Foliage colour influence on seed germination of *Bienertia cycloptera* in Arabian deserts

Arvind Bhatt, F. Pérez-García and Prakash C. Phondani

Bienertia cycloptera (Chenopodiaceae) produces two types of leaf foliage colour (reddish and yellowish). In order to determine the role of leaf colour variation in regulating the germination characteristics and salinity tolerance during germination, a study was conducted on seeds collected from plants of both colours. Seeds with and without pulp were germinated under two illumination conditions (12-h light photoperiod and continuous dark), three alternating temperature regimes (15/25°C, 20/30°C and 25/35°C), and several salinity levels at 20/30°C. Germination percentage was significantly higher for seeds without pulp as compared to the seeds with pulp. The response of *B. cycloptera* seeds to salinity depended on the leaf colour. Thus, the seeds collected from reddish coloured plants were able to tolerate higher salinity compared to those of yellowish coloured plant. The germination recovery results indicate that the seeds from both coloured plants could remain viable in saline condition and they will be able to germinate once the salinity level are decreased by rain. The production of different foliage colours by *B. cycloptera* seems to be an adaptative strategy which increases the possibility for establishment in unpredictable environments by producing seeds with different germination requirements and salinity tolerance.

Coloured compounds such as chlorophyll, anthocyanins and carotenoids are the main pigments responsible for producing colour by plants, and these pigments have various physiological functions in plants (Schaefer and Wilkinson 2004, Schaefer and Rolshausen 2006). Chlorophyll is involved in photosynthesis, anthocyanins are in protecting the photosynthetic apparatus against excess radiation (Gould et al. 2002, Gould 2004), and carotenoids act in light capture and photo protection of light-sensitive leaf organelles (Verhoeven et al. 1999, Hormaetxe et al. 2004). Generally, plants produce these pigments in vegetative tissues in response to drought stress, increased ultraviolet light and herbivore pressures (Whittall and Carlson 2009). Further, flower and fruit colours have been reported to enhance the reproductive success of plants by facilitating communication between plants, their pollinators and seed-dispersal agents (Ridley 1930, Stiles 1982, Schaefer and Schmidt 2004, Carlson and Holsinger 2010). However, production of bright colours of fruit/foliage is costly because plants need to allocate considerable resources to synthesize these pigments (Lomascolo et al. 2008, Lev-Yadun and Gould 2009).

Previous studies have reported that flower colour polymorphism occurred due to indirect selection on plant performance in distinct physical environments (Lacey and Herr 2005, Strauss and Whittall 2006). Therefore, different morphs have differences in tolerance to abiotic conditions which may be maintained by plants to cope with fluctuating environmental conditions (El-Keblawy et al. 2013). Differently coloured floral morphs have also been shown to vary with respect to germination and salinity tolerance (Takeno and Yamaguchi 1991, Warren and Mackenzie 2001, Schemske and Bierzychudek 2001, 2007, El-Keblawy et al. 2013). However, until now no information has been available regarding the factors that affects the leaf colour and how variation in these colours evolve within a species. Furthermore, it is important to know whether leaf colour diversity is driven by physiological demands or if there might be other additional selective agents.

Bienertia cycloptera (Chenopodiaceae) is an annual, succulent, glabrous herb, 10–40 cm tall, distributed throughout the Middle East, Iran, Pakistan and Afghanistan (Akhani et al. 2003). This species has a unique C4 photosynthesis mechanism which occurs within a single chlorenchyma cell (Akhani et al. 2005, Voznesenskaya et al. 2005). The species is reported to have dimorphic chloroplasts with different inner structure (and metabolism) in the leaf mesophyll cells (Voznesenskaya et al. 2001, Voznesenskaya et al. 2005). The colour of chromoplasts has been reported to play an important ecological role in attracting pollinators and seed dispersing frugivores (Solymosi and Keresztes 2012). Fruits of *B. cycloptera* are fleshy, orbicular, berry-like and surrounded by a fleshy circular wing (Mandaville 2004). The species has

the ability to self-fertilize and it produces a single seed per flower which is protected by the fleshy fruit until desiccation when this fleshy fruit ruptures and allows the dispersal of the seed (Clay 2006). However, we did not find any literature on the mode of seed dispersal in *B. cycloptera*. This species has good potential to be used as forage for camel and sheep (Bhat et al. 2013). We observed that this species has two distinct leaf colour morphs (reddish and yellowish) (Fig. 1). Yellow plants are more abundant than red morphs.

The ability of seeds to germinate fast at low water potential is an advantageous adaptation for species colonising water-stressed environments (Bochet et al. 2007). It has been shown in a large number of species that an increase in salt concentration usually delays and reduces seed germination (Zia and Khan 2004, El-Keblawy et al. 2007, El-Keblawy and Al-Shamsi 2008, Tlig et al. 2008). However, there is a wide range of variability in salt tolerance among species (Khan and Gulzar 2003, Khan and Gul 2006). Moreover, many seeds that are unable to germinate at high saline concentrations might recover the ability to germinate when salinity levels decrease (Baskin and Baskin 2001, Zia and Khan 2008).

