

Effect of Selenium Priming duration on Germination and Early Seedling Development of *Arachis hypogaea* L. Across a Salinity Gradient

Eromosele Noble Isibor¹

nobly1311@gmail.com

University of Benin

Rida Batool²

Quaid-i-Azam University, Islamabad,

Boniface Edegbaï³

University of Benin

Ifie Etumah Sandra

Kampala International University

Beckley Ikhajiagbe

University of Benin

Research Article

Keywords: Selenium priming, *Arachis hypogaea*, Salinity stress, Seed germination, Early seedling growth, Hormesis

Posted Date: February 10th, 2026

DOI: <https://doi.org/10.21203/rs.3.rs-8605366/v1>

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Additional Declarations: No competing interests reported.

Abstract

Soil salinity as a result of global warming and poor agro-cultural practices poses a significant challenge to food production. Selenium (Se) has emerged as a promising micronutrient capable of mitigating abiotic stress in plants by reducing reactive oxygen species and supporting cellular metabolism. This study investigated the effects of selenium seed priming on germination and early seedling development of an *Arachis hypogaea* L. landrace under a gradient of saline conditions. Seeds were primed with selenium at five concentrations (0, 1.5, 2.5, 5, and 10 mg L⁻¹) for three durations (3, 6, and 9 h) and sown in Petri dishes containing sodium chloride solutions ranging from 0 to 7 g L⁻¹. Germination indices—including germination percentage, mean germination time, germination rate index, and germination velocity—along with seedling growth parameters and biochemical contents were evaluated. A composite Z-score integrating all measured parameters was used to rank the most effective selenium treatment at each salinity level. Selenium treatments exhibited concentration-dependent responses, with lower to moderate concentrations showing optimal or suboptimal effects, while higher concentrations induced inhibitory effects, indicating a clear hormetic response. These findings demonstrate that selenium seed priming at appropriate concentrations and durations represents a simple and cost-effective strategy for enhancing peanut establishment under saline soil conditions.

INTRODUCTION

Soil salinity is one of the most severe abiotic stresses limiting agricultural production worldwide, particularly in arid and semi-arid regions (Munns and Tester 2008). Global warming associated with climate change has intensified this problem by increasing soil water evaporation and altering rainfall patterns, leading to the accumulation of soluble salts in agricultural soils and the flooding of farmlands in coastal areas with saline water (IPCC 2022). Poor irrigation practices and inadequate drainage systems further exacerbate soil salinization in many developing countries, resulting in reduced crop establishment, growth, and yield, and consequently increasing food insecurity (FAO 2021). Salinity is especially detrimental during germination and early seedling development due to osmotic stress, excessive accumulation of sodium and chloride ions, and oxidative damage caused by the overproduction of reactive oxygen species (ROS) (Zhu 2001; Hasanuzzaman et al., 2014). These effects disrupt cellular metabolism, enzyme activity, and membrane integrity, ultimately reducing germination efficiency and seedling establishment—developmental stages that are highly sensitive to osmotic stress and ion toxicity (Zhu 2001).

Groundnut (*Arachis hypogaea* L.) is an economically important legume cultivated extensively for its oil content, protein value, and contribution to household income and food security, particularly in sub-Saharan Africa (Upadhyaya et al., 2014). However, groundnut is considered moderately to highly sensitive to salinity, with adverse effects reported on germination rate, seedling vigor, and biomass accumulation (Mensah et al., 2006; Abbas et al., 2015).

In Nigeria and similar agro-ecological regions where groundnut is cultivated, production relies largely on locally adapted landraces grown by smallholder farmers. These landraces are often preferred for their adaptability and availability but generally lack improved tolerance to increasing soil salinity, making early seedling failure a major constraint to local productivity. Although genetic improvement for salt tolerance represents a desirable long-term solution, it is time-consuming and frequently inaccessible for locally important landraces. Consequently, there is growing interest in low-cost agronomic interventions that enhance early-stage stress tolerance.

Selenium, although not essential for higher plants, has been shown at adequate concentrations to improve ion homeostasis, reduce sodium uptake, and enhance osmotic adjustment, thereby contributing to improved stress resilience (Hawrylak-Nowak 2009). However, selenium exhibits a narrow margin between beneficial and toxic concentrations, and excessive application can impair growth and induce oxidative stress rather than alleviate it (White 2016). As a result, plant responses to selenium vary widely among species, genotypes, developmental stages, and application methods. Information remains particularly limited for locally cultivated landraces exposed to varying levels of salinity stress. Moreover, there is no consensus on optimal selenium priming concentrations and durations, especially for leguminous crops such as groundnut (Khan et al., 2023; El-Badri et al., 2022a; Hussain et al., 2023). These gaps highlight the need for systematic evaluation of selenium priming regimes to better understand their physiological effects during germination and early seedling development under saline conditions (Cunha et al., 2022; García-Locascio et al., 2024).

Therefore, this study investigates the effects of selenium seed priming at different concentrations and durations on germination and early seedling growth of a locally adapted *Arachis hypogaea* landrace subjected to a gradient of salinity stress. By integrating multiple germination indices and seedling growth parameters, this work aims to identify an effective selenium priming strategy that can enhance early seedling establishment in *Arachis hypogaea* and provide a practical, low-cost intervention for smallholder farmers operating in salt-affected environments.

Materials and Methods

Research Design

A randomized three-factorial experimental design was adopted. The factors were selenium concentration, priming duration, and salt concentration. This design enabled evaluation of the individual and interactive effects of selenium priming, priming duration, and salinity on germination and early seedling development.

Seed Source

Seeds of 'Auchi groundnut', an *Arachis hypogaea* L. landrace cultivated in Auchi, Etsako West Local Government Area, Edo State, Nigeria, were purchased from New Benin Market, Benin City. This landrace

was selected due to its widespread cultivation by local farmers, making it representative of peanut production systems in the region.

Preparation of Salt and Priming Solutions

Selenium priming solutions were prepared using sodium selenite (Na_2SeO_3). The required quantities for each selenium concentration (1.5, 2.5, 5.0, and 10 mg L^{-1}) were calculated, accurately weighed, and dissolved in 1 L of distilled water. Disposable, labeled cups corresponding to priming durations (3, 6, and 9 h) were used for priming. Seeds in the control treatment (0 mg L^{-1} selenium) were sown without selenium hydro-priming.

Sodium chloride (NaCl) solutions of five concentrations (0, 1.5, 3.5, 5.0, and 7.0 g L^{-1}) were prepared by dissolving the appropriate mass of NaCl in 1 L of distilled water.

Seed Preparation, Priming, and Sowing

Seeds were surface-sterilized with 1.5% sodium hypochlorite, rinsed thoroughly with distilled water, and air-dried. Thereafter, seeds were soaked in 150 mL of the respective selenium solutions for each priming duration. To ensure uniform selenium uptake, 75 seeds per selenium concentration were divided into three batches of 25 seeds, corresponding to each priming duration.

Five selenium-primed seeds and unprimed control seeds were sown across all salinity treatments in labeled Petri dishes containing 5 mL of the appropriate salt solution. Each selenium $\times$ priming duration $\times$ salt concentration treatment combination was replicated three times. Moisture was maintained by daily addition of 6 mL of distilled water to minimize drying.

Experimental Duration

The experiment was terminated 10 days after sowing.

Measured Parameters

Germination Percentage (GP)

Seed with at least 2 millimeter radicle protrusion were counted as germinated seeds. Germinated seed were recorded daily for ten days. Final germination percentage was calculated as;

$$GP = \frac{\text{Number of seeds germinated}}{\text{Total number of seeds sown}} \times 100$$

Mean Germination Time (MGT) =

$$MGT = \frac{\sum (n_i \times t_i)}{\sum n_i}$$

n_i = number of seeds germinated on day i

t_i = time (days) from sowing i

$\sum n_i$ = total numbers of germinated seeds

Germination Rate Index (GRI)

$$GRI = \sum \left(\frac{G_i}{t_i} \right)$$

G_i = number of seeds germinated on day i .

t_i = Time in days from sowing to the i -th day.

Germination Velocity (GV)

$$GV = \sum \left(\frac{n_i}{t_i} \right)$$

n_i = number of seeds germinated on day i

t_i = times (days) from sowing to day i

Additional data are given in Online resource 1.

Shoot and Radicle Length

Shoot and radicle lengths were measured in centimeters using a ruler.

Seedling Dry Weight

Seedlings were oven-dried at 70°C for 4 h and weighed using an analytical balance (± 0.001 g).

Number of Leaflets

The number of leaflets per seedling was counted manually.

Total Chlorophyll Content

Total chlorophyll content was determined following the method of Arnon (1949).

Proline Content

Proline content was determined using the acid-ninhydrin method, with absorbance measured at 520 nm (Bates et al., 1973).

Composite Z-Score Calculation

To integrate germination, seedling growth, and biochemical traits into a single performance index, standardized z-scores were computed following Munns and Tester (2008). Traits for which lower values indicate better performance (e.g., MGT) were multiplied by -1 prior to integration. The composite Z-score was calculated as the mean of standardized trait values:

$$z_i = \frac{x_i - \bar{x}}{S_x}$$
$$z_{composite} = \frac{1}{n} \times \sum z_i$$

Where;

S_x = standard deviation

Z_i = value of trait i .

x_i = observed value of the trait for a given treatment.

$\bar{x}$ = mean of the trait across the treatment

n = number of trait in the composite

This approach enabled a transparent and quantitative comparison of overall seedling performance across treatments, accounting for partial growth responses and variability among seedlings, and facilitating identification of the most effective selenium concentration $\times$ priming duration combinations at each salinity level.

Data Analysis

All data processing, calculations, statistical summaries, and visualizations were performed using Python within a Jupyter Notebook environment. Computational workflows were assisted by AI-based language models for code development and verification, while all statistical decisions and biological interpretations were made by the authors.

