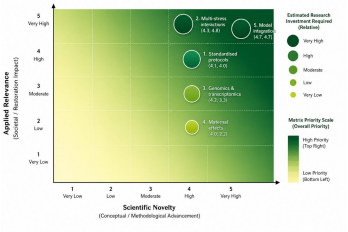

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Recovery germination as an overlooked dimension of seed responses to abiotic stress

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Abstract

Upon the alleviation of abiotic stress, seeds can resume development, a distinct physiological phenomenon termed recovery germination. While the inhibitory effects of salinity, extreme thermal regimes, heavy metals, and osmotic stress on initial germination are extensively documented, the reverse trajectory, the transition from stress-induced inhibition to successful germination post-relief, remains critically understudied. This study advances the hydrotime framework for post-stress kinetics, while evaluating the current state of knowledge across four major domains: salinity, heat, heavy metals and osmotic recovery. We further examine the ecological significance of recovery germination as an adaptive strategy underpinning persistence in fluctuating abiotic environments. Evidence is synthesized from experimental studies, population-level models, and field ecology to establish a conceptual framework for recovery germination as a measurable, heritable, and ecologically meaningful seed trait. We identify key knowledge gaps: the absence of standardized recovery germination protocols, the scarcity of multi-stress interaction studies, and the underrepresentation of recovery germination in predictive vegetation models. We propose a research agenda to address these deficiencies. The recovery germination concept has significant implications for crop improvement under climate change, ecological restoration, and seed bank management.

Keywords

Seed ecophysiology; Germination recovery; Osmotic stress; Hydrotime model; Seed ecology; Drought

Contents

1 Introduction

Seed germination is the most environmentally sensitive phase in the plant life cycle, defining the spatiotemporal window within which a new individual can establish itself (Bewley et al. 2013; Kheloufi 2022). For more than six decades, experimental seed biology has focused on how abiotic stressors suppress germination, including salinity (Bradford 1990; Katembe et al. 1998; Kheloufi and Mansouri 2026), supraoptimal temperatures (Argyris et al. 2010), osmotic stress (Welbaum and Bradford 1991), heavy-metal contamination (Seregin and Kozhevnikova 2009), and combinations of these (Pirasteh-Anosheh et al. 2015). Over the same period, an equally productive line of enquiry has examined how defined stimuli promote germination, notably light acting through phytochrome, nitric-oxide donors, and smoke-derived karrikins (Flematti et al. 2004; Nelson et al. 2008; Costa et al. 2016; Khosla et al. 2020). Together, these two literatures establish that germination output reflects the net balance between inhibitory and promotive signals. Recovery germination captures precisely this balance, since it measures what a seed does once an inhibitor is withdrawn. Running through this body of work, however, is a pervasive but rarely stated assumption. Stress-exposed seeds are held to be fated either to germinate at reduced rates and percentages or to remain quiescent until conditions become permissive.

What has remained largely neglected is the process by which seeds recover their germinative capacity following the removal or attenuation of stress, a scenario that is not only ecologically realistic but constitutes, in many environments, the predominant sequence of events. Coastal salt marshes experience episodic freshwater flushing events. Desert soils alternate between desiccation and rainfall pulses. Agricultural fields subject to saline irrigation may receive leaching rains. Riparian zones undergo periodic flooding and exposure of heavy-metal-contaminated sediments, followed by dilution events. In each of these contexts, seeds physiologically inhibited by

abiotic stress are abruptly returned to permissive conditions, and their germinative response to this reversal carries profound consequences for community assembly and ecosystem function.

Despite this ecological ubiquity, the phenomenon of "recovery germination," defined here as the resumption and completion of germination following the transfer of previously stressed seeds to optimal or near-optimal conditions, has no dedicated, comprehensive review in the seed biology literature. Isolated experimental studies have reported high recovery germination percentages following salinity (Almansouri et al. 2001; Patade et al. 2014) and osmotic treatments (Welbaum and Bradford 1991; Kheloufi and Mansouri 2026), and the priming literature implicitly documents a related phenomenon (Finch-Savage and Footitt 2017). However, these findings have not been conceptually unified, physiologically explained, or ecologically contextualized within a coherent research framework.

2 Defining recovery germination

We propose a formal definition: recovery germination is the proportion of seeds, expressed as a percentage of the original seed lot, that successfully completes germination (defined as radicle protrusion) following transfer from inhibitory stress conditions to conditions permissive for germination. This definition is distinct from: (a) stress-tolerant germination, which refers to germination occurring despite the continued presence of the stressor; (b) seed priming sensu stricto, which involves controlled hydration followed by drying before sowing; and (c) dormancy alleviation, which involves a shift in dormancy status rather than the removal of an external inhibitor (Bewley et al. 2013; Kheloufi 2022; Paparella et al. 2015; Finch-Savage and Footitt 2017).

The Recovery Index (RI) is proposed as a standardized quantitative metric and is calculated as follows:

$$RI = \frac{Grec\ (tr)}{Gcontrol\ (tc)}$$

where *Grec (tr)* is the cumulative recovery germination percentage scored at a designated time-point (tr, days after transfer to permissive conditions) and *Gcontrol (tc)* is the final germination percentage under unstressed control conditions scored at the standard, species-specific endpoint (*tc, days*). Both terms are expressed as percentages of the same initial seed lot, so that *RI* is dimensionless. This formulation explicitly accounts for the kinetic asymmetry between the two phases: *tc* follows standard seed-testing protocols through to a definitive germination plateau, whereas *tr* captures the characteristically accelerated post-stress kinetics. Symbols are defined here at first use and are applied consistently throughout the review; the hydrotime symbols introduced in Sections 6 and 7 are summarized in Table 2.

An RI approaching 1.0 indicates near-complete physiological reversibility of stress effects on germination; values substantially below 1.0 indicate persistent impairment, possibly reflecting irreversible cellular damage, dormancy re-induction, or accelerated ageing. Values exceeding 1.0, which have been reported in some priming-equivalent stress regimes, indicate stress-stimulated enhancement of germination potential, equivalent to a priming memory (Paparella et al. 2015).

Figure 1 brings these elements together: it contrasts the germination time-course under control, persistent-stress, and stress-relieved conditions (panel A), shows how the Recovery Index falls as stress intensity approaches the lethal threshold (panel B), and locates recovery germination alongside the related concepts of stress-tolerant germination and seed priming through the physiological pathways they share (panel C).

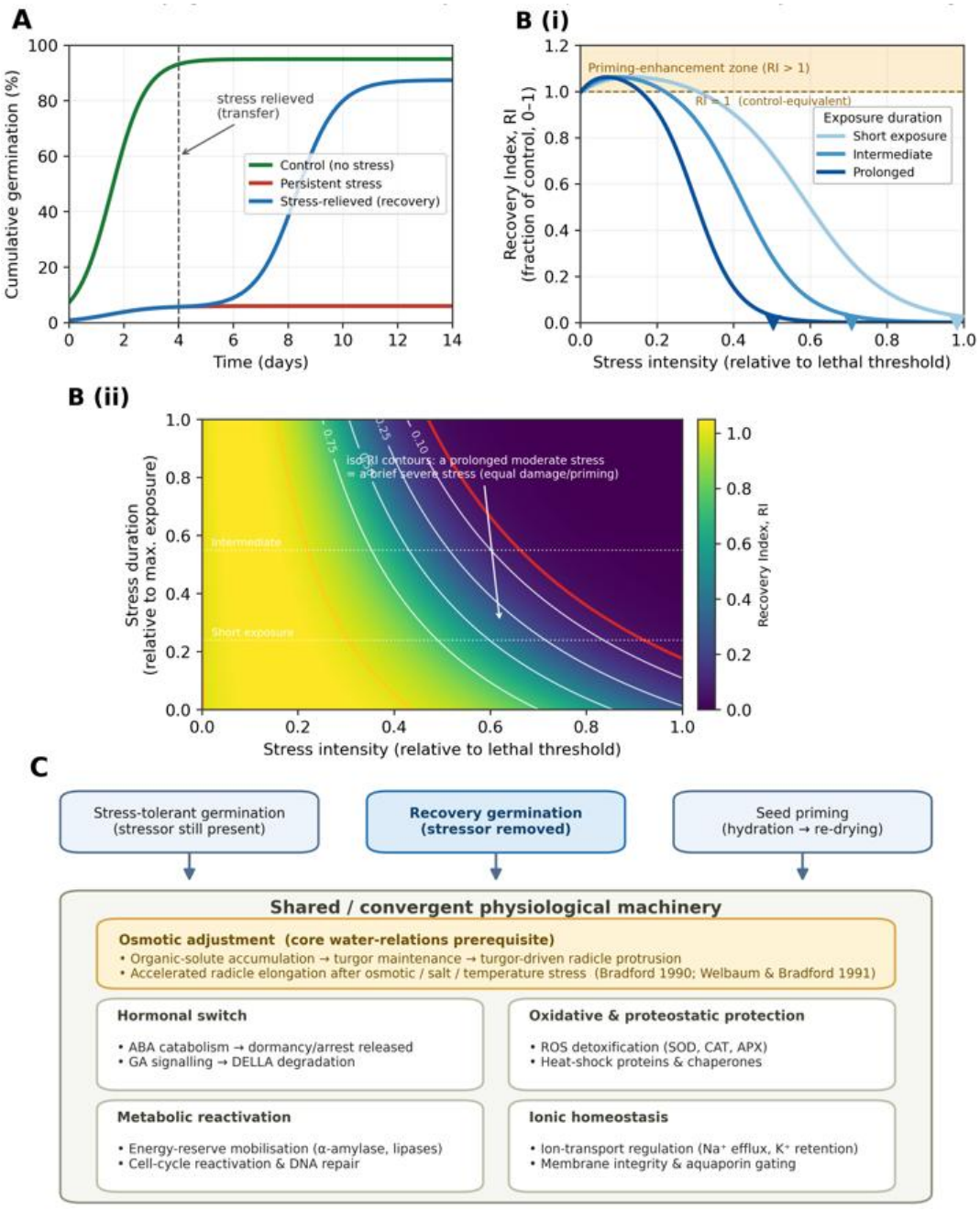

Figure 1. Conceptual framework of recovery germination.