In this study, we hypothesize that there might be a connection between leaf colour variation and the regulation of germination characteristics and salinity tolerance during the germination stage in *B. cycloptera*, which may consequently determine the survival strategy in unpredictable desert conditions. To test the success of germination in the two leaf morphs (reddish and yellowish), we assessed the impact of presence and absence of fruit pulp on the germination response of *B. cycloptera* seeds to light, temperature and salinity. We also assessed whether seeds that were not able to germinate in saline solutions could recover germination capacity following transfer to distilled water.

Material and methods

Plant material and storage

Mature fruits of *B. cycloptera* were collected in December 2014 from Al-Khor, Doha Qatar (25°65′N, 51°39′E, 2 m a.s.l.). Seeds from both colours of leaf foliage (reddish and yellowish) (Fig. 1) were collected separately and tested with and without pulp. Immediately after collection, seeds were cleaned and stored at room temperature (20 ± 2°C) until the experiment started (February 2015). The seed mass was determined by weighing three replicates, 50 seeds each, with and without pulp, from both the reddish and yellowish plants. Pulps were removed from the seeds by a hand-made rubber thresher and care was taken not to scarify the seed coat while removing the pulp.

Effect of light and temperature on seed germination

To investigate the effect of temperature and light requirements during germination, seeds with and without pulp of both reddish and yellowish plants were incubated in three incubators set at three temperature regimes:15/25, 20/30 and 25/35°C in either continuous darkness or 12-h light/12-h darkness. Lower temperatures correspond to the dark period, while higher temperatures to the light period. In the continuous dark treatment, the dishes were wrapped in aluminium foil to prevent exposure to light. The germination experiment was conducted in 9 cm tight-fitting Petri dishes containing one disk of Whatman no. 1 filter paper moistened with 10 ml of distilled water. Four replicates of 20 seeds each were used for each treatment. A seed was considered to have germinated when the emerging radicle had elongated to 2 mm. Germinated seedlings were counted and removed daily for 20 days following seed soaking. Seeds incubated in continuous dark were checked only after 20 days.

Effect of salinity on seed germination

To assess the salinity tolerance during germination, seeds without pulp of both reddish and yellowish colored plants were germinated under different salinity levels (0, 100, 200, 400 and 600 mM NaCl). Four replicates, each consisting of 20 seeds, were used for each treatment. Seeds were germinated in 9 cm diameter Petri dishes on two layers of Whatman no. 1 filter paper, moistened with 10 ml of the test solution. Petri dishes were sealed with parafilm to minimize evaporation and incubated at 20/30°C in either continuous dark or 12-h light photoperiod. For continuous dark treatment, the dishes were wrapped in aluminium
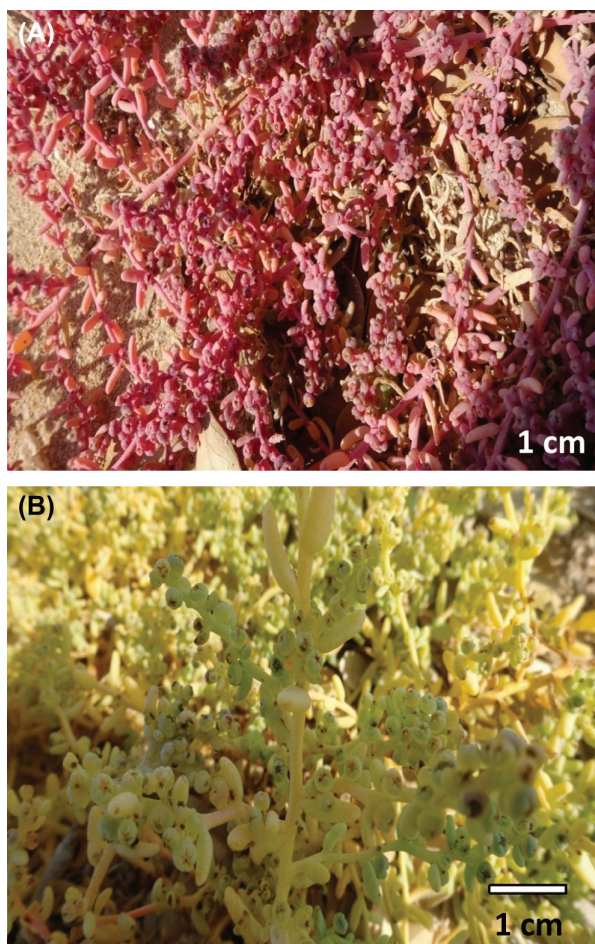

Figure 1. Variation in leaf colour foliage in *B. cycloptera* (A) reddish, (B) yellowish. Photograph taken from Al-Khor, Doha Qatar.

foil to prevent any exposure to light. Seed germination was recorded as above.

