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SEED GERMINATION PLASTICITY OF TWO ENDANGERED SPECIES OF *FERULA* IN THE CONTEXT OF CLIMATE CHANGE

ABSTRACT

Ferula assa-foetida and *F. gummosa*, *Apiaceae*, are important endemic and endangered medicinal plants. Survival of the species is threatened by climate change, overexploiting (as source of oleo-gum resin and forage) and lack of organized cultivation. Cultivation of these valuable medicinal plants is restricted by insufficient domestication knowledge. Germination characteristics of different populations of *Ferula* taxa were studied with the aim of describing and comparing their responses to continuous cold stratification condition. Germination cues for the species were complex, with dormancy mechanisms present to restrict germination until cold stratification are fulfilled. Results indicated that a period of 4 weeks of stratification is sufficient for germination of *F. assa-foetida*, but optimal germination of *F. gummosa* require stratification for periods of 8 weeks. Both species were able to germinate at very low temperatures (4°C). Within-taxon differences in dormancy breaking and seedling emergence may interpret as local adaptations. The continued regeneration and propagation of the species in the wild will depend on the temperature and moisture status of the soil during winter and the maintenance of conditions suitable for stratification for an appropriate length of time.

Key words: dormancy, global warming, highland, Iran, local adaptation

INTRODUCTION

Seed germination is a critical stage in the life cycle of plants, particularly when considering the effects of global warming on high-altitude species. This is due to the dependence of these species on specific temperature regimes to stimulate germination and ensure seedling development coincides with favorable growing conditions (Mondoni *et al.* 2008, 2011;

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Milbau *et al.* 2009). The germination emergence stage is a high-risk phase of the plant life cycle, and therefore seed-based research can be useful in identifying species at risk of extinction from climate change, i.e. species with a narrow germination niche in terms of temperature range and/or stratification requirement (Cochrane *et al.* 2011; Walck *et al.* 2011). Information of this type provides a link between environmental change and the mechanisms that control population processes (Ooi *et al.* 2009; Cochrane *et al.* 2011; Walck *et al.* 2011; Ooi 2012), and can thus help to improve the accuracy of models predicting plant response to climate change (Ooi 2012).

Ferula assa-foetida and *F. gummosa*, *Apiaceae*, are important endemic and endangered medicinal plants. The taxa are monocarpic, herbaceous and perennials spread at altitudes of 1500–2500 m, with an average annual precipitation of 350–700 mm of Iran (Safaian and Shokri 1993; Mozaffarian 1996; Ivan 2007; Amiri and Joharchi 2016). Recently, survival of the species is threatened by climate change, overexploiting (as source of oleogum resin and forage) and lack of organized cultivation. Cultivation of these valuable medicinal plants is restricted by edaphic and climatic factors, low percentage of seed set and seasonal dormancy, and insufficient domestication knowledge (Golmohammadi *et al.* 2016).

According to Baskin and Baskin (2014), linear embryos in the *Apiaceae* are under-developed, and seeds have morphological dormancy (MD) or morphophysiological dormancy (MPD). Normally, seeds with MD only need suitable temperature, moisture, oxygen, and of course time to germinate (Baskin and Baskin 2014). However, in many cases, the fully differentiated under-developed embryos also have physiological dormancy (PD), which imposes an additional constraint to germination; such embryos do not germinate in less than one month in suitable germination conditions. In this case, the dormancy is not just morphological but morphophysiological (MPD), and the embryos require additional treatment, such as cold, to complete their growth. Previous studies have classified *F. gummosa*, and *F. asafetida* as having deep morphophysiological dormancy, since cold stratification had been suggested as the main dormancy-breaking treatment (Otroshi *et al.* 2009; Rouhi *et al.* 2012). Formation of deep MPD seems to be an adaptation to regions with a very cold winter and a dry, cool summer. In these areas, temporary sporadic favorable temperatures (elevated temperature) in winter or too early in winter are threatening for seedling establishment. Therefore, the dormancy helps seeds to remain un-germinated throughout the winter. Moreover, the low temperatures alleviate dormancy and once dormancy *breaks, two possible scenarios might o*ccur: non-dormant seeds either wait for a mild and moist spring to germinate, or they germinate at low temperatures in the middle of winter in cold soil, even covered with heavy snow, until late winter; while the shoots grow and emerge above the soil surface with the increase in temperature (Baskin and Baskin 2014).

Different dormancy breaking and germination stimulating treatments have been tried with seeds of many species of *Apiaceae* (Baskin and

Baskin 1991; Baskin *et al.* 1992, 1995, 1999, 2000; Nadjafi *et al.* 2006; Amooaghaie 2009; Nowruzian *et al.*,, 2016; Fasih and Tavakkol Afshari 2018). Results of different treatments including various levels of gibberellic acid, HNO_3, chilling and soaking with water at different temperatures showed that moist-chilling and gibberellic acid treatments seem the most promising in *Ferula* species. The best treatments for *F. assa-foetida* was moist-chilling for 4 weeks at 5±1°C or for 2 weeks of moist-chilling (at 5±1°C) followed by soaking GA_3 (10 $mg \times l^{-1}$) solution for 24 h (Nowruzian *et al.*, 2016). In similar way treatment of moist-chilling for 6 weeks or 4 weeks followed by 500 ppm gibberellic acid is recommended for *F. ovina* (Fasih and Tavakkol Afshari 2018). Washing and chilling (5±1°C) for a period of 14 days was most effective in breaking dormancy in *F. gummosa* (Nadjafi *et al.* 2006).

