



Seed germination and seedling emergence in two populations of eastern dodder (*Cuscuta monogyna* Vahl.): evaluation of environmental factors and burial depth

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Abstract

To compare *C. monogyna* seed germination and the seedling emergence of two populations from Quchan and Bardaskan in Khorasan-e-Razavi-I province in north east of Iran, experiments were carried out. From the results, the highest germination percentages for Quchan (98%) and Bardaskan (97%) populations were observed at alternating 25/15 and 30/20 °C day/night temperatures, respectively. Germination percentage of both populations was 42–92% over a wide range of constant temperatures (10–35 °C). The NaCl concentration of 399.5 and 443.6 mM caused 50% inhibition of germination for Quchan and Bardaskan populations, respectively. The osmotic potential for 50% inhibition of germination was – 0.63 for Quchan and – 0.66 MPa for Bardaskan populations. The maximum emergence of Quchan (74%) and Bardaskan (80%) populations were recorded in the seeds placed at 0.5 cm with emergence failure at 5 cm soil depth. In another experiment in which seeds were after-ripened at different depths of soil in the field, seed germination was lower on the soil surface and 20 cm soil depth compared to 2, 5, 10 and 15 cm depth; and the highest seed emergence in the field was observed at 5 cm soil depth, 270 days after seed burial. The information of this study would be useful for determining the potential of this parasitic species to spread to new areas and arrange management strategies in different environmental conditions.

Keywords Salinity stress · Drought stress · Population · After-ripening · Parasitic weed

Introduction

Cuscuta spp (dodder) are classified as stem parasitic plants (Kuijy 1969). Among 200 *Cuscuta* species worldwide (Costea and Stefanovic 2010), 18 species have been identified in Iran (Zand et al. 2017), in which two species *C. campestris* Yuncker (field dodder) and *C. monogyna* Vahl. (eastern dodder) have the widest distribution (Rashed Mohassel et al. 2009; Zand et al. 2017). *C. monogyna* is a holoparasite flowering plant that infest economically important trees such as citrus, pomegranate (*Punica granatum* L.), vineyards (*Vitis vinifera* L.), oak (*Quercus persica* L.) and elm (*Ulmus campestris* L.) (Lanini and Kogan 2005; Nazari 2014; Holm et al. 1997; Ebrahimi and Eslami 2012a). Hosts infected

by *Cuscuta* become weak and have low growth and yield (Tsivion 1981; Cudney et al, 1992). When *C. monogyna* is not controlled, complete destruction of the host plant may eventually occur.

Cuscuta seedling activity is stimulated by wrapping around the above-ground parts of host plants and penetrating into internal structures. The parasitic infection continues to withdraw water and photosynthetic products through haustoria (Lanini and Kogan 2005). *C. monogyna* has relatively thicker stems than other *C. species* (Karimi 2001), and the seed is larger in *C. monogyna* (1.87 mm) in comparison with *C. campestris* (1.41 mm) (Fathoulla and Mosleh 2008). Besides seed germination, it is propagated by the stem fragments. However, vineyards trees are so close together, therefore if a piece of *C. monogyna* stem is placed on the other trees due to human activities and naturally, it can move from a parasitized plant to adjacent plants and can easily parasitize them (Karimi 2001).

Some environmental parameters such as temperature and light along with osmotic potential fluctuations can seriously affect plant species by restricting the germination process

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(De Cauwer et al. 2014; Chauhan and Johnson 2010; Ahmed et al. 2015). The dormancy mechanism is known as one of the main reasons for establishing the soil seed bank. Once the seed bank is formed in the soil, it is very difficult to control weeds. It is possible for *Cuscuta* seeds to survive in the soil for 20 years or even longer (Lanini and Kogan 2005) and then germinate independently of host plants (Dawson 1987). The appropriate soil temperatures for germination and emergence of *Cuscuta* seeds are 15–38 °C with the optimum of 30 °C (Hutchison and Ashton 1979), which corresponds with the prevailing temperatures during the late spring and early summer in Khorasan-e-Razavi province of Iran.

There is insufficient information regarding the effect of the time burial (time after seed burial in soil) and seed depth on breaking seed dormancy, germination, and seed fate in *C. monogyna*. Goldwasser et al. (2016) tested the scarified seeds of *C. campestris* under lab conditions and reported that at 5 °C, only 6.25% of seeds were germinated, whereas between 10 and 35 °C, 96.4–100% and, at 40 °C, 62.11% of the seeds were germinated. Temperature represents an important function in regulating seed germination time and organizing species distribution (Guan et al. 2009). Recognizing the effects of various environmental aspects on *C. monogyna* germination can be crucial to find out its emergence pattern and management in diverse agricultural systems. The environmental parameters experienced by the maternal plants of weeds may strongly influence the germination ecology of the produced seeds. Differences in soil characteristics, plant residues, moisture, temperature, light, and other environmental factors lead to geographical variations in germination and emergence ecology of weed species (Eslami 2011).

To advance weed management programs, it is crucial to have adequate information concerning seed dormancy, seed germination, seed decay, seedling emergence, and variations among different populations (Mennan and Ngouajio 2006). Therefore, the current experiment was aimed to study the influence of *Cuscuta* population and environmental parameters regarding dormancy behavior, seed germination, and seedling emergence.

Materials and methods

Site and seed description

Seeds from Quchan and Bardaskan populations were collected in October 2015 and December 2015 respectively from parasitized vineyards in both cities of Quchan (36°57' N, 58°31' E and 1526 m altitude) and Bardaskan (35°78' N, 57°92' E and 862 m altitude) located in Khorasan-e-Razavi province, Iran with semiarid and dry climate (Fig. 1). To prepare experimental samples, the seeds were randomly

collected from a vineyard plants at single orchard experimental samples and then manually cleaned and stored under room temperature (25 °C). The 1000-seed weight of Quchan and Bardaskan populations were 4.82 ± 0.09 and 5.87 ± 0.1 g, respectively. *C. monogyna* seeds do not need light to germinate (Ebrahimi and Eslami 2012a). Therefore, in the current study the experiments were carried out in light/dark conditions and to promote seed germination, seed dormancy was removed prior by soaking them in boiling water for 30 s (Ebrahimi and Eslami 2012a) in each experiment, except the last experiment in which the influence of time and burial depth on seed fate was investigated.

General protocol regarding germination tests

For both populations of *C. monogyna*, 4 replications of 25 seeds were placed in 9 cm Petri dishes (with two layers of Whatman No. 1 filter paper), and were moistened with 5 mL distilled water (control) or salinity and drought stress solution if required. To minimize evaporation, Petri dishes were competently sealed with parafilm and placed in the incubator (Grouc company, GER SET 1100 model). The incubation conditions were set as 14 days under 12 h/12 h light/dark at optimum temperature of 25/15 °C and 30/20 °C day/night for Quchan and Bardaskan populations, respectively, based on the results of next test. To create a photosynthetic photon-flux density of $85 \mu\text{mol m}^{-2} \text{s}^{-1}$, fluorescent lamps were installed. The germinated seeds were counted daily after reaching radicle length ≥ 2 mm. The final germination percentage was recorded 14 days after incubation.

Temperature

Experiment were run as various fluctuating temperatures (25/10, 25/15, 30/20 and 35/25 °C) and constant temperatures (5, 10, 15, 20, 25, 30, 35, and 40 °C) on germination of seeds under light/dark regime.