Recovery percentage

Non-germinated seeds from the 20 days NaCl incubation tests were transferred to distilled water and incubated for an additional 20 days at the same incubation temperature. Recovery percentage (RP) was calculated by the following formula: $RP = (a–b/c–b) \times 100$, where a is the number of seeds germinated in NaCl solution after a 20-d period plus those that recovered to germination in distilled water after another 20-d period, b is the number of seeds germinated in NaCl solution after a 20-d period, and c is the total number of seeds tested (Gul and Webber 1999, Yang et al. 2010). Initial germination was recorded as $(b/c) \times 100$, and final germination as $(a/c) \times 100$.

Data analysis

For all experiments, final germination percentages (mean value $\pm$ SE) were calculated. The values of final germination percentages were arcsine square-root transformed and then subjected to analysis of variance (ANOVA) using SPSS (untransformed data shown in Table 1–5). The effect of temperature regime (three levels), illumination conditions (12-h light photoperiod and continuous darkness), plant colour (reddish and yellowish green plants), and seed type (seeds with pulp and without pulp) on the final germination percentage were analysed by a four-way factorial ANOVA. A three-way factorial ANOVA was also used to test the effect of NaCl concentration (5 levels), plant colour (2 levels), and illumination conditions (2 levels) on seed germination. One-way factorial ANOVA was applied to test the effect of different concentrations of NaCl on the germination percentages (initial and final germination). Similarly, recovery percentage (RP) values were analysed by a one-way factorial ANOVA. Where ANOVA indicated a significant effect, a comparison of mean values was carried out through the least significant difference test (LSD) at 0.05 level of probability.

Results

Seed mass

For seeds collected from reddish plants, mean mass ($\pm$ SE) per 50 seeds was 0.152 ± 0.014 g for seeds with pulp and 0.076 ± 0.002 for seeds without pulp, and for seeds collected from yellowish plants, 0.178 ± 0.008 g and 0.073 ± 0.002 g, respectively.

Effect of temperature and light regimes

The effect of incubation temperature and illumination condition (12-h light photoperiod and continuous dark) on the final germination percentage of *B. cycloptera* seeds is shown in Table 1, and their correspondent ANOVA results are shown in Table 2. Illumination condition, seed type (seed with and without pulp), and plant colour (reddish and yellowish) had highly significant ($p < 0.001$) effects on seed germination; therefore the effect of temperature regime was lightly significant ($p = 0.049$). The two-way interactions were significant ($p < 0.01$ and $p < 0.001$, depending on interaction), except for the interaction between light and temperature ($p = 0.600$). For the three-way interactions, two of these were significant ($p < 0.01$) and the other two were not significant ($p > 0.05$) (Table 1). The four-way interaction was not significant ($p = 0.362$).

For illumination condition, seed type, and plant colour, a one-way ANOVA was used to compare final germination percentages. For all three temperature regimes and both illumination conditions assayed, the germination percentage of seeds without pulp was higher than that of seeds with pulp. Germination of seeds with and without pulp was in the range 0–29% and 35–96%, respectively (Table 1). Further, for seeds with pulp these values were always lower for seeds collected from reddish plants than for those from yellowish plants (Table 1). Thus, removal of pulp was found to be highly effective in promoting seed germination of *B. cycloptera*. The germination under 12-h light photoperiod was generally higher than that under continuous dark, except for seeds with pulp from reddish plants (Table 1).

Effect of NaCl concentration

The effects of different NaCl concentrations on germination of *B. cycloptera* seeds are shown in Table 3 and their correspondent ANOVA results are shown in Table 4. The highest germination was obtained in distilled water, except for seeds collected from reddish plants incubated under continuous darkness. Salt concentration, and illumination condition had significant ($p < 0.01$) effects on seed germination and were dependant on the plant colour (reddish and yellowish). The two-way interactions were significant ($p < 0.001$),

Table 1. Germination percentages (mean values $\pm$ SE) of *B. cycloptera* seeds collected from reddish and yellowish plants. Seeds with and without pulp were incubated at three alternate temperatures under two illumination conditions (12-h light photoperiod and continuous darkness). Means within a column followed by the same lowercase letters are not significantly different at the $p < 0.05$ level according to the LSD test. Likewise, means within a row followed by the same uppercase letters are not significantly ($p > 0.05$) different from each other.

