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Genetic analysis of sunflower fatty acids under optimum and water stressed conditions

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Abstract: In order to study the genetic control of sunflower fatty acids under optimum and water limited conditions a set of 12 sunflower hybrids were evaluated as randomized complete block design with three replications in two separate experiments during two years (2019 and 2020) in Karaj, Iran. The hybrids were obtained by crossing of four male sterile lines and three restorer lines as testers. Water limitation was imposed by water withholding during reproductive stage. Palmitic acid content was governed by both additive and non-additive effects and linoleic acid content by non-additive gene action under optimum and water limited conditions. Stearic acid content was controlled by both additive and non-additive effects in optimum but by additive effects under water limited condition. Oleic acid content was governed by non-additive factors in optimum, while by both additive and non-additive effects in water limited condition. Oil content and leaf temperature were inherited by additive and seed yield by additive and non-additive effects in both conditions. Relative water content and chlorophyll content were controlled by both additive and non-additive effects under optimum but by non-additive effects in water limited condition. According to these results hybrid breeding is suggested for improvement of main sunflower fatty acids under optimum and water limited condition except that selection-based methods for improvement of stearic acid content.

Keywords: drought stress; fatty acids; gene action; heritability

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1 Introduction

Sunflower with a cultivation area of about 27 million hectares is one of the main sources of vegetable oil worldwide (FAO 2019). Sunflower is cultivated as a spring-summer crop in cold regions and as an autumn-winter crop in sought regions of Iran with more than 100 years of cultivation background (Ghaffari et al. 2020). Standard sunflower oil in average is composed mainly of about 69 % linoleic (C18:2), 20 % oleic (C18:1), 7 % palmitic (C16:0) and 4 % stearic (C18:0) fatty acids (Seiler and Jan 2010; Skoric et al. 2008). Other fatty acids including arachidic (20:0), behenic (22:0), and lignoceric (24:0) acids constitute minor part of sunflower oil (Friedt et al. 1994).

Genotype is the most important factor that determines the fatty acid composition of an oil (Knowles 1988), but also environmental conditions as water availability affects the oil characteristics of sunflower (Baldini et al. 2000; Hassan et al. 2005). Seed yield and oil content of sunflower are the main sensitive parameters to water deficit during flowering and reproduction stages (Ghaffari et al. 2012; Kazemeini et al. 2009). Baldini et al. (2000) reported that water stress causes a reduction in oleic acid in standard sunflower hybrids but an increase in high oleic types. Petcu et al. (2001) also reported reduction of oleic acid but increasing of linoleic acid contents in sunflower. Ali et al. (2009) reported that sunflower genotypes express differential responses to water stress with respect to the fatty acids.

Genetic nature of characteristics associated with oil quality is complicated because of strong influences of environmental factors (Joksimović et al. 2001, 2006). Knowing the nature of gene action is an essential prerequisite to determine the breeding strategy in cross pollinated crops as sunflower. For traits under control of additive gene action selection-based methods and for those under control of non-additive effects, hybrid breeding is used to exploitation of heterosis (Skoric 2012). Line × tester mating design allows estimation of components of genetic variance in hybrid breeding programs (Kempthorne 1957; Singh and Chaudary 1985) and extensively has been used in sunflower studies (Chahal et al. 2019; Hladni et al. 2011; Joksimovic et al. 2006; Memon et al. 2015; Tyagi et al. 2020).

According to these studies, involvement of additive gene action has been reported in expression of oil content (Binodh et al. 2008; Leon et al. 2003; Mijić et al. 2008; Ortegon-Morales et al. 1992), although, non-additive gene action has been observed in inheritance of this trait (Hladni et al. 2011; Karasu et al. 2010; Memon et al. 2015; Parameswari et al. 2004; Skoric et al. 2000; Tan 2010). Prevalence of dominant gene action is reported in expression of oleic acid in sunflower (Fernandez-Martinez et al. 1989; Fick 1984; Perez-Vich et al. 2002a; Skoric et al. 1978; Urie 1984). Georgieva and Hristova (1975), Joksimovic et al. (2006) and Tan (2010) reported the importance of non-additive gene action in inheritance of linoleic acid content in sunflower. Simpson et al. (1989) reported that high linoleic acid content is controlled by a partially recessive gene.

Ivanov et al. (1988) reported more contribution of additive effects on expression of high palmitic acid content, while Sakthivel (2003) and Ortis et al. (2005) indicated the importance of non-additive gene action in inheritance of this trait in sunflower. Perez-vich et al. (1998) reported partial dominance for low palmitic acid content in sunflower. Miller and Vick (1999) showed that low palmitic and stearic acids content are under control of additive gene action. Perez-vich et al. (2002b) found that genes responsible for low stearic acid exhibited partial dominance over those for medium and high stearic acid content in sunflower. Madhavilatha et al. (2004) and Ortis et al. (2005) reported that stearic acid is under control of non-additive gene action in sunflower. Tan (2010) reported preponderance of non-additive gene action for governing of additive gene action for palmitic and stearic acid content and both types of gene action for seed yield and oil content. Chahal et al. (2019) reported that oil content, oleic and linoleic acids are controlled by additive gene action, whereas, palmitic, stearic acid and linolenic acids were predominantly under control of non-additive gene action. Tyagi et al. (2020) reported the major role of dominant effects for oil content and major fatty acids of sunflower under normal and drought stressed conditions.