The need for standardized recovery germination metrics has been increasingly acknowledged in the seed science community, yet significant methodological inconsistency persists across published studies. Traditional indices such as FGP (Final

Germination Percentage, %) and MGT (Mean Germination Time) are routinely reported under stress conditions but frequently omit the post-stress recovery phase. This omission conflates seed death with stress-enforced dormancy and systematically underestimates true seed lot viability (Kheloufi and Mansouri 2020; Mansouri and Kheloufi 2024; Kheloufi and Mansouri 2024; Kheloufi and Mansouri 2025; Kheloufi and Mansouri 2026).

To address this gap, a suite of complementary indices has been recently proposed. The Germination Recovery Ratio (SGRR), for instance, quantifies the proportion of lost germination potential restored upon stress removal, with a high SGRR indicating not only reversal of stress-induced dormancy but also possible activation of metabolic pathways that promote rapid subsequent germination and seedling establishment. The RI proposed here aligns conceptually with these developments, extending their scope by normalizing recovery germination against an unstressed control and enabling direct cross-study comparisons independently of baseline germination capacity. The superior discriminatory power of this approach is illustrated by the following example: gibberellin priming of wheat seeds under drought stress achieved a SGRR of 1.004, corresponding to complete germination recovery, versus 0.74 with hydro-priming under identical conditions, a distinction that final germination percentage alone would have obscured (Sedghi 2025).

The interpretation of RI values must account for the temporal dimension of recovery germination, which is rarely considered but critically informative. Seeds that recover germination slowly after stress removal may reflect sub-lethal cellular damage requiring repair, particularly to DNA strand integrity in embryo meristematic cells, before germination can proceed (Tariq et al. 2010). The DNA damage response (DDR) has been identified as an essential component of the germination process, preserving genome integrity of embryo cells during and after stress-induced imbibition (Macovei et al. 2025), and the activation of DDR pathways during stress exposure may partly account for the accelerated recovery germination rate, but not necessarily elevated final percentage, observed in seeds pre-exposed to sub-lethal stress.

The concept of a priming memory underlying RI values exceeding 1.0 now has mechanistic support in epigenetic frameworks. Stress priming can trigger chromatin remodeling and DNA methylation changes that serve as molecular memory imprints, enabling faster transcriptional re-activation of germination programs upon stress removal (Dobránszki et al. 2025). Distinguishing between physiological reversibility (RI near 1.0 with rapid recovery kinetics), stress-stimulated enhancement (RI > 1.0), and persistent impairment (RI << 1.0 with slow or arrested recovery) therefore requires reporting both the final recovery percentage and the germination rate index in the post-stress transfer period, a methodological standard this review advocates adopting universally.

3 Salinity recovery germination

3.1 Physiological basis of salinity-induced germination inhibition

High NaCl concentrations inhibit seed germination through two partially independent mechanisms: (i) an osmotic component attributable to low external water potential (Ψ, expressed in MPa), preventing imbibition; and (ii) an ionic component resulting from Na^+ and Cl^- accumulation within seed tissues, leading to ion toxicity,

disruption of enzyme function, and reactive oxygen species (ROS) overproduction (Hasegawa et al. 2000; Munns and Tester 2008). The relative contribution of each component varies with species, NaCl concentration, and exposure duration. At moderate salinity (< 100 mM NaCl), osmotic effects predominate; at higher concentrations, ion-specific damage becomes increasingly significant (Katembe et al. 1998).

The two components differ markedly in reversibility. The osmotic component is inherently reversible: desalination rapidly restores water potential, allowing imbibition to resume. The ionic component, however, may persist, as accumulated Na^+ and Cl^- must be actively excluded or compartmentalized, a process that depends on the energetic state and membrane integrity of the seed. Consequently, seeds of glycophytes are expected to exhibit lower RI values following prolonged high-salinity exposure compared to halophytes. This divergence is driven by embryo-level traits; while glycophytes lack dedicated ion exclusion mechanisms, halophytes benefit from constitutively expressed vacuolar Na^+/H^+ antiporters and other robust ion homeostasis systems (Flowers and Colmer 2015).

3.2 Recovery germination responses across species

The experimental literature consistently demonstrates that a substantial fraction of germination lost under salinity is recoverable upon desalination. Almansouri et al. (2001) found that durum wheat (*Triticum durum* Desf.) seeds inhibited at 200 mM NaCl achieved 78 to 91% germination upon transfer to distilled water, depending on variety. Patade et al. (2014) reported near-complete recovery (> 90%) in primed sugarcane under 100 mM NaCl stress. Remarkably, halophytes of the genus *Suaeda*, and *Suaeda fruticosa* in particular, have been reported to recover germination almost completely after exposure to salinities well above seawater strength, and in some experiments to germinate faster and to a higher final percentage after salinity release than in the unstressed control, which suggests a stimulatory hardening effect of moderate ionic stress (Gul et al. 2013, 2024).

These divergent glycophyte and halophyte trajectories are summarized in Figure 2, which tracks cumulative germination in durum wheat and *Suaeda fruticosa* under continuous salinity against transfer to distilled water, and reports the corresponding Recovery Index, including the supra-optimal recovery (RI > 1.0) reported for the halophyte.

The pattern of recovery germination strongly modulated by species identity, stress intensity, and the ionic versus osmotic nature of the imposed stress. Seeds of halophytes generally maintain viability even under extreme salinity and recover germination capacity when water potential of the medium increases, a feature considered a key indicator of salt tolerance at the germination stage. Recent work on *Halostachys caspica* Bieb., a perennial Amaranthaceae halophyte of Central Asian saline-alkali soils, confirmed that ungerminated seeds subjected to high salt concentrations exhibited markedly elevated recovery germination percentages upon stress removal (Zhang et al. 2024), corroborating the hypothesis that enforced dormancy rather than seed death underlies inhibition at supraoptimal salinities. Similarly, recovery germination tolerance in *Crithmum maritimum* L. was found to exceed levels previously reported for this species (Martins-Noguerol et al. 2024). These results collectively underscore the need to reassess recovery potential across wider

ranges of conditions and provenances. Collectively, these findings demonstrate that seed viability is far more resilient to ionic stress than germination percentages alone would imply, and that recovery assays constitute an indispensable complement to standard germination metrics in salinity tolerance studies.

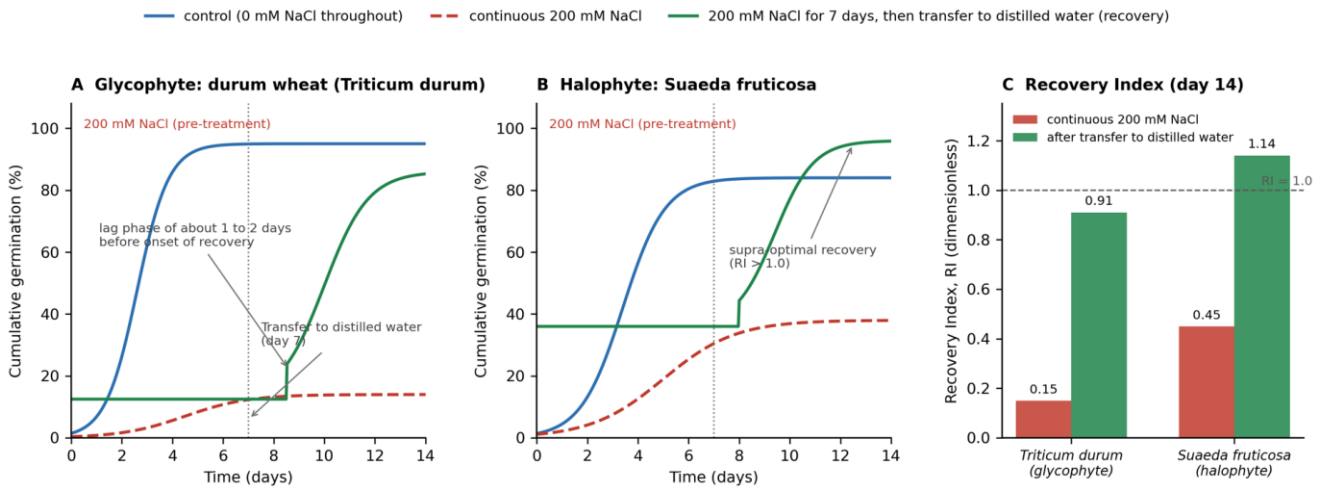

Figure 2. Salinity recovery germination kinetics (original schematic, drawn by the authors). (A) Cumulative germination of a glycophyte (*Triticum durum*) and (B) of an obligate halophyte (*Suaeda fruticosa*) under a control (0 mM NaCl), under continuous exposure to 200 mM NaCl, and after 7 days at 200 mM NaCl followed by transfer to distilled water. (C) Corresponding Recovery Index (RI, dimensionless; RI = Grec(tr)/Gcontrol(tc), Section 2), with the dashed line marking complete reversibility (RI = 1.0). The trajectories are illustrative and are not drawn to scale: they reproduce the direction and the relative magnitude of the responses reported by Almansouri et al. (2001) for durum wheat (78 to 91% recovery germination after 200 mM NaCl), and by Gul et al. (2013, 2024) and Zhang et al. (2024) for halophytes recovering from supraoptimal salinity. No value shown is a measured datum and no statistical comparison is implied.

3.3 Mechanisms of salinity recovery

The five stress domains examined here, together with their principal physiological targets, the recovery metric most relevant to each, and representative study species, are summarized in Table 1 and taken up in turn in the sections that follow.

Upon desalination, recovery germination involves several coordinated processes: (i) Restoration of water potential gradients enabling osmotic imbibition of the embryo and endosperm; (ii) Efflux of accumulated Na^+ via plasma membrane Na^+/H^+ antiporters (SOS1 pathway) and vacuolar sequestration via tonoplast antiporters (NHX1); (iii) Re-activation of antioxidant systems, particularly catalase (CAT), superoxide dismutase (SOD), and ascorbate peroxidase (APX), to neutralize residual ROS produced during the stress phase; (iv) ABA catabolism via CYP707A-family 8′-hydroxylases, releasing the ABA-mediated arrest of germination; and (v) Gibberellin (GA) signaling amplification, promoting DELLA protein degradation and enabling endosperm rupture and testa splitting (Blumwald et al. 2000; Rajjou et al. 2012).

A critical and underexplored question concerns the temporal dynamics of these recovery processes. ROS detoxification constitutes among the most rapid recovery responses (minutes to hours), while ion export and hormonal reprogramming may require days (Hasegawa et al. 2000). This hierarchy of recovery speeds may explain

observations of sigmoidal rather than exponential recovery germination curves in experimental studies, with an initial lag phase followed by rapid germination.

