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RESEARCH ARTICLE

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Seed Germination Responses of Dimorphic Seeds in *Atriplex sagittata* under Light, Salinity and Storage Conditions

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ABSTRACT. *Atriplex sagittata* Borkh. is an annual herbaceous plant belonging to the family Amaranthaceae with a wide geographical distribution. Like other *Atriplex* species, *A. sagittata* produces dimorphic seeds, brown and black, that differ in size and morphology. To assess the germination responses of these dimorphic seeds under different environmental conditions, the effects of light, salinity and storage conditions were investigated. Following collection, the seeds were stored for two years under two different conditions: +4 °C and +24 °C. After, the seeds were exposed to different salinity levels. To test the effect of light on germination, parallel dark treatments were included as controls. Germination assays revealed that storage conditions had no statistically significant effect, while light increased the germination rate of black seeds. In response to increasing salinity concentrations (50, 100, 200, 300, 400, 500 mM), the inhibitory effect of salt was first observed at 400 mM for brown seeds and at 50 mM for black seeds. Overall, brown seeds exhibited much higher germination rates and greater salt tolerance compared to black seeds. Mechanical scarification of black seeds demonstrated that their dormancy is mechanically imposed.

Keywords: *Atriplex sagittata, bet-hedging, germination, salinity, seed dimorphism*

INTRODUCTION

Seed heteromorphism is an adaptation that enhances the ability of species to disperse and establish in different habitats [1]. This adaptation is associated with a risk-spreading, bet-hedging strategy and is based on the production of seeds of different sizes, shapes or colours (morphs in general) by the same individual [2]. In addition to differences on the morphological level, seeds also vary in several other traits such as maturation time, endosperm content, and testa thickness [3]. The variation in traits like these results in distinct dispersal and germination requirements among morphs. This enables populations to persist under fluctuating environmental stresses by buffering against spatial and temporal variability [4–6].

Species with seed heteromorphism occur predominantly in xeric habitats where environmental unpredictability is a defining feature [7]. By spreading the risk of recruitment failure across time and space, heteromorphic seeds increase their chances of survival in unpredictable and variable habitat conditions [2]. Although intermediate forms may occur, many species in such habitats typically generate one seed morph that is more dormant than the other [3]. This strategy not only helps maintain the population in the already colonized habitat but also enables the establishment of new populations over long distances [2]. Seeds with lower dormancy generally contain more nutrient reserves, so they ensure the stability and expansion of the population by rapidly producing new individuals near the parent plant. In contrast, the dormant seeds delay germination, contributing to the formation of persistent soil seed banks that safeguard recruitment opportunities in future seasons [3,8]. Therefore, whether for dispersal to new habitats or for the maintenance of existing populations, the morphologically advantageous seed types germinate under specific environmental conditions, allowing the species to sustain its life cycle. In unpredictable habitats like deserts where favourable conditions may not occur for several seasons, annual plants gain a certain level of survival even in unfavourable years through heteromorphic seeds. Thus, this mechanism secures the long term health of populations and provides a buffer against periodic fluctuations in environmental conditions [1].

Seed heteromorphism has been documented in more than twenty plant families, including Asteraceae, Poaceae, and Brassicaceae [9]. This phenomenon is considered an adaptive mechanism that enhances the survival of species under stressful environmental conditions such as irregular rainfall regimes, high light intensity and salinity. From this perspective, in families rich in halophytic taxa like Amaranthaceae, this phenomenon is particularly notable. This is especially evident within the genera such as *Arthrocnemum*, *Atriplex*, *Chenopodium*, *Salicornia*, *Salsola*, *Spergularia*, and *Suaeda*, which successfully colonize saline and degraded habitats [7,10–14]. The genus *Atriplex* is particularly noteworthy for exhibiting both fruit (heterocarpy) and seed heteromorphism, as well as their remarkable species diversity [15]. With approximately 300 species worldwide, *Atriplex* includes annual or perennial herbs, subshrubs and shrubs [16]. Most species of *Atriplex* are well adapted to arid, saline or degraded habitats. In Türkiye, *Atriplex* is represented by 20 taxa, comprising 18 species and 2 subspecies. The genus is present in 48 provinces, typically inhabiting fields and roadsides, barren fields, ruderal habitats and salt steppes, ranging from 5 to 2000 meters above sea level [17].

