PLANT SCIENCE TODAY
Vol 13(sp1): 1-17
https://doi.org/10.14719/pst.10864

eISSN 2348-1900

REVIEW ARTICLE

Nutrient transporters in plants under abiotic and biotic stresses: Current insights and future perspectives

A S Priyanka[1], M K Kalarani[2]*, A Senthil[1], R Sivakumar[2], R Karthikeyan[2], M Umapathi[1], M Prasanthrajan[3] & D Selvi[4]

[1]Department of Crop Physiology, Tamil Nadu Agricultural University, Coimbatore 641 003, Tamil Nadu, India
[2]Directorate of Crop Management, Tamil Nadu Agricultural University, Coimbatore 641 003, Tamil Nadu, India
[3]Department of Environmental Science, Tamil Nadu Agricultural University, Coimbatore 641 003, Tamil Nadu, India
[4]Department of Soil Science and Agricultural Chemistry, Tamil Nadu Agricultural University, Coimbatore 641 003, Tamil Nadu, India

*Correspondence email - kalarani.mk@tnau.ac.in

Received: 24 July 2025; Accepted: 24 November 2025; Available online: Version 1.0: 26 February 2026

Cite this article: Priyanka AS, Kalarani MK, Senthil A, Sivakumar R, Karthikeyan R, Umapathi M, Prasanthrajan M, Selvi D. Nutrient transporters in plants under abiotic and biotic stresses: Current insights and future perspectives. Plant Science Today. 2026; 13(sp1): 1-17. https://doi.org/10.14719/pst.10864

Abstract

Nutrient transporters are integral membrane proteins that regulate the uptake, translocation and redistribution of essential nutrients in plants. Under abiotic and biotic stresses, their activity plays a pivotal role in maintaining ionic homeostasis, osmotic balance and stress signalling. This review explores how nutrient transporters respond to environmental cues and mediate stress tolerance. For instance, potassium transporters mediate stomatal closure under drought, maintain Na^+/K^+ homeostasis under salinity and facilitate structural adaptations such as adventitious root and aerenchyma formation under flooding. Similarly, plasma membrane H^+-ATPase maintains membrane integrity under heat stress, while metal transporters regulate the uptake and detoxification of heavy metals. In response to biotic stress, calcium and silicon transporters enhance structural defences and stimulate the biosynthesis of secondary metabolites. Collectively, these mechanisms underscore the central role of nutrient transporters in plants under stress and highlight their potential as targets for engineering crops with improved nutrient use efficiency and stress tolerance.

Keywords: abiotic stress; biotic stress; ionic homeostasis; nutrient transporters; stress tolerance

Introduction

The global population is estimated to reach 8.5 billion by 2030, with a subsequent increase to 9.7 billion in 2050 and a further rise to 10.4 billion by 2100. Food production needs to be doubled in developing countries to meet future food demands by 2050 (1). The challenge of doubling food production is complicated by the various stresses that plants encounter. As sessile organisms, plants are often exposed to various abiotic stresses, such as drought, salinity, heat stress, cold stress, heavy metal toxicity, flooding and nutrient imbalances (both deficiencies and toxicities), as well as biotic stresses, such as pathogen attack and pest damage. These stresses adversely affect photosynthesis, respiration and water and nutrient uptake, leading to excessive production of reactive oxygen species (ROS), disruption of ion homeostasis and hormonal imbalances, which ultimately impair plant growth and productivity, causing substantial economic losses and posing a serious threat to global food security (2). The maintenance of ion homeostasis is one of the critical mechanisms for optimal growth and development. Stress disrupts the structural integrity of the plasma membrane, which in turn impairs the function of membrane-embedded transporters. Consequently, the plant's ability to uptake, transport and distribute vital metabolites and nutrients across the membrane is significantly hindered (3).

