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REGULAR PAPER

Factors controlling germination and dormancy processes in dimorphic fruits of *Atriplex inflata* (Chenopodiaceae)

Abdallah Atia*, Mokded Rabhi, Ahmed Debez, Zouhaier Barhoumi, Chedly Abdelly & Abderrazak Smaoui

Laboratoire des Plantes Extrêmophiles, Centre de Biotechnologie, Technopole de Borj-Cédria, BP 901, Hammam-Lif, 2050, Tunisia
*Author for correspondence: atbdllh@yahoo.fr

Background and aims – Seed dimorphism is an adaptive feature to harsh environments such as arid and saline habitats. This is explained as an escape from inadequate conditions. In the current study, we investigated the seed germination of a dimorphic species *Atriplex inflata* Muell. (Chenopodiaceae). *A. inflata* occurs in saline habitats, namely in arid regions. Its bracteoles enclose a brown or a black fruit. This unit constitutes the diaspore.
Methods – Mature fruits were collected from Kelbia (35°46'06"N 10°07'34"E), located in the centre of Tunisia, with semi-arid climate. The effect of cold stratification, nitrate (KNO_3, 10 mM), light, dry storage (for seven months), chemical scarification and salt pretreatment on germination were determined in order to assess the factors that control germination and dormancy.
Key results – The results show that brown fruits germinated rapidly and the final germination percentage was 98% after twenty days. However, germination of black fruits was slower and reached only 19%. This confirms the fact that the difference in morphology is accompanied by a difference in germination capacity and dormancy in *A. inflata*. Chemical scarification and dry storage increased germination capacity of black fruits. Thus, the black fruit showed a physical dormancy and a non-deep physiological dormancy.
Conclusion – The production of two types of fruit in *A. inflata*, one dormant and the other non-dormant, is of high ecological importance for the survival of populations. Actually, this ensures both rapid germination (brown fruits) and a permanent seed bank (black fruits), which permit the persistence of the species and population establishment in disturbed environments.

Key words – *Atriplex inflata*, fruit dimorphism, physical dormancy, physiological dormancy, population survival.

INTRODUCTION

In some species belonging to the Asteraceae, Chenopodiaceae, Poaceae and Brassicaceae, a single individual produces different morphophysiological types of seeds that differ in colour, size, shape, germination and dormancy (Imbert 2002, Li et al. 2005, Mandák & Pyšek 2005). This phenomenon is known as seed dimorphism or seed polymorphism. This may be an adaptive feature to harsh environments (Mandák 1997). In halophytic species, including *Arthrocnemum*, *Atriplex*, *Chenopodium*, *Salicornia*, *Salsola*, *Spergularia* and *Suaeda*, seed polymorphism is considered as an adaption to saline environments (Li et al. 2005). It enables halophytes to respond to severe conditions and could provide multiple opportunities for germination and growth in saline ecosystems (Song et al. 2007). It is well known that in halophytes, seeds are exposed to severe salinity at the soil surface; this is not suitable for germination and seedling establishment. Upon salt dilution by rain, germination is maximal for non dormant seeds (Ungar 1995, Debez et al. 2004). However, in saline biotopes, salinity is in permanent fluctuation and the re-increase of soil salinity prevents germination (Easton & Kleindorfer 2008) and in some cases, it induces a secondary dormancy, like in seeds of *Suaeda aralocaspica* (Wang et al. 2008).

It is well known that many seeds are dormant at maturity. Baskin & Baskin (2004) define five classes of dormancy in seeds of Angiosperms. They include physiological dormancy, morphological dormancy, morphophysiological dormancy, physical dormancy and combined dormancy (physical and physiological dormancy). Several methods are used to break dormancy including physical and chemical treatments. These treatments are specific for each type of dormancy (Mandák & Pyšek 2001). For instance, the mechanical and acid scarifications are largely used for physically dormant seeds

in which germination is prevented by a hard testa. Nitrate, red light, gibberellins, cold storage and dry storage are used to alleviate physiological dormancy (Baskin & Baskin 2004, Finch-Savage & Leubner-Metzger 2006, Atia et al. 2009a).

