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Dual Drought–Lead Stress Tolerance in Solanaceae: Morphophysiological and Genetic Integration

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Abstract

Drought and lead (Pb) pollution are two major abiotic stress factors that often occur together in low-input and peri-urban farmlands. While both have been studied individually in crops such as tomato, pepper, and eggplant (Solanaceae), few studies have examined their combined effects. This is notable, as many farmers face both challenges simultaneously. Much of the existing literature focuses on either drought or heavy metals such as cadmium or arsenic, often overlooking Pb and drought as a dual stress. This review addresses that gap by examining how Solanaceae crops respond to both stresses at physiological, anatomical, and genetic levels. Based on a structured review of 83 peer-reviewed studies published between 2000 and 2024 and retrieved from Google Scholar, PubMed, Scopus, and Web of Science, the synthesis highlights key traits such as stomatal regulation, root system architecture, antioxidant enzyme responses, and detoxification pathways. Antioxidant activity and HMA3-mediated Pb sequestration emerged as convergent mechanisms supporting dual-stress resilience across Solanaceae species. The review draws on recent findings, including CRISPR-based gene editing in tomato, to highlight genes linked to stress tolerance. It also compares cultivated varieties and landraces to identify genotypes with improved adaptability. Gaps in the literature are emphasized, particularly the absence of dual-stress field trials, underutilization of wild relatives, and lack of genotype × environment × stress (G×E×S) data to guide breeding. A conceptual model is proposed to integrate these dimensions into future strategies aimed at developing Solanaceae crops that perform reliably under combined drought and Pb exposure.

Keywords: Dual Stress Tolerance, Drought, Lead Toxicity, Solanaceae, Antioxidant Response, Phytochelatins, CRISPR, Stress-Resilient Breeding.

Introduction

Climate change and environmental degradation have intensified the occurrence of abiotic stressors such as drought (Ojeilua et al., 2025) and heavy metal pollution in agricultural systems. Among these, drought remains a primary driver of global crop yield loss,

particularly in arid and semi-arid regions (Yang et al., 2021). Concurrently, the accumulation of heavy metals, especially lead (Pb), in soil due to industrial runoff, mining, and excessive use of agrochemicals poses a persistent threat to plant growth, soil health, and food safety (Sharma & Dubey, 2005; Kumar et al., 2020). These stressors increasingly overlap in the same agroecosystems, particularly in low-input and urban-adjacent lands, yet they are rarely studied together (Ur Rahman et al., 2024).

Solanaceae crops, including tomato (*Solanum lycopersicum*), pepper (*Capsicum annuum*), and eggplant (*Solanum melongena*), are vital sources of nutrition, income, and agro-industrial value worldwide (Foolad, 2007). However, their sensitivity to both drought and lead stress limits their productivity and adaptability under environmental duress (Mahmood et al., 2021). Although individual stress responses have been well characterized in these species, the combined impact of drought and Pb exposure remains poorly understood (Gao et al., 2022), with limited insights into how plants balance water conservation, nutrient uptake, and metal detoxification simultaneously. As illustrated in Figure 1, drought stress exerts its detrimental effects through multiple interconnected physiological and cellular pathways. Reduced water availability and lower water potential lead to a cascade of impairments, including decreased photosynthesis, oxidative stress via reactive oxygen species (ROS), membrane damage, and eventual cell death (Laxa et al., 2019). These disruptions collectively contribute to inhibited growth, impaired reproductive development, and overall yield reduction. Understanding these primary drought mechanisms provides a foundation for exploring how such responses interact or conflict with lead detoxification pathways in dual-stress environments.

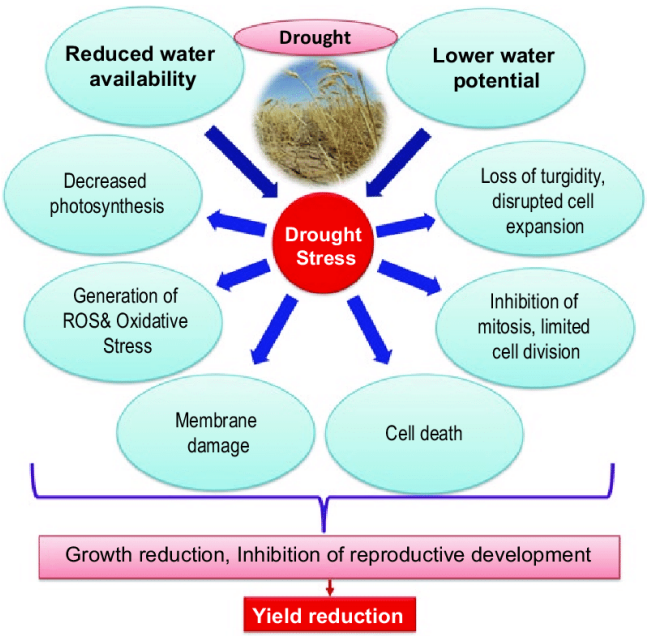


Figure 1. Conceptual model of plant responses to drought stress, showing morpho-physiological changes leading to yield resilience.

Source: Hasanuzzaman et al. (2018)

Statement of the Problem and Research Gap

Although both drought and lead (Pb) toxicity are recognized as serious abiotic stressors affecting crop performance, they are often studied in isolation. Numerous studies have addressed each stressor individually and, in some cases, simultaneously with other stress combinations (e.g., drought–salt or Pb–Cd). However, integrated studies that specifically examine drought and Pb stress together, particularly in Solanaceae crops, remain scarce. These stressors frequently co-occur in the same agroecosystems, especially in marginal lands, peri-urban zones, or areas exposed to both water scarcity and heavy metal contamination. The absence of dedicated research on their combined physiological, anatomical, and genetic effects leaves a major gap in our understanding of how plants simultaneously coordinate water-saving strategies with metal detoxification mechanisms.

Objective of the Review

This review provides an integrated examination of the physiological, anatomical, biochemical, and genetic responses of Solanaceae crops to drought and Pb toxicity, individually and in combination. It highlights shared stress signaling pathways, such as ABA and ROS-mediated responses, and emphasizes underexplored areas including epigenetic regulation, root plasticity, metal sequestration, and antioxidant defense. Furthermore, it identifies knowledge gaps and proposes directions for breeding strategies that leverage wild relatives, QTL mapping, CRISPR-based editing, and stress-adaptive scoring indices.

Materials and Methods

This review was conducted using a structured, systematic approach to compile and synthesize current knowledge on how Solanaceae crops respond to drought and lead (Pb) toxicity, both individually and in combination. The objective was to identify mechanistic trends at physiological, anatomical, biochemical, and genetic levels relevant to dual-stress tolerance in crops such as tomato (*Solanum lycopersicum*), pepper (*Capsicum* spp.), and eggplant (*Solanum melongena*).

Search Strategy and Data Sources

A comprehensive literature search was performed across four major academic databases: Google Scholar, Web of Science, PubMed, and Scopus. Boolean search strings were used in combination, including:

("Solanaceae" OR "tomato" OR "pepper" OR "eggplant") AND ("drought stress" OR "water deficit") AND ("lead toxicity" OR "Pb stress" OR "heavy metal stress") AND ("ROS" OR "antioxidant enzymes" OR "detoxification" OR "CRISPR" OR "epigenetic response")

No automated filters were applied. Searches were manually refined to capture relevant peer-reviewed primary research and review articles published between 2000 and 2024.

Inclusion and Exclusion Criteria

Studies were included if they addressed Solanaceae crops subjected to drought, lead (Pb), or combined stress and presented either primary data or synthesized findings on physiological, anatomical, biochemical, or genetic responses. Priority was given to studies that offered clear insights into stress tolerance mechanisms. By contrast, studies were excluded if they focused on non-Solanaceous species, investigated other heavy metals without specific reference to Pb, lacked peer review (such as preprints), were written in languages other than English, or were limited to conference abstracts.

Study Selection Process

The study selection process followed a structured and transparent approach aligned with best practices for systematic literature reviews. A total of 89 records were identified across the four databases. After removing duplicates and screening titles and abstracts for relevance, 83 studies were retained for full inclusion following full-text assessment. 6 articles were excluded due to insufficient biological relevance or lack of methodological clarity. The final dataset included both experimental investigations and integrative reviews addressing drought, lead (Pb) toxicity, or their combined effects in Solanaceae crops. An overview of the selection process is illustrated in Figure 2.

Data Extraction and Thematic Organization

Selected studies were organized by stress type (drought, Pb, or dual) and response level (physiological, anatomical, biochemical, detoxification, or genetic). Extracted findings were synthesized under key thematic areas, including stomatal regulation, root-to-shoot allocation, ROS dynamics, antioxidant enzyme activity, Pb sequestration via transporters such as HMA_3 and phytochelatins, and regulation of stress-related genes through CRISPR and epigenetic mechanisms.

This synthesis allowed for the identification of converging stress responses in Solanaceae crops and highlighted critical knowledge gaps such as the lack of dual-stress field trials, limited use of wild relatives, and insufficient genotype × environment × stress (G×E×S) studies for breeding applications.