Although there are numerous reports about the nature of gene action in inheritance of sunflower fatty acids in optimum water supply however to the best of our knowledge there is no information about the nature of gene action under drought stressed condition. This study conducted with the aim of study and comparison of genetic control of sunflower fatty acids under optimum and water limited conditions.

2 Materials and methods

The field study was conducted at research field of Seed and Plant Improvement Institute (SPII) in Karaj, Iran (35.84° N, 50.93° E; altitude of 1321 m above sea level) during two years (2019 and 2020). The region has a Mediterranean climate with hot-dry summers and cold-dry winters with average annual precipitation of 243 mm and annual temperature of 13.5 °C. Two years average physicochemical characteristics of soil in the experimental field is shown in Table 1. A set of 12 sunflower hybrids obtained by crossing between four restorer lines as the lines (L) and three cytoplasmic male sterile lines as the testers (T) evaluated in line × tester mating fashion as proposed by Singh and Chaudhary (1985) in randomized complete block design with three replications in optimum and water limited experiments. Each experimental plot consisted of three rows of four m length with 60 and 25 cm spacing between and within rows respectively. Fertilizers were applied at the rate of 100:70:90 $kgha^{-1}$ for N:P:K. All phosphate and potassium fertilizers and one third of nitrogen fertilizer were distributed before planting and the rest of the nitrogen fertilizer was applied in two

Table 1: Average physico-chemical characteristics of soil in the experimental field.

Electrical conductivity (ds/m)	pH	Organic carbon (%)	N (%)	P (ppm)
2.2	7.2	0.58	0.06	12.6
K (ppm)	Clay (%)	Silt (%)	Sand (%)	Soil texture
256	26	49	25	Clay loam

splits up to 8–10 leaf stage. Water limitation was imposed by water withholding in R4-R6 growth stages as defined by Schneiter and Miller (1981). Relative water content (RWC), leaf temperature (LT) and leaf chlorophyll concentration (LCC) were measured at the end of flowering stage (R6). The upper most fully expanded leaves were used for measurement of RWC using RWC = 100 × (fresh weight − dry weight)/(turgid weight − dry weight). Turgid weight was determined after 24 h rehydration at 4 °C in a dark room with the leaf discs placed in a container with distilled water and dry weight determined after oven drying for 24 h at 80 °C. Leaf chlorophyll concentration was assessed using an SPAD-502 chlorophyll meter (SPAD-502, Minolta). The measurements being taken at upper, middle and lower part of the leaf and average of them was considered as leaf chlorophyll concentration. Following the harvest at physiological maturity (R9) seed yield and oil characteristics were analyzed.

Oil content was determined using soxhlet extractor and fatty acid profile was identifies by gas chromatography. Fatty acid methyl esters (FAMEs) were prepared from the oil samples according to the method of Savage et al. (1997) and the hexane layer in final solution that contained the FAMEs was separated by centrifugation. The FAMEs were analyzed by GC according to the method described by Azadmard-Damirchi and Dutta (2006). Data of the physiological traits and main fatty acids (palmitic, stearic, oleic and linoleic acids) were subjected to the line × tester analysis (Singh and Chaudhury 1985) followed that, genetic components including additive and non-additive genetic components, dominance and heritability values were estimated.

3 Results and discussion

3.1 Analysis of variance

According to the combined analysis of variance there were significant differences among the hybrids for all of the physiological traits and fatty acids except leaf temperature under water limited condition (Tables 2 and 3), which allowed further analysis by line × tester analysis method. Tyagi et al. (2020) also reported significant variability among sunflower genotypes considering oil content and major fatty acids. Under optimum irrigation the variances due to the lines and testers were significant for all of the traits except linoleic acid of lines and seed yield and oil content of testers. Under limited condition the lines were more variable for physiological traits while testers for all of the fatty acids. The higher variability among the testers provided reasonable wide genetic base needed for testing of the

Table 2: Analysis of variance for physiological traits and the fatty acids of sunflower under optimum irrigation.

