



Germination Functional Traits in Seeds of Halophytes

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Abstract

Many families of halophytes rely on seeds for their natural regeneration. As a functional trait, germination is highly responsive to the environment including salinity. For some halophyte species, their seeds may avoid periods of high salinity through dormancy, which may be present in only one seed morph in species with heteromorphic seeds, and can be influenced by the maternal environment and transgenerational effects. Avoidance strategies are plastic and can

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vary among and within species as well as with habitat. Other species of halophytes are highly tolerant to salinity, with germination occurring in conditions more than twice the concentration of sodium chloride found in seawater, utilizing physiological mechanisms such as ion compartmentalization and osmotic adjustment. However, these strategies are not exclusive to halophytes and are sometimes found in germinating seeds of salt-tolerant non-halophytes. Quantification of the germination niche to the environment can be made using the population-based germination models thermal time (temperature), hydro time (water potential), and halo time (salinity). These models estimate environmental thresholds to germination and germination rate changes with the environment. Of the few examples of applying these models to salinity, the germination of halophytes appears no more tolerant to salinity than non-halophytes. More frequent application of these models is required to build a global view. As demonstrated by a case study in the Brazilian Caatinga (a semiarid ecosystem), validation of these germination models in situ, combined with climate and soil data, can be used to predict germination responses to climate change.

Keywords

Halophyte · Germination · Functional traits · Salinity · Population-based models

1 Introduction

For the majority of the 369,000 species of flowering plants (Royal Botanic Gardens, Kew 2016), seeds are the means by which natural regeneration occurs. Seeds provide the link between the adult plant and the next generation of plants, facilitating plant dispersal across spatial and temporal scales. It is, therefore, not surprising that seeds are frequently referred to as the “time capsules of life.” There are many halophyte families that reproduce by seed, with the highest number of genera belonging to the Amaranthaceae (45 genera), Asteraceae (24 genera), and Poaceae (29 genera) for those occupying salt marsh and salt desert habitats, and the Asteraceae (37 genera), Fabaceae (21 genera), and Poaceae (32 genera) for salt-tolerant species that inhabit beaches, cliffs, and dunes (Fig. 1; data taken from Baskin and Baskin 2014).

Mature seeds of most species (ca. 75–80%; Walters et al. 2013) are desiccation tolerant (orthodox) and undergo a process of maturation drying on the mother plant before being dispersed metabolically inactive (Berjak and Pammenter 2008). Species with this type of desiccation behavior include many crops (e.g., rice (*Oryza*), maize (*Zea mays*), and wheat (*Triticum*)) as well as wild species (e.g., halophytes in the *Atriplex* and *Suaeda* genera). Seeds of these species have the potential to form a soil seed bank, with life spans ranging from years to decades and even centuries (Baskin and Baskin 2014; Long et al. 2015). However, frequent cycles of hydration and dehydration may impact on their longevity (Kranner and Seal 2013). In some cases, hydration-dehydration cycles may enhance seed tolerance to abiotic stress factors, such as salinity (Matias et al. 2015), as hydration enables to

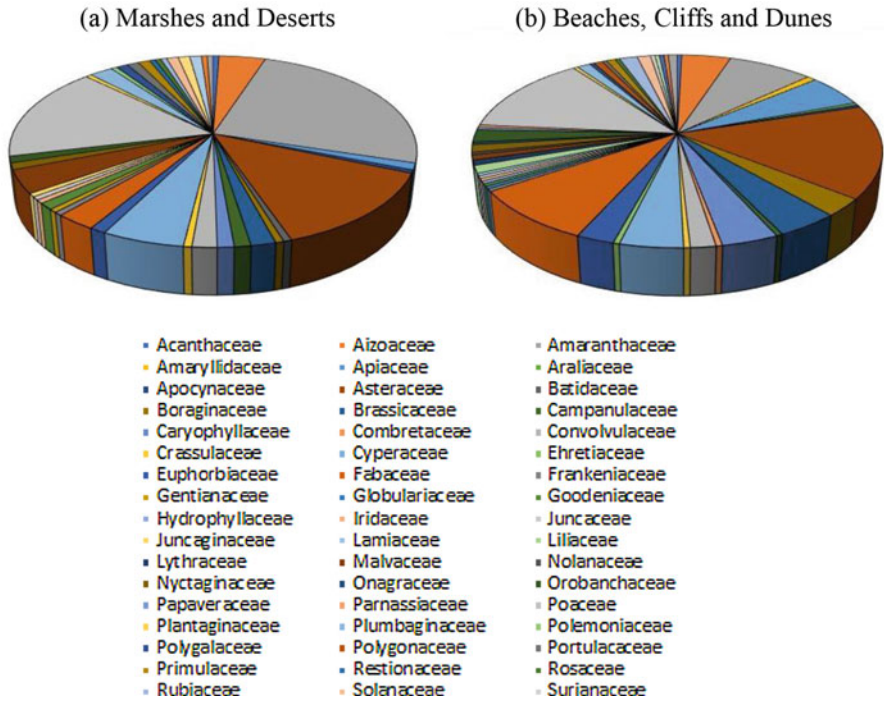


Fig. 1 Families containing genera of (a) halophytes from salt marshes and salt deserts and (b) salt-tolerant species from beaches, cliffs, and dunes. The highest number of genera belong to the Amaranthaceae (45 genera), Asteraceae (24 genera), and Poaceae (29 genera) for those occupying salt marsh and salt desert habitats and the Asteraceae (37 genera), Fabaceae (21 genera), and Poaceae (32 genera) for salt-tolerant species that inhabit beaches, cliffs, and dunes. (Data are summarized from Table 11.12 of Baskin and Baskin 2014)

repair processes to commence and the initiation of metabolic processes such as the synthesis of antioxidants (Kranner and Seal 2013). In contrast, a small proportion of species (ca. 5–10%) do not undergo maturation drying (Walters et al. 2013). Their seeds are sensitive to desiccation (recalcitrant) and are dispersed while hydrated and metabolically active (e.g., mangrove tree *Avicennia marina*, cocoa (*Theobroma cacao*), and oak (*Quercus robur*); Berjak and Pammenter 2008). Some species may also exhibit vivipary, where seeds germinate while still attached to the mother plant (e.g., the mangroves *Avicennia* and *Rhizophora*; Flowers and Colmer 2008).