Atriplex inflata Muell. (flat-topped saltbush), is an annual Chenopodiaceae species that reaches a height of about 50 cm. Beadle (1952) reported that it mainly occurs in saline habitats, namely in arid regions. This species is introduced in several regions in the world for its high forage value (Hyder 1981). Its bracteoles consist of a spongy envelope filled with air. This may enable fruit dispersal. Each spongy envelope encloses one fruit: a brown or a black one.

Numerous studies of seed heteromorphism in halophytes showed that in most species, seeds respond differently to salt. However, the identification of dormancy types and the release of dormancy as well as the effect of salinity on secondary dormancy induction remain unclear. Beadle (1952) showed that *A. inflata* fruit germination depended on fruit morph; brown fruits that germinated rapidly were not dormant, whereas dark fruits were dormant. By contrast, the longevity of the latter was higher than that of the former. However, information about the effect of nitrate, cold stratification, dry storage and salt pre-treatment were not reported in the paper of Beadle (1952). Furthermore, dormancy type was not identified in Beadle's (1952) paper. Thus, we carried out this study to investigate the effects of cold stratification, nitrate and acid scarification on dormancy and germination process as well as to study the effect of salt pre-treatment on germination and secondary dormancy induction in the dimorphic species, *A. inflata*.

MATERIALS AND METHODS

Fruit collection

Mature fruits were collected in July 2009 from natural populations growing in Kelbia (35°46'06"N 10°07'34"E), located in the centre of Tunisia. This site with a semi-arid climate is characterized by a mean annual rainfall that ranges from 200 to 300 mm and a monthly temperature average that varies between 20 and 26°C in autumn (September–November), between 10 and 16°C in winter (December–February), between 20 and 26°C in spring (March–May) and between 28 and 35°C in summer (June–August). Fruits were stored under laboratory conditions (at 20–26°C) in paper bags, until experiments started in September 2009.

Experiments

After the bracteoles were removed, fruits were separated in two groups based on their colour: brown or black. They were disinfected in a 3.5% calcium hypochlorite solution for 5 min before starting germination tests. They were placed in 9 cm diameter Petri dishes (25 fruits per Petri dish) and covered with a double layer of filter paper (type *Filtrak*) moistened with 5 ml distilled water or test solution. Each Petri dish was covered with transparent plastic film to reduce evaporation. The experiments ($n = 4$ for each) were carried out in a growth chamber (dark light: 8h–16h, temperature: 20°C (in dark) and 26°C (in light). Light was produced by OSRAM 40 W lamps (fluence rate: 35 µmol m^{-2} s^{-1}, 400–700 nm).

Germination of black and brown fruits in distilled water

Germination capacity of the two fruit morphs was tested. Four replicates of 25 fruits were used for each morph (black and brown). The fruits were incubated in 9 cm diameter Petri dishes containing a double layer of filter paper moistened with distilled water. This experiment was conducted for twenty days.

Effect of light, nitrate, stratification, dry storage and acid scarification on germination

The effect of cold stratification, nitrate (KNO_3, 10 mM), light, dry storage and acid scarification on germination were determined in order to assess the specific requirements to alleviate dormancy. For the cold stratification treatment, fruits were sown on filter paper moistened with distilled water in Petri dishes covered with aluminium paper then placed at 5°C for eight weeks. After that, germination tests were performed: fruits were gently washed with distilled water and placed in Petri dishes containing distilled water or nitrate solution (KNO_3, 10 mM). For germination test under dark conditions, the dark was ensured by wrapping each Petri dish with four layers of a black plastic film (Atia et al. 2009a). For dry storage, fruits were placed in paper bags for seven months at room temperature. All germination tests were carried out for twenty days.

The effect of acid scarification

The effect of acid scarification was also assessed followed by a germination test in distilled water or in 10 mM KNO_3 solution. For fruit scarification, a sufficient quantity of disinfected black fruits was placed in 75% H_2SO_4 solution for 5 min, then the acid solution was removed and the fruits were carefully washed with distilled water. Four replicates of 25 scarified or non-scarified fruits were used for the germination test. This experiment was conducted for twelve days.