Source of variation	DF	Seed yield	OC	RWC	LCC	LT	C16:0	C18:0	C18:1	C18:2
Year	1	489,103.4^{ns}	6.77^{ns}	7.0^{ns}	0.2^{ns}	0.8^{ns}	2.8**	0.1^{ns}	89.4**	40.7*
Replication/year	4	315,235.4	9.4	0.6	18.6	0.5	0.1	0.1	2.0	2.5
Hybrid	11	312,325.7**	8.0**	10.6**	22.5**	13.9**	1.2**	3.0**	63.3**	65.5**
Line	3	604,093.7**	18.1**	20.2**	33.5**	30.0**	0.5**	4.9**	5.3**	1.6^{ns}
Tester	2	130,243.2^{ns}	5.6^{ns}	9.3**	14.3**	11.6**	2.7**	3.9**	137.8**	153.7**
Line × Tester	6	227,135.9*	3.7^{ns}	6.2**	19.7**	6.5**	1.1**	1.8**	67.5**	68.0**
Year × Hybrid	11	373,884.2**	9.9**	1.1^{ns}	2.0^{ns}	0.6^{ns}	0.4**	1.4**	24.1**	27.8**
Year × line	3	110,909.1^{ns}	14.7**	0.5^{ns}	2.6^{ns}	0.5^{ns}	0.5**	1.5**	20.4**	22.9**
Year × tester	2	546,084.4**	6.8^{ns}	1.9^{ns}	2.5^{ns}	0.8^{ns}	0.5**	0.5**	21.6**	24.9**
Year × line × tester	6	447,971.7**	8.7**	1.2^{ns}	1.5^{ns}	0.6^{ns}	0.3**	1.7**	26.8**	31.2**
Error	44	83,914.6	2.2	0.8	4.9	4.9	0.1	0.0	0.4	1.0
Coefficient of variation (%)		10.9	3.4	1.0	6.0	8.2	4.3	3.7	3.1	1.5

ns, * and ** denote to the non-significant and significant differences at probability of 5 and 1 % of probability respectively. Oil content (OC), relative water content (RWC), leaf chlorophyll content (LCC), leaf temperature (LT), C16:0, C18:0, C18:1 and C18:2 are palmitic, stearic, oleic and linoleic acids respectively.

Table 3: Analysis of variance for physiological traits and the fatty acids of sunflower under water limited irrigation.

Source of Variation	DF	Seed yield	OC	RWC	LCC	LT	C16:0	C18:0	C18:1	C18:2
Year	1	52,488.0^{ns}	66.9*	2.8^{ns}	17.0^{ns}	76.5**	11.3**	2.0**	83.2**	82.8**
Replication/year	4	36,702.3	6.7	1.4	13.4	1.3	0.0	0.1	1.4	2.8
Hybrid	11	194,915.3**	6.4**	11.1**	25.3**	3.7^{ns}	2.1**	3.1**	63.9**	64.8**
Line	3	324,597.2**	16.6**	18.9**	45.4**	7.1*	1.7**	4.4**	1.3^{ns}	3.1^{ns}
Tester	2	158,205.4^{ns}	6.7**	3.1^{ns}	6.2^{ns}	1.3^{ns}	1.0**	3.1**	177.9**	166.8**
Line × Tester	6	142,310.9*	1.2^{ns}	9.9**	21.6*	2.8^{ns}	2.7**	2.5**	57.3**	61.6**
Year × Hybrid	11	63,321.3^{ns}	3.2**	1.0^{ns}	1.5^{ns}	0.4^{ns}	1.3**	3.1**	15.2**	18.9**
Year × line	3	16,820.9^{ns}	1.9^{ns}	2.8^{ns}	2.0^{ns}	0.1^{ns}	0.1^{ns}	2.7**	38.4**	29.8**
Year × tester	2	10,608.5^{ns}	6.4**	0.4^{ns}	0.0^{ns}	0.6^{ns}	1.9**	2.7**	8.1**	1.7^{ns}
Year × line × tester	6	104,142.4^{ns}	2.9*	0.3^{ns}	1.7^{ns}	0.6^{ns}	1.8**	3.4**	6.0**	19.3**
Error	44	56,645.2	1.0	1.2	8.5	2.5	0.1	0.0	1.1	1.2
Coefficient of variation (%)		12.8	2.5	1.6	7.5	6.2	3.4	2.4	5.5	1.6

ns, * and ** denote to the non-significant and significant differences at probability of 5 and 1 % of probability respectively.

lines. The variance due to the line × tester interaction was significant for all of the traits except oil content in both conditions and leaf temperature under limited irrigation, suggested the involvement of non-additive genetic effects on expression of fatty acids under optimum and water limited conditions. Variance due to the lines and testers is an indicator of general combining ability and provide a pre-estimate of additive gene action while variance due to the line × tester interaction is an indicator of specific combining ability and non-additive gene action (Kempthorne 1957). There were significant differences among the years for oil content, leaf temperature and all the studied fatty acids under water limited condition suggested that drought stress intensified the environmental effect of the years on these traits. The results displayed the importance of additive effects on inheritance of oil content in both conditions and on leaf temperature in water limited condition. Both additive and non-additive gene actions were involved in inheritance of the fatty acid contents.