According field observations of authors, cold stratification causes embryos to complete growth and germinate in the middle of winter in cold soil or covered with heavy snow. Shoots grow and emerge above the soil surface following increasing of temperature in early spring. Therefore the first objective of the present work is stimulation of the only natural treatment, cold stratification, and study of dormancy termination time and seedling growth in *F. assa-foetida*, *F. gummosa*. Differences of the present work with earlier are in unlimited cold stratification duration for dormancy breaking; and exposing moist chilling condition for seedling growth. Moreover, study of differences and similarities among closely related taxa in order to increase understanding of adaptations and changes in seed dormancy and germination preferences. One difficulty when comparing seed dormancy and germination between taxa is the intra-taxon variation. Variation within a taxon may depend on genetic differences, local weather during growth of mother plants and maturation of seeds, seed position on the mother plant, soil quality, or other naturally occurring factors. To be able to draw conclusions on a general level, for example for modeling or predicting changes in emergence pattern following climate change, knowledge about a taxon, including its variation, is needed. Therefore for investigation of the impact of the habitat variability, germination characteristics among different populations of *F. assa-foetida* and *F. gummosa* were studied under continuous moist chilling conditions. Information about germination can also improve the success rate of using seed for rehabilitation, which is critical to restoration of the high altitude rangelands.

MATERIALS AND METHODS

Seed material of 23 accessions of the two *Ferula* taxa from all over Iran were obtained from Natural Resources Gene Bank, Iran (Table 1).

Table 1

Some details of the studied wild *Ferula* populations.

Province	Pop.	Code	Latitude [decimal]	Longitude [decimals]	Altitude [m above sea level]	Mean annual precipitation [mm]
		F. assa-foetida				
Hormozgan	Bandar Abbas	FaBandarA1	28.17	56.83	2200	178
Hormozgan	Bandar Abbas	FaBandarA2	27.88	50.22	1845	179
Khorasan	Boshroye	FaBoshroye	33.96	57.17	893	94
Hormozgan	Haji Abad	FaHajiAbad	28.94	56.46	1900	179
Esfahan	Kashan	FaKashan	33.75	51.48	1800	137
Kerman	Kerman	FaKerman	30.09	57.76	2300	133
Fars	Lar	FaLar	27.46	54.39	2000	200
Yazd	Mehriz	FaMehriz	33.36	57.34	1565	84
Yazd	Tabas	FaTabas1	33.39	57.26	1536	56
Yazd	Tabas	FaTabas2	31.52	54.32	2090	56
Yazd	Taft	FaTaft	31.66	54.18	2122	60
Kerman	Zarand	FaZarand	30.88	56.88	2300	47
		F. gummosa				
Kohkeluye and Boyerahman	Dena	FgDena	30.50	51.72	2560	760
Elam	Elam1	FgEelam	33.63	46.41	1000	575
Hormozgan	Haji Abad	FgHajiAbad	28.12	56.84	2200	178
Charmahal Bakhtiali	Lordegan	FgLordegan	31.42	51.26	2683	555
Semnan	Shahrod	FgShahrod	35.87	56.65	950	139
Yazd	Tabas	FgTabas	33.36	57.34	1565	84
Yazd	Taft	FgTaft	31.56	54.16	2439	60
Kohkeluye and Boyerahman	Yasuj	FgYasuj1	30.48	51.79	2300	855
Kohkeluye and Boyerahman	Yasuj	FgYasuj2	31.94	51.44	1950	855
Kohkeluye and Boyerahman	Yasuj	FgYasuj3	30.45	51.65	2420	855
Kerman	Zarand	FgZarand	30.88	56.87	2400	47

For each accession 150 seeds were sterilized with 70% ethyl alcohol for five minutes, and then washed with distilled water. Three replicates (50 seeds per replicate) of sterilized seed were placed in Petri dishes on double Whatman papers (TP). For protection against moulds, the water used to moisten the seed samples and substrata contained 0.002% Binomial fungicide. The samples were immediately transferred into a germinator at 4±1°C and 12/12 h light (400 lux)/dark for 60 days. Following germination, the percent and speed of germination were recorded every two days until the end of the experiment (two months). The length of roots and shoots of 10 randomly-selected seedlings from each replicate were measured in 30 days seedlings. After measuring shoot and root lengths, the cary-

opses were cut from the seedlings and fresh seedling weight of each replicate was recorded. The seedlings were then placed in an oven at 80°C for 24 hours, after which the dry weight of each replicate was recorded as a percentage of the fresh weight. The vigor index measures seedling performance, relating together the germination percentage and growth of seedlings produced after a given time (Abdul-Baki and Anderson 1973).

Data analysis

Analyses of variance (ANOVA) were conducted for seed germination traits including dormancy termination (days), germination period (days), germination%, germination rate, germination Index, seed vigor index, radicle length [mm], shoot length [mm], seedling length [mm], radicle/shoot length ratio, seedling fresh weight [mg], seedling dry weight (mg] and seedling dry matter%; and seed morphology traits including seed weight [g], seed length (mm], seed width (mm] and 1000 seeds weight (g] using the SAS9 software (SAS Institute Inc). To assess the relationships among the 13 different traits Pearson's correlation coefficient was analyzed using statistical analysis system software (SAS version 9.1, SAS Institute, 2001). The standardized morphological data were employed to calculate the Euclidean distances among the 23 *Ferula* genotypes by NTSYS-pc version 2.1 (Rohlf 2002). Moreover, unweighted pair group methods of arithmetic mean (UPGMA) algorithm and SAHN clustering were also utilized to get the genetic relationships. The Principal component analysis (PCA) of 23 *Ferula* genotypes was determined by Minitab software (version 15).

RESULTS

Seeds Length, width and weight of *F. assa-foetida* (in length: 8 – 15 mm; in width: 4 – 7.7 mm; in weight: 9 – 23 mg) and *F. gummosa* (in length: 9-15 mm; in width: 6.5-10 mm; in weight: 7.7-32 mg) ranged among populations of each species (Table 2). ANOVA suggested significant differences among wild populations of *Ferula* species for the seed characteristics. A relatively high CV was obtained for seed weight (Table 2).