There are several seed traits that contribute towards a species function in an ecological context. Seed mass and size have been well studied, yet the scope of traits is broader than this. Biochemical (e.g., nutrient content, metabolic rate), physiological (e.g., embryo development, light and temperature requirements, stress tolerance, dormancy), and physical/morphological (e.g., shape, coat thickness) traits are also important and impact on the seed functions dispersal, persistence, germination timing, and establishment (Saatkamp et al. 2019).

Germination is highly responsive to the environment, with temperature and water availability acting as two critical drivers (Baskin and Baskin 2014). Germination may refer to the emergence of the radicle (early root) through the seed coat (physiological germination) or the emergence of a normal seedling (developed cotyledon(s), hypocotyl and roots, with a healthy appearance; see Matias et al. 2015). Ecologically, a plant can control the temporal or spatial environment a seedling will grow in through germination, maximizing the chances of reproductive success (Baskin and Baskin 2014). This includes the importance of the thermal memory, representing phenotypic plasticity that has arisen in response to thermal environments previous generations have experienced (Fernández-Pascual et al. 2019). Understanding and quantifying the germination niche of a species can also highlight its sensitivity to environmental perturbation, such as experienced through climate change (Porceddu et al. 2013; Seal et al. 2017; Gomes et al. 2019; Dantas et al. 2020).

In this chapter, we do not intend to repeat the thorough reviews on halophyte seed germination available in the literature (see Ungar 1978; Gul et al. 2013; Baskin and Baskin 2014; Rasheed et al. 2019) or the vast amounts of data available on the online database eHALOPH (2019). Rather, we will highlight common trends in germination functional traits and the latest approaches to quantifying these in halophyte seeds, as well as discuss their application in the context of global challenges in the future. For consistency, we define a halophyte as being listed in eHALOPH (2019), which uses the criterion based on the definition of Aronson (1989) of “known or presumed tolerance to electrical conductivity measuring (or estimated to be) at least 7.8 dS m^{-1} or, during significant periods of the plant’s entire life.”

2 Trends in Halophyte Germination Traits

As with halophyte plants, the seeds of halophytes are well adapted to the saline environments in which they germinate. The two main environmental constraints to completing the germination process are temperature and water availability, which can be further challenging in saline environments since saline soils may have a lower osmotic potential than the threshold osmotic potential for germination. Also, the salt ions dissolved in this water can be toxic to cells if not compartmentalized efficiently within vacuoles (Flowers and Colmer 2008). However, other factors may be important to certain habitats, such as tolerance to low oxygen or anoxia in habitats that are subjected to flooding (e.g., coastal salt marshes) and tolerance to high temperatures in salinized drylands with high evaporative demands. There is no “one rule fits all,” and different species cope with salinity during germination in different ways. However, broadly speaking, species can be split into two groups: those that avoid salinity and those which tolerate it.

2.1 Salinity Avoidance

Seed dormancy is an effective means by which the parent plant can control the timing of germination and avoid environmental conditions that are adverse for seedling

establishment (Finch-Savage and Leubner-Metzger 2006). Seed dormancy is a more complex trait than observing that a seed has not germinated, and several classifications exist to describe it, as reviewed by Finch-Savage and Leubner-Metzger (2006) and Baskin and Baskin (2014). Dormancy is present in 55 halophyte families including the Amaranthaceae and Poaceae (see Baskin and Baskin 2014 for a list of species and types of dormancy). Physiological dormancy is the most common form, in which radicle emergence is prevented by a “physiological inhibiting mechanism of the embryo” (Baskin and Baskin 2014). Often dormancy is present in annual species, which need to recruit from seed every year, and more frequently in species found in temperate than in subtropical regions (Gul et al. 2013). Once matured on the mother plant, orthodox seeds may be dispersed with primary dormancy and require a specific set of environmental cues before dormancy is broken. For example, the temperate herbs *Suaeda maritima* and *Salicornia patula* have physiological dormancy (Baskin and Baskin 2014). To release dormancy, seeds of these species require cold-wet stratification during an overwintering period, before germinating in the spring when temperatures become warmer and rainfall maintains low salinity concentrations (Seal et al. 2018). A change in environmental conditions may induce secondary dormancy, such as observed in some perennial species such as *Cyperus arenarius* from subtropical habitats (Gul et al. 2013). Induction of secondary dormancy by high salinity concentrations has also been reported (e.g., black seeds of *Suaeda aralocaspica*; Wang et al. 2008), but in some instances, this may reflect suboptimal conditions for nondormant seeds rather than dormancy per se (Seal et al. 2018). Dormancy may also facilitate the formation of a soil seed bank from which germinated seeds emerge in the future when environmental conditions become favorable. The length of time in which seeds remain viable depends on the species and habitat (Gul et al. 2013), as well as various seed quality traits, such as seed size and the specific characteristics of seed coats, appendages, and exudates (Long et al. 2015).

Salinity avoidance through dormancy is also common in species that produce more than one type or morph of seeds, called seed heteromorphism. Seeds may be morphologically different, such as in color or size, and exhibit different germination preferences (e.g., to light, temperature, and salinity) and dormancy status (e.g., nondormant and dormant) contributing to ecological differences between morphs. Seed heteromorphism is a bet-hedging strategy, spreading germination over time and minimizing the risk of losing an entire cohort of seedlings (Baskin and Baskin 2014). Recent reviews by Liu et al. (2018) and Rasheed et al. (2019) summarize what is currently known regarding heteromorphism in halophytes, including some species in the genera *Suaeda*, *Atriplex*, *Salicornia*, and *Salsola*.

The influence of the environment experienced by the mother plant can have a profound effect on the seed functional traits of the offspring including germination and dormancy (Fernández-Pascual et al. 2019) and may be transgenerational (Yang et al. 2015). In the halophyte *Spergularia marina*, the level of primary dormancy can vary across consecutive growth years (Ungar 1988). Other halophytes, such as *Suaeda aralocaspica*, show a dimorphic specific interaction with maternal salinity or nutrients (Wang et al. 2012). In summary, salinity avoidance strategies are plastic, varying among and within species as well as with habitat, and are influenced by the maternal environment.