3.1.1 Contribution of lines × testers on genetic variance

Relative contribution of lines, testers and their interaction effects on genetic variance of physiological traits and fatty acids of sunflower was estimated (Figure 1). Under optimum irrigation the lines (restorer lines) explained the bigger part of genetic variance for most of the traits as seed yield, oil content, RWC, leaf temperature and stearic acid, however contribution of the testers (male sterile lines) in variance of these traits were lower than the lines. Line × tester interactions were more important on variance of the remaining traits (Leaf chlorophyll concentration, palmitic, oleic and linoleic acids). Contribution of the lines in variance of two major fatty acids (oleic and linoleic acids) was negligible, on the contrary the effect of testers was considerable. In a similar study by Chahal et al. (2019) restorer lines explained most part of variability of oil content and fatty acid components of sunflower except palmitic acid content which male × female interaction was considerable for that.

Contribution of the lines in variance of seed yield, oil content, leaf chlorophyll concentration and leaf temperature were more than the other sources under water limited condition. The testes explained the most part of genetic variance for oleic acid content and like that optimum condition the lines didn't contribute in variance of oleic and linoleic acids. Line × tester interactions were more important concerning variance of RWC, palmitic, oleic and linoleic acids. Generally, the lines explained more variability of the physiological traits while testers and line × tester interaction effects more variability of the fatty acids. Contribution of the testers on variability of main oleic and linoleic acids increased considerably under water limited condition.

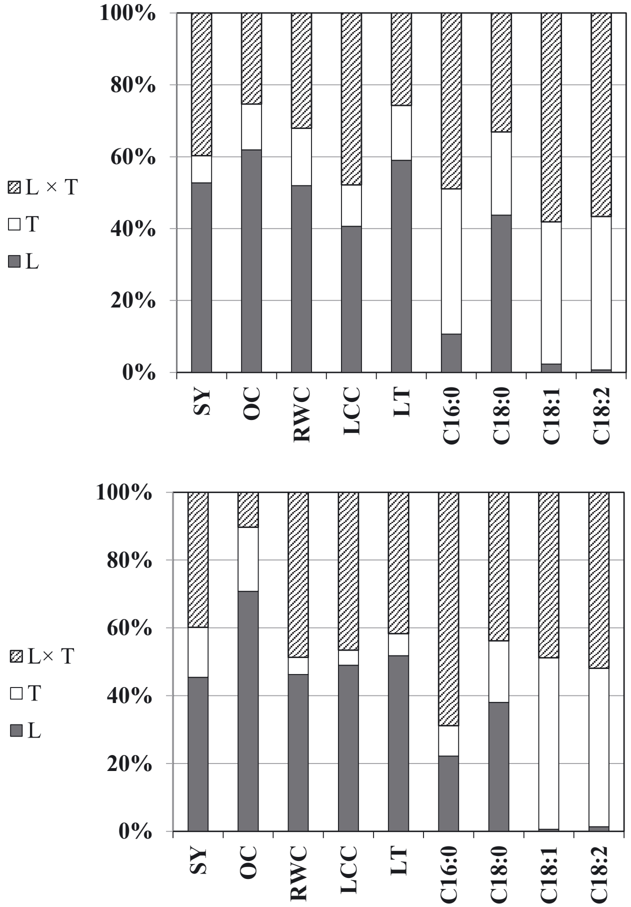

Figure 1: Relative contribution of different sources on genetic variance components of physiological traits and fatty acids of sunflower under optimum (above) and water limited conditions (down). The abbreviations are as: Seed yield (SY), oil content (OC), relative water content (RWC), leaf chlorophyll content (LCC), leaf temperature (LT), C16:0, C18:0, C18:1 and C18:2 are palmitic, stearic, oleic and linoleic acids respectively. L and T denote to the lines and testers respectively.

3.1.2 The fatty acids profile

The fatty acid composition of sunflower oil analyzed in optimum and water limited experiments. There were considerable differences among the experiments for unsaturated fatty acids. In both conditions linoleic acid constitute the most part of the oil; 65.6 % and 67.4 % in optimum and water limited conditions respectively

(Figure 2a), followed by mono-unsaturated oleic acid which constitute 21.7 % and 19.4 % of oil in optimum and water limited conditions respectively (Figure 2b). Oleic acid content decreased while linoleic acid content increased under water limited condition. Among the two saturated fatty acids; palmitic acid content increased (Figure 2c) while stearic acid content decreases under water limited condition (Figure 2d). There is evidence that environmental conditions affect fatty acid composition of sunflower (Demurin et al. 2000; Hassan et al. 2005). In accordance with the results of this study Baldini et al. (2000) reported that water stress causes a reduction in oleic acid content of sunflower oil. Petcu et al. (2001) also reported that palmitic and linoleic acids content of sunflower oil increases while stearic and oleic acids concentration decrease under drought condition. Flagella et al. (2002) reported a significant increase in stearic acid while an alternate decrease in palmitic acid content of sunflower oil under water stress. Ali et al. (2009) reported differential responses of sunflower genotypes to water stress with respect to the fatty acid contents. The changes of fatty acid content of sunflower under water limited condition may act as a protective or adaptability factor against drought condition. Differential changes of sunflower fatty acids under drought stress in different reports may be due to the different genotypes used in the studies and also imposition of drought stress at different growth stages.