Table 2

Mean comparisons of seed morphological characteristics of 23 populations of *Ferula assa-foetida* (with prefix Fa) and *F. gummosa* (with prefix Fg) constant cold stratification. Different letters indicate significant differences among different populations for the same species. P <0.05

Pop.	Seed weight [mg]	Seed length [mm]	Seed width [mm]
	F. assa-foetida		
FaBandA1	12.23 c-f	9.73 f	5.47 c
FaBandA2	13.57 cd	9.30 f	5.67 c
FaBoshro	13.00 cde	15.17 a	7.65 a
FaHajiAb	8.90 f	7.68 g	4.12 d
FaKashan	16.93 b	11.77 bcd	6.97 b
FaKerman	23.00 a	12.21 bc	6.95 b

Table 2

Continued

Pop.	Seed weight [mg]	Seed length [mm]	Seed width [mm]
	F. assa-foetida		
FaLar	15.23 bc	12.40 b	5.93 c
FaMehriz	9.23 f	11.23 cd	5.77 c
FaTabas1	10.33 def	10.07 ef	5.93 c
FaTabas2	10.13 ef	10.98 ed	5.87 c
FaTaft	10.33 def	11.82 bcd	6.80 b
FaZarand	17.77 b	12.08 bc	6.72 b
Mean	13.37	11.19	6.15
Cv	43.86	16.95	16.6
	F. gummosa		
FgDena	20.07 bc	12.60 b	7.30 bc
FgEelam	15.00 d	12.53 b	6.40 ef
FgHajiAb	14.70 d	10.72 cd	5.97 f
FgLordeg	32.17 a	14.75 a	7.60 b
FgShahro	22.20 b	12.75 b	10.08 a
FgTabas	7.70 e	9.92 d	6.50 def
FgTaft	6.17 e	8.87 e	5.32 g
FgYasuj1	19.77 bc	12.87 b	7.10 bcd
FgYasuj2	22.10 b	13.33 b	7.18 bc
FgYasuj3	17.00 cd	12.43 b	6.40 ef
FgZarand	15.57 d	11.13 c	6.75 ced
Mean	17.49	11.99	6.96
Cv	37.51	17.1	16.36

Both species *F. assa-foetida* and *F. gummosa*, failed to germinate without prior stratification. However, cold stratification stimulated the germination of both species. ANOVA suggested significant differences among wild populations of *Ferula* species for all the seed germination traits. A relatively high CV was obtained for germination period, germination rate, seed vigor index, seedling fresh weight and seedling dry weight; moderate to low values of CV were obtained for the remaining traits (Table 3). Comparison of means verified that the duration of dormancy termination was significantly longer in *F. gummosa* (ranged from 31-51 days, with average 42 days) than *F. assa-foetida* (ranged from 12-28 days, with average 19 days) (Table 3; Fig. 1). Different populations of *F. assa-foetida* species had the significantly higher germination period, germination%, germination rate, germination Index, seed vigor index and radicle length values (Table 3). In the species *F. assa-foetida* the highest germination characteristics (germination percentage, rate and index) were obtained in the population FaTabas1and the highest seedling parameters (radicle and shoot length, and seedling fresh weight) were obtained in the populations FaTaft and FaZarand; however, the seedling dry matter percentage for the FaTaft and FaZarand showed the lowest values. In the species *F. gummosa* the highest germination characteristics (germination per-

cent, rate and index) were obtained in the populations FgLordegan and FgTaft and the highest seedling parameters (radicle and shoot length, and seedling fresh weight and seedling dry matter percent) were obtained in the population FgYasuj2 (Table 3). Populations FgYasuj1, 2, 3 of the species *F. gummosa*, with closely similar habitats and geographical ranges, were found to have markedly different dormancy and germination characters (Table 3). Variation within a taxon may depend on genetic differences, local weather during growth of mother plants and maturation of seeds, seed position on the mother plant, soil quality, or other naturally occurring factors.

Table 3

Mean comparisons of seed germination characteristics of 23 populations of *Ferula assa-foetida* (with prefix Fa) and *F. gummosa* (with prefix Fg) under constant cold stratification. Different letters indicate significant differences among different populationsfor the same species. P <0.05

Pop.	Dormancy termination [days]	Germination period [days]	Germination [%]	Germination rate	Germination Index	Seed vigor index
Ferula assa-foetida						
FaBandA1	14.33 d	10 ab	50.67 cd	8.427 bc	478.2 cd	42.9 abc
FaBandA2	16.33 cd	16.67 ab	70.67 abc	6.3 cde	472.3 cd	32.4 a-d
FaBoshro	23 ab	10.67 ab	26.67 de	2.797 ed	220.4 de	14.94 dc
FaHajiAb	13.67 d	9.333 ab	46.67 cde	7.337 bcd	433.6 cd	17.28 bcd
FaKashan	21.67 bc	20.67 a	66.67 abc	7.95 bcd	562.7 bc	46.78 ba
FaKerman	28.33 a	20.67 a	58.67 abc	4.273 cde	390.6 cd	33.57 a-d
FaLar	28.33 a	20.67 a	20 e	1.343 e	122.9 e	6.51 d
FaMehriz	26.33 ab	16 ab	62.67 abc	5.86 cde	481.8 cd	26.45 a-d
FaTabas1	13 d	10 ab	86.67 a	15.19 a	824.5 a	39.8 abc
FaTabas2	12.33 d	6.667 b	80 ab	14.43 a	771.6 ab	42.93 abc
FaTaft	12.33 d	8 b	62.67 abc	11.63 ab	607.1 abc	53.4 a
FaZaran	17 cd	13.33 ab	53.33 bcd	7.817 bcd	486.7 cd	46.41 abc
Mean	18.89	13.56	57.11	7.78	487.71	33.61
Cv	16.93	45.19	26.36	36.0	29.1	48.27
Ferula gummosa						
FgDena	45 bcd	7.333 cb	20 c	0.763 e	91.77 d	13.28 ef
FgEelam	45 bcd	8.667 cb	30.67 c	1.133 de	138.5 d	12.98 ef
FgHajiAb	48.33 bc	4 c	69.33 ab	2.347 cd	295.8 c	29.25 cd
FgLordeg	38.33 de	11.33 cb	78.67 a	3.94 ab	439.1 ab	69.25 a
FgShahro	51.67 ab	4.667 c	29.33 c	0.823 e	106.7 d	13.03 ef
FgTabas	35 e	9.333 cb	65.33 ab	4.11 ab	417.2 abc	33.72 cb
FgTaft	32.33 e	14 b	72 ab	5.08 a	489.6 a	25.48 cde
FgYasuj1	33 e	22.67 a	70.67 ab	2.767 bc	322.4 bc	43.42 b
FgYasuj2	56.33 a	2.667 c	16 c	0.253 e	36.04 d	16.93 def
FgYasuj3	43 cd	10 cb	18.67 c	0.8 e	93.37 d	6.267 f
FgZarand	31.67 e	14.67 b	56 b	3.577 bc	359.6 abc	26.12 cde
Mean	41.79	9.94	47.88	2.33	253.63	26.34
Cv	8.72	45.04	24.69	32.93	28.13	28.83