Several *Atriplex* species show heteromorphism at both the fruit and seed levels. One of the most striking examples is *Atriplex sagittata*, which produces dimorphic seeds that differ in both morphology and ecological function in addition to its polymorphic fruit types [18]. One seed morph is comma-shaped, light green to light brown in colour (brown morph hereafter), and measures approximately 2.0-4.5 × 2.0-4.0 mm. The second morph is round, black (black morph hereafter), glossy, with dimensions of 1.60-2.75 × 1.50-2.50 mm (Fig. 1) [19].

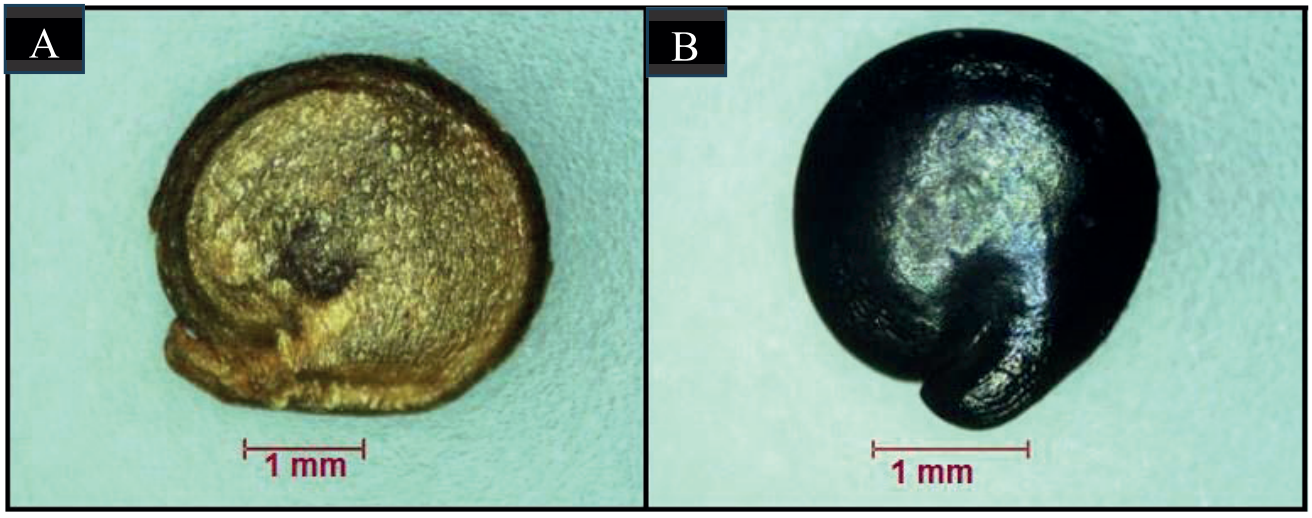


Figure 1: Dimorphic seeds of A. sagittata. Brown morph (A), black morph (B) [19].

Previous studies on *A. sagittata* have primarily focused on the relationship between fruit polymorphism and germination or seed bank dynamics [8,15,18,20,21]. However, these works have largely adopted a fruit-centered approach, with relatively few comprehensive analyses examining the combined effects of multiple environmental stress factors, such as cold-induced dormancy, light, and salinity on seed germination.

To address this gap, this study aims to provide a more integrative understanding of the ecological and physiological adaptation mechanisms of *A. sagittata* by evaluating the effects of different environmental parameters on seed germination. This approach offers new insights into how seed dimorphism contributes to the species' persistence and colonization capacity under variable and stressful habitat conditions.

MATERIALS AND METHODS

Seed Material and Pre-Treatment

Mature fruits of A. sagittata used in this study were collected randomly from ruderal habitats at Ankara University, Faculty of Agriculture (39.96317, 32.86052), on 3 November 2022. Until the experiments, the seeds were stored within their intact pericarps at two different conditions of +4 °C (refrigerated) and +24 °C (ambient laboratory conditions) to test if storage conditions influence germination. In both treatments, seeds were kept in permeable paper bags to ensure gas exchange and prevent moisture accumulation. While the storage environments were non-controlled, they typically maintained a low ambient relative humidity (estimated at 20-40%). Prior

to germination experiments, seeds were manually separated from the fruit structures and categorized based on their storage temperature and morphotypes as brown and black.

