIR1015×Ac-Sunset) under drought stress and non-stress conditions based on randomized complete block design with three replications. The results of generation mean analysis showed that for plant biomass in both stress and control conditions and for plant seed yield, number of head per plant in control condition m and [a] were the best fitted. For number of head per plant and number of branches in stress condition and for 100 seed weight in control condition, m, [a] and [d] were shown to be the best fit of generation means. The dominant variance of plant seed yield, 100 seed weight and number of branch in stress condition and plant height, plant seed yield, 100 seed weight and number of branch in control condition were higher than additive variance. Broad sense and narrow sense heritabilities of oil content were 59.82 and 89.47 in control and drought stress conditions, respectively. Yield traits such as plant seed yield, number of head per plant and oil content were controlled by additive effects, which suggest scope for breeding and selection for improved drought tolerance in safflower.

Key words: Broad sense heritability, Drought stress, Generation mean analysis, Narrow sense heritability, Oil content.

INTRODUCTION

Safflower (*Carthamus tinctorius* L.) is one of the important oilseed crops grown commercially in Iran. It seems that Iran is one of the centers of origin of the safflower in the old world (Knowels, 1969). The production of cultivars with high seed yield and oil content is the most important purpose of safflower breeding. Safflower is a self-pollinating crop, with some out crossing depending on genotype and insect activity (Weiss, 2000). So, the breeding methods of self-pollinating crops such as hybrid cultivars are also considered in breeding programs (Dajue and Mundel, 1996).

Local safflower seed oil has a fatty acid content made up of palmitic acid (6-8%), stearic acid (2-3%), oleic acid (16-20%) and linoleic acid (71-75%) (Golkar, 2014; de Oliveira *et al*., 2018). Achieving greater crop seed and oil yield per unit is one of the most important challenges for production in dry land environments (Deng, 2014). To plan the efficient breeding programs for developing drought tolerant varieties, obtaining information on the genetic basis of tolerance, mode of inheritance, magnitude of gene effects and their function are necessary.

Heritability is one of the genetic parameters used to determine the breeding methods, which also shows the phenotype and genotype adaptation degree (Pahlavani *et al*., 2007). The additive genetic variance portion

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is important for genotype selection; as in successful selection, it is essential for the additive variance portion to be high enough in genetic variance (narrow-sense heritability) (Poehlman, 1995). Simple phenotypic selection can be used in the traits showing a high heritability (Khan *et al.,* 2008).

Generation mean analysis provides an opportunity to estimate genetic components and measure epistasis effects. This also helps us to understand the performance of the parents used in the crosses and potentials for the crosses to be used either for heterosis exploitation or pedigree selection (Shahbazi and Saedi, 2007).

It is noted that if the strategy of a breeding program is to improve yield in both stress and non-stress environments, selection should be based on the yield under both conditions, when the breeder is looking for cultivars adapted to a wide range of environments (Sio-Se Mardeh *et al*., 2006; Mohammadi *et al*., 2018).

Previous studies showed that the dominance effects of the genes played a major role in the variation of seed yield number of heads per plant in safflower (Kotecha, 1981). Also, the influence of both additive and non-additive effects of genes on the number of heads per plant has been reported (Sahu and Tewari, 1993). However, for some traits such as height, days to 50% flowering, number of seeds per head and 100-seed weight additive genetic effects explained considerable amount of variation (Abel, 1976a; Sahu and Tewari, 1993). Abel (1976b) reported that broad sense heritability of seed yield in safflower was very low. Kotecha and Zimmerman (1978) found that narrow sense heritability for seed weight in safflower was high and varied from 66.0 to 85.5%. Heterosis for oil content and a wide range of heterosis for seed yield has been reported (Patil and Narkhede, 1996). The inheritance of flower color has been studied in safflower (Leus, 2016).

In order to obtain more precise estimates of gene effects of safflower cultivars under drought condition, generation mean analysis was used to determine the genetic control of drought tolerance during growth of safflower using F_1, F_2 and F_3 populations derived from crosses between KIR1015×Ac-Sunset lines.

