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ORIGINAL PAPER

Genetic Analysis of Oil Content and Fatty Acid Composition in Safflower (*Carthamus tinctorius* L.)

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Abstract The F_1 and F_2 progenies of eight-parent diallel crosses were used to investigate the mode of inheritance of fatty acids, oil, and protein in safflower (*Carthamus tinctorius* L.) seeds. The results indicated significant differences among the parents for general (GCA) and specific combining ability (SCA). Relatively high narrow-sense heritability was estimated for fatty acids including linoleic (0.84), oleic (0.77), palmitic (0.61), and stearic (0.6) acids. The high narrow-sense heritability and the high ratio of GCA/SCA mean squares for all the fatty acids investigated indicate the important role of additive gene action in controlling these traits. In our experiment, however, low narrow-sense heritability was obtained for oil (0.37) and protein (0.28) contents. Furthermore, the estimates of genetic variance components proposed the importance of non-additive genetic effects that contribute to variation in oil and protein content. The overall results indicated that K_{21} × Mex.22-191 cross could be employed for the production of high oil yielding and high oleic acid safflower lines in breeding programs.

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Introduction

Safflower (*Carthamus tinctorius* L.) ranks eighth after soybean, groundnut, rapeseed, sunflower, sesame, linseed, and castor crops grown worldwide [1]. It is grown commercially in Iran, the likely origin of this oilseed crop [1]. It has been cultivated locally for its oil and flower [2], more specifically for its colorful petals used as food coloring and flavoring agent, for producing vegetable oils, and for preparing textile dyes [1, 3]. The resultant meal after oil extraction is used for animal feed as it is rich in proteins [4].Safflower has recently attracted public attention, not for its colorful petals but because it is acknowledged as an important source of healthy vegetable oils [4]. The safflower seed is typically composed of 55–65% kernel and 33–45% hull [1]. Normal types of the whole seed contain 27–32% oil, 5–8% moisture, 14–15% protein, 2–7% ash, and 32–34% crude fiber [5]. Safflower is one of the crops with the greatest variability of fatty acid in its seed oil composition [6]. This has encouraged researchers to look for new genetic sources of fatty acid composition to improve oil quality of safflower seed [2]. Conventional safflower seed oil has a fatty acid profile made up of 6–8% palmitic acid, 2–3% stearic acid, 16–20% oleic acid, and 71–75% linoleic acid [4]. Unlike high oleic acid content, which can be found in other oilseed crops such as sunflower, the high linoleic acid content present in safflower oil is a distinct trait that is not available in any other commercial oilseed crop. Safflower oil rich in linoleic acid has interesting market niches for animal feed [7]. Because of its great stability and bland flavor, high-oleic safflower

oil makes a very good frying oil [5]. As an additional advantage, it has no linolenic fatty acid which is readily oxidized in oils such as soybean and canola [5].

Oil content is a quantitative trait, which is affected by genotype, environment, and genotype × environment interaction [8, 9]. Breeding efforts in safflower should emphasize improvement of both quality and quantity of oil [10]. Differences in fatty acid composition due to year, location and genotype have also been reported in safflower [6]. Studies have suggested that fatty acid content might be relatively easy to manipulate in a breeding program [11]. An understanding of the genetic control of fatty acid composition within potential donor species could help in using their genes for the improvement of oil crops [8]. Heritability and variance components are useful for designing new breeding programs, predicting response to selection, allocating resources in field performance trials, and constructing selection indices [12]. Improving oil yield requires adequate information regarding the nature of general combining ability (GCA) and specific combining ability (SCA) of the parents available in a wide array of genetic material to be used in the hybridization programs. Information is also required about the nature of gene actions involved in the expression of quantitative and qualitative traits [13, 14]. Diallel analysis provides a unique opportunity to test a number of lines in all possible combinations [12].

A recent study of safflower showed the potential role of modifying genes in the expression of high oleic acid content and hypothesized the effect of both modifying genes and minor genes in governing oleic acid content [10]. However, the quantitative nature of the oil content and oleic acid has been subjected to detailed study in other oilseed crops [8, 15]. Improvement of quantity and quality of oil in safflower, like in most oleaginous crops, is the major goal of breeding programs. In spite of great improvements in modifying the quantity and quality of oil, very little in known about the inheritance of protein content, oil content, and fatty acid composition in safflower. The present study was designed to investigate the inheritance of oil content, fatty acid composition and protein content of safflower seeds and to determine the superior parents and crosses on the basis of their general and specific combining abilities for oil content, fatty acids, and protein content for further improvement of oil quality and quantity in safflower.