2.2 Salinity Tolerance

Instead of avoiding the challenges imposed by salinity, some halophyte species show extreme tolerance to salinity during germination. For example, the concentration of sodium chloride required to reduce germination from 75–100% to around 10% is over 1 M (i.e., more than twice the concentration of sodium chloride found in seawater) for species such as *Haloxylon persicum*, *Neokochia americana* (syn. *Kochia americana*), *Suaeda aralocaspica*, and *Limonium vulgare* (Gul et al. 2013). This is in contrast to those most sensitive to salinity, such as *Lepidium latifolium*, *Spergularia rupicola*, and *Chenopodium album* that require just 0.3 M to reduce germination to around 10% (Gul et al. 2013). This concentration is lower than that required to produce the same response in some salt-tolerant non-halophytes, such as *Cenostigma pyramidale* and *Anadenanthera colubrina* (Dantas et al. 2020). Predicting a species tolerance to salinity during germination is difficult and appears independent of plant form (Gul et al. 2013). For many halophytes, and indeed some non-halophyte species, germination is maximal in water or in highly diluted saline solutions, not always reflecting the salt tolerance of the adult plant (Gul et al. 2013; Kranner and Seal 2013).

Growing evidence suggests that the seeds of halophytes which germinate at high salinities may accumulate salt ions and compartmentalize them into the seed coat away from the embryo. An early study by Khan et al. (1985) revealed that the salt-tolerant *Salicornia pacifica* var. *utahensis* accumulated Na^+ and Cl^- in the seed coat. For the halophytes *Suaeda physophora* and *Haloxylon ammodendron* that germinate to at least 20% in ca. 700 mM NaCl and recover well when transferred to water, the concentration of Na^+ in the seed coat was much higher than the embryo, whereas the xerophyte *Haloxylon persicum*, which does not germinate in ca. 700 mM NaCl, had a significantly lower seed coat/embryo ratio for Na^+ (Song et al. 2005). The importance of ion compartmentalization was also shown in seeds of *Ficinia nodosa* that do not germinate at high salinities but show high recovery when transferred to water, which localized Cl^- in the endosperm, in contrast to the more salt-sensitive *Spyridium globulosum* that accumulated Na^+ and Cl^- in the embryo, displacing K^+ (Guja et al. 2013). Fruits may also play a role in protecting seeds from ion toxicity, as suggested for *Atriplex canescens* where the bract was observed to accumulate Na^+ and Cl^- with lower concentrations found in the seed endosperm or embryo (Khan et al. 1985).

As well as protecting the embryo from ion toxicity, ion compartmentalization may be linked to osmotic adjustment. Just like adult plants that sequester ions into vacuoles, lowering the internal osmotic potential so that water can be taken up (Flowers and Colmer 2008), fruits and seeds may employ a similar technique to facilitate imbibition. The seeds of *Suaeda maritima* (Seal et al. 2018), *Suaeda physophora*, and *Haloxylon ammodendron* (Song et al. 2005) are thought to utilize this strategy. Compatible solutes may also contribute towards osmotic adjustment, with roles for proline and betaine in germinating seeds of *Kosteletzkya virginica* (Poljakoff-Mayber et al. 1994) and *Suaeda japonica* (Yokoishi and Tanimoto 1994), respectively. However, as discussed in the next section, the use of these osmolytes is not exclusive to the seed germination of halophytes.

2.3 Do Salt-Tolerant Non-halophytes Use the Same Tolerance Mechanisms During Germination as Halophytes?

Soil salinity is the most relevant abiotic stress for agriculture, affecting between 25% and 30% of cultivated (irrigated and nonirrigated) areas. The most affected agricultural areas (25%) are located in arid or semiarid regions, where evapotranspiration is higher than precipitation. In these drylands, 20% of the cultivated areas show secondary salinization, i.e., soil salinization due to human activities such as irrigated agriculture with fertigation and drainage, and are poorly designed (Shahid et al. 2018). Thus, tolerance to salinity has been widely studied in non-halophyte crop species. In spite of this, there are still some knowledge gaps due to the complex molecular mechanisms that plants invoke in response to salinity.

Arabidopsis thaliana salt-resistant mutants can absorb Na^+ and K^+ from the germination media, showing a possible relationship between tolerance capacity and the ability to take up these ions as osmotica (Saleki et al. 1993). This can only be accomplished upon ion compartmentalization for osmotic adjustment. This strategy is not exclusive to halophytes, as the xerophyte *H. persicum* (Song et al. 2005) and barley (Zhang et al. 2010) also present evidence for this.

Cellular osmotic adjustment with amino acids (e.g., proline), quaternary and other amines (e.g., glycine-betaine and polyamines), and a variety of sugars and sugar alcohols (e.g., mannitol and trehalose) is known to improve plant performance under salinity, in both halophyte and non-halophytes species. *Hibiscus cannabinus*, a halotolerant cultivar, showed an upregulation of the transcription factor WRKY70, which can be related to osmotic adjustment in halophytes that was not observed in the salt-sensitive cultivar (Kashif et al. 2020). On the other hand, seed coat impermeability and the timing of its breakdown can also be a mechanism of seed avoidance to salinity in non-halophytes, as shown in annual pasture legumes, notably in *Melilotus siculus* (Turra) Vitman ex B.D. Jacks (Nichols et al. 2009).

2.4 Environmental Cues for Germination

There is a close connection between germination and the environment. For halophytes germinating in tropical or subtropical habitats, water availability is important as rainfall is limited, whereas those from temperate habitats typically have sufficient water but are limited by temperature (Gul et al. 2013). Aside from salinity, other germination factors to consider are light, photoperiod, and oxygen availability (for a review see Baskin and Baskin 2014). With so much variation existing between and within species in response to environmental cues, defining the germination niche of species in a comparative approach is important. In the next section, we discuss a popular approach of achieving this using population-based germination models.