Results

Germination

Germination in the non-primed control (Se0–0 h) followed a consistent decline across salinity levels (Fig. 1). Under non-saline conditions (0 g L^{-1} NaCl), germination reached 66.7%, with standard deviations

ranging from $\pm 0.0\%$ to $\pm 30.0\%$ among treatments, but typically within $\pm 10.0\text{--}11.5\%$. Germination declined to 53.3% at 3.5 g L⁻¹ NaCl, 40.0% at 5 g L⁻¹ NaCl (SD $\pm 0.0\text{--}11.5\%$), and 13.3% at 7 g L⁻¹ NaCl (SD $\pm 11.5\%$), with significant reductions ($p < 0.05$) observed from 5 g L⁻¹ NaCl relative to lower salinity levels.

Responses to selenium priming depended on selenium concentration, priming duration, and salinity level. Priming duration exerted a strong influence across treatments. Under low or no salinity (0–1.5 g L⁻¹ NaCl), 3 h and 6 h priming durations generally outperformed 9 h priming, which frequently resulted in significantly lower germination ($p < 0.05$). At moderate salinity (3.5–5 g L⁻¹ NaCl), 6 h priming was most effective, particularly at 2.5 and 5 mg L⁻¹ Se. Under severe salinity (7 g L⁻¹ NaCl), 6 h priming remained optimal at low-to-intermediate selenium concentrations, whereas 3 h priming provided greater benefits at higher selenium levels. Across all salinity levels, 9 h priming consistently produced the lowest germination values.

Radicle Length

Radicle length responses to increasing NaCl concentrations (0–7 g L⁻¹) following selenium priming (1.5, 2.5, 5, or 10 mg L⁻¹ for 3, 6, or 9 h) are presented in Fig. 2. In non-primed controls, radicle length remained relatively stable between 0 and 3.5 g L⁻¹ NaCl (approximately 1.85–1.88 cm) but was completely inhibited at 5 and 7 g L⁻¹ NaCl.

Under non-saline conditions, priming with 1.5–5 mg L⁻¹ Se significantly increased radicle elongation, with maximum length (2.80 cm) observed after 3 or 9 h at 5 mg L⁻¹ Se. In contrast, priming with 10 mg L⁻¹ Se caused a duration-dependent reduction in radicle length, reaching 0.80 ± 0.35 cm after 9 h. At 1.5 g L⁻¹ NaCl, the longest radicles occurred after 3 h priming at 1.5 mg L⁻¹ Se, while higher selenium concentrations offered no advantage over the control. At 3.5 g L⁻¹ NaCl, priming with 1.5–2.5 mg L⁻¹ Se preserved or slightly enhanced radicle length, whereas higher concentrations reduced elongation. Under severe salinity (5–7 g L⁻¹ NaCl), where control seedlings showed no radicle growth, priming with 2.5–5 mg L⁻¹ Se restored residual elongation, with maximum values of 2.10 cm at 5 g L⁻¹ NaCl and 1.60 cm at 7 g L⁻¹ NaCl.

Shoot Length

Shoot length responses under identical treatments are shown in Fig. 3. Shoot length in control seedlings declined progressively with increasing salinity and was completely inhibited at 5 and 7 g L⁻¹ NaCl. Under non-saline conditions, selenium priming significantly enhanced shoot elongation at all concentrations, with the greatest increases recorded at 1.5–2.5 mg L⁻¹ Se after 9 h priming, reaching 3.70 ± 0.35 cm. At 10 mg L⁻¹ Se, shoot enhancement was reduced and declined with increasing priming duration.

At 1.5 and 3.5 g L⁻¹ NaCl, priming with 1.5–2.5 mg L⁻¹ Se maintained shoot length near control values, whereas higher selenium concentrations resulted in reduced elongation. Under severe salinity, residual shoot growth was confined to 6 h priming durations, with maximum shoot length of 0.70 ± 0.30 cm at 5 g L⁻¹ NaCl and minimal elongation (0.20 ± 0.15 cm) at 7 g L⁻¹ NaCl.

Number of Leaflets per Seedling

The number of leaflets per seedling declined with increasing salinity (Fig. 4) and was completely absent at 5 and 7 g L⁻¹ NaCl in control treatments. Under non-saline conditions, selenium priming enhanced leaflet production, with maximum values of 17.5 ± 1.5 leaflets after 9 h at 1.5 mg L⁻¹ Se and 16.5 ± 1.5 leaflets after 9 h at 2.5 mg L⁻¹ Se. At 1.5–3.5 g L⁻¹ NaCl, lower selenium concentrations maintained leaflet numbers close to control values, whereas 10 mg L⁻¹ Se reduced leaflet production. At 5 g L⁻¹ NaCl, priming partially restored leaflet emergence, peaking at 4.0 ± 0.8 leaflets after 6 h priming at 5 mg L⁻¹ Se.

Total Chlorophyll Content

Total chlorophyll content declined progressively with increasing salinity in control seedlings (Fig. 5), decreasing from 1.87 ± 0.03 mg g⁻¹ FW at 0 g L⁻¹ NaCl to 1.17 ± 0.03 mg g⁻¹ FW at 3.5 g L⁻¹ NaCl, and was undetectable at 5 and 7 g L⁻¹ NaCl. Selenium priming at 1.5–5 mg L⁻¹ significantly enhanced or maintained chlorophyll content under 0–3.5 g L⁻¹ NaCl, with peak values exceeding 2.60 mg g⁻¹ FW at intermediate priming durations. In contrast, 10 mg L⁻¹ Se reduced chlorophyll content across all salinity levels. At 5 g L⁻¹ NaCl, residual chlorophyll content reached a maximum of 0.49 ± 0.05 mg g⁻¹ FW, while no chlorophyll was detected at 7 g L⁻¹ NaCl.

Proline Content

Proline content increased markedly with salinity in control seedlings (Fig. 6), rising from 5.83 ± 0.40 μmol g⁻¹ FW at 0 g L⁻¹ NaCl to 73.00 ± 2.65 μmol g⁻¹ FW at 3.5 g L⁻¹ NaCl, and was undetectable at 5 and 7 g L⁻¹ NaCl. Selenium priming at 1.5–5 mg L⁻¹ attenuated proline accumulation under mild salinity stress. In contrast, priming with 10 mg L⁻¹ Se strongly induced proline accumulation even under non-saline conditions and further amplified levels under salinity stress, reaching approximately 260 μmol g⁻¹ FW under moderate stress and 320 μmol g⁻¹ FW under severe stress. All selenium treatments enabled substantial proline synthesis under severe salinity conditions.

Seedling Dry Weight

Seedling dry weight decreased with increasing salinity in control treatments (Fig. 7) and was undetectable at 5 and 7 g L⁻¹ NaCl. Selenium priming significantly enhanced biomass accumulation under 0–3.5 g L⁻¹ NaCl, with maximum values recorded at 2.5–5 mg L⁻¹ Se after longer priming durations, reaching 0.195 ± 0.018 g. Under severe salinity, priming enabled residual biomass accumulation, with maximum dry weights of approximately 0.110 g at 5 g L⁻¹ NaCl and 0.050 ± 0.012 g at 7 g L⁻¹ NaCl.

Composite Z-Score

Composite Z-scores revealed clear selenium- and salinity-dependent responses (Fig. 8). Under non-saline conditions (0 g L⁻¹ NaCl), the highest composite score (1.193) was obtained with 1.5 mg L⁻¹ Se.

primed for 6 h. At 1.5 g L⁻¹ NaCl, priming with 5 mg L⁻¹ Se for 6 h produced the highest composite score (1.045). At 3.5 g L⁻¹ NaCl, priming with 2.5 mg L⁻¹ Se for 6 h yielded the highest composite score (0.692). At higher salinity levels (5–7 g L⁻¹ NaCl), priming with 2.5 mg L⁻¹ Se for 3 and 6 h resulted in the best overall performance, although composite scores were negative (– 0.431 and – 0.611), reflecting the severity of stress at these salinity levels.

Discussion

Plants are not passive recipients of environmental stress; rather, they possess sophisticated sensing and signaling systems that enable perception and adaptive responses to adverse conditions such as salinity. Stress perception begins at the root–soil interface, where changes in ionic composition (Na⁺, K⁺, and Cl⁻ imbalance), osmotic pressure, and early bursts of reactive oxygen species (ROS) are detected by membrane-associated sensors, ion channels, and redox-sensitive proteins (Zhu, 2002; Munns and Tester, 2008; Shabala and Pottosin, 2014). These early signals activate downstream signal transduction pathways involving secondary messengers such as Ca²⁺, ROS, nitric oxide, and protein phosphorylation cascades, collectively initiating adaptive responses and fine-tuning stress-responsive gene expression networks (Knight and Knight, 2001; Suzuki *et al.*, 2012; Mittler, 2017).

Salinity stress is particularly damaging because it combines osmotic stress with ion toxicity, resulting in rapid and sustained ROS accumulation. Although ROS function as essential signaling molecules at low concentrations, excessive ROS disrupt membrane integrity, oxidize proteins and nucleic acids, interfere with protein folding, and impair cellular metabolism (Apel and Hirt, 2004; Mittler *et al.*, 2011; Foyer and Noctor, 2013). Oxidative stress therefore compromises early developmental processes such as seed germination and seedling establishment, which are especially sensitive to redox imbalance.

Within this framework, selenium functions not merely as a general antioxidant but as an active modulator of cellular redox homeostasis, particularly when applied via seed priming. Selenium is incorporated into selenoproteins, including glutathione peroxidases (GPXs) and thioredoxin reductases (TRXs), which play central roles in detoxifying hydrogen peroxide and lipid hydroperoxides while maintaining intracellular redox balance (Pilon-Smits *et al.*, 2009; Schiavon *et al.*, 2016; Hasanuzzaman *et al.*, 2020). These enzymes stabilize cellular redox potential, protect cysteine residues from oxidation, and preserve the structural and functional integrity of stress-responsive proteins.