Salinity stress

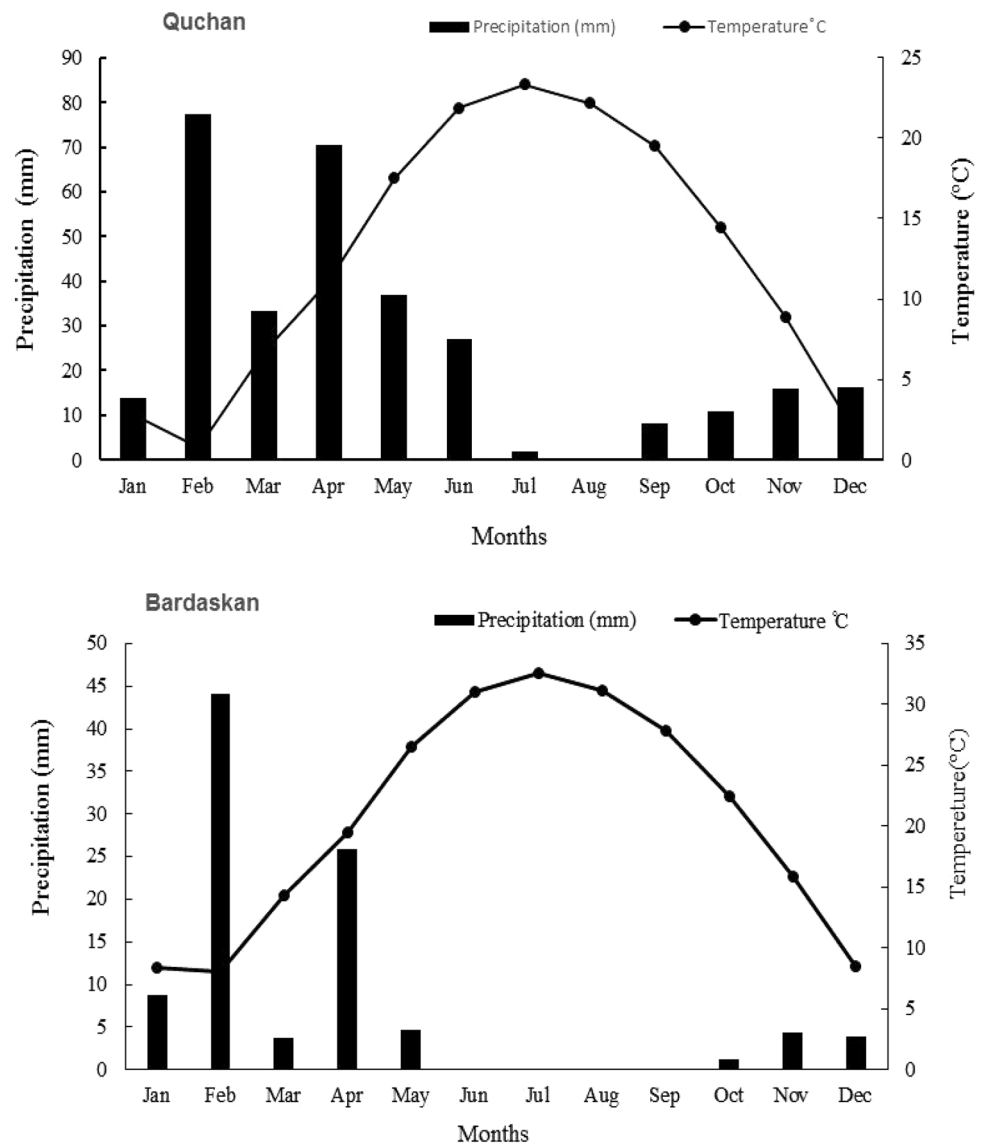
To impose salinity on the seeds, NaCl was dissolved in deionized water to achieve different solutions: 0 (control), 10, 20, 40, 80, 160, 320, 640, and 800 mM. Salinity solutions were set according to the osmotic effects that obtained from salinity levels and were determined using Eq. 1 (Richards 1954).

$$OP = -0.036 \times EC, \quad (1)$$

where, *OP* is osmotic potential and *EC* is electrical conductivity.

Petri dishes were incubated as previously described for general protocol. At the end of the test period (day

Fig. 1 Mean long-term (10 years) precipitation and temperature data for Quchan and Bardaskan during 2007–2016



14), germinated seeds were removed. In the following, the ungerminated seeds treated with 800 mM NaCl (the highest levels of salinity) transferred to Petri dishes and were rinsed by distilled water to indicate the effect of ion toxicity from osmotic potential (Recovery test).

Osmotic potential

C. monogyna seeds were germinated under 12/12 h (light/dark) in aqueous solutions of polyethylene glycol 6000 with osmotic potentials of 0 (Control), -0.1 , -0.2 , -0.4 , -0.6 , -0.8 , and -1.0 MPa. The Solutions were fixed by dissolving required content of PEG 6000 in distilled water as suggested by Michel (1983).

Seed burial depth on seedling emergence

This experiment was conducted in April 2016. Before seeds burial seeds were scarified by boiling water for 30 s and were buried at seven different soil depths (soil surface, 0.5, 1, 2, 3, 4 and 5 cm) in 15-cm-diameter plastic pots. An additional treatment included seeds being placed on the soil surface covered with three sheets of filter paper to provide constant water supply to the seeds. The filter paper was daily removed for emergence assessment. Control soil pots, in which *C. monogyna* seeds were not planted, were included to check the presence of *C. monogyna* in the study. The moist soil was placed over sown seeds to an appropriate depth and was gently compacted. For each burial depth, four pots (replicates), with 50 seeds per pot

were set. The soil used for this experiment was a loam comprised of 37% sand, 36% silt and 27% clay with 0.76% total organic matter and pH of 7.5. Pots from Quchan and Bardaskan populations were placed in two different incubators at a day/night temperature of 25/15 °C and 30/20 °C (12 h/12 h), respectively. The photoperiod was set at 12 h with fluorescent lamps used to produce a light intensity of 140 $\mu\text{mol m}^{-2} \text{s}^{-1}$. Pots were irrigated after seed sowing until each pot reached field capacity and the excess water leached from the bottom. Irrigation was repeated weekly (uniformly to all pots) or as the soil dried. Seedlings were counted as they emerged from the soil for 30 days after initial burial. At the end of the experiment, seeds buried at 5 cm depth were recovered to determine the fate of ungerminated seeds and their viability. The soil was filtered using a 0.1-mm mesh metal sieve to recover intact seeds and the decayed seedlings which failed to emerge after germination. This method could recognize dormant seeds from germinated seeds that failed to emerge due to excessive depth of burial.