Table 3

Continued

Pop.	Radicle length [mm]	Shoot length [mm]	Seedling length [mm]	Radicle/shoot length ratio	Seedling fresh weight [mg]	Seedling dry weight [mg]	Seedling dry matter [%]
			Ferula assa-foetida				
FaBandA1	28.13 a	46.45 abc	74.58 ba	0.613 ab	34.67 ab	2.333 b	6.72 d
FaBandA2	16.33 abc	29.73 cd	46.07 bcd	0.573 ab	20.73 ab	2.167 b	5.7 d
FaBoshro	18.52 abc	37.95 bcd	56.47 a-d	0.503 abc	19.5 ab	2.157 b	11.84 b
FaHajiAb	11.17 c	29.49 cd	40.66 dc	0.397 abc	22.69 ab	7.623 a	5.8 d
FaKashan	13.2 bc	55.03 ab	68.23 abc	0.253 c	34 ab	3.167 b	9.49 c
FaKerman	23.43 abc	34.07 bcd	57.5 a-d	0.7 a	34.33 ab	2.833 b	8.4 c
FaLar	11.92 c	19.36 d	31.28 d	0.627 ab	17.98 b	2.987 b	16.57 a
FaMehriz	14.2 bc	28.23 cd	42.43 dc	0.51 abc	25.26 ab	1.333 b	6.2 d
FaTabas1	16.9 abc	27.57 cd	44.47 bcd	0.6 ab	13.8 b	1.233 b	9.83 c
FaTabas2	21.1 abc	31 cd	52.1 bcd	0.653 ab	12.73 b	1 b	8.15 c
FaTaft	22.4 abc	60.97 a	83.37 a	0.357 bc	29.13 ab	1.833 b	6.49 d
FaZaran	25.73 ab	61.03 a	86.77 a	0.46 abc	40.63 a	2.4 b	6.07 d
Mean	18.59	38.41	56.99	0.52	25.46	2.59	15.35
Cv	37.6	30.2	28.53	30.36	44.94	60.57	14.36
			Ferula gummosa				
FgDena	22.99 cb	42.69 b	65.68 b	0.537 ab	36.4 b	4.067 c	11.53 bcd
FgEelam	8.817 d	36.44 cb	45.26 cd	0.26 b	17.31 cd	1.577 d	9.33 cde
FgHajiAb	13.87 cd	28.4 c	42.27 d	0.54 ab	26.87 cb	1.167 d	4.35 f
FgLordeg	23.13 cb	66.33 a	89.47 a	0.347 b	68.23 a	7.567 a	11.11 cd
FgShahro	14.2 cd	28.59 c	42.78 d	0.483 ab	11.06 d	1.263 d	11.97 cb
FgTabas	15.8 bcd	36.03 cb	51.83 bcd	0.44 ab	17.9 cd	1.633 d	7.257 e
FgTaft	11.6 d	24.13 c	35.73 d	0.483 ab	17.2 cd	1.3 d	7.51 e
FgYasuj1	25.2 b	36.27 cb	61.47 cb	0.697 a	36.87 b	3.267 c	8.977 de
FgYasuj2	42.1 a	62.19 a	104.3 a	0.673 a	18.71 cd	5.98 b	31.03 a
FgYasuj3	9.667 d	35.81 cb	45.47 cd	0.273 b	21.86 cd	3.167 c	14.2 b
FgZarand	13.8 cd	32.43 cb	46.23 cd	0.457 ab	19.33 cd	1.433 d	7.893 e
Mean	18.29	39.03	57.32	0.47	26.52	2.95	11.38
Cv	30.16	17.17	16.72	32.75	28.44	27.74	13.34

Using Pearson's correlation, an analysis was done to assess the relationship among the germination and seedling traits. It is useful to determine the relationship among the traits since this information will be useful in the utilization of the germplasm as well in the collection of the germplasm based on the target traits. The correlations among measured traits are shown in Table 4. Dormancy termination, as the most important trait, was positively and significantly correlated with important germination characters including germination percentage, germination rate and seedling vigor index; and negatively correlated with all seed morphological charac-

ters. Germination percentage exhibited a positive and significant correlation with germination rate, germination index and seedling vigor index (Table 4; Fig. 2).