Table 1. Summary of the five major abiotic stress categories covered in this review, with their primary physiological targets, the key germination recovery metric used in each, and the representative study species from which the cited evidence is drawn.

Stress type	Stress agent	Primary physiological target	Key recovery metric	Representative species	Key references
Salinity	NaCl / sea spray	Ion toxicity; osmotic imbalance; ROS overproduction	Final germination % post-desalination	*Suaeda maritima, Triticum durum*	Almansouri et al. 2001; Gul et al. 2013, 2024
High temperature	Supraoptimal thermal regime	Membrane phase transition; protein denaturation; enzyme inactivation	Germination recovery at optimum T after heat shock	*Lactuca sativa, Arabidopsis thaliana*	Argyris et al. 2010; Queitsch et al. 2000; Waters and Vierling 2020
Heavy metals	Cd, Pb, Cr, Cu, As	Enzyme inhibition ; radical damage ; disruption of radicle elongation	Final germination % after metal removal	*Cucurbita pepo, Pinus roxburghii*	Acila et al. 2024; Bibi et al. 2025
Osmotic stress	PEG 6000 ; mannitol	Low water potential; inhibition of imbibition kinetics	Rate and final % post-transfer to water	*Cucumis melo, Lactuca sativa*	Welbaum and Bradford 1991; Bradford 2002
Compound Climatic	NaCl + Extreme heat	Non-additive ABA/ROS signaling saturation; membrane collapse	Factorial recovery interaction coefficients	*Triticum aestivum, Halostachys caspica*	Yu et al. 2024; Zhang et al. 2024

4 Heat stress recovery germination

4.1 Supraoptimal temperature and thermoinhibition

High-temperature stress on germinating seeds can manifest as thermoinhibition (reduced germination percentage without dormancy re-induction) or thermodormancy (induction of dormancy requiring specific release signals) (Argyris et al. 2010; Bewley et al. 2013). The distinction is critical for recovery germination: thermoinhibited seeds retain their full germinative potential and resume germination upon return to optimal temperatures, whereas thermodormant seeds require additional dormancy-breaking treatments. The heat-shock threshold for thermoinhibition typically falls between 35–45°C, depending on species and the specific germination temperature optimum (Bradford 1990).

Heat stress disrupts germination through: (i) phase transitions in membrane lipids, compromising membrane integrity and disrupting proton gradients; (ii) denaturation of thermolabile proteins, including germination-promoting enzymes such as α-amylase; (iii) disruption of the cytoskeleton, impeding cell expansion in the emerging radicle; and (iv) inhibition of gibberellin biosynthesis, arresting DELLA protein degradation. The accumulation of heat shock proteins (HSPs, particularly Hsp70, Hsp90, and small HSPs) serves to buffer these effects through chaperone activity, protecting nascent polypeptides from misfolding (Waters and Vierling 2020).

4.2 Recovery mechanisms after heat stress

Recovery from heat stress involves the coordinated disaggregation of protein aggregates facilitated by Hsp70/Hsp40 chaperone systems and the AAA+ ATPase disaggregase Hsp101 (ClpB in bacteria) (Queitsch et al. 2000). Lipid membrane remodeling, involving adjustment of unsaturated fatty acid composition to restore membrane fluidity at the new (lower) temperature, is accomplished by temperature-sensitive fatty acid desaturases (FADs) (Los and Murata 2004). GA biosynthesis resumes upon temperature reduction, driving rapid progression through germination sub-processes previously arrested by heat.

Figure 3 captures both dimensions of this response: panel A maps final germination as a joint function of the germination-phase (stress) temperature and the recovery temperature *Arabidopsis thaliana*, showing that losses incurred at 40–45 °C are largely recovered on transfer to 22 °C whereas damage beyond roughly 48 °C is not, while panel B sets out the molecular sequence (chaperone-mediated disaggregation, restored GA biosynthesis and signaling, and ABA catabolism) that drives germination once heat stress is removed.

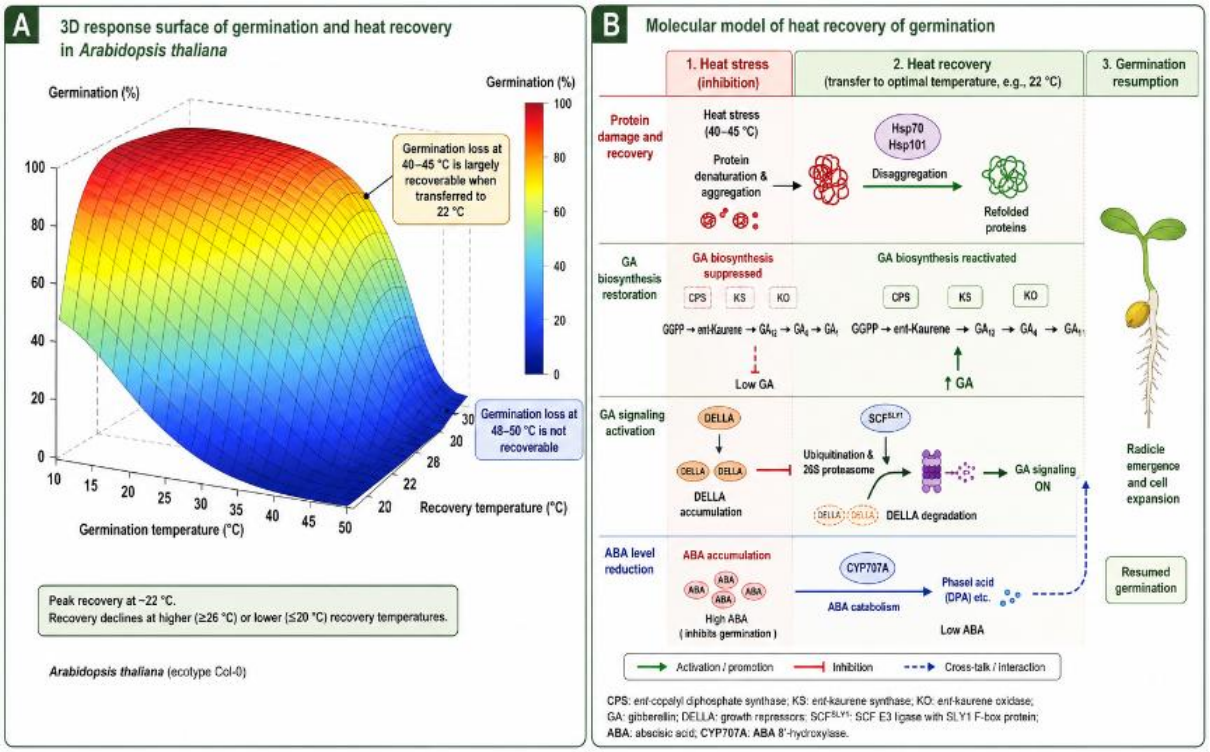

Figure 3. Temperature response and heat recovery model (original schematic, drawn by the authors). (A) Final germination as a joint function of the germination-phase temperature and the recovery temperature. The surface is illustrative: the thermoinhibition window and the recovery thresholds follow the ranges reported for lettuce (Argyris et al. 2010) and for *Arabidopsis thaliana* (Queitsch et al. 2000), and no value shown is a measured datum. (B) Molecular sequence following the relief of heat stress, compiled from Queitsch et al. (2000), Los and Murata (2004) and Waters and Vierling (2020).

A particularly intriguing observation is that brief heat shock treatments (e.g., 40°C for 1 h) can enhance subsequent recovery germination beyond control levels in some species. This may reflect HSP-mediated stabilization of germination-promoting proteins, rendering them more active once stress is removed (Wahid et al. 2007). This observation has potential biotechnological implications: controlled heat priming might improve germination performance in thermally variable agricultural environments.

5 Heavy metal recovery germination

5.1 Mechanisms of heavy metal toxicity in seeds

Heavy metals, including cadmium (Cd), lead (Pb), chromium (Cr), copper (Cu), and arsenic (As), suppress germination through multiple, often synergistic mechanisms. At the biochemical level, these metals competitively displace essential cations (Ca^{2+}, Mg^{2+}, Zn^{2+} etc.) from enzyme active sites, induce lipid peroxidation through Fenton-type reactions, and covalently modify thiol groups in proteins, disrupting redox regulation (Hossain et al. 2012; Meharg and Hartley-Whitaker 2002). At the cellular level, heavy metals impair mitotic activity in the radicle meristem, reducing cell division rates and thus slowing or preventing radicle elongation. At the tissue level, metal accumulation in the seed coat and endosperm can compromise the mechanical weakening of these structures that normally permits radicle protrusion.

The oxidative dimension of heavy metal toxicity during germination has attracted increasing mechanistic study. Heavy metals trigger the overproduction of reactive oxygen species (ROS) through Fenton-type and Haber–Weiss reactions, leading to lipid peroxidation of membrane phospholipids, protein carbonylation, and DNA strand breakage in embryonic tissues (Shoaib and Javaid 2021). In germinating seeds, where the antioxidant defense machinery is only partially reactivated during imbibition, this oxidative burst is particularly damaging. Cadmium and copper stress in *Cucurbita pepo* L. seeds have been shown to reduce glutathione content progressively with increasing metal concentration, while simultaneously elevating glutathione S-transferase activity at high Cd doses, a response pattern indicative of intensifying oxidative load and activation of detoxification conjugation pathways (Acila et al. 2024). The reduction in superoxide dismutase activity observed under both metals further compromises the seed's capacity to scavenge superoxide radicals, leaving embryonic axis cells vulnerable to oxidative damage at a developmental stage when membrane integrity is critical for water uptake and reserve mobilization.

At the hormonal and enzymatic level, heavy metals disrupt the signaling cascades that coordinate reserve mobilization and radicle elongation during germination. Cadmium has been specifically shown to inhibit α-amylase and invertase activities in germinating seeds, thereby impairing the hydrolysis of stored starch and sucrose and depriving the embryo of the soluble sugars required for cell expansion and mitotic activity (He et al. 2008). Concurrently, Cd^{2+} competes with Ca^{2+}, Mg^{2+}, and Fe^{2+} for access to membrane transport proteins (including both non-selective cation channels and active carriers), leading to nutrient imbalances that further compromise metabolic function (Sun et al. 2025). Heavy metal exposure also disrupts the GA/ABA hormonal balance. Elevated endogenous ABA and suppressed GA biosynthesis mimic a dormancy-reinforcing state, delaying or preventing radicle protrusion even under otherwise permissive osmotic conditions (Zuo and Xu 2020). Collectively, these multi-

target effects, oxidative, enzymatic, ionic, and hormonal, explain why heavy metal toxicity at germination is frequently irreversible at concentrations far below those that compromise seed viability outright.

