



# Seed Germination Strategies of Mediterranean Halophytes Under Saline Condition

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## Abstract

The study of the ecological strategies adopted by seed plants to ensure their success in different environments is closely related to germination ecology. This implies a careful knowledge of ecophysiology of seeds and, therefore, also of interaction between plants and the complexity of external factors. In particular, the environmental conditions of the area where a plant grows and produces seeds represent the main factors that influence successful seedling establishment. The physical-chemical features of habitats, and therefore their heterogeneity, affect the behavior of seeds in different ways. In addition to the timing of seed production, they can induce or terminate dormancy and/or germination and influence the germination pattern of different seeds in the same plant and so the composition and dispersal of soil seed banks. Salinity is a major abiotic stress affecting growth and plant productivity worldwide, constituting one of the main topics of study in the field of plant physiology. Halophytes are the plants that have the availability to survive and develop in different types of saline habitats. In this chapter, we consider some examples to illustrate the main adaptive strategies used by the seeds of halophytes on ecophysiological perspectives to survive in habitats affected by high levels of salinity. The focus is on the species that live in the

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brackish or salt coastal areas of the Mediterranean Basin. On these environments, the salt stress may act synergistically with intense anthropic pressure, generating profound alterations in the ecosystem and threatening the survival of the plant species very sensitive to the effects of climate change also. The results show the main diverse strategies, such as dormancy cycling, seed heteromorphism, and recovery capacity, from saline shock, favoring the chances of seed survival. The interaction between temperature and salinity during germination was also discussed assessing its crucial role as an ecological strategy.

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**Keywords**

Halophyte · Seed germination · Dormancy · Heteromorphism · Mediterranean Basin

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## 1 Introduction

Germination is a complex process widely recognized as one of the most important stages of the development cycle of seed plants. It also represents the period of maximum vulnerability to environmental changes, and it has the minimal potential for a homeostatic response or physiological rebalancing as reported by earlier studies (Ungar 1982; Khan and Ungar 1984; Donohue et al. 2010; Gul et al. 2013; Baskin and Baskin 2014).

The choice of the best time to germinate is a difficult choice by seed plants, also for the consequences that this choice will have on their subsequent development and reproduction.

In particular, the germination must take place in close connection with the environmental conditions characterizing the periods preceding and following the ripening of the seed. It is known that in the same species, changes in the conditions in which the seeds first develop, and then mature, can induce different behaviors from 1 year to the next, in the evolution of subsequent seed germination of a species (Penfield and Mac Gregor 2017). At the same environmental conditions, seed post-ripening and germination follow a strict logic, with very little variability over time that is typical of the biorhythm of each species. So, plant species, starting from the early stages of the life cycle, may exhibit a complementary set of adaptations/strategies aimed to survive despite critical environmental or biotic factors (Gutterman 2012). It is also well known that various external environmental factors act, either individually or interacting with each other, on the behavior of seeds, whose sensitivity can be specific for the species and their seed types (Khan and Ungar 1997; Gul et al. 2013; Kranner and Seal 2013). Temperature, humidity, intensity, duration and spectral composition of light, water availability, concentration of dissolved and non-dissolved gases in the water and the soil, and salts' ions in the soil circulating solution or in the water are among the most important and discussed factors affecting the germination processes.

In saline or brackish habitats, the concentration of salts is certainly the main factor of stress for plant species. In these critical and fragile environments, the salinity and its fluctuations influence the viability and germination of the seeds and can reach levels that seriously threaten the survival of a population (Redondo-Gómez et al. 2008; Delgado Fernandez et al. 2016).

Halophytes are plants that can survive and reproduce in this peculiar saline environment. They constitute a highly specialized type of vegetation with prominent variability in anatomical and morphological adaptations which confer significant tolerance to high levels of salinity. These species in the course of evolution have developed different mechanisms for regulating growth that ensure their survival in high-salt environments (inland or coastal areas, salt marshes, dunes, and deserts).

Besides different and changing environmental factors, the seed germination is also influenced by the health state of the seed and its intrinsic structural characteristics. These include, for example, the consistency of the integuments that regulate the permeability to water and gases, the stage of maturity of the embryo and of the seed as a whole, the mechanical resistance of the seminal integuments to the growth of the embryo in the initial stages of germination, and metabolic blocks of the embryo, requiring the presence or absence of light and/or low or high temperatures to be removed (Baskin and Baskin 2004; Finch-Savage and Leubner-Metzger 2006; Long et al. 2015).

Therefore, the germination of a seed is the result of the interaction of a set of multiple factors internal or external to the seed itself. These factors can be inhibiting, stimulating, or retarding its germination. This, together with the success of initial growth and the survival of the seedlings, acquires a particular ecological significance by representing how the plant species that is reproduced by seed can preserve the occupied territories and, by colonizing others, expand their areas of diffusion.

Ultimately, it can, therefore, be argued that the germination of seeds acts significantly as an essential vector for the success, distribution, and continuity in nature of a species and its populations (Huang et al. 2016). To ensure this, the species must “know” the right strategies to ensure adequate germination and their survival in the environment.

Seed germination, being also an irreversible process (Rosbakh and Poschold 2015; Costa et al. 2019), can never be a random event. The birth of new seedlings in a nonoptimal time for poor water supply or too high or too low temperatures or salinity values tending to increase could significantly slow down the growth and development of the sprouts causing also the disappearance, seriously endangering the species itself. It was, therefore, necessary for the seed species to develop the germination control mechanisms that are indispensable for successfully tackling and overcoming the most unfavorable periods.

This is even more important for species such as halophytes, which have to perform their life cycle in very critical environments due to the almost permanent presence of saline stress conditions. In this regard, many studies have shown that the seeds of almost all halophytes respond to germination similarly to glycophytes (plants sensitive to salinity) (Gul et al. 2013). It can be said that, although the exact salt concentration tolerated may vary from individual to individual, in both



**Fig. 1** A. Brackish area of San Rossore Estate (Tuscan coast, Italy) with typical species of halophilic vegetation

the number of germinated seeds is strongly reduced by the presence of high salt concentrations. Halophytes, on the other hand, adopt particular strategies at physiological and morphological level, in which glycophytes are not able to evolve at any stage of development.

The main objective of this chapter is to provide a brief but complete overview of the main germination strategies adopted by seeds of some halophytes from the Mediterranean Basin, to complete their life cycle, ensuring the continuity of a population in their natural and critical environments and plasticity that also provides ecological diversity. In particular, reference will be made to the species growing in the Mediterranean coastal salt areas, which represent very rich and highly valuable ecosystems at risk of degradation by human activities and also particularly sensitive to the effects of climate change (Hassan et al. 2017). The maritime marshes, often behind coastal dunes, are also subjected to periodic saltwater inundation. An example of a brackish area, along the Italian littoral, and characterized by typical species of halophilous vegetation is shown in Fig. 1.

