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Study of Half-Sib Families of Ajowan (*Carum copticum* L.) Provides New Insights into the Heritability of Some Important Traits

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ABSTRACT

We selected ten Ajowan parents (*Carum copticum* L.) from a genetically diverse population to evaluate gene effects, heritability, and correlations among their morphological traits. We poly-crossed the parents to produce half-sib genotypes. The evaluations comprised the number of days to flowering, plant height, number of fertile branches, number of umbrellas per plant, number of seeds per umbel, seed yield per plant, harvest index, essential oil percentage, and essential oil yield. Parents and polycross progeny seeds grew in a randomized complete block design with three replications at the University of Tehran, 2015-2017. The results showed broad-sense heritability ranged from 0.64 to 0.96 in parents and their progenies. Narrow-sense heritability appeared through the regression of progenies on the parents (h^2_{po}) and via progeny analysis (h^2n), suggesting that additive genes control these traits. The correlation of seed yield with plant height, number of fertile branches, number of umbrellas per plant, and number of seeds per umbel were positive and significant. The results indicated a significant negative correlation between thymol and γ- terpinene in parents and half-sib families. We reported wide variations and high heritability for most of the evaluated traits in the ajowan populations that can improve seed and essential oil yields.

Introduction

Ajowan (*Carum copticum* L.) is an open-pollinated annual herbaceous plant with grayish-brown fruits or seeds. It has an erect structure, is aromatic, glabrous, or minutely pubescent, and branched with striate stems and white flowers. This plant species can grow up to 90 cm tall. It is native to Egypt and is cultivated in India, Iran, Pakistan, Afghanistan, and Iraq (Minija, 2002). Its fruits or seeds contain 2-4% brown color essential oil known as Ajowan oil, with thymol as the main constituent (35-60%) (Khajeh et al., 2004), which is a potent germicide and is antispasmodic, antifungal, antimicrobial, and aromatic for perfumery and the toothpaste industry (Mahboubi and Kazempour, 2011). Ajowan is used traditionally as a stimulant, carminative, flatulence, diarrhea, abdominal pain, atonic dyspepsia, and piles. Its natural range falls into severe cold and rainfall below 450 mm/year (Hejazian, 2006).

Since Ajowan plants are open-pollinated and sexually propagated, having superior-bred cultivars with enhanced heterogeneous populations can best trigger improvement. To select parents and breed a variety, information on the individual general combining ability (GCA) is desirable and derivable from the analysis of half-sib progenies. It may emanate from covariance estimates between parents and HS progenies (Falconer and Mackay, 1996). Poly-cross and open-pollinated mating are beneficial as they help predict genetic advancement from selections. Thus, it is necessary to obtain information about heritability, correlations, the effects of genotype and environment, and their interactions (Mather and Jinks, 1982).

Heritability estimates indicate the expected response to selection in a segregating population

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and are beneficial in designing an effective breeding program. Researchers may reach heritability estimates from parental material (h^2_b), progeny analyses (h^2_n), and parent-offspring regressions (h^2_{po}). The heritability of different agronomic traits has been estimated in many medicinal plant species (Akbari et al., 2019; Niazian et al., 2017; Izadi et al., 2017). The magnitude of these estimates for this plant species has varied among the traits measured, with lower estimates for characteristics under complex genetic control like yield than for more simple-inherited features like plant height (Dalakani et al., 2012; Fadaei Heidari et al., 2016; Sadati et al., 2016).

The correlation between characters can indicate whether the selection of one character will affect another. In addition, researchers may practice selecting genotypes while considering highly heritable features associated with more complex traits such as performance. Correlations among traits have reached estimates in many medicinal plants. In a relevant study, Niazian et al. (2017) estimated phenotypic correlations among several features measured in Ajowan ecotypes. They reported that essential oil yield correlated with the number of umbel per plant and dry matter yield. Seed yield positively correlated with the number of branches, harvest index, and plant height.

There is little information on the fundamentals and methods for Ajowan crossbreeding. This research estimated the total genetic variance, broad-sense and narrow-sense heritability, and phenotypic correlation among different quantitative traits in half-sib Ajowan families.