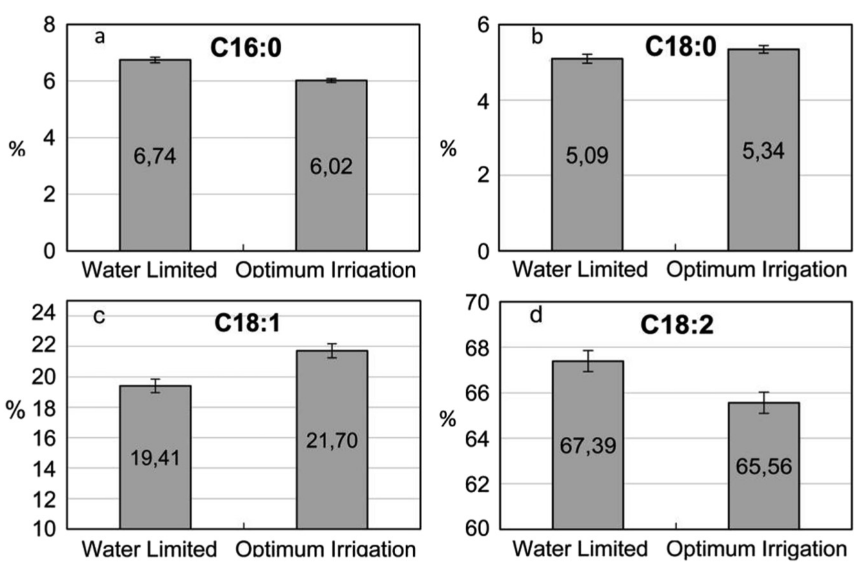

Figure 2: Major fatty acids profile of sunflower oil under optimum and water limited irrigation for palmitic acid (a), stearic acid (b), oleic acid (c) linoleic acid (d).

3.1.3 Genetic components

Estimation of genetic components revealed that oil content and leaf temperature are inherited by additive effects under optimum irrigation (Table 4). In most reports it is indicated that oil content of sunflower is governed mainly by additive gene action (Ghaffari et al. 2011; Leon et al. 2003; Miller et al. 1980; Singh et al. 1989) although the role of non-additive component is also reported (Hladni et al. 2006; Marinkovic 1993; Skoric et al. 2000). This made it possible to improvement of sunflower oil content through selection in the past (Skoric 2012). Oleic and linoleic acids content were under control of only non-additive gene action which is in accordance with numerous reports (Fernandez-Martinez et al. 1989; Fick 1984; Perez-Vich et al. 2002a; Skoric et al. 1978; Urie 1984), However Joksimovic et al. (2006) reported prevalence of additive and non-additive gene action in inheritance of oleic and linoleic acids contents respectively. Seed yield, RWC, leaf chlorophyll concentration, palmitic and stearic acid contents were under control of both additive and non-additive gene action. Involvement of both additive and non-additive variances in inheritance of seed yield in sunflower has been reported in various studies (Goksoy et al. 2002; Kaya 2004). Involvement of non-additive (Darvishzadeh et al. 2014) in inheritance of RWC has been reported in sunflower. Miller and Vick (1999) reported that low palmitic and stearic acids content is inherited by additive factors. Ivanov et al. (1988) also reported more contribution of additive effects on expression of high palmitic acid content in sunflower. According to the similar studies non-additive gene action was more important in inheritance of palmitic acid (Chahal et al. 2019; Ortis et al. 2005; Sakthivel 2003) and stearic acid (Madhavilatha et al. 2004; Ortis et al. 2005). This information expresses more effect of non-additive gene action in inheritance of main fatty acids of sunflower under optimum water supply and imply to the fact that hybrid breeding is more effective in improvement of these characteristics in sunflower.

Under water limited condition oil content, leaf temperature and stearic acid content were under control of only additive effects but RWC, leaf chlorophyll concentration and linoleic acid content were inherited only by non-additive factors (Table 4). Due to the nature of gene action which indicated involvement of non-additive effects in inheritance of RWC in this study direct selection could not be efficient in improvement of this trait but cross breeding is necessary to expression and exploitation of genetic variability of RWC in sunflower. Both additive and non-additive gene actions were involved in inheritance of seed yield, palmitic and oleic acids content. Involvement of non-additive gene action in inheritance of seed yield, RWC and chlorophyll content under drought stressed condition has been reported in sunflower (Darvishzadeh et al. 2014). Ghaffari and Shariati (2018) also reported that

Table 4: Genetic components for physiological characteristics and fatty acids of sunflower.

