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Phenological Traits, Seed Yield, and Essential Oil Yield of Fifty Populations of Bitter Fennel (*Foeniculum vulgare*)

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ABSTRACT

Bitter fennel (*Foeniculum vulgare* var. vulgare) is a commercial subspecies of fennel that is widely used in food, pharmaceutical, and perfume industries. Despite the economic importance of this crop and a growing demand for its products, most farmers cultivate local bitter fennel populations that are not necessarily high-yielding. Genetic variation in bitter fennel and relevant heritability studies have suggested that selection can be an efficient breeding method to increase bitter fennel yield. This experiment was conducted in the College of Aburaihan, University of Tehran, Pakdasht, Iran, from 2010 to 2014. Fifty fennel populations from different parts of Iran were collected and assessed for their maturity habit, life span, seed yield, essential oil content, and essential oil yield in a five-year field experiment. Results showed that these fennel populations, based on their maturity habits, comprised three distinctive groups of early, intermediate, and late-maturing, requiring 120, 175, and 230 days from seedling emergence to seed harvest, respectively. The life span of the fennel populations ranged from three to four years. In general, fennel populations in arid regions with extreme temperatures in summer and winter were early-maturing and had shorter life spans. Populations in humid or semi-humid regions with a rather temperate climate were late- or intermediate-maturing and had longer life spans. These observations showed how the causes of growth limitation such as extreme seasonal temperature changes, water accessibility, and competition for sunlight have shaped the phenological features of these fennel populations. During the first three years of the study, considering the minimum life span of all populations, essential oil yield among the early-maturing fennels ranged from 2.5 to 104.6 L ha^{-1} $year^{-1}$ (average 26.1±0.1). The essential oil yield ranged from 10.1 to 152.2 L ha^{-1} $year^{-1}$ (average 67.7±1) in intermediate-maturing fennels and from 7.5 to 160.9 L ha-1 year-1 (average 46.4±0.2) in late-maturing fennels. Populations with four and five-year life spans had a dramatic decrease in yield after the third year, although they produced considerable amounts of green biomass. Regarding average values in three years, the highest essential oil yield a mong early-maturing fennels occurred in the Fasa population (51.4 L ha^{-1}), among intermediate-maturing fennels in the Meshkin Shahr and Moqhan populations (140.5 and 124.9 L ha^{-1}, respectively), and among late-maturing fennels in the Sari population (52.1 L ha^{-1}). Identifying high-yielding early- and intermediate-maturing populations provides a platform for further evaluations on high-yielding fennel populations with stable performance in future studies.

Introduction

Fennel (*Foeniculum vulgare*) is a valuable spice plant from the Umbelliferae (Apiaceae) family and is cultivated in nearly all parts of the world (Damjanovic et al., 2005). It is a hardy, perennial, umbelliferous herb with yellow flowers and feathery leaves. Fennel plants can reach a height of up to 2.3 m with hollow stems. Its leaves can grow up to 40 cm long; they are finely lobated, with thread-like segments, and measure about 0.5 mm wide. Its flowers appear on terminal compound umbels. Its fruit is a dry seed, measuring 4–10 mm in length.

Fennel is generally considered indigenous to the shores of the Mediterranean (Gross et al., 2009). It is utilized in food and pharmaceutical industries, with its essential oil, commonly known as sweet fennel oil, finding applications in cosmetics, pharmaceuticals, perfumery, and as a food additive (Barros et al., 2010; Hamdy Roby et al., 2013; Diao et al., 2014; Kooti et al., 2015). Fennel is a valuable additive in condiments, liqueur products, and baked goods (Hornok, 1992). The most popular medical usage of fennel is as an anti-colic agent, especially for infants (Alexandrovich et al., 2003). Fennel can also improve feeding efficiency and increase body weights in cattle and poultry (Yazarloo et al., 2014; Teixeira et al., 2013). Fennel seeds contain essential oils that give them their flavoring and curative properties. Thus, its essential oil content and seed yield are the most important commercial aspects (Bogdanov et al., 2015; He and Huang, 2011; Gupta et al., 1995).

A subspecies of bitter fennel (*Foeniculum vulgare* var. vulgare) is a commercial subspecies for fennel-derived products, as it produces more seeds with high essential oil content and can be grown even in arid regions (Omidbaigi, 2009; Coşge et al., 2008). In bitter fennel, hereafter just called fennel, seeds can contain up to 6% essential oil with main compositions such as trans-anethole, methyl chavicol, fenchone, and limonene (Bowes and Zheljazkov, 2005; Zahid et al., 2008; Edoardo et al., 2010; He and Huang, 2011; Hamdy Roby et al., 2013; Shojaiefar et al., 2015; Bahmani et al., 2016). Seed yield in fennel can vary widely. It reportedly ranges from as low as 130 kg ha-1 to as high as 4140 kg ha^{-1} (Brijesh et al., 2016; Ayub et al., 2015; Ehsanipour et al., 2012; Al Dalain et al., 2012; Mehta et al., 2011).

Utilizing high-yielding cultivars is necessary to meet an increasing demand for fennel seeds. In fennel, additive and non-additive components of genetic variation play a significant role (Shojaiefar et al., 2015; Singh and Divakara Sastry, 2006). High broad-sense heritabilities for fennel yield and morphological traits have been reported (Izadi Darbandi et al., 2013). Therefore, regarding fennel as a rainfed crop, selection can be an efficient, cheap prerequisite for breeding.

The total world fennel seed production in 2022 was approximately 800 thousand tons, of which 5% was produced in Iran (FAO, 2022). Iran, as one of the origins of fennel, includes regions with different climates, such as warm to cold and dry to humid (Masodian, 2002). Since ancient times, Iranian farmers have farmed fennel in these regions using local fennel populations and landraces. Due to evolutionary adaptations to local growth conditions (Bogdanov et al., 2015; Ramırez Valiente et al., 2009), these populations have very diverse morphological (Bahmani et al., 2012a, 2015, and 2016; Shojaiefar et al., 2015) and phytochemical properties (Akbari et al., 2023; Izadi Darbandi et al., 2023; Bahmani et al., 2016). Also, they have diverse genetic features (Bahmani et al., 2012b and 2013; Shojaiefar et al., 2015).

Despite the economic importance of fennel seeds and essential oil, Iranian fennel populations are still unknown for their yield potential and even less known for their phenological features. This experiment attempted to characterize 50 fennel populations from different climates in Iran, considering their maturity habit, life span, seed yield, essential oil content, and essential oil yield. The results of this study can be beneficial to breeders and agronomists to formulate agronomic strategies, set breeding goals, and attempt further screening.

Materials and Methods

This experiment was conducted in a research farm in the College of Aburaihan, University of Tehran, Pakdasht, Iran. The farm was situated at 35°29' N latitude and 51°40' E longitude, with an estimated elevation of 1026 m above sea level. This region is characterized by a semi-arid climate (Table 1).

Plant materials

In autumn 2009, fifty bitter fennel populations (*Foeniculum vulgare* Mill) were gathered from different parts of Iran, each with a distinct climate, including variations in humidity, temperature, altitude, longitude, and latitude. These samples were then stored in a refrigerator at 5 °C (see Table 2) (Bahmani et al., 2016, 2015 and 2012a).

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Table 1. Climatic conditions of the experimental site.