Duration of seed burial and seed burial depth on seed fate

This experiment was only performed on Bardaskan population. For this purpose, the seeds of *C. monogyna* were collected in early November 2015 from parasitized vineyards and pomegranate orchards in Bardaskan. This experiment began on November 9, 2015 and ended on February 7, 2017 (450 days, duration of burial). The samples containing 25 dormant seeds of *C. monogyna* were placed in permeable plastics (7 × 7 cm) with three replications used to create a natural soil condition. The plastics (180 bags) were buried at the depth of 0, 2, 5, 10, 15 and 20 cm to evaluate the effect of tillage depth in *C. monogyna* management. The soil texture was determined as a sandy loam with 0.81% organic carbon and pH of 8. To prevent from being blown away by wind, the soil surface bags were anchor with iron nails. the bags were joined together by a wire to facilitate exhumation. After every 45 d (450 days including 10 sampling times), the ungerminated seeds from the bags were recovered and placed in Petri dishes and incubated for 14 days in day/night temperature of 30/20 °C (12/12 h) (Lab germination). Seed germination in the field was evaluated by counting only the emerged and decayed seedlings at the time of bag exhumation. The bags containing seeds were buried under the trees inside the pomegranate orchard, so whenever the trees were irrigated, the bags were irrigated at the same time with pomegranate orchard. The information regarding temperatures at the time of harvesting along with the total monthly rainfall are presented in Table 1.

Table 1 Minimum and maximum temperature at harvesting date and total rainfall in the month in the experiment effect of time and burial depth on seed fate

Harvesting date	Min T °C	Max T °C	Total rainfall in the month (mm)
Nov 9, 2015, Start the experiment	7.6	17.4	12.9
45 d=Dec 24th	1.9	9.8	11.8
90 d=Jan 7, 2016	5.7	20.1	7.5
135 d=Mar 23th	16.4	22.3	21.8
180 d=May 7th	24.9	35.3	4.2
225 d=June 23th	19.5	35.0	0.0
270 d=Aug 7th	22.6	37.3	0.0
315 d=Sep 24th	23.2	37.3	0.0
360 d=Nov 8th	11.4	19.2	0.0
405 d=Dec 23th	1.0	14.8	1.5
450 d=Feb7, 2017	-0.7	9.4	40.3

Min Minimum, *Max* Maximum, *T* Temperature, *d* Day

Statistical analyses

All the experiments were conducted twice (except the seed burial depth on seedling emergence and the effect of time and burial depth on seed fate, in which seeds were exhumed at different times), as a completely randomized design with four replicates per treatment. The experimental data was pooled for analysis, since there was no time-by-treatment interaction. A functional three-parameter logistic model (Chauhan et al. 2006; Ebrahimi and Eslami 2012b) of the form:

$$G(\%) = G_{\max} / \left\{ 1 + (x/x_{50})^{G_{rate}} \right\} \quad (2)$$

was fitted to the germination values (%) obtained at different concentrations of NaCl or osmotic potential using Sigma Plot (version 11.0, SyStat Software, Inc., Point Richmond, CA, USA). In this equation, G represents the total germination (%) at NaCl concentration or osmotic potential x ; G_{\max} is the maximum germination (%); x_{50} is the NaCl concentration or osmotic potential for 50% inhibition of the maximum germination, and G_{rate} indicates the slope. The seedling emergence (%) values obtained at different burial depths were fitted to a sigmoidal decay curve (Norsworthy and Oliveira 2006; Ebrahimi and Eslami 2012b) of the form:

$$E(\%) = E_{\max} / (\exp(-(x - x_{50}) / E_{rate})) \quad (3)$$

where E represents the seedling emergence (%) at burial depth x ; E_{\max} is the maximum seedling emergence; x_{50} represents the depth at which emergence is reduced by 50%, and E_{rate} indicates the slope. ANOVA and regression

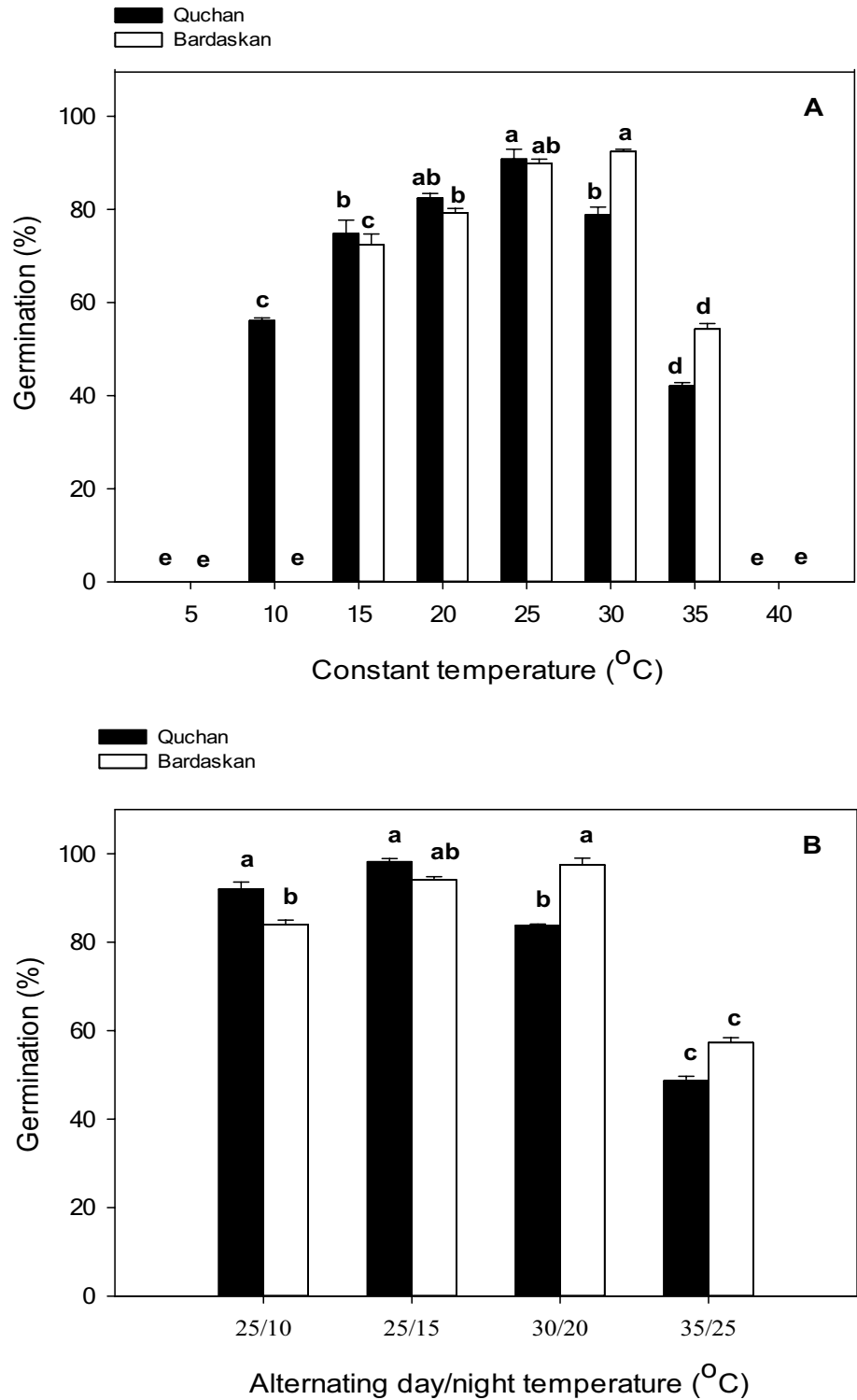
analysis were performed on non-transformed percentage germination data (SAS Version 9.0.3).