3 Population-Based Models for Quantifying Germination Traits in Salinity

3.1 Thermal, Hydro, and Hydrothermal Time Models

Temperature and water availability are two of the most important environmental factors that influence when and where a seed may germinate. To characterize the thermal and hydic germination niches for a species, it is necessary to germinate seeds under different conditions of temperature and water potential. However, niche characterization is largely dependent on the breadth of conditions chosen for the test. For the seeds of non-halophytes, the use of population-based models has increased over the last few decades as they can eliminate this constraint. For a population of seeds, the germination rate of nondormant seeds in relation to temperature or water potential typically follows a predictable, linear pattern that can be extrapolated to estimate values for germination functional traits. For temperature, the thermal time model (García-Huidobro et al. 1982; Covell et al. 1986) estimates the cardinal temperatures and a thermal time constant (θ_T) that describes the thermal units inside the cardinal temperature range that are required for germination to occur ($^{\circ}\text{C d}$) and a standard deviation of the population response (Fig. 2a). The cardinal temperatures are base temperature, T_b , below which no germination is predicted to occur; optimum temperature, T_o , where the germination rate is maximal; and the ceiling temperature, T_c , above which no germination is predicted to occur.

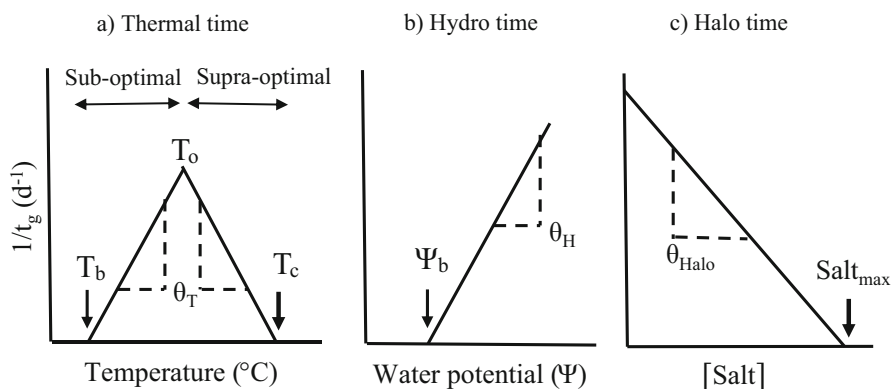


Fig. 2 Population-based models for quantifying germination under conditions of (a) temperature, (b) water potential, and (c) salinity. (a) Thermal time model estimates the cardinal temperatures: base temperature, T_b , below which no germination is predicted to occur; optimum temperature, T_o , where the germination rate is maximal; and the ceiling temperature, T_c , above which no germination is predicted to occur. θ_T is a thermal time constant that describes the thermal units required for germination to occur (units of $^{\circ}\text{C d}$) within the T_b to T_c range. (b) Hydro time model estimates the minimum or base water potential for germination (Ψ_b) and a hydro time constant (θ_H) that describes the accumulation of water potential above Ψ_b for germination to occur (units of MPa d). (c) Halo time model estimates the maximum salt concentration (Salt_{max}) in units of mM and a halo time constant (θ_{Halo}) that describes the accumulation of salt below Salt_{max} required for germination to occur (units of mM d).

temperature, T_c , above which no germination is predicted to occur. For water potential, often created by using solutions of polyethylene glycol, the hydro time model (Gummerson 1986; Bradford 1995) estimates the minimum or base water potential for germination (Ψ_b), a hydro time constant (θ_H) that describes the accumulation of water potential above Ψ_b for germination to occur (MPa d), and the standard deviation of the population response (Fig. 2b). The hydrothermal time model combines both of these conditions and can be used to predict germination at any combination of temperature and water potential (see Bradford 1995 for a review).

Thermal time and hydro time models were initially developed on crop species but have since been applied to the germination of hundreds of wild and domesticated species, of different life-forms (e.g., trees, shrubs, herbs) and from different habitats (see Dürr et al. 2015 for a review). These models have also been applied to species to describe dormancy loss (Porceddu et al. 2017) and field emergence (Porceddu et al. 2013) and to assess the germination risk of species to climate change (Seal et al. 2017; Gomes et al. 2019; Dantas et al. 2020). With such broad applications, population-based germination models have become powerful and popular tools to characterize seed functional traits.

3.2 Application of Population-Based Germination Models to Saline Environments

In the context of quantifying germination under salinity, there are far fewer examples of applying a population-based model than available for water potential created by using polyethylene glycol solutions. Germination thresholds to salinity and germination rate salinity constants may be estimated through the hydro time model (Ψ_b in units of MPa and θ in units of MPa d) or through the halo time model (maximum salt concentration, Salt_{\max} , in units of mM and a halo time constant, θ_{Halo} , in units of mM d (Seal et al. 2018); Fig. 2c). For conditions when temperature and salinity are considered together, the hydrothermal time (MPa °C d) and halothermal time (mM °C d; Seal et al. 2018) models may be applicable. Table 1 summarizes current data available for salinity in the published literature, where values derived from hydro time and hydrothermal time models have been converted to molarity units for comparison between methods.

Of the few published studies available, there is no consistent pattern in the maximum salt threshold to germination between species of non-halophytes and halophytes. Non-halophytes have a range of estimated thresholds from the most sensitive at 113 mM NaCl (or -0.28 MPa; *Myracrodruon urundeuva*) to the least at 953 mM NaCl (or -2.36 MPa; *Digitaria sanguinalis*) (Table 1). For halophytes, the range of estimated threshold values overlaps this for six species, with values of 393 mM NaCl (or -0.94 MPa; *Polygonum aviculare*) to 1021 mM NaCl (or -2.53 MPa; *Chloris virgata*), and just four species showing values well above these (the most tolerant being *Tecticornia indica* estimated at 2473 mM or -5.92 MPa; Table 1). The values of hydro time and hydrothermal time are

Table 1 Summary of estimated halo time and halothermal time models from the literature for germination in salinity. θ_{Halo} is the halo time constant, and θ_{HaloT} is the halothermal time constant