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## 2 Seed Dormancy/Nondormancy Cycles

To ensure germination in environmental conditions that are favorable for subsequent competition and reproduction, a lot of species adopt a strategy based on the cyclical state of quiescence in the seed, whose duration and typology differ from species to species. This condition must possibly be followed by the vegetative restart at the

most opportune and favorable moment. This biological defense system is what is called “seed dormancy.” Dormancy is typical behavior of the therophytes, one of the most common biological forms in critical habitats, and rather common also in the Mediterranean environment, especially in the coast, where the favorable conditions for the development of the species are met only a few months a year.

This is not the context to deal with the complexity of the physiology of dormancy. We only remember that the seed is defined as “completely dormant” when, despite being in perfect health, and in optimal environmental conditions, it is not able to germinate (Baskin and Baskin 2014). This status is, therefore, a real survival strategy acquired from seeds, also useful to escape the lethal effects of any alterations in environmental conditions that cause stress of various kinds, physical, biotic, and abiotic.

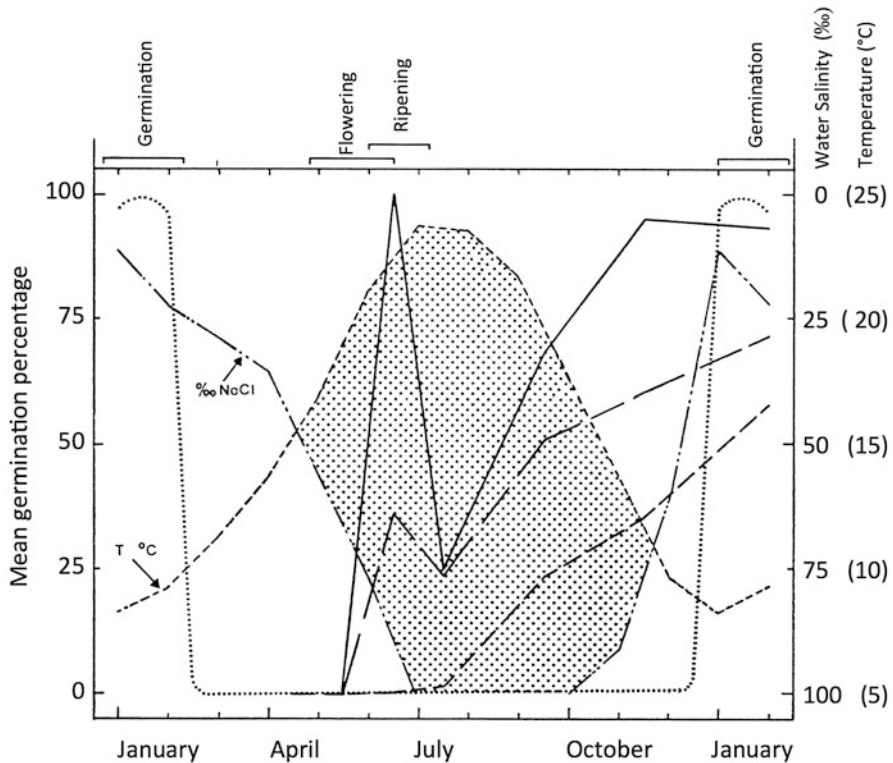
In an attempt to identify the causes and classify the various ways in which dormancy occurs, a wide range of scientific papers are available, some of which are very distant over time (Belderok 1961; Barton 1965; Nikolaeva 1977; Lang 1965; Khan 1977; Bewley 1997; Finch-Savage and Leubner-Metzger 2006; Qasem 2019).

The study of seed dormancy, with its types and duration, is a very important factor in the ecology of germination and on the specific strategies developed by plants at the germination stage, to manage with particular environmental conditions. It is easy to understand how it is of great importance for those species that have evolved to adapt, live, and reproduce, in difficult environmental conditions, such as the halophytes. These plants tolerate extreme temperatures and high salinities in the substrates due to the presence of  $\text{Na}^+$  and  $\text{Cl}^-$  that can also cause metabolic toxicity (Flowers et al. 2010).

The observations on the type of seed dormancy and the following germination behavior allow, in many cases, to draw interesting considerations on the ecology of the different species. The correlation of the data obtained in these investigations with the main environmental factors affecting seed germination and seedling development may also lead to the identification of species ecotypes.

In the halophyte, the seeds germinate only when the salinity of the substrate is reduced to levels that ensure the following development of the seedlings. This can be attributed to the presence of particular mechanisms of regulation of the dormancy whose duration is regulated by the annual cycles, temperatures, precipitations, and salt dilution.

In the regions of the Mediterranean Basin, the dormancy of the seeds normally presents the maximum intensity in the summer, a period that may be the most unfavorable for the survival of the seedlings. In fact, in these environments, during Summer high temperatures are associated with accentuated aridity, and consequently with increases of the substrate saline concentration due to water evaporation. These severe conditions may damage seedling post-germination stages. The annual modifications of the seeds dormancy/nondormancy status represent a form of adaptation to such environmental conditions and are implemented mainly in annual species, which entrust their reproduction exclusively to seeds and undergo a high demographic variability overtime (Fenu et al. 2013; Huang et al. 2016). However, cases of



**Fig. 2** Mean germination (%) of *Althenia filiformis* seeds at 20 °C in deionized water (—), 6.5 (---) and 13‰ (----), in relation to environment temperature (T °C) and water salinity (‰) annual fluctuation. (From Onnis and Pelosini 1976)

even perennial species that seem to have adopted this type of strategy are not uncommon.

Among the halophytes, one of the first species studied in the Mediterranean area is *Althenia filiformis* Petit, a rooted hydrohalophyte typically exists in brackish lagoon areas. The first studies on seed germination highlighted a very fine and complex regulation of seed dormancy. Such regulation resulted to be closely shaped on the salinity variations of the water in which the species grows and on the time of seeds ripening that normally takes place in the early summer. Figure 2, from the work of Onnis and Pelosini (1976), shows some of the most interesting data obtained in laboratory tests with *Althenia* achenes.

In deionized water, the germination capacity has two maximum peaks: one in early summer when the seeds mature and one in the following autumn. The high and rapid germination for freshly ripe seeds, interpretable as an expression of the lack of a dormant state, does not have real ecological meaning when compared to the environments where those species live. Indeed, such behavior does not seem coherent with what can truly occur in nature where the salinity of the substrate in the same

period is rather high and certainly inhibiting, almost completely, the germination that tends to decrease severely. The second seed germination peak, on the other hand, could be the consequence of a progressive decline of the dormancy that the seeds seem to (re)acquire in the middle of summer and is reached when in nature even the saline concentration of the water is close to the minimum values and temperatures drop.