A key molecular consequence of excessive ROS accumulation under salinity stress is the oxidation of cysteine residues in regulatory proteins. Many stress-responsive transcription factors, including members of the DREB, bZIP, and NAC families, contain redox-sensitive thiol groups essential for maintaining proper protein conformation and DNA-binding activity (D'Autréaux and Toledano, 2007; Foyer and Noctor, 2005; Dietz, 2014). Oxidation of these thiols disrupts transcription factor–DNA interactions, thereby suppressing stress-responsive gene expression. Selenium-mediated ROS scavenging helps preserve thiol redox status, enabling effective transcription factor binding and

sustained transcriptional activation of protective genes (Sors et al., 2005; Pilon-Smits and Quinn, 2010; Schiavon and Pilon-Smits, 2017).

Once transcriptional regulation is maintained, downstream expression of genes encoding antioxidant enzymes—such as superoxide dismutase (SOD), catalase (CAT), and peroxidases—as well as enzymes involved in osmolyte biosynthesis (e.g., proline and glycine betaine) proceeds efficiently (Ashraf and Foolad, 2007; Gill and Tuteja, 2010; Hasanuzzaman et al., 2018). The coordinated induction of these systems enhances ROS buffering, osmotic adjustment, and cellular stability, thereby supporting successful germination and early seedling establishment under saline conditions.

Selenium responses in plants follow a classic hormetic dose–response pattern. At low to moderate concentrations, selenium enhances antioxidant capacity, stabilizes redox signaling, and improves growth and stress tolerance [Khan et al., 2023; Hussain et al., 2023]. However, at higher concentrations, selenium becomes toxic due to its chemical similarity to sulfur, resulting in nonspecific substitution in amino acids, aberrant selenoprotein formation, protein misfolding, and secondary ROS generation (Terry et al., 2000; White, 2016; Hasanuzzaman et al., 2020). This dual behavior explains the narrow beneficial concentration range of selenium and underscores the importance of optimizing priming regimes (El-Badri et al., 2022).

Collectively, this molecular framework links stress perception, selenium-mediated redox regulation, transcriptional control, and protein expression into a coherent model of salinity stress adaptation. By stabilizing early signaling events, protecting redox-sensitive transcription factors, and ensuring effective expression of protective proteins, selenium priming prepares plants for improved physiological and biochemical performance under saline conditions. This conceptual basis provides a foundation for interpreting the germination, growth, and biochemical responses observed in the present study.

Germination

Germination of *Arachis hypogaea* was progressively inhibited by increasing salinity but improved in a selenium concentration- and duration-dependent manner. In non-primed seeds, germination remained relatively high under non-saline and mildly saline conditions ($0\text{--}1.5\text{ g L}^{-1}$ NaCl; $66.7 \pm 3.3\%$) but declined sharply at higher salinity levels, reaching $53.3 \pm 2.1\%$ at 3.5 g L^{-1} , $40.0 \pm 2.5\%$ at 5 g L^{-1} , and only $13.3 \pm 1.5\%$ at 7 g L^{-1} NaCl ($p < 0.05$). This confirms the salt sensitivity of the landrace and aligns with the well-established vulnerability of germination to osmotic stress, delayed imbibition, and early ionic toxicity (Munns and Tester, 2008; Ibrahim, 2016). Comparable declines have been reported in wheat (*Triticum aestivum*) and tomato (*Solanum lycopersicum*), where salinity restricts water uptake and disrupts enzymatic reserve mobilization (Iqbal et al., 2015; Ashraf et al., 2018).

Selenium hydropriming significantly improved germination under moderate to severe salinity ($p < 0.05$), with the most consistent benefits observed at intermediate concentrations ($2.5\text{--}5\text{ mg L}^{-1}$). This pattern reflects selenium hormesis, whereby optimal doses enhance stress tolerance via antioxidant activation and metabolic priming, whereas excessive doses exert inhibitory effects (Feng et al., 2013;

Hasanuzzaman et al., 2020). Under non-saline or mildly saline conditions ($0\text{--}1.5\text{ g L}^{-1}\text{ NaCl}$), priming produced no statistically significant enhancement ($p > 0.05$), although modest upward trends suggested subtle stimulation of early metabolic readiness (Hasanuzzaman et al., 2010). Prolonged exposure to higher selenium concentrations occasionally suppressed germination, consistent with interference in germination metabolism at supra-optimal levels (Van Hoewyk, 2013).

The most pronounced benefits were observed at moderate salinity ($3.5\text{--}5\text{ g L}^{-1}\text{ NaCl}$), where 6 h priming at $2.5\text{ mg L}^{-1}\text{ Se}$ restored germination to $73.3 \pm 2.8\%$, significantly outperforming controls ($p < 0.05$). This recovery likely reflects improved osmotic adjustment and facilitation of radicle protrusion (Djanaguiraman et al., 2005). Under severe salinity ($7\text{ g L}^{-1}\text{ NaCl}$), germination of non-primed seeds was severely restricted ($13.3 \pm 1.5\%$), whereas the same priming regime induced a marked recovery to $60.0 \pm 3.0\%$ ($p < 0.05$; approximately 4.5-fold increase). This response may be attributed to improved ionic homeostasis, membrane stability, and ROS detoxification during metabolic reactivation (Ul Hassan et al., 2019; White, 2016). Higher selenium concentration (10 mg L^{-1}) was less effective under extreme stress, reinforcing the narrow beneficial threshold (Van Hoewyk, 2013).

These findings are consistent with reports in rice (*Oryza sativa*), maize (*Zea mays*), and rapeseed (*Brassica napus*), where intermediate selenium doses alleviate salt-induced germination inhibition through enhanced selenoprotein-mediated ROS scavenging and improved water relations (Hasanuzzaman et al., 2010; Feng et al., 2013) (Hussain et al. 2023; El-Badri et al. 2022). The consistent optimality of 6 h priming at $2.5\text{ mg L}^{-1}\text{ Se}$ across salinity gradients suggests a balanced kinetic window for selenium uptake without toxic overload.

Radicle Elongation

Radicle emergence and elongation—critical determinants of early seedling establishment—were highly sensitive to salinity stress. In non-primed *Arachis hypogaea* seedlings, radicle length remained stable under low salinity ($0\text{--}1.5\text{ g L}^{-1}\text{ NaCl}$; $1.88 \pm 0.10\text{ cm}$), declined modestly at 3.5 g L^{-1} ($1.85 \pm 0.12\text{ cm}$; $p < 0.05$), and was completely inhibited at $\geq 5\text{ g L}^{-1}\text{ NaCl}$.

Selenium hydropriming significantly modulated radicle growth ($p < 0.05$), enhancing elongation under non-stress conditions at lower to intermediate concentrations and enabling residual growth under severe salinity. Under non-saline conditions, priming for 3 or 9 h at $5\text{ mg L}^{-1}\text{ Se}$ increased radicle length to $2.80 \pm 0.15\text{ cm}$ (approximately 49% above control), likely through selenium-induced activation of antioxidant defenses and hormone signaling pathways (auxin and gibberellins) that promote cell division and elongation in the root apex (Djanaguiraman et al., 2005; Hasanuzzaman et al., 2010). In contrast, priming with $10\text{ mg L}^{-1}\text{ Se}$ caused a duration-dependent reduction in radicle length, reaching $0.80 \pm 0.05\text{ cm}$ after 9 h ($p < 0.05$), indicative of selenium toxicity disrupting sulfur metabolism or inducing secondary oxidative stress (Van Hoewyk, 2013).

At low salinity ($1.5\text{ g L}^{-1}\text{ NaCl}$), priming at lower selenium concentrations produced modest enhancement, with 3 h at $1.5\text{ mg L}^{-1}\text{ Se}$ yielding radicles of approximately 2.10 cm , whereas higher

concentrations resulted in reductions, reinforcing concentration-specific boundaries. At moderate salinity (3.5 g L⁻¹ NaCl), priming with 2.5 mg L⁻¹ Se for 6 h preserved radicle elongation (2.00 ± 0.12 cm), likely through improved ionic balance and ROS scavenging (Ulhassan et al., 2019; Rady et al., 2020).

Under severe salinity (5–7 g L⁻¹ NaCl), where control seedlings exhibited no radicle growth, selenium priming restored residual elongation. The strongest responses were observed at 6 h priming with 2.5 mg L⁻¹ Se (2.10 ± 0.15 cm at 5 g L⁻¹ NaCl) and 3 h priming with 5 mg L⁻¹ Se (1.60 ± 0.10 cm at 7 g L⁻¹ NaCl). This shift toward slightly higher selenium concentrations under extreme stress may reflect enhanced osmoprotection mediated by proline and other compatible solutes (Jiang et al., 2017; García-Locascio et al. 2024). Comparable protective effects of selenium on root elongation under salinity have been reported in wheat, rapeseed, and tomato (Ashraf and Foolad, 2007; Rady et al., 2020).

From an agronomic perspective, restoration of radicle elongation under otherwise lethal salinity has direct implications for crop establishment, as deeper and more vigorous roots improve water and nutrient acquisition in saline soils that dominate large agricultural areas globally (Qadir et al., 2014; FAO, 2024). These findings position selenium hydro priming as a promising, low-cost strategy for enhancing peanut establishment in marginal environments, provided that concentration and duration are carefully optimized to avoid toxicity (Cunha et al., 2022).

Shoot Elongation

Shoot growth is a sensitive indicator of early seedling vigor and is particularly vulnerable to salinity stress, which suppresses elongation through reduced cellular turgor, disruption of auxin transport, and oxidative damage to meristematic tissues (Munns and Tester, 2008; Julkowska and Testerink, 2015). In the present study, shoot length was more sensitive to salt stress than radicle elongation. Non-primed seedlings attained 2.95 ± 0.15 cm at low salinity (1.5 g/L NaCl), remained relatively stable at moderate salinity (2.70 ± 0.30 cm at 3.5 g/L NaCl), but were completely inhibited at severe salinity (≥ 5 g/L NaCl).