Species ^a	Family ^a	Life-form	Habitat	Salt/temperature (°C) tested	Maximum threshold (50%) ^{c, d} mM	θ_{Halo} (mM d)	θ_{HaloT} (mM °C d)	Reference
Non-halophyte species ^b								
<i>Anadenanthera colubrina</i>	Fabaceae	Tree	Dry tropical forest	NaCl/25	440	977	–	Dantas et al. (2020)
<i>Cenostigma pyramidalis</i>	Fabaceae	Tree	Dry tropical forest	NaCl/25	428	589	–	Dantas et al. (2020)
<i>Cenostigma microphylla</i>	Fabaceae	Tree	Dry tropical forest	NaCl/25 & 30	727 (at 25 °C)	–	82,754	Gomes et al. (2019)
<i>Cichorium intybus</i>	Asteraceae	Herb	Widespread	NaCl/30	361	–	–	Vahabinia et al. (2019)
<i>Digitaria sanguinalis</i>	Poaceae	Herb	Saline grassland	NaCl/25	953	981	–	Zhang et al. (2012)
<i>Erica vesicaria</i>	Brassicaceae	Herb	Widespread	NaCl/30	257	40,774	–	Bakhshandeh et al. (2019)
<i>Myracrodruon urundeuva</i>	Anacardiaceae	Tree	Dry tropical forest	NaCl/25	113	222	–	Dantas et al. (2020)
Halophyte species ^b								
<i>Acanthus ilicifolius</i>	Acanthaceae	Shrub	Mangrove	NaCl/25	727	412	–	Wijayasinghe et al. (2019)
<i>Atriplex prostrata</i>	Amaranthaceae	Herb	Salt marsh	NaCl/10–30	505 (at 15 °C)	–	43,857	Allen et al. (2000)

<i>Beta vulgaris</i>	Amaranthaceae	Herb	Salt marsh	NaCl/6.7–14.3	730 (at 6.7 °C)	–	29,116	Gummerson (1986)
<i>Chloris virgata</i>	Poaceae	Herb	Saline grassland	NaCl/15–30	1021 (at 25 °C)	553	–	Zhang et al. (2012)
<i>Polygonum aviculare</i>	Polygonaceae	Herb	Inland salt steppe	NaCl/10–30	393 (at 15 °C)	–	12,948	Allen et al. (2000)
<i>Salicornia utahensis</i>	Amaranthaceae	Herb	Salt desert	NaCl/10–30	1236 (at 15 °C)	–	58,476	Allen et al. (2000)
<i>Suaeda maritima</i>	Amaranthaceae	Herb	Salt marsh	NaCl/5–25	1279.5 (at 5 °C)	11,847	70,804	Seal et al. (2018)
<i>Suaeda vermiculata</i>	Amaranthaceae	Shrub	Salt desert	NaCl/10–30	1370 (at 15 °C)	–	62,653	Allen et al. (2000)
<i>Tecticornia indica</i>	Amaranthaceae	Herb	Salt marsh	NaCl/10–30	2473 (at 15 °C)	–	79,360	Allen et al. (2000)
<i>Triglochin maritima</i>	Juncaginaceae	Herb	Salt marsh	NaCl/10–30	631 (at 15 °C)	–	37,592	Allen et al. (2000)

^aTaxonomy according to Plants of the World Online database (POWO 2019)

^bDefined as a halophyte according to eHALOPH (2019)

^cHighest mM threshold of conditions tested

^dExcept for *C. intybus*, *E. vesicaria*, and *Suaeda maritima*, data was originally in MPa, MPa d, or MPa °C d and estimated for mM NaCl, mM d, or mM °C d according to van't Hoff's equation (Ψ (atm) = 0.082 T (°K) C (M))

similarly variable. These data provide further evidence to support the notion that halophytes are not necessarily more tolerant to salinity during germination than non-halophytes.

Adding to this variable response to salinity across species is that saline thresholds to germination may be modulated by temperature even within a species. An analysis by Allen et al. (2000) demonstrated that the threshold to germination varied with temperature in three of the halophytes examined (*Atriplex prostrata*, *Polygonum aviculare*, and *Tecticornia indica*), with germination more tolerant to NaCl at lower temperatures than at higher temperature. Consistent with this, germination of *Suaeda maritima* was three times more tolerant to NaCl at 5 °C (maximum threshold of 1279 mM) than at 25 °C (maximum threshold of 447 mM; Seal et al. 2018). This was also observed in the non-halophyte *Cenostigma microphyllum* which had a higher tolerance to salt at 25 °C than at 30 °C (Gomes et al. 2019).

The relationship between germination rate and temperature may also become nonlinear at selected temperatures, such as observed in *Chloris virgata* imbibed in NaCl, where the germination rate changed linearly at low temperatures (15 °C) but became curvilinear at higher temperatures (20–30 °C; Zhang et al. 2012). Curvilinear fits were also more appropriate for four species of mangroves that did not follow the typical linear pattern of germination rate with salinity (Wijayasinghe et al. 2019).

Evidence for the physiological adjustment of halophyte seeds to saline conditions is most clearly demonstrated when germination in iso-osmotic solutions created by polyethylene glycol and salt are compared. A higher percentage of germination in salt than in polyethylene glycol has been demonstrated in some halophyte species such as *Haloxylon ammodendron* (Song et al. 2005) and *Zygophyllum xanthoxylon* (Tobe et al. 2001). However, this behavior may not be restricted to halophytes, as several non-halophytes including barley (Zhang et al. 2010) and *Eruca vesicaria* (Bakhshandeh et al. 2019) show higher tolerance to NaCl than polyethylene glycol. In other cases, some non-halophytes show few differences suggesting a lack of physiological adjustment (e.g., *Anadenanthera colubrina* var. *cebil* and *Cenostigma pyramidale*, Dantas et al. 2020). In the non-halophyte tree *Myracrodruon urundeuva*, Ψ_b was higher in polyethylene glycol (−0.72 MPa) than in NaCl (−0.28 MPa or 113 mM) at 25 °C (Dantas et al. 2020).

3.3 Conclusion

In summary, the application of population-based models to salinity enables a comparative approach to characterize and quantify seed functional traits across species. Currently, a lack of studies makes it difficult to identify trends between halophytes and non-halophytes and whether any variation exists with taxonomy or habitat. Interpretation of this type of functional data will largely depend on how well seeds cope with the influx of ions and the maintenance of water content, via physiological adjustment.

In this section we described the effects of salinity \times temperature and water potential \times temperature on germination of halophyte and non-halophyte seed populations by halothermal and hydrothermal time models. In the next section, we will describe how climate and specifically climate change with different patterns of rainfall, soil salinization, and temperature increase occurring at once will influence germination patterns of halophyte and non-halophyte species.