Incubation temperature (°C)	Illumination Condition	Reddish plant		Yellowish plant	
		With pulp	Without pulp	With pulp	Without pulp
15/25	Photoperiod	5.00 ± 1.77 aA	76.25 ± 2.07 bB	28.75 ± 4.80 cA	73.75 ± 4.46 abB
	Darkness	6.25 ± 3.25 aA	35.00 ± 1.77 aAB	12.50 ± 2.79 abA	66.25 ± 3.70 aB
20/30	Photoperiod	2.50 ± 1.25 aA	83.75 ± 2.07 bcB	18.75 ± 3.70 bcA	91.25 ± 3.25 bB
	Darkness	2.50 ± 1.25 aA	37.50 ± 2.79 aB	11.25 ± 2.07 abA	76.25 ± 2.07 abC
25/35	Photoperiod	0 aA	96.25 ± 1.08 cB	7.50 ± 2.16 abA	80.00 ± 1.77 abB
	Darkness	1.25 ± 1.08 aA	37.50 ± 2.79 aB	6.25 ± 1.08 aA	60.00 ± 1.77 aC

Table 2. Results of the four-way ANOVA regarding the effects of incubation temperature (15/25°C, 20/30°C, 25/35°C), plant colour (reddish and yellowish morphs), seed type (seeds with and without pulp), and illumination conditions (12-h light photoperiod and continuous darkness) on the germination of *B. cycloptera* seeds.

Source of variation	DF	MS	F	p
Temperature (T)	2	101.10	3.15	0.049
Plant colour (CP)	1	3073.72	95.64	<0.001
Seed type (ST)	1	45337.91	1410.71	<0.001
Light (L)	1	3558.39	110.72	<0.001
T × CP	2	228.37	7.11	0.002
T × ST	2	519.82	16.17	<0.001
T × L	2	16.54	0.51	0.600
CP × ST	1	391.19	12.17	0.001
CP × L	1	373.55	11.62	0.001
ST × L	1	1893.48	58.92	<0.001
T × CP × ST	2	85.30	2.65	0.077
T × CP × L	2	38.32	1.19	0.309
T × ST × L	2	209.83	6.53	0.002
CP × ST × L	1	1171.03	36.44	<0.001
T × CP × ST × L	2	33.15	1.03	0.362
Error	72	32.14		

Table 4. Results of the three-way ANOVA for the effects of NaCl concentration (0, 100, 200, 400, 600 mM), plant colour (reddish and yellowish plants), and illumination conditions (12-h light photoperiod and continuous darkness) on the germination of *B. cycloptera* seeds.

Source of variation	DF	MS	F	p
NaCl	4	1352.29	28.43	<0.001
Plant colour (CP)	1	2456.77	51.65	<0.001
Light (L)	1	435.29	9.15	0.004
NaCl × CP	4	875.59	18.41	<0.001
NaCl × L	4	341.73	7.18	<0.001
CP × L	1	142.18	2.99	0.089
NaCl × CP × L	4	106.25	2.23	0.076
Error	60	47.56		

Discussion

Bienertia cycloptera seeds collected from differently coloured plants (reddish and yellowish) showed morphological heterogeneity in seed mass and in germination response. This variability in germination might have an advantage under harsh environmental desert conditions that could favour the spread of germination in time and space, and it could also reduce the risk of seed bank depletion. Variation in seed size has been considered as a maternal outcome because mother plant tissues supply the nutrients to embryo (Giles 1990). Therefore, maternal environmental conditions such as nutrient availability, soil moisture content, temperature and pollination play an important role in determining seed size (Alexander and Wulff 1985, Quesada et al. 1996, Wright et al. 1999). In the present study, we collected the seeds of both leaf colour morphs from the same population, and therefore we assumed that there was no variation in resource availability that could affect the seed morphological traits.

Removal of pulp from the seeds proved to be effective in promoting seed germination of *B. cycloptera* (both reddish and yellowish colour morphs). This indicates that if the pulp is removed, seeds are able to germinate immediately after dispersal. We assumed that there might be some germination inhibitors in the fruit pulp. Furthermore, seeds with pulp have higher mass, which should be easily visible to frugivores. When eaten and passed through the digestive tract the seeds will be able to germinate either due to alteration of the mechanical or chemical structure of the seed coat and/ or removal of fruit pulp (Samuels and Levey 2005, Traveset et al. 2008). This can be further confirmed by the fact that *B. cycloptera* fruits do not have any dispersal structure. The

except for the interaction between light and plant colour (p = 0.089). The three-way interaction was not significant (p = 0.076) (Table 4).

For seeds collected from yellowish plants, significant (p < 0.05) differences were detected among final germination percentages from 0 (control) to the all different salt concentrations assayed; however, for seeds from reddish plants these significant differences only were detected for seeds incubated under photoperiod conditions (Table 3). For the two illumination conditions, no significant differences (p > 0.005) were detected among the final germination percentages reached at different salt concentrations (Table 3). The decreases in germination due to application of NaCl solutions were higher for seeds collected from yellowish plants than for seeds from reddish plants (Table 3). That is, seeds from red-coloured plants seem to have the highest salinity tolerance. Besides, for each salt concentration, there was no significant (p > 0.005) difference between the germination percentages reached under photoperiod and continuous dark (Table 3).

