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Physiological and Biochemical Mechanisms of Aluminum Tolerance in Maize (Zea mays L.): A PRISMA-ScR Guided Scoping Review and Systematic Evidence Map

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Abstract
Acidic soils present a critical challenge to maize (Zea mays L.) production worldwide, with aluminum toxicity serving as a primary physiological constraint that restricts root elongation and impairs nutrient acquisition. Historically, plant physiology research and crop breeding efforts heavily emphasized organic acid exudation—driven primarily by ZmMATE1 and ZmMATE6 citrate transporters—as the main mechanism for excluding toxic aluminum from sensitive root apex tissues. However, accumulating evidence demonstrates that aluminum tolerance in maize is inherently polygenic, relying on an interconnected network of apoplastic, symplastic, and transcriptional responses rather than a single biochemical pathway. This scoping review provides a synthesis of physiological, and transcriptomic literature published up to July 2026, conducted in strict adherence to PRISMA-ScR guidelines. A systematic search across Web of Science, PubMed, and Scopus retrieved 642 initial records, yielding 78 high-quality studies following rigorous dual-reviewer screening. From these curated studies, we systematically map 14 validated, heterologously expressed, and candidate genes associated with aluminum stress. Key findings emphasize the central regulatory module governed by ZmSTOP1, which orchestrates downstream defense networks. Beyond transcriptional control, we delineate essential apoplasmic modifications, particularly pectin methyl-esterification dynamics that dictate aluminum binding capacity within root cell walls. Additionally, we evaluate internal symplasmic protection pathways, including reactive oxygen species scavenging mediated by ZmAT6 to maintain cellular integrity. Finally, we address a major disconnect between short-term hydroponic seedling assays and mature field performance, offering a PRISMA-guided framework integrating multi-trait genetic tolerance with agronomic practices like liming.
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Keywords: *Zea mays, aluminum toxicity, ZmMATE1, ZmSTOP1, apoplast, cell wall pectin, ROS scavenging, PRISMA-ScR, evidence map*

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I. Introduction and Rationale

Acid soils (pH < 5.0) cover approximately 30% of the world's ice-free land surface (~3,950 million hectares) and nearly 50% of potential arable land globally (von Uexküll & Mutert, 1995; Kochian et al., 2015). Under acidic soil conditions, aluminum is solubilized from clay minerals into the phytotoxic trivalent cation species (Al^{3+}), which rapidly inhibits root elongation at micromolar concentrations (Kopittke et al., 2016). Because soil acidity is co-characterized by phosphorus (P) fixation, toxic manganese (Mn^{2+}) concentrations, and restricted subsoil rooting depth, Al toxicity often severely limits crop nutrient uptake and water acquisition (Rao et al., 2016; Magalhaes et al., 2018).

Maize (*Zea mays* L.) is a vital staple food and feed crop across extensive acid-soil regions in Sub-Saharan Africa, South America, and Southeast Asia. Due to its high genetic diversity and well-annotated genomic resources, maize has served as a primary model for dissecting complex abiotic stress responses, including aluminum toxicity (Guimarães et al., 2014). Historically, root citrate exudation mediated by Multidrug and Toxic Compound Extrusion (MATE) transporters—specifically ZmMATE1 and ZmMATE6—has been treated as the primary Al exclusion mechanism in maize (Maron et al., 2010; Du et al., 2021b). However, extensive evaluations of tropical maize germplasm (including East African and South American landraces) demonstrate that high Al tolerance frequently operates independently of ZmMATE1 expression or high citrate exudation rates (Piñeros et al., 2005; Matonyei et al., 2020).

While individual narrative reviews have addressed specific aspects of Al stress, a comprehensive scoping review that systematically maps validated versus putative candidate genes, evaluates cell-wall and internal detoxification pathways, and assesses the translational validity of hydroponic assays has been missing. This

scoping review applies the PRISMA-ScR framework to: (1) map empirical evidence across cellular subsites; (2) elucidate core transcriptional cascades (ZmSTOP1); (3) identify critical methodological gaps in current screening pipelines; and (4) propose an integrated framework combining multi-trait selection with agronomic soil amendments.

II. PRISMA-ScR Methodology and Evidence Accounting

2.1 Protocol and PCC Boundary Definitions

This review was conducted according to PRISMA-ScR guidelines (Tricco et al., 2018) and JBI scoping review methodology (Peters et al., 2020). The Population-Concept-Context (PCC) framework was defined as:

• Population: Maize (*Z. mays* L.) inbred lines, hybrids, landraces, and mapping populations.

• Concept: Physiological, biochemical, and structural mechanisms underlying Al^{3+} tolerance, exclusion, or internal detoxification or sequestration.