Materials and Methods

Six breeding lines (ISF_{14}, A_2, C_{111}, C_{4110}, K_{21}, IL.111) selected from various local populations of safflower along with two genotypes obtained from Germany (GE_{62918}) and Mexico (22-191) were used in this study (Table 1). Local lines were obtained by selfing individual plants selected from some Iranian safflower landraces. Eight genotypes were crossed in a complete-diallel mating design to provide 56 F_1 hybrids. The F_2 seeds were produced in a greenhouse by bagging F_1 plants of direct crosses during flowering period to produce 28 F_2 populations. Two experiments were subsequently conducted at the Research Farm of Isfahan University of Technology, Iran (51° 32′ E and 32° 32′ N, 1,630 m asl) in the spring seasons of 2007 and 2008, using the randomized complete block designs with three replications.

Table 1 Plant materials used for diallel cross-design in safflower

Entry	Parents	Origin
1	P_1 GE_{62918}	Germany
2	P_2 C_{111}	Selected from the Kouseh landrace
3	P_3 C_{4110}	Selected from the Kouseh landrace
4	P_4 ISF_{14}	Selected from the Isfahan landrace
5	P_5 A_2	Selected from the Azarbayejan landrace
6	P_6 K_{21}	Selected from the Kordestan landrace
7	P_7 Il.111	Selected from the Auroumieh landrace
8	P_8 Mex.22-191	Mexico

For the purpose of statistical analysis, complete diallel sets of F_1 and half diallel crosses of F_2 were conceived as two separate experiments. The parental lines along with their F_1 hybrids (64 genotypes) were included in the first experiment, while F_2 populations and their parental lines (36 genotypes) were allocated to the second experiment. Each plot comprised two 1.5 m rows spaced 50 cm apart and two 3 m rows spaced 50 cm apart in the first and second experiments, respectively. The flour samples were prepared separately from 10 to 30 individuals for F_1 and F_2 progenies, respectively, from each genotype with three replications. The percentage of oil, fatty acids and protein of safflower flour seeds of the genotypes were calculated by using near-infrared reflectance spectroscopy (NIR) (model 8200, Perten Instruments AB, Sweden). The 20-g flour samples from each genotype were scanned. Three-hundred samples (three field replications of parental lines, F_1 and F_2 progenies) were scanned three times. The fatty acid content of palmitic (C16:0), stearic (C18:0), oleic (C18:1), and linoleic (C18:2) were expressed as the percentage of the total fatty acids.

General combining abilities (GCA) and specific combining ability (SCA) of different parental genotypes were estimated according to methods I and II of Griffing [16] for all their traits. Since parental genotypes were selected from different sources, the data were analyzed as a fixed model. Moreover, analyses of components of variance of oil and protein contents were conducted using the Jinks-Hayman

method [17]. The relative importance of variances due to GCA and SCA were compared by the predictability factor $[2\sigma^2_{GCA}/(2\sigma^2_{GCA} + \sigma^2_{SCA})]$.

Narrow sense heritabilities of traits were estimated using variance components and calculated as $\hat{h}^2_n = \hat{\sigma}^2_A/(\hat{\sigma}^2_A + \hat{\sigma}^2_D + \hat{\sigma}^2_E)$ [18]. The validity of the assumptions for the Jinks-Hayman analysis was tested against the regression coefficient of Wr/Vr [17]. Since parental genotypes were selected from different sources, the data were analyzed as a fixed model. The collected data were subjected to analysis of variance (ANOVA) using general linear model (GLM) of Statistical Analysis System program [19]. Diallel analyses were carried out using SAS [20] and Diall98 [21] programs.