A proportion of ungerminated, salt-treated seeds were able to germinate when they were transferred to distilled water (Table 5). However, there were no significant (p > 0.005) differences among recovery percentages between seeds from the two plant colours (Table 5).

Table 3. Germination percentages (mean values ± SE) of *B. cycloptera* seeds without pulp collected from reddish and yellowish plants after incubation in different NaCl concentrations for 20 days at 20/30°C under two illumination conditions (12-h light photoperiod and continuous darkness). Means within a column followed by the same letters are not significantly different at the p < 0.05 level according to the LSD test. For each NaCl concentration and plant colour, the significance of differences between the results from photoperiod and darkness are shown as ***p < 0.001, *p < 0.05, n.s. = not significant.

NaCl concentration (mM)	Reddish plant		Yellowish plant	
	Photoperiod	Darkness	Photoperiod	Darkness
0	83.75 ± 2.07 b	37.50 ± 2.79 a ***	91.25 ± 3.25 b	76.25 ± 2.07 b *
100	63.75 ± 2.72 ab	55.00 ± 6.37 a n.s.	30.00 ± 3.06 a	36.25 ± 4.46 a n.s.
200	60.00 ± 4.68 a	53.75 ± 7.58 a n.s.	20.00 ± 3.95 a	28.75 ± 2.07 a n.s.
400	46.25 ± 1.08 a	57.50 ± 5.15 a n.s.	27.50 ± 3.75 a	22.50 ± 8.00 a n.s.
600	60.00 ± 4.68 a	50.00 ± 3.95 a n.s.	27.50 ± 6.49 a	23.75 ± 5.96 a n.s.

Table 5. Germination percentages (mean values ± SE) of *B. cycloptera* seeds without pulp collected from reddish and yellowish plants after incubation in different NaCl concentrations for 20 days at 20/30°C under 12-h light photoperiod (initial germination), and germination percentages when non-germinated seeds were incubated for another 20 days in distilled water (final germination). Means within a column followed by the same letters are not significantly different at the p < 0.05 level according to the LSD test.

NaCl concentration (mM)	Reddish plant			Yellowish plant		
	Initial germination	Final germination	Recovery percentage	Initial germination	Final germination	Recovery percentage
0	83.75 ± 2.07 b	83.75 ± 2.07 a	---	91.25 ± 3.25 b	91.25 ± 3.25 b	---
100	63.75 ± 2.72 ab	95.00 ± 1.77 a	85.90 ± 5.15 a	30.00 ± 3.06 a	77.50 ± 2.79 a	68.00 ± 3.35 a
200	60.00 ± 4.68 a	86.25 ± 4.10 a	63.50 ± 11.95 a	20.00 ± 3.95 a	75.00 ± 3.06 a	68.35 ± 4.45 a
400	46.25 ± 1.08 a	81.25 ± 2.07 a	64.72 ± 4.65 a	27.50 ± 3.75 a	70.00 ± 2.50 a	59.37 ± 3.72 a
600	60.00 ± 4.68 a	78.75 ± 3.70 a	46.05 ± 9.08 a	27.50 ± 6.49 a	76.25 ± 7.15 a	61.47 ± 3.59 a

seed mass of seeds with pulp collected from yellowish-coloured was higher than that of reddish-coloured plants, while the seed mass for seeds without pulp was very similar for the two morphs. The de-pulped seeds from the reddish-coloured plants attained showed higher germination ability (96.25%) than seeds of yellowish-coloured plants (91.25%), suggesting an absence of seed dormancy.

Light enhanced the germination of seeds, both with and without pulp, and from both reddish and yellowish plants. This indicates that *B. cycloptera* seeds have positive photoblastism and that they might be able to form a soil seed bank as they require light for germination (Bowers 2000, Rojas-Aréchiga et al. 2001, El-Keblawy et al. 2013, El-Keblawy and Bhatt 2015). However, the light response on seed germination in *B. cycloptera* seems to depended on plant colour. Seeds produced by reddish-coloured plants germinated significantly better in 12-h light photoperiod as compared to continuous dark. However, seeds produced by yellowish-coloured plants were able to germinate well in both illumination conditions. This could be explained by variation in light absorbance by two different pigments in the leaf foliage of *B. cycloptera*. Generally, light absorption varies with the colour of pigment, and yellow and red-coloured leaves show greater reflection of light (Moss and Loomis 1952). Therefore we may assume that lower absorbance by leaf colour pigments (reddish and yellowish) could be responsible for a greater light requirement during the germination of *B. cycloptera* seeds.