Water uptake

To assess the permeability of the fruit wall to water, an imbibition test was realized: fruit dry mass was determined in the beginning of the experiment, then fruits were placed in distilled water in Petri dishes as described for the germination test. After 24 h, relative increase in mass was determined as $W_r = [(W_f - W_i)/W_i] \times 100$, where W_i is the initial fruit weight and W_f is their weight after 24 h of imbibition (Wang et al. 2008). Four replicates of 25 dry fruits were used for each type.

Effect of salt pretreatment on germination

To determine the effect of salt pretreatment in the induction of secondary dormancy, scarified and non-scarified fruits were placed in Petri dish containing a double layer of filter paper moistened with salt solution (600 mM NaCl) for nine days. After that, they were carefully washed with distilled water.

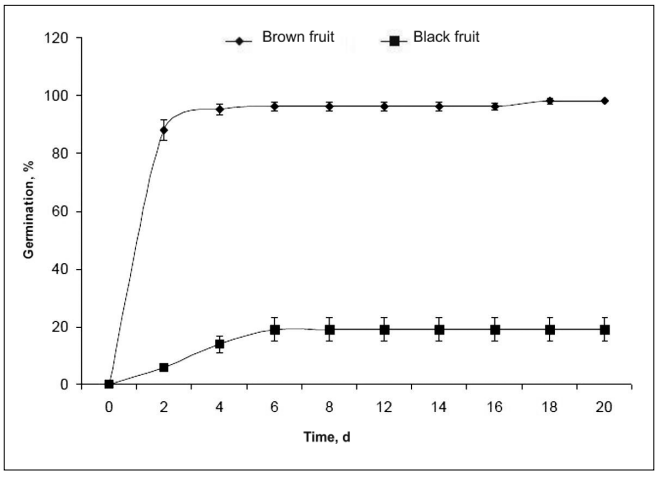

Figure 1 – Comparison of seed germination of two fruit types of *A. inflata* over time in distilled water (means of 4 replicates ± SE).

Then, a germination test in distilled water was performed for twelve days as described previously.

Data collection and statistical analyses

Germinated fruits were counted every two days; a fruit was considered as germinated when the radicle appeared (Côme 1982). Germinated fruits were discarded after counting. Germination data were arcsine square root transformed before statistical analysis. Three-way ANOVA was used to test the significance of main effects of seed type, light, nitrate and their interactive effects. The one-way ANOVA was used to test the significance effect of dry storage on germination, the effect of fruit type on imbibition and the effect of chemical scarification on germination. Duncan test (Duncan 1955) was used to identify significant differences among treatments ($P \leq 0.05$), using the statistical software SPSS 10.0 (1999).

RESULTS

Germination of non-treated fruits in distilled water

Brown fruits germinated rapidly in distilled water. The germination percentage reached 88% after two days of imbibition and exceeded 95% after four days. The final germination percentage was 98% after twenty days (fig. 1). However, the germination of black fruits did not exceed 6% after two days and reached only 14% after four days. On the sixth day, it reached 19% and no additional germination was observed after that (fig. 1).

Table 1 – **Results of three-way ANOVA analysis for the effect of light, nitrate and fruit type on fruit germination.**

Source of variation	*F*-values	*P*-level
Light	41.696	0.0001
Nitrate	0.110	0.743
Fruit type	1762.724	0.0001
Light × nitrate	0.227	0.638
Light × fruit type	57.871	0.0001
Nitrate × fruit type	0.018	0.895
Light × nitrate × fruit type	0.454	0.507

Table 2 – **Effects of light, nitrate and fruit type on final germination percentage (means of 4 replicates ± SE).**

	Light		Dark	
	Brown fruits	Black fruits	Brown fruits	Black fruits
Distilled water	98 ± 1.16	19 ± 4	100	0
Nitrate	99 ± 0.58	18 ± 2.23	99 ± 0.58	0

Effect of light, nitrate, stratification, dry storage and acid scarification on germination