The uptake of nutrients from the soil into the plant roots, followed by their transport to the root vascular tissues, is mediated by a range of nutrient transporters. Nutrient transporters are specialised membrane transporters that facilitate the movement of nutrients across cellular membranes, enabling plants to uptake nutrients from the soil and distribute them throughout the plant (Table 1) (19). Based on the type of nutrient ions they transport, transporters are categorised as cation transporters, which mediate the uptake of ions such as potassium (K^+), calcium (Ca^{2+}), magnesium (Mg^{2+}) and iron (Fe^{2+}) and anion transporters, which facilitate the transport of ions such as nitrate (NO_3^-) and chloride (Cl^-). These nutrient transporters are indispensable for maintaining nutrient homeostasis, which supports plant growth, development and stress adaptation (20). Plants employ various mechanisms to withstand stress, including osmotic adjustment, maintenance of ionic balance, activation of antioxidant defence systems, regulation of stomatal aperture, stabilisation of cellular membranes, protection of the photosynthetic apparatus and synthesis of secondary metabolites (21). Among these mechanisms, maintaining ionic homeostasis is critical for stress tolerance, with nutrient transporters playing a significant role in this process. Under stress conditions, nutrient transporters contribute to stress tolerance by improving nutrient-use efficiency (20).

Table 1. Major and micronutrient transporters in plants

S. No.	Nutrients	Transporter family	Transporter subtype	Primary function	Location	Reference
				Major nutrients		
1.	Nitrogen	Nitrate transporter 1/ Nitrate peptide family (NRT1/NPF)	NRT1.1 (NPF6.3)	Act as a dual-affinity nitrate transceptor	Epidermis near root tips, cortex or endodermis in mature roots, emerging leaves and reproductive parts such as style, stigma and anthers	(4)
			NRT1.2 (NPF4.6)	Act as a low-affinity nitrate transporter	Root hairs and root epidermis	(4)
			NRT1.5 (NPF7.3)	Involved in xylem loading and root-to-shoot translocation of nitrate	Xylem-pole pericycle	(4)
			NRT1.6 (NPF5.5)	Uptake of nitrate into ovules	Vascular tissues of the silique and funiculus	(4)
			NRT1.7 (NPF2.13)	Involved in nitrate remobilisation	Phloem of the minor veins in the old leaves	(4)
			NRT1.8 (NPF7.2)	Involved in xylem unloading of nitrate and stress tolerance	Xylem parenchyma cells of roots and leaves	(4)
			NRT1.9 (NPF2.9)	Involved in phloem loading of nitrate in roots	Companion cells of root phloem	(4)
			NRT1.11 and NRT1.12 (NPF1.2 and NPF1.3)	Involved in xylem-to-phloem nitrate redistribution in leaves	Companion cells of the major veins in expanded leaves	(4)
		Nitrate transporter 2 family (NRT2)	NRT2.1 and NRT2.2	Act as a high-affinity nitrate transporter	Older part of the main root	(5)
			NRT2.4 and NRT2.5	It acts as a high-affinity nitrate transporter, induced by N starvation	Younger part of the primary root and the distal region of lateral roots (NRT2.4); root hair zone of primary and lateral roots (NRT2.5)	(5)
			NRT2.6	Involved in plant defence	Leaves	(5)
			NRT2.7	Involved in vacuolar nitrate storage in seeds	Seed tonoplast	(5)
		Nitrate transporter 3/ Nitrate assimilation-related family (NRT3/ NAR2)	NRT3.1 and NRT3.2	Act as accessory proteins, modulate NRT2 function	Root plasma membrane (NRT3.1)	(5)
		Ammonium transporter family (AMT)	AMT1.1	Act as a high-affinity ammonium transporter	Outer cell layers of roots	(6)
			AMT1.2	Uptake of ammonium into the root epidermis supports symplastic transport	Endothelial cells	(6)
			AMT1.3	Act as a high-affinity ammonium transporter (Major contributor)	Outer cell layers of roots	(6)
			AMT1.4	Expressed in pollen, involved in reproductive development	Pollen grains and pollen tubes	(6)
			AMT1.5	Contributes to ammonium uptake, especially under limiting conditions	Roots	(6)
			AMT2.1	Involved in root-to-shoot ammonium translocation	Roots	(6)
			AMT2.2	Involved in ammonium transport and distribution	Leaves and petioles	(6)
2.	Phosphorus	Phosphorus transporter Family (PHT)	PHT1	Act as a high-affinity phosphate (Pi) transporter (Major contributor to root Pi uptake and initial translocation)	Root plasma membrane	(7)
			PHT2	It acts as a low-affinity Pi transporter and imports phosphate into chloroplasts	Chloroplast envelope	(7)
			PHT3	Transport Pi into mitochondria and supports ATP synthesis	Mitochondrial inner membrane	(7)
			PHT4	Transport Pi into the golgi bodies and other organelles	Plastid	(7)
			PHT5	Act as a Vacuolar Pi transporter and regulates cytosolic Pi homeostasis	Tonoplast	(7)
		PHO1 (SPX-EXS family) Family	PHO1	Xylem loading of Pi for root-to-shoot translocation	Root stellar cells are found in the lower part of the hypocotyl	(7)
		SULTR-like phosphorus distribution transporter (SPDT) family	SPDT	Allocation of Pi to seeds/grains in cereals	Xylem and phloem	(7)
		Phosphate Translocator Family	TPT, PPT, GPT and XPT	Metabolic exchange of Pi with phosphorylated intermediates across plastid envelope membranes	Plastids	(7)