Similar behaviors, described as biorhythms, have been documented for other halophytes in the Mediterranean Basin such as *Parapholis strigosa* (Host.) Parl., a Mediterranean Atlantic salt-soil species. The kernels of this species mature in the middle of summer and show a rhythmic pattern of dormancy and therefore of seed germination, similar to that of *Althenia*. At 20 °C, which proved to be the optimal temperature for laboratory tests, the seeds show their best vitality (after a rather long period of primary dormancy), in terms of percentage and germination speed, in the autumn-winter period. The behavior of the seeds in the following months, characterized by a drop of the seed germination capacity, at least until the beginning of the following spring, however, shows that dormancy does not completely disappear. Bocchieri et al. (1981) attributed this behavior to the persistence of a “residual dormancy” (Meletti 1964) that is evidenced in delayed germination with low germination energy in the first 3 days of culture as well as with the presence of intrinsic mechanism of the seed to rhythmically regulate germination based on the seasonal trend of environmental quality. This is a defense strategy to prevent inappropriate germination, which is confirmed in the species by its other responses at the germination level and precisely (1) reduction up to no germination at rising temperatures with the induction of a thermodormancy that prevents the germination in the summer period which, as already mentioned, in the Mediterranean Basin, represents the most unfavorable moment for the life of plants and (2) inhibition of the germination by an excessive salt concentration which, however, can be completely recovered by removing the salt from the water (the seeds maintain total germination capacity).

Dormancy cycling of seeds as an adaptation to survive in drought and salt environments (Finch-Savage and Leubner-Metzger 2006) was observed also in *Artemisia caerulescens*, a perennial aromatic rare halophyte (Lombardi et al. 2019). This species grows in the central and western Mediterranean regions in saline or brackish soils where it ripens in autumn. A recent study highlighted an evident seasonal biorhythm in the seeds NaCl sensitiveness. In particular, in springtime (when the species reaches the maximum germination activity), the germination of *A. caerulescens* is controlled by a NaCl-induced dormancy that, if salinity rises, makes most seeds remain dormant until the salinity goes down, avoiding its negative effects. The NaCl-induced dormancy of the seeds in spring could help *A. caerulescens* to avoid the exposure of seedlings to harmful rises of soil salinity, which are quite common in Mediterranean marshes (Lombardi et al. 2019). Such peculiar germination behavior of *A. caerulescens* could be due to the induction of a NaCl-conditional dormancy after the breaking of initial primary dormancy that makes the seeds germinate over a narrower range of salinity than nondormant seeds (Baskin and Baskin 2014).

This NaCl-conditional dormancy of *Artemisia caerulescens* could also be related to its peculiar distribution in nature. This species grows in the elevated zones of salt marshes with a salinity significantly lower than that of the adjacent depressions where, in summer, salinity may rise till about  $100 \text{ mmol}\cdot\text{L}^{-1}$  (Lombardi et al. 2019). In addition, as a supplementary strategy to avoid inappropriate germinations, *A. caerulescens* seeds maintain the dormancy under high temperature (thermodormancy) (Lombardi et al. 2019). This behavior may avoid germinations in the summertime, when after occasional rainfall moisture could be sufficient for germination, but not enough to sustain seedlings into the next autumn period when rainfall is more reliable.

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### 3 Salinity-Temperature Interactions

Interaction between salinity and temperatures was closely associated with the seed germination of many halophytes (Ungar 1982). Quantification of germination niche within this interaction is very important to understand, particularly the impacts of climate change on the sea level and increasing temperatures. Numerous works show that the study of these synergistic effects is not easy to establish a model of behavior. In higher saline conditions, the temperature can favor or slow down seed germination depending on the species and its natural ripening times. For instance, if seeds germinate in spring, a moist-chilling treatment probably promotes the breaking of the dormancy, while for a species that germinates in autumn, a warm stratification of the seeds is required.

In some Mediterranean species, high external temperatures have proved to be decisive in inducing a state of thermodormancy in the seeds.

The case of *Hordeum maritimum*, a common species in Mediterranean highly saline coastal sites, is rather interesting. Studies on the seasonal changes of seed germination of this species have shown a close correlation between dormancy and salinity, temperature, and seed after-ripening time (Meletti 1964; Lang et al. 1987). In this case, dormancy, induced by high temperature (thermodormancy) led to a total inhibition of germination, which, even in the lowest salinity conditions, was maintained until the autumn of the year following that of the harvest. Confirming a dormancy induced by high temperatures and not a loss of vitality by the seeds is the simultaneous high germination rates recorded at lower temperatures. As reported by the authors of the work, a possible ecological interpretation of the response of *H. maritimum* to high temperatures, above all if synergistic with high salinity, is that this species owns an effective system of control and defense against “suicide” germination. In nature, “suicidal” germination theoretically occurs after summer sudden storms, when transitory water availability could promote germination that, however, would not sustain an adequate plant development. Such meteorological conditions may occur with maximum temperatures of  $27\text{--}30 \text{ }^\circ\text{C}$  and 24‰ soil salinity (approximately very close to the highest concentration used in the tests) that in the Mediterranean Basin are recorded at the end of summer, with mean monthly rainfall of 24 mm as compared to 152 mm in October and 89 mm in March (Lombardi and Onnis 1999). So, *H. maritimum* seed dormancy represents



an important strategy which ensures, independently of salinity and temperature, a seedling emergence only under optimal conditions. This enables the species to reproduce itself even in environments with adverse pedoclimatic conditions (Fenner 1985).

The effect of the relationship between salinity and increasing temperatures on germination behavior of halophilic species has been highlighted in other typically Mediterranean halophytes. These include *Briza maxima* (Lombardi et al. 1998) from wild populations in a brackish lagoon in Tuscany; *Plantago coronopus* living behind the dunes in southeastern Sicily (Luciani et al. 2001); *Crucianella maritima* (Del Vecchio et al. 2012); *Limonium insigne* growing in southeastern Iberian Peninsula (Fernández et al. 2015); *Cakile maritima* from central Italy, Sardinia, and Mallorca (Del Vecchio et al. 2018); *Limonium supinum* an endemic halophyte from Iberian Peninsula (Melendo and Giménez 2019), but also in other non-Mediterranean climates such as *Salsola vermiculata* from the Canary Islands (Guma et al. 2010), *Urochondra setulosa* (Gulzar et al. 2001), *Phragmites karka* (Zehra and Khan 2007), and *Zygophyllum propinquum* (Manzoor et al. 2017) from Pakistan or *Suaeda maritima* from British salt marshes (Seal et al. 2018).

