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Antioxidant Enzyme Activity in Germinating Seeds Under Salinity Stress

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ABSTRACT

Seeds that germinate in saline soil or water face a double problem: the medium holds water back osmotically, and the sodium and chloride that do enter the tissues are toxic. Both pressures disturb the balance of reactive oxygen species, which are at once damaging and necessary for germination to proceed. Antioxidant enzymes such as superoxide dismutase, catalase and ascorbate peroxidase are therefore measured in a large share of the salinity literature, and higher activity is often read as a sign of tolerance. This narrative review asks how far that reading holds for germinating seeds specifically. It draws on published work on seed oxidative biology, on the antioxidant enzyme system, and on comparisons of tolerant and sensitive genotypes, and it reports no new data. Most of the genotype comparisons come from seedlings, roots and leaves, not from imbibing seeds, and the direction of enzyme change depends on tissue, timing, the severity of the treatment and the way activity is expressed. We argue that an enzyme activity is interpretable only alongside a marker of damage, an osmotic control and a clear account of the germination stage sampled, and we set out a short appraisal framework and a reading matrix for that purpose.

Keywords: Antioxidant enzymes; Seed germination; Salinity stress; Reactive oxygen species; Superoxide dismutase; Catalase; Narrative review

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Article Class: Narrative Review

1. Introduction

Soil and irrigation-water salinity limit crop production over large areas, and the damage is often decided at the very start of the crop's life, because a seedling that fails to establish never gets the chance to show tolerance later (1, 2). Germination is a short and exposed phase, in which the dry seed takes up water, restarts its metabolism

and sends out a radicle (3).

Salt acts through two routes at once. It lowers the water potential of the medium, and the sodium and chloride that enter the tissue are toxic once they accumulate (1, 4, 5). Either route can upset the balance of reactive oxygen species in the cell, and the literature on salt and drought stress treats that imbalance as a central feature of the



response (6, 7).

Reactive oxygen species are not simply a hazard. In seeds they take part in the release from dormancy and in the loosening of cell walls that lets the radicle grow, so that a seed with too little of them may germinate poorly and one with too much is damaged (8, 9). Antioxidant enzymes hold the balance, and measurements of superoxide dismutase, catalase and ascorbate peroxidase fill a great many papers on salinity. Higher activity under salt is usually reported as a sign of tolerance. This review asks how safe that reading is for germinating seeds, and it reports no new data. The aim is to separate what has been shown in germinating seeds from what has simply been carried over from seedlings.

2. Literature Review

2.1 Germination as an Oxidative Process

Germination is commonly described in three phases of water uptake: a rapid initial imbibition, a plateau in which metabolism is reorganised, and a renewed rise in uptake once the radicle emerges (3). Respiration resumes as soon as tissues rehydrate, and mitochondria generate reactive oxygen species from the first hours, so oxidative chemistry belongs to germination from the start (8, 10).

The positive roles are well documented. Protein oxidation was linked to dormancy release in sunflower embryos (11), hydroxyl radicals loosen cell walls during cress germination (12), and reactive oxygen release in radish seeds responds to light, gibberellin and abscisic acid (13). The same molecules can also trigger cell death when they accumulate, which is why the field speaks of a dual role (9, 14). The target is thus a window, not zero.

Whether a treatment counts as stress depends on whether it pushes the system

outside its normal range (15). Seed history matters too. In sunflower seeds, deterioration during accelerated ageing went together with more lipid peroxidation and changed enzyme activities (16), so that two seed lots can start a salt experiment from quite different positions. A high activity in a failing seed lot is not the same thing as a high activity in a healthy one.

2.2 The Enzymatic Antioxidant Machinery

Superoxide dismutase converts superoxide into hydrogen peroxide and oxygen, and it exists as several isoforms located in different compartments (17, 18). Hydrogen peroxide is then handled by catalase, which acts at high capacity but low affinity (19), and by ascorbate peroxidase, which uses ascorbate as the electron donor (20). Ascorbate and glutathione are kept in their reduced state through a linked cycle of enzymes, and that cycle is often described as the redox hub of the cell (21, 22). Table 1 summarises the main enzymes and the cautions that attach to each.