For surface sterilization, seeds were immersed in a 1% sodium hypochlorite (NaClO) solution for 5 minutes, followed by two rinses with distilled water for 1 minute to eliminate any residual sterilization solution.

Germination Experiments

To assess salt tolerance, NaCl solutions were prepared at concentrations of 0 (control), 50, 100, 200, 300, 400 and 500 millimolar (mM). Then, seeds were placed on pre-autoclaved sterile filter papers in 100 × 20 mm Petri dishes, with 25 seeds per dish and 3 replicates per treatment. Each dish was moistened with 4 mL of either distilled water (control) or the corresponding NaCl solutions, then sealed with parafilm to prevent moisture loss. To test the effect of light on germination, a parallel set of Petri dishes for control groups was wrapped in two layers of opaque black plastic film to create complete darkness. All dishes were incubated in a controlled growth chamber under 12/12-hour light/dark photoperiod and a temperature regime of 22/12 °C. Illumination was provided by five white fluorescent lamps (Sylvania Standard T8 30W/765, maintaining a light intensity of approximately 100 µmol m^{-2} s^{-1} at the shelf level.

Germination Monitoring and Data Collection

Germination was monitored at two-day intervals. Seeds were considered germinated when the radicle had protruded to 1 mm, after which they were removed from the Petri dishes under sterile conditions. The experiment was terminated after 21 days. For the recovery assessment, non-germinated seeds were rinsed twice with distilled water for 1 minute and re-incubated under the same conditions for an additional 21 days.

In addition to final germination percentages, germination speed was quantified using the Germination Rate Index (GRI) following Kader's work as below (Eqn. 1) [22].

$$\mathrm{GRI} = \sum_{i=1}^{n} \left(\frac{G_i}{i}\right)$$

Eqn 1: *Germination Rate Index Formula, proposed by Kader (2005) [22]. G_i is the number of seeds germinated on i^{th} day.*

Mechanical Scarification

To evaluate whether dormancy in black seeds was caused by physical seed coat impermeability, a mechanical scarification treatment was applied. The seed coats of black morphs were gently abraded with P220 grade sandpaper until the endosperm was just visible. Scarified seeds were then subjected to the same sterilization and germination procedures as described above.

Imbibition Test

An imbibition test was conducted to assess water uptake capacity of both seed morphs. One hundred seeds from each morph were randomly selected, and their initial weights recorded using an analytical balance. Seeds were then placed in microcentrifuge tubes containing distilled water. After 24 hours, excess surface moisture was gently removed, and the seeds were re-weighed. The imbibition percentage was calculated using the formula below.

$$Imbibition\ Percentage = \left(\frac{Final\ weight - Initial\ weight}{Initial\ weight}\right) \times 100$$

Eqn 2: *Imbibition percentage formula*

Statistical Analyses

Germination data consisted of bounded proportions with frequent zero values and highly unequal distributions among groups (including cases approaching 0% and 100% germination). Assumptions of normality and homogeneity of variances were evaluated using Shapiro-Wilk and Levene's tests, respectively. To meet these assumptions, germination percentages were arcsine square-root transformed prior to analysis. When assumptions were met, differences among groups were analyzed using one-way ANOVA followed by Tukey's HSD post-hoc test. When assumptions were violated ($P < 0.05$), the non-parametric Kruskal–Wallis test was applied, followed by Dunn's post-hoc test with Bonferroni correction. Because both parametric and non-parametric approaches yielded consistent conclusions regarding statistical significance, ANOVA results are primarily presented to facilitate ease of comparison across factors. All analyses were performed using SPSS v27.0.

RESULTS AND DISCUSSION

The results of the experiments demonstrated that seed heteromorphism in *A. sagittata* constitutes a sophisticated bet-hedging strategy. The brown and black morphs exhibited fundamentally different germination behaviors, dormancy mechanisms and environmental responses, which are statistically significant (Table 1).

Table 1: ANOVA results of the germination assays. (*: Statistically significant, **: could not be calculated because all seeds germinated in all groups.)