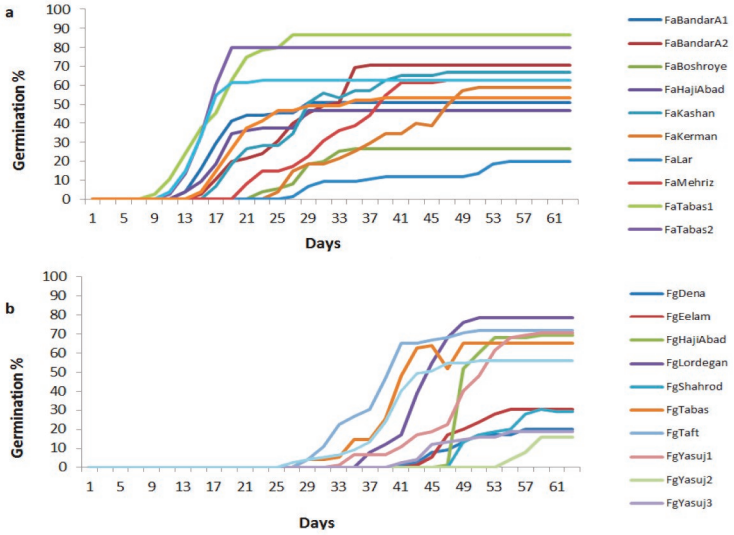

Fig.1. Comparison of germination percentage of different populations of *Ferula assa-foetida* (a); with prefix Fa) and *F. gummosa* (b); with prefix Fg) under constant cold stratification

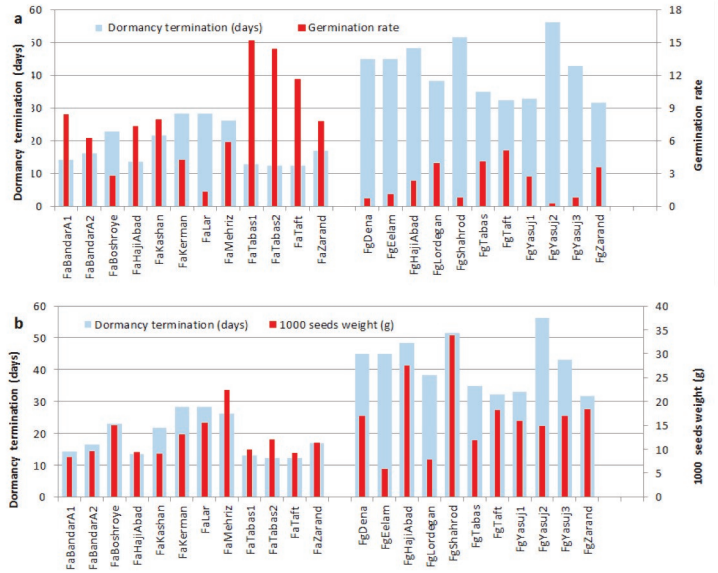

Fig. 2. Comparison of dormancy termination with germination rate (a) and with 1000 seeds weight (b) of different populations of *Ferula assa-foetida* (with prefix Fa) and *F. gummosa* (with prefix Fg) under constant cold stratification

Table 4

Pair wise correlation between seed (germination and morph) characteristics of different populations of Ferula taxa under constant cold stratification

	(1)	(2)	(3)	(4)	(5)	(6)	(7)	(8)	(9)	(10)	(11)	(12)	(13)	(14)	(15)	(16)
(1)	1.000															
(2)	-0.346	1.000														
(3)	-0.497*	0.246	1.000													
(4)	-0.83**	0.013	0.678**	1.000												
(5)	-0.79**	0.166	0.863**	0.944**	1.000											
(6)	-0.45*	0.178	0.778**	0.593**	.709**	1.000										
(7)	0.066	-0.188	-0.066	0.044	-0.034	0.335	1.000									
(8)	0.026	-0.172	-0.025	0.064	0.029	0.554**	0.634**	1.000								
(9)	0.044	-0.195	-0.044	0.063	0.007	0.521*	0.840**	0.952**	1.000							
(10)	-0.077	0.130	0.100	0.083	0.059	-0.016	0.529**	-0.281	0.012	1.000						
(11)	-0.013	0.244	0.224	-0.053	0.067	0.638**	0.340	0.649**	0.589**	-0.149	1.000					
(12)	0.139	-0.036	-0.216	-0.228	-0.242	0.085	0.327	0.450*	0.445*	-0.128	0.537**	1.000				
(13)	-0.101	-0.040	-0.194	-0.075	-0.143	-0.274	0.032	-0.092	-0.052	0.052	-0.169	0.533**	1.000			
(14)	0.506*	0.053	-0.222	-0.464*	-0.430*	0.170	0.397	0.481*	0.494*	0.019	0.623**	0.503*	-0.025	1.000		
(15)	0.432*	-0.005	-0.405	-0.446*	-0.478*	-0.005	0.318	0.437*	0.432*	-0.050	0.353	0.173	-0.318	0.700**	1.000	
(16)	0.511*	-0.148	-0.293	-0.397	-0.410	-0.010	0.223	0.298	0.297	-0.043	0.126	-0.059	-0.308	0.640**	0.731**	1.000

(1) Dormancy termination, (2) Germination period, (3) Germination%, (4) Germination rate, (5) Germination Index, (6) Seed vigor index, (7) Radicle length, (8) Shoot length, (9) Seedling length, (10) Radicle/shoot length ratio, (11) Seedling fresh weight , (12) Seedling dry weight, (13) Seedling dry matter %, (14) Seed weight, (15) Seed length, (16) Seed width