	SY	OC	RWC	LCC	LT	C16:0	C18:0	C18:1	C18:2
Optimum irrigation									
V(A)	26,672.87*	1.55**	1.62**	0.79**	2.72**	0.09*	0.48**	0.78^{ns}	1.84^{ns}
V(NA)	47,740.43*	0.51^{ns}	1.82**	4.92*	0.56^{ns}	0.34**	0.60**	22.34**	22.33**
Dominance	1.89	0.81	1.50	3.52	0.64	2.68	1.58	7.58	4.93
h2b	0.47	0.49	0.82	0.54	0.40	0.86	0.97	0.98	0.96
h2n	0.17	0.37	0.39	0.07	0.33	0.19	0.43	0.03	0.07
Water limited									
V(A)	18,874.37**	1.99**	0.20^{ns}	0.80^{ns}	0.26*	0.10*	0.23**	6.16*	4.44^{ns}
V(NA)	28,555.23*	0.06^{ns}	2.92**	4.37*	0.13^{ns}	0.87**	0.83^{ns}	18.71**	20.14**
Dominance	2.46	0.35	7.67	4.67	1.40	4.18	3.77	3.49	4.26
h2b	0.40	0.51	0.72	0.36	0.09	0.94	0.99	0.95	0.95
h2n	0.10	0.48	0.02	0.03	0.05	0.10	0.12	0.13	0.09

ns, * and ** are insignificant and significant differences in 5 and 1 % of probability respectively. V(A) and V(NA) denote the additive and non-additive variances respectively. The abbreviations are as: Seed yield (SY), oil content (OC), Relative water content (RWC), leaf chlorophyll content (LCC), leaf temperature (LT), C16:0, C18:0, C18:1 and C18:2 are palmitic, stearic, oleic and linoleic acids respectively. L and T denote to the lines and testers respectively.

oil content of sunflower is inherited by additive effects while seed yield by both additive and non-additive gene action under drought stressed condition. As the best of our knowledge there are no study concerning fatty acid inheritance in sunflower under water limited condition. The results of this study showed that the nature of gene action is similar for seed yield, oil content, leaf temperature and palmitic and linoleic acids in both optimum and water limited conditions; however there were differentiate response for RWC, Leaf chlorophyll concentration, stearic and oleic acids content. Beside agronomical characteristics of sunflower which are influenced by water availability (Ghaffari et al. 2012; Kazemeini et al. 2009), there are numerous reports indicate that the genetic nature of characteristics associated with oil quality is complicated due to the strong influences of environmental effects (Baldini et al. 2000; Hassan et al. 2005; Joksimovic et al. 2001, 2006). According to the results of this study selection of desirable genotypes could be efficient for improvement of stearic acid content under water limited condition while for improvement of palmitic and two major important fatty acids of sunflower; oleic and linoleic acids content, hybrid breeding is suggested for expression of desirable genotypes with optimum fatty acid profile. Venn diagram differentiated gene action for the studied traits in the two conditions (Figure 3). Oil content and leaf temperature were under control of only additive and linoleic acid content was governed by only non-additive effects in both optimum and water limited conditions.

Seed yield and palmitic acid content were inherited by both additive and none additive gene action in the both conditions (Table 4). The other traits were inherited differentially; RWC, leaf chlorophyll concentration and stearic acid content were controlled by both additive and non-additive gene action in optimum but by non-additive factors in the case of RWC and leaf chlorophyll concentration and by

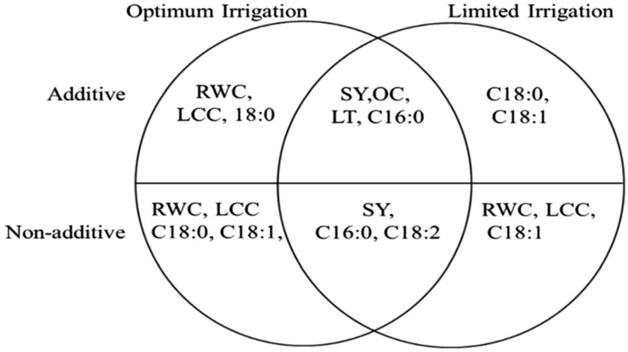

Figure 3: Venn diagram for discriminating gene action for physiological traits and fatty acids of sunflower under optimum and water limited condition. Abbreviations are as: Seed yield (SY), oil content (OC), relative water content (RWC), leaf chlorophyll concentration (LCC) and leaf temperature (LT).

additive effects in the case of stearic acid content under water limited condition. Oleic acid content was under control of non-additive factors in optimum irrigation, while it was under control of both additive and non-additive gene action under water limited condition. According to these results selection-based methods is suggested for improvement of oil content and leaf temperature and hybrid breeding for improvement of linoleic acid content in both optimum and water limited conditions. Selection-based methods followed by hybrid breeding are suggested for improvement of seed yield, RWC, Leaf chlorophyll concentration, palmitic and stearic acids content and hybrid breeding for improvement of oleic acid content. Under water limited condition selection-based methods followed by hybrid breeding are suggested for improvement of seed yield, palmitic and oleic acids content and hybrid breeding for improvement of RWC, Leaf chlorophyll concentration and linoleic acid content.