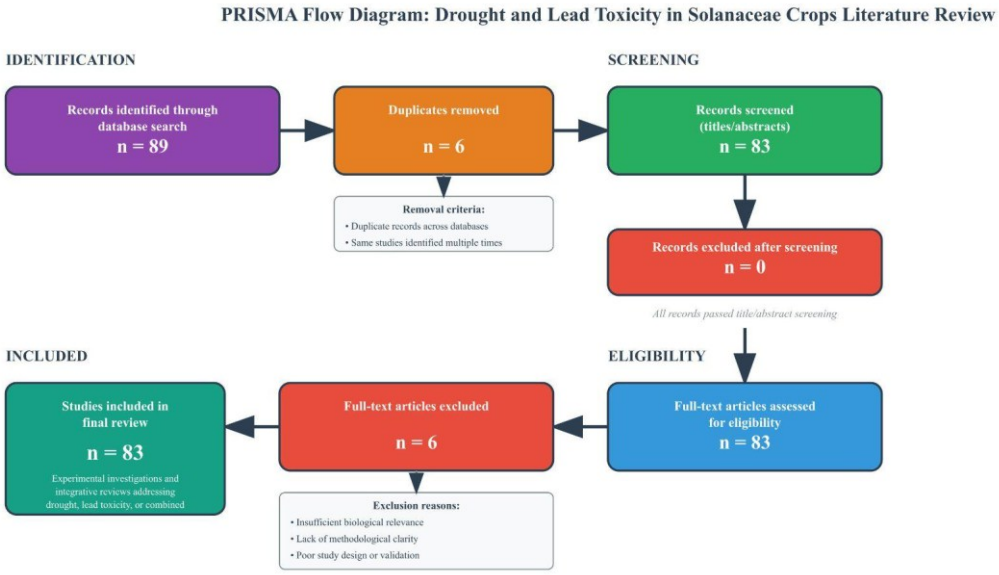


Figure 2. PRISMA-style flow diagram summarizing the selection process for studies included in the review of drought and lead (Pb) toxicity in Solanaceae crops adapted from Page et al. (2021). A total of 89 records were identified; after removing 6 duplicates and excluding 6 full-text articles for insufficient relevance or methodological clarity, 83 studies were included in the final synthesis.

Discussion

Physiological and Anatomical Responses to Drought in Solanaceae

The aftermath of drought stress stays longer on the plants, even after the stress is gone; most times, the plant is unable to recover or survive afterwards (Seleiman et al., 2021). These plants, especially the Solanaceae family, such as *Solanum lycopersicum* (tomato) and *Capsicum annuum* (pepper), can cope with or live through this stress by developing a set of physiological traits that confer or help them adjust their lifestyle during and after the stressor is removed (Mirzayeva et al., 2023; Trejo-Paniagua et al., 2024).

One of the most common physiological responses is the closure of stomata (these are tiny openings on leaf surfaces that control gaseous exchange and water loss in plants). This response is activated by a hormone called abscisic acid (ABA), which is produced in the root and leaves region of the plant during drought stress (Muhammad Aslam et al., 2022). The accumulation of these hormones sends a signal to the guard cells that surround each stoma, causing it to lose pressure and close (Munemasa et al., 2015). This helps the plant to conserve the limited water available to it, thereby reducing the rate of transpiration, but this closure also restricts the intake of carbon dioxide that is vital for photosynthetic activities in the plants (Lawson & Blatt, 2014).

Besides the closing of plant stomata, plants that suffer during drought also minimize the transport of water throughout their leaves as a result of decreasing the level of aquaporin activity, special water pipes in the cell membrane (Yang et al., 2021). This reduces the

velocity of transpiration via the leaf tissues, and it additionally ensures that the inner parts of the plants remain hydrated on the interior (Kayak et al., 2022).

The other notable adaptation of plants to the condition of drought is osmotic adjustment. In this case, the stress causes the plant to start to synthesize and accumulate such small molecules as proline and glycine betaine (Khan et al., 2018). With such molecules, they can equalize the pressure within their cells, defend their membranes and proteins, and retain as much available water as possible (De la Torre-Gonzalez et al., 2018). As an illustration, on the one hand, proline contributes to the prevention of the destructions linked to oxidative stress (an issue that causes the decrease in the photosynthesis speed of the plant because of the lack of carbon dioxide) (Pang et al., 2024), whereas on the other hand, glycine betaine protects plants against drought because it binds to the hydrophilic and hydrophobic residues of biomolecules, thus, retaining the structure and functionality of enzymes in a plant under drought stress (Yang et al., 2021).

Antioxidant enzymes such as catalase, superoxide dismutase, and ascorbate peroxidase are also produced by plants to enhance their internal protective mechanisms, particularly during the acute stress of drought, whereby toxic byproducts called reactive oxygen species (ROS) are produced (Turan et al., 2023). This assists in neutralizing these reactive intermediates and protects the cells in the plant against oxidation.

The other typical response is enhancement of the root-to-shoot ratio. When plants are exposed to drought, they may have reduced vegetative growth, especially of the shoot, and thus direct more vital energy towards the development of their root system (Kalra et al., 2023). The change provides them the chance of being able to utilize water at deeper areas of soil, and they stand a better chance of surviving the long-term drought stress.

Drought not only affects the behavioral pattern, which in this case, the anatomy of the plant, but it also causes some visible changes in its structure. In many Solanaceae crops, the leaves become thicker under drought stress (Yavas et al., 2023). These structural changes help to reduce the evaporational rate from the leaf surface, and they also increase the tissue capacity to hold water (Coneva et al., 2017).

Another common adaptation mechanism is the production of more trichomes (these are tiny, hair-like structures on the leaf surfaces of a plant). These structures act as a protective barrier against heat and desiccation by reflecting sunlight, increasing the leaf boundary layer, and reducing transpiration (Chen et al., 2022). In tomato species, especially the wild relatives, drought results in non-glandular trichomes becoming denser than usual, an occurrence that has been observed and linked to ways plants avoid drought (Kang et al., 2009). Sometimes, when leaf pubescence is combined with a thicker cuticle, it further reduces evaporative water loss in exposed conditions.

Some plants respond to drought by rolling or folding their leaves slightly to reduce water loss. These structural behaviors may be triggered by changes in turgor pressure within the leaf tissues, and they help to reduce the surface area exposed to direct sunlight. The resulting shape, which is tube-like in appearance, allows the leaves to create a more humid

microclimate around the stomata. This helps to reduce water vapor loss (Kadioglu & Terzi, 2007). Although this adaptation technique is more common in monocotyledonous plants, equivalent leaf-rolling behaviors have also been observed in tomato and pepper under progressive drought or when exposed to high vapor pressure deficits (Nuruddin et al., 2003). Changes in the vascular system occur inside the plant. Depending on the intensity of the stress, the vascular bundles can be enlarged or reduced (translocating the water and the nutrients within the plant) (Agusti & Blazquez, 2020). This adaptation assists the plant in preserving the flow of water even in cases where the moisture is low. The xylem vessels will, in some instances, be slimmer and this reduces the risks of the formation of air bubbles and the creation of obstructions to water movement in the cell (Venturas et al., 2017).

Figure 3 illustrates a summary of the discussed tomato landraces in a visual format with some of their most occurring drought-tolerant characteristics which include; off high relative water content, osmolyte accumulation, water-use efficiency, root-to-shoot plasticity capacities and antioxidant functions as tested in different conditions of droughts like limited irrigation, progressive stress and field appointments.

These responses from hormonal signaling and water conservation to solute accumulation and internal protection form a coordinated survival strategy that keeps Solanaceae crops alive during water scarcity (Kadioglu et al., 2012).

Drought-Tolerant Tomato Landraces with High Water Use Efficiency

Some tomato landraces that have developed adaptive traits that enhance their resilience to drought in semi-arid regions, these adapted varieties outperform modern cultivars in terms of physiological stability and water-use efficiency (WUE). These landraces serve as a valuable genetic resource for breeding programs that are aimed at enhancing drought tolerance in cultivated tomatoes.

One good example is the Mediterranean long shelf-life landrace *Tomàtiga de Ramellet*, which exhibits robust adaptation to limited irrigation. Under water deficit, this genotype maintains higher leaf relative water content, increased osmolyte accumulation (notably proline and soluble sugars), and stable photosynthetic efficiency (Fv/Fm). Its ability to balance transpiration with carbon assimilation helps to improve intrinsic WUE and sustains high fruit yield under field conditions (Fullana-Pericàs et al., 2019).

Similarly, Grozeva et al. (2024) evaluated five Bulgarian tomato landraces under 50% irrigation and identified Landrace 1352 as a superior performer. This genotype retained good fruit yield, chlorophyll fluorescence parameters (e.g., Fv/Fm), and leaf turgor, indicating that the genotype has a high level of physiological resilience. As observed by the authors, it performed similarly or even better than commercial hybrids, and therefore, it is a possible prospect to develop drought-resilient cultivars.

As well as the structural modifications identified, drought-tolerant tomato cultivars are also notable for increased antioxidation capacity. As an example, a study conducted in a controlled greenhouse environment, the cherry tomato plants (*Solanum lycopersicum* var. Cerasiforme) were treated with severe water deficit, the response revealed that superoxide

dismutase (SOD) activity performed a spectacular 4.7-fold increase, ascorbate peroxidase (APX) showed 19 fold increase and glutathione reductase (GR) increased by 12.2-folds. This was not so in the control replicates (Rao et al., 2023). Such enzyme responses were highly correlated to increased stability of photosystem II and low electrolyte loss, implying that these responses effectively neutralized reactive oxygen species (ROS) stimulated by drought. In the receiver of the study, it was concluded that the antioxidant strength of genotypes plays a major role in terms of their drought tolerance and recovery ability.

The second one is the landrace Ciettaicale that was reported by Rigano et al. (2014) and demonstrated a higher root-to-shoot ratio with a large quantity of water stored in the root system during drought stress than the commercial cultivar of 'Moneymaker'. These characteristics are adaptively plastic about the utilization of resources that impact increased water intake and maintenance of hydration inside the body.