The three-way ANOVA indicates that light, fruit type and their interaction significantly affect germination percentage whereas no significant effect was observed for nitrate (table 1). In addition, differences between the two fruit types were detected; for brown fruits, germination was not influenced by the dark (table 2). However, for black fruits, germination process was inhibited by the dark (table 2). Cold stratification for eight weeks significantly reduced their germination percentage (Duncan test, $P \leq 0.05$; fig. 2). Nitrate treatment after cold stratification increased it to 26%, but this increase remained statistically insignificant (Duncan test, $P > 0.05$; fig. 2). In addition, the one-way ANOVA analysis revealed that dry storage significantly increased the germination percentage of black fruits ($F = 20.542$, $P < 0.05$), which was also confirmed by the Duncan test ($P \leq 0.05$; fig. 2). For black fruits, a one-way ANOVA revealed a significant difference in germination percentage between scarified and non-scarified fruits ($F = 36.762$, $P < 0.05$). Their germination percentage after scarification reached 64% (fig. 2). Moreover, the addition of nitrate solution to the imbibition medium after fruit scarification significantly increased germination

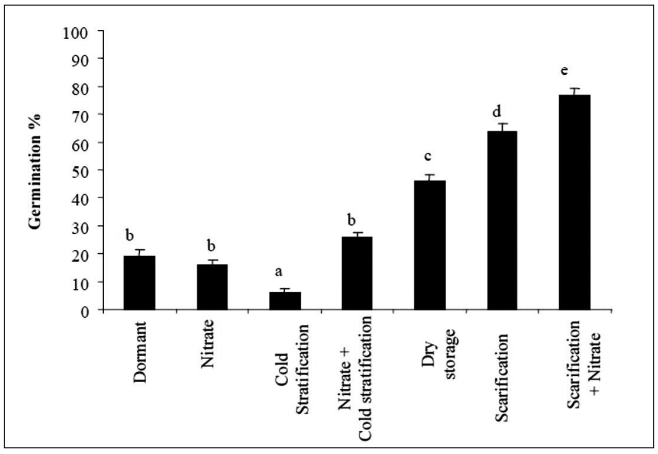

Figure 2 – Effects of nitrate, cold stratification, dry storage and acid scarification on germination of black fruits of *A. inflata* (means of 4 replicates ± SE). Means with different letters are significantly different at ($P < 0.05$).

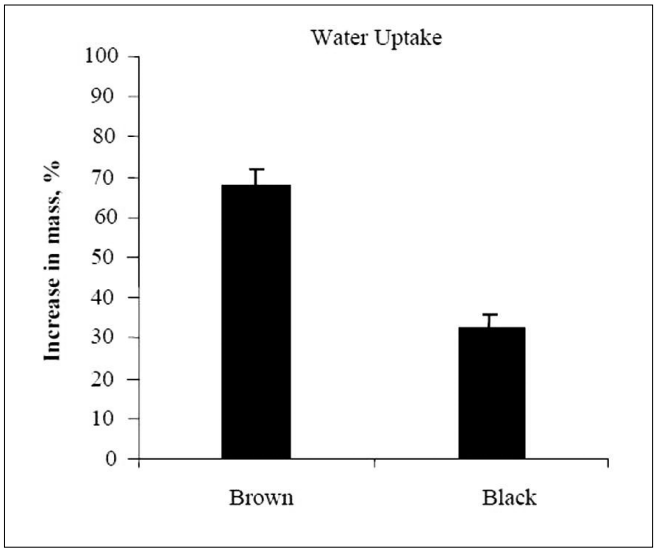

Figure 3 – Comparison of water uptake by brown and black fruits (means of 4 replicates ± SE).

percentage, which reached 77% (Duncan test, $P \leq 0.05$; fig. 2).

Water uptake

The one-way ANOVA analysis revealed a significant difference in imbibition between brown and black fruits ($F = 17.842$, $P < 0.05$). The imbibition test showed that the mass of brown fruits increased by 67.5% after 24 h of soaking in distilled water, whereas that of black fruits increased by only 32.2%, indicating a slower water uptake (fig. 3).

Effect of salt pretreatment on germination

Salt pretreatment did not alter germination percentage in brown fruits and scarified black fruit, but significantly reduced it in dry-stored black fruits (Duncan test, $P \leq 0.05$; fig. 4). Thus, salinity probably induced a secondary dormancy in black fruits.