• Context: Laboratory hydroponic assays, growth chamber experiments, glasshouse pot trials, and acid-soil field evaluations across global research settings.

2.2 Literature Search Strategy and Study Selection

A systematic search was executed on July 25, 2026 across Web of Science Core Collection, PubMed, and Scopus databases. The search string utilized Boolean combinations: (``Zea mays'' OR ``maize'') AND (``aluminum toxicity'' OR ``Al tolerance'' OR ``citrate exudation'' OR ``ZmMATE'' OR ``cell wall'' OR ``ROS scavenging'' OR ``STOP1''). Searches were restricted to peer-reviewed primary and secondary research articles and mechanistic reviews published up to July 2026. Grey literature and non-English publications without English abstracts were excluded.

Title and abstract screening, followed by full-text eligibility assessment, was conducted independently by two reviewers, with consensus resolution for discrepancies. Studies were included if they provided empirical data or comprehensive bibliography on maize physiological or biochemical responses to Al stress. Studies focusing exclusively on other plant species without direct maize comparative data or heterologous maize gene characterization were excluded.

2.3 Systematic Study Accounting and PRISMA Flow Metrics

The database search yielded 642 initial records (Web of Science: 284, Scopus: 226, PubMed: 132). After removing 188 duplicate entries, 454 titles and abstracts were screened. Of these, 326 records were excluded for failing to meet eligibility criteria (e.g., non-maize studies, lack of Al toxicity focus). Full texts of 128 articles were assessed, resulting in the final inclusion of 78 studies and key mechanistic benchmarks. Figure 1 summarizes the PRISMA-ScR selection accounting.

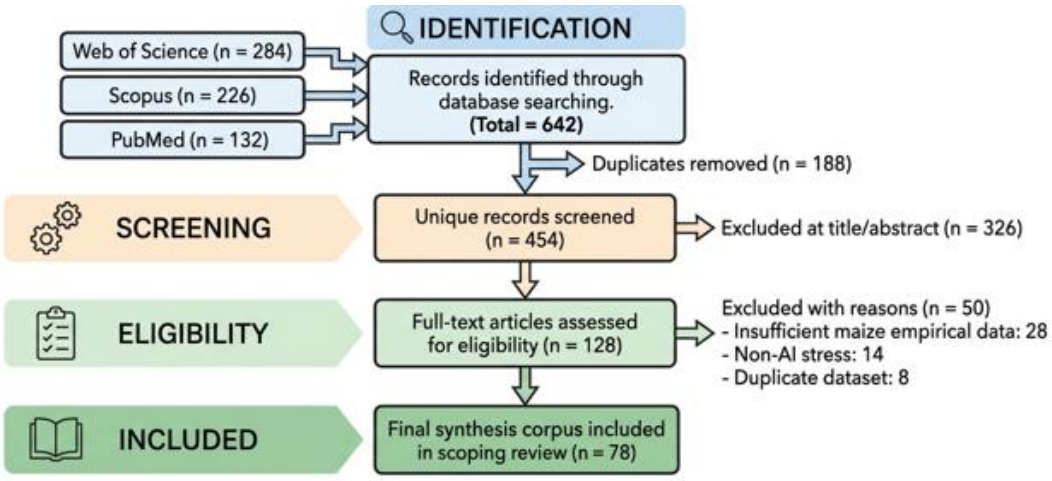


Figure 1: PRISMA-ScR Selection Accounting Flow Metrics

III. Primary Lesions and Physiological Manifestations of Al^{3+} Injury

3.1 Apoplastic Cell Wall Stiffening & Ca^{2+} Displacement

The primary site of Al toxicity in maize occurs within minutes of exposure in the apoplast of the root apex, specifically within the distal transition zone (DTZ, 1–2 mm from the tip), where root cells transition from cell division to rapid elongation (Sivaguru & Horst, 1998; Kopittke et al., 2015). Trivalent Al^{3+} binds with high affinity

to negatively charged unmethylated pectin carboxyl groups in the cell wall. This binding displaces essential divalent calcium (Ca^{2+}) ions, forming rigid pectin-Al cross-links that impair cell wall extensibility and halt root elongation prior to significant symplastic Al entry (Horst et al., 2010; Kopittke et al., 2016).

3.2 Plasma Membrane Disruption & ROS Accumulation

Subsequent to apoplastic binding, Al^{3+} interacts directly with plasma membrane phospholipids, inducing membrane rigidity, inhibiting plasma membrane H^+-ATPase proton pumping, and triggering callose (β-1,3-glucan) accumulation that plugs plasmodesmata (Yamamoto et al., 2002; Zhang et al., 2017). This membrane disruption triggers an oxidative burst, generating reactive oxygen species (ROS) such as hydrogen peroxide (H_2O_2) and superoxide radicals (O_2^-), leading to lipid peroxidation and mitochondrial dysfunction in sensitive genotypes (Giannakoula et al., 2008; Yu et al., 2024).