Material and Methods

Plant material

The ten parental plants (Table 1) in this study were from 23 different Ajowan ecotypes (Mirzahosseini et al., 2017) obtained from the gene bank of the Research Institute of Forests and Rangelands (RIFR). The parental ecotypes were selected based on simultaneous flowering time and similar height. Seeds of 10 selected parents were spaced-planted in a Latin square design with five replications. Polycross seeds were obtained during the spring of 2015. Polycross seeds and parental seeds were grown and evaluated during the spring of 2016 according to a randomized complete block design with three replications. Each plot was a 5 m row containing ten plants 40 cm apart. We measured eight plant traits (Table 2) in 2016-2017.

This experiment was located at an experimental field, College of Aburaihan, University of Tehran, 2015-2017. The plants grew on a Typic Haplargid soil with a clay loam texture, pH 7.5, and 1% organic matter. Fertilizers for soil enrichment were 200 Kg N ha-1 and 200 Kg P ha-1 before sowing.

Table 1. Ajowan family codes and their origin.

	code	origin	Latitude	Longitude	Elevation
1- Shiraz	12313	Fars	29° 33'N	52° 40' E	1472m
2- Arak	14492	Markazi	34°00'N	49°40'E	1737m
3- Beshruye	38913	Khorasan	28°32'N	54°26'E	879m
4- Shahediye	37251	Yazd	31°46'N	54°36'E	1193m
5- Ardebil	1085	Ardebil	38°15'N	48°18'E	1352m
6- Karaj	906	Alborz	35°48'N	51°00'E	1312m
7- Qom	7893	Qom	34°40'N	51°0'E	936m
8- Sarbishe	37477	Khorasan	32°30'N	59°40'E	1817m
9- Hamedan	14322	Hamedan	34°52'N	48°32'E	1818m
10- Yazd	31831	Yazd	31°46'N	54°36'E	1222m

Table 2. Abbreviation and unit of measurement for the ten plant traits in 2015 and 2017.

character	Abbreviation	Unit of measurement
Number of days to flowering	NDF	Day
Plant height	PH	Cm
Number of branches	NFB	
Number of umbrellas per plant	NUP	
Number of seeds per umbel	NSU	
Seed yield per plant	SYP	g
Harvest index	HI	
Essential oil percentage	EOP	
Essential oil yield	EOY	g

Essential oil extraction

The harvested samples were from the inflorescence stage. They were dried and powdered by an electrical grinding mill. Fifty g of each sample group was hydro-distilled (500 ml) in a Clevenger-type apparatus for four hours in three replications (Niazian et al., 2017; Noori et al., 2017). The essential oil extraction followed a method recommended by the British Pharmacopoeias (British Pharmacopoeia 1988). The accumulated oil was dried over anhydrous sodium sulfate and stored at 4 °C.

Gas chromatography-mass spectrometry analysis (GC/MS)

Essential oil components of seven ecotypes (parents and progeny) with higher yield were detected using Gas Chromatography. The GC/MS analysis was performed on a GC/MS apparatus using the HP (Agilent Technology) 7890 Network GC System gas chromatograph connected to a mass detector (5973 Network Mass Selective Detector). The gas chromatograph was equipped with an HP-5MS capillary column (fused silica column, 30 m × 0.25 mm i.d., Agilent Technologies) and an EI mode with ionization energy of 70 eV, mass range of 40-460 amu, and scan time of 0.4 s. One µl of diluted samples (1/100; v/v, in methanol) was manually injected in splitless mode. The interface temperature was 290 °C. Helium gas was selected as a carrier gas with the same flow rate (1 ml min^{-1}) for GC/FID. The oven temperature was programmed from 60 to 250 at 4 °C min^{-1} using helium as the carrier gas (1.1 ml min^{-1}). The oil compounds were identified by comparing their retention indices (RI), mass spectra fragmentation with NIST (National Institute of Standards and Technology) Adams library spectra, Wiley 7 n.1 mass computer library, and with those reported in the literature (Adams 2007).

Data analysis

Analysis of variance was performed to examine differences among the genotypes, and to estimate the variance components, using the general linear model (GLM) of SAS (SAS Institute, Inc. 1987). The variance components, genetic coefficient of variation, correlation, and broad-sense heritability were computed as suggested by Falconer (1996). Half-sib families were evaluated in a randomized complete block design with an equal number of plants in each plot and the data were obtained on all individual plants with the family variance component (σ^2_F) as the genetic variance among HS families, based on equation 1:

$$\sigma^2{}_F = cov\ (HS) = \frac{1}{4}\sigma^2{}_A$$

The within-plot variance is estimable in this analysis and is composed of the remainder of total genetic variance and within-plot environmental variance.