	Black Morphs				Brown Morphs			
	df	***Mean Sq***	***F***	***Sig.***	***df***	***Mean Sq***	***F***	***Sig.***
Light	1	0,109	11,361	**0,005***	1	0,000	- **	-**
Salinity	6	0,067	14,167	**<0,001***	6	1,513	385,297	**<0,001***
Storage Conditions	1	0,045	4,042	0,091	1	0,000	- **	- **
Salinity x Storage	6	101,601	3,862	**0,004***	6	6,619	3,055	,014

Divergent Germination Strategies and the Role of Light

The germination strategies of the two seed morphs were fundamentally distinct, confirming that heteromorphism is a primary driver of population dynamics. The results showed a highly significant difference in their germination rates ($F = 388.186$, $p < 0.001$), whereas post-dispersal storage conditions had no significant effect ($p > 0.05$). This indicates that the observed differences are intrinsic to the morphs themselves (Fig. 2).

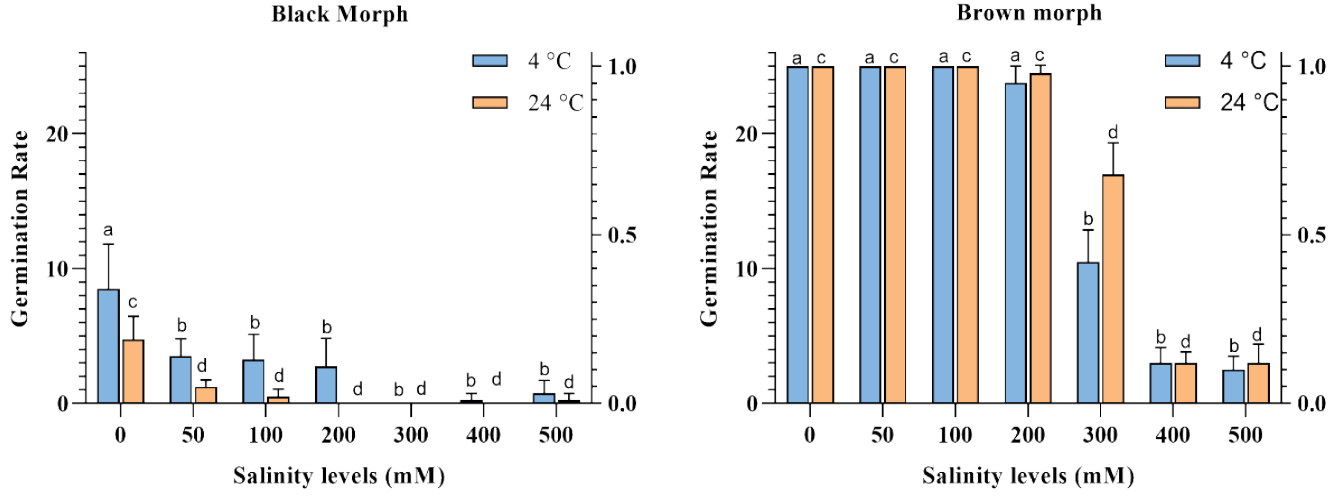


Figure 2: Salinity tolerance assay results.

A key divergence was the morphs' response to light (Fig. 3). Brown morphs germinated regardless of light exposure, which is characteristic of non-dormant, opportunistic strategists. In contrast, black morphs were photoblastic to a degree, with germination significantly enhanced by the presence of light ($F = 11.361$, $p < 0.05$). This shows light is a crucial environmental cue for dormancy release in the dormant morph, a well-documented phenomenon in halophytes that ensures germination only when seeds are near the soil surface [12,21,23–26].