Months	Monthly average temperature (˚C)					Monthly relative humidity (%)					Monthly total rainfall amount (mm)				
	2010	2011	2012	2013	2014	2010	2011	2012	2013	2014	2010	2011	2012	2013	2014
January	12.8	8.2	9	10.9	9.5	4.4	0.4	0.3	1.6	1.3	49	59.4	49.5	45.3	52.7
February	12.8	10.8	8	13.7	9.7	4.3	1.7	-0.4	4.4	0.7	48.9	48.1	51.4	42.3	42.9
March	19.1	15.1	14.1	18.4	17.1	9.2	5.4	3.5	8.1	6.8	40.4	43.5	30.8	33.8	34.7
April	23.4	23.6	23	23.2	23.3	11.7	13.4	13.1	12.6	12.6	35.1	26.4	36.8	28.5	30.1
May	28.5	29.1	29.3	27.8	30	17.4	17.9	18.5	16	18.3	26.6	26.8	22.4	26.4	22.9
June	35.8	35.6	33.5	34.5	35.2	23.9	18.5	21.6	21.3	22.3	15.6	18.5	20.6	19.1	16.9
July	38	37.5	36.3	38.3	37.4	25.9	26.2	24	24	25.4	17.7	16.6	21.9	20.5	18.4
August	34.5	35.8	36.2	35.1	36.8	23.6	23.5	24.6	22.9	25.3	20.6	26.2	17.3	22.8	15.3
September	31.2	31.2	31.2	33	33.1	20	20.1	19.2	21.7	24.4	23.3	23.7	23.3	17.6	18.1
October	27.6	23.4	24.8	24.3	22.8	17	13.2	14.7	12.7	13.1	26.2	34.2	32.5	30.3	36
November	18	11.4	16.7	16.4	13.9	8	4	8.4	8.5	5.5	39.1	66.2	52.2	52.4	47.9
December	14.7	5	9.9	9.3	11.3	4.4	1.3	2.5	1.1	3.5	35.8	54.1	63.6	49.1	52.3
Average	24.8	22.7	22.7	23.8	23.5	14.2	12.6	12.6	12.9	13.1	31.3	36.9	35.1	32.3	32.3
	Average of annual temperature					Annual precipitation (mm)									
	2010	2011	2012	2013	2014	2010	2011	2012	2013	2014					
	19.4°	17.7	17.8	18.5	18.6	471.9	346.9	237.2	248.6	87.6					

Field trial design

Fennel seeds were planted in a field under a randomized complete block design with three replications in the College of Aburaihan (Table 2). Each population was sown in a one m^2 plot. The soil texture was sandy loam (Table 3). After seedling emergence, the plots were thinned out to a final plant density of ten plants per plot (Khorshidi et al., 2010; Falzari et al., 2006; El-Gengaihi and Abdallah, 1978; Abdellaoui et al., 2020). The field had been under wheat cultivation two years before our study, and the wheat residues were incorporated into the soil. In our experiment, no fertilizer was applied. Weeding was done manually and regular irrigation maintained 50% field capacity. During the growing season, no diseases or pests were observed.

Plant characterization

From 2010 to 2014, we measured fennel life spans, maturity habits, seed yield (t ha^{-1}), essential oil yield (L ha^{-1}), essential oil content (%), plant density (p m^{-2}), days to reach 70% dried seed stage, germination rate (%), plant height (cm), inflorescent number, and 1000-seed weight (g) among the fifty fennel populations. Each year, the plants overwintered as rosettes and regrew in the next spring. The threshold of three plants per m^2 for plant density was decided as a criterion for life span. To determine a population's life span, from 2010 to 2014, we counted the years for as long as the plant density of any given population remained more than three plants per m2. Maturity habits of the populations were determined by counting the number of days that a population needed to reach 70% mature seeds (harvest time) from the planting date in the first year and for the rest of the study from mid-March when the average tridaily temperature in the field stayed above 5 °C. Seeds from each population were harvested when 70% of them had reached maturity and dried.

Table 2. Geography profile of regions home to Iranian fennel populations.

No	Ecotype	Altitude (m)	Latitude	Longitude	No	Ecotype	Altitude (m)	Latitude	Longitude
1	Meshkin shahr	1568	38 23 N	47 40 E	26	Tehran	1190	35 41 N	51 19 E
2	Fozveh	1612	32 36 N	51 26 E	27	Yazd	1230	31 54 N	54 24 E
3	Sari	23	36 33 N	53 0 E	28	Bajestan	1265	34 51 N	58 17 E
4	Kaleibar	1180	38 52 N	47 1 E	29	Qazvin	1278	36 15 N	50 0 E
5	Sanandaj	1373	35 20 N	47 0 E	30	Fasa	1288	28 58 N	53 41 E
6	Shiraz	1488	29 36 N	52 32 E	31	Oromie	1313	37 32 N	45 5 E
7	Sabzevar	977	36 12 N	57 43 E	32	Ardabil	1332	38 15 N	48 17 E
8	Kohin	1527	36 36 N	49 67 E	33	Shabestar	1350	38 0 N	46 11 E
9	Mahalat	1775	33 91 N	50 45 E	34	Tabriz	1361	38 5 N	46 17 E
10	Chahestan	27	27 13 N	56 22 E	35	Arak	1708	34 6 N	49 46 E
11	Kashan	982	33 59 N	51 27 E	36	Hamedan	1749	34 51 N	48 32 E
12	Khash	1394	28 13 N	61 12 E	37	Kamyaran	1464	34 47 N	46 56 E
13	Ahvaz	22	31 20 N	48 40 E	38	Alamot	1500	36 45 N	50 47 E
14	Moqhan	31	39 39 N	47 55 E	39	Marvdasht	1502	29 80 N	52 83 E
15	Barazjan	80	29 26 N	51 20 E	40	Saqez	1522	36 15 N	46 16 E
16	Inche boron	460	37 53 N	55 57 E	41	Esfahan	1550	32 37 N	51 40 E
17	Sarpol zahab	548	34 27 N	45 54 E	42	Rafsanjan	1580	30 25 N	55 54 E
18	Aran bidgol	850	34 70 N	52 30 E	43	Kerman	1753	30 15 N	56 58 E
19	Qom	877	34 42 N	50 51 E	44	Khalkhal	1769	37 38 N	48 31 E
20	Haji abad	931	28 19 N	55 55 E	45	Razan	1870	35 21 N	49 4 E
21	Ardakan	1620	30 13 N	52 26 E	46	Dehgolan	1970	35 10 N	47 30 E
22	Nairiz	1632	29 12 N	54 20 E	47	Hasht gerd	1426	35 65 N	50 43 E
23	Sardasht	1670	36 9 N	45 30 E	48	Damavand	2000	35 43 N	52 15 E
24	Givi	1682	37 41 N	48 28 E	49	Abade	2030	31 11 N	52 40 E
25	Tafresh	1978	34 41 N	50 1 E	50	Divandare	2142	36 4 N	46 55E

Table 3. Chemical and physical properties of soil at 0–50 cm depth.

Soil bulk density (g cm^{-3})	Sand%	Silt%	Clay%	pH	Soil	EC (ms cm)	Soil depth (cm)
1.36	28.8	52	19.2	7.4	Silty loam	3.55	0–30

Life span and maturity habit

To measure the life span of the populations, the criterion was the number of years that a fennel population survived winter and regrew in spring. Given that in the first year, the plant density for all populations was 10 plants per m^2, we considered a population alive each year if its plant density had not declined to fewer than 3 plants per m^2. This trait was monitored and recorded for six years when we learned that the fifth year was the maximum number of years that any Iranian fennel can live. In the sixth year, the plant density of all populations declined to fewer than 3 plants per m^2.

Regarding the maturity habit, we counted the number of days that each population in each year needed to reach 70% dried seed stage as the earliest time for seed harvest. In the first year, we started counting days from the day that seedlings emerged from the soil. In the second year, the starting day was the day when the average daily temperature did not fall below 5 °C.

Seed yield, essential oil content, and essential oil yield

Fennel seeds were evaluated throughout the life span of each population. Seed yield was reported as tons per hectare (ton ha^{-1}). Seeds were harvested when 70% of them had dried. After harvesting the seeds manually and cleaning them, they were weighed on a precise scale.

Each year, essential oils were extracted from the harvested seeds of the fifty populations. The extraction process involved grinding a 20 g seed sample from each genotype using an electric mill. Subsequently, the resulting powder was combined with 500 mL of deionized water and subjected to heating at 100 °C. The collected oil was obtained using a Clevenger-type apparatus (Boyadzhieva and Angelov, 2014; Akbari et al., 2015). There were three replications per extraction. The essential oil yield was determined by the following formula: seed yield × essential oil content) / 100 (Ramadan, 2007).

Statistical analysis
Analysis of variance was performed using SAS 9.0 according to a split plot in time. Clustering was conducted by SPSS 18 and graphs were drawn in Microsoft Excel.

Results
Analysis of variance was performed on life span, maturity habit, seed yield, and essential oil content. Since interactions between population and year were significant for each trait, a separate analysis of variance was conducted per trait each year.

Life span
In the first, second, and third years of the study, the number of plants per plot for all populations was above three plants per plot, resulting in a minimum life span of three years for all populations. Based on life span, the 50 fennel populations were divided into three groups:
1. Populations with a five-year life span (Sari, Qazvin, Chahestan, Kaleibar, Haji Abad, Khalkhal, Meshkin Shahr, and Ardabil).
2. Populations with a four-year life span (Khash, Marvdasht, Fozve, Kohn, Damavand, Alamo, Givi, Moqan, Rafsanjan, Fasa, and Hamedan).
3. Populations with a three-year life span (rest of the populations) (Tables 4 and 5).