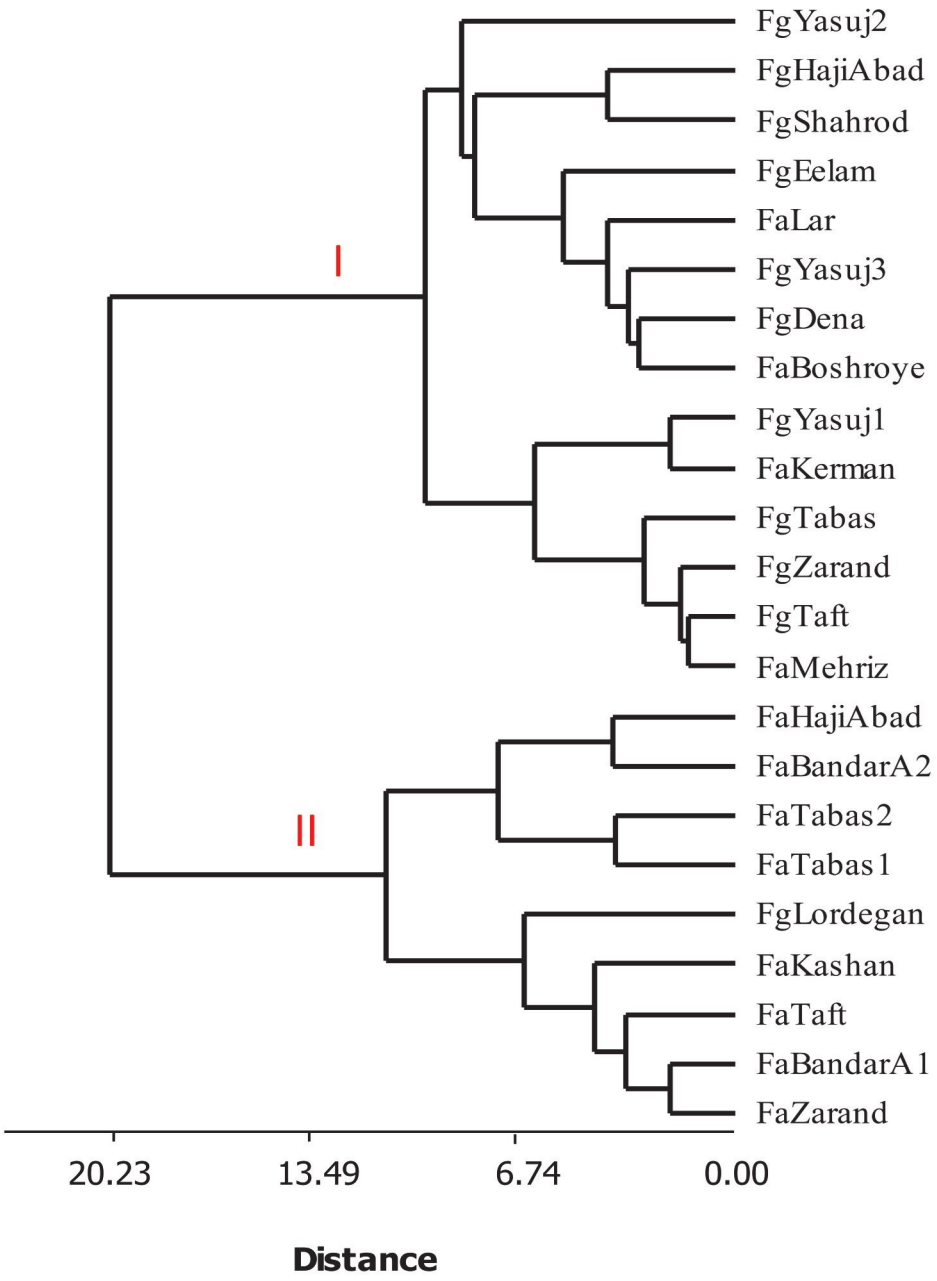

Fig. 3. Dendrograms of the 23 populations of *Ferula assa-foetida* (with prefix Fa) and *F. gummosa* (with prefix Fg) under constant cold stratification based on studied traits

Table 5

Pearson correlation analyses for the relationship between seed (germination and morphological) characteristics within different populations of Ferula taxa under constant cold stratification and some ecological parameters

Characters / Ecological parameters	Latitude	Longitude	Altitude	Mean annual precipitation
Dormancy termination	0.200	-0.321	-0.028	0.61**
Germination period	-0.218	-0.028	0.195	-0.112
Germination%	-0.017	0.203	0.224	-0.45*
Germination rate	0.032	0.286	0.037	-0.6**
Germination Index	0.037	0.307	0.116	-0.6**
Seed vigor index	0.002	0.052	0.361	-0.224
Radicle length	-0.084	-0.004	0.275	0.319
Shoot length	0.140	-0.265	0.264	0.274
Seedling length	0.065	-0.187	0.294	0.319
Radicle/shoot length ratio	-0.328	0.331	0.131	-0.020
Seedling fresh weight	-0.218	-0.157	0.56**	0.267
Seedling dry weight	-0.238	-0.271	0.330	0.495*
Seedling dry matter%	-0.345	-0.247	-0.079	0.155
Seed weight	0.016	-0.315	0.262	0.535**
Seed length	0.343	-0.263	-0.106	0.444*
Seed width	0.574**	-0.057	-0.263	0.206

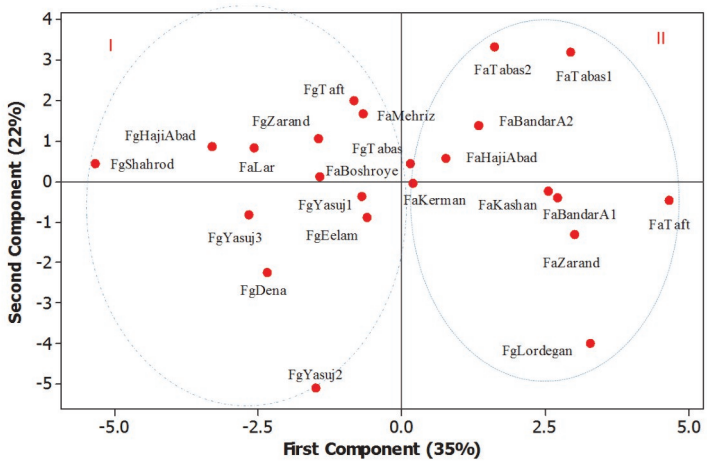

Fig. 4. Scatter diagram of the 23 populations of *Ferula assa-foetida* (with prefix Fa) and *F. gummosa* (with prefix Fg) under constant cold stratification based on studied traits