The enzymes are only one part of the system. Non-enzymatic antioxidants contribute as well (23), and plants carry a large, redundant network of genes that adjust redox balance, so a change in one enzyme can be offset elsewhere (24, 25). When the balance fails, lipids, proteins and nucleic acids are oxidised (26, 27); lipid peroxidation is the damage most often followed, usually by a colorimetric assay easily distorted by other compounds in the extract (28). Total superoxide dismutase activity, moreover, says nothing about which isoform or compartment changed, and glutathione-linked enzymes are often left unmeasured altogether. Absence of a change in one enzyme is not absence of a change in the system.



Table 1. Principal antioxidant enzymes discussed in the salinity literature on seeds.

Enzyme	Main reaction	Interpretive caveat
Superoxide dismutase	Converts superoxide to hydrogen peroxide (17, 18)	Several isoforms; total activity hides which one changed
Catalase	Breaks hydrogen peroxide into water and oxygen (19)	Assay reads a high-capacity, low-affinity enzyme
Ascorbate peroxidase	Reduces hydrogen peroxide using ascorbate (20)	Unstable if extraction lacks ascorbate
Glutathione-linked enzymes	Recycle ascorbate and glutathione (21, 22)	Often not measured, so the cycle is seen only in part

Note: Qualitative summary; the interpretive caveats are those raised in the cited methodological and review literature.

2.3 Salinity: Osmotic, Ionic and Oxidative Components

In a germinating seed the osmotic and ionic parts of salt injury are hard to separate. Work on durum wheat compared salt solutions with ion-free osmotic solutions and found that both delayed and reduced germination (2). A study without an iso-osmotic, non-salt control cannot say how much of an enzyme change belongs to the ions.

The route from either stress to oxidative imbalance is described in reviews of drought and salinity (7, 29, 30), and the capacity to keep reactive oxygen species in check has been proposed as one of the features that separates halophytes from ordinary crops (31). Figure 1 sketches how the pressures reach the antioxidant system and where a typical assay samples it.

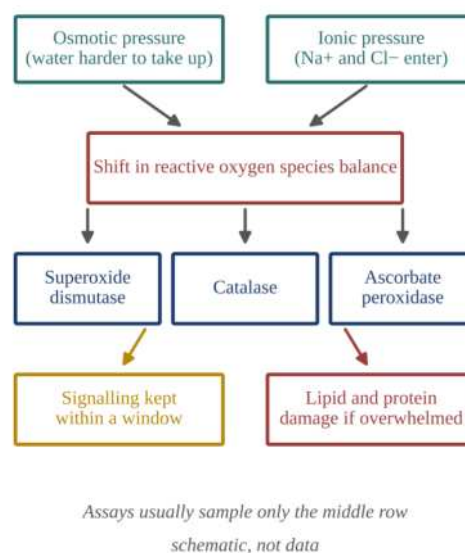


Figure 1. How salinity reaches the antioxidant system and where an enzyme assay samples it (schematic, not data).

2.4 Evidence from Tolerant and Sensitive Genotypes

Many studies ask whether a tolerant genotype keeps higher enzyme activity under salt than a sensitive one. They exist for rice, barley, wheat and several other species (32), and Table 2 lists a selection. The usual finding is that tolerant material mounts a stronger or better-coordinated antioxidant response, but the details vary, and the studies differ in which enzyme moved, in which tissue and at what time.

A limitation runs through the table. Almost all of these studies sampled seedlings, roots or leaves, not imbibing seeds, and the seed has its own reserves, compartments and a developmental programme that changes hour by hour. Extending seedling results to germination is thus an assumption, and the evidence that would test it directly is much thinner. Even among seedling studies, salt concentration, sampling time and tissue differ so widely that a ranking of tolerance from one paper may not hold in another. That is a cautious statement, but it is the one the published work will currently bear.