DISCUSSION

In *A. inflata*, the difference in morphology is accompanied by a difference in germination capacity and dormancy. Brown fruits were non-dormant, but a large part of black fruits were dormant. Indeed, brown fruits germinated rapidly in distilled water and their final germination percentage was 98%, whereas the germination rate of black fruits did not exceed 19%. These results confirm those observed by Beadle (1952) in the same species. More recently, the same dimorphism was observed in genus *Atriplex*, such as in *A. triangularis* (Khan & Ungar 1985), *A. sagittata* (Mandák & Pyšek 2001), *A. prostrata* (Carter & Ungar 2003) and *A. hortensis* (Mandák 2003). In other halophytes, this phenomenon characterises the seeds of *Salicornia europaea* (Carter & Ungar 2003), *Suaeda salsa* (Li et al. 2005, Song et al. 2007) and *S. aralocaspica* (Wang et al. 2008).

In black fruits, germination was inhibited in the dark, contrarily to that of brown fruits. In other halophytes, germination was largely dependent on light and nitrate (Atia et al. 2009a, 2009b). For example, small seeds of *A. prostrata* and *S. europaea* were found to be dormant and germination of large seeds in the field was controlled by light (Carter & Ungar 2003). In *A. sagittata*, which produces one type of non-dormant fruits (type C) and two types of dormant ones (types A and B), dormancy was significantly alleviated by nitrate and reduced by the dark in all fruit types (Mandák & Pyšek 2001). This was not the case of *A. inflata*, since germination of black fruits was not stimulated by nitrate treatment. A non-significant nitrate stimulating effect was observed only after cold stratification for eight weeks. It is known that in physiologically dormant seeds, germination is stimulated by cold stratification or by dry storage (Mandák & Pyšek 2001, Baskin & Baskin 2004). For instance, in the case of *S. aralocaspica*, black seeds were physiologically dormant and needed cold stratification or dry storage (Wang et al. 2008).

Contrarily to cold stratification that did not stimulate germination of black fruits of *A. inflata*, dry storage significantly increased it (fig. 2). These results confirm those observed by Beadle et al. (1952) for the same species. Thus, a non-deep physiological dormancy exists in fruits of *A. inflata*. Indeed, this type of dormancy is alleviated by dry storage (Baskin & Baskin 2004, Finch-Savage & Leubner-Metzger 2006). This phenomenon was observed in some Geraniaceae, Fabaceae and Rhamnaceae. For instance, the dry storage increased the germination percentage in *Portulaca oleracea* (El-Keblawy & Al-Ansari 2000), *Bromus tectorum* (Allen & Meyer 2002), *Onopordum acanthium* (Qaderi et al. 2003) and *Prosopis juliflora* (El-Keblawy & Al-Rawai 2006). The ecologic significance of dormancy loss induced by dry storage is associated with the temperature fluctuations that occur in natural habitats. These conditions induce physical and chemical modifications that alter strength of seed coats

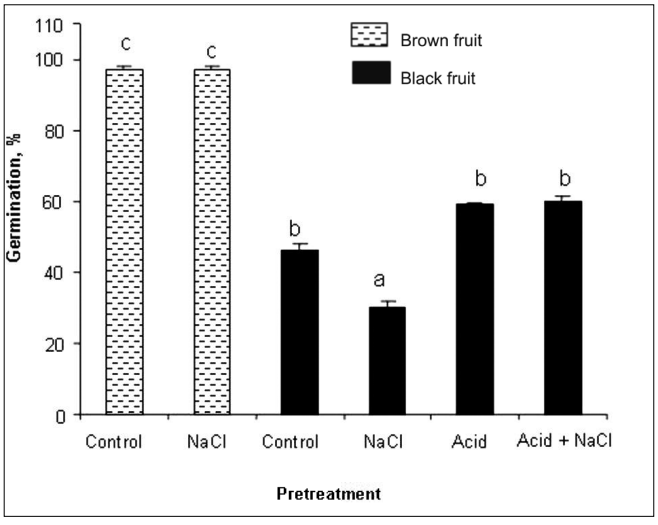

Figure 4 – Effects of salt pretreatment on germination of two fruit types of *A. inflata*. This experiment was conducted after seven months of dry storage at room temperature (means of 4 replicates ± SE). Means with different letters are significantly different ($P < 0.05$). The control designates fruits germinated in distilled water.

and subsequently increase their permeability to water and gases, which allow germination to occur (Qaderi et al. 2003).