Results

Effect of temperature

Germination of *C. monogyna* populations was affected by

Fig. 2 Effect of constant (A) and alternating (B) day/night temperatures on seed germination percentage of *C. monogyna* Quchan and Bardaskan populations



constant temperature regimes (Fig. 2A.). The highest germination percentages of Quchan (90%) and Bardaskan (92%) populations were observed at 25 °C and 30 °C respectively (Fig. 2A). Germination was recorded to be completely failed at 5 °C in Quchan population and up to 10 °C in Bardaskan population.

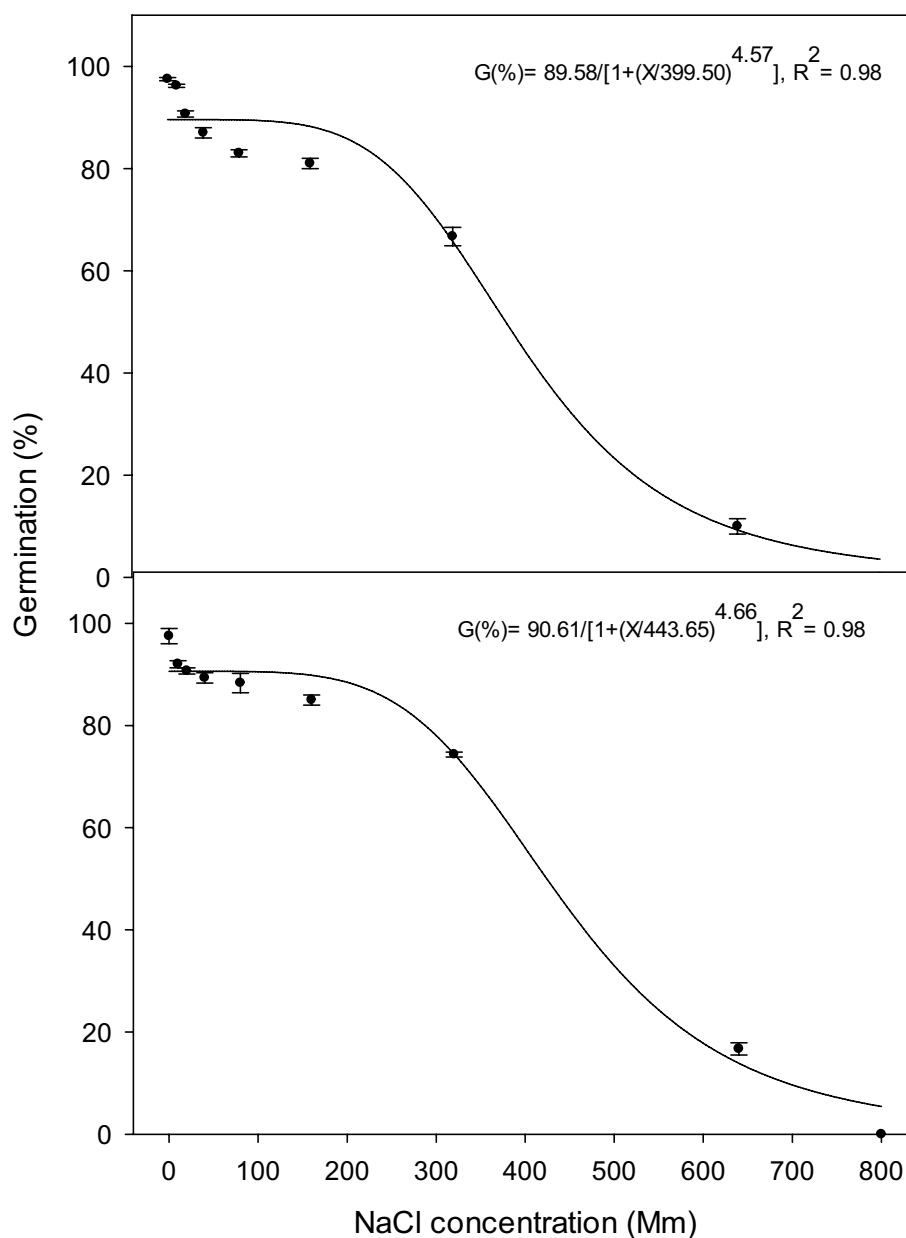
Alternating temperature regimes affected *C. monogyna* germination remarkably ($P < 0.01$), (Fig. 2B) and germination of both populations under alternated temperatures increased compared with constant temperatures. The maximum germination percentage regarding Quchan (98%) and Bardaskan (97%) populations were recorded at 25/15 °C and 30/20 °C day/night, respectively (Fig. 2B). For both populations, the lowest percentage of seed germination was at

35/25 °C day/night. In Quchan and Bardaskan populations, 92 and 84% germination occurred at 25/10 °C day/night temperature, respectively (Fig. 2B).

Effect of salinity

The germination percentage of both populations of *C. monogyna* were strongly affected by all levels of salinity. By increasing salt concentration final germination percentage decreased significantly. In both populations, germination was $> 80\%$ in NaCl concentrations up to 160 mM. By increasing salinity up to 640 mM, the germination percentage of Quchan and Bardaskan populations decreased to 10 and 17% respectively. Seeds failed to germinate at 800 mM

Fig. 3 Effect of NaCl concentrations on seed germination percentage of *C. monogyna* Quchan and Bardaskan populations. The line represents the functional three-parameter logistic model. Vertical lines represent standard error (\pm SE)



NaCl concentration (Fig. 3). Based on the three-parameter logistic model, a suitable fit is provided for the seed germination response to salinity stress. NaCl concentration required for 50% inhibition of seed germination (X_{50} parameter) was 399.5 and 443.65 mM for Quchan and Bardaskan populations respectively (Fig. 3). After recovering the ungerminated seeds by 800 mM salinity solution and then re-incubating using distilled water, the germination of 69% for Quchan and 73% for Bardaskan populations were observed.

Effect of osmotic potential

The seed germination of *C. monogyna* from either population was induced by osmotic stress (Fig. 4) and germination

was > 70% by decreasing osmotic potential to -0.4 MPa. By decreasing the osmotic potential to -0.8 MPa, the germination percentage in Quchan and Bardaskan populations reduced to 9 and 18%, respectively and seeds failed to germinate at -1 MPa osmotic potential (Fig. 4). As previously stated, the three-parameter logistic model can present a precise fit for germination response against drought stress conditions. The osmotic potential required for 50% inhibition of seeds germination was -0.63 and -0.66 MPa for Quchan and Bardaskan populations, respectively (Fig. 4).