5.2 Recovery germination after heavy metal exposure

The physiological constraints governing heavy metal recovery germination stem directly from the coordination chemistry of toxic divalent and trivalent cations within the seed coat (testa) and endosperm. Unlike monovalent sodium ions Na^+ which are highly soluble and subject to active efflux via plasma membrane Na^+/H^+ antiporters (the SOS1 pathway) upon desalination, heavy metal cations establish stable, immobilized complexes within the seed apoplast (Rekha et al., 2021). Cations such as Cd^{2+}, Pb^{2+}, and Cr^{3+} covalently bind to the negatively charged carboxyl, hydroxyl, and phenolic groups of cell-wall pectins, cellulose, and suberin matrices. This binding triggers an immediate mechanical hardening of the outer seed investment layers, structurally impeding the cell expansion required for radicle protrusion even after external concentrations decrease. Furthermore, sub-lethal heavy metal exposure leaves a persistent biochemical legacy within the storage tissues (Loix et al., 2017). Cadmium exposure significantly down-regulates the activity of crucial hydrolytic enzymes, specifically α-amylase and proteases, within the seed storage tissues (cotyledons and endosperm. This enzymatic impairment halts starch and reserve protein mobilization. Because these intracellular heavy metal fractions are actively sequestered into vacuoles via ATP-binding cassette (ABC) and heavy metal ATPase (HMA) transporters rather than being excreted, the metabolic suppression persists long into the post-stress window (Loix et al., 2017; Rekha et al., 2021). Consequently, recovery assays under heavy metal regimes do not merely evaluate the restoration of water potential gradients, but rather measure the capacity of the embryonic axis to function under a sustained internal toxic load.

Figure 4 sets out both aspects of this behavior: panel A gives dose–response curves for cadmium, lead, and chromium under continuous exposure versus recovery after transfer to clean solution, identifying a recovery threshold for each metal, and panel B outlines the detoxification and redox-restoration machinery, phytochelatin and metallothionein chelation, vacuolar sequestration, and the ascorbate–glutathione cycle, on which any post-exposure recovery depends.

Rigorous experimental designs featuring precise washout-recovery assays, wherein seeds are exposed to a heavy metal solution for a discrete duration, thoroughly rinsed with deionized water or chelating buffers, and subsequently transferred to a metal-free substratum, remain remarkably absent from the published literature. This omission constitutes a major knowledge gap that limits current understanding of post-toxic recovery kinetics. The mechanistic framework outlined above is therefore partly inferential, extrapolated from studies that quantified germination and seedling vigor under continued metal exposure rather than after stress removal. Studies on *Cucurbita pepo* L. (Acila et al., 2024) and *Pinus roxburghii* Sarg. (Bibi et al., 2025) for instance, reported final germination percentages of 86–93% and comparably stable values across Cd, Cu, and Pb concentration gradients (30–180 mg L^{-1}), respectively, but neither study included a post-exposure washout phase; both datasets therefore describe tolerance under sustained stress rather than true recovery capacity. These thresholds are mass-based (mg L^{-1}) rather than equimolar. Since atomic mass increases from Cu (63.5) through Cd (112.4) to Pb (207.2 g mol^{-1}), an equal mg L^{-1} loading delivers fewer moles

of the heavier ion, so the molar phytotoxicity thresholds for Pb^{2+} and Cd^{2+} may be reached at lower µM concentrations than for Cu^{2+}, a caveat when comparing metals on a mass basis. Direct evidence for recovery germination after heavy metal stress remains largely confined to studies employing chelating agents (e.g., EDTA, citrate) or antioxidant priming agents applied during stress rather than following it, and controlled washout experiments that measure germination percentage, mean germination time, and radicle elongation before and after metal removal are urgently needed to validate or refute the mechanistic inferences drawn here.

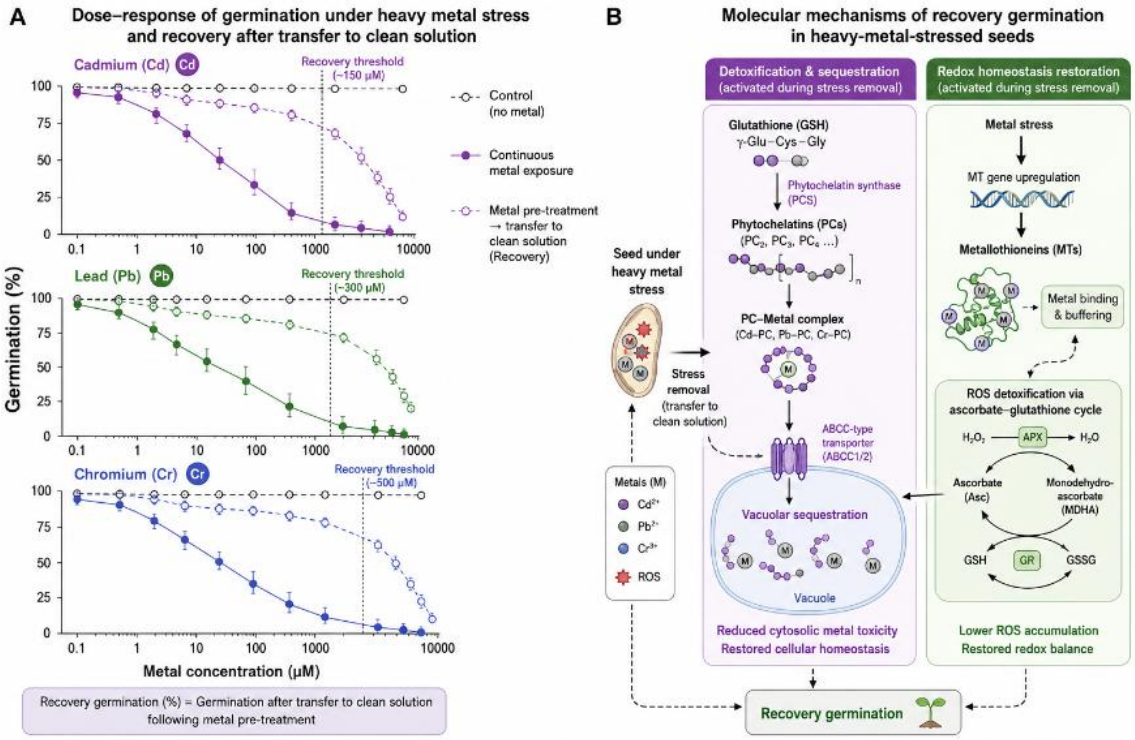

Figure 4. Heavy metal recovery germination: Dose-response and mechanism. (Acila et al. 2024; Bibi et al. 2025; Loix et al. 2017; Rekha et al. 2021).

Notwithstanding this limitation, the existing evidence illuminates two ecophysiologically critical principles. First, the extent of phytotoxicity is strongly metal-specific and cannot be predicted from concentration alone. In *C. pepo*, Cd caused significantly greater suppression of seed vigor indices and mean germination time than equimolar Cu concentrations, despite broadly similar final germination percentages, indicating that germination completion *per se* is an insensitive endpoint that can mask substantial sub-lethal injury to the embryonic axis and cotyledonary reserve-mobilization machinery (Acila et al., 2024). Cadmium has independently been shown to impair protease activity and starch degradation in cotyledons at highly phytotoxic concentrations (100–200 µM) (well above the ≈50 µM free-Cd^{2+} level generally regarded as severe in aqueous seed bioassays) a biochemical legacy expected to persist after stress removal and to compromise post-germination establishment (Grobelak et al. 2019). Second, species adapted to metalliferous or drought-prone soils may deploy constitutive tolerance mechanisms, including antioxidant enzyme induction and

compatible-solute accumulation, that buffer germination completion even under elevated Pb and Cd loads, as demonstrated in *P. roxburghii* (Bibi et al., 2025), yet the functional integrity of the resulting seedlings under metal-free conditions has not been assessed. Taken together, these findings underscore that a comprehensive evaluation of heavy metal phytotoxicity at the seed germination stage requires the integration of multiple endpoints (final germination percentage, seed vigor index, radicle elongation rate, and, critically, post-stress recovery germination) rather than reliance on any single metric. Establishing standardized washout protocols analogous to those routinely employed in salinity recovery studies should therefore be accorded high priority in future experimental designs.

6 Osmotic stress recovery germination

6.1 PEG-induced osmotic stress as an experimental system

Polyethylene glycol (PEG 6000) is widely used to impose controlled water potential stress on seeds without ionic side effects, making it an ideal experimental system for studying pure osmotic effects on germination (Welbaum and Bradford 1991). Seeds incubated in PEG solutions whose water potential lies below the base water potential (Ψb, MPa; the threshold water potential below which a given seed fraction cannot complete germination) remain in a state of arrested germination and, by the construction of the hydrotime model, accumulate no hydrotime (θH, MPa·h; the hydrotime constant, that is, the water-potential-time integral above Ψb that a seed fraction must accumulate in order to complete germination), since hydrotime accrues only while Ψ > Ψb (Bradford 1990). Such seeds nevertheless remain hydrated and metabolically active. The critical question addressed by osmotic recovery studies is therefore whether the physiological progress made during sub-threshold hydration is retained and expressed once the water potential rises above Ψb (Section 7.1), or whether seeds must start over from a fully non-imbibed state.

Welbaum and Bradford (1991) provided pivotal evidence that seeds of muskmelon (*Cucumis melo* L.) exposed to −1.0 MPa PEG for 7 days germinated significantly faster upon transfer to water than non-primed controls, demonstrating that sub-threshold imbibition at suboptimal water potential constitutes genuine physiological priming. This is the mechanistic basis for the commercially important technique of osmopriming. Critically, the same phenomenon constitutes the mechanistic basis for recovery germination in field soils: seeds that have partially imbibed during a sub-threshold soil moisture event, perhaps a light rain insufficient to raise soil Ψ above Ψb, will germinate faster than naive seeds when a subsequent, larger rain event creates permissive conditions.