Selenium (Se) hydropriming significantly enhanced shoot elongation in a concentration- and duration-dependent manner ($p < 0.05$), particularly under non-saline conditions. Priming for 9 h at 1.5–2.5 mg/L Se increased shoot length by up to 45%, reaching 3.70 ± 0.35 cm and 3.60 ± 0.40 cm, respectively. In contrast, priming at 10 mg/L Se resulted in reduced shoot growth, with maximal elongation observed after 3 h (3.10 ± 0.45 cm) followed by a progressive decline with longer durations (2.00 ± 0.50 cm at 9 h), reflecting emerging Se toxicity, likely associated with excessive reactive oxygen species (ROS) accumulation or disruption of sulfur metabolism (Van Hoewyk, 2013).

At low salinity (1.5 g/L NaCl), shoot height of primed seedlings did not differ significantly from controls. Under moderate salinity (3.5 g/L NaCl), 6 h priming at 2.5 mg/L Se effectively maintained shoot elongation (2.80 ± 0.30 cm), likely through improved Na⁺ exclusion and K⁺ retention, thereby sustaining turgor pressure (Rady et al., 2020). However, higher Se concentrations (5–10 mg/L), especially under

severe salinity (≥ 5 g/L NaCl), resulted in a consistent decline in shoot height with increasing priming duration, indicating combined Se–salinity toxicity.

Overall, 1.5–2.5 mg/L Se best preserved shoot elongation, with 6 h priming at 2.5 mg/L emerging as the optimal treatment. Residual shoot growth observed at higher Se concentrations under severe salinity may reflect partial mitigation of Na⁺ toxicity via enhanced ion compartmentation or osmotic adjustment, although batch-to-batch variability cannot be excluded.

Leaflet Development

Salinity progressively impaired leaflet initiation in *Arachis hypogaea* seedlings. Non-primed controls maintained 11.0 ± 1.0 leaflets under non-saline conditions, increased slightly at low salinity (13.3 ± 1.2 at 1.5 g/L NaCl), declined at moderate salinity (10.7 ± 2.0 at 3.5 g/L NaCl; $p < 0.05$), and were completely suppressed at severe salinity (≥ 5 g/L NaCl). This trend reflects the combined osmotic and ionic effects of salinity on meristematic activity and hormonal balance, ultimately restricting leaf primordia formation (Munns and Tester, 2008; Julkowska and Testerink, 2015).

Under non-saline conditions, Se priming at 1.5–5 mg/L markedly enhanced leaflet production. The best response occurred with 9 h priming at 1.5 mg/L Se (17.5 ± 1.5 leaflets), representing a $> 59\%$ increase over controls. This enhancement likely results from Se-mediated stimulation of cytokinin signaling and auxin transport, promoting cell division in the shoot apical meristem (Hasanuzzaman *et al.*, 2010; Zhu *et al.*, 2017; Khan *et al.*, 2023). Longer priming durations (6–9 h) were generally more effective at lower Se concentrations, allowing sufficient Se uptake without inducing toxicity. In contrast, 10 mg/L Se significantly reduced leaflet number, with 9 h priming yielding only 8.0 ± 2.5 leaflets, indicative of inhibitory effects associated with oxidative and metabolic disruption (Van Hoewyk, 2013; Hussain *et al.*, 2023).

At moderate salinity (3.5 g/L NaCl), lower Se concentrations (1.5–2.5 mg/L) preserved or slightly enhanced leaflet numbers, with 6 h priming at 2.5 mg/L Se producing 12.5 ± 1.5 leaflets. This retention suggests Se-mediated mitigation of ionic imbalance and maintenance of hormonal homeostasis required for leaf initiation (Rady *et al.*, 2020). Higher Se concentrations (5–10 mg/L) significantly reduced leaflet number ($p < 0.05$), highlighting the narrow margin between Se benefit and toxicity.

Under severe salinity (5 g/L NaCl), Se priming enabled partial recovery of leaflet development, with the best response observed at 6 h priming with 5 mg/L Se (4.0 ± 0.8 leaflets), followed by 6 h at 10 mg/L Se (3.0 ± 1.0 leaflets). This partial rescue likely reflects enhanced ROS detoxification and osmoprotectant synthesis, sustaining minimal meristematic activity under extreme stress (Ul Hassan *et al.*, 2019; García-Locascio *et al.*, 2024). No leaflet formation occurred at 7 g/L NaCl across treatments, indicating an upper limit to Se-mediated protection.

Chlorophyll Content

Chlorophyll content, a sensitive indicator of photosynthetic capacity and oxidative stress tolerance, responded strongly to Se priming under salinity stress. Under non-saline conditions, priming with 1.5–5 mg/L Se significantly increased chlorophyll content, with the highest value (2.51 ± 0.03 mg/g FW) recorded after 6 h priming at 5 mg/L Se—a 34% increase over controls. This enhancement likely reflects Se's antioxidant role in reducing ROS and stabilizing chloroplast membranes, possibly through modulation of chlorophyll biosynthesis pathways (Feng et al., 2013; Cunha et al., 2022).

In contrast, high Se concentration (10 mg/L) reduced chlorophyll content across durations, with 9 h priming yielding only 1.08 ± 0.02 mg/g FW, indicative of phytotoxicity associated with excessive seleno-amino acid incorporation or sulfur metabolic disruption (Van Hoewyk, 2013).

As salinity intensified, Se's protective effects became more evident under moderate stress but insufficient under extreme conditions. At 3.5 g/L NaCl, 3 h priming at 1.5 mg/L Se retained the highest chlorophyll content (1.75 ± 0.08 mg/g FW), representing a 50% improvement over controls, likely through enhanced antioxidant enzyme activity and preservation of chloroplast integrity (Rady et al., 2020). Under severe salinity (5 g/L NaCl), residual chlorophyll was detectable only in primed seedlings, with 6 h priming at 5 mg/L Se producing the highest retention (0.49 ± 0.05 mg/g FW). No chlorophyll was detectable at 7 g/L NaCl, marking the threshold beyond which Se protection failed.

Proline Accumulation

Proline accumulation is a hallmark of plant responses to salinity stress, contributing to osmotic adjustment, protein stabilization, and ROS scavenging (Szabados and Saviouré, 2010). Selenium priming significantly modulated proline content in a concentration- and duration-dependent manner.

Under non-saline and low-salinity conditions (0–1.5 g/L NaCl), low to intermediate Se concentrations (1.5–5 mg/L) caused only modest increases in proline relative to controls, remaining well below stress-induced levels and reflecting metabolic priming rather than stress perception. In contrast, 10 mg/L Se induced pronounced proline accumulation even in the absence of salt stress (up to 92.0 ± 4.0 μ mol/g FW after 9 h), suggesting that high Se acted as a mild stressor, activating osmolyte synthesis pathways similar to responses observed in Se-hyperaccumulator species (Freeman et al., 2006).

At moderate salinity (3.5 g/L NaCl), Se priming synergistically enhanced proline accumulation, particularly with longer priming durations. For instance, 9 h priming at 5 mg/L Se increased proline to 127.0 ± 5.0 μ mol/g FW (74% above control), supporting improved osmotic adjustment. However, 10 mg/L Se triggered extreme accumulation (260.0 ± 8.0 μ mol/g FW), approaching levels associated with metabolic imbalance (Verbruggen and Hermans, 2008; El-Badri et al., 2022).

Under severe salinity (≥ 5 g/L NaCl), unprimed seedlings showed no detectable proline, whereas Se priming enabled substantial accumulation. At 5 g/L NaCl, 9 h priming at 5 mg/L Se yielded 200.0 ± 8.5 μ mol/g FW, while 10 mg/L Se reached 290.0 ± 7.5 μ mol/g FW. At 7 g/L NaCl, maximal accumulation

($320.0 \pm 9.0 \mu\text{mol/g FW}$) occurred with 9 h priming at 10 mg/L Se, reflecting a compensatory response to combined Se and salinity stress (Hasanuzzaman et al., 2014; Ulhassan et al., 2019).

Seedling Dry Weight

Seedling dry weight, an integrative measure of biomass accumulation and overall vigor, was strongly influenced by Se priming under salinity stress. In non-primed controls, dry weight remained relatively stable under low to moderate salinity (0.094–0.117 g at 0–3.5 g/L NaCl) but declined to zero at ≥ 5 g/L NaCl, indicating failure of seedling establishment due to osmotic shock and ionic toxicity (Munns and Tester, 2008).

At low salinity (1.5 g/L NaCl), Se priming significantly enhanced biomass accumulation, with 6 h priming at 5 mg/L Se producing 0.185 ± 0.018 g, over 60% higher than controls. This response highlights an optimal Se uptake window that balances antioxidant protection with growth promotion (Rady et al., 2020) (Cunha et al. 2022).

Under moderate salinity (3.5 g/L NaCl), intermediate Se concentrations maintained or slightly increased dry weight, with 6 h priming at 5 mg/L Se yielding 0.135 ± 0.018 g. In contrast, 10 mg/L Se produced neutral or inhibitory effects, consistent with early toxicity symptoms.

At severe salinity (≥ 5 g/L NaCl), Se priming enabled residual biomass accumulation where unprimed seedlings failed. At 5 g/L NaCl, 6 h priming at 2.5–5 mg/L Se resulted in ~ 0.110 g dry weight, while at 7 g/L NaCl, the highest value (0.050 ± 0.012 g) occurred with 6 h priming at 2.5 mg/L Se. This shift toward lower Se under extreme stress suggests a trade-off between osmoprotection and metabolic cost, emphasizing the narrow margin of Se efficacy under lethal salinity (Jiang et al., 2017; Ulhassan et al., 2019).

