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, Iran, highland, 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; Milbau et al. 2009). The germination emergence stage is a high-risk phase of the plant life cycle, and there-
fore 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 oleo-gum 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 ungerminated throughout the winter. Moreover, the low temperatures alleviate dormancy and once dormancy breaks, two possible scenarios might occur: 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, HNO3, chilling and soaking with water at different temperatures showed that moist-chilling and gib-
berellic 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 GA3 (10 mgL⁻¹) solution for 24 h (Nowruzian et al., 2016). In similar way treatment of moist-chilling for 6 weeks or 4 weeks followed by soaking gibberellic acid is recommended for *F. ovina* (Fasih and Tavakkol Afshari 2018). Washing and chilling (5±1C) 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 aims of the present work were stimulating the cold stratification (the treatment that occurs in nature), 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, studied 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 or populations of the two *Ferula* taxa from all over Iran were obtained from Natural Resources Gene Bank, Iran (Table 1).

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. Once the seeds started to germination, the number of germinated seeds 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 caryopses 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).

Table 1

| Province | Population | Code       | Latitude (decimal) | Longitude (decimals) | Altitude (m above sea level) | Mean annual precipitation (mm) |
|----------|------------|------------|--------------------|----------------------|-------------------------------|--------------------------------|
| Horm     | Bandar Abbas | FaBandarA1 | 28.17              | 56.83                | 2200                          | 178                            |
| Horm     | Bandar Abbas | FaBandarA2 | 27.88              | 50.22                | 1845                          | 179                            |
| Khor     | Boshroye    | FaBoshroye | 33.96              | 57.17                | 893                           | 94                             |
| Horm     | Haji Abad   | FaHajiAbad | 28.94              | 56.46                | 1900                          | 179                            |
| Esfah    | Kashan      | FaKashan   | 33.75              | 51.48                | 1800                          | 137                            |
| Kerm     | 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                             |
| Kerm     | Zaran       | FaZaran    | 30.88              | 56.88                | 2300                          | 47                             |
| K&B      | Dena        | FgDena     | 30.50              | 51.72                | 2560                          | 760                            |
| Elam     | Elam1       | FgElam     | 33.63              | 46.41                | 1000                          | 575                            |
| Horm     | Haji Abad   | FgHajiAbad | 28.12              | 56.84                | 2200                          | 178                            |
| Ch B     | Lordegan    | FgLordegan | 31.42              | 51.26                | 2683                          | 555                            |
| Semn     | 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                             |
| K&B      | Yasuj       | FgYasuj1   | 30.48              | 51.79                | 2300                          | 855                            |
| K&B      | Yasuj       | FgYasuj2   | 31.94              | 51.44                | 1950                          | 855                            |
| K&B      | Yasuj       | FgYasuj3   | 30.45              | 51.65                | 2420                          | 855                            |
| Kerm     | Zaran       | FgZaran    | 30.88              | 56.87                | 2400                          | 47                             |

Horm - Hormozgan; Khor - Khorasan; Esfah - Esfahan; Kerm - Kerman; K&B - Kohkeluye and Boyerahman; Ch B - Charmahal Bakhtiali; Semn - Semnan
Data analysis

Variance analysis (ANOVA) were conducted for seed germination traits including dormancy termination, germination period, germination percentage, 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], seedling dry matter %; and seed morphology traits including seed weight [g], seed length [mm], seed width [mm], and 1000 seeds weight [mg] 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 populations by NTSYS-pc version 2.1 (Rohlf, 2002). Moreover, unweighted pair group methods of arithmetic mean (UPGMA) algorithm and SAHN clustering were utilized to get the genetic relationships. The Principal component analysis (PCA) of 23 Ferula populations 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 traits. A relatively high CV was obtained for seed weight (Table 2).

Table 2
Mean comparisons of seed morph 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