3.1.4 Dominance ratio

Dominance ratio was more than unit for seed yield, RWC, leaf chlorophyll concentration, and all fatty acids under optimum irrigation (Table 4), suggesting involvement of over dominance in inheritance of these traits. Over dominant gene action was observed for all of the traits except for oil content under water limited condition. Over dominant gene action has been reported for many traits of sunflower as for seed yield and oil content (Gangappa et al. 1997; Goksoy et al. 2002). Involvement of dominance in inheritance of oleic acid (Fernandez-Martinez et al. 1989; Fick 1984; Perez-Vich et al. 2002a; Skoric et al. 1978; Urie 1984; Velasco et al. 2000) and linoleic acid (Georgieva and Hristova 1975) has been reported, while partial dominance reported in the case of palmitic and stearic acids (Ivanov et al. 1988; Perez-vich et al. 1998), which are in accordance with the results of this study. Regarding the over dominant gene action in expression of the fatty acids under optimum and water limited conditions hybrid breeding is suggested for exploiting of heterosis and improvement of the sunflower main fatty acids.

3.1.5 Heritability

Broad sense heritability values were considerably high for RWC and all of the studied fatty acids under optimum irrigation (Table 4). The values for narrow sense heritability were low for most of the oil features except for oil content, RWC and stearic acid content in this condition suggesting that non-additive gene effects play a major role in inheritance of fatty acid components of sunflower oil. These results are in accordance with Chahal et al. (2019) who reported intermediate narrow sense heritability for oil content and stearic acid content while lower values for palmitic, oleic and linoleic acid.

Estimates for broad sense heritability values under water limited condition was almost high for all of the fatty acids however the values for narrow sense heritability were low except for oil content (Table 4). These results indicated that, additive effects had lower impact than that of non-additive effects on expression of physiological traits and major fatty acids of sunflower under optimum and water limited conditions, which in turn cause lower narrow sense heritability for these traits, so higher effects of environmental is concluded. The additive variance is the main determinant of the observable genetic properties of the population and selection response (Falconer and Mackay 1996). Relative higher heritability and predominately additive gene action for oil content in both conditions facilitate selection in early generations of inbreeding and cultivar development (Miller and Fick 1997), while lower values for oleic and linoleic acid indicate the affectability of these traits by environmental conditions and lower efficiency of selection for improvement of them. It is concluded again that hybrid breeding is necessary to exploiting of heterosis in improvement of sunflower fatty acids.

3.1.6 Comparison of genetic components in two irrigation treatments

Comparison of genetic components revealed a differentiate response of sunflower fatty acids to optimum and water limited conditions. In both conditions additive and non-additive variances for palmitic and stearic acids were negligible while variances for non-additive variance due to oleic and linoleic acids were considerably high (Figure 4a and b).

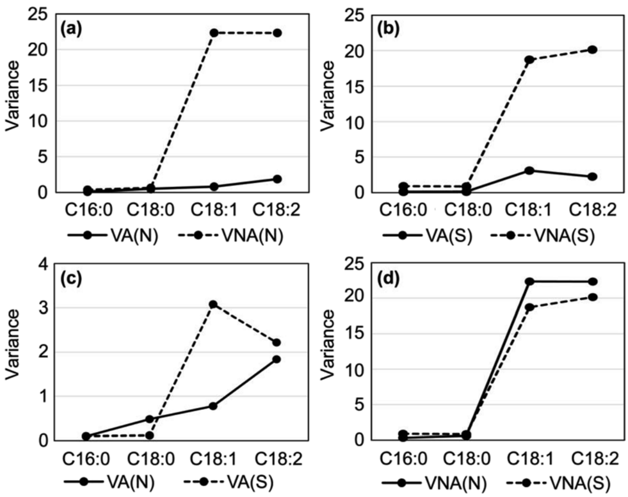

Figure 4: Comparison of genetic components for sunflower fatty acids in optimum (a) and water limited conditions (b), comparison of additive (c) and non-additive variances (d) for fatty acid inheritance in optimum and water limited conditions. V(A), VNA denote to the additive and non-additive variances respectively. N and S denote to the optimum and water limited conditions respectively.