6.2 Kinetic analysis of osmotic recovery germination

A sophisticated analysis of osmotic recovery germination requires probit-transformed time-to-germination data for individual seed fractions, allowing estimation of population parameters including Ψb(50) (median base water potential of the population, MPa) and σΨb (standard deviation of Ψb across the population, MPa) (Bradford 2002). Two distinct responses to osmotic recovery have been described in the literature: (a) Acceleration without improvement: seeds germinate faster post-transfer but final germination percentage does not exceed the control; and (b) Acceleration with

enhancement*:* both rate and final percentage are improved, consistent with a priming-equivalent effect. Acceleration accompanied by an increase in final germination, that is, the priming-equivalent response, predominates under moderate osmotic stress, with the ambient water potential held just below the base water potential (Ψb − 0.5 MPa ≤ Ψ < Ψb) for 3 to 7 days, conditions typical of effective osmopriming (Welbaum and Bradford 1991; Bradford 2002; Corbineau et al. 2023).

Severe stress (Ψ ≪ Ψb) more often yields acceleration without enhancement, or no measurable recovery, consistent with damage accrual outweighing physiological advancement.

Notably, seeds that undergo recovery germination following osmotic stress display altered Ψb distributions. Populations previously exposed to sub-lethal osmotic stress often exhibit a leftward shift in mean Ψb, i.e., a lower base water potential, compared with non-stressed controls. This shift implies that stressed-and-recovered seeds can germinate at lower soil water potentials than naive seeds of the same population, a potential adaptive advantage in arid environments where safe-site water potential may be marginal.

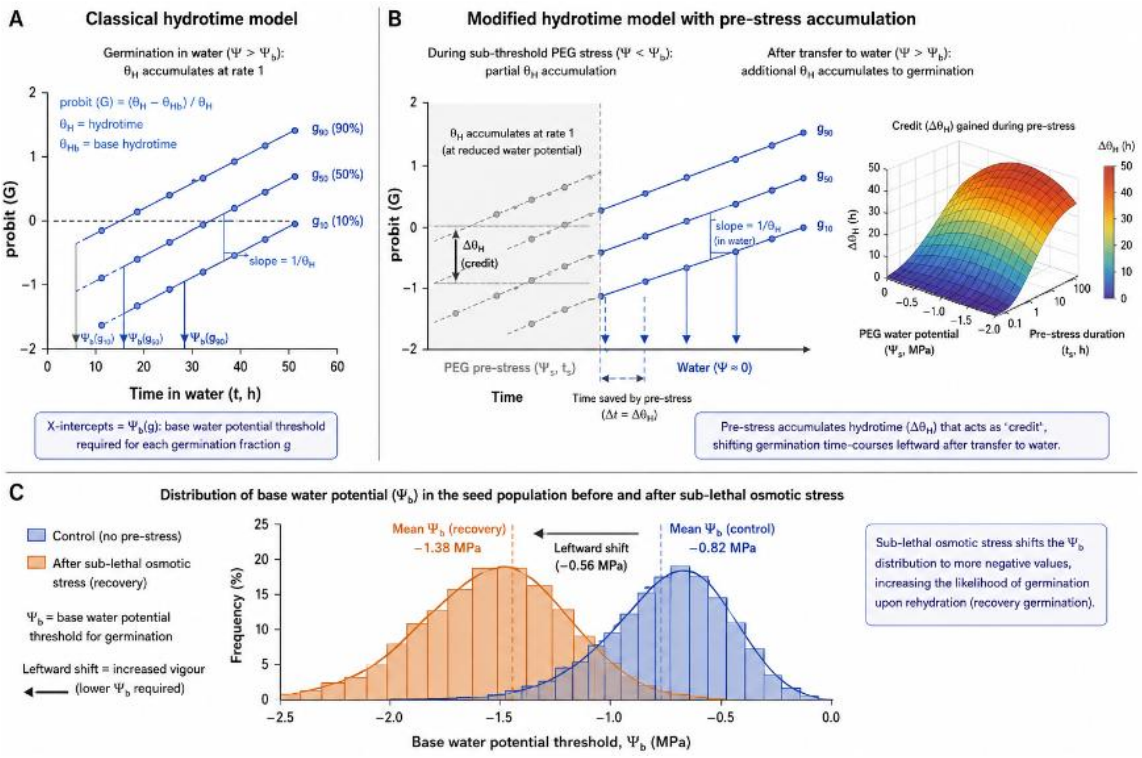

Figure 5. Hydrotime model applied to osmotic recovery germination (original schematic). (A) The classical hydrotime model, GR(g) = (Ψ − Ψb(g))/θH, with the base water potential (Ψb) and hydrotime constant (θH) defined and parameterised as in Bradford (1990, 2002) and Welbaum and Bradford (1991). (B) The modified formulation proposed in the present review (Section 7.1), in which sub-threshold hydration lowers the effective base water potential (Ψb' = Ψb − A) and thereby displaces the post-transfer time-course leftward. (C) The corresponding leftward shift of the population Ψb distribution under sub-lethal osmotic pre-treatment. Panels B and C are theoretical constructs of this review and are illustrative rather than fitted to a specific empirical dataset; the classical parameter. values in panel A are those of Bradford (1990, 2002).

Figure 5 places these dynamics within the hydrotime framework, setting the classical model (panel A) against a modified formulation in which sub-threshold imbibition accrues a hydrotime "credit" that shifts the post-transfer time-course leftward (panel B), and showing how sub-lethal osmotic pre-treatment displaces the population base-water-potential distribution toward more negative values (panel C). The classical parameters underlying panel A are those of the Bradford (1990, 2002) hydrotime framework, whereas the modified formulation in panels B and C is that developed in Section 7.1 of the present review and is presented as a theoretical construct rather than a fit to measured data.

7 Hydrotime model reinterpretation in context of stress recovery

The hydrotime model (Bradford 1990; 2002) describes germination rate as a linear function of water potential above the base water potential: GR(g) = (Ψ − Ψb(g)) / θH, where GR(g) is the germination rate of seed fraction g (the reciprocal of the time to radicle protrusion of that fraction, h^{-1}), Ψ is the ambient water potential, Ψb(g) is the base water potential of that fraction, and θH is the hydrotime constant (MPa·h). This model has been widely validated in predicting germination time-courses under uniform water potential conditions and has been extended to incorporate temperature (the hydrothermal time model) (Bradford 2002). However, the classical hydrotime model was developed for static water potential conditions and does not explicitly address situations where Ψ changes during imbibition, precisely the scenario encountered in recovery germination. Several theoretical and empirical extensions are necessary:

7.1 Sub-treshhold advancement and the effective base water potential

To integrate recovery dynamics into the classical hydrotime framework, it is essential to respect the domain over which hydrotime is defined. In the Bradford formulation, hydrotime accumulates only while the ambient water potential exceeds the base water potential (Ψ > Ψb), the germination rate of fraction g being GR(g) = (Ψ − Ψb(g)) / θH (Bradford 1990, 2002; Welbaum and Bradford 1991). Below the threshold (Ψ < Ψb) the rate term is negative, so sub-threshold imbibition cannot, by construction, contribute positive hydrotime. The physiological advancement that nonetheless occurs during a sub-threshold hydration episode must therefore be represented not as accumulated hydrotime, but as a stress-induced lowering of the base water potential itself. We formalise this as a non-negative advancement functional, A(g), that accrues only within a hydration window in which imbibition is sufficient to sustain pre-germinative metabolism yet insufficient for irreversible radicle elongation:

$$A(g) = \int_0^{t_1} \varphi(\Psi)\, dt, \qquad \varphi(\Psi) \geq 0 \quad \text{for} \quad \Psi_{min} \leq \Psi < \Psi_b$$

$$\Psi_b'(g) = \Psi_b(g) - A(g)$$

$$GR(g) = \frac{\Psi - \Psi_b'(g)}{\theta_H}, \qquad \Psi_b'(g) \leq \Psi_b(g)$$

where t_1 is the time of stress alleviation, ϕ(Ψ) is the advancement rate over the metabolic hydration window bounded below by Ψ_min, and Ψb'(g) is the resulting effective (primed) base water potential of fraction g.

This advancement is mediated by the stabilisation and activation of the pre-germinative metabolic machinery. During sub-threshold hydration, seeds initiate mitochondrial maturation, DNA damage-response (DDR) activation, and transcription of aquaporin isoforms (notably PIP1 and PIP2 variants), without progressing to irreversible cell elongation (Macovei et al. 2025; Maurel et al. 2008). Upon stress relief, the pre-existing pool of water-transport proteins and repaired genomic templates lowers the water-potential threshold for germination and accelerates water influx, which accounts for the characteristically sigmoidal acceleration of post-stress germination kinetics.

Because the physiological progress made under stress is stored as a shift in Ψb rather than as hydrotime, post-transfer germination proceeds by the ordinary, strictly non-negative hydrotime accumulation, now referenced to the primed threshold:

$$GR(g) = (\Psi - \Psi b'(g)) / \theta H$$

Since $\Psi b'(g) \leq \Psi b(g)$, a seed that has experienced and recovered from sub-lethal stress reaches radicle protrusion sooner, at any given ambient Ψ, than a naive seed of the same fraction. This preserves the central hypothesis of faster-than-naive recovery while eliminating the sign inconsistency inherent in accumulating hydrotime below the threshold. Formulating the sub-threshold contribution as $\Delta\Psi b(g) = -A(g) \leq 0$, where $\Delta\Psi b(g)$ is the stress-induced change in the base water potential of fraction g (MPa) and A(g) is the non-negative advancement functional defined above, also unifies this subsection with the stress-induced modification of Ψb treated in Section 7.2 and depicted in Figure 5C, so that a single mechanism (a downward displacement of the base water potential) governs both the accelerated kinetics and the leftward shift of the population Ψb distribution. This reinterpretation carries direct implications for predictive models of seedling emergence in fluctuating soil-water environments, which currently assume that germination timing is set solely by the instant at which Ψ first exceeds a fixed base water potential and therefore neglect the stress-induced lowering of Ψb (Venable 2007).