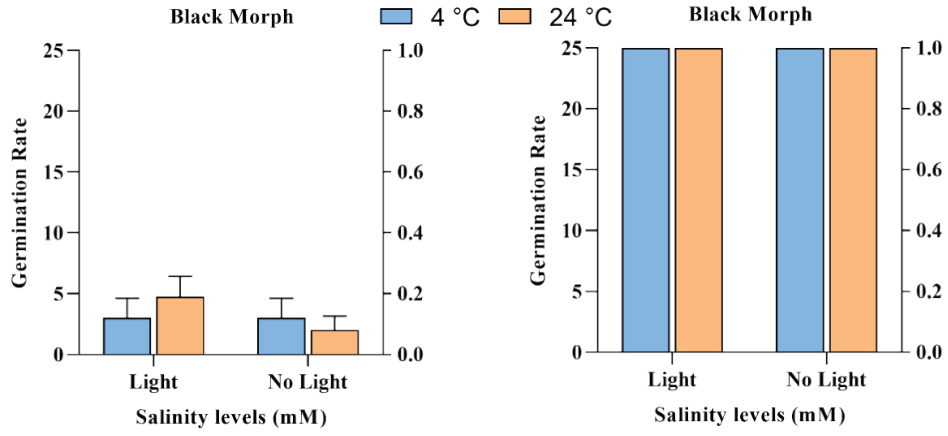
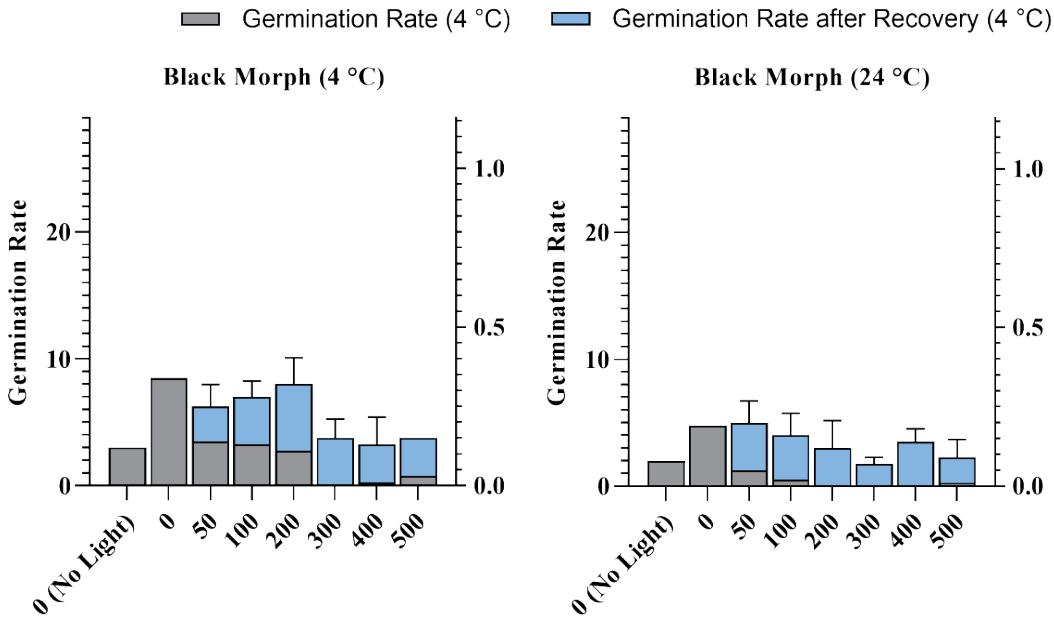


Figure 3: Germination Results of control groups

Differential Salinity Tolerance and Recovery Capacity

Salinity acted as a strong inhibitory factor for both morphs, while their tolerance thresholds differed. Germination of the black morphs was suppressed even at 50 mM NaCl. In contrast, the brown morph maintained high germination percentages up to 300 mM, with a gradual decline only at higher concentrations (Fig. 2). This pattern indicates that brown morphs are not only non-dormant but also possess a greater physiological tolerance to salinity stress. This allows brown morphs to germinate rapidly, whenever the conditions are favourable, even in moderately saline soil. Recovery assays confirmed that inhibition of germination by salinity was largely reversible, as both morphs remained viable and germinated at different rates once salinity stress was removed (Fig. 4). This high recovery capacity suggests that salinity is acting mostly as a temporary constraint rather than a toxic one, allowing the species to persist through fluctuating salinity. For the black morphs, high sensitivity to salinity likely complements their light requirement, restricting germination to early spring in saline habitats, when increased precipitation dilutes surface salts and light cues signal favorable microsites [27,28]. This contrast illustrates a divergent germination strategy between morphs, supporting a bet-hedging mechanism that enhances population persistence under variable conditions.