All these studies prove beyond doubt that the drought-tolerant landraces of *Solanum lycopersicum* possess a set of favorable characteristics (including effective stomata control and osmotic adjustments to increase root architecture and antioxidant defense), making them productive even in water-limited environments. Their use in breeding programs raises a promising solution to achieving high-yielding tomato cultivars that are stress resistant.

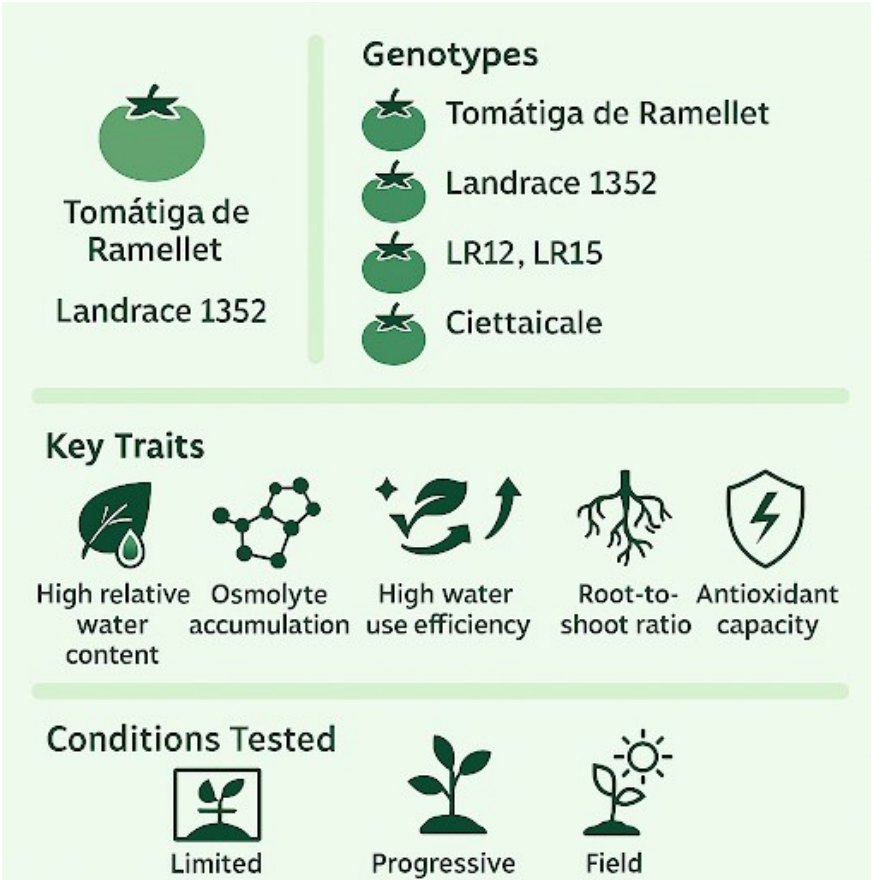


Figure 3. Drought-tolerant tomato landraces and their key adaptive traits.
Source: Adapted from Fullana-Pericàs et al., 2019; Grozeva et al., 2024; Rigano et al., 2014.

Pb Uptake and Transport in Solanaceae

Lead (Pb^{2+}) is mostly absorbed via the root organ into most plant systems using two cross routes; apoplastic and symplastic, apoplastic route, the lead is taken up passively along the cell membranes and the cell-to-cell interspaces, and the symplastic route involves active transport into the cytoplasm, followed by intercellular movement via the plasmodesmata (He et al., 2023; Ur Rahman et al., 2024). Pb in the apoplast may bind to negatively charged cell wall constituents, including pectins and hemicelluloses, which owes to its short term toxicity (Krzesłowska et al., 2016). This defense however is overcome when Pb is highly concentrated and is able to make entry into the symplast rather than to be prevented by the Casparian strip and forced via the apoplast in the apo stele region (Kumar et al., 2020). Once Pb crosses into the symplast, its uptake and internal movement depend on several membrane-bound metal transporters that are not specific to lead but can facilitate its transport due to chemical similarities with essential divalent cations (Ur Rahman et al., 2024). Among these, ZIP (ZRT-IRT-like Protein) transporters, originally recognized for their role in zinc and iron uptake, have a broad substrate range that includes Pb^{2+}, particularly under metal stress or zinc-deficient conditions when their expression is upregulated (Tan et al., 2020). Similarly, members of the NRAMP (Natural Resistance-Associated Macrophage Protein) family, including NRAMP1 and NRAMP6, contribute to the transport of Fe^{2+}, Mn^{2+}, and Cd^{2+}, and have been implicated in Pb uptake in hyperaccumulator species where they operate at the plasma membrane and tonoplast to mediate both cellular entry and vacuolar sequestration (Thomine & Schroeder, 2013). HMA (Heavy Metal ATPase) transporters, particularly the P_1B-type ATPases such as HMA2, HMA3, and HMA4, further assist in lead transport by actively pumping ions across membranes using ATP; in Solanaceae, these proteins are believed to facilitate xylem loading and intracellular detoxification, with HMA3 playing a particularly important role in tonoplast-localized vacuolar sequestration of Pb to minimize cytosolic toxicity (Mohabubul Haque et al., 2022). This process is summarized in Figure 4, which illustrates the glutathione-dependent phytochelatin synthesis pathway, Pb–PC complex formation, and vacuolar sequestration via ABC transporters in Solanaceae. After the successful loading of Pb into the xylem, it is then carried upward to aerial tissues through the transpiration stream, a process closely tied to environmental conditions, particularly the rate of transpiration driven by stomatal behavior (Ur Rahman et al., 2024; Zhou et al., 2018). In the event of or with the accumulation of abscisic acid (ABA) during drought stress, stomatal closure restricts transpirational pull, which in turn limits Pb mobility from roots to shoots (Zhou et al., 2018). However, not all Pb makes this journey. A significant portion is left behind in the root system, either they are compartmentalized into vacuoles or bound to cell wall components as part of the plant's detoxification strategy (Gao et al., 2022). This selective retention helps to explain why many Solanaceae crops accumulate high levels of Pb in roots while there is a minimal translocation to the fruits or edible tissues.

Recent transcriptomic studies have revealed that exposure to Pb toxicity induces an upregulation of metal transporter genes and a concomitant up-regulation of metal-chelation biosynthesis including phytochelatins and metallothioneins (Zhu et al., 2022). In the cytoplasm, these molecules also bind Pb ions and, in effect, inhibit free circulation, thereby lowering their toxic effects prior to the complex being carried out in the long-range translocation process (Riyazuddin et al., 2021; Abid et al., 2020). The combination of these multifarious networks, viz. passive and active transport machineries + intracellular detoxification + stress-responsive gene regulation = constitutes the characteristic lead-accommodating regime in Solanaceae species, which both determines their tolerance levels and build up patterns (Kisa, 2019).

Table 1. Summary of key transporter genes involved in Pb uptake and detoxification in Solanaceae

Transporter Family	Gene Examples	Primary Function	Subcellular/Cellular Localization	Pb Affinity	Reference(s)
ZIP	ZIP1, ZIP3, ZIP4	Uptake of Zn^{2+} and Fe^{2+}; non-specific transport of Pb^{2+} under stress conditions	Plasma membrane (roots)	Moderate (especially under Zn-deficiency)	Tan et al., 2020; Ur Rahman et al., 2024
NRAMP	NRAMP1, NRAMP6	Transport of Fe^{2+}, Mn^{2+}, Cd^{2+}, and Pb^{2+}; cellular entry and vacuolar sequestration	Plasma membrane and tonoplast	Confirmed in hyperaccumulators	Thomine & Schroeder, 2013
HMA (P_1B-ATPase)	HMA2, HMA3, HMA4	Active transport of Pb^{2+} into vacuoles or xylem loading for detoxification	Tonoplast (HMA3), plasma membrane (HMA2, HMA4)	High (especially HMA3 for vacuolar sequestration)	Mohabubul Haque et al., 2022
ABC Transporters	Not gene-specific	Pb–phytochelatin (PC) complex transport into vacuoles	Tonoplast	Indirect (complex-mediated)	Summarized in Figure 4
Chelators	Phytochelatins, Metallothioneins	Bind Pb^{2+} in cytoplasm to reduce free ion toxicity	Cytoplasm	High binding capacity	Zhu et al., 2022; Riyazuddin et al., 2021

Cellular and Anatomical Effects of Lead (Pb) Toxicity in Solanaceae

In Solanaceae crops, Lead (Pb) toxicity causes significant cellular and anatomical disruptions in their overall well-being. One significant impact is felt, particularly in their root development, oxidative homeostasis, and chloroplast integrity. These effects do not just impair growth and nutrient uptake, but they also compromise photosynthetic efficiency and stress resilience.

Pb exposure is known to be associated with the disruption of the cells in the root network. High Pb concentrations inhibit primary root elongation, reduce lateral root density, and lead to the general shortening of the growth that occurs in the root system. In tomato (*Solanum lycopersicum*), Pb stress has been shown to suppress the activities in the root meristematic and also promote cell wall stiffening, likely due to disrupted auxin gradients

and altered expression of cell wall-modifying enzymes such as expansins and peroxidases (Sharma & Dubey, 2005). Images obtained from the microscopic analysis of eggplant (*Solanum melongena*) have also revealed that under Pb stress, there is root tip deformation, cortical cell disintegration, and the collapse of xylem vessels, which indicates a direct interference with cell division and tissue organization (Magioli & Mansur, 2005).