The different temperature requirement for germination of seeds between seeds with and without pulp and seeds from reddish- and yellowish-coloured plants, indicate that the colour of the plants could play a significant role in the survival strategy of this species in deserts. Seed without pulp were able to germinate in all the tested temperatures. Although they achieved maximum germination (reddish = 96.25% and yellowish = 91.25%) at higher (25/35°C) and moderate (20/30°C) temperature; which is approximately the temperature of March in their geographic range (Feulner 2006). Usually, *B. cycloptera* seeds mature and disperse during December, when the average temperature is around 15/25°C. At this time, all the dispersed seeds have pulp that might hinder their germination. However, the alleviation of its effect could be through heavy rains that leach the allelochemicals or through decomposition of the pulp. When rain occurs in March, most of the seeds germinate as their pulp would be decomposed. Further these results

suggest that final seed germination percentage of *B. cycloptera* may not be related to seed size, as seed size did not show any significant difference during the germination. Similar results were obtained for *Miscanthus sinensis* (Christian 2012). The ability of *B. cycloptera* seeds to germinate over a wide range of temperatures might be advantageous as it most probably is the availability of water that decide the timing of germination under the field conditions (Grime et al. 1981).

Seeds collected from red-coloured plants seem to have higher salinity tolerance than those collected from yellowish-coloured plants. The production of seeds with different germination characteristics and salinity tolerance indicates that the different foliage colours shown by this species may be an adaptation strategy which increases the possibilities for establishment in unpredictable environments. Under NaCl solutions of different concentration, seeds obtained from reddish-coloured plants germinated better than seeds from yellowish-coloured plants. Variability in salinity tolerance depending on seed characteristics have been reported in other desert halophytes, such as *Atriplex centralasiatica* (Li et al. 2008), *Suaeda aralocaspica* (Wang et al. 2008), *Suaeda splendens* (Redondo-Gómez et al. 2008) and *Salsola rubencence* (El-Keblawy et al. 2013). We found that salinity result in a greater germination decrease in seeds collected from yellowish-coloured plants, and if salinity stress is not reduced during the germination season, it might be assumed that they may enter secondary dormancy and possibly form a seed soil bank. These differences between seeds obtained from plant morphs with different foliage colour presumably represent a combination of different complementary adaptive strategies that have ecological significance and are of importance for the successful survival of the species in deserts condition. Yellow foliage plants re much more abundant than red-coloured ones. Generally, smaller seeds have an advantage because they have a better chance of dispersal and colonization of new habitats (Muller-Landau 2010, Skarpaas et al. 2011). However, seeds of *B. cycloptera* obtained from different-coloured plants did not show any difference in germination recovery after exposure to saline conditions. This indicates that the seeds from both colour morphs do remain viable in saline condition and may able to germinate once the salinity is decreased by rain. Similar results have been obtained for other desert species such as *Aeluropus lagopoides* (Gulzar and Khan 2001), *Urochondra setulosa* (Gulzar et al. 2001), *Limonium stocksii* (Zia and Khan 2004) and *Halopeplis perfoliata* (El-Keblawy and Bhatt 2015).

To conclude, our results show that the response of *B. cycloptera* seeds to salinity dependeds on the leaf colour of the mother plant. Seeds from reddish plants were more tolerant to salt stress than those from yellowish plants. The presence of morphs with different foliage colour in *B. cycloptera* thus seems to be an adaptation strategy which increases the possibility of establishment in unpredictable environments by producing seeds with differences in germination requirements and salinity tolerance. *Bienertia cycloptera* seeds showed a high capacity for germination recovery after exposure to saline conditions, suggesting that seeds of this species are tolerant to salt stress. The results of the present study indicate that the degree of salt tolerance shown by *B. cycloptera* may be sufficient to permit seed germination at the levels of salinity found in the soils of its natural habitat in Arabian deserts, and therefore this species may be used in rehabilitation programs of degraded lands in arid regions and for reducing desertification processes.

References

Akhani, H. et al. 2003. Ecology, biogeography and pollen morphology of *Bienertia cycloptera* Bunge ex Boiss. (Chenopodiaceae), an enigmatic C4 plant without Kranz anatomy. – Plant Biol. 5: 167–178.

Akhani, H. et al. 2005. *Bienertia sinuspersici* (Chenopodiaceae): a new species from southwest Asia and discovery of a third terrestrial C4 plant without Kranz anatomy. – Syst. Bot. 30: 290–301.

Alexander, H. M. and Wulff, R. 1985. Experimental ecological genetics in *Plantago*. X. The effects of maternal temperature on seed and seedling characters in *P. lanceolata*. – J. Ecol. 73: 271–282.

Baskin, C. C. and Baskin, J. M. 2001. Seeds. Ecology, biogeography, and evolution of dormancy and germination. – Academic Press.

Bhat, N. R. et al. 2013. Application of biosaline agriculture strategies for sustainable plant production in Kuwait. – J. Agricult. Biodiv. Res. 2: 33–43.