Table 4. Analysis of variance for plant density.

SOV	df	Plant density (p m^{-2})
Landrace (L)	49	25.8^{**}
Block	2	2.14^{*}
Error 1	98	1.2
Year (Y)	5	2422.1^{**}
Landrace×Year	245	3.4^{**}
Error 2	500	0.5
Mean	-	5
CV (%)	-	14.3

Table 5. Analysis of variance for plant density in separate years.

SOV	df	Year 1	Year 2	Year 3	Year 4	Year 5	Year 6
Block	2	-	4.7^{**}	0.9^{ns}	0.3^{ns}	0.1^{ns}	0.1^{ns}
Landrace	49	-	3.6^{**}	14.8^{**}	17.7^{**}	6.1^{**}	0.7^{**}
Error	98	-	0.8	0.8	1.6	0.3	0.1
Mean	-	10	8.5	6.4	3.8	0.9	0.2
CV (%)	-	-	10.6	14.4	33	61	166

Maturity habit
Based on the number of days required to reach 70% dried seeds, the fifty fennel populations were divided into three groups:
1. Late maturity populations with 230 days to seed harvest (Sari, Kaleibar, Qazvin, Chahestan, and Haji Abad).
2. Intermediate maturity populations with 175 days to seed harvest (Moqhan, Kohn, Meshkin Shahr, Alamot, Khalkhal, Damavand, Ardabil, Marvdasht, Kashan, Givi, Khash, and Fozve).
3. Early maturity populations with 120 days to seed harvest (the rest of the populations) (Tables 6 and 7).

Table 6. Analysis of variance on days required to reach 70% dried seeds.

SOV	df	Days to 70% dried seed
Landrace (L)	49	16453.5^{**}
Block	2	97.1^{*}
Error 1	98	29.1
Year (Y)	4	18476.7^{**}
L×Y	123	2771.4^{**}
Error 2	254	19.8
Mean	-	153.2
CV (%)	-	2.9

Table 7. Analysis of variance on days required to reach 70% dried seeds in separate years.

SOV	df	Year 1	Year 2	Year 3	Year 4	Year 5
Block	2	34.2ns	0.1ns	298.6**	18.8ns	9.3ns
Landrace	49	5703.1**	3455.4**	4894.3**	4890.6**	3228.5**
Error	98	30.1	13.7	25.5	9.1	16.5
Mean	-	154.2	154.4	139.1	169.8	187.5
CV (%)	-	3.6	2.4	3.6	1.8	2.1

The late-maturing fennels had a longer life span (five years), the intermediate-maturing ones had a four to five-year life span, and early-maturing ones had a three to four-year life span (Table 8).

Table 8. Classification of the landraces based on their maturity habits and life spans.

Maturity habit	Landrace	Life span (years)
Late maturing (230 days)	Sari, Kaleibar, Qazvin, Chahestan, Haji abad	5
Medium maturing (175 days)	Meshkin, Ardebil, Khalkhal, Kohin	5
	Khash, Fozve, Kashan, Alamot, Damavand, Moqhan, Marvdasht, Givi	4
Early maturing (120 days)	Rafsanjan, Hamedan, Fasa	4
	Rest of the landraces	3

Evolutionary adaptation to harsh environments

Evolutionary adaptation to harsh environments in plants has led to defense mechanisms such as escape, avoidance, and tolerance. Escape, meaning maturity before stress arrival, including sensitivity to day periods (as an alarm for coming hot/cold and dry periods), is one of the most common mechanisms seen in many species (Farsi and Baqheri, 2006). Iranian fennels also use this escape mechanism to avoid extreme temperatures and water deficiency. The escape strategy was evaluated by considering climatic data in the regions where some populations originated (downloadable from www.weather.ir) and using ambrothermic graphs to investigate temperature range and water availability throughout the year.

Sari represented an example of a region that is the origin of late-maturing fennels. Sari ambrothermic graph (Fig. 1) showed the co-presence of high precipitation and moderate temperature for almost nine months of the year (Mar-Nov), allowing plants in the wild and rainfed farms to grow for such a long period. Rich and fertile soils in this region usually result in vigorous plants, explaining why these fennels tend to live longer (usually five years).

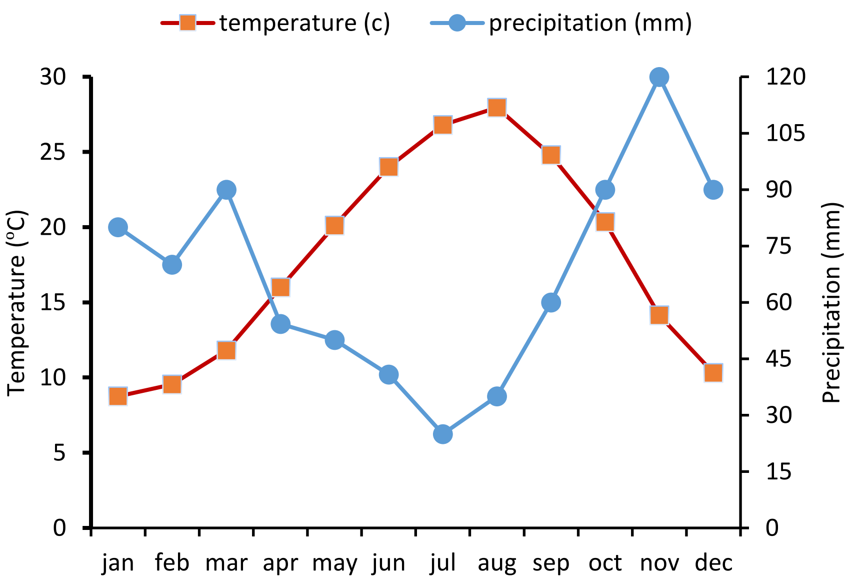

Fig. 1. Ambrothermic graph of Sari showing suitable temperature and humidity from March to November.

Sanandaj represented an example of a region home to early maturing fennels. Sanandaj ambrothermic graph (Fig. 2) showed the co-presence of high precipitation and moderate temperature for almost four months a year (April-July), allowing plants in the wild and rainfed farms to grow during these four months. Limiting factors in regions like Sanandaj are cold winters and dry summers. Due to harsh winters and summers in these climates, plants tend to live shorter (usually three years).

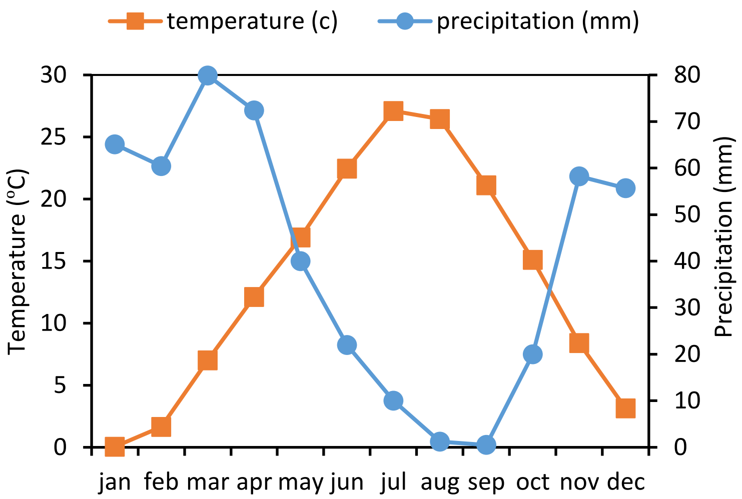

Fig. 2. Ambrothermic graph of Sanandaj showing suitable temperature and humidity from April to July.

Damavand represented an example of a region home to intermediate-maturing fennels. Damavand ambrothermic graph (Fig. 3) showed the co-presence of high precipitation and moderate temperature for almost six months a year (March-August), allowing plants in the wild and rainfed farms to grow during these six months. Limiting factors in regions like Damavand were cold winters and dry summers.