4 Future Perspectives

4.1 Impact of Climate Change

A massive change in climate has been occurring in the past decades, with stochastic rainfall events, increasing temperature, and aridization/desertification of several vulnerable areas in the world. Climate change is predicted to impact on the spatial pattern of soil salinity, in both coastal and inland agricultural and natural ecosystems, by changing patterns of temperature, precipitation, and evapotranspiration. Pessimistic future climate scenarios with 30% reduction in precipitation and/or 10% increase in evapotranspiration are expected to increase more than twofold the soil salinity of irrigated fruit orchards in a semiarid area of Spain (Aragüés et al. 2015). Due to an average temperature increase of up to 1.5 °C, sea-level rise (causing coastal flooding) and saltwater intrusion, over 70% increase in soil salinity is expected by 2050 in the coastal areas of Bangladesh (Dasgupta et al. 2015).

Effects of climate change (increased temperature; extreme weather events; and sea-level rise) on mangrove forests and salt marshes, where salinity is expected to rise by 0.5%, may vary from lower seedling recruitment and loss of root biomass, causing vegetation coverage to diminish (for a review see Schaeffer-Novelli et al. 2016).

Population-based germination models can be used to predict germination events, not only in different habitats (Fernández-Pascual et al. 2019) but also in different climate scenarios, e.g., decrease in rainfall during the rainy season (Fig. 3), which can induce salinization of the soil (Aragüés et al. 2015). Even if precipitation/evapotranspiration is not altered, measured soil salinity increases by 0.249 dS/m for each 1 °C increase in maximum monthly temperature (Dasgupta et al. 2015). A general model describing germination events (based on heat sum and seed thermal requirements and thresholds), and its relationship with precipitation reduction in a future climate (adapted from Dantas et al. 2020 and Gomes et al. 2019), is presented in Fig. 3. Seeds need a minimum osmotic potential in the soil, in order to uptake water, and this is related to a minimum precipitation volume and the soil salinity that are reduced with rainfall events due to leaching of the accumulated salts (Aragüés et al. 2015). This model, which was applied to four dryland specialist tree and shrub species, can be applied to several other halophytes and salt-tolerant non-halophytes, once information on germination requirements and thresholds are available.

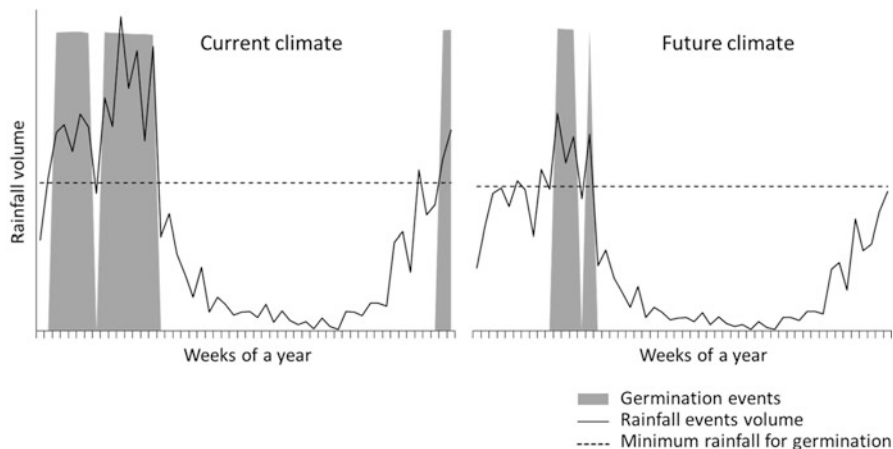


Fig. 3 Germination events during a year of a hypothetical tropical dryland specialist species in response to rainfall volume in current and future climate. (Adapted from Dantas et al. 2020; Gomes et al. 2019). Germination events (gray columns) are based on available heat sum for germination (i.e., the temperature accumulated by the seed per day, above the minimum or base temperature threshold), which in tropical areas is not usually limiting. Thus, germination events occur when water is available. A minimum rainfall volume (dashed horizontal lines) can provide enough water for decreasing soil salinity and/or supporting water uptake during seed imbibition. Pessimistic predictions point to a future climate with a reduction of up to 40% in precipitation volume (continuous lines) in relation to current climate, reducing the available time for germination and initial seedling development

4.2 Application of Cutting Edge Techniques to Halophytes and Non-halophytes

Parallels between halophyte and non-halophyte salt tolerant seeds can lead to understanding the highly complex tolerance mechanisms and allow glycophyte transformation for salt stress during germination, plant development, and crop production. The new genome-editing technique clustered regularly interspaced short palindromic repeat (CRISPR)-associated protein (CRISPR/Cas), which is highly specific and efficient, has been widely tested in major crops (Bortesi and Fischer 2015), suggesting its importance in improving abiotic stress tolerance (Osakabe and Osakabe 2017) as well as to promote better germination and initial development in salinized soil. New research has successfully applied this technique to enhance glycophyte crops for salt tolerance, such as rice (Zhang et al. 2019). On the other hand, the possibility of using CRISPR/Cas technique on economically important halophytes can support the enhancement of nutritional quality of fodder species and faster growth of wood biofuel enabling biosaline agriculture and thus salinized land reclamation.

5 Conclusion

Seed germination is an important plant functional trait that is highly responsive to the environment. Just like the plant growth of halophytes, halophyte seed germination is well adapted to saline environments. Some species employ avoidance strategies,

such as dormancy and the formation of a soil seed bank, favoring germination at low salinity concentrations, while other species show extreme salinity tolerance through the utilization of mechanisms such as ion compartmentalization and osmotic adjustment. The use of population-based germination models is facilitating the characterization of the germination niche in response to different environmental parameters, particularly temperature and water availability, but data for salinity is currently sparse. As popularity for applying this approach to salinity grows, the validation of laboratory-based data in the field is essential and, when combined in a multi-disciplinary approach with climate and soil data, can be used to predict the response of seed germination under future climates.