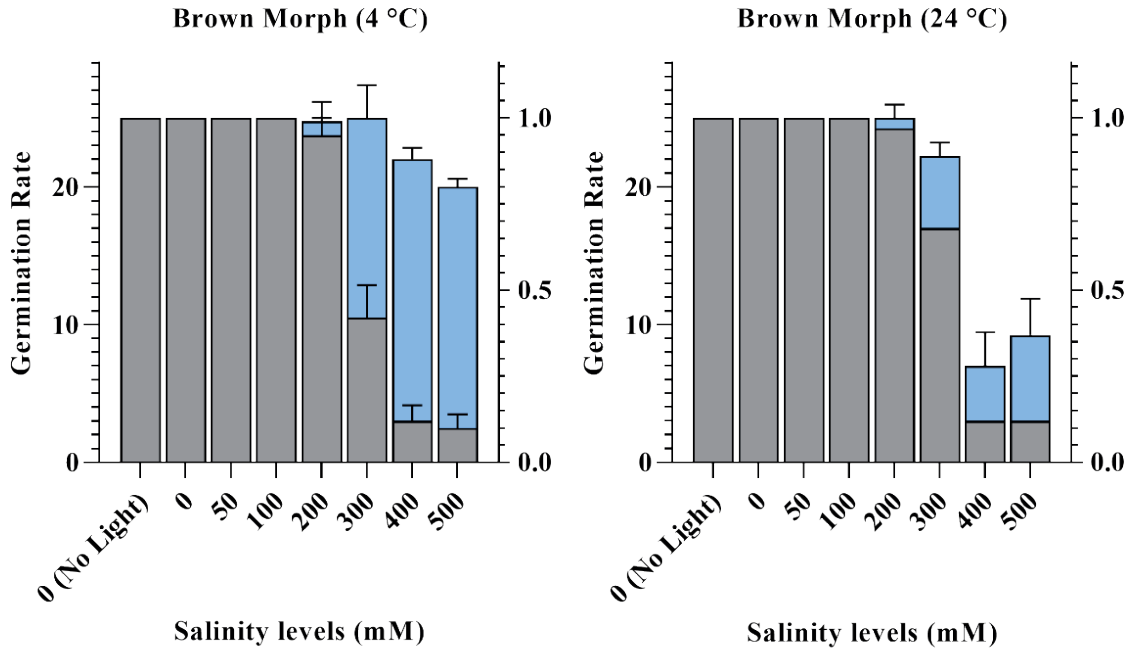


Figure 4: Recovery results of all groups

Analysis of germination speed via the Germination Rate Index (GRI) revealed that the germination velocity of brown morphs was significantly reduced at 100 mM NaCl, even though final germination percentages remained high (Fig. 5). This shows that the early physiological processes of germination are more sensitive to osmotic stress than the overall germination capacity, a critical consideration for seedling establishment in naturally fluctuating saline environments.

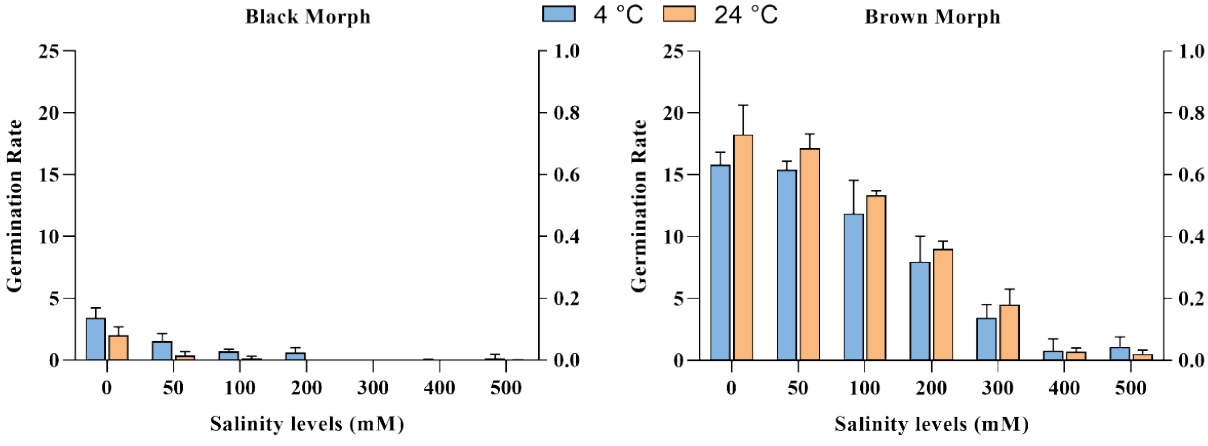


Figure 5: Germination Rate Index (GRI)