Pb exposure induces excessive accumulation of reactive oxygen species (ROS) in plant cells, which involves superoxide anions (O_2^-), hydrogen peroxide (H_2O_2), and hydroxyl radicals (OH•), all of which induce oxidative stress and cause damage to their cells. This oxidative burst causes an overwhelming reaction in the antioxidant defense system, causing lipid peroxidation, protein oxidation, and damage to the DNA (Ur Rahman et al., 2024). In response, Solanaceae plants activate a suite of antioxidant enzymes to neutralize ROS (Zandi & Schnug, 2022). Notably, tomato and pepper plants exposed to Pb show increased activities of superoxide dismutase (SOD), catalase (CAT), ascorbate peroxidase (APX), and glutathione reductase (GR), which collectively form a detoxification shield that mitigates oxidative damage (Maia et al., 2022). These enzymatic defenses are often complemented by non-enzymatic antioxidants such as ascorbic acid and glutathione, which help maintain redox balance and protect cellular structures.

Pb toxicity also impairs chlorophyll biosynthesis and damages chloroplast ultrastructure, thereby hampering photosynthetic performance. In *Solanum lycopersicum*, chlorophyll a and b contents decline sharply under Pb stress, accompanied by reduced activity of key biosynthetic enzymes like δ-aminolevulinic acid dehydratase (ALAD) and protochlorophyllide oxidoreductase (POR) (Sharma & Dubey, 2005). Transmission electron microscopy has revealed swollen thylakoids, disrupted grana stacking, and increased plastoglobuli formation in Pb-exposed tomato leaves, indicating severe photodamage. These alterations tally with the low net photosynthetic rate (Pn), stomatal conductance (gs), and chlorophyll fluorescence parameters (e.g., Fv/Fm), all of which ultimately reduce plant productivity (Zhang et al., 2014).

Pb exposure in Solanaceae initiates a cascade of anatomical and cellular disturbances, disrupting the integrity of the cells in the root, generating oxidative stress, and degrading chloroplast function. These effects collectively undermine the plant's physiological resilience and growth potential. However, the induction of antioxidant defenses and differential anatomical responses among genotypes provide valuable targets for identifying or engineering Pb-tolerant cultivars.

Detoxification of Lead in Solanaceae

To balance off the physiological burden that is triggered by lead (Pb) toxicity, Solanaceae crops engage with multiple detoxification mechanisms, mainly but not limited to metal chelation and antioxidant defense systems. These responses reduce Pb bioavailability, neutralize secondary oxidative damage, and help to stabilize cellular metabolism under metal stress.

Chelation of Lead Ions

A primary strategy used for Pb detoxification is the chelation of Pb^{2+} ions in the cytosol through the synthesis of specialized ligands. Chief among these are phytochelatins (PCs) and metallothioneins (MTs). Phytochelatins, enzymatically synthesized from glutathione (GSH) by phytochelatin synthase (PCS), bind Pb ions into stable PC–Pb complexes. These are then actively sequestered into vacuoles via ABC transporters, minimizing cytosolic toxicity (Marques et al., 2025). In *Solanum lycopersicum*, PCS expression increases with Pb concentration and is associated with upregulated expression of glutathione biosynthetic genes, such as γ-ECS (gamma-glutamylcysteine synthetase).

Metallothioneins are low-molecular-weight, cysteine-rich proteins with high metal-binding affinity. In *Capsicum annuum*, Pb exposure has been associated with significant upregulation of MT2 and MT3 transcripts, particularly in roots, based on transcriptomic analyses (Kısa et al., 2016). While their precise roles under Pb stress require further functional validation, these isoforms are thought to contribute to cytoplasmic Pb detoxification by chelating free Pb ions.

Antioxidant Enzyme Responses

Pb-induced oxidative stress is a hallmark of toxicity, as lead interferes with both photosynthetic and respiratory electron transport chains, leading to excessive production of reactive oxygen species (ROS). To neutralize this oxidative pressure, plants activate a well-coordinated network of antioxidant enzymes that buffer redox imbalance. Key antioxidant enzymes, previously discussed (see Section 3.1), such as SOD, CAT, APX, and GPX, are upregulated under Pb stress, particularly in roots and leaves (Tomanek, 2015). In parallel, guaiacol peroxidase (POD) helps detoxify lipid peroxides, contributing to membrane stability during Pb-induced oxidative stress.

Proteomic profiling of Pb-stressed eggplant has revealed the upregulation of APX1, Cu/Zn-SOD, and monodehydroascorbate reductase (MDHAR) in roots and leaves, indicating a tissue-specific antioxidant strategy under Pb challenge. These enzymatic defenses often coincide with increased non-enzymatic antioxidants, such as ascorbic acid, glutathione, and phenolic compounds, reinforcing redox homeostasis (Tomanek, 2015).

Omics-Based Insights into Pb Detoxification

Recent transcriptomic and proteomic studies have provided profound insights into the regulatory mechanisms driving Pb tolerance in Solanaceae. RNA-Seq analyses in tomato and pepper have shown coordinated upregulation of genes encoding metal transporters (ZIP, NRAMP, HMA), vacuolar sequestration components, glutathione S-transferases (GSTs), and transcription factors such as WRKYs and bZIPs, which modulate stress responses (Singh et al., 2016).

Under Pb stress, methylation changes in promoter regions of detoxification genes have been observed, suggesting stress-induced epigenetic priming may help regulate tolerance and memory of metal exposure (Fasani et al., 2023).

Impact of Drought on Detox Pathways

The effect of drought pressure + Pb detoxification on the overall structure of the Solanaceae group is great. In another example, one can find that stomatal closure curbs transpiration, although this curbs Pb translocation to aerial tissues, which can be viewed as a possible protective measure. Nevertheless, drought also draws the cycles of glutathione, inhibits metabolic energy provision, both of which are required in the synthesis of the chelators, as well as those that rely on ATP to transport metals, such as HMA3 and ABC transporters (Zhang et al., 2014).

Besides, drought increases the basal ROS levels that can overcome the antioxidant systems that are already strained by the oxidative stress produced by Pb. Experimental findings in dual-stressed tomato demonstrate a slowness of APX and SOD genes up regulation, a decrease in phytochelatin content, and the acceleration in lipid peroxidation than single treatments of stress with Pb, signaling the trade-offs and boundaries in the defense mechanism under the presence of compounded stress situations.

Genotype-Specific Responses in Solanaceae

Detoxification capacity under Pb stress varies widely among Solanaceae genotypes, with landraces and wild relatives often showing superior tolerance traits compared to commercial cultivars. For instance, *Solanum nigrum*, a wild relative of eggplant, exhibits strong vacuolar Pb sequestration, sustained root biomass, and higher basal expression of PCS and MT genes, making it a model for phytoremediation and donor of metal-tolerance traits (Yu et al., 2015).

Local *Capsicum annuum* landraces from metal-polluted areas often display elevated antioxidant enzyme activity (e.g., increased SOD and CAT) and tend to accumulate less Pb in fruits compared to commercial hybrids, suggesting genetic adaptation for reduced translocation and enhanced detoxification. However, evidence for specific molecular mechanisms such as HMA3 upregulation under combined drought–Pb stress remains limited and requires dedicated research.

Tomato genotypes (*Solanum lycopersicum*) differ significantly in antioxidant efficiency and metal compartmentalization. Cherry-type tomatoes (*var. cerasiforme*) often show elevated APX, GSH, and phenolic levels under Pb exposure, along with better maintenance of photosystem II integrity and reduced Pb mobility to reproductive organs (Constán-Aguilar et al., 2013). These traits are desirable for breeding programs targeting both yield stability and safe edible quality under soil contamination.

Breeding Implications

The growing understanding of detoxification pathways, particularly from omics-enabled studies, opens opportunities for targeted breeding in Solanaceae. Perhaps the most important route is to incorporate high-expression alleles of PCS, MT, and HMA3 of wild or tolerant landraces to elite lines through introgression. The other potential is with the help

of the marker-assisted selection (MAS) using SNPs that are linked with a high capacity to scavenge ROS or low Pb translocation (Foolad, 2007).

Genomic selection may equally be used on the models in which the detox efficiency indices could be accommodated, like vacuolar sequestration rate or antioxidant enzyme kinetics. Since several advances have been made in this field of study, genomic editing devices such as CRISPR-Cas9 currently offer accurate solutions, adjusting important genes like HMA3 or transporters that are on the tonoplast, without affecting growth or productivity (Tiwari et al., 2023).

It is unknown why, but the combined effect of the two stress screens in common, that is, simultaneous exposure to Pb and drought, at early breeding stages, can aid the identification of genotypes with high redox plasticity, low metal uptake, and physiological stability under natural conditions at the soil level.

Table 2. Effects of Pb Stress in Selected Solanaceae Crops

Crop Species	Observed Pb Stress Effects	Adaptive or Detox Responses
Solanum lycopersicum	Root shortening, chlorophyll loss, oxidative stress, and disrupted grana stacking	Upregulation of SOD, CAT, APX; phytochelatin and metallothionein biosynthesis; vacuolar Pb sequestration
Capsicum annuum	Root cell damage, reduced photosynthetic parameters	MT2/MT3 expression; HMA3-mediated Pb transport; SOD and GR enhancement
Solanum melongena	Root meristem collapse, cortical disintegration	Upregulation of APX1, MDHAR in root and shoot tissues
Solanum nigrum	Maintains root biomass under Pb; strong vacuolar sequestration	High PCS and MT expression; Pb buffering in the vacuole
S. lycopersicum var. cerasiforme	Reduced Pb mobility to fruits; stable photosystem II	High APX and GSH levels; increased phenolic content; reduced lipid peroxidation

Note: The information presented in Table 1 is based on peer-reviewed primary studies that experimentally assessed physiological, biochemical, and molecular responses of Solanaceae species to Pb stress. Classification (e.g., PCS expression, vacuolar sequestration) reflects direct measurements such as gene expression (qRT-PCR), Pb content (AAS, ICP-MS), and stress indicators under controlled exposure.