**Table 2.** Examples of tolerant versus sensitive comparisons and what they report.

System	Tissue studied	Reported pattern
Wheat genotypes	Seedlings	Tolerant genotypes kept higher antioxidant activity (33)
Cultivated tomato and wild relative	Roots	Wild tolerant species up-regulated its defences (34, 35)
Rice cultivars	Roots	Tolerance linked to less lipid damage; tissue-specific (36)
Pea	Whole plant, long exposure	Tolerance linked to induced defences (37)
Plantago species	Leaves	Enzymes responded differently in tolerant and sensitive species (38)

Note: Findings are paraphrased qualitatively from the cited papers; none of the studies listed sampled imbibing seeds as the main material.

3. Materials and Methods

3.1 Scope and Question

The review asks one question in two parts. What do published measurements of antioxidant enzymes under salinity show about germinating seeds, and how far can an increase in activity be read as evidence of tolerance? None of these choices is exotic, but each one leaves a trace in the numbers that follow.

3.2 Literature Assembly

The review draws on peer-reviewed work on seed oxidative biology, the enzyme system and its assays, salinity physiology, and comparisons of tolerant and sensitive material. Studies of seedlings are used to show what the enzymes do, and not as proof of what happens in the seed.

We ran no formal systematic search and claim none; this is a narrative synthesis and the choice of sources reflects the authors' judgement. The review is

therefore a better guide to how a measurement should be read than to the size of any effect, and it quotes no numerical results.

3.3 Appraisal Framework

To judge how far a report can be trusted we used four questions. Which stage and tissue were sampled, given how differently the phases of water uptake behave (3)? Was there an osmotic control (2)? How was activity expressed, and by what assay (39, 40)? And was a damage marker reported alongside (28)? Table 3 sets out why each matters. A reader comparing two papers needs to know how each of these was handled before comparing a single value.

Table 3. Design points that change how an enzyme result can be read.

Design point	Why it matters	Reporting need
Tissue and stage	Axis and storage tissue differ; so do phases of water uptake (3)	Name the stage and tissue
Osmotic control	Salt effects are partly osmotic (2)	Iso-osmotic non-salt treatment
Expression of activity	Per protein, per fresh weight and per seed differ (39)	State the basis used
Damage marker	Activity without damage data is ambiguous (28)	Report peroxidation alongside
Seed lot history	Ageing alters enzymes and lipids (16)	Report storage and vigour

Note: Points are drawn from the methodological papers cited; they are not attributed to any single study.

4. Results

4.1 Enzyme Responses Are Real but Not Uniform

Across the studies in Table 2, salt changed antioxidant enzyme activity in nearly every system, and in tolerant material the change



more often pointed towards stronger defence. The pattern was not uniform, however. Different enzymes moved in different directions, one tissue responded while another did not, and sometimes the sensitive genotype showed the larger rise, presumably under greater oxidative load (36, 38, 41). A higher activity can thus mean a better-defended tissue or a more heavily stressed one.

Time adds another layer: tolerance in pea was reported as a feature of prolonged treatment, with defences induced over time (37), so a single sampling time may capture a transient and call it a trait. The same enzyme can therefore tell different stories depending on when the seeds were sampled.

4.2 Timing and Tissue in the Germinating Seed

The seed adds problems that seedling work does not. Figure 2 places the oxidative events described above on the three phases of water uptake: reactive oxygen species appear as respiration restarts (8, 10), and signalling roles follow as germination proceeds (11, 12). Measurements on a whole seed average over embryonic axis and storage tissue, which differ in function, so a change in one can be masked by the other.

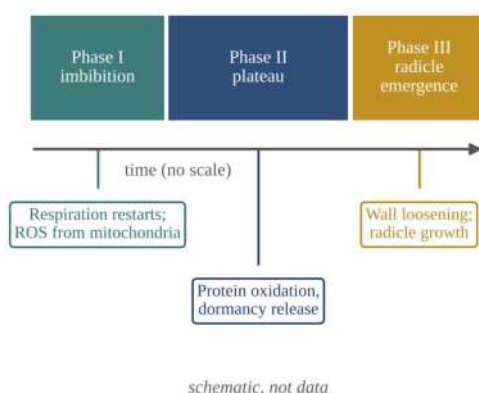


Figure 2. Phases of water uptake in germination with the oxidative events discussed in the text (schematic, not data).