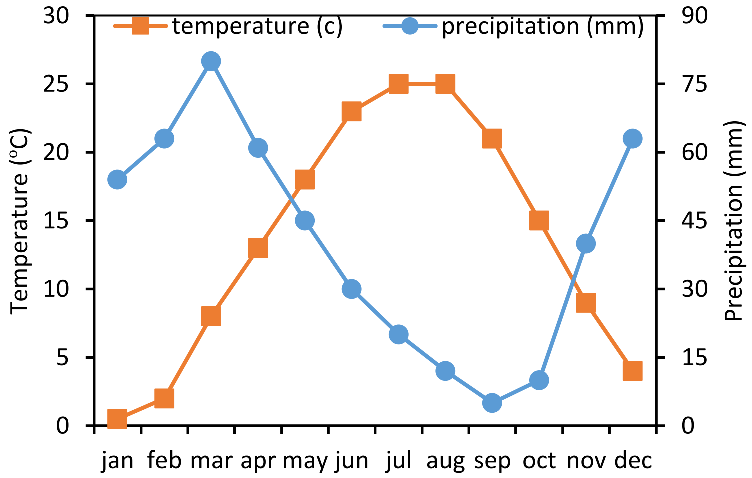

Fig. 3. Ambrothermic graph of Damavand showing suitable temperature and humidity from March to August.

These patterns show an evolutionary adaptation of phenological features to the environmental conditions experienced by fennel ancestors for long periods, confirmed by a relevant report by Fenner (1998) because such natural growth season in any given region determines the life

cycle of that region's fennels.
The 1000-seed weight (Fig. 4) in late-maturing fennels from shaded areas (regions with humid and temperate climates) was lower. Regarding early-maturing fennels from exposed areas (regions with dry and warm/cold climates), the 1000-seed weight was higher. This observation was similar to previous reports by Ramırez Valiente et al. (2009) and Silveira and Oliveira (2013).

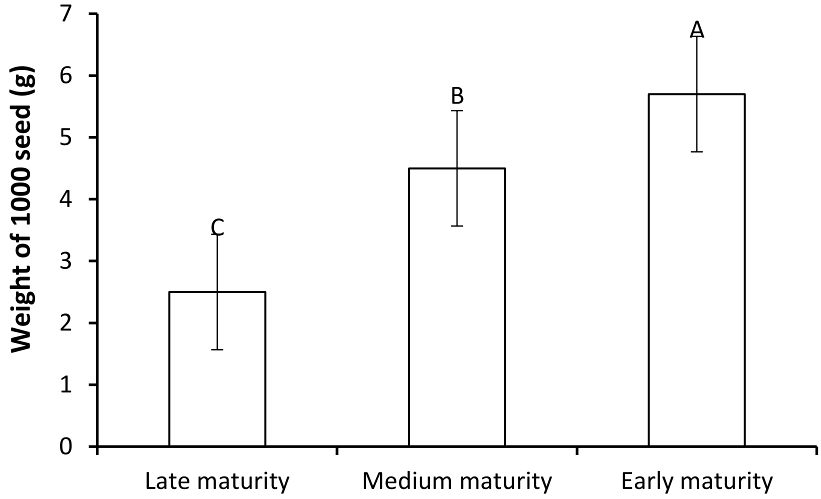

Fig. 4. Average 1000-seed weight (g) for the three maturity groups.

The seeds (Fig. 5) of late-maturing fennels from shaded areas had faster germination, and early-maturity fennels from exposed regions had slower germination. Similar results about other species exist in the literature (Mut and Akay, 2010; Kos and Poschlod, 2008; Leishman and Westoby, 1994).

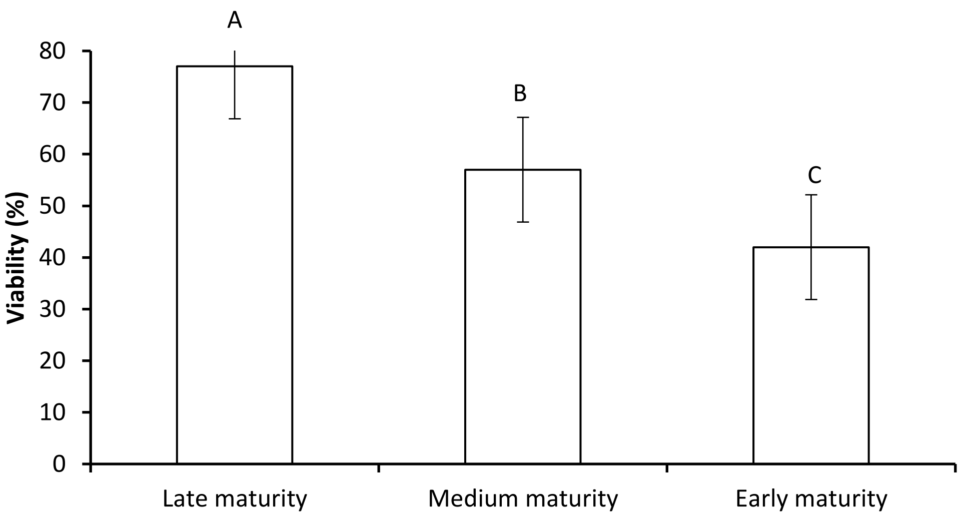

Fig. 5. Average germination rate (%) for the three maturity groups after 15 days.

Regarding plant height and inflorescent count (Figs. 6 and 7), the late-maturing fennels were taller and had more inflorescences. The early-maturing fennels were shorter and had fewer inflorescences.

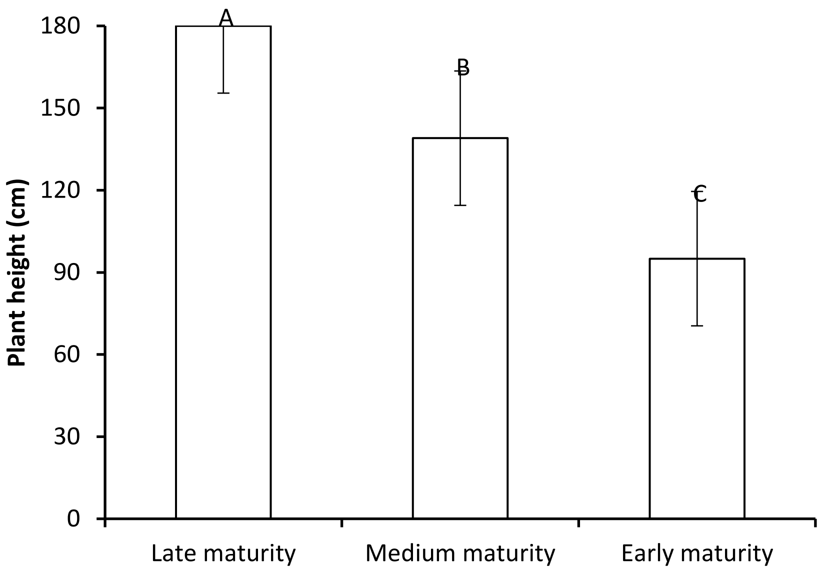

Fig. 6. Average plant height (cm) for the three maturity groups.

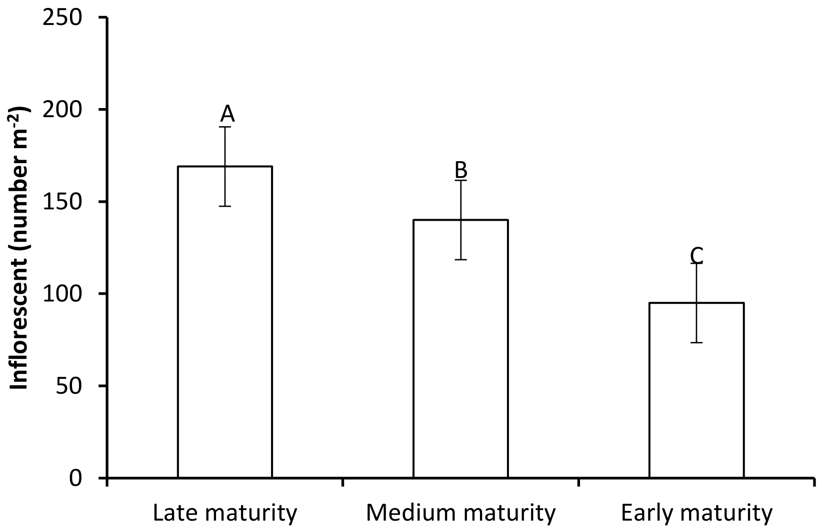

Fig. 7. Average inflorescent count for the three maturity groups.

Seed yield

Among the populations regarding seed yield, there were significant differences in each year. Seed yields in fennel populations ranged from 0.015 to 10.7 tons ha^{-1} $year^{-1}$. Out of the fifty fennel populations, only three had seed yield in the fifth year, and only 16 fennel populations yielded seeds in the fourth year (Tables 9 and 10). Average seed yield for all fennel populations in the first, second, third, fourth, and fifth year of the study were 1.44±0.09 tons ha^{-1} (in all fifty fennel populations), 2.11±0.15 tons ha^{-1} (in all fifty populations), 1.46±0.23 tons ha^{-1} (in all fifty populations), 1.14±0.20 tons ha^{-1} (in 16 of the populations), and 0.48±0.13 tons ha^{-1} (in three of the fennel populations), respectively. These fennels had their maximum seed yield in their second year (Table 11).