However, it should be emphasized that, from the available data, it is not always possible to establish whether the germination drops recorded in the presence of high salt concentrations and high temperatures are due to a momentary thermodormancy induced by an osmotic effect or by a toxic effect of the same salinity. It is widely known that salinity can inhibit the germination of halophyte seeds by inducing one or both of these effects (Gul et al. 2013). Important indicators in studies of this type to understand the nature of thermodormancy would be the recovery, in deionized water, of the germination in seeds not germinated in the presence of salt (a symptom of osmotic effect) or the actual mortality of seeds (an irreversible symptom of toxic effects).

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## 4 Germination Recovery

The seeds of various halophytes remain dormant at lower water potential without losing their vitality. They can germinate readily if transferred into deionized water after high salinity treatments. This germination behavior seems to distinguish halophytes from salt-sensitive plants that survive for shorter periods in seawater salinity exposure and fail to germinate as a result of reduced salt concentration. The ability of the seeds to recover their germination capacity after a dormancy period induced by external factors is a vital adaptive trait ensuring the success of halophytic plants in their native ecosystem. In Mediterranean saline environments, this type of germination strategy is often found to be very important. In these habitats, field observations showed that seed germination usually occurs during the spring or autumn after ripening or in the more elevated soils. In this way, seeds take advantage of the lower salinity levels and adequate water availability. This type of response to salt stress in the seeds of species growing in coastal salt marshes could also be of great importance by inhibiting germination in submerged conditions due to sea advancement.

Studies conducted on *Cakile maritima*, an annual halophyte that grows on the coastal sand dunes of semiarid coast of Tunisia, have also revealed some of the molecular mechanisms involved in this type of strategy. In this species, high salinity inhibits and delays germination, as occurs in most halophilic species, but significantly stimulates the vigor of the seeds in the recovery phase. All of this has been physiologically explained as a consequence of the low osmotic potential that is generated with high salt concentrations (e.g., NaCl). A low osmotic potential would prevent the development of a sufficient turgor pressure to allow the cell division and differentiation necessary for the radicle emergence and start of germination. The seeds would, therefore, remain quiescent but always active and ready to germinate in more favorable conditions (less saline stress). The seed protein and lipid pool would be involved in this germination behavior change. Proteomic analyses have shown that the massive conversion of reserve proteins into 20 amino acids that could be transformed into other amino acids and of fatty acids into carbohydrates is slowed down in the presence of salt but quickly reinduced in conditions favorable for recovery (Debez et al. 2018).

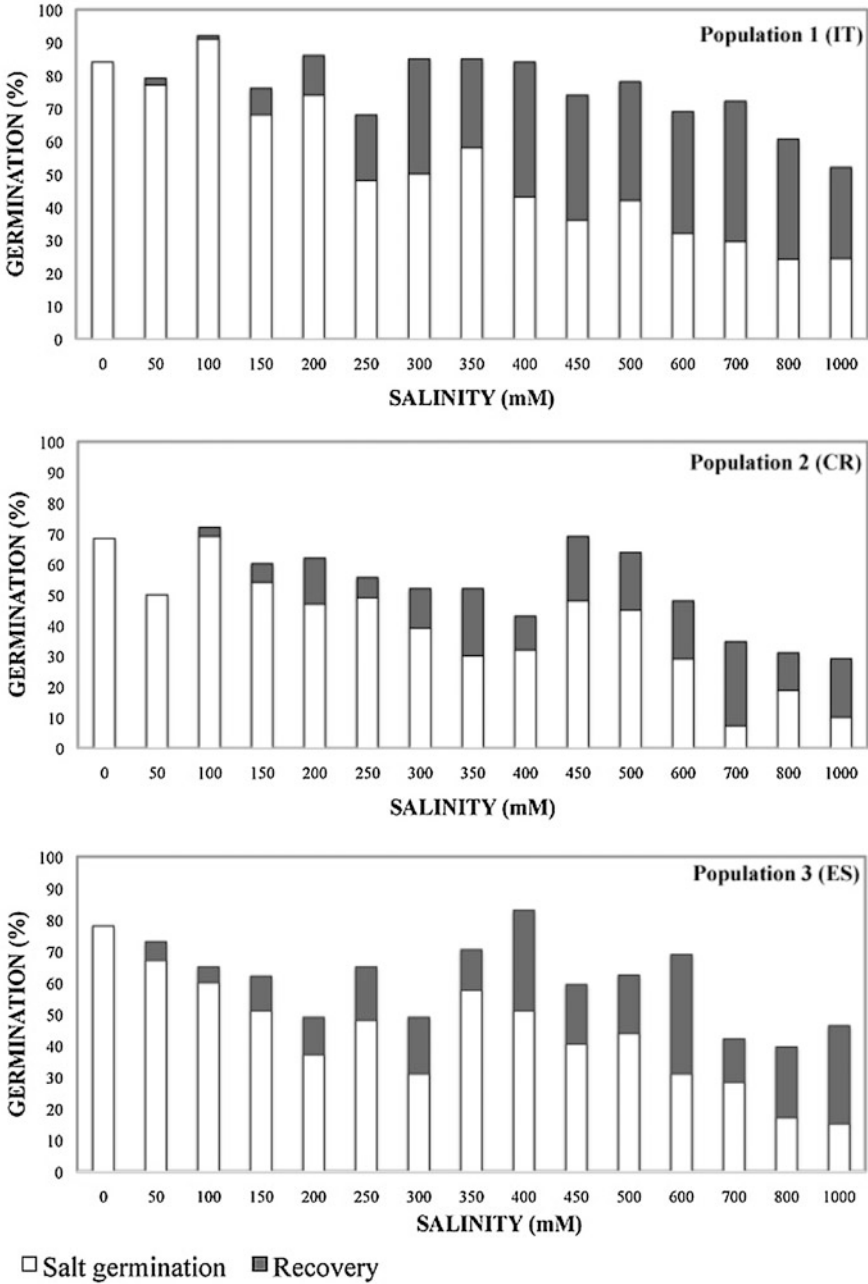
In the Mediterranean area, further confirmations on the implication of the osmotic potential in the establishment of a state of dormancy in seeds subjected to salt stress conditions are given by research conducted on some both perennial and annual halophytes of the southeast coast of Spain. Following exposure to different salts and osmotic potentials ranging between  $-2.37$  and  $-3.90$  M, it was confirmed that low osmotic risks stimulate the germination rate with the subsequent rapid evolution of the seedlings before the osmotic potentials decreased again promoting dormancy. This has been observed in all species, both annual and perennial (Pujol et al. 2000).