A seed sampled after a fixed number of hours in salt may be at a different phase from its control, because salt delays germination (2), so the enzyme difference mixes the effect of salt with that of developmental stage. A seed that has barely begun to take up water behaves differently from one with a protruding radicle.

4.3 Reading the Numbers: Activity and Damage Together

Because activity can rise for opposite reasons, we read it together with a damage marker; Figure 3 gives the matrix. Higher activity with less lipid damage is the usual evidence for effective defence; higher activity with more damage suggests defence that is present but overwhelmed; lower activity with more damage is a failure of the system; and lower activity with little damage may mean that the stress has not reached the seed or that other protection is acting (26, 27). The distinction matters, because only one of these readings predicts a seed that will go on to establish.

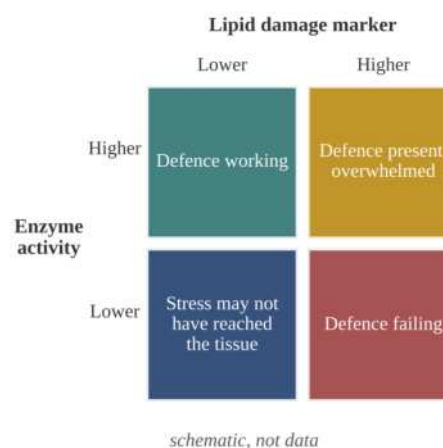


Figure 3. Reading matrix for an enzyme result paired with a damage marker (schematic, not data).

Few papers report both quantities on the same tissue, though some do (36, 41). The way activity is expressed adds to the uncertainty, since a value per unit protein, per fresh weight or per seed can move



differently as imbibition proceeds (19, 39). This is one reason why apparently identical treatments give conflicting reports.

5. Discussion

5.1 Interpretation

The main finding is a qualified one. Enzyme activity does respond to salinity, and tolerant material often responds more effectively, but a rise in activity is not by itself evidence of tolerance, least of all in seeds. The strongest support comes from seedlings and plants, and it travels to the seed only with assumptions that are rarely tested (32, 33, 35). Nothing in this reading argues against measuring enzymes; it argues for measuring them with their context.

A second point concerns the dual role of reactive oxygen species. If they are needed for germination, strong antioxidant capacity could also dampen useful signalling (9, 14). That is a hypothesis from the signalling literature, not a result, but it is a reason not to treat higher activity as always better. Reviews of this kind are more useful when they mark where the evidence stops than when they smooth it over.

5.2 Limitations

This is a narrative review and shares the limitations of that form. The selection of sources reflects judgement, and no formal search or quality scoring was done. A reader who needs an effect size should consult the original papers, applying the questions in Table 3. It is a habit worth keeping even when the result looks expected.

5.3 Future Work

Three needs stand out: studies that sample imbibing seeds at defined phases, with axis and storage tissue separated; designs that pair every salt treatment with an

iso-osmotic control and report damage markers; and work that follows isoforms and the ascorbate and glutathione cycle, so that a change in total activity can be traced to its source (18, 22). These cautions apply to any stress treatment, not only to salt.

6. Conclusion

Antioxidant enzyme activity in germinating seeds under salinity is a useful but easily over-read measurement. Salt changes it, tolerant material often differs from sensitive material, and reactive oxygen species have a role in germination as well as in injury. What the literature does not yet show is that higher activity in the imbibing seed means greater tolerance. An enzyme assay should be read with a damage marker, an osmotic control and a clear statement of the stage and tissue sampled.

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9. Conflict of Interest

The authors declare no conflict of interest.

10. Author Contributions

A.Z. conceived the review and wrote the sections on seed biology and salinity. L.J. wrote the sections on the antioxidant enzyme system and assays. I.A. wrote the sections on genotype comparisons and study design. All authors revised the manuscript and approved the final version.

11. Ethics Statement

This is a review of published literature. No human participants or animals were involved and no ethical approval was



required.

12. Data Availability

No new data were generated. All sources are cited in the reference list.

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