MATERIALS AND METHODS

Experimental procedure

In this study, two improved lines were used as the parents. The line KIR1015 was isolated from Kurdistan landrace which was obtained by single plant selection from Iranian local populations and then selfing for three generations and Ac-Sunset a registered Canadian cultivar (Mundel *et al.,* 1992). The parental genotypes were chosen based on their genetic variation for traits such as seed yield. The genotype of KIR1015 was considered as P_1 and the genotype of Ac-Sunset was taken as P_2, in crosses. The crosses between parental genotypes were carried out manually in spring 2013. F_2 seeds were produced by bagging F_1 plants in paper bags prior to the flowering period in summer 2013. The generations of F_3 were produced by bagging the F_2 plants in paper bags prior to the flowering period in summer 2014. The populations were cultivated at the Research Farm in Isfahan, Iran during the growing seasons of 2015. All five populations were evaluated in a randomized block design under two irrigation conditions (normal irrigation or control and low irrigation or water stress). Under the normal irrigation, plants were well watered whenever soil moisture reached the field capacity point while under stress condition after the onset of flowering, watering was delayed until the wilting point took place (Alizadeh Yeloojeh and Saeidi, 2020). There was no effective rainfall during stress adopting. The experimental design at each site was a randomized complete block design with three replications. For each one of the P_1, P_2 and F_1 generations one line, F_2 three lines and F_3 families, 80 lines in each replication were planted. All lines were completely randomized within each of the three blocks before cultivation took place. The distance between rows was 50 cm, it was 15 cm in rows and the length of each row was 2 m.

Data collection was performed from all the studied populations. Generation mean analysis was applied for each trait using Mather and Jinks method (Mather and Jinks, 1982). The traits assessed were plant biomass (g/m^2), plant height (cm), number of head per plant, number of seeds per head, 100 seed weight (g), plant seed yield (g) and oil content of the seeds (%). Samples for each plot were analyzed in three replications, and their means were considered for statistical analysis.

Statistical analysis

The generation mean analysis of the five populations (P_1, P_2, F_1, F_2 and F_3) and associated scaling tests (Mather, 1949; Cavalli, 1952) were performed based on the assumption that populations have non-homogeneous variances (Mather and Jinks, 1971). A statistical explanation supports the theory that the variance of the populations will not be homogeneous (Beaver and Mosjidis, 1988). The variation in the parental lines and their F1 is environmental, whereas variation in later generations has both genetic and environmental components (Mather and Jinks, 1971).

The data was analyzed using SAS 9.0 software. The goodness of fit for additive-dominance model was observed using joint scaling and chi-square tests. In case that the additive-dominance model has not revealed all the genetic changes in the trait of interest, the five-parameter fitness model was used. In this study, only three and four-parameter models were tested by goodness of fit test using chi-square test with one and two degrees of freedom for goodness of fit, and the five-parameter model could not be tested due to the lack of sufficient generations and zero degree of freedom of chi-square test.

Genetic variance components as well as environmental effect variance were estimated according to Hallauer and Miranda (1988) based on expected mean squares (Table 1):

$$\sigma_g^2\bar{F}_3 = (1/2)A + (1/16)D = (M32 - M2)\,/\,r$$

$$\sigma_g^2 F_3 = (1/4)A + (1/8)D = M12 - M11$$

$$E1 = M11$$

$$E2 = M2\,/r$$

$$VE1 = \frac{2M_{11}^2}{rn(k-1)+2}$$

$$VE2 = \frac{2M_2^2}{[(r-1)(n-1)]+2}$$

$$VA = \frac{128}{9r^2}\left[\frac{M_{32}^2}{P+1} + \frac{M_2^2}{[(r-1)(n-1)]+2}\right] + \frac{32}{9}\left[\frac{M_{12}^2}{rp(k-1)+2} + \frac{M_{11}^2}{rh(k-1)+2}\right]$$

$$VD = \frac{512}{9}\left\{\left[\frac{4M_{12}^2}{rp(k-1)+2} + \frac{4M_{11}^2}{rh(k-1)+2}\right] + \frac{1}{r^2}\left[\frac{M_{32}^2}{P+1} + \frac{M_2^2}{[(r-1)(n-1)]+2}\right]\right\}$$

The gene effects were estimated from the joint scaling test as proposed by Mather and Jinks (1982). The genetic components of mean for the selected traits were observed using joint scaling test including Mean (m), additive effect (d), dominate effect (h), additive×additive effect (i), and dominate×dominate effect (l) parameters. The heritability in broad sense and narrow sense (h^2_b and h^2_n, respectively) and degree of the dominance ratio (D) were estimated as follows:

$$\mathrm{h}_\mathrm{n}^2 = \frac{V_A}{V_P}$$

$$\mathrm{h}_\mathrm{b}^2 = \frac{V_A + V_D + V_{AD}}{V_P}$$

$$D = \sqrt{\frac{V_D}{V_A}}$$

RESULTS AND DISCUSSION

Successful development of drought tolerant cultivars presupposes a careful study to determine inheritance of traits in the target environment since water deficit stress might affect gene action (Khodadadi *et al.,* 2017; Gholizadeh *et al.,* 2018). In plants, most of the phenotypic variations are continuously distributed and could be considered as quantitative traits. The complexity of their genetic control is high because the involved genes are numerous, with usually minor effects and very sensitive to the environment.