7.2 Stress-induced modification of Ψb

Sub-lethal stress may lower the effective Ψb of a seed population through several mechanisms: (i) Stress-induced ABA catabolism reduces the ABA concentration required to maintain dormancy, shifting Ψb downward; (ii) Partial cell wall loosening in the endosperm during the stress phase reduces the mechanical resistance that germination must overcome, effectively lowering the water potential threshold for cell expansion (Nonogaki 2017); (iii) Upregulation of aquaporin genes (particularly PIP1 and PIP2 family members) during stress may enhance water conductivity through seed tissues, facilitating faster imbibition at a given Ψ post-stress (Maurel et al. 2008).

Table 2 sets the principal hydrotime parameters as defined in the classical Bradford framework against their reinterpretation under post-stress recovery, and links each to the ecological consequence it implies.

Table 2. Comparison of key hydrotime model parameters as defined in the classical Bradford (1990, 2002) framework and their reinterpretation in the context of post-stress recovery germination. Ψ, water potential (MPa); Ψb, base water potential (MPa); Ψb(50), median base water potential of the population (MPa); Ψb', effective (primed) base water potential after sub-threshold hydration, Ψb' = Ψb − A(g) (MPa); A(g), advancement functional of fraction g (MPa); θH, hydrotime constant (MPa·h); σΨb, standard deviation of Ψb across the seed population (MPa); GR(g), germination rate of fraction g (h^{-1}).

Parameter	Classical hydrotime model	Post-stress recovery reinterpretation	Ecological implication
Base water potential (Ψb(50))	Fixed for a seed lot; species-specific constant	Dynamically shifted by sub-lethal stress pre-conditioning; priming lowers Ψb(50)	Seeds can exploit lower soil water potentials post-rain pulses
Hydrotime constant (θH)	Accumulated above Ψb; linear with germination rate	θH is a property of the seed lot and is not itself altered by sub-lethal stress; no hydrotime accrues below Ψb. Post-stress acceleration arises because germination after transfer proceeds against the lowered threshold Ψb' = Ψb − A(g) (Section 7.1)	Explains faster-than-expected recovery germination in fluctuating desert soils
Seed-to-seed variation (σΨb)	Normally distributed around population mean	Stress may select for lower-Ψb sub-populations via maternal effects	Micro-habitat variation shapes population-level recovery capacity
Thermal time interaction	Hydrotime and thermal time operate multiplicatively	Heat stress modifies Ψb independently of θH accumulation	Compound stress–recovery (heat + drought) requires dual-model framework
Priming memory	Not accounted for in classical model	Sub-lethal stress acts as priming: the advancement A(g) acquired during sub-threshold hydration is stored as a persistent lowering of Ψb and is retained after the stress is removed	Seeds arriving in favorable microsites germinate before competitors

8 Ecological significance of recovery germination

8.1 Recovery germination as an adaptive strategy

From an evolutionary perspective, recovery germination capacity can be viewed as a bet-hedging strategy enabling seeds to exploit transient favorable conditions following episodes of abiotic stress. In fluctuating environments, characterized by alternating periods of stress and permissive conditions, seeds that retain high germination potential across stress-recovery cycles will have a substantial fitness advantage over seeds that suffer permanent germination inhibition after a single stress episode (Venable 2007; Gremer and Venable 2014).

This argument is particularly compelling for two major vegetation types: (i) Desert ephemerals, where seed germination is tightly coupled to rainfall pulses that

may be preceded by prolonged desiccation and heat episodes; and (ii) Coastal halophytes, where seeds experience alternating high-salinity inundation and freshwater flushing on tidal timescales. In both cases, the degree to which seeds retain germinative capacity across stress-recovery cycles, i.e., their recovery germination resilience, may be a primary determinant of fitness and of species distribution boundaries.

Table 3 generalizes beyond these two cases to a wider set of contexts (salt marsh, arid desert, metal-contaminated soil, saline-irrigated cropland and post-fire habitat), specifying for each the stress episode, the recovery trigger, the adaptive strategy enabled and the resulting functional outcome. Following the logic of Table 2, each scenario is also assigned an evidence base, and the epistemic status of that evidence is stated explicitly, since the five contexts are not equally supported: recovery germination has been measured directly in salt marsh and saline-cropland systems (Almansouri et al. 2001; Patade et al. 2014; Gul et al. 2013, 2024; Zhang et al. 2024; Kheloufi and Mansouri 2024, 2026), whereas the metal-contaminated and post-fire scenarios are extrapolations from studies that did not include a post-stress transfer phase (Acila et al. 2024; Bibi et al. 2025; Flematti et al. 2004; Nelson et al. 2008).

8.2 Community assembly and competitive dynamics

Figure 6 illustrates how this plays out in a fluctuating salt marsh. Panel A shows a synthetic 30-day series of tidal wetting and drying cycles in which soil water potential (Ψsoil) repeatedly crosses the base water potential (Ψb) of a glycophyte and of a halophyte, opening recurrent windows for recovery germination; the two threshold values used (about −1.4 MPa for the glycophyte and about −0.6 MPa for the halophyte) lie within the range reported for these two functional groups (Bradford 1990, 2002; Flowers and Colmer 2015), and the accompanying soil NaCl series spans the concentrations typical of temperate salt marshes (Gul et al. 2013). Panel B models the consequences with a stochastic cohort simulation written for this review, in which three hypothetical species differing only in Recovery Index (RI = 0.5, 0.75 and 1.0, a range that brackets the values reported for glycophytes and halophytes in Section 3.2) germinate whenever Ψsoil crosses Ψb: species with higher recovery capacity generate larger and more frequent cohorts and, over a 50-year horizon of increasing hydroclimatic variability (IPCC 2021), rise in relative abundance. The simulation is a heuristic construct rather than a fit to field data, and its outputs should be read as qualitative expectations.

Recovery germination timing also influences competitive dynamics between co-occurring species in disturbed habitats. Species with higher RI values and faster recovery germination kinetics will capture available safe sites more rapidly following stress relief, potentially excluding slower-recovering competitors. This mechanism may contribute to the dominance of particular stress-tolerant species (e.g., *Suaeda* spp., *Puccinellia* spp.) in salt marsh communities and to the successional dynamics following flooding, drought, or soil pollution events.

An underexplored dimension of this competitive ecology is the interaction between recovery germination and the soil seed bank. Seeds in the persistent soil seed bank are regularly subjected to cycles of sub-lethal stress and alleviation (Fenner and Thompson 2005). If stress exposure modifies Ψb (as mentioned in Section 7.2), then soil seed bank populations may gradually accumulate lower Ψb values over time, a form of population-level physiological conditioning that could explain why seed bank seeds of

some species germinate more readily than freshly harvested seeds from the same mother plant.

Table 3. Ecological scenarios in which recovery germination is ecologically significant, with the relevant stress episode, the recovery trigger, the adaptive strategy enabled, the functional ecological outcome and the supporting evidence. Ψ, water potential; Ψb, base water potential (Section 6.1). The final column states, for each scenario, both the key references and whether recovery germination in that context has been measured directly (documented), partly measured (partly documented), or is projected from related evidence (inferred or hypothesized). The scenarios therefore illustrate the breadth of contexts in which recovery germination capacity is expected to confer a fitness advantage, and at the same time identify where that expectation still awaits an experimental test.

Ecological context	**Stress episode**	**Recovery trigger**	**Adaptive strategy enabled**	**Functional outcome**	**Evidence base and status (key references)**
Coastal salt marsh	Tidal inundation (NaCl surge); soil water potential falls below Ψb	Freshwater flooding or rainfall dilution; Ψ rises above Ψb	Halophytic persistence; competitive exclusion of glycophytes	Niche partitioning along the salinity gradient	Documented. Recovery germination after transfer from saline to fresh water is repeatedly reported for salt-marsh Chenopodiaceae, including *Suaeda fruticosa* and *Halostachys caspica* (Flowers and Colmer 2015; Gul et al. 2013, 2024; Zhang et al. 2024)
Arid and semi-arid desert	Summer drought combined with a heat pulse	Autumn rain event raising Ψ above Ψb	Bet-hedging germination; subdivision of the cohort	Temporal spread of risk; formation of a seedling bank	Partly documented. Bet-hedging and rainfall-cued germination are well established (Venable 2007; Gremer and Venable 2014); the recovery germination component itself is inferred from sub-threshold hydration experiments (Welbaum and Bradford 1991; Bradford 2002)
Heavy-metal contaminated soil	Continuous Cd or Pb exposure	Leaching, chelation by soil organic matter, or liming	Colonisation by pioneer species	Seedling establishment for phytoremediation	Hypothesized. Germination under sustained metal load has been quantified (Acila et al. 2024; Bibi et al. 2025), but no washout-recovery assay has been published; the scenario follows from the sequestration and cell-wall binding mechanisms reviewed in Section 5.2 (Loix et al. 2017; Rekha et al. 2021)
Agricultural field under saline irrigation	Irrigation-induced salinity event	Rainfall leaching or drainage	Crop recovery; restoration of stand density	Yield maintenance under variable irrigation quality	Documented at the germination stage. Recovery after desalination has been quantified in wheat and in crop and rangeland species (Almansouri et al. 2001; Patade et al. 2014; Kheloufi and Mansouri 2024, 2026); the stand-level consequence remains to be tested (Bailly and Gomez Roldan 2023)
Post-fire habitat	Heat shock during fire	Post-fire rainfall on cooled soil, with smoke-derived karrikins in the soil solution	Smoke-stimulated germination following heat inhibition	Rapid colonization; fire-follower guild	Inferred. Karrikin-stimulated germination is well characterized (Flematti et al. 2004; Nelson et al. 2008; Khosla et al. 2020), but the sequence heat inhibition followed by recovery has not been tested as a recovery germination assay; identified here as a priority (Section 9.1)

