



Mechanisms of Tolerance to Acidic Soil Stress in Joha Rice Cultivars

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Abstract

Soil acidity is a major abiotic stressor that significantly limits rice growth and productivity, particularly in acid-prone regions where low soil pH, nutrient imbalances, and aluminium toxicity adversely affect plant development and performance. This review summarises the morpho-physiological, biochemical, and molecular responses underlying acidic soil stress tolerance in rice, with particular emphasis on Joha rice cultivars. Acidic stress impairs root development, photosynthetic efficiency, biomass accumulation, and membrane stability through oxidative damage, ion toxicity, and metabolic disruption. In contrast, tolerant cultivars exhibit enhanced growth performance, robust antioxidant defence systems, greater accumulation of osmoprotectants, and efficient activation of stress-responsive signalling pathways compared with sensitive cultivars. Key tolerance mechanisms include reactive oxygen species detoxification, maintenance of cellular pH homeostasis, aluminium exclusion and detoxification, and the activation of signalling networks mediated by Ca²⁺, abscisic acid (ABA), mitogen-activated protein kinases (MAPKs), and OsART1-regulated transcriptional responses. A comprehensive understanding of these adaptive mechanisms provides valuable insights for the identification, screening, and breeding of acid-tolerant rice cultivars, thereby contributing to sustainable rice production in acid-affected soils.

Keywords: Acidic soil stress, Aluminium stress, Antioxidant defence, Joha rice cultivar

Introduction

Rice (*Oryza sativa* L.) is the staple food for nearly half of the global population, particularly in developing countries, and is cultivated on approximately 160 million hectares worldwide, predominantly across Asia (IRRI, 2016). With the global population projected to reach nearly nine billion by 2050, increasing rice productivity under diminishing arable land resources remains one of the major challenges for global food security (Ai *et al.*, 2015) [22]. Among the various abiotic stresses constraining sustainable rice production, soil acidity is a major global concern, affecting nearly 30% of the world's land area and more than 50% of potentially arable soils with a pH below 5.0 (Mattiello *et al.*, 2010; Ngoune Tandzi *et al.*, 2018) [28, 32]. In India, particularly in North-East India, where nearly 80% of agricultural soils are acidic, acid soil stress poses a serious limitation to crop productivity (Saikia *et al.*, 2018; Mishra *et al.*, 2020) [29, 34].

Acidic soils are characterized by low pH, nutrient deficiencies, and increased solubility of toxic ions such as Al³⁺, Fe²⁺, and Mn²⁺, with phosphorus deficiency representing a major nutritional constraint (Kochian *et al.*, 2015; Kar *et al.*, 2021) [21, 22]. Among these, aluminium toxicity is recognized as one of the principal growth-limiting factors in acid soils, causing inhibition of root growth, membrane damage, nutrient imbalance, and oxidative stress through excessive generation of reactive oxygen species (ROS) (Awasthi *et al.*, 2019; Ofoe *et al.*, 2022; Liu *et al.*, 2022; Chakraborty *et al.*, 2024) [3, 7, 25, 33]. In rice, aluminium toxicity induces lipid peroxidation, disrupts ion transport, compromises membrane stability, and may ultimately trigger programmed cell death (Awasthi *et al.*, 2019; Sharma *et al.*, 2019) [3, 36].

Although rice is considered one of the most acid-tolerant cereal crops, substantial genotypic variation exists in tolerance mechanisms (Famoso *et al.*, 2010; Zhao *et al.*, 2018; Ma *et al.*, 2018; Yamaji *et al.*, 2018) [11, 40, 42]. Recent studies have revealed that aluminium tolerance in rice is mediated through integrated mechanisms involving organic acid secretion, antioxidant defence systems, and signalling pathways regulated by ART1/STOP1-related transcriptional networks (Wang *et al.*, 2024; Huang and Ma, 2025) [18, 39]. Acidic stress also activates ROS-mediated signalling, calcium-dependent MAPK cascades, ABA-regulated pathways, and plasma membrane H⁺-ATPases involved in intracellular pH homeostasis (Zhang *et al.*, 2020 [41]; Li *et al.*, 2021; Formentin *et al.*, 2018; Lim *et al.*, 2022; Bharath *et al.*, 2021; Haruta *et al.*, 2019; Duby and Boutry, 2021) [5, 10, 12, 16, 24].