Table 1. Analysis of variance and expected mean square of parents, F_1, F_2 and F_3.

Source of variation	Df	Mean square	Expected mean square
Replication	r-1	-	-
treatment	n-1	M_3	-
Between generations	g-1	M_{31}	σ^2+r σ^2_g
Between F3 families	p-1	M_{32}	σ^2+ r $\sigma^2 g\bar{F}_3$
Error	(r-1)(n-1)	M_2	σ^2
Total	rn-1	-	-
Within generations	rn(k-1)	M1	-
Within F3 families	rp(k-1)	M_{12}	σ^2_{wg+} σ^2_{we}
Within Homogeneous generations	rh(k-1)	M_{11}	σ^2_{we}

r: Number of replications, n: Number of genotypes, g: Number of generations, p: Number of F3 families, k: Number of observations, h: Number of homogeneous generations.

The results of ANOVA showed that parents significantly differed for the evaluated agro-morphological traits (data not shown). The means and standard deviations for traits in different generations are shown in Table 2.

The KIR1015 parental genotype showed superior means compared to Ac-Sunset parental genotype for all the traits under drought stress condition. For most of the traits, F_1 revealed higher means than F_2 individuals. This may be due to the inbreeding dispersion. The means of offspring observed between two parents for some characteristics such as plant biomass indicated that there may be additive effects in controlling these traits. The average of F_1 progenies were closer to one parent for 100 seed weight, this indicates a partial or complete dominance effects controlling this trait.

The average of most of the measured traits decreased due to the negative effect of drought stress. The highest reduction was observed in the parental genotypes for plant seed yield, number of heads per plant, number of branches and 100 seed weight. Guttieri *et al.* (2001) reported that the main reason for the reduction of the seed yield were decrease of 100 seed weight in the first step, and secondly reduction of the number of seeds per unit area.

The results of generation mean analysis based on joint scaling test for the measured characters are shown in Table 3. The best model was selected using the non-significant chi square (χ^2) value and lowest standard error for all traits. For plant biomass in both conditions and plant seed yield, number of heads per plant in control condition two parameters m and [a] were shown to be best fitted for the observed to the expected generation means. Inter-allelic interaction was not found significant. The genetic variation between generations was explained alone by additive effects in these traits. But for all other traits, both additive and non-additive gene effects were involved to explain genetic variation between the generation means.

Alizadeh Yeloojeh and Saeidi (2020) implied the importance of additive gene effects on the genetic control of seed yield, but their finding is inconsistent with those of Rajab and Fried (1992), Mandal and Banerjee (1997), and Singh *et al.* (2008), who observed that dominance predominantly controlled seed yield.

Three parameters m, [a] and [d] were shown to be the best fit for the observed to the expected generation means for the number of heads per plant and number of branches in drought stress condition and for 100 seed weight in control condition. Three- parameter m, [a] and [i] was fitted for number of branch in stress condition and 100 seed weight in normal condition (Table 3). In the study of Pahlavani *et al.* (2007) number of heads per plant was the important component of the yield for those dominant gene effects responsible. Shahbazi

Table 2. Comparisons of means (±standard errors) for various characters in five populations of cross KIR1015×Ac-Sunset grown in control (C) and drought (S) treatments (each value is an average of three replications).