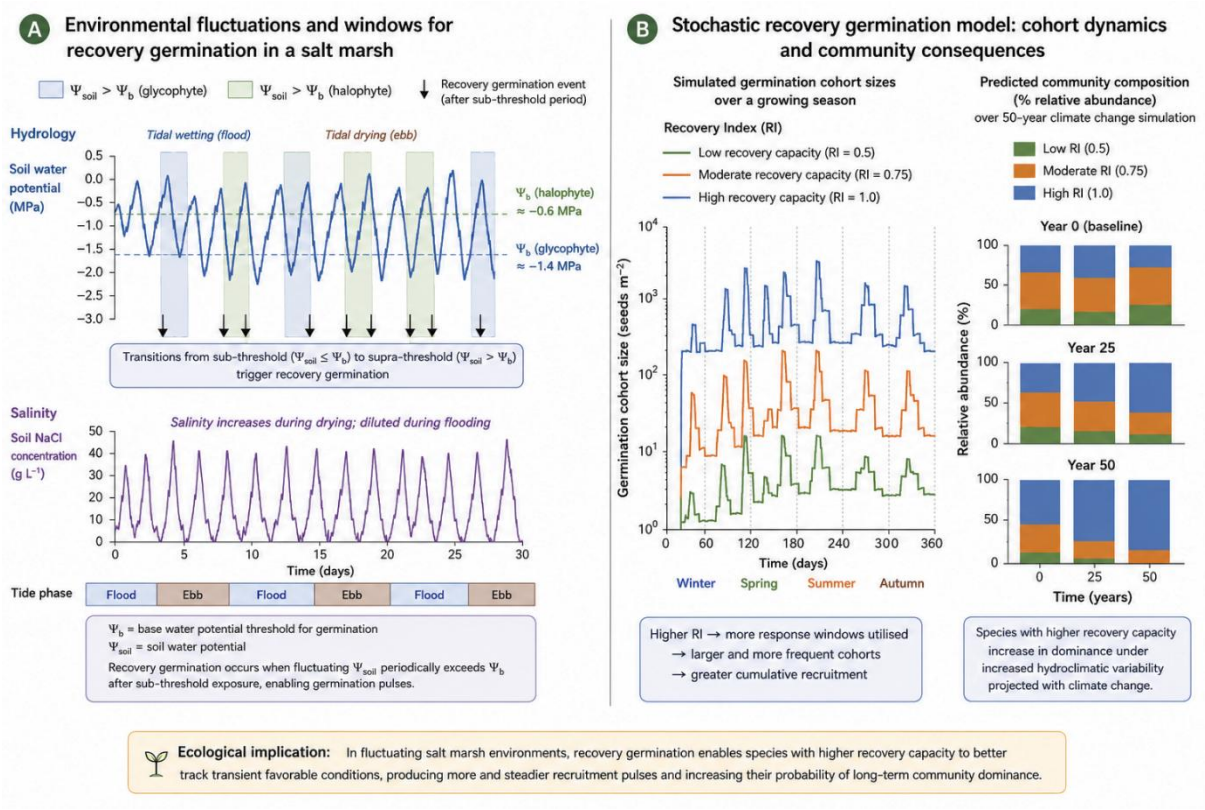

Figure 6. Ecological framework: recovery germination in fluctuating environments (original figure, produced by the authors). (A) Synthetic 30-day series of soil water potential (Ψsoil, MPa) and soil NaCl concentration (g L^{-1}) in a tidally flooded salt marsh. Shading marks the intervals in which Ψsoil exceeds the base water potential (Ψb) of a glycophyte (Ψb ≈ −1.4 MPa) or of a halophyte (Ψb ≈ −0.6 MPa) and arrows mark the resulting recovery germination events. The wetting and drying amplitude, the salinity range and the two Ψb values were chosen to lie within the ranges reported for temperate salt marshes and for glycophyte and halophyte seeds respectively (Bradford 1990, 2002; Gul et al. 2013; Flowers and Colmer 2015). (B) Output of a stochastic recovery germination model written for this review. Three hypothetical species differing only in Recovery Index (RI = 0.5, 0.75 and 1.0; RI as defined in Section 2) germinate whenever Ψsoil rises above Ψb after a sub-threshold period; left, simulated cohort size (seeds m^{-2}, log scale) over one growing season; right, predicted relative abundance at years 0, 25 and 50 under a scenario of increasing hydroclimatic variability (IPCC 2021). The RI values used span the range of recovery responses reported in Sections 3 to 6 (Almansouri et al. 2001; Patade et al. 2014; Gul et al. 2013, 2024; Zhang et al. 2024). Both panels are original constructs: the curves are simulation output and schematic series, not measured data, and the axis values should not be interpreted as empirical observations.

8.3 Implications for climate change

Under projected climate change scenarios, abiotic stress events relevant to germination, drought, heat waves, saline intrusion in coastal agricultural zones, are predicted to increase in both frequency and intensity (IPCC 2021). Critically, climate projections also predict changes in the duration of stress events and the temporal spacing between stress and recovery periods. This double exposure, more intense stresses followed by more erratic recovery windows, may exceed the recovery

germination resilience thresholds of many crop and wild plant species, with consequences for both agricultural productivity and natural ecosystem dynamics.

Recovery germination capacity is therefore a functionally important trait that should be incorporated into models of species distribution change under climate warming. Current process-based vegetation models largely treat germination as a binary event (stress prevents germination; favorable conditions enable it) without accounting for the history-dependence and kinetic complexity of recovery germination dynamics documented in this review. Integrating hydrotime-based recovery germination models into dynamic global vegetation models (DGVMs) represents an important methodological challenge for the next generation of climate-change impact assessments.

9 Knowledge gaps and research priorites

Despite the evidence reviewed above, recovery germination remains an underdeveloped research field. Figure 7 positions the five priority areas identified below on a matrix of scientific novelty against applied relevance, with marker size indicating the relative research investment each is likely to require. The scores are not derived from a bibliometric survey: they are the authors' qualitative assessment, made on a five-point scale, of the gaps documented in Sections 9.1 to 9.5 and of the state of the literature cited there (ISTA 2024; Sedghi 2025 for protocols; Li et al. 2022; Yu et al. 2024 for multi-stress interactions; Gao et al. 2021; Dai et al. 2022; Liu et al. 2024 for genomic and transcriptomic approaches; Bilichak and Kovalchuk 2016; Zhang et al. 2026; Kovalchuk 2026 for maternal and epigenetic effects; Challinor et al. 2016; Banerjee and Mondal 2022; Gavasso-Rita et al. 2023 for model integration). On this assessment, multi-stress interaction studies and model integration emerge as the highest-priority targets.

9.1 Absence of standardized protocols

No universally adopted protocol exists for quantifying recovery germination. Studies vary in stress duration, stress intensity, recovery medium, recovery duration, and whether dormancy-breaking treatments are applied before or after stress exposure. A coordinated effort, potentially through the Seed Ecology and Seed Technology working groups of the International Society for Seed Science (ISSS), to develop standardized recovery germination protocols analogous to the ISTA germination testing rules would substantially improve cross-study comparability.

The scale of this challenge is illustrated by the breadth of existing ISTA germination testing infrastructure. The ISTA International Rules for Seed Testing already cover more than 600 species across agricultural, horticultural, forestry, and medicinal categories, and the Germination Technical Committee continues to update these methods (ISTA 2024). Yet recovery germination is entirely absent from this framework. Establishing recovery germination as a distinct, formally recognized testing category within such international frameworks would be a critical first step.

Beyond institutional recognition, there is a practical need to define the minimum set of variables that any recovery germination assay must report. These should include pre-stress seed moisture content, stress agent identity and concentration, exposure duration and temperature, the medium and duration of the recovery phase, and final germination counts taken at standardized intervals. Recent

work on integrated assessment of germination performance under abiotic stress has reinforced the value of reporting multiple complementary germination indices alongside germination percentage alone (Sedghi 2025), a principle that applies equally to recovery germination assays. Agreement on a minimal reporting checklist, even before full protocol standardization, would meaningfully reduce the interpretive barriers currently faced when comparing results across laboratories and species.

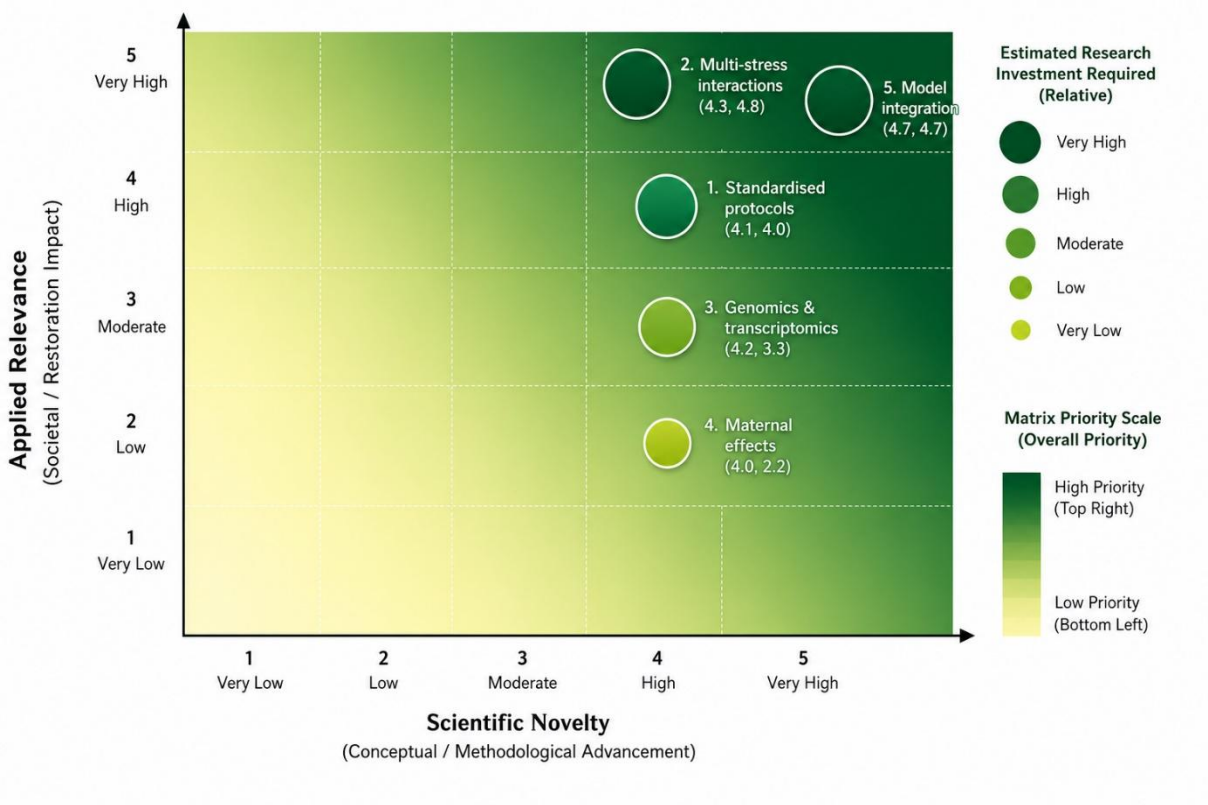

Figure 7. Research priority matrix for recovery germination science (original figure, produced by the authors). The five priority areas set out in Sections 9.1 to 9.5 are plotted against scientific novelty (conceptual and methodological advancement) and applied relevance (societal and restoration impact); the score pair given in parentheses beside each label gives the position of that area on the two axes, and the area of each marker is proportional to the relative research investment it is estimated to require. The scores are an expert assessment by the authors on a five-point scale, derived from the gap analysis presented in Section 9 and from the literature cited there (ISTA 2024 and Sedghi 2025 for standardised protocols; Li et al. 2022 and Yu et al. 2024 for multi-stress interactions; Gao et al. 2021, Dai et al. 2022 and Liu et al. 2024 for genomics and transcriptomics; Fenner 1991, Bilichak and Kovalchuk 2016, Springer and Schmitz 2017, Zhang et al. 2026 and Kovalchuk 2026 for maternal and epigenetic effects; Challinor et al. 2016, Banerjee and Mondal 2022, Gavasso-Rita et al. 2023 and Chen et al. 2025 for model integration).