Broad-sense heritability (h^2_b) and narrow-sense heritability (h^2_n) were calculated based on parental mean values and family mean values, respectively. Estimates of genetic components from parental analyses were used for calculating the h^2_b. Estimates of genetic variance components from progeny analyses were used for calculating the h^2_n.

Broad-sense (h^2_b) and narrow-sense (h^2_n) were calculated based on equation 2 and 3, respectively (Majidi et al., 2009).

$$h^2{}_b = \frac{\sigma^2{}_{gp}}{(\sigma^2{}_{gp} + \frac{\sigma^2{}_{ep}}{r})}$$

$$h^2{}_n = \frac{\sigma^2{}_{gF}}{(\sigma^2{}_{gF} + \frac{\sigma^2}{r} + \frac{\sigma^2{}_w}{rn})}$$

Where σgp, σgF represents variance components in parents and families, respectively; σep represents residual mean squares in the ANOVA for parental genotypes and σ^2, σ^2_w represent replication × HS-family interaction (error) and variance within HS-families, respectively. The r and n show the number of replications and number of individual plants per plot, respectively. The linear regression coefficient between parent and half-sib progeny is an estimate of narrow-sense heritability (h^2_{po}) which is multiplied by two (Falconer, 1989).

Phenotypic correlation was obtained as described by Falconer and Macky (1996). General combining ability was calculated as the deviation of each half-sib progeny from the whole population (Wricke and Weber, 1986).

The genotypic coefficient of (CVg) was calculated as

$$CV_g = (\frac{\sigma_g}{\mu}) \times 100$$

σg is the standard deviation of the genotypic effect and μ the phenotypic mean (Falconer and Macky, 1996).

Results

Genetic variation and heritability

There were significant differences among parents and half-sib families regarding all evaluated plant traits (Table 3). The highest and lowest seed-yielding half-sib families were Hamedan and Shahediyeh, respectively. In parental ecotypes, Yazd had the highest seed yield. Ardebil had the maximum and Hamedan the minimum essential oil yield in half-sib families (Table 4).

The range of NDF in half-sib families was 66 (Sarbishe) to 88 (Karaj) days (data not shown). Yazd, Ardebil, Karaj, and Sarbishe families had the highest and the lowest PH, respectively. The lowest and the highest HI were related to Karaj and Qom, respectively (Table 4).

Table 3. Analysis of variance for agro-morphological traits in parents and half-sib Ajowan progenies.

	Mean square			
Trait	Parents	Error	half-sib families	Error
NDF	168.9**	6.43	95.57**	4.89
PH	282.73**	40.94	386.44**	41.89
NFB	2.87**	0.32	2.65**	0.35
NUP	921.5**	13.3	1263.57**	16.95
NSU	29.2**	7.8	37.86**	12.32
SYP	40.08**	5.15	29.91**	4.3
HI	32.42**	6.06	23.74**	8.49
EOP	1.62**	0.001	6.31**	0.027
EOY	329.92**	40.55	599.32**	53.31

*; **: significant at p<005 p<001 respectively.

NDF, Number of days to flowering; PH, Plant height; NFB, Number of fertile branches; NUP, Number of umbrellas per plant; NSU, Number of seeds per umbel; SYP, Seed yield per plant; HI, Harvest index; EOP, Essential oil percentage; EOY, Essential oil yield.

Table 4. Genetic coefficient of variation, broad-sense heritability, and narrow-sense heritability of plant traits in parents and half-sib Ajowan families.

Plant trait	Genetic coefficient of variation (%)		Broad-sense heritability (%)	Narrow-sense heritability (%)	Parent-offspring regression (h^2_{nop}%)
	Half-sib	parent			
NDF	7.03	9.18	96.19	82.05	69.59
PH	11.13	12.6	85.5	70.48	48.20
NFB	8.5	9.9	84.9	60.36	32.86
NUP	22.6	24.3	78.52	53.68	37.53
NSU	8.1	8.9	73.05	62.25	41.56
SYP	11.7	25.2	87.57	39.54	22.50
HI	12.96	20.04	81.14	52.39	39.70
EOP	28.98	30.4	89.01	68.14	37.24
EOY	27.53	27.9	94.14	70.32	40.66

NDF, Number of days to flowering; PH, Plant height; NFB, Number of fertile branches; NUP, Number of umbrellas per plant; NSU, Number of seeds per umbel; SYP, Seed yield per plant; HI, Harvest index; EOP, Essential oil percentage; EOY, Essential oil yield.