Results and Discussion

The results obtained from analyses of variances indicated significant genotypic effects in both F_1 and F_2 diallel experiments for all of the seed-quality traits (Table 2). A considerable genetic variability was observed among the parents for all the traits evaluated. Means of oil content in parental lines averaged over the two experiments varied between 32.66% (Mex.22-191) and 25.1% (IL.111). The parental lines C_{4110} and Mex.22-191 produced the highest (75.23%) and the lowest values of (55.82%) linoleic acid content, respectively. Mex.22-191 and C_{4110} had the highest (35.26%) and the lowest (15.40%) oleic acid contents among the parental lines, respectively (Table 3). While GE_{62918} (9.09) had the highest palmitic acid content, IL.111 (7.05) had the lowest value of this acid among the parental genotypes (Table 3). The highest and the lowest mean values of stearic acid were recorded for A_2 (1.7) and K_{21} (3.81), respectively (Table 3). The highest and the lowest values of protein content (%) belonged to A_2 and IL.111, respectively (Table 3).

A novel finding of this study involves the identifying of new genotypes with increased levels of oleic acid (>20%) relative to the levels found in normal genotypes. The Mex.22-191 parental line, with an average oleic acid of 35% is defined as an oleic safflower oil type. Therefore, this genotype could be used in safflower breeding programs aiming at producing frying oil with a high oleic acid content.

The mean squares of GCA in F_1 and F_2 diallel experiments were highly significant for all the traits (Table 4). The proportion of GCA variance to that of SCA varied from trait to trait. SCA mean squares were significant for all the traits in F_1 and F_2 diallel experiments (Table 4).

Table 2 Results of analysis of variance for protein content, oil content, and fatty acid composition in F_1 and F_2 generations of safflower

Source of variation	Mean square						
	df	Oil (%)	Linoleic acid (%)	Oleic acid (%)	Palmitic acid (%)	Stearic acid (%)	Protein (%)
F_1 hybrids							
Replication	2	17.5	57.49**	14.12**	21.01**	51.73**	32.79**
Genotypes	64	11.01**	100.7**	88.27**	2.18**	15.13**	4.47**
Residual	126	4.59	6.05	6.62	0.73	3.13	2.39
F_2 populations							
Replication	2	20.9**	9.36*	26.41**	33.57**	51.59**	31.04**
Genotypes	35	11.29**	69.11**	93.7**	2.63**	25.82**	5.47**
Residual	70	3.03	2.48	4.92	0.17	1.87	1.65

*,** Significant at $P < 0.05$ and $P < 0.01$, respectively

Table 3 Mean of biochemical traits of eight safflower genotypes used as parental lines in diallel mating design

Trait (%)	GE_{62918}	C_{111}	C_{4110}	ISF_{14}	A_2	K_{21}	IL.111	Mex.22-191	$LSD_{0.05\%}$
Oil content	25.53	27.37	27.80	29.73	26.50	30.66	25.10	32.66	4.54
Linoleic acid*	69.29	74.09	75.23	72.96	74.72	66.80	73.27	55.82	7.35
Oleic acid	19.54	16.24	15.40	15.88	15.73	20.84	15.82	35.26	5.49
Palmitic acid	9.09	8.16	7.99	9.74	7.69	8.89	7.05	7.64	1.82
Stearic acid	2.08	2.51	2.26	2.04	1.7	3.81	3.17	1.89	1.84
Protein content	18.40	19.56	21.8	19.93	22.3	19.23	15.46	17.56	3.30

* The values of palmitic (C16:0), stearic (C18:0), oleic (C18:1), linoleic (C18:2) fatty acids expressed as percent by weight of total fatty acid content

Table 4 Analysis of variance for combining ability of different traits in the F_1 and F_2 generations of safflower