Under water limited condition additive variances due to the oleic and linoleic acids were more than optimum irrigation and especially there was a considerable difference between additive variance of oleic acid under two conditions (Figure 4c). In spite of additive variance, non-additive variances for oleic and linoleic acid contents in optimum irrigation were clearly more than water limited condition (Figure 4d). So the clear response was increasing of additive variance (Figure 4c) while reduction of non-additive variances for both oleic and linoleic acid contents under water limited condition (Figure 1d).

As indicated before, environmental conditions affect fatty acid composition of sunflower (Demurin et al. 2000; Hassan et al. 2005) and these changes could be a protective or adaptability response to drought condition. It is concluded that water limitation makes it possible to express more variability in additive variance for oleic acid which in turn increases heritability of this fatty acid under water limited condition. According to the results of this study due to the involvement of both additive and non-additive effects in inheritance of oleic acid under water limited condition it is possible to impose selection followed by crossing of suitable parent lines to expression of heterosis for improvement of this fatty acid in sunflower. Because selection in the target environment increases the selection efficiency (Ceccarelli 1987), so due to the expression of higher additive variance of oleic acid in water limited condition, selection in this condition could be efficient in improvement of oleic acid content.

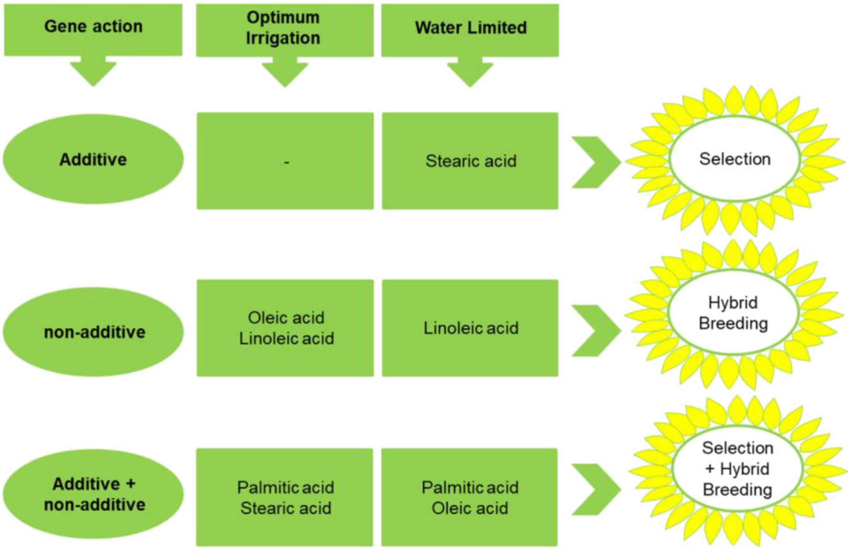

Figure 5: Summary of gene action and suggested breeding strategy for sunflower fatty acids under optimum and water limited conditions.

4 Conclusions

According to the results of this study oleic and stearic acids content decreased while linoleic and palmitic acids content increased under water limited condition. The changes of fatty acid content of sunflower under water limited condition may act as a protective or adaptability factor against drought condition. Higher expression of oleic acid content in water limited condition could be aroused from activation of the related drought responsive genes (Oncel et al. 2000; Shao et al. 2008; Skoric 2009). Palmitic acid content was under control of both additive and non-additive gene actions and linoleic acid content by non-additive gene action in both optimum and water limited conditions. Stearic acid content was controlled by both additive and non-additive effects in optimum but by additive effects under water limited conditions. Oleic acid content was governed by non-additive factors in optimum, while by both additive and non-additive effects in water limited conditions. The results indicated that oil content and leaf temperature are inherited by additive and seed yield by additive and non-additive effects in both conditions. Relative water content and chlorophyl content were controlled by both additive and non-additive effects under optimum but by non-additive effects in water limited condition. The results of this study showed that the nature of gene action is similar for seed yield, oil content, leaf temperature and palmitic and linoleic acids in both optimum and water limited conditions, however there were differentiate response for RWC, leaf chlorophyll concentration, stearic and oleic acids.

Additive variance was increased while non-additive variance reduced for oleic and linoleic acids content under water limited condition. It is concluded that water limitation makes it possible to express more variability in additive variance for oleic acid which in turn increases possibility for selection of inbred lines with higher content of oleic acid. As yield improvement for stressed conditions requires selection under target condition (Ceccarelli 1987) due to the expression of higher additive variance for oleic acid content in water limited condition, selection in this condition may enhance the selection efficiency in improvement of this fatty acid. Lower values of heritability for oleic and linoleic acids indicated affectability of these traits by environmental effects and lower efficiency of selection for improvement of them in both conditions. According to the results of this study hybrid breeding is suggested for improvement of main fatty acids of sunflower under optimum irrigation. Under water limited condition hybrid breeding is suggested for improvement of oleic, linoleic and palmitic acids content while selection-based methods for improvement of stearic acid content (Figure 5).

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