Moreover, recent advances in transcriptomics and molecular breeding have significantly improved our understanding of low-pH adaptation mechanisms in rice and offer promising opportunities for the development of acid-tolerant cultivars (Chen *et al.*, 2023; Singh *et al.*, 2024; Gupta *et al.*, 2025) [8, 15, 37]. Under acidic stress conditions, oxidative damage is mitigated by antioxidant defence systems comprising both enzymatic and non-enzymatic components, which play critical roles in stress adaptation and cellular protection (Bose *et al.*, 2018; Turkan, 2018; Das *et al.*, 2021) [6, 9, 38]. Furthermore, chlorophyll fluorescence has emerged as a powerful non-destructive tool for evaluating photosynthetic performance and understanding plant responses to acidic environments (Murchie and Lawson, 2013) [31], while morpho-physiological screening has been widely employed to identify tolerant rice genotypes under acid soil conditions (Shandilya and Tanti, 2020; Aung and Masuda, 2020) [2, 35].

Properties of Acidic Soil

Soil pH exerts profound effects on soil health and plant growth by influencing nutrient availability, toxic metal solubility, microbial activity, root cell integrity, and cation exchange capacity (Ngoune Tandzi *et al.*, 2018; Mishra *et al.*, 2020) [29, 32]. Acidic soils, generally characterized by a pH below 5.5, occupy nearly 30% of the global land area and are widely distributed across different regions of the world, with approximately 40.9% occurring in the Americas, 26.4% in Asia, 16.7% in Africa, 9.9% in Europe, and 6.1% in Australia and New Zealand (Ngoune Tandzi *et al.*, 2018) [32]. Approximately 4.5% of the global agricultural land is severely affected by soil acidity, making it a major constraint to crop productivity (Bose *et al.*, 2018; Sharma *et al.*, 2019) [6, 36].

In India, acidic soils are predominantly distributed in high-rainfall regions such as North-East India and the south-western zones, where nearly two-thirds of soils have a pH below 5.5 (Mishra *et al.*, 2020; Saikia *et al.*, 2018) [29, 34]. These soils are commonly associated with nutrient deficiencies, particularly of phosphorus, calcium, and magnesium, together with increased solubility of phytotoxic ions such as aluminium (Al^{3+}), iron (Fe^{2+}), and manganese (Mn^{2+}), which severely restrict plant growth and productivity (Kochian *et al.*, 2015; Awasthi *et al.*, 2019; Ofoe *et al.*, 2022) [3, 22, 33].

In highly weathered tropical soils, such as Acrisols and Ferralsols, aluminium toxicity and poor nutrient availability represent major limitations to crop performance (Ngoune Tandzi *et al.*, 2018) [32]. Soil acidification is often aggravated by excessive rainfall, nutrient leaching, unsustainable management practices, and fluctuating redox conditions, which alter iron chemistry and intensify toxicity, particularly under flooded conditions (Becker and Asch, 2005; Aung and Masuda, 2020) [2, 4].

One of the most damaging consequences of low pH is the increased release of Al^{3+} into the soil solution, as aluminium becomes progressively more soluble with decreasing pH (Ma *et al.*, 2018; Liu *et al.*, 2022) [25]. Aluminium toxicity is widespread in South Asia and sub-Saharan Africa and frequently co-occurs with iron toxicity, imposing combined stress on rice growth (Kar *et al.*, 2021; Chen *et al.*, 2023; Gupta *et al.*, 2025) [8, 15, 21]. Excess Al^{3+} inhibits root elongation, damages root apices, alters cell wall structure, disrupts nutrient uptake, and interferes with root system architecture (Yamaji *et al.*, 2018; Chakraborty *et al.*, 2024; Das *et al.*, 2021; Singh *et al.*, 2024) [7, 9, 37, 40]. Likewise, iron toxicity induces oxidative stress through disruption of electron transport and excessive ROS generation, while aluminium stress similarly promotes ROS accumulation and membrane damage (Kar *et al.*, 2021; Bose *et al.*, 2018; Turkan, 2018) [6, 21, 38].

Collectively, these stresses share common physiological consequences, including oxidative injury, impaired nutrient absorption, and severe growth inhibition (Sharma *et al.*, 2019; Kar *et al.*, 2021; Yamaji *et al.*, 2018; Wang *et al.*, 2024) [21, 36, 39, 40]. Therefore, root growth reduction under acidic conditions is driven not only by proton toxicity but also by associated metal toxicities and oxidative damage, making acid soil stress a complex and multifactorial limitation to crop productivity (Awasthi *et al.*, 2019; Das *et al.*, 2021; Singh *et al.*, 2024) [3, 9, 37].