Composite z-score

Selenium priming exerted a clear influence on overall seedling performance across salinity gradients, as reflected by composite z-scores integrating all measured parameters. Under non-saline conditions (0 g/L NaCl), priming with 1.5 mg/L Se for 6 h produced the highest composite score (1.193). At this low Se dose, seedlings likely benefited from enhanced chlorophyll retention and improved basal metabolic activity, supporting efficient photosynthesis, energy production, and early growth without imposing metabolic costs (Hasanuzzaman et al., 2020; Khan et al., 2023). This response suggests that low-dose Se primes cellular metabolism through selenoprotein-mediated reactive oxygen species (ROS) scavenging and modulation of growth-related hormonal signaling pathways.

At mild salinity (1.5 g/L NaCl), the optimal treatment shifted to 5 mg/L Se for 6 h, yielding a composite score of 1.045. This shift indicates an increased Se requirement under osmotic stress, where intermediate Se concentrations likely enhanced antioxidant defenses, improved water relations, and

sustained nutrient acquisition (Hussain et al., 2023). Consequently, seedlings maintained relatively higher chlorophyll content and overall vigor compared with other treatments.

Under moderate salinity (3.5 g/L NaCl), priming with 2.5 mg/L Se for 6 h produced the highest composite score (0.692), suggesting an optimal balance between selenium's protective effects and the onset of toxicity at higher concentrations. Similar dose-dependent responses to Se under salt stress have been reported in other crops (Hawrylak-Nowak et al., 2014; Ziegler & Fageria, 2021).

At higher salinity levels (5–7 g/L NaCl), the best-performing treatments also involved 2.5 mg/L Se; however, composite scores were negative (– 0.431 at 5 g/L and – 0.611 at 7 g/L). These negative values indicate that overall seedling performance was severely constrained by extreme salinity. Nevertheless, the selected Se treatments still conferred relative advantages by increasing germination rate, sustaining residual chlorophyll content and metabolic activity, reflecting a narrow balance between selenium-mediated osmotic and oxidative protection and avoidance of supra-optimal toxicity (García-Locascio et al., 2024).

Overall, the composite z-score analysis demonstrates that selenium priming modulates seedling performance in a dose- and stress-dependent manner. Positive z-scores identify treatments that optimize integrated physiological performance, whereas negative values highlight conditions under which seedlings remain constrained but still respond most favorably to specific selenium regimes. These findings underscore the importance of carefully matching selenium dose and stress intensity when interpreting in vitro responses, without extrapolating directly to field performance.

Conclusion

This study demonstrates that selenium hydro-priming enhances early seedling establishment of *Arachis hypogaea* under saline conditions, primarily by accelerating germination and promoting radicle development. Seedling survival under salinity was driven more by enhanced germination and early root growth than by later biomass accumulation, highlighting the importance of rapid establishment in stress-prone environments.

Across salinity levels, low to intermediate selenium concentrations combined with short to intermediate priming durations consistently produced the most favorable responses, reflecting selenium's hormetic behavior.

From these results, sweet spots for selenium priming can be identified: a priming duration of 6 h consistently produced the highest composite z-scores across different salt levels, while the optimal selenium concentration depended on salt stress: 1.5 mg/L for 0 g/L, 5 mg/L for 1.5 g/L, and 2.5 mg/L for 3.5–7 g/L. These patterns indicate that selenium can enhance relative seedling performance in vitro by supporting chlorophyll content and metabolic processes, even under increasing salt stress. Negative z-scores highlight the constraints imposed by high salinity, but the treatments identified as optimal

consistently produced the highest relative composite performance, emphasizing the importance of selenium dose and priming duration in moderating salt stress effects.

While these findings provide strong physiological evidence for the effectiveness of selenium hydropriming, field-based validation under variable soil and environmental conditions is required to confirm the consistency, scalability, and agronomic relevance of this approach. Overall, selenium hydropriming represents a practical, low-cost strategy for improving the establishment of *Arachis hypogaea* landraces in saline soils, provided that concentration and exposure time are carefully optimized.

Abbreviations

Se	Selenium
NaCl	Sodium chloride
SD	Standard deviation
h	Hour(s)
mg/L	Milligrams per liter
g/l	Grams per liter
cm	Centimeter
$\text{mg g}^{-1} \text{FW}$	Milligram per gram Fresh Weight
$\mu\text{mol g}^{-1} \text{FW}$	Micromoles per Gram Fresh Weight
ZISCO	Composite z-score index
ROS	Reactive oxygen species
MGT	Mean Germination Time
GV	Germination Velocity
GRI	Germination Rate Index

Declarations

Ethics and Consent to participate: The plant material (*Arachis hypogea* L.) used in this study was cultivated under standard agronomic practices in, Etsako West Local Government Area, Edo State, Nigeria. All procedures complied with local and national guidelines for the use of the cultivated plant material. No wide or endanger species were used and no specific permission or license were required.

Consent to publish: Not applicable.

Availability of data and material: All data generated or analyzed are included in this manuscript except for the germination indices MGT, GV and GRI, for sake of convenience have been placed as supplementary data.

Competing interests : The authors declare no competing interests.

Funding: This work was personally funded by the authors; no external funding was received.

Author's contributions:

Conceptualization: Eromosele Noble Isibor

Methodology: Eromosele Noble Isibor; Boniface Edegbai.

Formal Analysis and investigation: Eromosele Noble Isibor.

Writing-Review and editing: Rida Batool; Ifie Etumah Sandra. Eromosele Noble Isibor

Supervision: Eromosele Noble Isibor; Boniface Edegbai; Beckley Ikhajiagbe

Acknowledgments: I will like to appreciate Happy and Christopher, undergraduate students of the department of Science Laboratory Technology, Faculty of Life Sciences, University of Benin for their assistance in data collection. Also Mrs. Enabele, Chief laboratory officer at the department of Plant Biology and Biotechnology for granting us access to the lab for the experiment.

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Figures

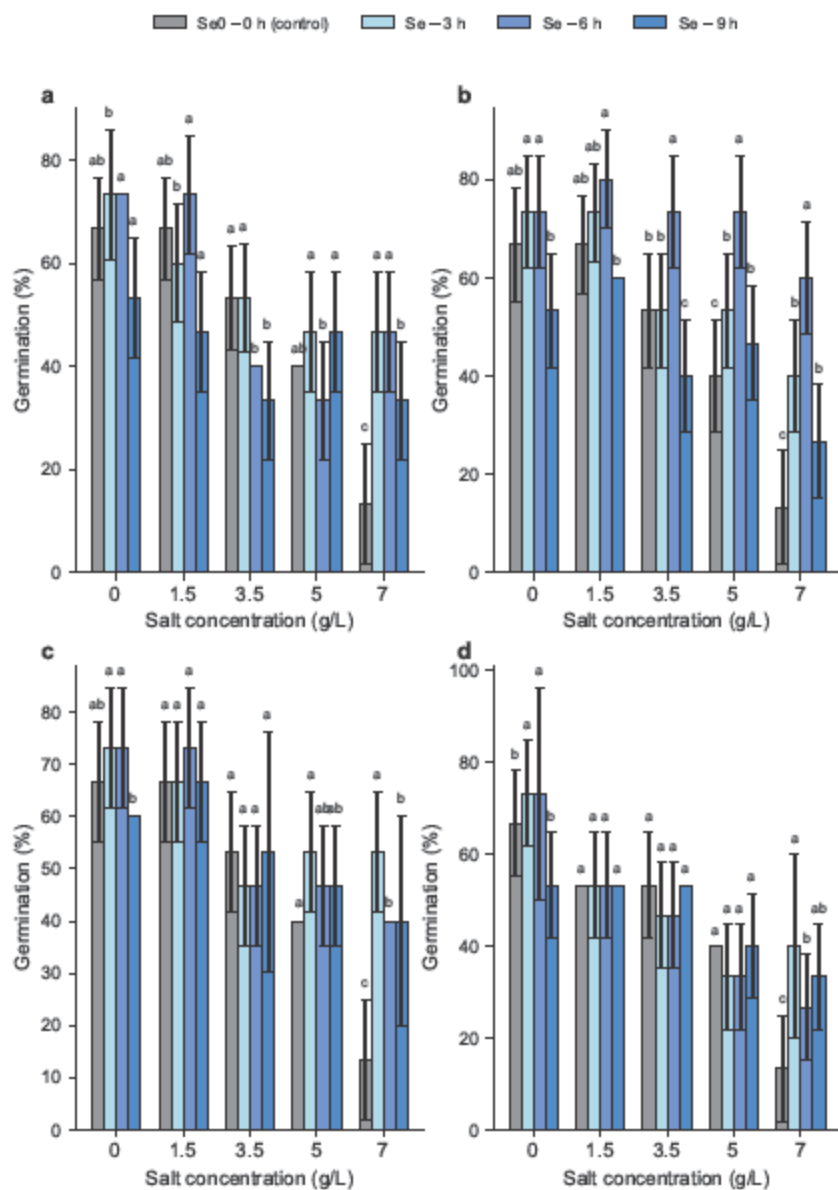


Figure 1

Germination percentage (%) of Auchi groundnut, a landrace of *Arachis hypogaea* L., pretreated at different selenium (Se) durations (3h, 6h, 9h) and exposed to increasing salinity levels (0, 1.5, 3.5, 5, and 7 g/L NaCl). Panels represent Se pretreatment concentrations of (a) 1.5 mg/L, (b) 2.5 mg/L, (c) 5 mg/L, and (d) 10 mg/L. Final germination percentage was determined after 10 days of sowing. Error bars represent ± SD (n = 3). Different lowercase letters indicate significant differences among treatments within each salt concentration (p < 0.05; Tukey's test).