Some studies have shown that the germination recovery of the seeds after exposure to salinity depends also on the environmental characteristics of the place of origin of the analyzed species. In a work focused on the seed germination pattern of *Salicornia patula* related to the localities where the seeds of the populations studied were collected (Italy, Spain, and Croatia), a close relationship between recovery and soil moisture was highlighted. This is well expressed by the data summarized in Fig. 3. The seeds of populations growing in the areas where there is average annual precipitation ranging between 757 and 579 mm did not seem to be affected by a permanent inhibition and had the best germination values in the recovery phase. Instead, the seeds collected where the average annual rainfall is 1194 mm had a permanent inhibition in the recovery phase after high salt concentrations were removed (Gasparri et al. 2016).

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## 5 Seed/Fruit Heteromorphism

A phenomenon little studied for the halophilous species distributed in the Mediterranean Basin is the production, in the same species, of heteromorphic seeds/fruits. This polymorphism, occurring commonly in Asteraceae, Amaranthaceae, and Poaceae, means the production of seeds or fruits that differ in color, shape, weight, size, external structure, and position in inflorescences and that have different



**Fig. 3** Germination percentages indicating the salinity effect (white) and total germination (light gray) after recovery in seeds from population 1, Sentina Natural Regional Reserve (IT); population 2, Blace (CR); population 3, Sant Pere Pescador, Girona (ES) at 25 °C. (Adopted from Gasparri et al. 2016)

physiological characteristics (Venable and Levin 1985; Baskin and Baskin 2014). The phenomenon is often found in plants growing in habitats with frequent changes in environmental conditions, such as deserts and salt marshes (Ungar 1987; Wei et al. 2007).

As many studies have confirmed, the presence of heteromorphic seeds plays an important ecological role in promoting the diffusion and conservation of the species. In particular, the differences in germination behaviors, a consequence of the seminal structures especially at the level of the integuments and of the different photo-thermoperiodic requirements for overcoming dormancy, represent a significant advantage for the species that live in nonhomogeneous environments and increase the possibility of adaptation to the variations of the environmental conditions. This is especially important in particular microenvironments where the variations can be dangerous for the seedlings in the early stages of their development and growth (Ungar 1982). Many transitional and unstable areas of the Mediterranean coasts belong to these microenvironments, where the beginning of the flood period and the drought period can vary deeply from year to year, depending on the irregular distribution of the autumn and winter rains (Berger 1985).

Many halophyte species show seed or fruit heteromorphism (Table 1), and among these species, most of halophytic species are annual, and only a few species belong to perennials (Khan and Gul 1998; Yan et al. 2011). Most of the species used to characterize the germination model and the dormancy mechanism in heteromorphic dispersal units of halophytes, belong in particular to Amaranthaceae. Among the first plants investigated, there are *Atriplex dimorphostegia* inhabiting saline soils of south Israel (Koller 1957), *Atriplex patula* var. *hastata*, and *Salicornia europaea* from salt marshes of North America (Ungar 1971, 1979) and *Salicornia patula* from the Mediterranean coast of France (Grouzis et al. 1976). Focusing on the latter case, several authors have found a very different behavior of the dispersion units on the bases of their position in the inflorescences. *S. patula* is a species colonizing unstable transition zones where the beginning of the flooding period and of the dry period may vary from year to year with large fluctuations in phreatic water level and soil moisture salinity. For some populations of Mediterranean salt marshes, a somatic dimorphism with two types of seed, central seeds larger and lateral seeds smaller and free from perianth envelopes, was confirmed. This polymorphism is linked with a physiological “dimorphism” concerning some requirements for germination and dispersal. The lateral seeds are dispersed shortly before the central seeds, have poor flotation properties, and stay in the bare soil zones between permanent unvegetated muds and perennial vegetation. It has been also shown that lateral seeds, contrary to central seeds, have higher longevity and an innate dormancy which can be removed by a cold and wet pretreatment. The innate dormancy of the lateral seeds, associated with a general percentage of germination reduced at low temperatures, prevents massive germination in the autumn (Berger 1985). If for some reasons, seedlings born from nondormant seeds do not survive to unsuitable environmental conditions, the presence of dormant seeds, acting as a seed bank, is a guarantee of survival of the species. Similar results have been obtained in studies on populations of *S. patula* collected along the coast of Croatia. In these investigations,

**Table 1** Examples of main halophytes producing heteromorphic seeds. (From Liu et al. 2018, modified)

<i>Species</i>	Morphs	Habitat
<i>Arthrocnemum macrostachyum</i> <sup>a</sup>	Brown; black	Coastal salt marshes
<i>Arthrocnemum indicum</i>	Large; small	Coastal salt marshes
<i>Atriplex aucheri</i>	Brown; black	Desert, saline soil
<i>Atriplex centralasiatica</i>	Brown; black	Desert, saline soil
<i>Atriplex inflata</i>	Brown; black	Saline soil
<i>Atriplex micrantha</i> <sup>a</sup>	Brown; black	Desert, saline soil
<i>Atriplex patens</i>	Brown; black	Saline soil
<i>Atriplex prostrata</i> <sup>a</sup>	Large; small	Inland and coastal marshes
<i>Atriplex rosea</i> <sup>a</sup>	Brown (larger); black (smaller)	Salt marshes
<i>Atriplex sagittata</i> <sup>a</sup>	Large; medium; small	Salt steppe and riparian habitats
<i>Halogeton glomeratus</i>	Green; yellow	Inland salt deserts
<i>Salicornia europaea</i> <sup>a</sup>	Large; small	Inland and coastal marshes
<i>Salicornia patula</i> <sup>a</sup>	Large; small	Lagoon
<i>Salicornia ramosissima</i> <sup>a</sup>	Large (central); small (lateral)	Saline soil, coastal marshes
<i>Salsola komarovii</i>	Long winged; short winged	Coastal regions
<i>Salsola affinis</i>	*Types A, B, C	Gravel desert, saline soil
<i>Salsola ferganica</i>	Large with or without winged perianth (WP); medium with or without WP; small with or without WP	Cold desert
<i>Suaeda acuminata</i>	Brown; black	Salinized desert
<i>Suaeda aralocaspica</i>	Brown (larger), black (smaller)	Salinized desert
<i>Suaeda corniculata</i>	Brown; black	Saline-alkaline soils
<i>Suaeda glauca</i>	Brown; black	Saline soil
<i>Suaeda kossinskyi</i>	Brown; black	Saline soil
<i>Suaeda linifolia</i>	Brown; black	Saline soil
<i>Suaeda moquinii</i>	Brown (soft); black (hard)	Salt marshes
<i>Suaeda paradoxa</i>	Brown; black	Saline soil

(continued)