| Population     | Seed weight [mg] | Seed length [mm] | Seed width [mm] |
|----------------|------------------|------------------|-----------------|
| *F. assa-foetida* |                  |                  |                 |
| FaBandA1       | 12.23            | 9.73             | 5.47            |
| FaBandA2       | 13.57            | 9.30             | 5.67            |
| FaBoshro       | 13.00            | 15.17            | 7.65            |
| FaHajiAb       | 8.90             | 7.68             | 4.12            |
| FaKashan       | 16.93            | 11.77            | 6.97            |
| FaKerman       | 23.00            | 12.21            | 6.95            |
| FaLar          | 15.23            | 12.40            | 5.93            |
| FaMehriz       | 9.23             | 11.23            | 5.77            |
| FaTabas1       | 10.33            | 10.07            | 5.93            |
| FaTabas2       | 10.13            | 10.98            | 5.87            |
| FaTaft         | 10.33            | 11.82            | 6.80            |
| FaZarand       | 17.77            | 12.08            | 6.72            |
| Mean           | 13.37            | 11.19            | 6.15            |
| Cv             | 43.86            | 16.95            | 16.6            |
Both species *F. assa-foetida* and *F. gummosa*, failed to germinate without prior stratification. However, cold stratification stimulated the germination and growth of seedlings 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 percentage, 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 FaTabas1 and the highest seedling parameters (radicle and shoot length, and seedling fresh weight) were observed in the populations FaTaft and FaZarand; however, these two populations showed lowest values of seedling dry matter percentage. In the species *F. gummosa* the highest germination characteristics (germination percentage, 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 FgYa-suj1, 2, 3 of the species *F. gummosa*, with similar habitat and geographical range, 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 2

| Population  | Seed weight [mg] | Seed length [mm] | Seed width [mm] |
|-------------|------------------|------------------|-----------------|
| 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 e          | 11.99 c          | 6.96            |
| Cv          | 37.51            | 17.10            | 16.36           |
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 populations for the same species. *P* <0.05

| Population      | Dormancy termination [days] | Germination period [days] | Germination [%] | Germination rate | Germination Index | Seed vigor index | Radicle length [mm] |
|-----------------|-----------------------------|---------------------------|-----------------|------------------|-------------------|-------------------|-------------------|
| *F. assa-foetida* |                             |                           |                 |                  |                   |                   |                   |
| FaBandA1        | 14.33 d                     | 10 ab                     | 50.67 cd        | 8.427 bc         | 478.2 cd          | 42.9 abc          | 28.13 a           |
| FaBandA2        | 16.33 cd                    | 16.67 ab                  | 70.67 abc       | 6.300 cde        | 472.3 cd          | 32.4 a-d          | 16.33 abc         |
| FaBoshro        | 23 ab                       | 10.67 ab                  | 26.67 de        | 2.797 ed         | 220.4 de          | 14.9 dc           | 18.52 abc         |
| FaHajiAb        | 13.67 d                     | 9.33 ab                   | 46.67 cde       | 7.337 bcd        | 433.6 cd          | 17.3 bcd          | 11.17 c           |
| FaKashan        | 21.67 bc                    | 20.67 a                   | 66.67 abc       | 7.950 bcd        | 562.7 bc          | 46.8 ba           | 13.20 bc          |
| FaKerman        | 28.33 a                     | 20.67 a                   | 58.67 abc       | 4.273 cde        | 390.6 cd          | 33.6 a-d          | 23.43 abc         |
| FaLar           | 28.33 a                     | 20.67 a                   | 20.00 e         | 1.343 e          | 122.9 e           | 6.5 d             | 11.92 c           |
| FaMehriz        | 26.33 ab                    | 16.00 ab                  | 62.67 abc       | 5.860 cde        | 481.8 cd          | 26.4 a-d          | 14.20 bc          |
| FaTabas1        | 13.00 d                     | 10.00 ab                  | 86.67 a         | 15.190 a         | 824.5 a           | 39.8 abc          | 16.90 abc         |
| FaTabas2        | 12.33 d                     | 6.67 b                    | 80.00 ab        | 14.430 a         | 771.6 ab          | 42.9 abc          | 21.10 abc         |
| FaTaft          | 12.33 d                     | 8.00 b                    | 62.67 abc       | 11.630 ab        | 607.1 abc         | 53.4 a            | 22.40 abc         |
| FaZaran         | 17.00 ed                    | 13.33 ab                  | 53.33 bcd       | 7.817 bcd        | 486.7 cd          | 46.4 abc          | 25.73 ab          |
| Mean            | 18.89 13.56                 | 57.11 7.780               | 7.780 487.7     | 33.6 18.59       |
| Cv              | 16.93 45.19                 | 26.36 36.000              | 29.1 48.3       | 37.60            |
| Population | Dormancy termination [days] | Germination period [days] | Germination [%] | Germination rate | Germination Index | Seed vigor index | Radicle length [mm] |
|------------|-----------------------------|---------------------------|----------------|-----------------|------------------|------------------|-------------------|
| **F. gummosa** |                             |                           |                |                 |                  |                  |                   |
| FgDena     | 45.00                       | bcd                       | 7.33           | eb              | 20.00            | 0.763            | e                 | 91.8             | d                | 13.28            | ef               | 22.99            | cb               |
| FgElaam    | 45.00                       | bcd                       | 8.67           | eb              | 30.67            | 1.133            | de               | 138.5            | d                | 12.98            | ef               | 8.817            | d                |
| FgHajiAb   | 48.33                       | bc                        | 4.00           | c               | 69.33            | 2.347            | cd               | 295.8            | c                | 29.25            | cd               | 13.87            | cd               |
| FgLordeg   | 38.33                       | de                        | 11.33          | eb              | 78.67            | 3.940            | ab               | 439.1            | ab               | 69.25            | a                | 23.13            | cb               |
| FgShahro   | 51.67                       | ab                        | 4.67           | c               | 29.33            | 0.823            | e                | 106.7            | d                | 13.03            | ef               | 14.20            | cd               |
| FgTabas    | 35.00                       | e                         | 9.33           | eb              | 65.33            | 4.110            | ab               | 417.2            | abc              | 33.72            | cb               | 15.80            | bcd              |
| FgTaft     | 32.33                       | e                         | 14.00          | b               | 72.00            | 5.080            | a                | 489.6            | a                | 25.48            | cde              | 11.60            | d                |
| FgYasuj1   | 33.00                       | e                         | 22.67          | a               | 70.67            | 2.767            | bc               | 322.4            | bc               | 43.42            | b                | 25.20            | b                |
| FgYasuj2   | 56.33                       | a                         | 2.667          | c               | 16.00            | 0.253            | e                | 36.0             | d                | 16.93            | def              | 42.10            | a                |
| FgYasuj3   | 43.00                       | cd                        | 10.00          | eb              | 18.67            | 0.800            | e                | 93.3             | d                | 6.27             | f                | 9.67             | d                |
| FgZarand   | 31.67                       | e                         | 14.67          | b               | 56.00            | 3.577            | bc               | 359.6            | abc              | 26.12            | cde              | 13.80            | cd               |
| Mean       | 41.79                       |                            | 9.94           |                 | 47.88            | 2.330            | bc               | 253.6            |                 | 26.34            |                 | 18.29            |                 |
| Cv         | 8.72                        |                            | 45.04          |                 | 24.69            | 32.93            |                  | 28.1             |                 | 28.83            |                 | 30.16            |                 |
Table 3
Continued