Table 5 shows the genetic coefficient of variation, broad-sense heritability, and narrow-sense heritability in parents and half-sib families. EOP (30.4%, 28.99%) and EOY (27.9%, 27.53%) had the highest genetic coefficient of variation in parents and half-sib families. NDF, EOP, EOY, and PH in both parents and offspring had the highest h^2_b and h^2_n, showing that genetic factors control this trait. The large amount of h^2_n in these traits showed that additive factors are in control, and selection would effectively improve these plant traits. In parents, NSU and NUP (73.05 and 78.52, respectively), and in half-sib families, HI and NSU (64.25 and 67.41, respectively) had the lowest h^2_b value. NSY had the lowest amount of h^2_n in parents and half-sib families, showing that non-additive factors control this trait.

Narrow-sense heritability based on parent-offspring regression appeared in Table 5. Narrow-sense heritability for NDF and PH was high (more than 50%) but moderate for NSU, HI, and NUP. The large amounts of h^2_n reveal that breeding for these traits is effective.

Essential oil composition

The EO components of ecotypes varied in parents and progenies (Table 6). For parents, Ardebil (53%) and Qom (53%) ecotypes had the highest thymol, and Yazd and Arak had the highest γ-terpinene in the essential oil (Table 6). Previous studies (Mirzahosseini et al., 2017; Davazdahemami et al., 2011; Dehghan Abkenar et al., 2006; Zarshenas et al., 2014) showed that three substances, i.e., thymol, γ-terpinene, and p-cymene are the main components of Ajowan essential oils, comprising between 90 and 97% of EO components, as demonstrated in this research. In half-sib families, the Arak and Ardebil ecotypes had 73% and 42% as the highest and lowest percentages of thymol in essential oils, respectively. The Ardebil ecotype, with 25%, and the Arak ecotype, with 9%, had the maximum and minimum amounts of γ-terpinene in the essential oil. As for another prominent component, the p-cymene in Ardebil (19%) and Arak ecotype (9%) had the highest and lowest amounts, respectively. The methyl chavicol in the essential oils of Ardebil and Boshruye ecotypes were 8.47 and 7.77, respectively. The beta-pinene in the EOs of Ardebil, Boshruye, Arak, and Yazd ecotypes was more than 1%. Other compounds were less than 1% of the total essential oil.

Correlation

SYP correlated with PH, NFB, NUP, NSU, HI, EOP, and EOY positively, with significant values (Table 7). EOY also positively correlated with NFB, NUP, NSU, SYP, HI, and EOP. Meanwhile, PH, NFB, and NFU significantly correlated with NDF. The correlation between NFB and other evaluated traits was positive and significant, except for NUP. There was a significant correlation among NUP and SYP, EOP and EOY. The correlation between NSU and other traits was positive and significant, except for PH and NUP (Table 7). Correlation coefficients of plant traits between the parents and offspring were insignificant for most plant traits, except for NDF and PH (Table 8).

General combining ability

The general combining ability of traits for ten half-sib families became apparent (Table 9). GCA for NDF was the highest in Karaj (8.53) and the lowest in the Sarbishe family (-10.8). Yazd and Sarbishe families had the highest and lowest GCA regarding pH, respectively. The range of GCA for NFB was 1.07 (Yazd) to -1.92 (Sarbishe), and for NUP ranged from 24.47 (Sarbishe) to -26.53 (Shiraz). The GCA for NSU varied from 5.76 (Hamedan) to -6.5 (Sarbishe). Ardebil (22.95) and Sarbishe (-14.13) had the highest and lowest GCA for EOY, respectively. Ardebil, Hamedan, and Yazd families had positive GCA for most of the evaluated traits and can assist in breeding new varieties.