**Table 1** (continued)

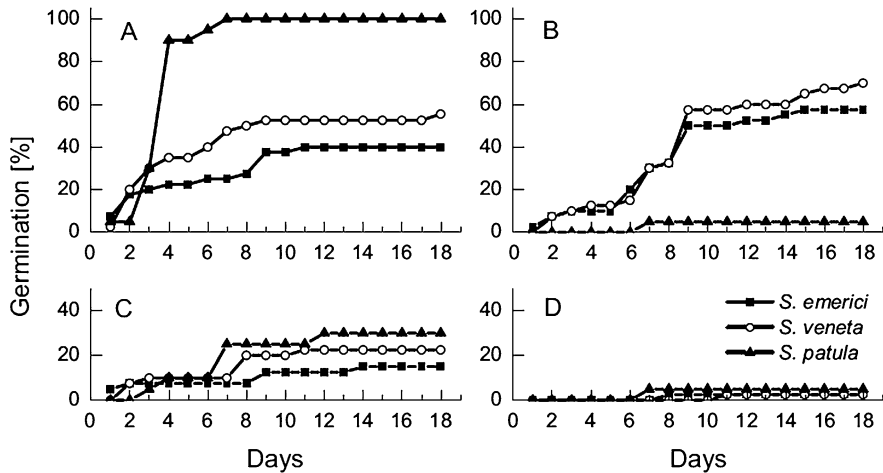
<i>Species</i>	Morphs	Habitat
<i>Suaeda salsa</i>	Brown (larger); black (smaller)	Saline soil
<i>Suaeda splendens</i> <sup>a</sup>	Brown; black	Saline soil
<i>Chenopodium album</i> <sup>a</sup>	Brown (larger); black (smaller)	Light-saline soil
<i>Halopyrum mucronatum</i>	Summer; winter	Coastal dune
<i>Tamarix ramosissima</i> <sup>a</sup>	Spring; summer	Piedmont Gobi Desert, valleys, saline soil
<i>Cakile edentula</i>	Large; small	Coastal dune
<i>Zannichellia pedunculata</i> <sup>a</sup>	Fruits with or without crest	Lagoon

Type A fruits have lignified perianths with long wings and green utricles; Type B fruits have lignified perianths with short wings, or no wings, and green utricles; Type C fruits have tepals without wings and yellow utricles

<sup>a</sup>Mediterranean species

the seed germination patterns were discussed to explain the habitat preferences of *S. patula* with respect to other species in the same region but in areas different for the tidal regime and nutrient flow, such as *Salicornia emerici* (Šajna et al. 2013). The differences of environmental requirement also in these cases seem to be closely related to differences in the germination rate of the two seed types (central and lateral) occurring in both species and to the number of seeds that germinated for fertile shoot greater in *S. emerici*. The authors suggest that the presence of lateral persistent and hardly germinating seeds represents a seed bank for the recovery of the plant population after drastic events such as flooding. In this environment, the rarity of *S. patula* could be explained with a difficulty of the species to cope with strong environmental perturbations that make it able to occupy only more stable habitats, although potentially drought and with high salt concentration. Figure 4 shows clearly the differences in the germination rate related to salinity, for central and lateral seeds of *S. patula* and *S. emerici*.

In the Mediterranean area, another example of species with dimorphism in the dispersion units is represented by *Zannichellia palustris*, a facultative hydrohalophyte living in freshwater as well as in coastal and inland saline waters (Adam 1977; Van Vierssen 1982a, b). The populations investigated by Lombardi et al. (1996) grow in a marine lagoon of Tuscany (Italy) and at maturity (June), show the contemporary presence of two fruit types differing for the morphology of the pericarp dorsal side and the germination response. The serrated-crested achenes showed higher germination percentage than the non-crested ones. Actually, in these fruits, the morphological differences were linked to a different degree of seed maturity. Therefore, the seed bank contains seeds characterized by different dormancy. Furthermore, the ratio of the two achene types in the seed bank may be affected by environmental conditions. The production of physiologically different



**Fig. 4** Germination percentage of central (A, C) and lateral (B, D) seeds of *Salicornia patula* and *S. emerici*, in non-saline (A, B) and saline (C, D) condition. (From Šajna et al. 2013)

seeds may favor the dispersal and the preservation of a species in unstable environments (Lombardi et al. 1996). In particular, in hypersaline habitats, the extreme variability of the environment represents a risk for the seedling, especially in their early developmental stages. In this habitat, the phenomenon of seed dimorphism represents a particular strategy for survival that provides multiple opportunities for a population to maintain its continuity (Phillipupillai and Ungar 1984; Khan and Ungar 1986; Gul et al. 2013).

## 6 Conclusion

Halophytes species, maintaining the ecological stability of saline coastal areas and arid and semiarid inland soils, have an indispensable role in habitat protection. The tolerance of these species to the salt stress is a complex mechanism at both physiological and molecular levels that is influenced by different environmental factors. The different forms of adaptation and survival strategy of halophytes that make them survive extreme conditions represent a valid resource to cope with the salinization phenomena due to climate change and anthropogenic activities. In the ongoing climate change scenario, the risk of soil salinization is one of the major threats to the coastal ecosystem and agriculture. For that, in the past few years, halophytes have received great attention, not only for their importance for ecosystems but also as model species in salt tolerance research, reclamation of salt-affected and heavy metal-contaminated areas, as well as for their use for potential forage, fiber, and biomass crops.

However, the exploitation of halophilous species is still hampered by a fundamental lack of knowledge of the mechanisms of salt tolerance. Among the main

adaptive strategies adopted by halophytes, the regulation of the germination is pivotal for survival in saline and arid habitats where the environmental conditions and their variations can become very critical. Therefore, a thorough understanding of the mechanisms underlying the regulation of germination of halophyte seeds is essential to overcome the lack of knowledge of the salt tolerance mechanism.