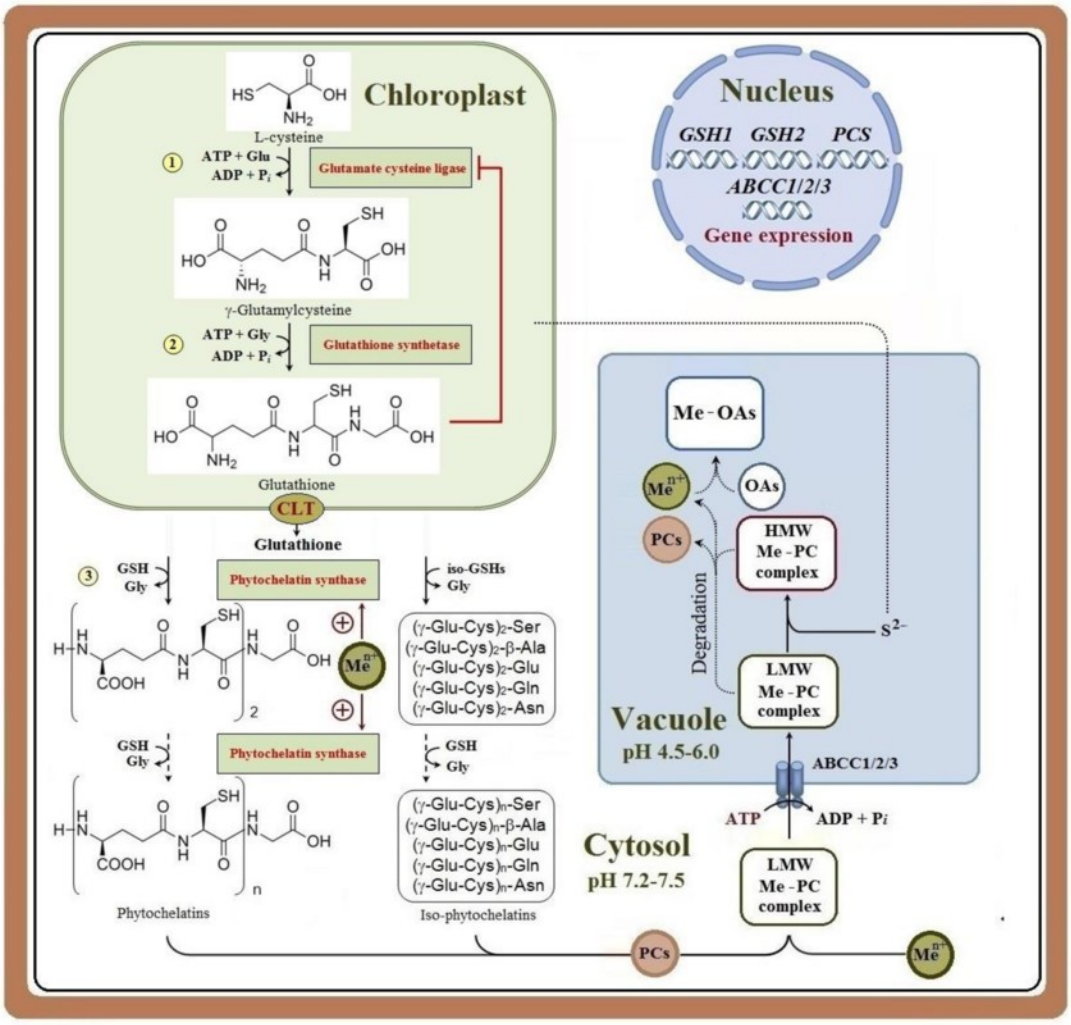


Figure 4. Phytochelatin-mediated lead detoxification pathway based on established heavy metal detox models.

Source: Seregin & Kozhevnikova. (2023)

Stress Signaling Under Lead and Drought in Solanaceae

Plants rarely face just one abiotic factor in isolation. What is obtainable in the real world is that most plants that are experiencing threat from one abiotic stress are likely to encounter another. In Solanaceae, the co-occurrence of drought stress and heavy metal pollution may be unavoidable, as water used for irrigation can even introduce lead unknowingly, or even the usage of fertilizer to improve yield (Sharma & Dubey, 2005; Kumar et al., 2020).

Plants respond to these stresses by activating complex signaling molecules like reactive oxygen species (ROS), abscisic acid (ABA), calcium ions (Ca^{2+}), and stress-related protein kinases. These signals do not act alone; they communicate with each other, causing a crosstalk across gene networks and metabolic pathways, which shapes how the plant adapts to combined stress conditions (Choudhury et al., 2016; Kambona et al., 2023).

Although it is often hypothesized that drought-induced ABA accumulation restricts transpiration and subsequently limits Pb translocation from root to shoot, empirical

evidence specific to Solanaceae remains limited. Some studies, such as Zhou et al. (2018), have observed reduced Pb mobility under drought in non-Solanaceous crops, suggesting that this may be a plausible but context-dependent mechanism. However, further controlled studies are required in Solanaceae to confirm whether drought consistently reduces Pb accumulation in aerial tissues.

Shared Stress Regulators: ROS, ABA, and Calcium

ROS molecules such as hydrogen peroxide (H_2O_2), superoxide radicals (O_2^-), and hydroxyl radicals (•OH) are quickly produced as a trigger to both Pb exposure and drought exposure. They are not only destructive, these molecules also serve as secondary messengers allowing to enhance the signal of stress. ROS production in Pb stress is mediated mainly due to a dysfunctional electron transport chain in mitochondrion and chloroplast whereas oxidative stress under drought stress is developed due to decreased carbon fixation and stomatal closure. The various sources still tend to share downstream targets and in many cases end up being similar, which may include antioxidant enzymes and redox-sensitive transcription factors (Choudhury et al., 2016).

Another key determinant in the central signaling status of both types of stress is abscisic acid (ABA). When drought occurs, the buildup of ABA signals the regulation of stomatal closure, osmotic balance, and stress gene expression. ABA levels also increase under Pb stress, and research shows that ABA signaling components, including PYR/PYL receptors and SnRK2 kinases, are upregulated during metal-induced stress (Kumar et al., 2022). The hierarchical relationship of hormone activity suggests that ABA is a central coordinator in dual-stress signaling. Notably, ABA also controls ROS production by NADPH oxidases, linking hormonal and redox signaling.

The other convergence point of the combined stresses is calcium signaling. Pb causes loss of Ca^{2+} homeostasis due to its ability to displace calcium at binding sites, but also causes transient Ca^{2+} spikes, which trigger the activation of calcium-dependent protein kinases (CDPKs). On the other hand, drought induces a cytosolic Ca^{2+} burst that controls the expression of genes, pathways of ion transport, and membrane reconstitution. These calcium waves interact with the ABA and ROS in regulating the plant's resistance to the two stressors. Dual Pb ion drought stress has been reported to cause stronger Ca^{2+} transient in tomato roots, as compared to individual modality (Kour et al., 2023).

MAPK Cascade and Downstream Transduction

Mitogen-activated protein kinase (MAPK) cascades denote a fundamental downstream transduction unit in Solanaceae stress signaling. MAPKs, including MPK3 and MPK6, are also phosphorylated under both Pb and drought conditions, and serve as a carrier to deliver messages of upstream receptors to the nucleus. Such cascades are the transcription factors WRKY, MYB, and bZIP, which regulate the expression of antioxidant enzymes in addition to the genes that synthesize the chelators and osmoprotectants.

The analysis of Transcriptomics in Pb-stressed pepper and tomato drought-stamba indicates that the MAPKKK–MAPKK–MAPK modules appear to be activated to a large extent, indicating that there is a possibility of signal integration that takes place at the level of kinases. Remarkably, these cascades could be activated much longer under the different stress types: drought would lead to prolonged activation of MAPK signaling, whereas Pb would induce acute yet short-lived activation of the kinase (depending on cytotoxicity) (Taj et al., 2010).

Overlap in Antioxidant Defense Networks

The majority of the open research literature is not concerned with the joint impacts of drought and lead stress per se. They are more likely to classify lead together with other heavy metals such as cadmium or arsenic, so it is hard to come up with clear statements about the interaction between Pb and drought. Such non-segregation imposes an embargo that restrains our insight into how these two stresses affect each other in the actual field (Krzyżak et al., 2023).

It has also been demonstrated in some studies that a combination of Pb and drought stress makes it difficult to regulate the balance between antioxidant defenses and oxidative stress. Indeed, the cost of the process of detoxifying Pb might take resources that should have been used on osmotic adjustment or other protective mechanisms of response to droughts (Cervilla et al., 2007). Severe situations may cause a reduction of photosynthetic activity and reduce recovery during and after the removal of specific stress.