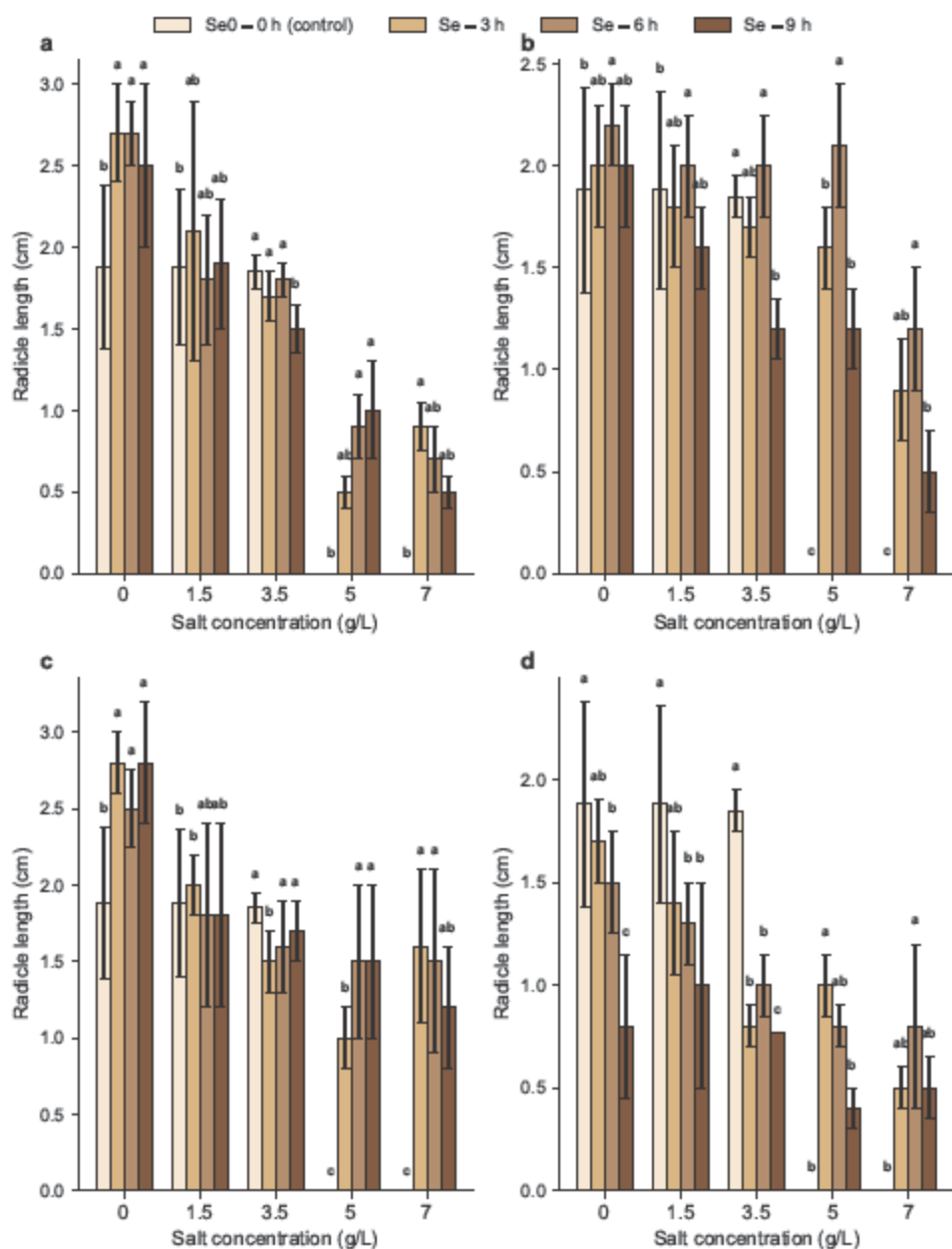


Figure 2

Radicle length (cm) of seedlings of Auchi groundnut, a landrace of *Arachis hypogaea* L., pretreated with different of selenium (Se) durations (3h, 6h, 9h) and grown under varying salt concentrations (0, 1.5, 3.5, 5, and 7 g/L NaCl). Panels correspond to Se pretreatment concentrations of (a) 1.5 mg/L, (b) 2.5 mg/L, (c) 5 mg/L, and (d) 10 mg/L. Radicle length was measured 10 days after sowing. Error bars represent $\pm$ SD (n = 3). Different lowercase letters denote significant differences among treatments within each salt concentration (p < 0.05; Tukey's test).

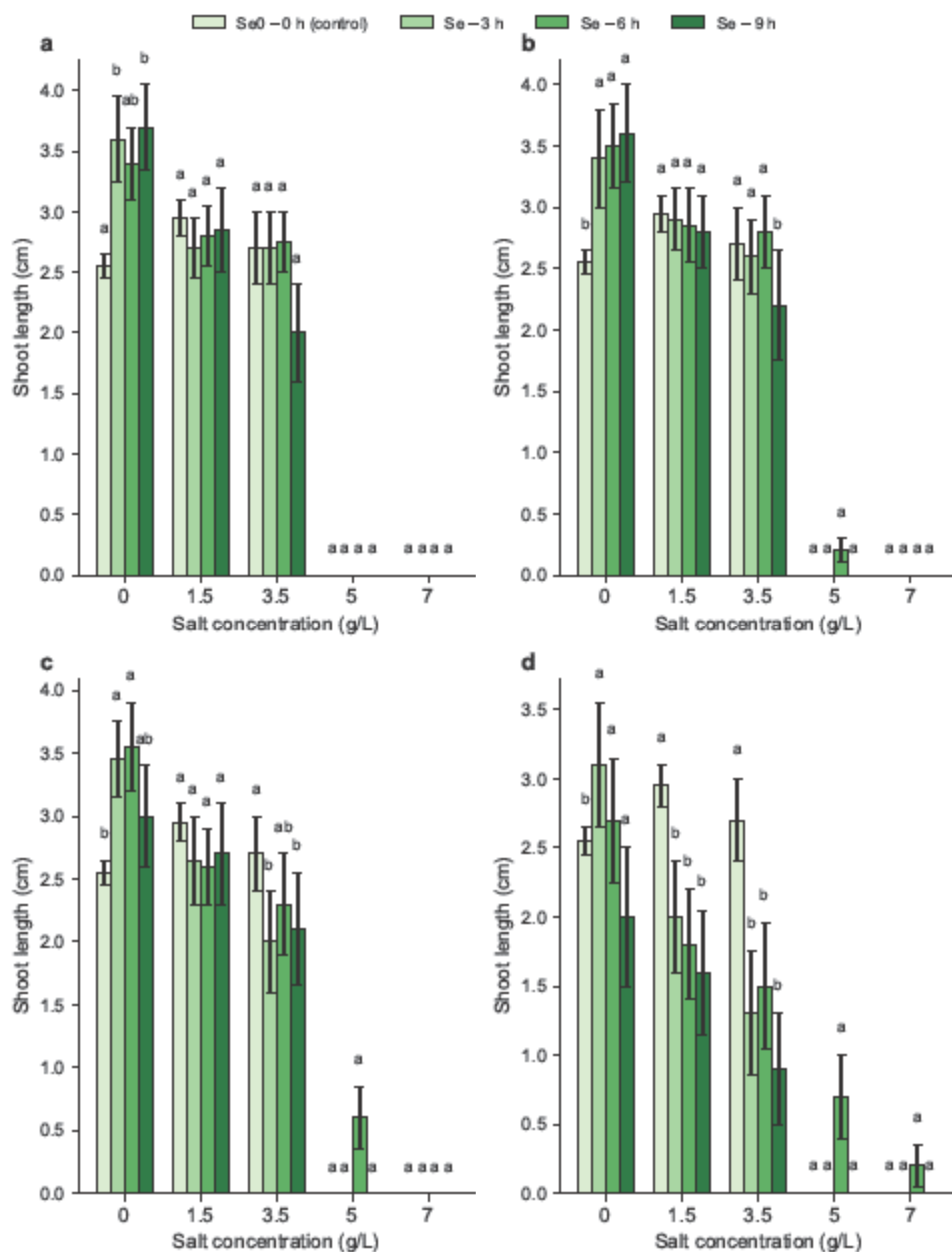


Figure 3

Shoot length (cm) of seedlings of Auchi groundnut, a landrace of *Arachis hypogaea* L., pretreated with different durations of selenium (Se) (3h, 6h, 9h) and subjected to increasing salinity levels (0, 1.5, 3.5, 5, and 7 g/L NaCl). Panels represent Se pretreatment concentrations of (a) 1.5 mg/L, (b) 2.5 mg/L, (c) 5 mg/L, and (d) 10 mg/L. Shoot length was measured 10 days after sowing. Error bars represent $\pm$ SD (n = 3). Different lowercase letters indicate significant differences among treatments within each salt concentration (p < 0.05; Tukey's test).