9.2 Multi-stress interaction studies

Almost all published recovery germination studies address a single stressor. In natural and agricultural environments, compound stress exposure (e.g., salinity + heat; osmotic stress + heavy metals) is common. The interaction between multiple stressors in conditioning recovery germination capacity is unknown and may involve non-additive

effects due to shared molecular targets (e.g., ROS detoxification systems, ABA signaling).

The molecular basis for such non-additivity is becoming increasingly tractable. ABA plays an important role in plant adaptive responses to multiple stresses including drought, salt, osmotic, and cold conditions, while ROS are widely produced under biotic and abiotic stress; the production of apoplast ROS is itself induced and regulated by ABA and participates in the ABA signaling pathway (Li et al. 2022). Because ABA and ROS signaling are deeply interconnected, simultaneous activation by two stressors could either amplify or attenuate the recovery response in ways that no single-stress study could predict. Seed sensitivity to ABA, gibberellin, ethylene, and brassinosteroid is fundamental to germination regulation (Corbineau et al. 2023; Bailly and Gomez-Roldan 2023).

Encouragingly, some recent work has begun to address the germination consequences of combined stresses at the physiological level. Combined salinity and heat stress hinder germination and can lead to ROS production which, within a certain concentration range, may actually facilitate germination, with the signaling molecule GABA shown to promote germination under simultaneous heat and salinity stress via NADPH oxidase-mediated hydrogen peroxide signaling (Yu et al. 2024). Such findings suggest that the interactions between co-occurring stressors during recovery are biologically rich and potentially exploitable for agronomic purposes. Systematic factorial experiments crossing common field-relevant stressors, followed by explicit quantification of recovery germination indices, are urgently needed to determine whether compound stress exposure leaves seeds more or less recoverable than single-stress exposure of equivalent intensity.

9.3 Genomic and transcriptomic basis

The genetic architecture of recovery germination capacity is essentially unexplored. QTL mapping and GWAS studies for stress recovery traits could identify genomic loci and candidate genes associated with high RI values, providing targets for crop improvement. Transcriptomic studies comparing the recovery phase across stress types would likely reveal both shared core recovery pathways and stress-specific elements.

Encouraging progress in adjacent areas demonstrates the feasibility of this approach. A GWAS conducted on 346 diverse rice accessions identified 51 significant SNPs arranged into six QTL regions associated with seed germination rate, seedling shoot length, and shoot fresh weight, with integration of gene expression, annotation, and haplotype analysis revealing 21 strong candidate genes significantly associated with seed vigor (Dai et al. 2022). Similarly, GWAS on 541 worldwide rice varieties identified three QTLs for germination under salt stress, with the TATA modulatory factor OsTMF identified as a candidate gene whose expression was up-regulated in roots and shoots after salt exposure, and whose knockout mutants showed delayed germination under salt stress (Liu et al. 2024). Analogous mapping populations specifically designed to contrast high- and low-recovery genotypes would be a natural extension of this work, with recovery index values providing a quantitative trait ideally suited to genome-wide association approaches.

At the transcriptomic level, the recovery phase itself has received minimal direct attention. Transcriptomic analysis of *Brassica napus* seeds under heat stress

identified 442 differentially expressed genes, with enrichment in genes involved in post-translational modification, protein turnover, chaperones, carbohydrate transport, and secondary metabolite biosynthesis, with small heat shock proteins and specific transcription factors emerging as key contributors to heat stress tolerance (Gao et al. 2021). Whether these same gene categories are consistently mobilized during the recovery phase across different stress types, or whether recovery-specific transcriptional programs exist, remains unknown. Time-resolved RNA-sequencing across the stress-to-recovery transition, designed to capture the transcriptome at the moment stress is relieved and at subsequent intervals, would represent the most direct way to characterize the molecular program of recovery germination.

9.4 Maternal and epigenetic effects

Seeds from mother plants grown under mild abiotic stress frequently display altered germination behavior, suggesting maternal provisioning of stress tolerance mechanisms (Fenner 1991). Whether maternal effects also modify recovery germination capacity, and whether such modifications are epigenetically transmitted across generations, is unknown. Given the growing evidence for transgenerational epigenetic inheritance in plants (Springer and Schmitz 2017), this represents a potentially important and unexplored dimension of recovery germination biology.

The mechanistic pathways through which maternal stress experience could modify seed recovery capacity are beginning to come into view. Epigenetic marks induced by environmental stress can be transmitted inter- and transgenerationaly through maintenance, resetting, and selective passage of DNA methylation and histone modifications during the gamete-to-zygote transition (Bilichak and Kovalchuk, 2016). Small RNAs also influence germination and seedling vigor under water deficit and heat stress. The seed itself is a composite structure containing tissues of different genetic origins, the maternal seed coat, the embryo, and the endosperm, meaning that all three compartments could in principle carry maternally derived epigenetic information relevant to germination and recovery behavior. This understanding has led to proposals to capitalize on the ability of plants to naturally adjust their responses to fluctuating environments and transmit stress-induced information to the next generation, with maternal stress memory being explored as a priming strategy to produce seed lots with enhanced stress tolerance (Zhang et al. 2026).

There is also evidence that transgenerational stress memory can extend beyond a single filial generation. A growing number of reports indicate that plants can maintain a memory of stress exposure throughout their ontogenesis and transmit it faithfully to the following generation, with features of transgenerational memory including elevated genome instability, higher tolerance to stresses experienced by parents, and cross-tolerance; a likely contributing factor is the absence of full-scale reprogramming of the epigenetic landscape during gametogenesis, allowing epigenetic marks to escape reprogramming and be passed to progeny (Kovalchuk 2026). Whether this inherited memory extends specifically to recovery germination capacity, that is, whether offspring of stressed parents recover more completely from a subsequent stress episode, is an entirely open question. Controlled multi-generation experiments combining mother-plant stress treatments with offspring recovery germination assays would test this hypothesis directly and could reveal whether stress memory is a tractable lever for improving seed lot resilience.

9.5 Integration with vegetation and crop models

The inclusion of recovery germination dynamics in process-based models of crop stand establishment and natural vegetation dynamics would improve predictive accuracy under variable abiotic conditions. Collaboration between seed biologists and modelers is urgently needed to develop appropriate sub-models and parameterize them from experimental data.

Current process-based crop models represent germination primarily as a function of temperature and soil water potential, with limited capacity to simulate sub-lethal stress exposure followed by recovery. Widely used crop models such as DSSAT, APSIM, EPIC, and CropSyst represent physiological mechanisms of crop development, growth, and yield formation under biotic and abiotic stresses as well as farming management practices such as tillage and irrigation, yet none of these frameworks currently incorporates a recovery germination sub-model that would allow the simulation of stand establishment following transient stress pulses (Banerjee and Mondal 2022; Gavasso-Rita et al. 2023).

A recognized problem in process-based crop modelling is that the choice of thresholds above which stress factors are activated, and the way these factors interact in multi-stress environments, are not always clear, with modelers sometimes relying on calibration or optional subroutines to improve model fit (Challinor et al. 2016), a situation that could be improved substantially by embedding empirically derived recovery germination parameters.

The development of recovery germination sub-models will require, in the first instance, the kind of standardized experimental data called for in Section 9.1, since model parameterization demands consistent, species-resolved recovery germination curves across a range of stress intensities and durations. The feasibility of assembling data at that scale has been demonstrated for germination under osmotic stress. Chen et al. (2025) characterized seed germination and seedling emergence across 242 populations of *Leptochloa chinensis* over a gradient of osmotic potentials and burial depths, producing exactly the kind of population-resolved response surface that a recovery germination sub-model would require, except that no post-stress transfer phase was included. Extending such designs to include a recovery phase, beginning with major crops for which parameterization data are most abundant, would provide a tractable pathway toward models capable of predicting crop establishment under the episodic and multi-stress conditions expected to intensify under climate change.

10 Conclusions

This review establishes recovery germination, the resumption of germination following abiotic stress removal, as a physiologically distinct, ecologically significant, and scientifically underexplored dimension of seed biology. Across the five domains examined (salinity, heat, heavy metals, osmotic stress, and the hydrotime framework), a consistent picture emerges: seeds inhibited by sub-lethal stress retain substantial germinative potential that is realized rapidly and at high percentage upon return to permissive conditions. Critically, this recovery capacity is not passive. It is actively mediated by stress-induced physiological changes (antioxidant upregulation, hormonal reprogramming, and a stress-induced lowering of the base water potential to $\Psi b' = \Psi b - A(g)$) that collectively advance the seed to a more primed germinative state than an equivalent unstressed seed would occupy.

The ecological implications are considerable. Recovery germination enables plants to exploit transient favorable windows in chronically stressful environments, shapes community assembly dynamics in disturbed habitats, and constitutes a functional trait of direct relevance to species distribution responses under accelerating climate change. The hydrotime reinterpretation advanced here, treating sub-threshold hydration as lowering the effective base water potential (Ψb') rather than as accumulating hydrotime below the threshold, provides a mechanistically grounded framework for incorporating recovery germination into predictive phenological models.

We therefore urge that recovery germination be elevated from an incidental observation in stress-physiology studies to a first-class research objective, equipped with standardized assay protocols, a comparative cross-species database, and an integrated theoretical framework. The ecophysiology of recovery germination is, in the broadest sense, the ecophysiology of plant resilience, and it warrants commensurate scientific investment.

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