Effect of seed burial depth on seed emergence

Seed burial depth greatly affected seedling emergence of either population, and the response was similar among the

Fig. 4 Effect of osmotic potentials on seed germination percentage of *C. monogyna* Quchan and Bardaskan populations. The line represents the functional three-parameter logistic model. Vertical lines represent standard error (\pm SE)

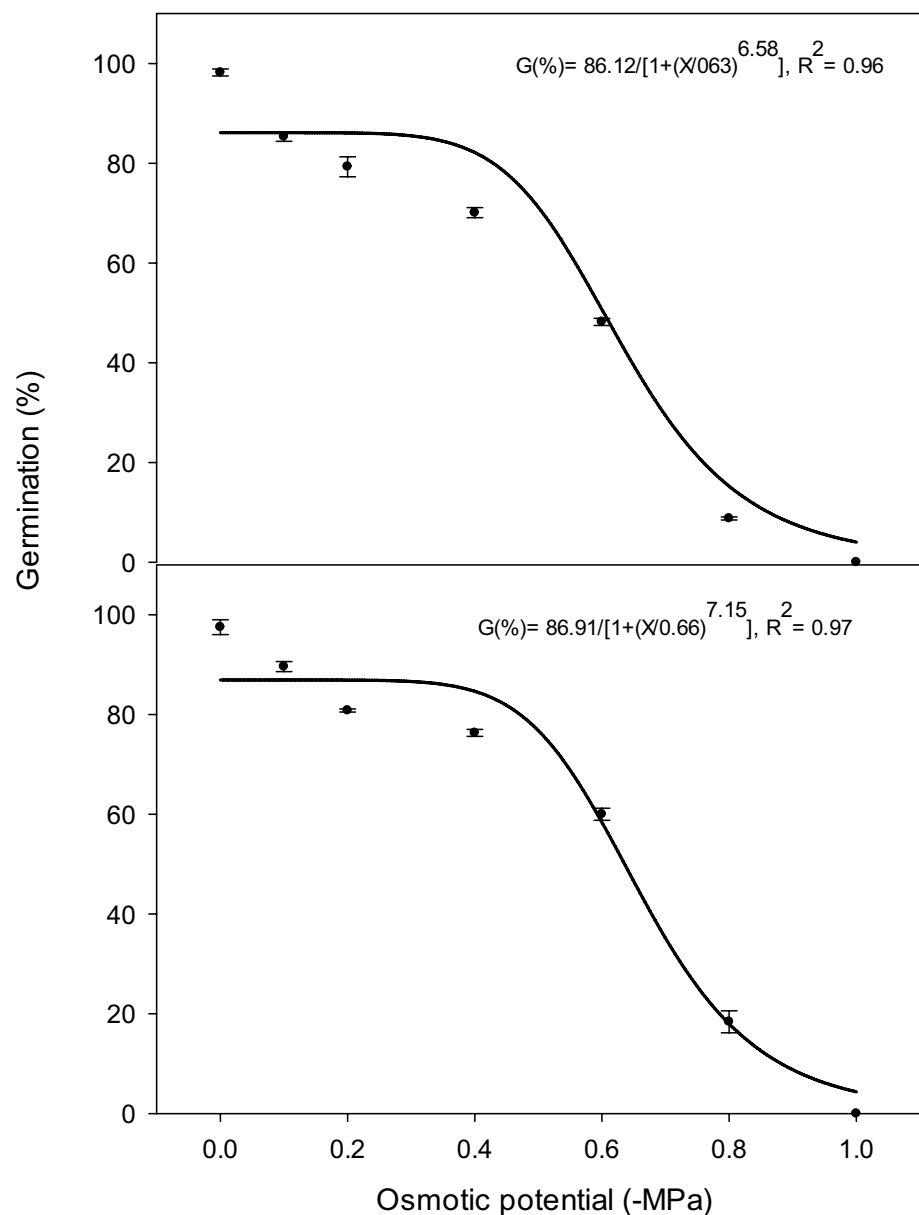
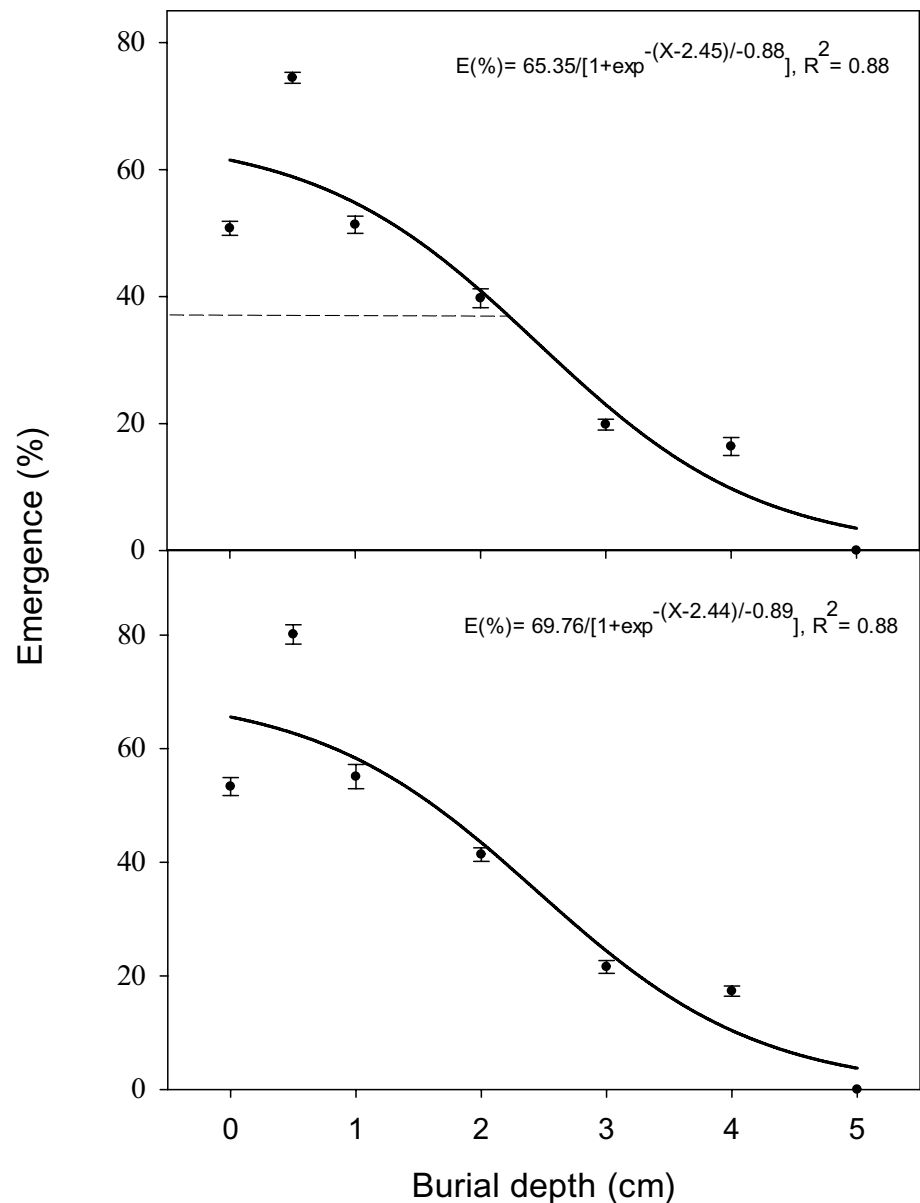


Fig. 5 Effect of seed burial depth on seedling emergence percentage of *C. monogyna* Quchan and Bardaskan populations. The line represents a three-parameter sigmoid model fitted to the data. Vertical lines represent standard error (\pm SE)



populations (Fig. 5). As the depth of seed burial increased, a severe decrease in seedling emergence of populations was recorded. In both populations, the highest seedling emergence observed for seeds placed on the soil surface under three layers of filter paper. The percentage of seedling emergence in depth of 0.5 cm for Quchan and Bardaskan populations were 74 and 80%, respectively (Fig. 5).