The imbibition test showed that brown fruit mass increased by 67.5% after 24 h of sowing in distilled water. However, black fruits absorbed water slowly with a mass increase of 32.2% after 24 h (fig. 3). These results suggest that in black fruit (dormant type), fruit wall restrains water uptake, which reduces germination capacity. The same trend was also observed in seeds of *Suaeda salsa* (Li et al. 2005) and *Suaeda aralocaspica* (Chenopodiaceae) (Wang et al. 2008). Furthermore, acid scarification significantly increased germination percentage of black fruits that reached 64%. This leads to conclude that in black fruits, the main germination inhibitor is the hard testa. Thus, black fruits of *A. inflata* exhibit a physical dormancy. In *Atriplex tatarica*, both cold and mechanical scarifications stimulated germination. In dormant fruits of *Atriplex sagittata*, germination was not stimulated by cold stratification but was maximal (100%) after mechanical scarification (Mandák 2003). It is well known that physical dormancy, developed during seed maturation, is caused by a water-impermeable seed coat. More precisely, it is caused by a densely packed layer of palisade cells impregnated with water-repellent substances, which inhibits imbibition (Baskin & Baskin 1998). Hence, under field conditions, prevention of imbibition process in species with seeds or fruits physically dormant maintain them dormant until some factors render the covering layer permeable to water. These factors include temperature fluctuation, fire, drying, freezing and passage through digestive tract of animals (Baskin et al. 2000).

The addition of nitrate solution in the imbibition medium after seed scarification significantly increased germination in black fruits of *A. inflata*. Nitrate may stimulate the process by alleviating fruit physiological dormancy. This result confirms the fact that black fruits of *A. inflata* exhibit two types of dormancy; a physical dormancy that may be alleviated by chemical scarification and a physiological dormancy that may be alleviated by dry storage.

Seed dormancy prevents plant establishments under unfavourable conditions so that germination only occurs when conditions for plant survival are likely to be suitable (Bewley 1997). However, the induction of secondary dormancy is possible, namely in disturbed environments (Finch-Savage & Leubner-Metzger 2006). In halophytes, Wang et al. (2008) demonstrated that high salt concentration induces a secondary dormancy in seeds of *Suaeda aralocaspica*. In *A. inflata*, salt pretreatment did not alter the germination percentage of brown fruits and scarified black fruits, but reduced that of dry-stored black ones. Thus, salinity may induce a secondary dormancy in black fruits of *A. inflata*. But, why does salinity pretreatment reduce germination of non-scarified fruits and not alter germination of brown fruits or black scarified fruits? We can speculate that salinity may reduce growth potential of the embryo to a too low point to overcome the mechanical resistance of the fruit coat. This phenomenon is usually observed in physiologically and physically dormant seeds (Finch-Savage & Leubner-Metzger 2006).

In halophytes, two strategies have been developed to overcome salt stress during germination stage. On the one hand, upon early autumn rain, some species show rapid germination. These species have an opportunistic germination strategy (Wei et al. 2008). Such a phenomenon is of high significance since any delay in this process could adversely affect their establishment if salinity re-increased (Easton & Kleindorfer 2008). On the other hand, persistence of permanent seed bank is of high importance for these species. This strategy allows germination when salt is highly diluted or leached from the soil surface. This is common in dry regions when rainfalls are occasional and irregular. Thus, the production of a second kind of fruit with impermeable wall ensures a permanent seed bank in which germination can occur after some months or in the next season when some of the hard fruits become permeable (Nichols et al. 2008) or when embryo growth potential becomes sufficient to overcome mechanical resistance of fruit envelope (Baskin & Baskin 2004). Thus, the production of dormant and non-dormant fruits in *A. inflata* is obviously of great ecological value because such differences ensure population survival.

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