	Mean square						
	df	Oil content (%)	Linoleic acid (%)	Oleic acid (%)	Palmitic acid (%)	Stearic acid (%)	Protein content (%)
F_1 hybrids							
GCA	7	47.70**	680.05**	599.6**	7.79**	72.37**	10.78*
SCA	28	9.22**	19.65**	28.23**	2.01**	7.84**	5.12**
Reciprocal	28	3.56	39.11**	22.06	0.98	8.17**	2.24
Residual	126	4.53	6.07**	6.79	0.74	3.32	2.38
GCA/SCA		5.17*	34.6**	21.23**	3.87**	3.27**	2.10
δ_A^2		1.6	27.52	24.10	0.16	2.68	0.22
δ_D^2		0.87	2.54	4.01	0.10	1.28	0.51
P.F		0.64	0.91	0.86	0.61	0.67	0.30
h_b^2		0.62	0.93	0.92	0.86	0.76	0.51
h_n^2		0.35	0.86	0.81	0.65	0.62	0.21
F_2 populations							
GCA	7	25.43**	255.96**	342.11**	9.39**	58.16**	12.8**
SCA	28	7.76**	22.47**	31.59**	0.95**	17.74**	3.63**
Reciprocal	28	–	–	–	–	–	–
Residual	70	3.03	2.48	4.92	0.17	1.87	1.65
GCA/SCA		3.27**	11.39**	10.82**	9.88**	9.23**	3.52**
P.F		0.43	0.72	0.71	0.70	0.72	0.48
δ_A^2		1.16	15.56	20.10	0.34	2.68	0.60
δ_D^2		1.57	6.01	8.89	0.24	1.20	0.65
h_b^2		0.76	0.95	0.93	0.92	0.84	0.65
h_n^2		0.39	0.82	0.73	0.58	0.59	0.35

*,** Significant at $P < 0.05$ and $P < 0.01$, respectively

h_b^2 broad-sense heritability, h_n^2 narrow-sense heritability, *P.F* predictability factor

This result indicates that the development of hybrid cultivars could also be considered as an effective breeding procedure to improve seed quality traits in safflower.

The reciprocal effects in F_1 diallel crosses estimated by Griffing's analysis were significant for linoleic acid and stearic acid. No significant reciprocal effects were detected for the remaining seed-quality related traits in the present study. These results indicate that extra-nuclear genes also have a significant contribution in controlling linoleic and stearic acids in seed oil of safflower. Further study is clearly required to confirm this result and to elucidate the possible interactions between nuclear and extra-nuclear genes in governing these two fatty acids.

The GCA/SCA mean square ratio was significant for all the studied traits in both generations, except for protein content in F_1 generation (Table 4). This ratio ranged from 2.10 (for protein content) to 34.6 (for linoleic acid) in F_1 diallel analysis. In F_2 diallel analysis, the lowest and highest ratios of GCA/SCA mean squares were 2.6 (for protein content) and 11.39 (for linoleic acid) (Table 4). The predictability factor was close to unity for fatty acids, but it represented a deviation from unity for oil and protein content. Predictability factor calculated from GCA and SCA variances reflects the degree to which trait is transmitted to the progeny. Therefore, the predictability of progeny performance based on the GCA-effect should be reliable for fatty acids in safflower.

Estimates for GCA effects varied between −1.11 (GE_{62918}) and 1.58 (Mex.22-191) in F_1, and between −1.65 (IL.111) and 0.93 (Mex.22-191) in F_2 diallel analysis for oil content. The greater GCA value of Mex.22-191 implies the capacity of this parent to produce superior progenies for oil content when combined with another parent. GCA effects for linoleic acid showed a range from −8.27 (Mex.22-191) to 2.75 (C_{111}) in F_1 and −4.47 (K_{21}) to 2.5 (C_{111}) in F_2 diallel analysis. C_{111}, C_{4110}, ISF_{14} and A_2 may be recommended as superior parents for breeding programs aimed at increasing the linoleic acid content. The rest of the parents were inferior for increasing linoleic acid because of their poor general combining effects. For increasing the oleic acid content (%), K_{21} and Mex.22- 191 were found to be the best general combiners (Table 5). In the case of palmitic acid content (%), IL.111, and Mex.22-191 possessing poor GCA effects were found suitable for breeding

Table 5 General combining ability (GCA) effects for eight parents in F_1 and F_2 diallel analyses in safflower