Bochet, E. et al. 2007. Soil water availability effects on seed germination account for species segregation in semiarid road slopes. – Plant Soil 295: 179–191.

Bowers, J. E. 2000. Does *Ferocactus wislizenii* have a between-year seed bank? – J. Arid Environ. 45: 197–205.

Carlson, J. E. and Holsinger, K. E. 2010. Natural selection on inflorescence color polymorphisms in wild *Protea* populations: the role of pollinators, seed predators, and inter-trait correlations. – Am. J. Bot. 97: 934–944.

Christian, E. J. 2012. Seed development and germination of *Miscanthus sinensis*. – PhD thesis, Iowa State Univ., USA, paper 12880.

Clay, C. N. 2006. Non-leaf chlorenchyma in *Bienertia cycloptera* and *Suaeda aralocaspica* (chenopodiaceae) exhibit single cell CG photosynthesis. – PhD thesis, Washington State Univ., USA.

El-Keblawy, A. and Al-Shamsi, N. 2008. Effects of salinity, temperature and light on seed germination of *Haloxylon salicornium*, a common perennial shrub of the Arabian deserts. – Seed Sci. Technol. 36: 679–688.

El-Keblawy, A. and Bhatt, A. 2015. Aerial seed bank affects germination in two small-seeded halophytes in Arab Gulf desert. – J. Arid Environ. 117: 10–17.

El-Keblawy, A. et al. 2007. Salinity, temperature and light affect germination of *Salsola imbricata*. – Seed Sci. Technol. 35: 272–281.

El-Keblawy, A. et al. 2013. Perianth colour affects germination behaviour in wind-pollinated *Salsola rubescens* in Arabian deserts. – Can. J. Bot. 92: 69–75.

Feulner, G. R. 2006. Rainfall and climate records from Sharjah airport: historical data for the study of recent climatic periodicity in the UAE. – Tribulus 16: 3–9.

Giles, B. E. 1990. The effects of variation in seed size on growth and reproduction in the wild barley *Hordeum vulgare* ssp. *spontaneum.* – Heredity 64: 239–250.

Gould, K. S. 2004. Nature's Swiss army knife: the diverse protective roles of anthocyanins in leaves. – J. Biomed. Biotechnol. 5: 314–320.

Gould, K. S. et al. 2002. Do anthocyanins function as antioxidants in leaves? Imaging of H_2O_2 in red and green leaves after mechanical injury. – Plant Cell Environ. 25: 1261–1269.

Grime, J. P. et al. 1981. A comparative study of germination characteristics in a local flora. – J. Ecol. 69: 1017–1059.

Gul, B. and Webber, D. J. 1999. Effect of salinity, light, and temperature on germination in *Allenrolfea occidentalis*. – Can. J. Bot. 77: 240–246.

Gulzar, S. and Khan, M. A. 2001. Seed germination of a halophytic grass *Aeluropus lagopoides*. – Ann. Bot. 87: 319–324.

Gulzar, S. et al. 2001. Effect of temperature and salinity on the germination of *Urochondra setulosa*. – Seed Sci. Technol. 29: 21–29.

Hormaetxe, K. et al. 2004. Role of red carotenoids in photoprotection during winter acclimation in *Buxus sempervirens* leaves. – Plant Biol. 6: 325–332.

Khan, M. A. and Gul, B. 2006. Halophyte seed germination. – In: Khan, M. A. and Weber, D. J. (eds), Ecophysiology of high salinity tolerant plants. Springer, pp. 11–30.

Khan, M. A. and Gulzar, S. 2003. Light, salinity and temperature effects on the seed germination of perennial grasses. – Am. J. Bot. 90: 131–134.

Lacey, E. P. and Herr, D. 2005. Phenotypic plasticity, parental effects, and parental care in plants? I. An examination of spike reflectance in *Plantago lanceolata* (Plantaginaceae). – Am. J. Bot. 92: 920–930.

Lev-Yadun, S. and Gould, K. S. 2009. Role of anthocyanins in plant defense. *Anthocyanins*. – Springer.

Li, W. et al. 2008. The effect of light, temperature and bracteoles on germination of polymorphic seeds of *Atriplex centralasiatica* under saline conditions. – Seed Sci. Technol. 36: 325–338.

Lomascolo, S. B. et al. 2008. Correlated evolution of fig size and color supports the dispersal syndromes hypothesis. – Oecologia 158: 783–796.

Mandaville, J. P. 2004. Bedouin ethnobotany: plant concepts and plant use in a desert pastoral world.

Moss, R. A. and Loomis, W. E. 1952. Absorption spectra of leaves. I. The visible spectrum. – Plant Physiol. 27: 370.

Muller-Landau, H. C. 2010. The tolerance-fecundity trade-off and the maintenance of diversity in seed size. – Proc. Natl Acad. Sci. USA 107: 4242–4247.