3.	Potassium	Potassium transporter/high-affinity K$^+$ transporter/ K$^+$ uptake permease family	KT/HAK/KUP	It acts as a high-affinity potassium transporter and is involved in root-to-shoot translocation	Root plasma membrane	(8)
		High-affinity K$^+$ transporter family	HKT	It acts as a K$^+$/Na$^+$ co-transporter and is involved in Na$^+$ exclusion and K$^+$ homeostasis, especially under salt stress	Plasma membrane of root stele cells	(8)
		K$^+$ efflux antiporter family (KEA)	KEA1, KEA2, KEA3, KEA4, KEA5 and KEA6	Act as a K$^+$/H$^+$ antiport and are involved in K$^+$ and pH homeostasis in chloroplasts, endomembranes and vacuoles	Chloroplast inner envelope (KEA1 & 2); thylakoid membrane (KEA3); endomembrane compartments (KEA4,5 & 6)	(8)
		Cation/H$^+$ exchanger family	CHX17 and CHX21	Transport K$^+$ and other cations and involved in pH regulation, pollen tube growth and osmotic adjustment	Root plasma membrane (CHX17); chloroplast envelope (CHX21)	(8)
		Shaker-like K$^+$ channel family	AKT1, AKT2, KAT1, SKOR and GORK	Act as a low- and high-affinity K$^+$ transporter and are involved in K$^+$ loading into xylem, guard cell function and long-distance transport	Root periphery (AKT1); phloem tissues (AKT2); root xylem sap (SKOR); guard cells (KAT1 & 2)	(8)
		Tandem-pore K$^+$ channel family	TPK1, TPK2, TPK3, TPK4 and TPK5	Involved in K$^+$ flux across vacuolar and endomembrane systems, osmotic adjustment	Tonoplast	(8)
		K$^+$ inward rectifier channel family	Kir-like proteins	Act as an inward-rectifying K$^+$ channel involved in K$^+$ uptake in specific tissues	Tonoplast	(8)
4.	Magnesium	Magnesium transporters (MGT)	MGT1, MGT6 and MGT7	Involved in Mg^{2+} uptake from soil and long-distance transport	Root plasma membrane	(9)
			MGT2 and MGT3	involved in the maintenance of Mg^{2+} homeostasis in mesophyll cells	Tonoplast	(9)
			MGT4, MGT5 and MGT9	Involved in the active transport of Mg^{2+} for pollen development	Various membranes and predominantly found in anther and pollen cells	(9)
			MGT10	Import Mg^{2+} into chloroplasts, essential for photosynthesis	Chloroplast envelope	(9)
		Mg^{2+}/H$^+$ exchanger	MHX	Involved in Mg^{2+}/H$^+$ exchange and Mg^{2+} sequestration into the vacuole	Tonoplast	(9)
5.	Calcium	Ca^{2+}-permeable channels (Cyclic nucleotide-gated channels, Depolarisation-activated Ca^{2+} Channels, Hyperpolarisation-activated Ca^{2+} Channels, Glutamate receptor-like receptors and Nucleotide-binding leucine-rich repeat receptors)	CNGCs, DACCs, HACCs, GLRs and NLRs	Mediates Ca^{2+} influx into the cytosol, crucial for signalling and stress responses	Plasma membrane	(10)
		Ca^{2+}-ATPases (Autoinhibited Ca^{2+}-ATPases, ER-type Ca^{2+}-ATPases)	ACAs and ECAs	Use ATP to pump Ca^{2+} out of the cytosol into organelles or apoplast, maintaining low cytosolic Ca^{2+}	Plasma membrane (ACAs); endoplasmic reticulum (ECAs)	(10)
		Ca^{2+}/Cation antiporters (Ca^{2+}/H$^+$ exchangers), Ca^{2+}/ Cation exchangers, Na$^+$/Ca^{2+} exchangers)	CAXs, CCXs and NCXs	Exchange Ca^{2+} with protons or other cations, sequester Ca^{2+} into the vacuole or the ER for homeostasis.	Tonoplast	(10)
6.	Sulphur	Sulphate transporters (SULTR)	SULTR1.1, SULTR1.2 and SULTR1.3	It acts as a high-affinity sulphate transporter and is involved in phloem loading and redistribution.	Epidermis and cortex of roots (SULTR1.1, SULTR1.2), phloem (SULTR1.3),	(11)
			SULTR2.1 and SULTR2.2	Act as Low-affinity sulphate transporters and are involved in long-distance sulphate translocation.	Vascular tissue of both the leaves and the roots (SULTR2.1) and phloem of roots and vascular bundle sheath in leaves (SULTR2.2)	(11)
			SULTR3.1, SULTR3.2, SULTR3.3, SULTR3.4 and SULTR3.5	Import sulphate into plastids and modulate other SULTRs	Chloroplast	(11)
			SULTR4.1 and SULTR4.2	Efflux of sulphate from the vacuole to the cytosol	Tonoplast	(11)