References

- Allen, P. S., Meyer, S. E., & Khan, M. A. (2000). Hydrothermal time as a tool in comparative germination studies. In M. Black, K. J. Bradford, & J. Vázquez-Ramos (Eds.), *Seed biology: Advances and applications* (pp. 401–410). Wallingford: CAB International.
- Aragüés, R., Medina, E. T., Zribi, W., Clavería, I., Álvaro-Fuentes, J., & Faci, J. (2015). Soil salinization as a threat to the sustainability of deficit irrigation under present and expected climate change scenarios. *Irrigation Science*, *33*, 67–79.
- Aronson, J. A. (1989). *HALOPH a data base of salt tolerant plants of the world*. Tucson: Office of Arid Land Studies, University of Arizona.
- Bakhshandeh, E., Pirdashti, H., Vahabinia, F., & Gholamhossieni, M. (2019). Quantification of the effect of environmental factors on seed germination and seedling growth of *Eruca (Eruca sativa)* using mathematical models. *Journal of Plant Growth Regulation*. <https://doi.org/10.1007/s00344-019-09974-1>.
- Baskin, C., & Baskin, J. (2014). *Ecology, biogeography and evolution of dormancy and germination* (2nd ed.). San Diego: Academic, 1600 pp.
- Berjak, P., & Pammenter, N. W. (2008). From *Avicennia* to *Zizania*: Seed recalcitrance in perspective. *Annals of Botany*, *101*(2), 213–228.
- Bortesi, L., & Fischer, R. (2015). The CRISPR/Cas9 system for plant genome editing and beyond. *Biotechnology Advances*, *33*(1), 41–52.
- Bradford, K. J. (1995). Water relations in seed germination. In J. K. Galili (Ed.), *Seed development and germination* (pp. 351–396). New York: Marcel Dekker.
- Covell, S., Ellis, R. H., Roberts, E. H., & Summerfield, R. J. (1986). The influence of temperatures on seed germination rate in grain legumes. A comparison of chickpea, lentil, soybean and cowpea at constant temperatures. *Journal of Experimental Botany*, *37*, 705–715.
- Dantas, B. F., Moura, M. S. B., Pelacani, C. R., Angelotti, F., Taura, T. A., Oliveira, G. M., Bispo, J. S., Matias, J. R., Silva, F. F. S., Pritchard, H. W., & Seal, C. E. (2020). Rainfall, not soil temperature, will limit the seed germination of dry forest species with climate change. *Oecologia*, *192*(2), 529–541.
- Dasgupta, S., Hossain, M. M., Huq, M., & Wheeler, D. (2015). Climate change and soil salinity: The case of coastal Bangladesh. *Ambio*, *44*(8), 815–826.
- Dürr, C., Dickie, J. B., Yang, X. Y., & Pritchard, H. W. (2015). Ranges of critical temperature and water potential values for the germination of species worldwide: Contribution to a seed trait database. *Agricultural and Forest Meteorology*, *200*, 222–232.
- eHaloph. (2019). Halophytes database. Version 3.19. <https://www.sussex.ac.uk/affiliates/halophytes/index.php>. Accessed 02 Oct 2019.
- Fernández-Pascual, E., Mattana, E., & Pritchard, H. W. (2019). Seeds of future past: Climate change and the thermal memory of plant reproductive traits. *Biological Reviews*, *94*(2), 439–456.
- Finch-Savage, W. E., & Leubner-Metzger, G. (2006). Seed dormancy and the control of germination. *The New Phytologist*, *171*(3), 501–523.

- Flowers, T. J., & Colmer, T. D. (2008). Salinity tolerance in halophytes. *The New Phytologist*, 179, 945–963.
- García-Huidobro, J., Monteith, J. L., & Squire, G. R. (1982). Time, temperature and germination of pearl millet (*Pennisetum typhoides* S. & H.). I. Constant temperature. *Journal of Experimental Botany*, 33, 288–296.
- Gomes, S. E. V., de Oliveira, G. M., Araujo, M. N., Seal, C. E., & Dantas, B. F. (2019). Influence of current and future climate on the seed germination of *Cenostigma microphyllum* (Mart. ex G. Don) E. Gagnon & G. P. Lewis. *Folia Geobotanica*, 54, 19–28.
- Guja, L., Wuhrer, R., Moran, K., Dixon, K. W., Wardell-Johnson, G., & Merritt, D. J. (2013). Full spectrum X-ray mapping reveals differential localization of salt in germinating seeds of differing salt tolerance. *Botanical Journal of the Linnean Society*, 173(1), 129–142.
- 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.
- Gummerson, R. J. (1986). The effect of constant temperatures and osmotic potentials on the germination of sugar beet. *Journal of Experimental Botany*, 37, 729–741.
- Kashif, M. H., Tang, D., Li, Z., Wei, F., Liang, Z., & Chen, P. (2020). Comparative cytological and gene expression analysis reveals potential metabolic pathways and target genes responsive to salt stress in Kenaf (*Hibiscus cannabinus* L.). *Journal of Plant Growth Regulation*. <https://doi.org/10.1007/s00344-019-10062-7>.
- Khan, M. A., Weber, D. J., & Hess, W. M. (1985). Elemental distribution in seeds of the halophytes *Salicornia pacifica* var. *utahensis* and *Atriplex canescens*. *American Journal of Botany*, 72(11), 1672–1675.
- Kranner, I., & Seal, C. E. (2013). Salt stress, signalling and redox control in seeds. *Functional Plant Biology*, 40(9), 848–859.
- 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.
- 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(1), 31–59.
- Matias, J. R., Ribeiro, R. C., Aragão, C. A., Dantas, B. F., & de Araújo, G. G. L. (2015). Physiological changes in osmo and hydroprimed cucumber seeds germinated in biosaline water. *Journal of Seed Science*, 37(1), 7.
- Nichols, P. G. H., Malik, A. I., Stockdale, M., & Colmer, T. D. (2009). Salt tolerance and avoidance mechanisms at germination of annual pasture legumes: Importance for adaptation to saline environments. *Plant and Soil*, 315, 241.
- Osakabe, Y., & Osakabe, K. (2017). Genome editing to improve abiotic stress responses in plants. In *Progress in molecular biology and translational science* (Vol. 149, pp. 99–109). Cambridge, MA: Academic.
- Poljakoff-Mayber, A., Somers, G. F., Werker, E., & Gallagher, J. L. (1994). Seeds of *Kosteletzkya virginica* (Malvaceae): Their structure, germination, and salt tolerance. II. Germination and salt tolerance. *American Journal of Botany*, 81, 54–59.
- Porceddu, M., Mattana, E., Pritchard, H. W., & Bacchetta, G. (2013). Thermal niche for in situ seed germination by Mediterranean mountain streams: Model prediction and validation for *Rhamnus persicifolia* seeds. *Annals of Botany*, 112(9), 1887–1897.
- Porceddu, M., Mattana, E., Pritchard, H. W., & Bacchetta, G. (2017). Dissecting seed dormancy and germination in *Aquilegia barbaricina*, through thermal kinetics of embryo growth. *Plant Biology*, 19(6), 983–993.
- Rasheed, A., Nisar, F., Gul, B., Khan, M. A., & Hameed, A. (2019). Ecophysiology of seed heteromorphism in halophytes: An overview. In M. Hasanuzzaman, S. Sergey Shabala, & M. Fujita (Eds.), *Halophytes and climate change: Adaptive mechanisms and potential uses* (pp. 104–114). Wallingford: CABI.