Table 5. Mean comparison of traits in parents (P) and offspring (O) obtained from poly-cross in ten ecotypes of Iranian Ajowan.

	ndf		ph		nfb		nup		nsu		syp		hi		eop		eoy	
	P	O	P	O	P	O	P	O	P	O	P	O	P	O	P	O	P	O
Shiraz	72^{d}	73^{e}	86^{b}	88^{bc}	10^{ab}	10^{b}	79^{d}	64^{e}	33^{bcd}	39^{a}	11^{c}	15^{cd}	15^{ab}	20^{ab}	5^{a}	8^{a}	35^{bcd}	67^{ab}
Arak	71^{d}	74^{e}	845^{b}	94^{bc}	9^{c}	11^{ab}	86^{c}	98^{abc}	28^{d}	35^{abc}	13^{bc}	18^{abc}	18^{a}	17^{bc}	42^{abc}	4^{e}	425^{abc}	41^{ef}
Beshruye	74^{d}	76^{de}	88^{b}	96^{a}	8.6^{c}	9^{cd}	94^{b}	102^{b}	31^{cd}	31^{bc}	16^{ab}	17^{abc}	17^{a}	17^{bc}	5^{b}	5^{d}	47^{ab}	48^{cde}
Shahediye	83.6bc	82bc	86.43b	90^{bc}	9^{bc}	10^{b}	44^{e}	50^{f}	32^{bcd}	36^{ab}	6^{d}	16^{bcd}	8^{c}	15^{bc}	4^{e}	5^{d}	13^{e}	35^{ef}
Ardebil	87^{ab}	82^{bc}	101^{a}	108^{a}	10^{ab}	11^{a}	95^{b}	100^{bc}	36^{abc}	35^{abc}	17^{ab}	20^{ab}	18.3^{a}	20^{ab}	3.3^{f}	6^{b}	32^{cd}	72^{a}
Karaj	91^{a}	88^{a}	103^{a}	110^{a}	10^{abc}	11^{a}	100^{b}	93^{c}	36^{abc}	39^{a}	15^{bc}	16^{cd}	14^{ab}	14^{c}	3.79^{e}	4^{e}	34^{cd}	39^{ef}
Qom	82^{c}	78^{cd}	86^{b}	89^{bc}	9^{c}	10^{b}	82^{cd}	76^{d}	39^{a}	36^{abc}	13^{bc}	16^{cd}	15.25^{ab}	23^{a}	3.09^{g}	5d	32^{cd}	45^{de}
Sarbishe	71^{d}	66^{f}	83^{b}	82^{c}	7^{d}	8^{d}	79^{d}	115^{a}	33^{bcd}	29^{c}	11^{c}	13^{d}	12^{bc}	17bc	4.29d	6^{b}	29.1d	59abc
Hamedan	87^{ab}	81^{bc}	105^{a}	92^{bc}	11^{a}	10^{b}	86^{c}	110^{a}	37^{ab}	42^{a}	14^{bc}	21^{a}	14^{ab}	17bc	4.28d	2f	36.7bcd	28f
Yazd	82^{c}	81^{bc}	106^{a}	118^{a}	10^{ab}	11^{a}	109^{a}	95^{bc}	32^{bcd}	36^{ab}	19^{a}	17^{abc}	17^{a}	14^{bc}	4.49^{c}	5^{d}	52^{a}	56^{bcd}

The presence of common letters between the data in each column indicates no significant difference.
NDF, Number of days to flowering; PH, Plant height; NFB, Number of fertile branches; NUP, Number of umbrellas per plant; NSU, Number of seeds per umbel; SYP, Seed yield per plant; HI, Harvest index; EOP, Essential oil percentage; EOY, Essential oil yield.

Table 6. Chemical composition of essential oils of parents and half-sib Ajowan families.

Ecotype	thymol		γ-terpinene,		p-cymene		Methyl chavicol		Beta pinene		Beta Myrcene		Total	
	parent	Half-sib	parent	Half-sib	parent	Half-sib	parent	Half-sib	parent	Half-sib	parent	Half-sib	parent	Half-sib
Arak	47.00[b]	73.28[a]	32 [a]	9.62 [b]	17 [a]	9.39 [b]	0.63 [b]	3.52[a]	0.74 [a]	1.07[a]	0.63 [a]	0.31[a]	98 [a]	97.19[a]
Boshruye	50.00 [a]	51.70[a]	26 [a]	21.24[b]	16 [a]	13.70[b]	-	7.77	4.64[a]	1.33[a]	0.35[a]	0.78[a]	96.99[a]	96.52[a]
Ardebil	53.00[a]	42.00[b]	26.00[a]	25.08[a]	18.00 [a]	19.00[a]	-	8.46	0.17[b]	1.31[a]	0.35[a]	0.78[a]	97.52[a]	96.64[a]
Karaj	50.00[b]	61.04[a]	30.00[a]	17.59[b]	17.00[a]	14.28[b]	0.63[a]	1.25[a]	0.61[a]	0.72[a]	0.35[a]	0.62[a]	98.59[a]	95.50[b]
Qom	53.00[b]	60.34[a]	26.00[a]	15.77[b]	17.00[a]	16.96[a]	0.59 [a]	2.44[a]	0.77[a]	0.95[a]	0.51[a]	0.59[a]	97.87[a]	97.05[a]
Sarbishe	48.00 [b]	59.62[a]	24.00[a]	17.92[b]	22.00[a]	15.30[b]	0.50[a]	2.43[a]	3.06[a]	0.78[b]	-	-	97.56[a]	96.05[b]
Yazd	41.00[a]	53.59[b]	33.00[a]	19.11[b]	20.00[a]	17.47[b]	0.73[a]	2.98[a]	2.48[a]	1.04[a]	0.69[a]	0.73[a]	97.9 [a]	94.92[b]
LSD $_{(p=0.05)}$	3.56	4.32	2.23	3.14	1.24	1.48	0.25	1.68	0.97	0.47	0.23	0.25	1.45	1.87