Morpho-Physiological Responses of Joha Rice Cultivars under Acidic Soil Conditions (pH 4.5)

Soil acidity is a major abiotic stress that severely limits rice growth and productivity, particularly in acid-prone ecosystems where aluminium and manganese toxicity, coupled with deficiencies of phosphorus, calcium, and magnesium, adversely affect plant performance (Awasthi *et al.*, 2019; Saikia *et al.*, 2018; Ofoe *et al.*, 2022) [3, 33, 34]. In rice, low-pH conditions inhibit root growth, reduce nutrient uptake, and impair overall plant development through proton toxicity and associated metal toxicities (Ma *et al.*, 2018; Yamaji *et al.*, 2018; Liu *et al.*, 2022) [12, 25, 40].

Joha rice cultivars exhibit distinct morpho-physiological responses under acidic stress, making them valuable genetic resources for understanding tolerance mechanisms (Shandilya and Tanti, 2020; Das *et al.*, 2021) [9, 35]. Under acidic soil conditions (pH 4.5), reduced root elongation caused by aluminium toxicity results in stunted root systems, decreased shoot length, and reduced biomass accumulation due to impaired nutrient acquisition (Zhao *et al.*, 2018; Chakraborty *et al.*, 2024) [7, 42]. In some tolerant genotypes, thicker roots and enhanced lateral root formation may serve as adaptive traits that improve nutrient absorption under stress conditions (Ma *et al.*, 2018; Haruta *et al.*, 2019; Duby and Boutry, 2021; Bharath *et al.*, 2021) [10, 16].

Acidic stress also negatively affects seed germination and early seedling establishment by disrupting enzymatic activity, weakening seed vigour, and restricting root penetration into the soil (Shandilya and Tanti, 2020) [35]. The toxic accumulation of Al^{3+} and Fe^{2+} under low-pH conditions interferes with root cell integrity and nutrient homeostasis, thereby reducing plant growth and inducing visible stress symptoms (Kar *et al.*, 2021; Aung and Masuda, 2020) [2, 21].

Comparative studies have shown that tolerant cultivars exhibit superior performance under acidic soil conditions compared with sensitive cultivars, maintaining better shoot and root growth, higher fresh and dry biomass, and improved root architecture under stress (Shandilya and Tanti, 2020; Das *et al.*, 2021) [9, 35]. Their enhanced tolerance is likely associated with more efficient exclusion or compartmentalization of toxic ions, improved nutrient uptake, and maintenance of cellular homeostasis (Awasthi *et al.*, 2019; Singh *et al.*, 2024) [3, 37]. In contrast, sensitive cultivars exhibit reduced branching, poor seedling establishment, and severe growth inhibition, reflecting greater susceptibility to acid stress.

Photosynthetic performance is also markedly affected under acidic conditions, with chlorophyll degradation, impaired chloroplast function, and reduced carbon assimilation commonly observed (Murchie and Lawson, 2013; Das *et al.*, 2021) [9, 31]. Acid-induced oxidative stress promotes excessive ROS accumulation, membrane lipid peroxidation, and elevated malondialdehyde (MDA) levels, particularly in sensitive cultivars (Bose *et al.*, 2018; Sharma *et al.*, 2019) [6, 36]. However, tolerant cultivars such as Bakul and Bahuboli maintain lower MDA accumulation, greater membrane stability, higher relative water content, and prolonged chlorophyll retention, thereby sustaining physiological activity under stress conditions (Shandilya and Tanti, 2020; Das *et al.*, 2021) [9, 35].

These morpho-physiological traits, together with stress injury indices, provide valuable selection criteria for breeding rice cultivars adapted to acidic soils (Fig. 1).