| Population | Shoot [mm] | Seedling [mm] | Radicle/shoot length ratio | Seedling fresh weight [mg] | Seedling dry weight [mg] | Seedling dry matter [%] |
|------------|------------|----------------|---------------------------|-----------------------------|--------------------------|--------------------------|
| FaBandA1   | 46.45 abc  | 74.58 ba       | 0.613 ab                   | 34.67 ab                    | 2.333 b                  | 6.72 d                   |
| FaBandA2   | 29.73 cd   | 46.07 bcd      | 0.573 ab                   | 20.73 ab                    | 2.167 b                  | 5.70 d                   |
| FaBoshro   | 37.95 bcd  | 56.47 a-d      | 0.503 abc                  | 19.50 ab                    | 2.157 b                  | 11.84 b                  |
| FaHajiAb   | 29.49 cd   | 40.66 dc       | 0.397 abc                  | 22.69 ab                    | 7.623 a                  | 5.80 d                   |
| FaKashan   | 55.03 ab   | 68.23 abc      | 0.253 c                    | 34.00 ab                    | 3.167 b                  | 9.49 c                   |
| FaKerman   | 34.07 bcd  | 57.50 a-d      | 0.700 a                    | 34.33 ab                    | 2.833 b                  | 8.40 c                   |
| FaLar      | 19.36 d    | 31.28 d        | 0.627 ab                   | 17.98 b                     | 2.987 b                  | 16.57 a                  |
| FaMehriz   | 28.23 cd   | 42.43 dc       | 0.510 abc                  | 25.26 ab                    | 1.333 b                  | 6.20 d                   |
| FaTabas1   | 27.57 cd   | 44.47 bcd      | 0.600 ab                   | 13.80 b                     | 1.233 b                  | 9.83 c                   |
| FaTabas2   | 31.00 cd   | 52.10 bcd      | 0.653 ab                   | 12.73 b                     | 1.000 b                  | 8.15 c                   |
| FaTart1    | 60.97 a    | 83.37 a        | 0.357 bc                   | 29.13 ab                    | 1.833 b                  | 6.49 d                   |
| FaZaran    | 61.03 a    | 86.77 a        | 0.460 abc                  | 40.63 a                     | 2.400 b                  | 6.07 d                   |
| Mean       | 38.41      | 56.99          | 0.520 a                    | 25.46                       | 2.590 b                  | 15.35                    |
| Cv         | 30.20      | 28.53          | 30.360 a                   | 44.94                       | 60.570 b                 | 14.36                    |