Parent	Oil content (%)	Linoleic acid (%)	Oleic acid (%)	Palmitic acid (%)	Stearic acid (%)	Protein content (%)
GE_{62918}						
F_1	−1.11**	0.54	−0.79*	0.59**	−1.01**	−0.37*
F_2	−0.59*	−1.24**	−0.83*	0.97**	−1.48**	−0.70**
C_{111}						
F_1	0.64*	2.75**	−0.94**	−0.07	0.71**	−0.2
F_2	0.64*	2.5**	−1.02**	−0.11	1.05**	−0.25
C_{4110}						
F_1	−0.05	2.24**	−2.62**	0.24*	0.98**	0.72**
F_2	0.90**	2.09**	−3.08**	0.46**	0.74**	0.93**
ISF_{14}						
F_1	1.07**	2.23**	−2.57**	0.26*	−1.55**	0.13
F_2	0.26	1.73**	−0.96**	0.15*	−1.54**	0.35
A_2						
F_1	−0.63*	1.58**	−1.92**	−0.14	−1.26**	0.03
F_2	−0.76*	2.46**	−1.15**	−0.69**	−0.58*	0.05
K_{21}						
F_1	−0.55	−2.71**	1.53**	−0.02	0.92**	0.62**
F_2	0.26	−4.47**	2.17**	0.17**	1.60**	0.44*
IL.111						
F_1	−0.95**	1.51**	−0.61	−0.56**	1.70**	−0.51**
F_2	−1.65**	0.99**	−2.12**	−0.51**	1.58**	−0.91**
Mex.22-191						
F_1	1.58**	−8.27**	7.94**	−0.28**	−0.51*	−0.43
F_2	0.93**	−4.13**	6.92**	−0.44**	−1.35**	−0.36
Correlation coefficient[a]						
F_1	0.68*	0.97**	0.96**	0.80*	0.91**	0.67
F_2	0.74*	0.93**	0.94**	0.94**	0.81*	0.86**

*,** Significant at $P < 0.05$ and $P < 0.01$, respectively

[a] Calculated correlation (r) between the mean value for trait and the value for GCA of eight genotypes

programs aimed at reducing the palmitic acid content, a saturated fatty acid. In both generations, GE_{62918}, ISF_{14}, A_2 and Mex 22-191 had negative GCA effects for stearic acid content (%) (Table 5). Thus, because of their poor combining ability effects, these parental lines may be suggested in breeding programs for decreasing the stearic acid content. Concerning protein content (%), C_{4110} and K_{21} were found to be superior parents in breeding programs aimed at protein-quality improvement (Table 5). C_{4110} had the highest GCA effect in the two diallel analyses. Also, this parent was a superior combiner in breeding programs for increasing the protein content. Almost similar trends were observed in both F_1 and F_2 generations for general combining ability effects of the parents. There was a slight instability observed in estimating GCA effects for oil content when estimated by F_1 compared to when F_2 progenies were used for estimation. This indicates the importance of dominance gene effects in the genetic control of oil and protein contents.

The GCA estimates significantly and positively correlated with parental values for all the traits in both generations with the exception of protein content in F_1 (Table 5). Moreover, the crosses having a positive GCA effect recorded a higher mean for different fatty acids in this study. These data provide further evidence for the greater importance of GCA than SCA for the fatty acids and in turn indicate the important role of additive gene action in controlling these traits.

The means of the crosses for oil content varied from $GE_{62918} \times A_2$ (24.41%) to $K_{21} \times$ Mex.22-191 (36.14%) in F_1, and from $ISF_{14} \times$ IL.111 (22.76%) to $ISF_{14} \times$ Mex.22-191 (34.8%) in F_2 diallels, respectively. For linoleic acid contents in F_1 and F_2 diallels, $C_{111} \times$ IL.111 (75.85%) and $ISF_{14} \times A_2$ (76.32%) had the highest means among the genotypes, respectively. The highest mean of the oleic acid content in both generations belonged to $K_{21} \times$ Mex.22-191 (30.76 and 31.4 for F_1 and F_2, respectively). $A_2 \times$ IL.111 cross had the least means

among all the genotypes for palmitic acid in F_1 and F_2 generations (7.76 and 8.17, respectively). Regarding the breeding aims of decreasing saturated fatty acids in safflower and improving the nutritional quality of its oil, $C_{4110} \times$ Mex.22-191 in both generations was found to have the lowest means for stearic acid (1.27 and 1.1 for F_1 and F_2, respectively). Thus, this cross was the best among all the crosses for reducing this fatty acid. As for protein content, the means varied from $GE_{62918} \times$ Mex.22-191 (15.75%) to $GE_{62918} \times K_{21}$ (21.62%) in F_1 and from $GE_{62918} \times$ C111 (18.56%) to $C_{4110} \times K_{21}$ (21.8%) in F_2 diallels.