Table 9. Analysis of variance on seed yield during the five years of the study.

SOV	df	Seed yield (ton ha^{-1})
Landrace (L)	49	66166.3**
Block	2	3926.1^{ns}
Error 1	98	2024.8
Year (Y)	4	173329.3**
L×Y	115	30453.5**
Error 2	238	2630.2
Mean	-	159.2
CV (%)	-	32

Table 10. Analysis of variance on seed yield in separate years.

SOV	df	Seed yield (ton/ha)				
		Year 1	Year 2	Year 3	Year 4	Year 5
Block	2	18721.3**	9207.1*	16357**	6343.6**	11.09^{ns}
Landrace	49	13945.5**	36019.3**	81943.8**	18517.6**	1502.6^{ns}
Error	98	1620.7	3509.8	2057.5	855.5	223.6
Mean	-	144.3	210.6	145.7	108.6	47.2
CV (%)	-	27	28	31	27	31

During the first three years of the study, i.e., the minimum life span for all the populations, seed yield data for the early-maturing fennels ranged from 0.0158 to 40.33 tons ha^{-1} year^{-1} (average 12.93 tons ha^{-1} year^{-1} ± 0.65), for the intermediate-maturing from 5.03 to 106.93 tons ha^{-1} year^{-1} (average 27.19 tons ha^{-1} year^{-1} ± 3.11), and for the late-maturing from 3.34 to 34 tons ha^{-1} year^{-1} (average 16.22 tons ha^{-1} year^{-1} ± 2.48) (Fig. 8). The highest average of seed yields during the first three years of the study among the early-maturing belonged to Fasa (232.1 tons ha^{-1} in three years) and Rafsanjan (214.3 tons ha^{-1} in three years). Among the intermediate-maturing, it belonged to Meshkin Shahr (675.5 tons ha^{-1} in three years) and Moqhan (522.8 tons ha^{-1} in three years). Regarding the late-maturing, it belonged to Haji Abad (206.6 tons ha^{-1} in three years). Late-maturing fennels in the last year of their life span (the fifth year) did not have seed yields higher than 0.01 tons ha^{-1}. The only populations with over 0.01 tons ha^{-1} seed yield in the fifth year were Meshkin Shahr, Khalkhal, and Ardabil, i.e., intermediate-maturing fennels. The only early-maturing fennels with seed yields in the fourth year were Fasa, Rafsanjan, and Hamedan.

Essential oil content

Significant differences occurred each year among fennel populations regarding their essential oil content. The essential oil content of fennel populations ranged from 0.9-5.1%. The late- and intermediate-maturing fennels had the highest essential oil contents (Tables 12 and 13). Average essential oil content for all populations in the first, second, third, fourth, and fifth year of the study were 2.54%±0.05 (for the fifty fennel populations), 2.42%±0.16 (for the fifty populations), 1.77%±0.04 (for the fifty populations), 1.79%±0.09 (for 16 of the populations), and 1.23%±0.16 (for three of the population), respectively. These fennels had their maximum essential oil content in their second year (Table 14).

Table 11. Comparison of means on seed yield (ton ha-1) of the fifty fennel landraces during their life spans.

Landraces	Seed yield (ton ha^{-1})					Landraces	Seed yield (ton ha^{-1})				
	Year 1	Year 2	Year 3	Year 4	Year 5		Year 1	Year 2	Year 3	Year 4	Year 5
Chahestan	2.46 B-D	0.98 O-S	1.25 G-L	0.69 EF	.	Yazd	1.73 D-H	2.58 D-J	1.01 G-N	.	.
Haji abad	1.36 E-K	3.35 C-F	1.47 E-J	0.87 D-F	.	Tehran	1.07 G-L	1.07 N-S	8.6 I-N	.	.
Qazvin	1.61 E-I	2.37 E-M	0.52 K-N	0.41 F	.	Bajestan	1.31 F-L	2.18 F-N	1.46 E-J	.	.
Sari	0.80 I-L	3.40 C-E	0.78 I-N	0.61 F	.	Hamedan	1.44 E-J	1.07 N-S	0.98 H-N	0.97 C-F	.
Kaleibar	1.30 F-L	2.35 E-M	0.35 L-N	0.43 F	.	Abade	1.30 F-L	2.12 G-O	0.88 H-N	.	.
Alamot	1.82 D-G	3.62 CD	2.18 D-F	1.20 C-E	.	Ahvaz	1.25 F-L	1.40 J-S	0.96 H-N	.	.
Kashan	1.33 E-L	1.42 L-S	0.50 K-N	.	.	Dehgolan	1.24 F-L	1.33 K-S	0.62 J-N	.	.
Khash	2.11 C-E	2.33 E-M	3.27 C	1.45 C	.	Sardasht	0.97 H-L	1.20 L-S	1.32 F-K	.	.
Kohin	1.25 F-L	3.37 C-E	2.83 CD	2.40 B	.	Saqez	0.65 J-L	3.12 C-G	1.34 F-K	.	.
Meshkin shahr	3.95 A	4.87 B	10.69 A	3.34 A	0.66 A	Sarpolzahab	1.40 E-J	2.15 G-O	1.15 G-M	.	.
Damavand	1.61 E-I	2.43 E-K	1.50 E-J	.	.	Kamyaran	1.01 G-L	1.18 M-S	0.93 H-N	.	.
Khalkhal	2.42 B-D	2.87 D-H	1.78 E-H	0.66 EF	0.52 AB	Barazjan	0.55 KL	0.97 O-S	1.03 G-N	.	.
Marvdasht	2.40 B-D	2.47 E-K	1.90 E-G	0.97 C-F	.	Tabriz	1.24 F-L	1.65 I-S	1.05 G-N	.	.
Moqhan	3.00 B	6.10 A	5.97 B	0.93 C-F	.	Sanandaj	2.85 BC	0.88 P-S	.85 I-N	.	.
Givi	1.14 G-L	0.97 O-S	7.2 I-N	.	.	Divandare	0.84 I-L	1.10 N-S	1.24 G-L	.	.
Fozveh	2.70 BC	2.72 D-I	2.25 DE	.	.	Shabestar	1.05 G-L	0.62 RS	0.24 MN	.	.
Ardabil	2.05 C-F	2.13 G-O	3.44 C	1.40 CD	0.22 B	Fasa	1.31 F-L	4.03 BC	1.61 E-I	0.45 F	.
Arak	1.50 E-I	1.65 I-S	7.9 I-N	.	.	Shiraz	0.87 I-L	0.48 S	0.73 I-N	.	.
Kerman	1.25 F-L	2.08 G-O	1.22 G-L	.	.	Qom	0.52 L	0.67 Q-S	0.48 K-N	.	.
Tafresh	1.55 E-I	2.37 E-M	0.82 I-N	.	.	Oromie	1.25 F-L	2.38 E-L	0.68 I-N	.	.
Mahalat	0.83 I-L	1.32 K-S	0.21 N	.	.	Esfahan	0.90 I-L	1.77 H-R	1.03 G-N	.	.
Ardakan	1.31 F-L	1.83 H-Q	1.04 G-N	.	.	Rafsanjan	1.40 E-J	2.75 D-I	2.26 DE	0.60 F	.
Hasht gerd	1.30 F-L	1.95 G-P	0.42 K-N	.	.	Razan	0.63 J-L	1.42 J-S	0.63 J-N	.	.
Incheboron	1.31 F-L	2.45 E-K	0.58 J-N	.	.	Sabzevar	0.85 I-L	2.50 D-K	1.07 G-N	.	.
Nairiz	1.11 G-L	1.88 H-P	1.31 F-K	.	.	Aran bidgol	1.05 G-L	1.65 I-S	0.68 J-N	.	.