Quesada, M. et al. 1996. Effects of pollen selection on progeny vigour in a *Cucurbita pepo* × *C. texana* hybrid. – Theor. Appl. Genet. 92: 885–890.

Redondo-Gómez, S. et al. 2008. Carry-over of differential salt tolerance in plants grown from dimorphic seeds of *Suaeda splendens*. – Ann. Bot. 102: 103–112.

Ridley, H. N. 1930. The dispersal of plants throughout the world. – L. Reeve & Co.

Rojas-Aréchiga, M. et al. 2001. Seed germination of wild and cultivated *Stenocereus stellatus* (Cactaceae) from the Tehuacán-Cuicatlán Valley, central Mexico. – J. Arid Environ. 49: 279–287.

Samuels, I. A. and Levey, D. J. 2005. Effects of gut passage on seed germination: do experiments answer the question they ask? – Funct. Ecol. 19: 365–368.

Schaefer, H. M. and Rolshausen G. 2006. Plants on red alert: do insects pay attention? – BioEssays 28: 65–71.

Schaefer, H. M. and Schmidt, V. 2004. Detectability and content as opposing signal characteristics in fruits. – Proc. R. Soc. B. 271: S370–S373.

Schaefer, H. M. and Wilkinson, D. M. 2004. Red leaves, insects and coevolution: a red herring? – Trends Ecol. Evol. 19: 616–618.

Schemske, D. W. and Bierzychudek, P. 2001. Perspective: evolution of flower color in the desert annual *Linanthus parryae*: Wright revisited. – Evolution 55: 1269–1282.

Schemske, D. W. and Bierzychudek, P. 2007. Spatial differentiation for flower color in the desert annual *Linanthus parryae*: was Wright right? – Evolution 61: 2528–2543.

Skarpaas, O. et al. 2011. Are the best dispersers the best colonizers? Seed mass, dispersal and establishment in *Carduus* thistles. – Evol. Ecol. 25: 155–169.

Solymosi, K. and Keresztes, Á. 2012. Plastid structure, diversification and interconversions II. Land plants. – Curr. Chem. Biol. 6: 187–204.

Stiles, E. W. 1982. Fruit flags: two hypotheses. – Am. Nat. 120: 500–509.

Strauss, S. Y. and Whittall, J. B. 2006. Non-pollinator agents of selection on floral traits. – Ecol. Evol. Flowers 208: 120–138.

Takeno, K. and Yamaguchi, H. 1991. Diversity in seed germination behavior in relation to heterocarpy in *Salsola komarovii* Iljin. – Bot Mag. 104: 207–215.

Tlig, T. et al. 2008. Germination responses of *Diplotaxis harra* to temperature and salinity. – Flora 203: 421–428.

Traveset, A. et al. 2008. Seed trait changes in dispersers' guts and consequences for germination and seedling growth. – Ecology 89: 95–106.

Verhoeven, A. S. et al. 1999. Xanthophyll cycle pigment localization and dynamics during exposure to low temperatures and light stress in *Vinca major*. – Plant Physiol. 120: 727–737.

Voznesenskaya, E. V. et al. 2001. Kranz anatomy is not essential for terrestrial C_4 plant photosynthesis. – Nature 414: 543–546.

Voznesenskaya, E. V. et al. 2005. Differentiation of cellular and biochemical features of the single-cell C4 syndrome during leaf development in *Bienertia cycloptera* (Chenopodiaceae). – Am. J. Bot. 92: 1784–1795.

Wang, L. et al. 2008. Germination of dimorphic seeds of the desert annual halophyte *Suaeda aralocaspica* (Chenopodiaceae), a C4 plant without Kranz anatomy. – Ann. Bot. 102: 757–769.

Warren, J. and Mackenzie, S. 2001. Why are all colour combinations not equally represented as flower-colour polymorphisms? – New Phytol. 151: 237–241.

Whittall, J. and Carlson, M. 2009. Plant defense: a pre–adaptation for pollinator shifts. – New Phytol. 182: 5–8.

Wright, K. J. et al. 1999. Influence of soil moisture on the competitive ability and seed dormancy of *Sinapis arvensis* in spring wheat. – Weed Res. 39: 309–317.

Yang, X. et al. 2010. Role of mucilage in the germination of *Artemisia sphaerocephala* (Asteraceae) achenes exposed to osmotic stress and salinity. – Plant Physiol. Biochem. 48: 131–135.

Zia, S. and Khan, M. A. 2004. Effects of light, salinity, and temperature on seed germination of *Limonium stocksii*. – Can. J. Bot. 82: 151–157.

Zia, S. and Khan, M. A. 2008. Seed germination of *Limonium stocksii* under saline conditions. – Pakistan J. Bot. 40: 683–695.