*F. assa-foetida*
Table 3

| Population | Shoot length [mm] | Seedling length [mm] | Radicle/shoot length ratio | Seedling fresh weight [mg] | Seedling dry weight [mg] | Seedling dry matter [%] |
|------------|-------------------|----------------------|-----------------------------|---------------------------|--------------------------|-------------------------|
| F. gummosa |                   |                      |                             |                           |                          |                         |
| FgDena     | 42.69  b          | 65.68  b             | 0.537 ab                    | 36.40  b                  | 4.067  c                 | 11.53 b                 |
| FgEelam    | 36.44  cb         | 45.26  cd            | 0.260 b                     | 17.31  cd                 | 1.577  d                 | 9.33  cde               |
| FgHajiAb   | 28.40  c          | 42.27  d             | 0.540 ab                    | 26.87  cb                 | 1.167  d                 | 4.35 f                  |
| FgLordeg   | 66.33  a          | 89.47  a             | 0.347  b                    | 68.23  a                  | 7.567  a                 | 11.11 cd                |
| FgShahro   | 28.59  c          | 42.78  d             | 0.483 ab                    | 11.06  d                  | 1.263  d                 | 11.97 cb                |
| FgTabas    | 36.03  cb         | 51.83  bcd           | 0.440 ab                    | 17.90  cd                 | 1.633  d                 | 7.26 e                  |
| FgTaft     | 24.13  c          | 35.73  d             | 0.483 ab                    | 17.20  cd                 | 1.300  d                 | 7.51 e                  |
| FgYasuj1   | 36.27  cb         | 61.47  cb            | 0.697  a                    | 36.87  b                  | 3.267  c                 | 8.98 de                 |
| FgYasuj2   | 62.19  a          | 104.3  a             | 0.673  a                    | 18.71  cd                 | 5.980  b                 | 31.03 a                 |
| FgYasuj3   | 35.81  cb         | 45.47  cd            | 0.273  b                    | 21.86  cd                 | 3.167  c                 | 14.20 b                 |
| FgZarand   | 32.43  cb         | 46.23  cd            | 0.457  ab                   | 19.33  cd                 | 1.433  d                 | 7.893 e                 |
| Mean       | 39.03  57.32      | 0.470  26.52         | 2.950  11.38               |                           |                          |                         |
| Cv         | 17.17  16.72      | 32.750  28.44        | 27.740  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 characters. Germination percentage exhibited a positive and significant correlation with germination rate, germination index and seedling vigor index (Table 4; Fig. 2). The correlation analysis indicated that some phenotypic traits had significant correlation ($p \leq 0.05$) with climate factors (Table 5). The mean 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 mean annual precipitation plays an important role in influencing the dormancy and germination traits of the Ferula taxa.
Table 4

Pair wise correlation between seed (germination and morph) characteristics of different populations of *Ferula* taxa

| Characters                  | 1. | 2. | 3. | 4. | 5. | 6. | 7. | 8. | 9. | 10. | 11. | 12. | 13. | 14. | 15. | 16. |
|-----------------------------|----|----|----|----|----|----|----|----|----|-----|-----|-----|-----|-----|-----|-----|
| 1. Dormancy termination     | 1.000 |   |    |    |    |    |    |    |    |     |     |     |     |     |     |     |
| 2. Germination period       | -0.346 | 1.000 |    |    |    |    |    |    |    |     |     |     |     |     |     |     |
| 3. Germination%             | -0.497* | 0.246 | 1.000 |    |    |    |    |    |    |     |     |     |     |     |     |     |
| 4. Germination rate         | -0.83** | 0.013 | 0.678** | 1.000 |    |    |    |    |    |     |     |     |     |     |     |     |
| 5. Germination Index        | -0.79** | 0.166 | 0.863** | 0.944** | 1.000 |    |    |    |    |     |     |     |     |     |     |     |
| 6. Seed vigor index         | -0.45* | 0.178 | 0.778** | 0.593** | 0.799** | 1.000 |    |    |    |     |     |     |     |     |     |     |
| 7. Radicle length           | 0.066 | -0.188 | -0.066 | 0.044 | -0.034 | 0.335 | 1.000 |    |    |     |     |     |     |     |     |     |
| 8. Shoot length             | 0.026 | -0.172 | -0.025 | 0.064 | 0.029 | 0.554** | 0.634** | 1.000 |    |     |     |     |     |     |     |     |
| 9. Seedling length          | 0.044 | -0.195 | -0.044 | 0.063 | 0.007 | 0.521* | 0.840** | 0.952** | 1.000 |    |     |     |     |     |     |     |
| 10. Radicle/shoot length    | -0.077 | 0.130 | 0.100 | 0.083 | 0.059 | -0.016 | 0.529** | -0.281 | 0.012 | 1.000 |    |     |     |     |     |     |
| 11. Seedling fresh weight   | -0.013 | 0.244 | 0.224 | -0.053 | 0.067 | 0.638** | 0.340 | 0.649** | 0.589** | -0.149 | 1.000 |    |     |     |     |
| 12. Seedling dry weight     | 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. Seedling dry matter%    | -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. Seed weight             | 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. Seed length             | 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. Seed width              | 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 |