Values of each composition for parents and half-sib families in rows followed by the same letters are not statistically significant based on the LSD test (p≤0.05).

Table 7. Correlation coefficient between traits in half-sib families.

Character	NDF	PH	NFB	NUP	NSU	SYP	HI	EOP	EOY
NDF	1								
PH	0.56**	1							
NFB	0.60**	0.58**	1						
NUP	-0.18ns	0.17ns	-0.25ns	1					
NSU	0.42*	0.09ns	0.47**	-0.23ns	1				
SYP	0.06ns	0.54**	0.54**	0.65**	0.64**	1			
HI	-0.21ns	-0.24ns	0.44**	-0.02ns	0.54**	0.45**	1		
EOP	-0.39*	-0.04ns	0.55**	0.44**	0.42*	0.42*	0.40*	1	
EOY	-0.29ns	-0.12ns	0.42*	0.54**	0.45**	0.40*	0.45**	0.83**	1

ns, *; **: not significant, significant at p<0.05, p<0.01, respectively.
NDF, Number of days to flowering; PH, Plant height; NFB, Number of fertile branches; NUP, Number of umbrellas per plant; NSU, Number of seeds per umbel; SYP, Seed yield per plant; HI, Harvest index; EOP, Essential oil percentage; EOY, Essential oil yield.

Table 8. Correlation coefficient of traits between parent (column) and offspring (row).

Character	NDF	PH	NFB	NUP	NSU	SYP	HI	EOP	EOY
NDF	0.59*								
PH	0.25	0.54*							
NFB	0.31	-0.01	0.40						
NUP	0.16	0.15	0.10	0.17					
NSU	0.25	0.21	0.18	0.24	0.28				
SYP	0.21	0.24	0.21	0.18	0.26	0.21			
HI	0.32	0.18	0.17	0.12	0.15	0.16	0.31		
EOP	0.39	-0.26	0.39	0.22	0.42	0.24	0.25	0.21	
EOY	0.40	-0.05	0.23	0.26	0.05	0.32	0.18	0.14	0.18

* significant at p<0.05
NDF, Number of days to flowering; PH, Plant height; NFB, Number of fertile branches; NUP, Number of umbrellas per plant; NSU, Number of seeds per umbel; SYP, Seed yield per plant; HI, Harvest index; EOP, Essential oil percentage; EOY, Essential oil yield

Table 9. General combining ability for agro-morphological traits of Ajowan genotypes.

Family	NDF	PH	NFB	NUP	NSU	SYP	HI	EOP	EOY
Shiraz	-5.13	-8.33	-0.26	-26.53	2.76	-2.10	2.24	2.60	17.89
Arak	-4.13	-3.08	0.40	7.8	-0.53	0.84	-0.37	-0.76	-8.03
Beshruye	-2.10	-0.66	-1.26	11.47	-4.5	0.72	0.01	-0.39	-1.00
Shahediye	3.86	-7.14	0.4	-13.87	-0.20	-4.02	-2.87	-0.36	-14.13
Ardebil	4.20	11.07	0.74	9.80	-0.53	2.9	2.29	1.10	22.95
Karaj	8.53	13.47	0.74	2.47	2.79	-1.07	-3.42	-0.79	-9.76
Qom	-0.13	-7.24	0.07	-13.87	-0.20	-0.66	5.60	-0.29	-3.86
Sarbishe	-10.8	-14.83	-1.92	24.47	-6.5	-0.50	-0.43	1.10	10.07
Hamedan	2.53	-4.24	0.07	19.80	5.76	3.73	0.0001	2.60	20.72
Yazd	3.2	21	1.07	4.47	0.46	0.18	-2.98	0.50	6.60
LSD	0.70	2.42	0.52	3.25	0.46	0.42	0.18	0.33	4.56