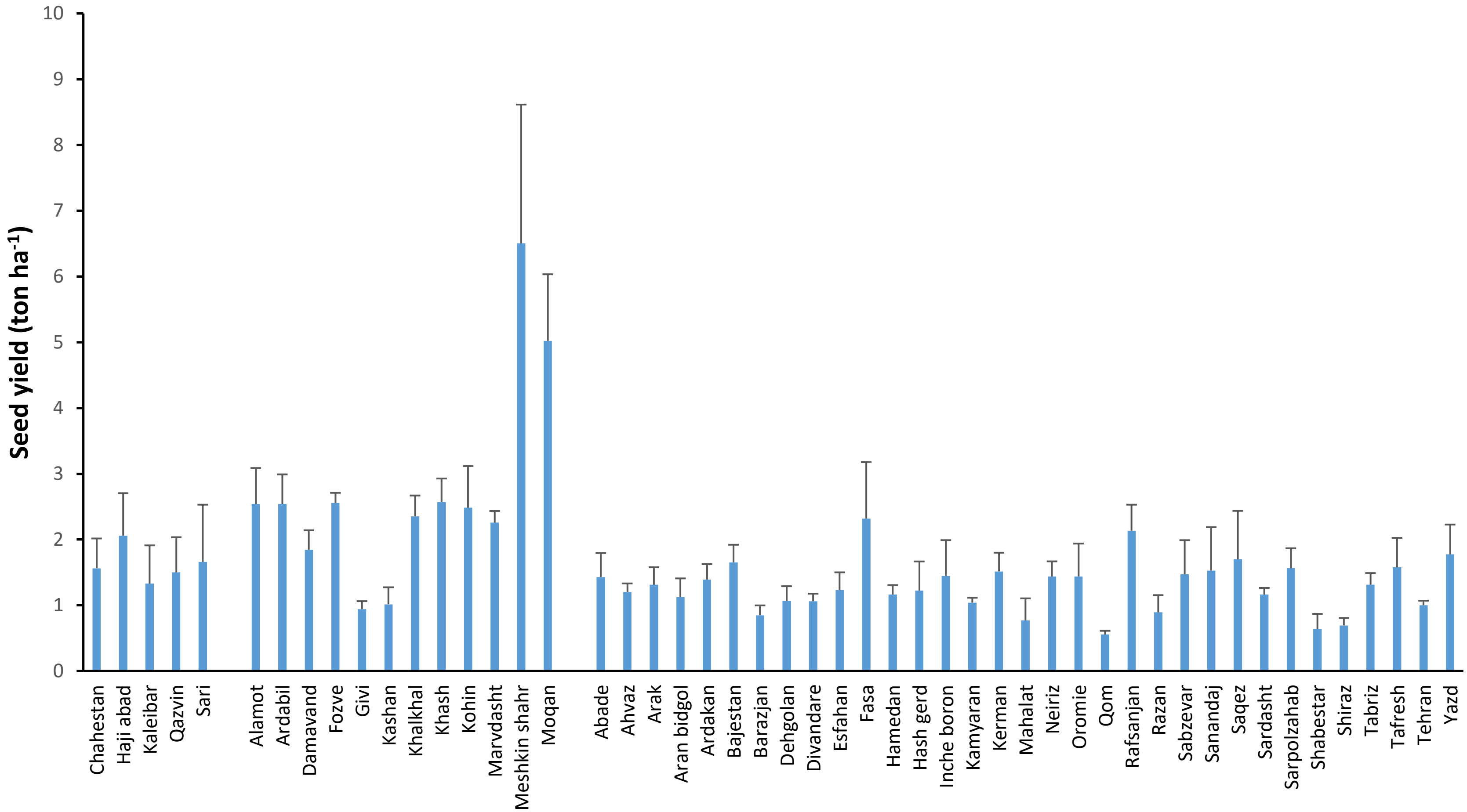

Fig. 8. Average seed yield (ton ha^{-1}) for all populations in the first three years of the study. Fennel populations: left: late-maturing, middle: intermediate-maturing, right: early-maturing.

Table 12. Analysis of variance on essential oil content in separate years.

SOV	df	Essential oil content (%)				
		Year 1	Year 2	Year 3	Year 4	Year 5
Block	2	0.15^{ns}	0.27*	0.18**	0.39^{ns}	0.01^{ns}
Landrace	49	0.36**	3.98**	0.34**	0.50**	0.26^{ns}
Error	98	0.09	0.06	0.03	0.11	0.04
Mean	-	2.54	2.41	1.77	1.76	1.2
CV (%)	-	12	11	11	19	17

Table 13. Analysis of variance on essential oil content during five years of the study.

SOV	DF	Essential oil content (%)
Landrace (L)	49	2.38**
Block	2	0.08^{ns}
Error 1	98	0.06
Year (Y)	4	17.32**
L×Y	115	1.09**
Error 2	238	0.07
Mean	-	2.18
CV (%)	-	13

During the first three years of the study, i.e., the minimum life span of all populations, essential oil content data ranged from 0.6 to 5.1% year^{-1} (average 2% ± 0.06) in early-maturing fennels, from 1.2 to 4.2% year^{-1} (average 2.6% ± 0.13) in intermediate-maturing fennels, and from 1.5 to 4.7% year^{-1} (average 2.9% ± 0.23) in late-maturing fennels (Fig. 9). The highest average of essential oil content during the first three years of the study among the early-maturing fennels belonged to Razan (3.44%) and Arak (2.9%). Among the intermediate-maturing fennels, it belonged to Fozveh (3.19%), Kashan (3.11%), and Marvdasht (3.10%). Among the late-maturing fennels, it belonged to Kaleibar (3.18%) and Sari (3.13%). Generally, higher essential oil contents appeared in intermediate- and late-maturing fennels.

Essential oil yield

In the first three years of the study, essential oil yields ranged from 2.5 to 104.6 L ha^{-1} year^{-1} (average 26.1±0.1) in early-maturing fennels, from 10.1 to 152.2 L ha^{-1} year^{-1} (average 67.7±1) in intermediate-maturing fennels, and from 7.5 to 160.9 L ha^{-1} year^{-1} (average 46.4±0.2) in late-maturing fennels. Also, during these three years, the highest average essential oil yield among the early-maturing fennels occurred in the Fasa landrace (51.4 L ha^{-1}), among the intermediate-maturing ones in the Meshkin Shahr and Moqhan landraces (140.5 and 124.9 L ha^{-1}, respectively), and among late-maturing ones in the Sari landrace (52.1 L ha^{-1}). High essential oil-yielding populations were intermediate- and early-maturing landraces, which have good potential for domestication (Fig. 10).

Table 14. Comparison of means regarding essential oil content (%) of the fifty fennel landraces during their life spans.