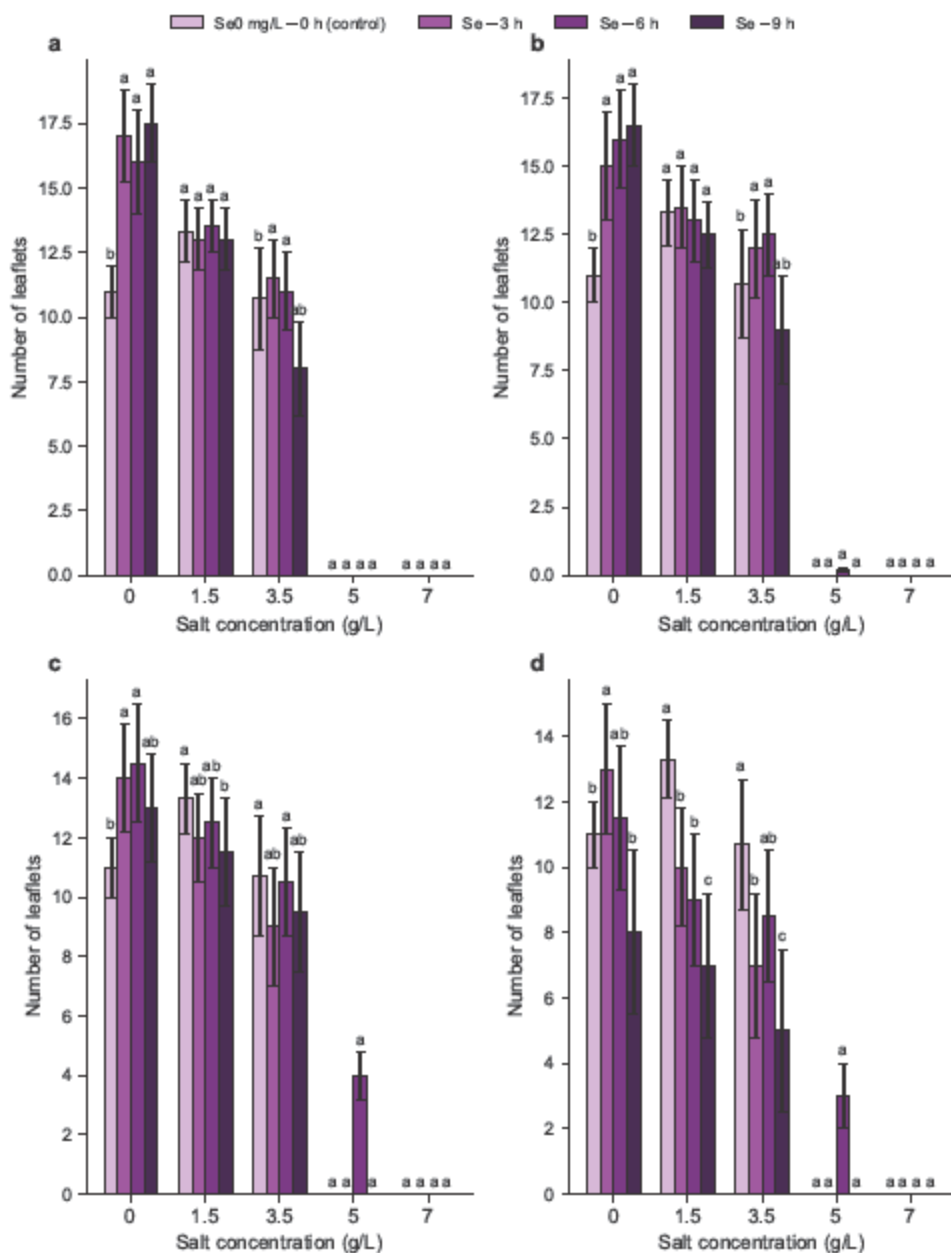


Figure 4

Number of leaflets per seedling of Auchi groundnut, a landrace of *Arachis hypogaea* L., as influenced by selenium (Se) pretreatment duration (3h, 6h, 9h) under different salt concentrations (0, 1.5, 3.5, 5, and 7 g/L NaCl). Panels correspond to Se pretreatment concentrations of (a) 1.5 mg/L, (b) 2.5 mg/L, (c) 5 mg/L, and (d) 10 mg/L. Leaflet number was recorded 10 days after sowing. Error bars represent $\pm$ SD (n = 3). Different lowercase letters denote significant differences among treatments within each salt concentration (p < 0.05; Tukey's test).

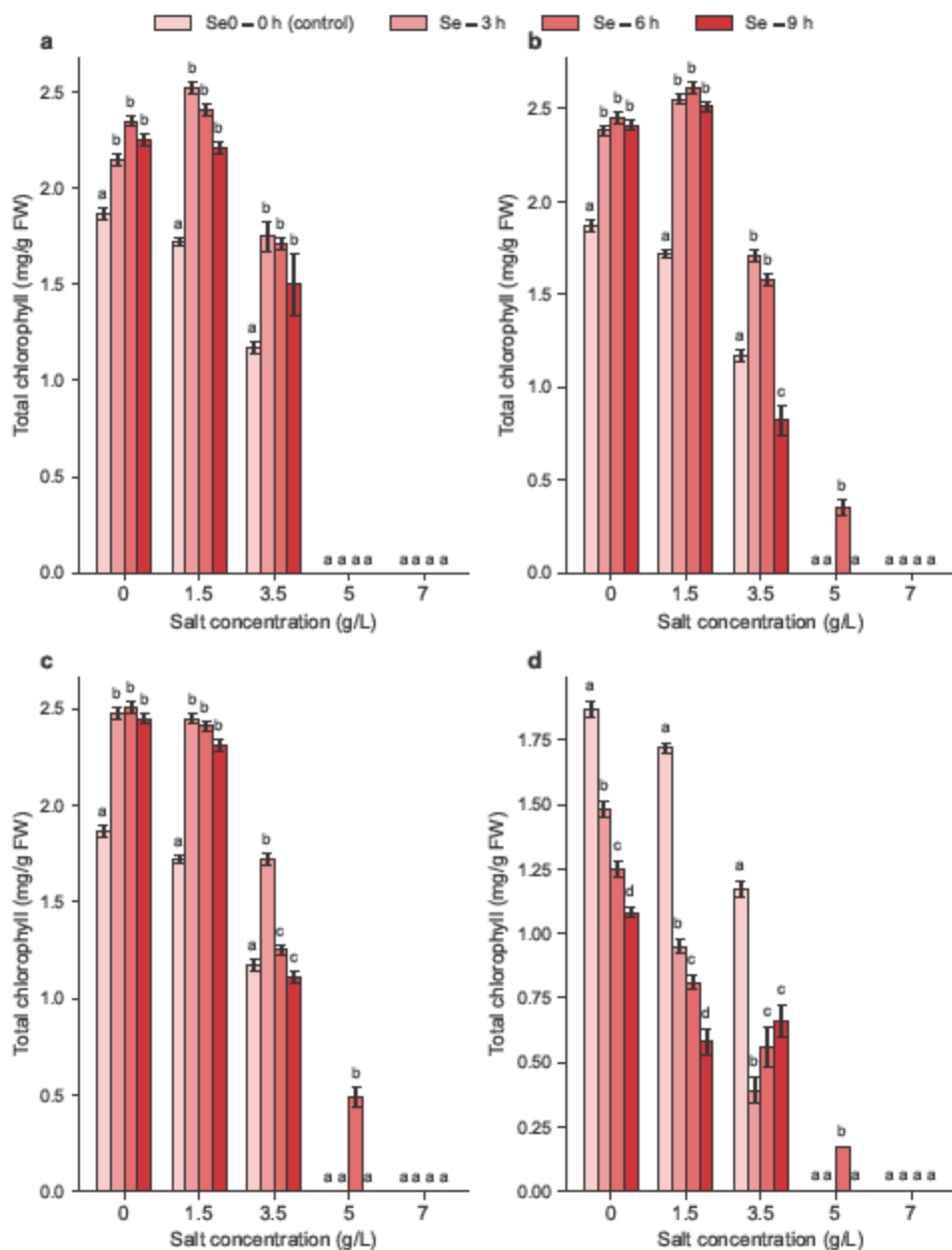


Figure 5

Total chlorophyll content (mg g^{-1} fresh weight) of seedlings of Auchi groundnut, a landrace of *Arachis hypogaea* L., pretreated at different selenium (Se) durations (3h, 6h, 9h) and exposed to increasing salt stress (0, 1.5, 3.5, 5, and 7 g/L NaCl). Panels represent Se pretreatment concentrations of (a) 1.5 mg/L, (b) 2.5 mg/L, (c) 5 mg/L, and (d) 10 mg/L. Chlorophyll content was determined 10 days after sowing. Error bars represent $\pm$ SD (n = 3). Different lowercase letters indicate significant differences among treatments within each salt concentration (p < 0.05; Tukey's test).