NDF, Number of days to flowering; PH, Plant height; NFB, Number of fertile branches; NUP, Number of umbrellas per plant; NSU, Number of seeds per umbel; SYP, Seed yield per plant; HI, Harvest index; EOP, Essential oil percentage; EOY, Essential oil yield.

Discussion

Knowledge about the nature and size of genetic variation helps plant breeders select the best way for plant improvement. In genetic variance, the additive part of gene action is the main factor responsible for heritable variation in many agronomic traits (Aastiveit and Aastiveit, 1990). In this study, the high broad- and narrow-sense heritability found for NDF, PH, EOP, and EOY in the present study confirmed that these traits are mainly under additive genetic control in Ajowan. Selection can be effective. Heritability estimates for essential oil yield were generally similar to or higher than estimates in the literature on Ajowan (Ghanshyam et al., 2015; Dalkani et al., 2012) and fennel (Izadi-Darbandi et al., 2013).

The estimates of broad-sense heritability for EOP (85%) in the present study were generally lower than those previously reported for Ajowan (Ghanshyam et al., 2015) and fennel (Izadi-Darbandi et al., 2013). These heritability estimates for seed yield have been moderate to high in the literature (*Carum copticum*, Dalkani et al., 2012; *Trachyspermum ammi*, Fadaei Heidari et al., 2013). Furthermore, Izadi-Darbandi et al. (2013) indicated that a large portion of the genetic variance for this trait in fennel is additive. Regression between parents and offspring is commonly used in open-pollination breeding to estimate narrow-sense heritability. The regression method provides a more reliable estimate of narrow-sense heritability than the sib analysis method. There was little agreement between them in most cases (Nguyen and Sleper, 1983). In the current study, narrow-sense heritability from sib-analysis correlated insignificantly with parent-offspring regression regarding the evaluated traits.

A simple correlation between the essential oil components in the columns (Table 6) showed a significant negative relationship between thymol and γ- terpinene in parents and half-sib families. These findings indicated that an increase in thymol caused a reduction in γ-terpinene and vice versa (Table 6). A negative correlation between γ-terpinene and thymol reportedly occurred in Carvalho Filho et al. (2006). Thymol took form by changes in γ-terpinene structure (Carvalho Filho et al., 2006).

From the positive and significant correlation between SYP and PH, NFB, NUP, and NSU, one can mention that indirect selection may effectively improve SYP. Niazian et al. (2017) reported a highly significant correlation between these traits. In the present study, the correlation between SYP and EOY was significantly similar to previous findings by Sadati et al. (2017). Selection would be effective in simultaneously improving the plant traits.

Genetic diversity between parents is necessary for transgressive segregation and to obtain a high degree of allelic diversity within cultivars to increase the adaptability and fitness of populations (Reed and Frankham, 2003; Amini et al., 2011). In this study, a wide range of general combining abilities occurred for most traits, especially EOY. This variation shows that the polycross could discriminate parental ecotypes as a rapid way to identify superior genotypes to breed varieties since general combining ability reveals additive gene actions (Mather and Jinks, 1982).

Studying different crops indicates that breeding for yield was not simple. The interactions with environmental variations resulting from site, season, and management tend to make genetic gains in plant yield elusive. These have assisted in intensively planted field crops, with resources and thousands of years of domestication behind them. Some of this technology is premature in species for which we have limited knowledge about their quantitative or qualitative genetics, such as Ajowan. There are resources of untapped genetic variation in Ajowan collections (Niazia et al., 2017; Sadati et al., 2017; Fadaei Heidari et al., 2016; Choudhary, 2006), and most Ajowan breeding pools in the world have probably been through very few generations of selection.

We concluded that there were significant variations and high heritability for most of the evaluated traits in the Ajowan populations to improve seed yield and essential oil yield. This research is the first report on heritable plant traits in Ajowan and the procedure of breeding varieties worldwide.

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Data archiving statement

The authors confirm that the data supporting the findings of this study are available within the article.

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Conflict of Interest

The authors indicate no conflict of interest for this work.

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