3.3 Hormonal Reprogramming in the Root Transition Zone

Al^{3+} stress rapidly stimulates localized ethylene (ET) biosynthesis in the root apex. This stimulation upregulates local auxin biosynthesis (mediated by TAA1/YUCCA modules) and alters auxin transport toward the DTZ (Sun et al., 2010; Yang et al., 2014). Localized auxin accumulation acts as a signaling cascade that actively inhibits cell expansion, demonstrating that root elongation arrest is a coordinated developmental response operating alongside physical cell-wall stiffening.

IV. Systematic Evidence Map of Al^{3+} Tolerance Genes in Maize

To provide a systematic evidence map, candidate and validated genes identified in the scoping review were categorized by cellular subsite, function, and empirical level of evidence in maize. Table 1 outlines these functional components, explicitly distinguishing direct maize genetic validation from heterologous or bioinformatic inferences.

Table 1: Evidence Map of Characterized, Heterologously Validated, and Candidate Al Tolerance Genes in Maize

Gene Symbol	Molecular Function / Pathway	Cellular Subsite	Evidence Level in Zea mays	Experimental Validation Model	Key References
ZmMATE1	MATE Citrate Transporter	Plasma Membrane	Fully Validated	Maize NILs, Copy Number (CNV) QTL, qPCR	Maron et al. (2010, 2013)
ZmSTOP1	C2H2 Zinc-Finger Transcription Factor	Nucleus	Fully Validated	Maize mutants, RNA-seq, promoter binding	Iuchi et al. (2007); Li & Tian (2023)
ZmAT6	Aldehyde Dehydrogenase (ROS Scavenging)	Cytosol	Fully Validated	Transgenic maize overexpression, MDA assays	Du et al. (2020)
ZmALMT2	ALMT Anion Efflux Transporter	Plasma Membrane	Validated	Xenopus oocyte electrophys, maize expression	Piñeros et al. (2008); Ligaba et al. (2012)
ZmMATE6	MATE Citrate Transporter	Plasma Membrane	Heterologous Validation	Transgenic Arabidopsis, maize QTL mapping	Du et al. (2021b)
ZmXTH	Xyloglucan Endotransglucosylase	Cell Wall / Apoplast	Heterologous Validation	Transgenic Arabidopsis overexpression	Du et al. (2021a)
ZmNrat1	Nramp Al^{3+} Influx Transporter	Plasma Membrane	Putative Candidate	Inferred via homology to OsNrat1	Guimarães et al. (2014); Matonyei (2020)
ZmALS1	Tonoplast ABC Transporter	Tonoplast / Vacuole	Putative Candidate	Inferred via homology to OsALS1	Huang et al. (2012); Kochian (2015)

4.1 Rhizosphere Exclusion & Transposon-Driven Promoter Variation

Citrate exudation into the rhizosphere remains the best-characterized exclusion mechanism in maize. Chelation of Al^{3+} by citrate forms a non-toxic Al-citrate complex, preventing Al interaction with cell wall pectin (Ma et al.,

2001; Kochian et al., 2004). Maron et al. (2013) demonstrated that natural variation in maize Al tolerance is strongly driven by copy number variation (CNV) at the ZmMATE1 locus. Tolerant genotypes carry multiple tandem copies of ZmMATE1 driven by a retrotransposon insertion in the promoter region, leading to higher ZmMATE1 transcript abundance, expanded root-tip expression, and sustained citrate release.

4.2 Transcriptional Control: The ZmSTOP1 Regulatory Cascade

Citrate exudation and acid-soil acclimation are governed at the transcriptional level by Sensitive to Proton Rhizotoxicity 1 (STOP1), a multi-C2H2 zinc-finger transcription factor (Iuchi et al., 2007; Li & Tian, 2023). Under Al^{3+} and low pH stress, ZmSTOP1 is post-translationally stabilized (avoiding RAE1-mediated proteasomal degradation) and binds to specific promoter motifs to activate ZmMATE1, ZmMATE6, and genes involved in proton tolerance and organic acid metabolism (Tokizawa et al., 2015; Zhang et al., 2019). Thus, ZmSTOP1 functions as a master regulator coordinating simultaneous responses to Al toxicity and proton stress.