Landraces	Essential oil content (%)					Landraces	Essential oil content (%)				
	Year 1	Year 2	Year 3	Year 4	Year 5		Year 1	Year 2	Year 3	Year 4	Year 5
Chahestan	2.4 F-L	3.49 DE	1.7 J-Q	1.75 B-E	.	Ardakan	2.33 F-L	2.28 H-L	1.5 N-S	.	·
Haji abad	2.53 C-L	1.87 L-Q	1.52 M-S	1.59 DE	.	Bajestan	2.03 KL	1.54 O-S	1.6 L-R	.	·
Qazvin	3.06 A-D	2.3 H-L	2.5 AB	2.25 A-C	.	Hamedan	2.66 B-J	2.29 H-L	2.33 A-D	1.67 C-E	·
Sari	2.56 C-K	4.73 A	2.1 C-I	2.55 A	.	Abade	2.3 F-L	1.36 R-U	1.4 P-S	.	·
Kaleibar	3.03 A-E	4.26 B	2.25 A-F	2.25 A-C	.	Ahvaz	2.2 H-L	1.51 P-T	1.45 O-S	.	·
Alamot	2.86 A-G	3.69 CD	1.85 G-N	1.55 DE	.	Dehgolan	2.13 I-L	2.18 I-M	1.5 N-S	.	·
Kohin	2.76 B-H	4.16 B	1.75 I-P	2.35 AB	.	Sardasht	2.23 H-L	0.95 UV	1.54 M-S	.	·
Khash	2.63 B-K	3.23 EF	1.9 F-M	1.25 E	.	Saqez	2.73 B-I	1.66 N-S	1.6 L-R	.	·
Kashan	3.23 AB	4.09 BC	2 D-K	.	.	Kamyaran	2.4 F-L	1.97 K-P	2.3 A-E	.	·
Fozveh	3.4 A	3.98 BC	2.2 A-G	.	.	Nairiz	2.43 E-L	3.2 EF	2.05 C-J	.	·
Meshkin shahr	2.33 F-L	2.83 FG	1.32 Q-S	1.75 B-E	1.46 A	Barazjan	2.3 F-L	0.56 V	1.7 J-Q	.	·
Damavand	2.43 E-L	1.27 R-U	2.16 B-H	.	.	Tabriz	1.93 L	2.48 G-J	1.75 I-P	.	·
Ardabil	2.53 C-L	2.12 I-N	1.37 P-S	1.3 E	0.9 B	Rafsanjan	2.5 D-L	1.02 T-V	1.8 H-O	2.1 A-D	·
Khalkhal	3.06 A-D	2.4 G-K	1.22 RS	1.25 E	1.33 AB	Sanandaj	2.9 A-F	2.48 G-J	1.53 M-S	.	·
Marvdasht	3.13 A-C	4.23 B	1.95 E-L	1.55 DE	.	Divandare	2.36 F-L	2.02 J-O	1.85 G-N	.	·
Moqhan	2.86 A-G	2.49 G-J	2.1 C-I	1.5 DE	.	Shabestar	2.26 G-L	1.5 P-T	1.46 N-S	.	·
Givi	3.23 AB	2.85 FG	2.05 C-J	.	.	Shiraz	2.53 C-L	2.56 G-I	2.53 A	.	·
Hasht gerd	2.6 C-K	1.39 Q-U	1.65 K-Q	.	.	Qom	2.13 I-L	1.65 N-S	1.55 M-R	.	·
Tafresh	2.4 F-L	1.19 S-U	1.5 N-S	.	.	Oromie	2.7 B-I	2.85 FG	1.7 J-Q	.	·
Sarpolzahab	2.33 F-L	0.57 V	1.54 M-S	.	.	Esfahan	2.43 E-L	1.56 O-S	1.8 H-O	.	·
Incheboron	2.3 F-L	2.43 G-K	1.55 M-R	.	.	Mahalat	2.13 I-L	1.4 Q-U	1.16 S	.	·
Kerman	2.4 F-L	1.73 M-R	1.65 K-Q	.	.	Razan	2.8 B-H	5.13 A	2.4 A-C	.	·
Yazd	2.23 H-L	1.31 R-U	1.6 L-R	.	.	Sabzevar	2.03 KL	4.18 B	1.25 R-S	.	·
Arak	2.86 A-G	4.22 B	1.6 L-R	.	.	Fasa	2.7 B-I	2.50 D-K	2 D-K	1.57 DE	·
Tehran	2.06 J-L	0.98 UV	2 D-K	.	.	Aran bidgol	2.63 B-K	1.65 I-S	1.95 E-L	.	·

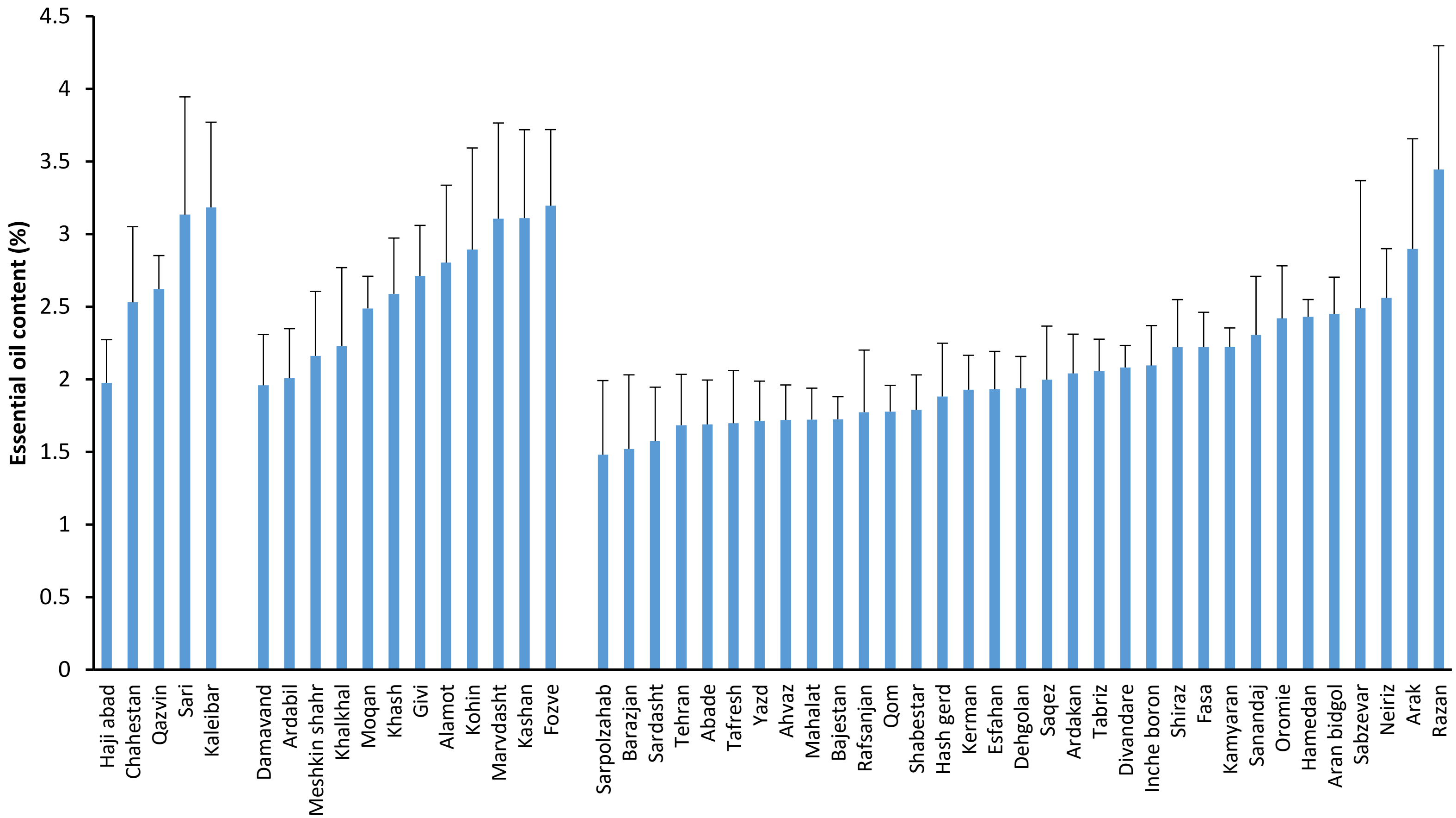

Fig. 9. Average essential oil content of the populations in the first three years of the experiment. Fennel populations: left: late-maturing, middle: intermediate-maturing, right: early-maturing.