Activation of antioxidant systems is one of the most salient axes of convergence in the Pb and drought signalling. The two stresses cause oxidative bursts, necessitating a strong detoxification of ROS. Superoxide dismutase (SOD), catalase (CAT), and ascorbate peroxidase (APX) are two examples of antioxidant enzymes, which are upregulated by the two stresses typically using transcriptional regulators (e.g., WRKY33, DREB2A, and NAC1). Tomato and eggplant subjected to combined stress of Pb and drought show an extra additive or even synergistic increase of SOD and GPX activities, especially in the root and leaves (Laxa et al., 2019)

The central roles are also played by non-enzymatic antioxidants, glutathione (GSH), ascorbic acid (AsA), and phenolic compounds. An example would be glutathione, which, in addition to being an ROS scavenger, is also utilized in phytochelatin biosynthesis, i.e., its protective role (dual stress) is two-fold; it functions in oxidative buffering and heavy metal chelation.

Hormonal and Transcriptional Crosstalk

Drought and Pb exposure also affect the biosynthesis and signaling of ethylene (ET), salicylic acid (SA), and jasmonic acid (JA), forming a complex hormonal web. For instance, Pb stress sometimes may cause an elevation in the level of ET, which interacts antagonistically with ABA, while JA tends to cooperate with ABA in defense gene induction.

This hormonal web is regulated by a suite of transcription factors, notably WRKYs, bZIPs, and NACs, that are often co-expressed in Solanaceae under both metal and drought stress. Certain transcription factors like WRKY25 and WRKY33 play a key role during drought and Pb stress by binding to W-box elements in the promoter regions of genes that control both antioxidant enzymes and metal transport. In tomato, dual stress conditions have been shown to increase the expression of WRKY33 and bZIP60, suggesting that these stresses activate some shared gene networks that help the plant tolerate them (Dong et al., 2023). A comparison of gene expression patterns under each stress gives a clearer picture of this relationship. For instance, genes like superoxide dismutase (SOD), catalase (CAT), and WRKY33 are commonly upregulated in both drought and Pb stress. However, drought tends to trigger more genes linked to osmotic regulation and ABA signaling, while Pb stress specifically activates genes responsible for producing metal-binding proteins and those that help move toxins into vacuoles for safe storage. This distribution is illustrated in Figure 5.

Genotypic Plasticity and Stress Priming

Different Solanaceae genotypes exhibit variable signaling responses under combined Pb and drought exposure. Wild relatives such as *Solanum nigrum* show stronger early activation of calcium–ABA pathways, while landraces of *Capsicum annuum* from metal-contaminated regions display higher MAPK and antioxidant enzyme activity under dual stress. This plasticity suggests the existence of stress memory or priming, where prior exposure to one stress enhances the response to another.

Epigenetic changes, such as DNA methylation in stress-responsive promoter regions, further suggest that signal integration can lead to semi-stable stress "memory," allowing some genotypes to mount faster and more robust defenses under recurring stress combinations (Sun et al., 2022).

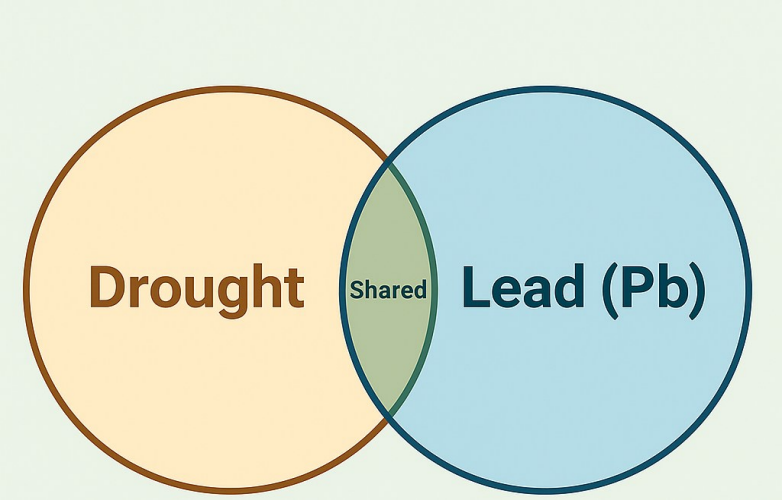


Figure 5. Comparative stress-responsive gene regulation under drought and lead exposure in Solanaceae.

Table 3: Shared and Unique Stress-Responsive Genes/Pathways Under Lead and Drought Stress in Solanaceae

Category	Drought Stress (Unique)	Shared Between Pb and Drought	Lead (Pb) Stress (Unique)
Key Signaling Molecules	ABA accumulation for stomatal closureCa^{2+} bursts for osmotic regulation	ROS (H_2O_2, O_2^-), ABA, Ca^{2+}, MAPK cascades (MPK_3, MPK6)	Pb-induced Ca^{2+} displacement Disruption of membrane transport
Transcription Factors	DREB2A, MYC2	$WRKY_{25}$, $WRKY_{33}$, bZIP60, NAC1	HSFs (involved in heavy metal tolerance), Specific WRKYs tied to metal detox
Antioxidant Enzymes	Peroxidase (POD) activity under dehydration	SOD, CAT, APX, GPX	Elevated GR (glutathione reductase) levels specific to Pb stress
Chelation & Transporters	Not prominent	Increased GSH and AsA (shared antioxidants), Induction of ABC transporters	Phytochelatin synthase (PCS), Metallothioneins (MT), HMA_3, ZIP, NRAMP genes
Hormonal Crosstalk	ABA–JA cooperation	ABA–ROS interaction activation and cross-talk	ABA–ET antagonism under metal exposure
Epigenetic Response	Histone H_3 acetylation in drought genes	Stress memory via DNA methylation and chromatin remodeling WRKY promoter priming	Methylation of metal transport gene promoters

Note: This table integrates data from peer-reviewed studies on Solanaceae crops, summarizing molecular responses to drought and lead (Pb) stress. Stress-specific pathways (e.g., DREB2A, MYC2, PCS, MTs, HMA_3) and shared mechanisms (e.g., ROS–MAPK signaling, WRKYs, SOD, APX) were identified through transcriptomics, physiological assays, and enzymatic profiling. Drought-related traits emphasize osmotic adjustment and ABA signaling, while Pb-related responses reflect metal chelation and sequestration. Source studies include Dong et al. (2023), Kisa (2019), Fasani et al. (2023), Ur Rahman et al. (2024), and Zhou et al. (2018).

Potential Synergy or Antagonism

Drought and lead (Pb) toxicity do not act in isolation. When they occur together, their interaction may either reduce or intensify overall stress symptoms in Solanaceae crops, depending on how the plant's internal systems respond.

In some cases, drought stress may reduce the amount of Pb that enters the plant. This occurs because when stomata close to conserve water, transpiration slows down. Since the upward movement of water through the xylem also drives the transport of minerals like Pb,

this reduced pull can limit how much Pb is taken up from the roots into the shoots (Mensah et al., 2025).

But this is not always a good thing. Sometimes, lead (Pb) stress can make things worse for the plant instead of helping it. For example, Pb can damage the roots by disrupting the cell membranes, blocking water channels like aquaporins, and disturbing the balance of important ions in the root zone (Ur Rahman et al., 2024). All of these make it harder for the plant to take up water. Now imagine this happening during drought, when water is already scarce, the plant ends up under more pressure from both lack of water and metal toxicity. So, rather than coping better, the plant may suffer more.

The majority of the open research literature are not concerned with the joint impacts of drought and lead stress per se. They are more likely to classify lead together with other heavy metals such as cadmium or arsenic, so it is hard to come up with clear statements about the interaction between Pb and drought. Such non-segregation imposes an embargo that restrains our insight into how these two stresses affect each other in the actual field (Krzyżak et al., 2023).

It has also been demonstrated in some studies that a combination of Pb and drought stress makes it difficult to regulate the balance between antioxidant defenses and oxidative stress. Indeed, the cost of the process of detoxifying Pb might take resources that should have been used on osmotic adjustment or other protective mechanisms of response to droughts (Cervilla et al., 2007). Severe situations may cause a reduction of photosynthetic activity and reduce recovery during and subsequent to the removal of specific stress (Choudhury et al., 2016).

Epigenetic and Stress Memory Considerations

Plants do not just respond to stress in the moment; they also 'remember' it. This stress memory, often driven by epigenetic modifications, allows Solanaceae crops to respond more quickly and efficiently to future episodes of drought or heavy metal exposure. When a plant faces drought or lead (Pb) stress, certain genes involved in defense, transport, and detoxification are activated. Over time, the way these genes are regulated can change at the chromatin level, without altering the underlying DNA sequence (Fasani et al., 2023; Ojeilua et al., 2025)..

One of the key mechanisms involved is histone modification. Under stress, chemical groups like acetyl or methyl can be added to specific histone tails, which affects how tightly the DNA is wrapped around them. When DNA is loosely packed, stress-responsive genes become more accessible and are expressed more easily. In tomato and pepper, stress-induced acetylation of histone H_3 has been associated with higher expression of drought and metal transport genes, suggesting a role in rapid gene activation when stress strikes again (Li et al., 2021).

Before lasting stress memory can be established, plants must first decode overlapping drought and Pb signals through shared signaling hubs. These include reactive oxygen

species (ROS), calcium, MAPKs, and abscisic acid (ABA). A simplified flowchart of these signal integration pathways is presented in Figure 6.

Another major process is DNA methylation, where methyl groups are added to cytosine bases in the genome. This modification can either silence or stabilize genes depending on the region. In Solanaceae, drought and Pb stress have been shown to alter methylation patterns in both promoter regions and transposable elements (Ur Rahman et al., 2024). These changes are not always temporary; in some cases, they are retained across cell divisions and even passed on to the next generation, offering what is known as transgenerational stress memory (Bhadouriya et al., 2021; Ojeilua et al., 2025).