As shown in Fig. 5, the sigmoidal decline model presented a satisfactory fit for *C. monogyna* seedling emergence data regarding burial depth treatments. The X_{50} parameter (the burial depth at which emergence of *C. monogyna* is reduced by 50%) predicted from the model (Eq. 3) was 2.45 and 2.44 cm for Quchan and Bardaskan populations respectively (Fig. 5). The recovery of ungerminated seeds buried at 5 cm showed that emergence

failure was due to fatal germination (70%), rather than depth imposed dormancy.

Effect of duration of seed burial and seed burial depth on seed fate

The fate of *C. monogyna* in soil was influenced by *duration of seed burial*, *seed burial depth* and the interaction of them. Gradually (days after seed burial), seed dormancy decreased at all burial depths while seed germination increased in the field experiment (Table 2). The maximum seed germination (98%) in the field was observed at the depth of 5 cm 270 days after seed burial (Early August 2016), and the minimum germination index was recorded in the depth of 0 and 20 cm (Table 2). The highest germination in the laboratory

Table 2 Effect of duration and burial depth on seed dormancy of Bardaskan population *C. monogyna* seeds

Depth (cm)	Time (days)	Seed germination (%)			Depth (cm)	Time (days)	Seed germination (%)		
		Field germination	Lab germination	Dormancy			Field germination	Lab germination	Dormancy
0	0	0.00±0.00	0.00±0.00	100±0.00	10	0	0.00±0.00	0.00±0.00	100±0.00
	45	0.00±0.00	4.00±0.50	96.00±0.50		45	20.00±1.20	2.68±0.30	77.32±0.60
	90	0.00±0.00	8.00±1.00	92.00±0.60		90	5.32±0.60	40.00±0.50	54.68±0.30
	135	0.00±0.00	37.32±2.10	62.68±0.70		135	38.68±2.00	28.00±0.80	33.32±0.80
	180	30.68±4.20	12.00±1.20	57.32±1.00		180	66.68±2.30	2.64±0.40	30.68±1.00
	225	16.00±2.50	18.68±1.40	65.32±0.60		225	66.68±2.60	0.00±0.00	33.32±1.00
	270	30.68±4.30	5.32±0.70	64.00±0.60		270	86.68±4.20	4.00±0.40	9.32±0.80
	315	65.32±5.10	6.68±0.70	28.00±1.20		315	93.32±5.80	0.00±0.00	6.68±1.00
	360	25.32±1.70	4.00±0.00	70.68±1.10		360	96.00±4.30	0.00±0.00	4.00±0.60
	405	34.68±3.50	21.32±1.50	44.00±1.00		405	93.32±1.90	5.32±0.60	1.32±0.70
450	52.00±2.8	26.68±1.30	21.32±1.60	450	98.68±2.70	1.32±0.30	0.0±0.00		
2	0	0.00±0.00	0.00±0.00	100±0.00	15	0	0.00±0.00	0.0±0.00	100±0.00
	45	4.00±0.60	5.32±0.80	90.68±0.50		45	16.00±0.80	10.68±0.50	73.32±2.00
	90	12.00±1.20	2.68±0.50	85.32±0.60		90	5.32±0.70	36.00±0.80	58.68±0.60
	135	25.32±1.80	10.68±0.70	64.00±1.00		135	41.32±1.80	34.68±0.40	24.00±2.40
	180	29.32±0.70	8.00±1.00	62.68±0.30		180	41.32±1.60	1.32±0.00	57.32±1.70
	225	45.32±1.00	8.00±0.70	46.68±2.00		225	65.32±2.20	4.00±0.70	30.68±0.80
	270	69.32±3.20	1.32±0.00	29.32±2.30		270	77.32±4.20	1.32±0.20	21.32±0.60
	315	88.00±5.10	0.00±0.00	12.00±1.30		315	96.00±2.50	0.00±0.00	4.00±0.40
	360	74.68±3.20	17.32±1.20	8.00±1.30		360	88.00±3.00	1.32±0.10	10.68±0.80
	405	100.00±2.30	0.00±0.00	0.00±0.00		405	93.32±3.20	4.00±0.50	2.68±0.30
450	100.00±5.50	0.00±0.00	0.00±0.00	450	85.32±2.10	14.68±1.00	0.0±0.00		
5	0	0.00±0.00	0.00±0.00	100±0.00	20	0	0.00±0.00	0.0±0.00	100±0.00
	45	12.00±1.10	6.68±0.60	81.32±0.40		45	16.00±1.20	4.00±0.30	80.00±1.60
	90	16.00±1.10	17.32±1.20	66.68±0.70		90	9.32±1.00	42.68±1.20	48.00±1.40
	135	53.32±2.40	28.00±2.00	18.68±0.60		135	22.68±2.00	56.00±1.00	21.32±0.80
	180	62.68±3.40	4.00±0.50	33.32±0.40		180	34.68±1.80	4.00±0.60	61.32±0.50
	225	82.68±3.20	5.32±0.30	12.00±1.10		225	45.32±2.80	2.68±0.30	52.00±1.00
	270	98.68±4.50	0.00±0.00	1.32±0.60		270	53.33±2.20	1.33±0.20	45.34±0.80
	315	94.68±4.00	1.32±0.00	4.00±0.10		315	60.00±3.00	4.00±0.60	36.00±1.20
	360	98.68±5.30	0.00±0.00	1.32±0.50		360	73.32±3.20	2.68±0.50	24.00±0.70
	405	93.32±2.80	5.32±0.30	1.32±0.30		405	68.00±3.60	17.32±1.00	14.68±0.80
450	93.32±4.10	5.32±0.60	1.32±0.20	450	76.00±1.90	17.32±0.80	6.68±0.70		

Seeds were after-ripened at 0, 2, 5, 10, 15 and 20 cm

Parentheses represent standard error (±SE)

was observed at 20 cm (56%) followed by the soil surface seeding treatment (37%) 135 days (Late March 2016) after seed burial (Table 2).

Discussion

According to the results, both *C. monogyna* populations could germinate in a wide range of constant and alternating temperatures from 10 up to 30 °C provides *C. monogyna* to germinate in cool temperatures of early spring up to warm temperatures of mid-summer and could parasitize host plants. Benvenuti et al. (2005) studied the influence of temperature on *C. campestris* germination and discovered that 60% and 80% of the seeds had germinated at 20 and 30 °C, respectively. Similarly, Krsmanovic et al. (2013)

reported that the seeds of *C. campestris* did not germinate at 5 and 45 °C which is in agreement with observed results. According to Salimi and Shahraeen (2000), the germination process of *C. monogyna*, *C. campestris*, and *C. planiflora* were recorded to be optimum at 20, 20, and 25 °C, respectively. However, in both *cuscuta* populations, seed germination index was found to be higher in alternated temperatures than constant temperatures. Booth et al. (2003). Also reported similar results. It is stated that alternating temperature arouses seed germination through activating some specific physiological processes; because maximizing germination requires an alternate day/night temperature (Malik et al. 2010). According to the results, the germination of both populations declined at 35 °C and 35/25 °C.

Based on climatic conditions, the population of Quchan was not exposed to high temperatures during spring and

early summer; while during similar periods, temperatures above 30 °C were recognized as a prevalent phenomenon in Bardaskan. On the other hand, the maximum germination of Quchan population was observed at lower temperature than Bardaskan population, possibly due to its higher tolerance to low temperatures. The results could imply that this parasitic weed could spread from east to other areas of Iran with similar temperature conditions and parasitize the host trees. In Vineyards of Quchan and Bardaskan, *C. monogyna* has a seedling emergence peak in early June in Quchan and in late March in Bardaskan, when the average of the soil surface temperature is about 20 to 25 °C, consistent with the optimum germination temperature of *C. monogyna* populations observed in this study.