Estimates for the various components of genetic variances for oil and protein contents based on the Jinks-Hayman method [17] given in Table 6 confirmed the results obtained by Griffing's method. The "D" parameter estimating the additive effect was much smaller than the dominance parameter "H_1" for oil content in both F_1 and F_2 generations. These results confirm those revealed by the Wr/Vr graph (data not shown) regarding overdominance as measured by $(H_1/D)^{0.5}$ ratio that reached 1.05 and 1.67 in F_1 and F_2 generations, respectively, indicating the action of the overdominant gene. The value of the balance between positive and negative alleles ($H_2/4H_1$) indicated that the UV value was not equal to 0.25, indicating the non-equal distribution of the dominant and recessive alleles.

The value for the "D" parameter estimating the additive effect was slightly smaller than that of the dominance parameter "H_1" for protein content. However, for both F_1 and F_2 generations, the value of the "D" parameter was much larger than that of the "H_2" parameter (Table 6). The average degrees of dominance as measured by the $(H_1/D)^{0.5}$ were 1.03 and 1.05 for F_1 and F_2 generations, respectively, indicating complete-dominance for the genetic control of protein content. The deviation of UV value ($H_2/4H_1$) from 0.25 indicates the non-equal distribution of dominant alleles governing protein content.

For these two traits in F_1 and F_2 generation, the positive value of the sum of the product of the additive value and dominance effects (F) indicated that the parents harbored a larger number of dominant genes than recessive ones.

A considerable genetic variability was observed among the parents for all the traits evaluated. This was not surprising since these genotypes originated from different genetic backgrounds. In both F_1 and F_2 diallels, it was found that the variance due to GCA was higher than those of SCA. Therefore, the additive-dominance genetic model was adequate for all the traits [22] and it was concluded that both kinds of gene effects were important for controlling the inheritance of all the traits studied [12]. Significant effects of GCA and SCA have also been reported for the inheritance of different fatty acids in oil castor [14], peanut [13], sunflower [23] and *Brassica juncea* L. [24]. The greater importance of SCA compared to GCA has been reported in peanut oil for oil quantity and quality [13]. The significance ratio of GCA/SCA mean squares, comparing of σ^2_A and σ^2_D and the predictability factor for fatty acid composition (close to unity) indicate the predominance of additive gene effects in the genetic control of these seed quality related traits in safflower. On the other hand, deviation of the predictability factor from unity and comparing of σ^2_A and σ^2_D for oil and protein contents (Table 4) indicates that the non-additive gene action was predominant for these traits [22].

The GCA mean square was considerably larger than that of SCA for linoleic, oleic, and palmitic acids, indicating that additive genetic effects were of major importance in governing these fatty acids. The additive–genetic control of these fatty acids in safflower as found by the present study is also confirmed by the findings reported by previous researcher for oleic acid [10]. For the studied traits, when the GCA effects of the parents obtained in the two generations were plotted against each other, a clear relationship was observed (data not shown). This result indicates that GCA variation among the parents had an acceptable consistency in the two generations. Also, there was a good homogeneity for the estimates of genetic components across the generations (Tables 4, 5). Thus, it seems that

Table 6 Estimation of the derived parameters of genetic variance components and regression coefficients between Wr/Vr in F_1 and F_2 progenies from diallel crosses of safflower genotypes

Genetic parameters									
Trait	D	H_1	H_2	F	h	H_1-H_2	$H_2/4H_1$	$(H_1/D)^{0.5}$	b (Wr/Vr)
Oil content (%)									
F_1	4.46**	5.01*	3.16*	3.76	−1.41*	1.84	0.15	1.05	1.34 ± 0.30
F_2	3.13*	8.84**	6.59**	1.86	−1.99**	2.25	0.18	1.67	0.42 ± 0.95
Protein content (%)									
F_1	4.11**	4.19*	1.84	5.78*	1.33*	2.35	0.11	1.03	1.03 ± 026
F_2	4.37**	4.83**	2.59**	5.31**	1.56**	2.24	0.13	1.05	1.25 ± 0.16

*,** Significant at $P < 0.05$ and $P < 0.01$, respectively

either F_1 or F_2 diallel analysis can provide similar results for estimating such genetic parameters as GCA effects [12]. The proportion of dominant genes was higher for all the traits in F_2 generation than those in F_1. There is no genetic reason for this finding except low sample size and sampling variation within F_2 populations may be involved. This is in agreement with the findings of previous report on safflower [25] and in contrast to those on sesame [22] and those of on bread wheat [12].