			Micronutrients			
1.	Iron	Iron-regulated transporter family	IRT1	Transports Fe^{2+} into the root after Fe^{3+} reduction	Root plasma membrane	(12)
		Natural resistance-associated macrophage protein (NRAMP)	NRAMP1, NRAMP3, and NRAMP4	Involved in vacuolar Fe mobilisation	Plasma membrane or vacuoles	(12)
		Yellow stripe-like (YSL)	YSL1, YSL2 and YSL3	Responsible for the transport of Fe complexes such as Fe-nicotianamine/Fe-phytosiderophore and involved in long-distance transport of Fe	Plasma membrane and phloem	(12)
		Vacuolar iron transporter (VIT)	VIT1 and VIT2	Involved in the storage and sequestration of Fe into vacuoles	Tonoplast	(12)
		Mitochondrial iron transporter (MIT)	MIT1 and MIT2	Import Fe into mitochondria	Mitochondrial membrane	(12)
		Ferric reductase oxidase (FRO)	FRO2	Reduces Fe^{3+} to Fe^{2+} for uptake	Plasma membrane	(12)
		Ferric Reductase Defective 3	FRD3	Critical for Fe solubilization and translocation through xylem by loading citrate into the root vasculature	Plasma membrane	(12)
		Oligopeptide transporter (OPT)	OPT3	Transport Fe into the phloem and helps in long-distance signalling	Plasma membrane and phloem	(12)
		Permease In Chloroplasts (PIC)	PIC1	Import Fe into chloroplasts	chloroplast inner envelope	(12)
		Transporter of mugineic acid (TOM)	TOM1 and TOM2	Essential for the secretion and internal movement of phytosiderophores, which resulted in iron chelation and uptake	Plasma membrane	(12)
		Nicotianamine synthase	NAS1 and NAS2	Synthesise nicotianamine, a chelator for Fe transport	Cytosol	(12)
2.	Manganese	Natural resistance-associated macrophage protein family (NRAMP)	NRAMP1, NRAMP2, NRAMP3, NRAMP4, NRAMP5 and NRAMP6	Involved in the transport of Mn^{2+} into the cytosol	Epidermal cells (NRAMP1), trans-golgi network (NRAMP2), xylem and phloem (NRAMP3), tonoplast (NRAMP4), exodermis and endodermis (NRAMP5), Golgi apparatus and trans-golgi network (NRAMP6)	(13)
		Zinc-regulated transporter/Iron-regulated transporter (ZRT/IRT)-related protein family	ZIP1 and ZIP2			
		Yellow stripe-like family (YSL)	YSL1, YSL2, YSL3 and YSL6		Plasma membrane	
		Cation diffusion facilitator/Metal transport protein family (CDF/MTP)	MTP8, MTP9, MTP10 and MTP11		Vacuole (MTP8), plasma membrane (MTP9), plasma membrane of parenchyma cells around the xylem (MTP10) and Golgi apparatus, pre-vacuolar compartment and trans-Golgi network (MTP11)	
		Vacuolar iron transporter family (VIT)	VIT1 and VIT2	Involved in the transport of Mn^{2+} out of the cytosol	Vacuole	(13)
		Ca^{2+}/Cation antiporter superfamily (CaCA)	CAX1, CAX2, CAX3 and CAX4		Vacuole	
		Bivalent cation transporter family (BICAT)	BICAT1 and BICAT2		Chloroplast	
		P2A-type ATPase family	ECA1 and ECA3		Endoplasmic reticulum and nuclear envelope (ECA1) and Golgi apparatus, pre-vacuolar compartment and trans-golgi network (ECA3)	