*: significant at 0.05 level; **: significant at 0.01 level
Table 5
Pearson correlation analyses for the relationship between seed (germination and morph) characteristics within different populations of Ferula taxa and some ecological parameters

| Parameters             | Dormancy termination | Germination period | Germination % | Germination rate | Germination Index | Seed vigor index | Seed weight | Seed length | Seed width | Seedling length | Radicle/shoot length ratio | Radicle length | Shoot length |
|------------------------|----------------------|--------------------|---------------|------------------|------------------|------------------|--------------|-------------|------------|------------------|-----------------------------|----------------|--------------|
| Latitude               | 0.200                | -0.218             | -0.017        | 0.032            | 0.037            | -0.002           | -0.084      | 0.140       | 0.265      | 0.61**           | -0.112                      | -0.6**         | 0.274        |
| Longitude              | -0.321               | -0.028             | 0.203         | 0.286            | 0.307            | 0.052            | -0.004      | -0.265      | -0.6**     | -0.224           | 0.319                      | 0.275          | -0.264       |
| Mean annual precipitation | 0.028                | 0.195              | 0.224         | 0.033            | 0.116            | 0.361            | 0.275       | 0.264       | 0.274      | 0.319**          | 0.343                      | 0.574**        | 0.057        |

*: significant at 0.05 level; **: significant at 0.01 level

The Euclidean distances matrix was subjected to agglomerative hierarchical clustering utilizing UPGMA method to construct a dendrogram (Fig. 3). 23 populations of the Ferula taxa were classified into two main groups. Cluster I consisted of 10 populations of F. gummosa and 4 populations of F. asa-foetida; cluster II included eight populations of F. asa-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 time, 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 seed germination and 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).

Fig. 3. Dendrograms of the 23 populations of Ferula assa-foetida (with prefix Fa) and F. gummosa (with prefix Fg) based on studied traits
Seed germination plasticity of two endangered species of Ferula in context…

Fig. 4. Scatter diagram of the 23 populations of Ferula assa-foetida (with prefix Fa) and F. gummosa (with prefix Fg) 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)

| Group | Dormancy termination [days] | Germination period [days] | Germination [%] | Germination rate | Germination Index | Seed vigor index | Radicle length [mm] | Shoot length [mm] |
|-------|-----------------------------|---------------------------|-----------------|------------------|------------------|-----------------|-------------------|------------------|
| I     | 36.85a                      | 12.40a                    | 46.53b          | 2.78b            | 274.18b          | 22.80b          | 17.55a            | 34.14b           |
| II    | 17.28b                      | 11.67a                    | 66.70a          | 9.38a            | 570.14a          | 42.43a          | 19.45a            | 43.71a           |

| Group | Seedling length [mm] | Radicle/shoot length ratio | Seedling fresh weight [mg] | Seedling dry weight [mg] | Seedling dry matter [%] | Seed weight [mg] | Seed length [mm] | Seed width [mm] |
|-------|----------------------|---------------------------|---------------------------|------------------------|----------------------|-----------------|-----------------|-----------------|
| I     | 51.69b               | 0.52a                     | 23.18b                    | 2.38a                  | 10.78b               | 18.26a          | 12.17a          | 6.87a           |
| II    | 63.15a               | 0.48a                     | 29.41a                    | 3.23a                  | 18.04a               | 10.72b          | 10.77a          | 6.03a           |
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

| 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  |
soil temperatures likely to be encountered in the field in high altitude Iran (Tabari and Talaei 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 studying 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 Diggie 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 seed origin. 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; Shimo 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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