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## References

- Adam, P. (1977). The ecological significance of “halophytes” in the Devonian flora. *The New Phytologist*, *78*, 237–244.
- Barton, L. V. (1965). Seed dormancy: General survey of dormancy types in seeds, and dormancy imposed by external agents. In A. Lang (Ed.), *Differenzierung und Entwicklung/Differentiation and development* (pp. 2346–2367). Berlin/Heidelberg: Springer.
- Baskin, J. M., & Baskin, C. C. (2004). A classification system for seed dormancy. *Seed Science Research*, *14*, 1–16.
- Baskin, C. C., & Baskin, J. M. (2014). *Seeds: Ecology, biogeography, and evolution of dormancy and germination* (2nd ed.). San Diego: Academic/Elsevier.
- Belderok, B. (1961). Studies on dormancy in wheat. *Proceedings of the International Seed Testing Association*, *26*, 697–760.
- Berger, A. (1985). Seed dimorphism and germination behavior in *Salicornia patula*. *Vegetation*, *61*, 137–143.
- Bewley, J. D. (1997). Seed germination and dormancy. *Plant Cell*, *9*, 1055–1066.
- Bocchieri, E., De Martis, B., & Marchioni, A. (1981). *Parapholis incurva* (L.) CE Hubbard (Gramineae); il contributo sulla ecologia della germinazione. *Bollettino della societa sarda di scienze naturali*, *20*, 131–138.
- Costa, A. S., Dias, L. S., & Dias, A. S. (2019). Imbibition, germination, and early seedling growth responses of light purple and yellow seeds of red clover to distilled water, sodium chloride, and nutrient solution. *Sci*, *1*, 51.
- Debez, A., Belghith, I., Pich, A., Taamalli, W., Abdelly, C., & Braun, H. P. (2018). High salinity impacts germination of the halophyte *Cakile maritima* but primes seeds for a rapid germination upon stress release. *Physiologia Plantarum*, *164*, 134–144.
- Del Vecchio, S., Mattana, E., Acosta, A. T. R., & Bacchetta, G. (2012). Seed germination responses to varying environmental conditions and provenances in *Crucianella maritima* L., a threatened coastal species. *Comptes Rendus Biologies*, *335*, 26–31.
- Del Vecchio, S., Porceddu, M., & Fantinato, E. et al. (2018). Risposte di germinazione delle popolazioni mediterranee di *Cakile maritima* a luce, salinità e temperatura. *Folia Geobot*, *53*, 417–428.
- Delgado Fernandez, I. C., Gimenez Luque, E., Gomez Mercado, F., & Pedrosa, W. (2016). Influence of temperature and salinity on the germination of *Limonium tabernense* Erben from Tabernas Desert (Almería, SE Spain). *Flora*, *218*, 68–74.
- Donohue, K., Rubio de Casas, R., Burghardt, L., Kovach, K., & Willis, G. C. (2010). Germination, post germination adaptation, and species ecological ranges. *Annual Review of Ecology, Evolution, and Systematics*, *41*, 293–319.
- Fenner, M. (1985). *Seed ecology*. New York: Chapman and Hall.
- Fenu, G., Cogoni, D., Ulian, T., & Bacchetta, G. (2013). The impact of human trampling on a threatened coastal Mediterranean plant: The case of *Anchusa littorea* Moris (Boraginaceae). *Flora*, *208*, 104–110.
- Fernández, I. C. D., Luque, E. G., Mercado, F. G., & Marrero, J. M. (2015). Germination responses of *Limonium insigne*(Coss.) Kuntze to salinity and temperature. *Pakistan Journal of Botany*, *47* (3), 807–812.



- Finch-Savage, W. E., & Leubner-Metzger, G. (2006). Seed dormancy and the control of germination. *The New Phytologist*, *171*, 501–523.
- Flowers, T. J., Galal, H. K., & Bromham, L. (2010). Evolution of halophytes: Multiple origins of salt tolerance in land plants. *Functional Plant Biology*, *37*, 604–612.
- Gasparri, R., Casavecchia, S., Galié, M., Pesaresi, S., Soriano, P., Estrelles, E., & Biondi, E. (2016). Germination pattern of *Salicornia patula* as an adaptation to environmental conditions of the specific populations. *Plant Sociology*, *53*, 91–104.
- Grouzis, M., Berger, A., & Heim, G. (1976). Polymorphisme et germination des graines chez trois espèces annuelles du genre *Salicornia*. *Oecol Platzt*, *11*, 41–52.
- Gul, B., Ansari, R., Flowers, T. J., & Khan, M. A. (2013). Germination strategies of halophyte seeds under salinity. *Environmental and Experimental Botany*, *92*, 4–18.
- Gulzar, S., Khan, M. A., & Ungar, I. A. (2001). Effect of temperature and salinity on the germination of *Urochondra setulosa*. *Seed Science and Technology*, *29*, 21–29.
- Guma, I. R., Padrón-Mederos, M. A., Santos-Guerra, A., & Reyes-Betancort, J. A. (2010). Effect of temperature and salinity on germination of *Salsola vermiculata* L. (Chenopodiaceae) from Canary Islands. *Journal of Arid Environments*, *74*, 708–711.
- Gutterman, Y. (2012). *Survival strategies of annual desert plants*. Springer Science & Business Media, Springer GmbH & Co. KG: Berlin/Heidelberg, Germany.
- Hassan, A. L., Estrelles, M., Soriano, E., López-Gresa, P., Bellés, M. P., Boscaiu, J. M., & Vicente, O. (2017). Unraveling salt tolerance mechanisms in halophytes: A comparative study on four Mediterranean *Limonium* species with different geographic distribution patterns. *Frontiers in Plant Science*, *8*, 1438.
- Huang, Z. Y., Liu, S. S., Bradford, K. J., Huxman, T. E., & Venable, D. L. (2016). The contribution of germination functional traits to population dynamics of a desert plant community. *Ecology*, *97*, 250–261.
- Khan, A. A. (1977). Preconditioning, germination and performance of seeds. In A. A. Khan (Ed.), *The physiology and biochemistry of seed dormancy and germination* (pp. 283–316). New York: Elsevier/North-Holland Biomedical Press.
- Khan, M. A., & Gul, B. (1998). High salt tolerance in germinating dimorphic seeds of *Arthrocnemum indicum*. *International Journal of Plant Sciences*, *159*, 826–832.
- Khan, M. A., & Ungar, I. A. (1984). The effect of salinity and temperature on germination of polymorphic seeds and growth of *Atriplex triangularis*. *American Journal of Botany*, *71*, 481–489.
- Khan, M. A., & Ungar, I. A. (1986). Life history and population dynamics of *Atriplex triangularis*. *Vegetation*, *66*, 17–25.
- Khan, M. A., & Ungar, I. A. (1997). Effects of light, salinity, and thermoperiod on the seed germination of halophytes. *Canadian Journal of Botany*, *75*, 835–841.
- Koller, D. (1957). Germination regulating mechanisms in some desert seeds, IV. *Atriplex dimorphostegia* Kar. et Kir. *Ecology*, *38*, 2–13.
- Kranner, I., & Seal, C. E. (2013). Salt stress, signalling and redox control in seeds. *Functional Plant Biology*, *40*, 848–859.
- Lang, A. (1965). Effects of some internal and external conditions on seed germination. In *Differenzierung und Entwicklung/Differentiation and development* (pp. 2495–2540). Berlin/Heidelberg: Springer.
- Lang, G. A., Early, J. D., Martin, G. C., & Darnell, R. L. (1987). Endo-, para- and ecodormancy: Physiological terminology and classification for dormancy research. *Horticultural Science*, *22*, 371–377.
- Liu, R., Wang, L., Tanveer, M., & Song, J. (2018). Seed heteromorphism: An important adaptation of halophytes for habitat heterogeneity. *Frontiers in Plant Science*, *9*, 1515.
- Lombardi, T., & Onnis, A. (1999). Seasonal changes in the germination responses of *Hordeum maritimum* and *H. murinum* seeds in relation to salinity, temperature and after-ripening time. *Plant Biosystems*, *133*, 289–296.
- Lombardi, T., Bedini, S., & Onnis, A. (1996). The germination characteristics of a population of *Zannichellia palustris* subsp. *pedicellata*. *Aquatic Botany*, *54*, 287–296.