4.3 Apoplastic Adaptation & Cell-Wall Remodeling

In genotypes where citrate exudation is low, apoplastic modifications provide vital protection. Tolerant maize lines display lower overall pectin content and a higher degree of pectin methyl-esterification in the root apex, resulting in fewer free carboxyl groups to bind Al^{3+} (Eticha et al., 2005; Horst et al., 2010). Furthermore, cell-wall remodeling enzymes such as xyloglucan endotransglucosylase/hydrolases (e.g., ZmXTH) alter hemicellulose structure and maintain wall extensibility under stress (Du et al., 2021a).

4.4 Symplastic Detoxification & ROS Scavenging

While symplastic Al uptake transport pathways in maize (such as ZmNrat1 and ZmALS1) remain putative and inferred from rice homologs, internal ROS scavenging systems are functionally verified. Overexpression of the aldehyde dehydrogenase gene ZmAT6 in maize directly reduces lipid peroxidation and maintains root growth under Al stress (Du et al., 2020). Secondary osmolytes, including proline and soluble sugars, further stabilize cytosolic osmotic balance during chronic exposure (Giannakoula et al., 2008).

V. Critical Knowledge Gaps and Methodological Disconnects

5.1 ZmMATE1-Independent Tolerance Pathways

Screening of East African (Kenyan) and South American landraces demonstrates that high levels of Al tolerance frequently occur without elevated ZmMATE1 expression or high citrate exudation rates (Piñeros et al., 2005; Matonyei et al., 2020). Identifying uncharacterized non-citrate QTLs and structural variants present in these diverse germplasm pools represents a high-priority research gap.

5.2 Hydroponic Seedling Assays vs. Field-Scale Translation

The vast majority of functional studies rely on short-term (24–72 h) hydroponic seedling assays evaluating primary root growth inhibition. However, as presented in Table 2, field toxicity in acidic soils is characterized by prolonged multi-stress interactions involving chronic phosphorus deficiency, seasonal water stress, subsoil physical impedance, and spatial soil heterogeneity (Lynch, 2019; Gallego-Tévar et al., 2024). High performance in hydroponic nutrient solutions does not consistently predict mature root system architecture, P acquisition efficiency, or grain yield under field conditions.

Table 2: Methodological Comparison of Al Tolerance Evaluation Screening Systems

Evaluation System	Duration & Scale	Primary Measured Parameters	Key Methodological Advantages	Translational Limitations
Hydroponic Nutrient Assay	24–72 hours (Seedling)	Net root elongation (NRE), callose hematoxylin staining	High throughput, precise Al^{3+} activity control, non-destructive	Lacks P interaction, soil matrix, microflora, and subsoil impedance
Glasshouse Pot Assays	3–6 weeks (Vegetative)	Root biomass, adventitious rooting, P uptake, shoot dry weight	Captures soil-P interaction and rhizosphere dynamics	Root confinement effects, disturbed soil structure
Acid-Soil Field Trials	Full season (Grain yield)	Root depth penetration, drought avoidance, grain yield, agronomic efficiency	Real-world multi-stress evaluation, agronomic validity	High spatial soil variability, weather confounding, labor intensive

VI. Agronomic Translation and Integrated Soil Management

6.1 Synergy Between Genetic Tolerance and Agronomic Amendments

Genetic tolerance and soil amendments (lime and phosphorus fertilizers) serve complementary physiological roles. While citrate exudation excludes Al^{3+} from the root apex, it does not correct subsoil acidity or supply deficient nutrients. Combining Al-tolerant maize hybrids with strategic surface liming and targeted banding of P

fertilizer maximizes root penetration into subsoils, enhancing drought resilience and P-recovery efficiency (Kisinyo et al., 2014; Magalhaes et al., 2018).

6.2 Multi-Trait Selection Strategies in Maize Breeding

Breeding programs should transition from single-trait selection (e.g., screening exclusively for ZmMATE1 alleles or citrate exudation) toward integrated multi-trait selection pipelines. Combining ZmMATE1-mediated exclusion, STOP1-mediated proton tolerance, ZmAT6-driven ROS scavenging, and desirable cell-wall pectin profiles will build durable, broad-spectrum adaptation to complex acid-soil syndromes.

VII. Conclusions

Aluminum tolerance in maize is a multi-faceted trait governed by interconnected apoplastic, symplastic, and transcriptional networks. While ZmMATE1-mediated citrate exudation represents a major exclusion mechanism, alternative pathways involving apoplastic cell-wall modification, STOP1-directed transcription, and ROS scavenging are vital for the full span of phenotypic resilience. Future research must prioritize functional validation of putative internal transporters in maize and establish robust correlations between seedling physiological markers and agronomic performance in field soils.

Declarations and Transparency Statements

• Protocol Preparation: The scoping review protocol was prepared following PRISMA-P recommendations.
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