Based on GCA effects of parental lines (Table 5), it may be concluded that Mex.22-191 had a good genetic potential for improving oil and oleic acid contents. The considerable association between GCA effects and mean parental traits implies that this value, rather than the GCA effects, can be used to choose parents with better combining ability [22]. Thus, both GCA and SCA effects need to be considered for obtaining the best safflower oil quality cultivars.

The present results indicate that oil, protein, oleic acid and palmitic acid concentrations are controlled mainly by the nuclear genome of the embryo (Table 4) and that the effect of the embryonic cytoplasm plus the maternal effect of the mother plant were only of minor importance. However, considering the significant reciprocal effects on the genetic control of linoleic and stearic acids in F_1, it was observed that the cytoplasmic effect might have an important role in the genetic control of these traits. No study has yet been reported about the prevailing cytoplasmic effect on the inheritance of linoleic and stearic acids in safflower. Non-persistence of the reciprocal effects from F_1 to F_2 generations, however, indicates the non-significant influences of extra-nuclear factors on the inheritance of linoleic and oleic acid compositions in sesame [26] and palmitic acid in soybean [27]. On the other hand, Ramachandram and Goud [25] reported a significant reciprocal effect for oil content in diallel crosses in safflower. The high narrow-sense heritability and the high ratio of GCA/SCA mean squares for all the fatty acids including oleic, linoleic, palmitic, and stearic indicate the important role of additive gene action in controlling these traits. This result is in agreement with report of accumulation of genes with a minor effect for oleic acid inheritance in safflower by another researcher [10].

Graphical Hayman analysis was applied for the two complex quantitative traits of oil content and protein content. Additive-genetic controls with partial dominance and complete dominance were observed for the four different fatty acids and the protein content, respectively. The greater magnitude of GCA effects rather than SCA effects and the significance of reciprocal effects in genetic control of seed protein in *B. juncea* was reported [24]. Non-additive genetic variance via over-dominance was obtained for genetic control of oil content. Consistent with our results, Ramachandran and Goud [25] had reported the non-equal distribution of dominant and recessive alleles among parental genotypes in diallel crosses for oil content in safflower.

The highest broad-sense heritability was related to oleic acid content among the different traits. High estimates of narrow-sense heritability for linoleic and oleic acids indicated that additive genetic variances for these fatty acids were relatively large (Table 3). The low heritability of oil content was also reported in other oilseed crops [8, 15, 24, 28, 29].

The high significant ratio of GCA/SCA mean squares, the high narrow-sense heritability estimates, and the low degrees of dominance for linoleic, oleic, palmitic and stearic acids indicated the prime importance of additive genetic effects on the genetic control of these traits. Hence, breeding procedures based on selection among lines derived from the hybridization program/recurrent selection (if applicable) should result in efficient progress for these traits. Low narrow-sense heritability estimates and the high degree of dominance for oil and protein contents indicated the importance of non-additive genetic efficiency. Hence development of hybrid cultivars would be suggested to improve oil and protein content in safflower. It may also be worthwhile to attempt bi-parental mating in the segregating generation among selected crosses to permit superior recombinations. The greater GCA values of Mex.22-191 for oil content and oleic acid, C_{111} for linoleic acid and C_{4110} for protein content imply the capacity of these parents to produce superior progenies when combined with another parent for improving the noted traits, respectively.

Conclusion

Since genetic improvement of oil yield and its quality is a major goal of safflower breeding, the superior genotypes in this study could be used in recombination breeding programs to accumulate suitable genes that are responsible for improving oil quality Thus, diallel selective mating, which may allow inter-mating of the selects in different cycles and exploit both additive and non-additive gene effects, could be useful in the genetic improvement of oil yield and its quality for nutritional purposes.

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