Physical Dormancy is the Primary Mechanism in Black Seeds

The dormancy mechanism in black morphs was identified as physical dormancy (PD), following the classification proposed by Baskin & Baskin [3]. Mechanical scarification resulted in the rapid and complete germination of all previously dormant black morphs within two days. This immediate response confirms that the primary barrier to germination

is the functionally impermeable testa, preventing sufficient water uptake to initiate germination.

Imbibition tests directly corroborated this finding, revealing a big difference between morphs. Brown morphs exhibited nearly four times greater water uptake than black morphs over 24 hours (Table 2). This can be attributed to structural differences in the seed coat, such as the presence of suberized layers, phenolic compounds like tannins, or heavily lignified palisade layers [3,29–31]. Testa-mediated dormancy mechanism can be seen as an adaptive strategy within the species of the family Amaranthaceae [7,29]. The reduced permeability in dormant morphs is documented in other *Atriplex* species and successful dormancy release via acid scarification of the testa in *Atriplex inflata* provides direct evidence for a physical barrier controlling water uptake [32,33]. This barrier is likely also a bet-hedging strategy; the dormant black seeds can persist in the soil seed bank, waiting until slow, cumulative processes, such as mechanical abrasion from soil movement or gradual temperature shifts that will overcome the testa impermeability and trigger germination.

Table 2: Imbibition results

	Dry Weight (g)		Imbibed Weight (g)		Water Intake (%)	
	24 °C	**4 °C**	**24 °C**	**4 °C**	**24 °C**	**4 °C**
Black Morphs	0,00180	0,00174	0,00221	0,00217	22,778%	24,713%
Brown Morphs	0,00386	0,00438	0,00732	0,00779	89,637%	77,854%

A Hierarchical Model for Dormancy Release

The germination behavior of black seeds suggests a sophisticated, multi-stage dormancy release process. After-ripening, a physiological process occurring during dry storage that gradually reduces primary dormancy and increases the seed's responsiveness to environmental cues, may function as a primary fundamental prerequisite [33,34]. Once this physiological preconditioning has occurred, germination appears to be regulated by two key environmental factors. Specifically, the high sensitivity to salinity may serve to restrict germination until seasonal precipitation sufficiently lowers soil salinity to tolerable levels. Subsequently, light could act as a final "safe site" signal, facilitating germination primarily when seeds are situated near the soil surface [35]. While this hypothesized sequence aligns with our observations of deferred germination, further physiological studies are required to confirm the specific transitions between these dormancy states.

CONCLUSION

This study elucidates the adaptive significance of seed heteromorphism in *Atriplex sagittata*. The species produces two distinct seed types that employ complementary strategies; brown seeds act as an opportunistic morph, germinating rapidly to exploit favourable conditions, while black seeds function as a dormant, soil seed bank-oriented morph, whose germination is carefully gated by time and environmental cues. This dual strategy buffers populations against temporal and spatial heterogeneity, maximizing long-term persistence in the unpredictable arid and saline habitats which *Atriplex* characteristically occupies. The different responses to light, salinity, and the clear mechanism of physical dormancy provide a physiological basis for a classic bet-hedging strategy.

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CONFLICT OF INTEREST

The authors declared that there is no conflict of interest.

AUTHORSHIP CONTRIBUTIONS

Concept: İ.B., A.E.Y., Design: İ.B., A.E.Y., Data Collection or Processing: N.N.Ö., B.A., Analysis or Interpretation: S.B., N.N.Ö., B.A., A.E.Y., Literature Search: S.B., N.N.Ö., B.A., Writing: S.B., A.E.Y

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