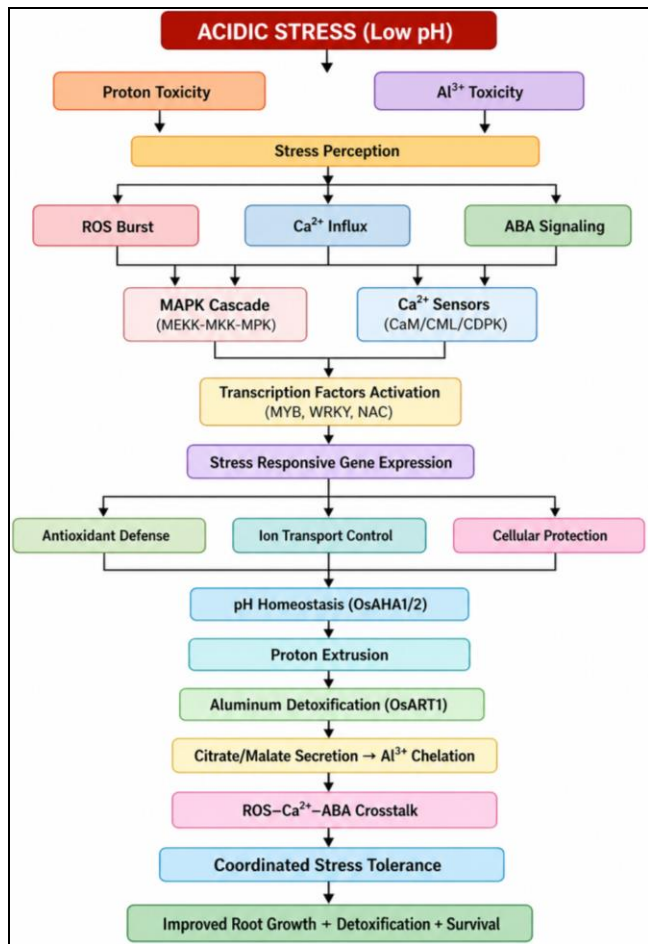


Fig 1: Diagrammatic representation of acidic stress (low pH) stress mechanisms (Acidic stress-responsive signalling pathways in rice)

Molecular Signalling and Adaptive Mechanisms of Rice under Acidic Soil Stress

Low-pH conditions severely impair rice growth, particularly in highly weathered and acid sulphate soils, by disrupting cellular homeostasis, root development, and nutrient acquisition (Awasthi *et al.*, 2019; Saikia *et al.*, 2018; Chen *et al.*, 2023) [3, 8, 34]. Rice plants perceive acidic stress through interconnected signalling networks involving reactive oxygen species (ROS), calcium (Ca^{2+}) signalling, and phytohormones such as abscisic acid (ABA), which collectively regulate adaptive responses required for survival under adverse environmental conditions (Bharath *et al.*, 2021; Lim *et al.*, 2022) [5, 24]. Similar to other abiotic stresses, acidic stress rapidly initiates molecular signalling cascades that alter gene expression and activate stress-responsive pathways essential for cellular protection and physiological adaptation (Li *et al.*, 2021; Singh *et al.*, 2024) [9, 37].

One of the earliest cellular responses to low-pH stress is the rapid accumulation of ROS accompanied by an elevation in cytosolic Ca^{2+} concentration, both of which function as crucial secondary messengers in stress signal transduction (Bose *et al.*, 2018; Turkan, 2018; Zhang *et al.*, 2020) [6, 38, 41]. Increased ROS production and calcium influx activate mitogen-activated protein kinase (MAPK) cascades involving MEKK–MKK–MPK signalling modules, which relay stress signals to downstream transcriptional regulators (Zhang *et al.*, 2020; Li *et al.*, 2021) [21, 41]. Activated MPKs subsequently phosphorylate transcription factors such as MYB, WRKY, and NAC proteins, thereby modulating the

expression of genes involved in stress tolerance, detoxification, and cellular protection (Li *et al.*, 2021; Bharath *et al.*, 2021) [5, 21]. Through this coordinated signalling network, rice plants fine-tune their physiological and molecular responses to acidic stress.

A critical adaptive mechanism in rice under acidic conditions involves the regulation of intracellular pH through plasma membrane H^+ -ATPases, particularly OsAHA1 and OsAHA2, which actively extrude excess protons from the cytosol to maintain pH homeostasis (Haruta *et al.*, 2019; Duby and Boutry, 2021) [10, 16]. Both the expression and activity of these proton pumps are enhanced under acidic conditions, helping to alleviate proton toxicity, preserve membrane integrity, and sustain normal cellular function (Chen *et al.*, 2023) [8]. Their activation is mediated through phosphorylation of the C-terminal regulatory domain, followed by interaction with 14-3-3 proteins, which stabilize the active conformation of the pumps and promote sustained proton extrusion (Haruta *et al.*, 2019; Duby and Boutry, 2021) [10, 16]. Calcium-mediated signalling may further regulate H^+ -ATPase activity via kinase-dependent phosphorylation, thereby linking ion signalling pathways with pH homeostasis (Zhang *et al.*, 2020) [41].