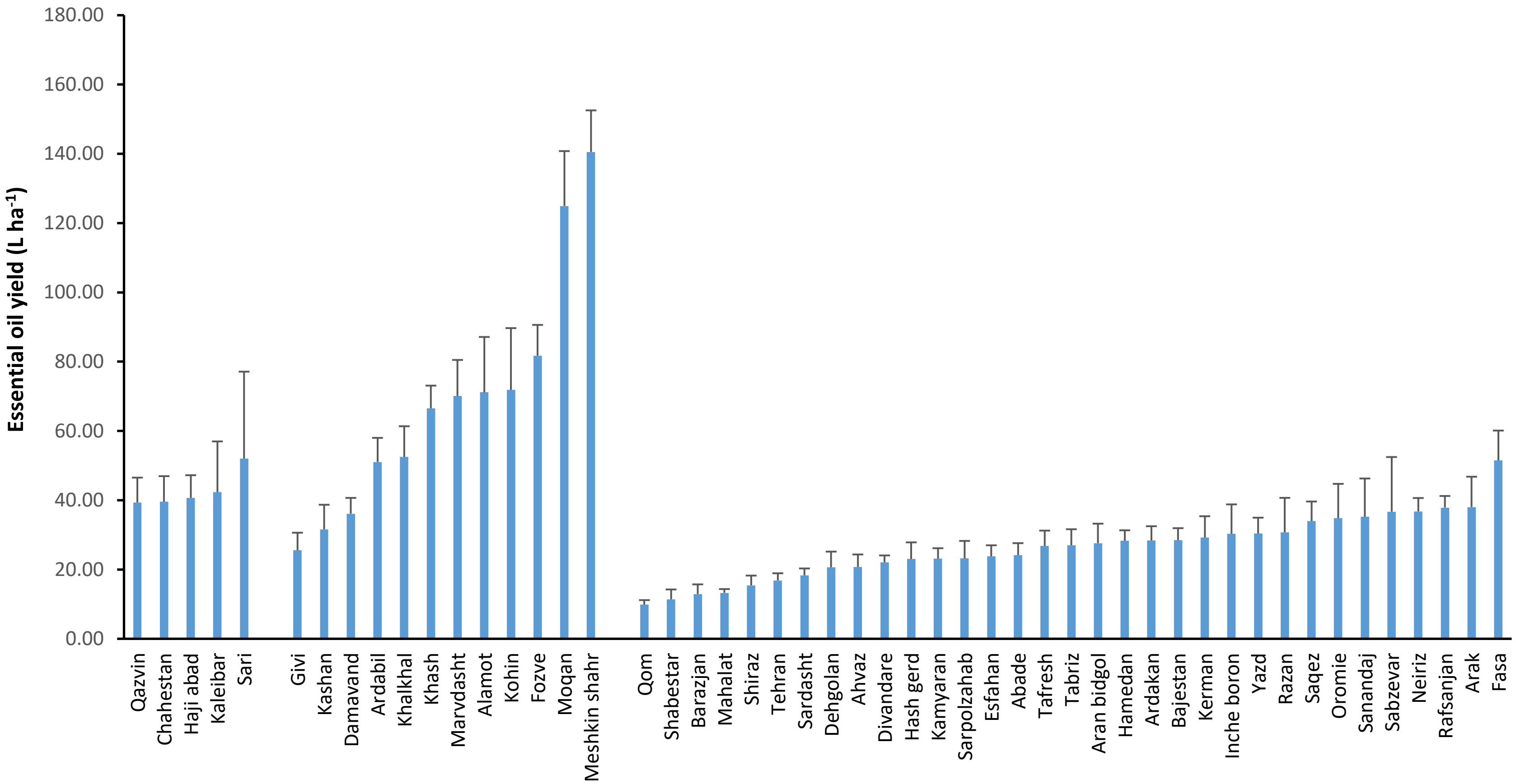

Fig. 10. Average essential oil yield (L ha^{-1}) of the populations in the first three years of the experiment. Fennel populations: left: late-maturing, middle: intermediate-maturing, right: early-maturing.

Discussion

Fennel is predominantly suitable for cultivation in arid and warm regions, such as the Mediterranean, where it appears as a traditional crop (Barazani et al., 2002). The production of fennel essential oil exhibits significant variability and is contingent upon various factors. Key determinants influencing the yield of fennel include genotype, climatic and soil conditions, and agricultural practices (Garcia-Jimenez et al., 2000; Barazani et al., 2002; Avci, 2013).

According to the analysis of variance, we observed a significant variation among the populations, years, and interaction between fennel populations and years for all the examined characteristics, indicating considerable variation among genotypes in the germplasm. Several previous reports, such as the ones by Shojaiefar et al. (2015) and Lal (2008), indicated a vast range of variability among genotypes and between years regarding economically crucial characteristics in fennel.

The studied fennel populations comprised three groups based on lifespan and number of days required to reach 70% dried seeds. It seems all fennel populations originated from regions with a similar climate, exhibiting similar maturity habits and lifespans. For example, those originating from dry areas were grouped as early-maturing with a short lifespan, while fennels from humid areas were late-maturing with a long lifespan. The remaining populations from regions with intermediate climates were intermediate-maturing with an intermediate lifespan.

Among environmental conditions, water, temperature, and light are the most influential limiting factors to plant growth. Likewise, Hawkins et al. (2003) claimed that the water-energy dynamics hypothesis is a driving factor when determining plant properties. When confronted with these limiting factors, especially drought and temperature stresses, plants may adopt one of these solutions: escape, avoidance, and tolerance. Escape means when the plant reaches maturity before receiving significant stress signals and includes signal responses to daylight (as an alarm that warm and dry weather can arrive soon). While it is the easiest solution (Chai et al., 1993), Iranian fennels appear to use escape to avoid water and temperature stresses.

According to Pearcy et al. (2004) and Chen et al. (2010), plants from dry and hot/cold areas, also known as exposed areas, have fewer flowers, larger seeds, slower seed germination, and shorter plants with low biomass. Plants from humid and temperate regions, also known as shaded areas, have more flowers, smaller seeds, faster seed germination, and taller plants with more biomass. To test this hypothesis in our study, we evaluated some morphological data, including the 1000-seed weight, germination rate in 15 days, plant height, and inflorescent number of the same fifty Iranian fennels in each of the three maturity habits (Figs. 4, 5, 6, and 7, respectively). The morphological data originated from Bahmani et al. (2016). It was evident that late-maturing fennels were taller, had more inflorescences, faster seed germination, and a lower 1000-seed weight, and vice versa for early-maturing fennels. Intermediate-maturing fennels stood between early and late-maturing ones. Usually, shaded areas have denser vegetative coverage, and plants may encounter problems in carbon assimilation due to sunlight limitations (Bedetti et al., 2011), which results in less photosynthesis and smaller seeds. However, sunlight limitations can trigger plants to grow taller and have more vegetative and reproductive growth. This growth can lead to more seeds per plant and more energy consumption to transfer food over a longer distance between sources and sinks. All these factors result in fewer nutrients for every single seed. The reverse of this narrative is true for early-maturing fennels in exposed areas. Intermediate-maturing fennels have an intermediate state between late- and early-maturing fennels.

In exposed areas, water-deficit stress has always been a grave reason for seedling death, so seeds have forcibly developed defense mechanisms, including delayed and scattered germination, to increase the chance of seedling survival and establishment (Sales et al., 2013; Moles and Westoby, 2004; Larcher, 2000; Baskin and Baskin, 1998). The cause of delayed and scattered germination of seeds can be a thicker seed cover and water-soluble germination inhibitors that take longer to dissolve and let the seed germinate (Abdollahi et al., 2012; Al-Taisan et al., 2010). In shaded areas in temperate regions, plants often do not have to deal with water and temperature stresses. However, sunlight shortages occur due to high competition among densely grown plants. Thus, mechanisms leading to faster germination and growth can provide seedlings with more time and less competition. Fast germination may enhance seed survival by shortening their exposure time to seed eaters and pathogens (Silveira and Oliveira, 2013; Bedetti et al., 2011; Verdu and Traveset, 2005).

In shaded areas, growth conditions are more suitable. Plants can have higher vegetative and reproductive growth, so plants have to grow taller to intercept more sunlight (Silveira and Oliveira, 2013; Pearcy et al., 2004). Plants in exposed

regions are limited in vegetative and reproductive growth because of water deficiency and extreme temperatures. They reduce the evaporation surface, so less vegetative growth is vital (Chen et al., 2010; Ramírez Valiente et al., 2009). These indications confirm the observations in this study. Iranian fennels in the second year had their maximum seed yield. In a report by Ehsanipour et al. (2012), the seed yield of four studied fennels ranged from 44 to 105 g m^{-2} (without applying fertilizers). In another report by Shojaiefar et al. (2015), the seed yields of eighteen studied fennels, while applying fertilizers, in the first and second years ranged from 40 to 390 g m-2 and from 24 to 420 g m^{-2}, respectively. They also reported that the seed yield in the second year was about 50% more than in the first year, which confirms the current results. Also, Iranian fennels in the first and second years showed the most essential oil content. In a report by Ehsanipour et al. (2012), the essential oil content of four studied fennels ranged from 1.2 to 1.62%. In another report by Shojaiefar et al. (2015), the essential oil contents of eighteen studied fennels, while applying fertilizers, in the first and second years ranged from 1.5 to 4.4% and from 2 to 3.7%, respectively. The same authors also reported that fennel essential oil content in the first year was about 12% more than in the second year.
Furthermore, Aprotosoaie et al. (2010) showed that fennel essential oil contents in the first and second years were much higher than in the third, which confirms our results. Higher essential oil contents appeared in intermediate- and late-maturing fennels. Intermediate- and late-maturing populations originated in regions with longer and proper growth conditions. This circumstance is an evolutionary mechanism that led them to higher vegetative growth and higher secondary metabolite production. Similar results appeared from a study by Zahid et al. (2008), indicating that late-maturing fennel populations with higher vegetative growth have higher essential oil content.

Conclusion

This study showed wide diversity among Iranian fennels regarding life span, maturity habit, seed yield, essential oil content, and essential oil yield. Our results showed how limiting growth factors such as extreme seasonal temperature changes and accessibility to adequate water and light over time can shape phenological and morphological features in Iranian fennels. This fennel germplasm can be a primary source of diversity and gene pool for future fennel breeding programs. Some populations, such as Fasa and Meshkin Shahr, can become a focus in future studies that consider genotype interactions with environments.

Conflict of Interest

The authors indicate no conflict of interest in this work.

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