Character	Condition	Populations				
		KIR1015	Ac-Sunset	F1	F2	F3
Plant biomass (g/m^2)	C	114.43±1.78^{a}	76.16±0.46^{c}	103.41±3.83^{b}	115.51±4.19^{a}	98.93±1.90^{b}
	S	89.74±1.84^{a}	64.89±1.21^{b}	81.74±4.28^{a}	82.05±2.39^{a}	79.74±7.21^{a}
Plant height (cm)	C	104.72±0.15^{b}	84.17±0.42^{e}	113.42±0.94^{a}	94.71±0.78^{d}	100.89±1.22^{c}
	S	103.03±0.27^{b}	78.30±0.40^{d}	110.78±1.22^{a}	101.34±1.45^{bc}	98.45±1.29^{c}
Number of branches	C	37.15±0.18^{a}	27.22±0.22^{c}	24±0.00^{d}	29.97±0.99^{b}	24.31±0.46^{d}
	S	24.19±0.04^{a}	14.43±0.44^{c}	17.48±1.39^{bc}	18.27±0.41^{b}	18.06±1.24^{b}
100 seed weight (g)	C	48.91±0.35^{a}	39.50±0.17^{b}	51.70±3.26^{a}	53.01±1.94^{a}	48.45±0.43^{a}
	S	39.32±0.19^{a}	28.99±0.28^{b}	42.85±3.08^{a}	41.40±0.14^{a}	40.76±0.88^{a}
Number of heads per plant	C	41.15±0.18^{a}	32.50±0.10^{c}	28.72±0.49^{d}	37.48±1.99^{b}	29.41±0.29^{d}
	S	29.37±0.13^{a}	20.73±0.43^{c}	23.19±2.19^{bc}	26.03±0.70^{ab}	25.59±1.27^{ab}
Plant seed yield (g)	C	42.46±0.10^{b}	31.86±0.46^{d}	46.98±2.07^{a}	43.15±0.75^{b}	38.24±0.29^{c}
	S	31.68±1.29^{a}	19.05±0.35^{c}	28.67±2.16^{ab}	25.05±0.39^{b}	23.94±1.40^{b}
Plant oil content (%)	C	0.31±0.04^{c}	6.89±0.76^{a}	1.25±0.05^{bc}	1.32±0.11^{bc}	1.79±0.11^{b}
	S	0.49±0.03^{d}	7.55±0.26^{a}	1.07±0.06^{dc}	1.16±0.30^{c}	1.83±0.03^{b}

and Saeidi (2007) showed that additive×additive and dominance×dominance epistasis had important roles in the genetic control of number of heads per plant and 100 seed weight. Sahu and Tewari (1993) reported on the importance of additive-dominance model for its genetic control.

Gupta and Singh (1988b) reported that additive gene effects played an important role in the control of number of branches, however, Narkhede and Patil (1987) claimed epistasis effects had a significant role in controlling the number of branches per plant. The results of Golkar *et al*. (2012) indicated a non-significant effect of epistasis in this regard which is in agreement with the results of our research.

Four-parameter models were fitted for plant height and plant seed yield in stress condition. This suggests that selection should be carried out in later generations and the interaction should be fixed by selection under selfing conditions. A 5-parameter model was fitted for plant height in control condition (Table 3). Previous studies reported plant height as an important morphological trait under the effect of additive gene action (Kotecha, 1981; Shahbazi and Saeidi, 2007; Golkar *et al.,* 2012).

Signs associated with different estimates of epistasis indicate the direction in which gene effects influence the population means. Mather and Jinks (1982) proposed the association or dispersion of genes in the parents based on signs associated with epistatic gene effects. These signs were in opposite directions and significant in the control for plant height. A negative sign for these parameters indicates an interaction between increasing and decreasing alleles, thus providing some evidence for the existence of dispersion in the parental genotypes which hinders early selection for such traits.

The higher estimate of dominance effect rather than additive effect for plant seed yield, plant height and 100 seed weight in both conditions revealed parental dominant genes join together in offspring hybrids. Although, the additive effects were significant for some characters but the quantities were smaller than dominant effects. Based on multi gene assumption less additive gene effect was not unexpected in this research (Mather and Jinks, 1982; Kearsey and Pooni, 1998).

The estimates of additive, dominance and environmental components of variance, broad-sense heritabilities and narrow-sense heritabilities and degree of dominance for different traits in control and drought treatments are presented in Table 4. The dominant variance of plant seed yield, 100 seed weight and number of branches in stress condition and plant height, plant seed yield, 100 seed weight and number of branches in control condition were higher than additive variance. Number of head per plant and number of branches exhibited high broad-sense heritabilities (more than 90%) in both control

Table 3. Estimates of gene effects in control (C) and drought stress (S) for various traits in the cross KIR1015×Ac-Sunset of safflower using the Mather and Jinks (1982) five-parameter model.