Table 6

Mean comparisons of seed (germination and morph) characteristics of populations that separated in two clusters of Fig. 4. Different letters indicate significant differences among different populations for the same species. P <0.05

Characters / Cluster	I	II
Dormancy termination	36.85a	17.28b
Germination period	12.40a	11.67a
Germination %	46.53b	66.70a
Germination rate	2.78b	9.38a
Germination Index	274.18b	570.14a
Seed vigor index	22.80b	42.43a
Radicle length [mm]	17.55a	19.45a
Shoot length [mm]	34.14b	43.71a
Seedling length [mm]	51.69b	63.15a
Radicle/shoot length ratio	0.52a	0.48a
Seedling fresh weight [mg]	23.18b	29.41a
Seedling dry weight [mg]	2.38a	3.23a
Seedling dry matter [%]	10.78b	18.04a
Seed weight [mg]	18.26a	10.72b
Seed length [mm]	12.17a	10.77a
Seed width [mm]	6.87a	6.03a

The correlation analysis indicated that some phenotypic traits had significant correlation (p>0.05) with climate factors (Table 5). The annual precipitation had positive correlation with dormancy termination time, seed weight and length; but showed negative correlation with the germination percentage, germination rate, and germination index. Seedling fresh weight had positive correlation with altitude. There was also positive correlation between seed width and latitude. The above correlations implied that the annual precipitation plays an important role in influencing the dormancy and germination traits of *Ferula* taxa.

The Euclidean distances matrix was subjected to agglomerative hierarchical clustering utilizing UPGMA method to construct a dendrogram (Fig. 3). 23 populations of *Ferula* taxa were classified into two main groups. Cluster I consisted of 10 populations of *F. gummosa* and 4 populations of *F. assa-foetida*; cluster II included eight populations of *F. assa-foetida* and only one population of *F. gummosa* (Fig. 3). Comparison of means of two clusters indicated that populations in cluster I have significantly higher dormancy termination, germination period and seed weight, however populations cluster II showed higher germination percentage, germination rate, germination index, seed vigor index and seedling length (Table 6). UPGMA trees of germination morphological characters partially separated the two species, a behavior also supported by PCA plot (Fig. 4). However, almost within each species cluster, the populations differed

somewhat from each other and were joined together with different distances. Therefore, there was no obvious relationship between phenotypic traits and the origin of these *Ferula* populations. PCA analysis of seed germination and morphological data revealed that the first 4 components comprise about 77% of total variance (Table 7). The first component accounted for 34.4% of the total variation in the data set while the second and third principal components contributed 21.2% and 14.4%, respectively. Together, these three components could explain 68% of the total variation in the characterized the *Ferula* populations. Analysis of the factor loadings of the characters in the retained PCs indicated that any of seed germination and morphological traits showed positive loadings in PC 1-3 (Table 7).

Table 7

Factor loadings (eigenvectors) for the different seed characteristics of *Ferula* populations for the principal components retained

Variable	PC1	PC2	PC3	PC4
Dormancy termination	-0.295	-0.267	0.048	0.174
Germination period	0.068	0.105	-0.028	0.204
Germination%	0.236	0.24	0.271	0.177
Germination rate	0.308	0.268	0.101	-0.133
Germination Index	0.31	0.285	0.154	0.01
Seed vigor index	0.323	-0.03	0.312	0.197
Radicle length	0.105	-0.3	0.363	-0.345
Shoot length	0.214	-0.392	0.1	0.075
Seedling length	0.192	-0.393	0.214	-0.084
Radicle/shoot length ratio	-0.056	0.089	0.403	-0.438
Seedling fresh weight	0.172	-0.293	0.189	0.265
Seedling dry weight	0.057	-0.343	-0.1	-0.233
Seedling dry matter%	-0.005	-0.057	-0.296	-0.537
Seed weight	-0.322	0.067	0.274	-0.015
Seed length	-0.267	0.144	0.261	-0.131
Seed width	-0.263	0.069	0.315	-0.053
Eigenvalue	6.1832	3.8224	2.2375	1.6753
Proportion	0.344	0.212	0.124	0.093
Cumulative	0.344	0.556	0.68	0.773

DISCUSSION

Germination cues for *F. assa-foetida* and *F. gummosa* were complex, with dormancy mechanisms present to restrict germination until cold stratification or other requirements are fulfilled (Nadjafi *et al.* 2006; Amooaghaie, 2009,

Nowruzian *et al.* 2016; Fasih and Tavakkol Afshari 2018). The existence of morphophysiological dormancy (MPD) is very frequent in the Apiaceae (Baskin *et al.* 1992, 1995, 2000; Phartyal *et al.* 2009; Vandelook *et al.* 2008, 2009; Scholten *et al.* 2009; Yaqoob and Nawchoo 2015; Fasih and Tavakkol Afshari 2018). Cold stratification temperature used in this experiment (4°C) provides an adequate moist chilling treatment. The temperature is also within the range of soil temperatures likely to be encountered in the field in high altitude Iran (Tabari and Talaee 2011; Ghasemi, 2015; Aghajanlou and Ghorbani 2016; Shirvani *et al.* 2018). This cold stratification temperature has been reported as successful in breaking dormancy in studies of alpine and high altitude species (Baskin and Baskin 2014).