Through this memory, previously stressed plants often respond more strongly or efficiently when the same stress reoccurs. This process, known as priming, equips them to better withstand subsequent drought or toxic metal exposure. For instance, a tomato seedling exposed to mild Pb stress may show enhanced activation of phytochelatin synthase and antioxidant genes if exposed again later in life, a form of biological preparedness encoded epigenetically (Kambona et al., 2023).

What makes these mechanisms stand out is their flexibility. Epigenetic changes can fine-tune gene expression in a way that is reversible, responsive, and context-dependent, making them ideal for complex stress environments where drought and heavy metals co-occur (Mirouze & Paszkowski, 2011). However, current research in Solanaceae is still in its early stages, and most findings are drawn from model species like Arabidopsis. There remains a clear gap in species-specific studies that investigate how tomato, pepper, or eggplant leverage epigenetic memory to navigate dual stress conditions (Kariñho Betancourt et al., 2024).

If we can identify stable epigenetic markers associated with drought-Pb tolerance, it could open up new routes for selecting resilient varieties without needing to edit their genetic code.

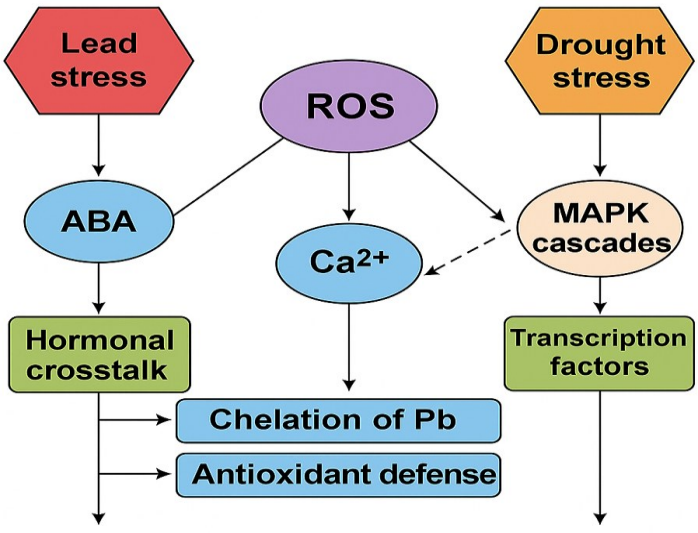


Figure 6: Signaling Pathways Under Combined Drought and Lead Stress in Solanaceae

Comparative Stress Tolerance in Solanaceae Crops

Solanaceae crops exhibit varying degrees of physiological and biochemical adaptation when exposed to drought and lead (Pb) stress. These differences are shaped by their intrinsic antioxidant systems, metal uptake pathways, and stress-responsive gene networks. Among the major cultivated species, tomato (*Solanum lycopersicum*) typically shows moderate drought tolerance, relying on osmotic regulation and partial stomatal control. However, it tends to accumulate relatively high levels of Pb in its roots, with limited translocation to aerial parts (Sharma & Dubey, 2005). Its antioxidant response under stress is modest, involving moderate induction of SOD, CAT, and APX, yet often insufficient under dual stress conditions. Consequently, tomato's field-level resilience under combined Pb and drought remains moderate, with yield penalties under prolonged exposure.

In contrast, pepper (*Capsicum annuum*) displays higher drought tolerance, particularly in landraces from semi-arid zones (Mahmood et al., 2021). Although Pb uptake occurs, it is generally lower than in tomato, with some shoot transfer reported. Notably, pepper mounts a robust antioxidant response, characterized by strong activation of enzymes such as SOD, CAT, and glutathione reductase, along with elevated levels of non-enzymatic antioxidants like ascorbate and phenolics (Yuce et al., 2024). This biochemical strength translates into superior field resilience, even under dual stress conditions.

Eggplant (*Solanum melongena*) exhibits variable drought tolerance across different cultivars, but its overall performance under combined stress conditions remains an underexplored venture. The intake of lead (Pb) by eggplant is typically measured from low to moderate, with minimal translocation to aerial parts, likely due to root-based sequestration mechanisms (Maia et al., 2022). However, its antioxidant defense system is comparatively weak, reducing its capacity to mitigate oxidative stress, particularly under simultaneous exposure to heavy metals and drought. Consequently, *S. melongena* often displays significant physiological and morphological disruptions under such conditions, leading to poor field performance (Singh et al., 2016).

Black nightshade (*Solanum nigrum*), a wild relative of the Solanaceae group, is emerging as a resilient model for dual stress tolerance. It demonstrates high Pb tolerance, mediated by vacuolar sequestration and efficient root compartmentalization (Kambona et al., 2023). Its drought tolerance is moderate to high, supported by early ABA and calcium signaling. The antioxidant machinery in *S. nigrum* is well-developed, with notable increases in GPX, GSH, and secondary metabolites like anthocyanins under stress (Fasani et al., 2023). These attributes give it high adaptability in marginal soils, suggesting potential for phytoremediation and stress-resilient breeding.

Similarly, wild peppers (*Capsicum chinense*) have been proven to be innately tolerant to drought, having a high-temperature and low-water environment (Zhu et al., 2022). Their translocation of Pb shoots is limited because it is kept by improved root-level chelation. They also possess a high antioxidant response, their biosynthesis of flavonoid is increased and their glutathione cycles remain similar in experimental conditions. Such characteristics

imply that they are genetically resistant to field stress, which makes them potential genetic materials in breeding dual-stress programs.

According to the researchers, Solanaceae wild relatives (*S. pennellii, S. chilense, and Capsicum baccatum*) have been reported to also bear important quantitative trait loci (QTLs) associated with drought tolerance, well-developed antioxidant mechanisms, and restricted uptake of heavy metals (Springer & Schmitz, 2017). These QTLs offer valuable targets for introgression into elite cultivars through marker-assisted selection or genomic approaches.

Table 4. Comparative drought and Pb stress tolerance traits across Solanaceae crops and wild relatives

Species	Drought Tolerance	Pb Uptake	Antioxidant Capacity	Field Resilience
Tomato (*S. lycopersicum*)	Moderate	High root accumulation	Moderate (SOD, CAT, APX induction)	Moderate
Pepper (*Capsicum spp.*)	High	Some shoot transfer	Strong (SOD, CAT, GR, AsA, phenolics)	High
Eggplant (*S. melongena*)	Variable	Low to moderate	Weak enzymatic buffering	Low
Black nightshade (*S. nigrum*)	High	Moderate with root sequestration	High (GPX, GSH, anthocyanins)	High
Wild pepper (*C. chinense*)	Moderate to high	Low shoot transfer	Strong (flavonoids, glutathione cycling)	Moderate to high
Wild tomato (*S. pennellii*)	Very high	Low	Moderate to strong (QTLs for stress traits)	High (especially drought)
Desert tomato (*S. chilense*)	High	Not well documented	Likely strong (heat/drought adaptive mechanisms)	High
Wild pepper (*C. baccatum*)	Moderate	Very low shoot transfer	Strong (enhanced ROS scavenging)	Moderate to high

Note: Table 4 presents a comparative summary of drought and lead (Pb) stress tolerance traits in cultivated and wild Solanaceae species. Classifications are based on peer-reviewed studies involving physiological, biochemical, and genetic data. Drought performance reflects field and pot trials under water-deficit conditions; Pb uptake and translocation data were derived from AAS or ICP-MS assays; and antioxidant capacity was assessed through enzymatic activities and gene expression.

Genetic and Biotechnological Strategies for Dual Stress Tolerance

Enhancing Solanaceae resilience to concurrent drought and lead (Pb) toxicity hinges on identifying and integrating tolerance-conferring alleles into elite backgrounds. Advances in

quantitative genetics and functional genomics offer pathways to accelerate dual-stress breeding using both conventional and molecular tools.

Marker-Assisted Selection (MAS) and QTL Mapping

Marker-assisted selection (MAS) remains a valuable tool for targeting quantitative trait loci (QTLs) linked to drought resilience, including traits such as root system architecture, transpiration efficiency, and hormonal regulation. In tomato, major-effect QTLs influencing relative water content and stress-responsive chlorophyll fluorescence have been mapped in segregating populations, providing anchor points for selection under field drought scenarios (Foolad, 2007). Similarly, loci correlated with Pb exclusion efficiency or low translocation to reproductive tissues have been identified, enabling pyramiding of both stress traits in breeding lines (Fatemi et al., 2022). Incorporation of dual-stress phenotyping in MAS pipelines will ensures that the important traits are not lost at the expense of yield and quality. Introduction of MAS in African breeding activities can be simplified by collaborating with genomic consortia and harmonized with the local biosafety regulations that facilitate the use of conventional breeding supported, stress tolerant cultivars.

CRISPR and Genome Editing

Emerging genome editing technologies, particularly CRISPR-Cas9, allow precise modulation of stress-related genes in Solanaceae. Editing of metal transporter genes such as HMA_3 has demonstrated potential in limiting Pb translocation to edible tissues, while maintaining nutrient homeostasis (Fatemi et al., 2022). Overexpression of transcription factors regulating both detoxification and drought response pathways, such as WRKYs and DREBs, can amplify systemic tolerance traits. However, in many African countries, regulatory uncertainty and limited transformation capacity still constrain the practical deployment of genome-edited crops. Ongoing continental biosafety dialogues may help clarify the regulatory status of non-transgenic CRISPR edits, opening avenues for their responsible use in public breeding programs.