- Royal Botanic Gardens, Kew. (2016). The state of the world's plants report – 2016. Royal Botanic Gardens, Kew. <https://stateoftheworldsplants.org/2016/>
- Saatkamp, A., Cochran, A., Commander, L., Guja, L. K., Jimenez-Alfaro, B., Larson, J., Nicotra, A., Poschlod, P., Silveira, F. A., Cross, A. T., & Dalziel, E. L. (2019). A research agenda for seed-trait functional ecology. *The New Phytologist*, 221(4), 1764–1775.
- Saleki, R., Young, P. G., & Lefebvre, D. D. (1993). Mutants of *Arabidopsis thaliana* capable of germination under saline conditions. *Plant Physiology*, 101(3), 839–845.
- Schaeffer-Novelli, Y., Soriano-Sierra, E. J., do Vale, C. C., Bernini, E., Rovai, A. S., Pinheiro, M. A. A., Schmidt, A. J., de Almeida, R., Coelho Júnior, C., Menghini, R. P., Martinez, D. I., Abuchahla, G. M. O., Cunha-Lignon, M., Charlier-Sarubo, S., Shirazawa-Freitas, J., & Cintrón-Molero, G. (2016). Climate changes in mangrove forests and salt marshes. *Brazilian Journal of Oceanography*, 64(spe2), 37–52.
- Seal, C. E., Daws, M. I., Flores, J., Ortega-Baes, P., Galíndez, G., León-Lobos, P., Sandoval, A., Ceroni Stuva, A., Ramírez Bullón, N., Dávila-Aranda, P., Ordoñez-Salanueva, C. A., Yáñez-Espinosa, L., Ulián, T., Amosso, C., Zubani, L., Torres Bilbao, A., & Pritchard, H. W. (2017). Thermal buffering capacity of the germination phenotype across the environmental envelope of the Cactaceae. *Global Change Biology*, 23(12), 5309–5317.
- 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.
- Shahid, S. A., Zaman, M., & Heng, L. (2018). *Soil salinity: Historical perspectives and a world overview of the problem*. Cham: Springer.
- Song, J., Feng, G., Tian, C., & Zhang, F. (2005). Strategies for adaptation of *Suaeda physophora*, *Haloxylon ammodendron* and *Haloxylon persicum* to a saline environment during seed germination stage. *Annals of Botany*, 96, 399–405.
- Tobe, K., Zhang, L. P., Qiu, G. Y. Y., Shimizu, H., & Omasa, K. (2001). Characteristics of seed germination in five non-halophytic Chinese desert shrub species. *Journal of Arid Environments*, 47, 191–201.
- Ungar, I. A. (1978). Halophyte seed germination. *The Botanical Review*, 44(2), 233–264.
- Ungar, I. A. (1988). Effects of the parental environment on the temperature requirements and salinity tolerance of *Spergularia marina* seeds. *Botanical Gazette*, 149(4), 432–436.
- Vahabinia, F., Pirdashti, H., & Bakhshandeh, E. (2019). Environmental factors' effect on seed germination and seedling growth of chicory (*Cichorium intybus* L.) as an important medicinal plant. *Acta Physiologiae Plantarum*, 41(2), 27.
- Walters, C., Berjak, P., Pammenter, N., Kennedy, K., & Raven, P. (2013). Preservation of recalcitrant seeds. *Science*, 339(6122), 915–916.
- Wang, L., Huang, Z., Baskin, C. C., Baskin, J. M., & Dong, M. (2008). Germination of dimorphic seeds of the desert annual halophyte *Suaeda aralocaspica* (Chenopodiaceae), a C4 plant without Kranz anatomy. *Annals of Botany*, 102(5), 757–769.
- Wang, L., Baskin, J. M., Baskin, C. C., Cornelissen, J. H. C., Dong, M., & Huang, Z. (2012). Seed dimorphism, nutrients and salinity differentially affect seed traits of the desert halophyte *Suaeda aralocaspica* via multiple maternal effects. *BMC Plant Biology*, 12(1), 170.
- Wijayasinghe, M. M., Jayasuriya, K. G., Gunatilleke, C. V. S., Gunatilleke, I. A. U. N., & Walck, J. L. (2019). Effect of salinity on seed germination of five mangroves from Sri Lanka: Use of hydrotime modelling for mangrove germination. *Seed Science Research*, 29(1), 55–63.
- Yang, F., Yang, X., Baskin, J. M., Baskin, C. C., Cao, D., & Huang, Z. (2015). Transgenerational plasticity provides ecological diversity for a seed heteromorphic species in response to environmental heterogeneity. *Perspectives in Plant Ecology, Evolution and Systematics*, 17(3), 201–208.
- Yokoishi, T., & Tanimoto, S. (1994). Seed germination of the halophyte *Suaeda japonica* under salt stress. *Journal of Plant Research*, 107, 385–388.

- Zhang, H. X., Irving, L. J., McGill, C., Matthew, C., Zhou, D. W., & Kemp, P. (2010). The effects of salinity and osmotic stress on barley germination rate: Sodium as an osmotic regulator. *Annals of Botany*, *106*, 1027–1035.
- Zhang, H., Irving, L. J., Tian, Y., & Zhou, D. (2012). Influence of salinity and temperature on seed germination rate and the hydrotimic model parameters for the halophyte, *Chloris virgata*, and the glycophyte, *Digitaria sanguinalis*. *South African Journal of Botany*, *78*, 203–210.
- Zhang, A., Liu, Y., Wang, F., Li, T., Chen, Z., Kong, D., Bi, J., Zhang, F., Luo, X., Wang, J., & Tang, J. (2019). Enhanced rice salinity tolerance via CRISPR/Cas9-targeted mutagenesis of the OsRR22 gene. *Molecular Breeding*, *39*, 47.