In both *C. monogyna* populations, salinity stress resulted in a decrease in germination index; however, salt tolerance varied between the populations. In Bardaskan population, germination was found to be > 16% over a range of 640 mM salinities, while in Quchan population, the germination reduced by 10% at 640 mM. In this concentration (640 mM), the seedling length of *C. monogyna* in both populations was about 1 cm, whereas in the control treatment (0 mM) seedlings had an average length of 12 cm. It means at high salinity conditions, *C. monogyna* cannot produce a strong seedling for parasitizing the host trees and due to seed germination, soil seed bank is only depleted. However, based on X_{50} parameter indicated a higher salt tolerance of Bardaskan compared to Quchan. Waisel (1972) stated that increasing salinity leads to reduced or delayed germination through osmotic stress or toxicity. In Bardaskan, some pomegranate and vineyards orchards are irrigated by salt water (≥ 7 dS m^{-1}); therefore, it is possible that the seeds of Bardaskan population can germinate under such conditions and parasitize the host trees. In such situations, it is recommended to cultivate non-host trees and salt-tolerant plants such as pistachios (*Pistacia vera* L.). Amini et al. (2017) reported that NaCl concentration caused 50% inhibition of germination in *Caucalis platycarpus* L. was 8.83 and 5.71 dS m^{-1} for Azerbaijan and Kermanshah populations, respectively. *C. monogyna* seeds demonstrated 68% and 73% germination recovery in Quchan and Bardaskan populations, respectively. It means that enforced seed dormancy in *C. monogyna* was mainly due to an osmotic effect, as opposed to toxicity owing to an ionic effect. In general, the germination data suggests that *C. monogyna* seeds can germinate under soil conditions in north and south of Khorasan-e-Razavi. This would provide the chance for the invasion of *C. monogyna* into new areas. Our results indicate that *C. monogyna* may tolerate higher salinity concentrations like *Ceratocarpus arenarius* L. (with X_{50} of 401 mM NaCl) (Ebrahimi and Eslami 2012b) which grows in the north of Khorasan.

The results showed the higher drought stress tolerance of Bardaskan compared with Quchan population, which is

likely referred to be a better adaptation to the low-rainfall. It seems that the adaptability of certain weed species to water stress depends on environmental conditions. Eslami (2011) mentioned that a xeric population of *Chenopodium album* L. from Iran maintained > 65% seed germination up to an osmotic potential of -0.4 MPa, while decreasing osmotic potential from 0 to -0.4 MPa caused an 80% reduction in germination of the same weed species from Denmark. Decreased water potential due to drought stress has been reported to be the cause of a slow germination in the seed, just as osmotic stress has a similar effect under salinity conditions. The occurrence of changes in medium changes the properties of the tegument of seeds, so that a low water potential leads to a reduced water content in tegument and limited water diffusion into the seeds (Hadas 1976). In the following, reduced enzyme activities and delayed developmental processes may be provoked.

It is possible for *C. monogyna* seedlings to emerge from a burial depth of 4 cm. Decreased seedling emergence due to increased burial depth may principally be associated with limited seed energy reserves (Mennan and Ngouajio 2006). The more inadequate gas exchange is considered the main cause of decreased emergence at greater depths (Benvvenuti et al. 2001; Huarth et al., 2016; Nosratti et al. 2017; Amini et al. 2017). Because of the seed size in *Cuscuta* spp (1–2 mm in diameter), the emergence is mostly limited to the upper 1 to 1.5 cm of soil (Lanini and Kogan 2005). Lower germination from seeds located at the soil surface compared to 0.5 cm depth is not surprising, since reduced seed contact with soil particles along with inadequate moisture frequently results in limited germination at the soil surface (Ghorbani et al. 1999). However, seeds that were placed on the soil surface and covered with filter paper had the highest emergence percentage. This indicates that germination of seeds on the soil surface might be increased under field conditions by the presence of host trees residue, which creates better soil–seed contact and preserves moisture content. The recovery of ungerminated seeds at the depth of 5 cm showed that emergence failure was the result of fatal germination (70%), not enforced dormancy. This indicates that non-dormant seeds of *C. monogyna* cannot form a persistent seed bank. However, dormant seeds, due to physical coating, may behave differently, as the seed coat appears to inhibit germination while it encloses the seed. Such seeds are likely to be stable in the soil seed bank during harsh conditions such as drought and salinity, because of seed coat inhibition. Physical dormancy is known as ecological adaptation, which ensures seedling survival and enhances seed persistence by regulating germination time, especially under arid conditions (Hu et al. 2009; Ebrahimi and Eslami 2012b).

On the soil surface, seed dormancy decreased from 96%, 45 days after burial to 21%, 450 days after burial which accounts for a 77% reduction in seed dormancy. In 20 cm

depth, seed dormancy rate was not completely released, and 7% of seeds were still dormant after 450 days after burial in this depth. Seed germination in the field at all depths except the soil surface and 20 cm depth, is due to available moisture and the activity of soil microorganisms which results in increased metabolic activity of seeds and dormancy breaking. The germination was observed in the lab, but not in the field until 135 days after seeds burial (Late March, 2016), assumingly due to harsh conditions of winter. According to the results, during cold months of the year (45, 90, 135, 405, and 450 days after seed burial), germination increased at all depths (except at 2 cm depth) in the laboratory compared to warm months (180, 225, 270, 315, and 360 days after seed burial), which is probably due to reduced seed dormancy caused by moist chilling. These seeds (0 and 20 cm) were germinated when they were transferred to the laboratory and exposed to optimum temperatures. The breaking of dormancy and germination were highest at the depth of 5 cm which occurred 270 days after burial, also with the burial of seeds at lower depths, the longevity of the seeds increased.

These results show that the farming operations that can maintain a large proportion of seeds at the depth of 5 cm, may result in a more accelerated depletion of the soil seed bank in the absence of seed replenishment. By the end of the study (450 d after seed burial), the seeds of the soil surface and 20 cm depth were 21% and 7% dormant, respectively, probably because these seeds have physical dormancy due to their hard seed coats and create a constant seed bank in the soil. The recovery test of ungerminated seeds at 5 cm burial depth showed the average 95% germination indicating the viability of seeds and enforced dormancy in this depth.

Conclusion

According to the observed results, *C. monogyna* populations naturalized in Quchan (semiarid climate) and Bardaskan (dry climate) regions could germinate in a wide temperature range (from constant to alternated). Relatively, Quchan population somewhat required lower temperatures for its optimal germination compared to Bardaskan population. On the other hand, Bardaskan population had a higher salinity and osmotic stress tolerance than Quchan population. Despite the fact that Quchan population has smaller seeds, seedling emergence was similar in both populations. The seed collections of *C. monogyna* from other locations in Iran or outside the country have different responses to environmental factors because of populations' biological diversity. *C. monogyna* seed germination is influenced by physical dormancy. This work only achieves a partial understanding of the germination patterns of these *C. monogyna* populations. The experimental set up should elucidate each component of *C. monogyna* dormancy for each population.