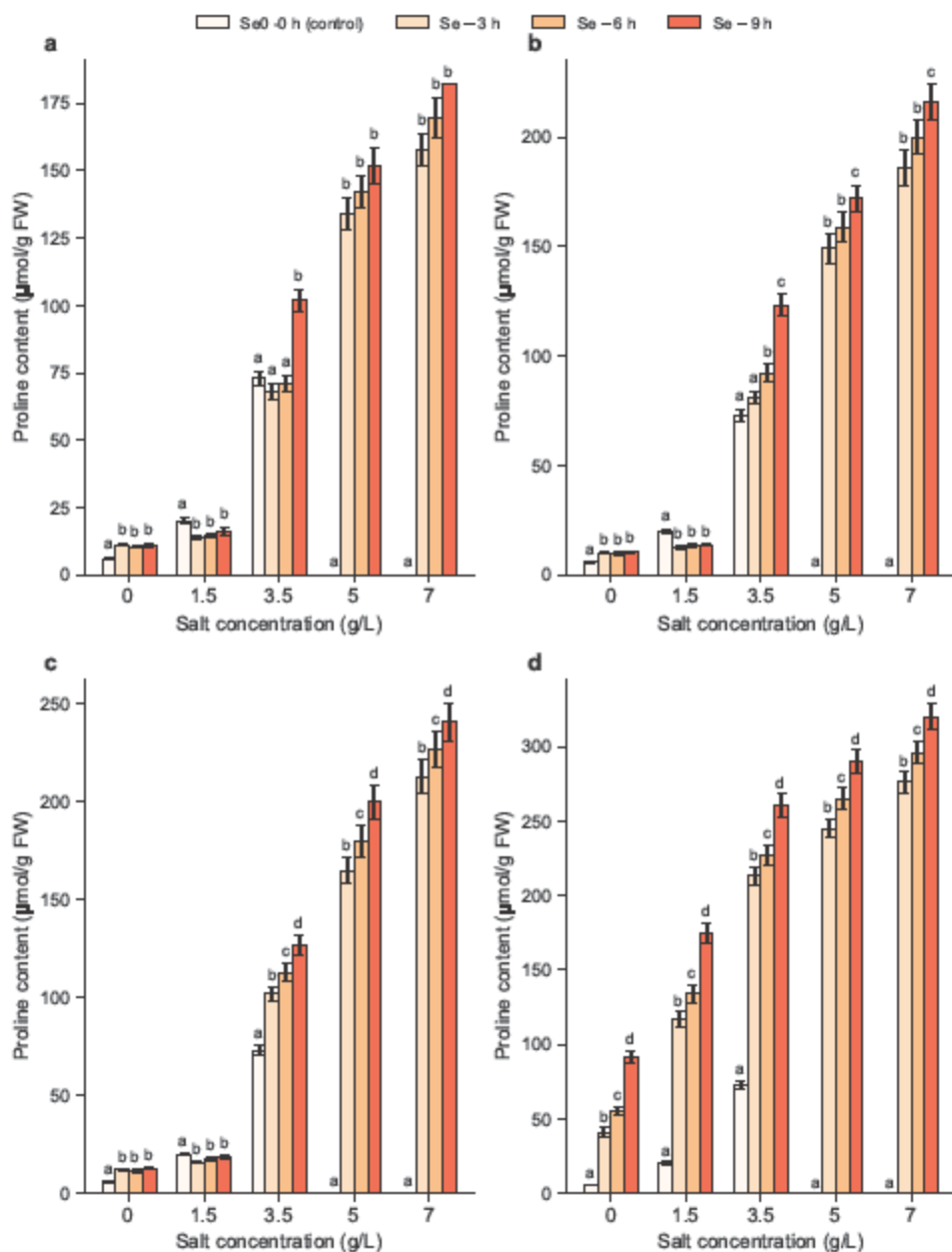


Figure 6

Proline content ($\mu\text{mol g}^{-1}$ fresh weight) of seedlings of Auchi groundnut, a landrace of *Arachis hypogaea* L., pretreated with different selenium (Se) durations (3h, 6h, 9h) and subjected to increasing salt stress (0, 1.5, 3.5, 5, and 7 g/L NaCl). Panels represent Se pretreatment concentrations of (a) 1.5 mg/L, (b) 2.5 mg/L, (c) 5 mg/L, and (d) 10 mg/L. Proline content was quantified 10 days after sowing. Error bars represent $\pm$ SD ($n = 3$). Different lowercase letters indicate significant differences among treatments within each salt concentration ($p < 0.05$; Tukey's test).

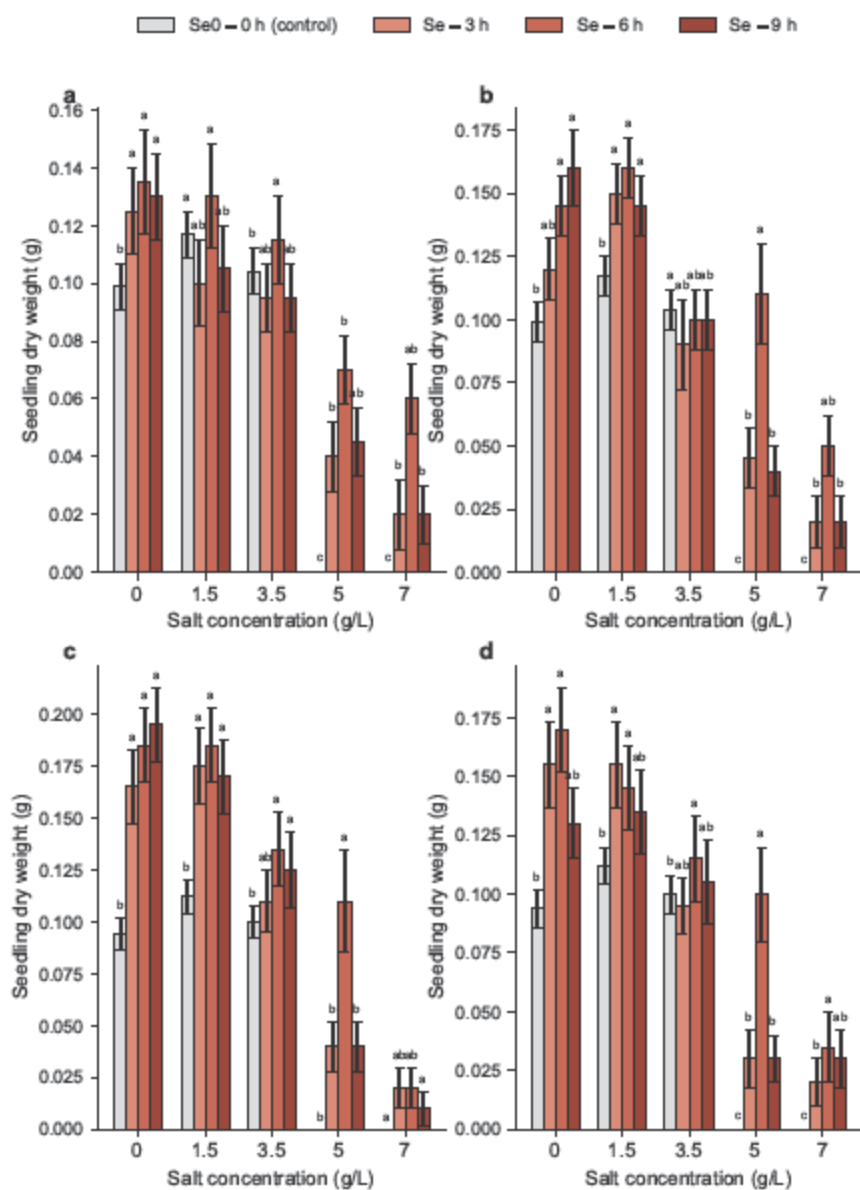


Figure 7

Dry seedling weight (g) of Auchi groundnut, a landrace of *Arachis hypogaea* L., pretreated with different durations of selenium (Se) (3h, 6h, 9h) and grown under varying salinity levels (0, 1.5, 3.5, 5, and 7 g/L NaCl). Panels correspond to Se pretreatment concentrations of (a) 1.5 mg/L, (b) 2.5 mg/L, (c) 5 mg/L, and (d) 10 mg/L. Dry weight was measured 10 days after sowing following oven drying to constant weight. Error bars represent $\pm$ SD (n = 3). Different lowercase letters denote significant differences among treatments within each salt concentration (p < 0.05; Tukey's test).

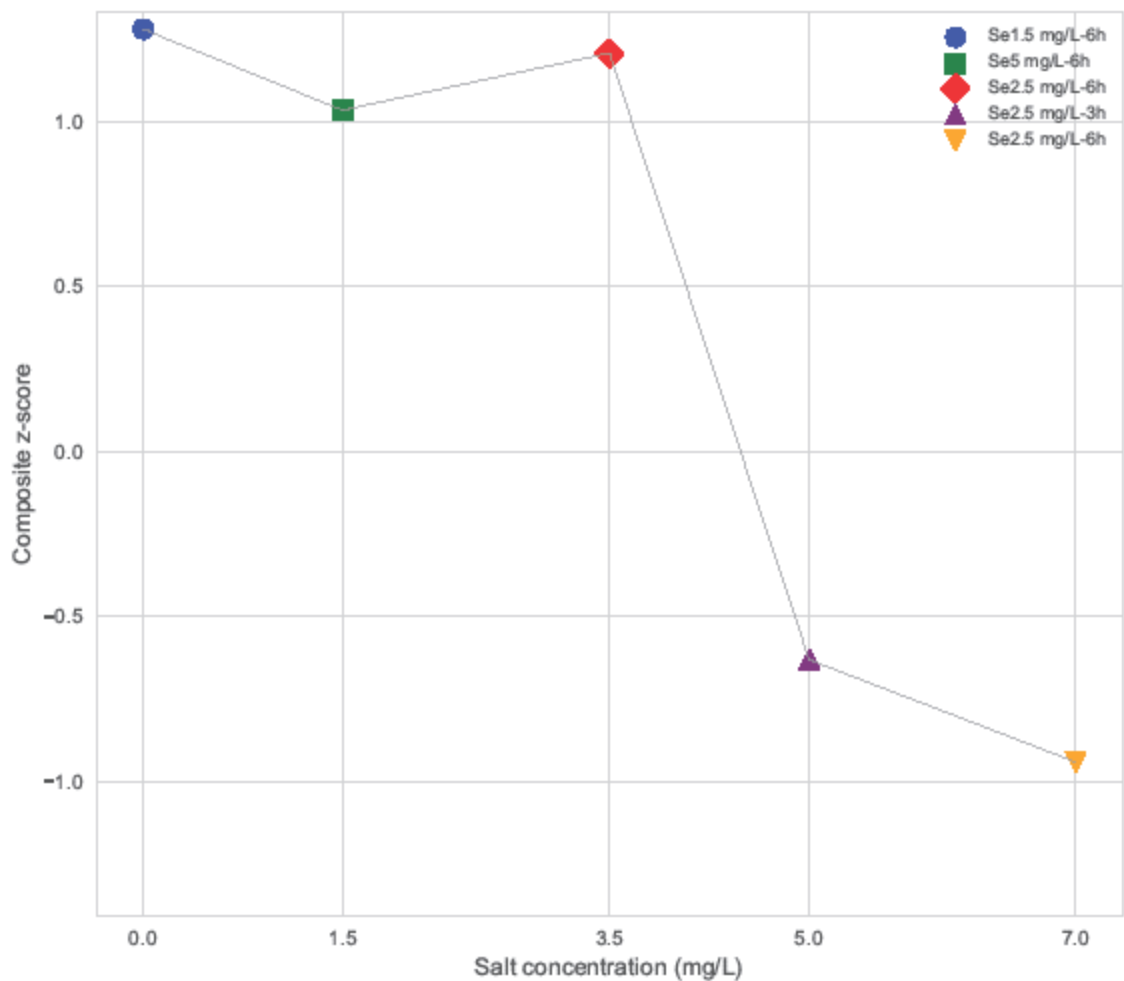


Figure 8

Composite Z-score index (ZISCO) integrating all measured germination, growth, physiological, and biochemical parameters of Auchi groundnut, a landrace of *Arachis hypogaea* L. The figure compares the best selenium (Se) pretreatment across different salt concentrations (0, 1.5, 3.5, 5, and 7 g/L NaCl), summarizing overall performance under salinity stress.

Supplementary Files

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