3.	Copper	Copper transporter family (COPT)	COPT1, COPT2, COPT3 and COPT4	Act as a high-affinity copper transporter	Plasma membrane	(14)
			COPT5	Act as a vacuolar copper exporter, critical for remobilizing stored copper under deficiency	Tonoplast	(14)
			COPT6	Involved in copper uptake and redistribution, especially important for copper allocation to aerial tissues and seeds	Plasma membrane-localized (notably in vasculature and reproductive tissues)	(14)
		ZIP (ZRT/IRT-like Protein)	ZIP2 and ZIP4	Involved in Cu^{2+} uptake	Plasma membrane	(14)
		Yellow stripe-like	YSL1, YSL2 and YSL3	Involved in the transport of Cu-nicotianamine (Cu-NA) complexes	Plasma membrane	(14)
		P-type ATPases (HMA family)	HMA1, HMA5, HMA6, HMA7 and HMA8	Involved in Cu efflux from the cytosol, delivery to chloroplasts and thylakoids, detoxification, ethylene receptor biogenesis.	Plasma membrane, chloroplast envelope, thylakoid membrane	(14)
4.	Zinc	ZRT/IRT-like Protein (ZIP)	ZIP1, ZIP2, ZIP3, ZIP4, ZIP5, ZIP9, ZIP10, ZIP11 and ZIP12	Responsible for absorbing Zn^{2+} from the soil, importing it into the symplast and contributing to zinc redistribution within the plant.	Plasma membrane	(15)
		Heavy metal ATPase (HMA)	HMA2 and HMA4	Involved in the Zn^{2+} efflux, loading into xylem for root-to-shoot translocation	Plasma membrane and xylem parenchyma	(15)
		Cation diffusion facilitator/metal transporter protein (CDF/MTP)	MTP1 and MTP3	Involved in Zn^{2+} sequestration into the vacuole	Tonoplast	(15)
		Yellow Stripe-Like (YSL)	YSL1 and YSL3	Involved in the transport of Zn-nicotianamine (Zn-NA) complexes	Plasma membrane	(15)
		Lazarus (LAZ) family	LAZ1, LAZ2, LAZ3 and LAZ4	Involved in Zn^{2+} uptake and homeostasis	Plasma membrane	(16)
5.	Molybdenum	Molybdate transporter (MOT)	MOT1	It acts as a high-affinity molybdate transporter responsible for molybdate uptake from the soil into root cells.	Root epidermis and plasma membrane	(17)
			MOT2	Involved in molybdate transport and redistribution from roots to shoots through the vascular tissues, facilitating long-distance translocation.	Xylem and phloem	(17)
6.	Boron	Boron exporter family (BOR)	BOR1	Efflux of boron from roots to shoots	Plasma membrane of root stele cells	(18)
			BOR2	Essential for distributing boron in the root cell wall, facilitating root elongation under boron-limited conditions.	Root plasma membrane	(18)
			BOR4	Exports excess B to prevent toxicity under high B conditions	Root epidermis	(18)