Results indicated that the duration of dormancy termination was significantly longer in *F. gummosa* than *F. assa-foetida*. A period of 4 weeks of stratification is sufficient for germination of *F. assa-foetida*, but *F. gummosa* require cold stratification for periods of 8 weeks for optimal germination. The final germination percentage of *Ferula* taxa at present study was higher than the previous experiences (Nadjafi *et al.* 2006; Amooaghaie 2009, Nowruzian *et al.*,, 2016; Fasih and Tavakkol Afshari 2018), in which *Ferula* seeds transferred to standard germination condition following limited cold stratification treatment. Sommerville *et al.* (2013) by studding of several species of Australian Alps suggested species requiring stratification for periods of 8 weeks or more for optimal germination may be particularly sensitive to climate change. High altitude ecosystems are considered to be among the most sensitive to climate changes (Hughes 2003; Laurance *et al.* 2011), and recent declines in average snow depth have been observed in alpine and high altitude areas in both the Northern and Southern Hemispheres (Hughes 2003; Nicholls 2005; Hennessy *et al.* 2007; Rosenzweig *et al.* 2007; Amiri and Eslamian 2010). For species in Apiaceae depend on cold moist conditions (wet stratification) to break dormancy; reduced snow cover during winter may threaten the survival of these species, even if subsequent temperatures are suitable for germination (Liu *et al.* 2011). Although the seed of some species may be able to tolerate winter temperatures in the absence of snow, a reduction in snow cover may also mean a reduction in the amount of available water (in total precipitation in winter and spring). As the level of seed hydration plays a role in breaking seed dormancy (Hoyle *et al.* 2008; Walck *et al.* 2011; Baskin and Baskin 2014), relative drought during winter and spring may prove to be more important in limiting the germination of these species than the lack of snow cover *per se* (Liu *et al.* 2011). Results of this research also indicated significant correlation between precipitation and germination traits.

Both species were able to germinate at very low temperatures (4°C). The ability to germinate at very low temperatures has been observed in several high altitude species (Wardlaw *et al.* 1989; Sommerville *et al.* 2013). The capacity to germinate at low temperatures may provide an advantage during a short growing season by allowing germination to begin under snow banks (Meyer *et al.* 1995; Forbis and Diggle 2001; Walck and Hidayati 2004). *Aciphylla glacialis* (Apiaceae) germinated optimally at low temperatures, similar to the Asian and North American Osmorhiza species (Walck *et al.* 2002; Baskin *et al.* 1995;

Walck and Hidayati 2004) in the same family (Apiaceae). Cold stratification response having similar effects to high altitude and alpine species: improving final germination, widening the range of temperatures for germination, decreasing germination time, and synchronizing germination by reducing variability in time to germination (Shimono and Kudo 2005).

The study species were highly variable in their dormancy and germination response to the moist chilling treatment. Variation of the dormancy termination duration parameter was significant among different populations of each species; ranging from 31 to 51 days in the *F. gummosa*, and from 12 to 28 days in the *F. assa-foetida*. Dormancy is a genetic seed characteristic, but it strongly interacts with environmental factors. Dormancy intensity depends on age, nutritive conditions and water supply of the plant, as well as the weather conditions during seed ripening (Andersson and Milberg 1998). Ecological factors, such as temperature, humidity, oxygen and light, greatly influence the seed's dormancy period interruption, and there is a significant distinction of causes of dormancy discontinuance among species (Podrug *et al.* 2014; Mahmoudi *et al.* 2015; Mazangi *et al.* 2016; Mirzaei Mossivand *et al.* 2018; Aghajanlou *et al.* 2018). In concordance with the researches significant correlation were found between germination characteristics (including dormancy termination) and precipitation.

The germination responses of *F. assa-foetida*, *F. gummosa* seeds was significantly affected by populations. Several studies have been published of attempts to interrelate the germination responses of populations of a particular species collected in different parts of its range. Haasis and Thrupp (1931) and Skordilis and Thanos (1995) working with coniferous species, and McNaughton (1966) with *Typha* species all reported variations in germination of different ecotypes. Lauer (1953), on the other hand, failed to distinguish notable differences between populations of *Agrostemma githago* and *Datura stramoniam* collected in various locations in Europe. The variety of observed responses to germination is expected, as high altitude environments exhibit significant spatio-temporal variability (Kaye 1997; Shimono and Kudo 2005; Noroozi *et al.* 2013, 2015). Even within a particular habitat, germination responses are unlikely to be consistent. For each species, germination is likely to vary between altitudes and populations. Variability in germination is an important strategy to ensure species survival in unpredictable environments, reducing the risk of exposing the entire seedling cohort to poor growing conditions (Giménez-Benavides *et al.* 2005; Venn, 2007; Mondoni *et al.* 2008). For example, in the genus *Penstemon*, Meyer (1995) suggests that germination of most species combines predictive mechanisms (e.g. fulfillment of cold stratification requirements) with the potential for development of a persistent seed bank.

CONCLUSIONS

Cold stratification is the main prerequisite for breaking deep complex dormancy in *F. assa-foetida* and *F. gummosa*. A period of 4 weeks of stratification is sufficient for germination of *F. assa-foetida*, but *F. gummosa* require stratification for periods of 8 weeks for optimal germination. Both species were

able to germinate at very low temperatures (4°C). The characteristics of deep MPD in the taxa are part of the plant's adaptation to its environment. Highly significant intraspecific population differences in the germination parameters of the taxa might reflect local adaptation to a particular environment. Pronounced differences occurred within both *F. assa-foetida* and *F. gummosa*, even though the some studied sites in each taxon were adjacent sites. Variation within a taxon may depend on genetic differences, local weather during growth of mother plants and maturation of seeds, seed position on the mother plant, soil quality, or other naturally occurring factors. To be able to draw conclusions on a general level, for example for modelling or predicting changes in emergence pattern following climate change, knowledge about a taxon, including its variation, is needed. Therefore, studies of germination behavior should include several populations from the same species.

The continued regeneration of the species in the wild will depend on the temperature and moisture status of the soil during winter and the maintenance of conditions suitable for stratification for an appropriate length of time. In this context temperature is a critical driver of plant regeneration, directly influencing seed dormancy, germination and vegetative reproduction. Therefore changing climate not only affect the dormancy and germination traits, but also is likely to impact on the germination response of these species through maternal effects on the developing seed. These species could be targeted for conservation in *ex situ* collections, whilst monitoring their response in the field.

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