Epigenetic and Priming-Based Approaches

Epigenetic changes, including promoter demethylation under drought and Pb exposure, have been observed in Solanaceae genotypes (Sun et al., 2022). Seed priming using low-level abiotic stimuli has also improved early antioxidant responses and transporter activation (Janah et al., 2025). Although such responses are not stably inherited, they offer a low-cost, non-GMO option to enhance early-stage resilience in high-risk production zones, especially where biotechnological infrastructure is limited.

Table 5. Key genes and QTLs associated with drought and Pb stress tolerance in Solanaceae crops

Gene/QTL	Function	Stress Type	Crop(s)
HMA3	Tonoplast Pb^{2+} transporter; vacuolar sequestration of heavy metals	Pb	Tomato, Pepper
PCS1	Phytochelatin synthase; chelation of Pb^{2+} in cytosol	Pb	Tomato, Eggplant
MT2, *MT3*	Metallothioneins bind Pb^{2+} and reduce cytotoxicity	Pb	Pepper
GSH1	Glutathione biosynthesis supports antioxidant and chelation responses	Pb, Drought	Tomato
WRKY33	Transcription factor regulating antioxidant genes and stress responses	Dual	Tomato
DREB2A	Drought-responsive transcription factor; induces dehydration tolerance genes	Drought	Tomato, Pepper
SOD, *APX*, *CAT*	Core antioxidant enzymes mitigate ROS under stress	Dual	Tomato, Pepper, Eggplant
QTL-drt9.1	Associated with root depth and drought recovery traits	Drought	Tomato
Sm-PbEx1 (Solanum melongena Pb Exclusion QTL 1)	Linked to reduced Pb translocation and higher shoot tolerance	Pb	Eggplant
NAC072	TF is involved in ROS regulation and stress recovery	Dual	Tomato
GSTU19	Glutathione S-transferase detoxifies ROS and xenobiotics	Pb	Tomato
RWC-QTL4	Controls relative water content under water deficit	Drought	Tomato, Pepper

Note: Table 5 compiles Pb- and drought-responsive genes and QTLs in Solanaceae crops based on peer-reviewed functional and genetic studies. Functional annotations are supported by transcriptomic, qPCR, and mutant evidence.

CRISPR-Modified Tomato Lines for Heavy Metal Resilience

Recent gene-editing efforts in *Solanum lycopersicum* have illuminated how targeted manipulation of stress-regulatory genes can reshape tolerance to drought, heat, and heavy metal toxicity. One of the notable examples is the CRISPR/Cas9-mediated knockout of *SlNPR1*, a master regulator traditionally known for pathogen defense. Edited lines exhibited heightened drought sensitivity, with increased stomatal aperture, elevated ROS levels, and suppressed expression of key drought-response genes such as *SlGST*, *SlDHN*,

and *SlDREB* (Li et al., 2019). These results highlight the key role *SlNPR1* plays in maintaining oxidative balance and protective signaling under water deficit.

In contrast, knockout of *SlMAPK3*, a mitogen-activated protein kinase, enhanced thermotolerance in tomato plants. Mutants showed reduced ROS accumulation, less membrane damage, and upregulation of heat shock transcription factors (HSFs) and heat shock proteins (HSPs), indicating that *SlMAPK3* functions as a negative regulator of heat stress response (Yu et al., 2019). The improved thermotolerance was associated with stronger antioxidant enzyme activity and a more stable redox environment under high temperatures.

Complementing these CRISPR-based knockouts, overexpression of *SlHMA3,* a tonoplast-localized P_1B-type ATPase, led to improved detoxification of lead ions through enhanced vacuolar sequestration. Transgenic lines retained more Pb^{2+} in roots, exhibited reduced translocation to shoots, and maintained better photosynthetic performance and biomass under lead stress (Tiwari et al., 2023).

These studies demonstrate how gene-specific editing and overexpression can fine-tune abiotic stress responses in tomatoes. They highlight both the positive and negative regulators of tolerance and emphasize the importance of functional validation in designing CRISPR-based strategies for crop improvement.

Future Directions

Although considerable progress has been made in dissecting the individual effects of drought and heavy metal stress in Solanaceae crops, there is still a limited understanding of how these stressors interact under realistic, multi-factorial field conditions. Most current studies rely on single-stress treatments in controlled environments, which do not reflect the complex genotype × environment × stress (G×E×S) interactions found in real-world fields. In natural settings, fluctuating moisture levels, uneven Pb contamination, and microbe-driven changes in metal mobility result in dynamic plant responses that cannot be fully captured in pots or growth chambers. This calls for expanded dual-stress field trials that go beyond isolated responses and instead explore the physiological and molecular trade-offs that arise when drought and Pb toxicity occur together.

A key priority is the deeper integration of omics technologies. Although transcriptomic and proteomic analyses have offered insights into individual stress signaling pathways, their application under combined stress is still uncommon. Future studies should focus on transcriptomic profiling under dual stress across both tolerant and sensitive genotypes to pinpoint critical regulatory hubs that coordinate responses between antioxidant activity and metal detoxification. Proteomic and metabolomic profiling is also needed to track enzyme shifts, redox dynamics, and the biosynthesis of protective molecules in real time. In addition, recent findings on stress-triggered DNA methylation and chromatin remodeling suggest that epigenetic control plays a role under dual stress, but this area remains largely unexplored. Building a unified omics-based platform would allow

researchers to identify reliable biomarkers for selection and accelerate the breeding of cultivars with durable resilience.

Another promising area lies in the use of wild Solanaceae relatives and traditional landraces that have evolved under low-input, stress-prone environments. Many of these genotypes show natural tolerance to both drought and heavy metals and may possess beneficial alleles linked to deeper roots, enhanced metal exclusion, or stronger antioxidant defenses. Incorporating these resources into breeding programs and screening them early under dual stress conditions could help unlock new sources of tolerance that are often missing in modern cultivars. However, the absence of uniform evaluation metrics continues to delay their use.

To overcome this, researchers must develop composite indices that reflect the plant's overall performance under stress. Rather than focusing on isolated traits like root length or chlorophyll concentration, these indices should combine factors such as biomass maintenance, ROS suppression, Pb sequestration, and yield consistency. Such multi-trait tools can help breeders screen large populations more efficiently and select high-potential lines before committing to field trials.

As illustrated in Figure 7, a full model for incorporating dual-stress adaptation into breeding should track the entire pathway, from external stress inputs, through intermediate biological processes, to final yield-related outcomes. Feedback loops from field evaluations, combined with omics-driven trait discovery and functional gene validation, can support ongoing improvements through each breeding cycle. Moving forward, advancing Solanaceae breeding will depend on shifting from single-stress research toward systems-based thinking that treats dual-stress tolerance as a unified and selectable trait.

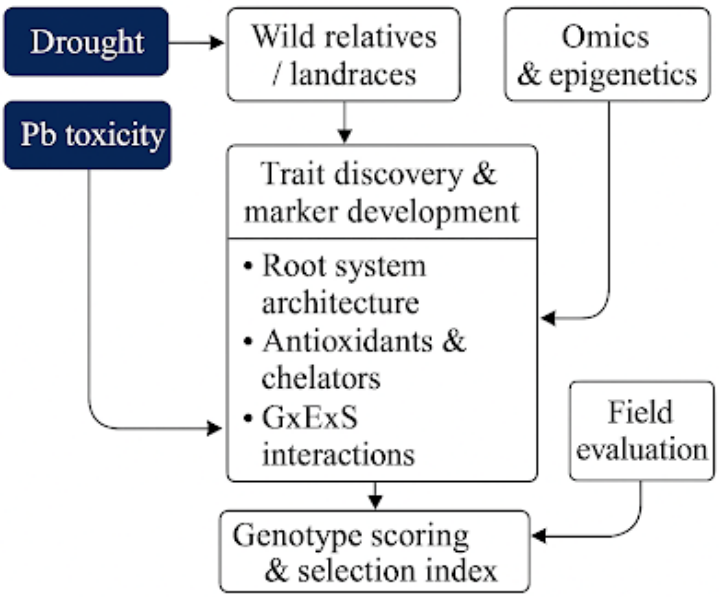


Figure 7: Model for dual-stress trait integration into Solanaceae breeding pipelines

Conclusion

In closing, this review has shown that drought and lead (Pb) toxicity, though well-studied individually, are rarely investigated as a combined stress, despite occurring together in real farming conditions. By bringing together findings on physiology, anatomy, detoxification, and gene-level responses in Solanaceae crops, this work not only identifies key tolerance traits but also exposes the major gaps holding back progress. Without dual-stress data, field validation, or proper use of wild relatives, breeding efforts will remain one-sided. Moving forward, researchers and breeders must shift from lab-based single-stress models to integrated dual-stress screening that reflects actual field realities. It is only through this kind of grounded, systems-based approach that we can develop tomato, pepper, and eggplant varieties capable of performing under the combined weight of drought and heavy metal stress. The tools are available, from omics to CRISPR, but they must be used with clear field targets in mind.

Recommendations

Future research should prioritize integrated field trials that simulate real-world dual stress conditions, particularly drought and lead exposure in Solanaceae crops. There is also a need to incorporate wild relatives and landraces into screening programs to uncover overlooked tolerance traits. Molecular tools such as CRISPR and transcriptome profiling should be applied to dissect shared and unique pathways involved in dual-stress adaptation. Finally, breeding efforts should consider genotype × environment × stress (G×E×S) interactions to ensure practical gains in stress resilience.

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