- Lombardi, T., Fochetti, T., & Onnis, A. (1998). Germination of *Briza maxima* L. seeds: Effects of temperature, light, salinity and seed harvesting time. *Seed Science and Technology*, 26, 463–470.
- Lombardi, T., Bedini, S., & Bertacchi, A. (2019). Germination ecology of the aromatic halophyte *Artemisia caerulescens* L.: influence of abiotic factors and seed after-ripening time. *Folia Geobotanica* 54 (1-2), 115–124.
- Long, R. L., Gorecki, M. J., Renton, M., Scott, J. K., Colville, L., Goggin, D. E., Commander, L. E., Westcott, D. A., Cherry, H., & Finch-Savage, W. E. (2015). The ecophysiology of seed persistence: A mechanistic view of the journey to germination or demise. *Biological Reviews*, 90, 31–59.
- Luciani, F., Cristaudo, A., & Aricò, D. (2001). Germination ecology of three *Plantago* L. (Plantaginaceae) species living in a saline environment. *Plant Biosystems*, 135, 213–221.
- Manzoor, S., Hameed, A., Khan, M. A., & Gul, B. (2017). Seed germination ecology of a medicinal halophyte *Zygophyllum propinquum*: Responses to abiotic factors. *Flora*, 233, 163–170.
- Melendo, M., & Giménez, E. (2019). Seed germination responses to salinity and temperature in *Limonium supinum* (Plumbaginaceae), an endemic halophyte from Iberian Peninsula. *Plant Biosystems*, 153, 257–263.
- Meletti, P. (1964). Nuove prospettive nello studio dei fattori che controllano la germinazione dei semi. *Giornale Botanico Italiano*, 71, 372–384.
- Nikolaeva, M. G. (1977). Factors controlling the seed dormancy pattern. In A. A. Khan (Ed.), *The physiology and biochemistry of seed and germination* (pp. 51–74). Amsterdam: Elsevier/North–Holland Biomedical Press.
- Onnis, A., & Pelosini, F. (1976). *Athenia filiformis* Petit: ecologia e significato dell'andamento della germinazione in relazione alle variazioni di temperatura e salinità del substrato nel periodo estivo–autunnale. *Giornale Botanico Italiano*, 110, 127–136.
- Penfield, S., & Mac Gregor, D. R. (2017). Effects of environmental variation during seed production on seed dormancy and germination. *Journal of Experimental Botany*, 68, 819–825.
- Phillipupillai, J., & Ungar, I. A. (1984). The effect of seed dimorphism on the germination and survival of *Salicornia europaea* L. populations. *American Journal of Botany*, 71, 542–549.
- Pujol, J. A., Calvo, J. F., & Ramirez–Díaz, L. (2000). Recovery of germination from different osmotic conditions by four halophytes from southeastern Spain. *Annals of Botany*, 85, 279–286.
- Qasem, J. R. (2019). Weed seed dormancy: The ecophysiology and survival strategies. In J. C. Jimenez–Lopez (Ed.), *Seed dormancy and germination*. IntechOpen. Available from: <https://www.intechopen.com/books/seed-dormancy-and-germination/weed-seed-dormancy-the-ecophysiology-and-survival-strategies>
- Redondo–Gómez, S., Mateos–Naranjo, E., Cambrollé, J., Luque, T., Figueroa, M. E., & Davy, A. J. (2008). Carry–over of differential salt tolerance in plants grown from dimorphic seeds of *Suaeda splendens*. *Annals of Botany*, 102, 103–112.
- Rosbakh, S., & Poschod, P. (2015). Initial temperature of seed germination as related to species occurrence along a temperature gradient. *Functional Ecology*, 29, 5–14.
- Šajna, N., Regvar, M., Kaligari, S., Škvorc, Z., & Kaligari, M. (2013). Germination characteristics of *Salicornia patula* Duval–Jouve, *S. emerici* Duval–Jouve, and *S. veneta* Pign et Lausi and their occurrence in Croatia. *Acta Botanica Croatica*, 72, 347–358.
- Seal, C. E., Barwell, L. J., Flowers, T. J., Wade, E. M., & Pritchard, H. W. (2018). Seed germination niche of the halophyte *Suaeda maritima* to combined salinity and temperature is characterised by a halothermal time model. *Environmental and Experimental Botany*, 155, 177–184.
- Ungar, I. A. (1971). *Atriplex patula* var. *hastata* seed dimorphism. *Rhodora*, 73, 548–551.
- Ungar, I. A. (1979). Seed dimorphism in *Salicornia europaea* L. *Botanical Gazette*, 140, 102–108.
- Ungar, I. A. (1982). Germination ecology of halophytes. In D. N. Sen & K. S. Rajpurchit (Eds.), *Contributions to the ecology of halophytes* (pp. 143–154). Dordrecht: Springer.
- Ungar, I. A. (1987). Population ecology of halophyte seeds. *The Botanical Review*, 53, 301–334.

- Van Vierssen, W. (1982a). The ecology of communities dominated by *Zannichellia* taxa in western Europe. I. Characterization and autoecology of the *Zannichellia* taxa. *Aquatic Botany*, *12*, 103–155.
- Van Vierssen, W. (1982b). The ecology of communities dominated by *Zannichellia* taxa in western Europe. II. Distribution, synecology and productivity aspects in relation to environmental factors. *Aquatic Botany*, *13*, 385–483.
- Wei, Y., Dong, M., & Huang, Z. Y. (2007). Seed polymorphism, dormancy and germination of *Salsola affinis* (Chenopodiaceae), a dominant desert annual inhabiting the Junggar Basin of Xinjiang, China. *Australian Journal of Botany*, *55*, 464–470.
- Yan, C., Yang, M., & Yan, W. (2011). Comparative germination of *Tamarix ramosissima* spring and summer seeds. *EXCLI Journal*, *10*, 198–201.
- Zehra, A., & Khan, M. A. (2007). Comparative effect of NaCl and seasalt on germination of halophytic grass *Phragmites karka* at different temperature regimes. *Pakistan Journal of Botany*, *39*, 1681–1694.