Under acidic soil conditions, proton toxicity is frequently accompanied by aluminium toxicity, which activates additional signalling pathways associated with aluminium detoxification and tolerance (Shandilya and Tanti, 2020; Das *et al.*, 2021) [9, 35]. A key regulator of aluminium tolerance in rice is the transcription factor OsART1, which controls the expression of genes involved in the secretion of organic acids such as citrate and malate. These organic acids chelate toxic Al^{3+} ions in the rhizosphere, thereby reducing aluminium toxicity and protecting root apices from cellular damage (Yamaji *et al.*, 2018; Ma *et al.*, 2018) [40]. Recent studies have further highlighted the roles of OsAIR3, STOP1-related signalling pathways, and antioxidant defence mechanisms in strengthening aluminium tolerance in rice (Wang *et al.*, 2024; Huang and Ma, 2025; Chakraborty *et al.*, 2024) [7, 18, 39]. Collectively, these mechanisms contribute to the maintenance of root growth and cellular integrity under acidic stress.

Calcium signalling also plays a central role in acidic stress adaptation. Elevated intracellular Ca^{2+} levels are sensed by calmodulin, calmodulin-like proteins (CMLs), and calcium-dependent protein kinases (CDPKs), which activate downstream transcription factors including MYB, WRKY, and NAC proteins that regulate ion transport, oxidative defence, and stress-responsive gene expression (Zhang *et al.*, 2020; Li *et al.*, 2021) [21, 41]. In addition, ABA signalling contributes substantially to acidic stress adaptation. Under low-pH conditions, increased ABA accumulation activates ABF transcription factors that bind to ABA-responsive elements (ABREs) in promoter regions, inducing genes such as *OsNAC* involved in stress adaptation, water balance regulation, and oxidative stress protection (Formentin *et al.*, 2018; Lim *et al.*, 2022) [12, 24]. Crosstalk among ABA, ROS, and calcium signalling pathways further refines stress perception and coordinates adaptive gene expression responses (Bharath *et al.*, 2021) [5].

Recent transcriptomic and integrative omics studies have revealed that acidic stress tolerance in rice is governed by highly coordinated signalling networks involving proton pumps, ROS-mediated pathways, hormone crosstalk, and transcriptional regulation (Chen *et al.*, 2023; Singh *et al.*,

2024; Gupta et al., 2025) [8, 15, 37]. The efficiency, integration, and spatial-temporal coordination of these signalling pathways ultimately determine the ability of rice plants to survive, adapt, and maintain productivity under acidic soil conditions ((Awasthi et al., 2019; Ofoe et al., 2022) [3, 33]).

Conclusion

Rice cultivation is increasingly threatened by acidic soils, which significantly impair plant growth, development, and productivity through proton toxicity, nutrient imbalance, and associated aluminium stress. Acidic stress induces pronounced morphological abnormalities, including poor root development, reduced tillering, and stunted growth, while simultaneously disrupting physiological and biochemical processes through oxidative damage, membrane destabilization, and metabolic imbalance.

To withstand such adverse conditions, rice plants activate multiple adaptive mechanisms, including enhanced antioxidant defence systems, osmoprotectant accumulation, and induction of stress-responsive genes that collectively maintain cellular homeostasis and reduce oxidative injury. A major component of acid tolerance involves the regulation of cytosolic pH through plasma membrane proton pumps such as OsAHA1 and OsAHA2, together with signalling networks mediated by ROS, Ca²⁺, and ABA that regulate downstream stress-responsive gene expression. In addition, aluminium detoxification pathways involving OsART1 and associated transport systems further reinforce tolerance mechanisms under acidic soil conditions.

Acid-tolerant rice cultivars exhibit superior coordination of these morphological, physiological, biochemical, and molecular responses, enabling improved survival and sustained growth under acidic stress. Therefore, future research integrating signalling biology, transcriptomics, functional genomics, and molecular breeding approaches will be essential to unravel the complex regulatory networks governing acid tolerance and to facilitate the development of resilient rice cultivars suited for acid-affected agroecosystems.

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