For each population, we should determine the duration of physical dormancy, level of physiological dormancy and cold stratification requirements to break it, influence of temperature on germination of non-dormant seeds (subjected to scarification and cold stratification).

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Declarations

Conflict of interest No conflicts of interest have been declared.

References

- Ahmed S, Opena JL, Chauhan BS (2015) Seed germination ecology of doveweed (*Murdannia nudiflora*) and its implication for management in dry-seeded rice. *Weed Sci* 63:491–501
- Amini R, Gholami F, Ghenepour S (2017) Effects of environmental factors and burial depth on seed germination and emergence of two populations of *Caucalis platycarpus*. *Weed Res* 57:247–256
- Benevenuti S, Macchia M, Miele S (2001) Quantitative analysis of emergence of seedlings from buried weed seeds with increasing soil depth. *Weed Sci* 49:528–535
- Benevenuti S, Dinelli G, Bonetti A, Catixone P (2005) Germination ecology' emergence and host detection in *Cuscuta campestris*. *Weed Res* 45:270–278
- Booth BD, Murphy SD, Swanton CJ (2003) Weed ecology in natural and agricultural systems. CAB International, Wallingford, pp 93–94
- Chauhan BS, Johnson DE (2010) The role of seed ecology in improving weed management strategies in the tropics. *Advances in Agron* 105:221–262
- Chauhan BS, Gill G, Preston C (2006) Factors affecting seed germination of annual sowthistle (*Sonchus oleraceus*) in southern Australia. *Weed Sci* 54:854–860
- Costea M, Stefanovic S (2010) Evolutionary history and taxonomy of the *Cuscuta umbellate* complex (Convolvulaceae): Evidence of extensive hybridization from discordant nuclear and plastid phylogenies. *Taxon* 59:1783–1800
- Cudney DW, Orloff SB, Reints JS (1992) An integrated weed management procedure for the control of dodder (*Cuscuta indecora*) in alfalfa (*Medicago sativa*). *Weed Tech* 6:603–606
- Dawson JH (1987) *Cuscuta* (Convolvulaceae) and its control. In: Parasitic Flowering Plants. Proc. 4th International. Symposium, Marburg, Germany, pp 137–149
- de Cauwer B, Devos R, Cearhout S, Bulcke R, Reheul D (2014) Seed dormancy, germination, emergence and seed longevity in *Galinsoga parviflora* and *G. quadriradiata*. *Weed Res* 54:38–47
- Ebrahimi E, Eslami SV (2012a) Effect of different treatments on dormancy breaking and seed germination of Eastern dodder (*Cuscuta*

- monogyna* Vahl) and African rocket (*Malcolmia africana* L. (R.Br.)). Plant Prot 26:191–198
- Ebrahimi E, Eslami SV (2012b) Effect of environmental factors on seed germination and emergence of invasive *Ceratocarpus arenarius*. Weed Res 52:50–59
- Eslami SV (2011) Comparative germination and emergence ecology of two populations of common lambsquarters (*Chenopodium album* L.) from Iran and Denmark. Weed Sci 59:90–97
- Fathoulla CN, Mosleh MS (2008) Biological and anatomical study of different *Cuscuta* species. Kurdistan Conf Biol 11:22–39
- Ghorbani R, Seel W, Leifert C (1999) Effects of environmental factors on germination and emergence of *Amaranthus retroflexus*. Weed Sci 47:505–510
- Goldwasser MH, Rubin B, Eizenberg H (2016) Field Dodder (*Cuscuta campestris*)- a new model describing temperature-dependent seed germination. Weed Sci 64:53–60
- Guan B, Zhuo D, Zhang H, Tian Y, Japhet W, Wang P (2009) Germination responses of *Medicago ruthenica* seeds to salinity, alkalinity and temperature. Arid Environ 73:135–138
- Hadas A (1976) Water uptake and germination of leguminous seeds under changing external water potential in osmotic solutions. J Exp Bot 27:480–489
- Holml DJ, Panch J, Harbeeger J (1997) World weeds: natural histories and distribution. John Willey & Sons, New York, USA
- Hu XW, Wang YR, Wu YP (2009) Effects of the pericarp on imbibition, seed germination, and seedling establishment in seeds of *Hedysarum scoparium* Fisch. et Mey. Ecological Res 24:559–564
- Huarth HR, Zorraquin MRP, Bursztyn EM, Zapiola ML (2016) Effects of environmental factors on seed germination and seedling emergence of common teasel (*Dipsacus fullonum*). Weed Sci 64:421–429
- Hutchison JM, Ashton FM (1979) Effect of desiccation and scarification on the permeability and structure of the seed coat of *Cuscuta campestris*. Am J Bot 66:40–46
- Karimi H (2001) Weeds of Iran. Tehran, Iran, p 419
- Krsmanovic MS, Bozic D, Pavlovic M, Radivojevic L, Vrbnicanin S (2013) Temperature effects on *Cuscuta campestris* seed germination. Pestic Phyt 28:187–193
- Kuijy J (1969) The biology of parasitic flowering plant. University of California Press, Berkeley, CA, p 246
- Lanini WT, Kogan M (2005) Biology and management of *Cuscuta* in crops. INV Agric 32:165–179
- Malik MS, Norsworthy J, Riley MB, William B (2010) Temperature and light requirements for Wild Radish (*Raphanus raphanistrum*) germination over a 12-month period following maturation. Weed Sci 58:136–140
- Mennan H, Ngouajio M (2006) Seasonal cycles in germination and seedling emergence of summer and winter populations of catchweed bedstraw (*Galium aparine*) and wild mustard (*Brassica kaber*). Weed Sci 54:114–120
- Michel BE (1983) Evaluation of the water potentials of solutions of polyethylene glycol 8000 both in the absence and presence of other solutes. Plant Physiol 72:66–70
- Nazari S (2014) Introducing *Cuscuta monogyna* as Oak Trees Parasite, its Biology, and Method to Fight in Lorestan province. Bull Environ Pharmacol Life Sci 3:164–168
- Norsworthy JK, Olivera MJ (2006) Sicklepod (*Senna obtusifolia*) germination and emergence as affected by environmental factors and burial depth. Weed Sci 54:903–909
- Nosrati I, Abbasi R, Bagheri A, Bromandan P (2017) Seed germination and seedling emergence of Iberian starthistle (*Centaurea iberica*). Weed Biol and Manag 17:144–149
- Rashed Mohassel MH, Najafi H, Akbarzadeh MD (2009) Weed biology and control, 2nd edn. Ferdowsi University of Mashhad Press, p 404
- Richards LA (1954) Diagnosis and Improvement of Saline and Alkali Soils. USDA Agricultural Handbook 60, Washington
- Salimi H, Shahraeen N (2000) Study on comparison of seed dormancy and germination of three species of dodder. Rostaniha 1:33–36
- Tsvion Y (1981) Suppression of axillary buds of its host by parasitic *Cuscuta* I. competition among sinks and indirect inhibition. New Phytol 87:91–99
- Waisel Y (1972) Biology of halophytes. Academic Press, New York and London
- Zand E, Baghestani MA, Shimi P, Nezamabadi N, Mousavi MR, Mousavi SK (2017) Chemical weed control guideline for major crops of Iran. Ferdowsi University of Mashhad Press, p 224

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