Character	Condition	Gene effects					x^2	p-value
		m	a	d	aa	dd		
Plant biomass (g/m^2)	C	105.41**	-21.31**	9.72	-	-	0.74	0.23
	S	85.86**	-14.59**	5.67	-	-	1.00	0.35
Plant height (cm)	C	124.10**	-11.28**	-87.11**	-23.66**	83.05**	-	
	S	101.40**	-14.36**	15.72**	-5.74**	-	0.97	0.26
Number of branch	C	24.01**	-4.97**	0.03	8.18**	-	0.14	0.13
	S	18.7**	-4.54**	-1.89*	-	-	0.34	0.16
100 seed weight (g)	C	45.6**	-5.29**	8.64**	-	-	0.98	0.28
	S	40.03**	-5.16**	2.77	-5.88**	-	0.78	0.25
Number of head per plant	C	25.86**	-4.5**	-1.69	-	-	1.00	0.32
	S	31.94**	-7.5**	-3.93**	-	-	0.36	0.14
Plant seed yield (g)	C	22.85	-5.14**	5.91	-	-	0.79	0.26
	S	21.46**	-6.31**	9.73*	3.90*	-	0.62	0.18
Plant oil content (%)	C	2.26**	2.01**	-1.39	-	-	0.77	0.24
	S	2.76**	2.41**	-1.45	-	-	0.79	0.32

Table 4. Different components of genetic variances, degree of dominance and heritability estimates of various traits studied under control (C) and drought stress conditions (S) in safflower.

Character	Condition	Additive variance (D)	Dominance variance (H)	E1	Environmental variance or error (E2)	Degree of dominance	Broad-sense heritability h^2b	Narrow-sense heritability h^2n
Plant biomass (g/m^2)	C	0	946.14	344.87	64.66	-	69.79	-
	S	0	721.56	384.20	120.07	-	58.86	-
Plant height (cm)	C	19.06	69.06	22.45	4.52	2.69	76.57	16.56
	S	52.5	0	32.71	13.34	-	53.27	53.27
Number of branches	C	0	84.58	4.67	2.06	-	92.63	-
	S	0	25.33	17.86	3.44	-	54.32	-
100 seed weight (g)	C	31.22	50.44	33.83	6.30	1.80	67.05	25.63
	S	14.73	19.07	43.30	6.87	1.61	40.25	17.55
Number of heads per plant	C	0	99.66	4.57	2.45	-	93.42	-
	S	0	61.43	24.81	5.26	-	67.14	-
Plant seed yield (g)	C	0	209.83	36.26	7.17	-	82.58	-
	S	0	85.74	68.66	13.73	-	51.00	-
Plant oil content (%)	C	2.56	0	0.85**	0.05**	-	58.72	58.72
	S	3.28	0	0.17**	0.02**	-	89.47	89.47

and stress treatments (Table 4). For 100 seed weight, a low heritability was observed in both environments. The degree of the dominance ratio was less than one, except for 100 seed weight in both conditions and for plant height in normal. This indicates the presence of partial or incomplete dominance types of gene action in the inheritance of these traits (Table 4). Selection of these characters must therefore be delayed until the F_3 or F_4 generation. This delay permits a loss of non-additive genetic variance through inbreeding, so that the additive genetic variance can be more clearly evaluated (Farshadfar *et al*., 2001). The degree of the dominance ratio was upper than one for 100 seed weight and plant height indicated the over dominant gene effect controlling these traits. Gardner (1963) suggested that values in early generations tend to be overestimated due to an upward bias from the repulsion phase of linkage and, in further generations, the linkage will be broken due to recombination and a low degree of dominance.

Safflower is an oil seed crop, therefore, breeding efforts should emphasize on the improvement of both quality and quantity of oil (Hamdan *et al*., 2008). In this study the results showed that additive affects control this trait. The previous studies reported that both additive (Golkar *et al.,* 2011) and dominance (Gupta and Singh, 1988) gene effects are observed in the genetic control of seed oil yield. In the study of Pahlavani *et al.* (2007) epistatic effects had a significant impact on the genetic control of safflower oil. While quantitative inheritance is reported for safflower oil content, non-additive gene effects have also been reported for the genetic control of oil content (Golkar *et al.,* 2011). Positive and significant relationships between seed-oil yield and other tested traits were found in the study of La Bella *et al.,* 2019.

Broad sense and narrow sense heritability of oil content were 59.82 and 89.47 in control and drought stress conditions, respectively (Table 4). Both broad and narrow–sense heritabilities have also been reported for oil content of safflower. Hamdan *et al.* (2008) reported that additive gene effects are important for the genetic control of oil content. Zhao *et al.* (2021) reported that heritability varied from low to moderate across traits. Heritability was low for grain yield and flowering period at 0.31 and 0.32, respectively. Plant height had a moderate heritability (0.68).

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