Stress influences the function, localisation and expression of nutrient transporter proteins. For instance, drought stress induces depolarisation of the plasma membrane, which activates guard cell outward rectifying K^+ (GORK) channel, a type of potassium (K) channel. This activation promotes the efflux of K^+ions from guard cells, resulting in stomatal closure as a critical adaptive response to enhance drought stress tolerance (22). Similarly, biotic stress also induces the activation of GORK channels, leading to K^+ loss and subsequent programmed cell death, which contributes to the plant's defence against biotic stress (23). In addition to their crucial role in the plant stress response, the regulation of nutrient transporters is essential for their effective function. At the transcriptional level, stress-specific transcription factors, such as Dehydration-Responsive Element Binding protein (DREB), tryptophan-arginine-lysine-tyrosine (WRKY) and NAC (NAM, ATAF1/2 and CUC2), modulate the expression of ion transporter genes, thereby facilitating their timely activation or inactivation in response to environmental cues (24, 25). Furthermore, Post-transcriptional mechanisms such as microRNA (miRNA) - mediated gene silencing and post-translational modifications such as phosphorylation and ubiquitination enable the rapid activation or inactivation of nutrient transporter protein activity (26-28). This multi-level regulation of nutrient transporters ensures plant tolerance to various stresses.

Recent transcriptomic studies have provided valuable insights into the stress-responsive regulation of nutrient transporters across different plant species. For instance, transcriptomic analyses revealed that low nitrogen (N) conditions induce the expression of NO_3^- transporters (NRTs) such as *NRT1*, *NRT2.4* and *NRT2.5* in lettuce and *NRT2.2* and *NRT2.5* in maize, suggesting enhancement in NO_3^- uptake and nitrogen use efficiency (NUE) (29, 30). Complementary to transcriptomic approaches, clustered regularly interspaced short palindromic repeats/CRISPR-associated (CRISPR/Cas) system-based functional genomics has emerged as a powerful tool to validate the roles of nutrient transporters in stress adaptation. For example, knockout studies of High-Affinity K^+ Transporter (HAKs) such as *OsHAK8* and *OsHAK1* in rice confirmed their roles in K^+ uptake, translocation and ion homeostasis, while genome editing of *OsHAK3* enhanced nutrient-use efficiency and stress tolerance, highlighting the potential of combining these approaches for developing resilient crops (31). This review summarises current insights into the effects of abiotic and biotic stresses on the function and regulation of nutrient transporters, emphasises their crucial roles in plant stress tolerance and explores their potential application in the development of climate-resilient crops.

Drought stress and nutrient transporters

Drought stress is a significant abiotic stress that reduces soil moisture and nutrient mobility, thereby limiting the mass flow of nutrients to root cells and disrupting ionic balance in plants. This nutrient imbalance, coupled with reduced water availability, triggers stomatal closure as a drought response mechanism. While stomatal closure helps conserve water, it simultaneously restricts CO_2 uptake, thereby limiting photosynthesis and ultimately reducing plant productivity (32). Drought stress also impairs root hydraulic conductivity, further restricting nutrient absorption. N uptake, which largely relies on the mass flow of water, is significantly constrained under drought conditions because of reduced mineralisation and diffusion. Similarly, phosphorus (P) and potassium (K) uptake are affected, as reduced soil water availability limits their transport under stress conditions (33).

Drought induces the dynamic regulation of NO_3^- transporters: short-term drought upregulates NRT1.1 and NRT1.5 to increase nitrate uptake and transport, whereas long-term stress downregulates these transporters to conserve energy and prioritise root nitrate allocation (34). High-affinity transporters such as NRT2.1 and NRT2.4, which could be key NO_3^- sensors under drought, become dominant under low-N conditions (35). Ammonium (NH^{4+}) uptake through ammonium transporters (AMTs) is also critical under drought, with AMT1.1 and AMT1.2 functioning as transceptors. Their activity is tightly regulated by post-transcriptional phosphorylation to prevent ammonium toxicity and maintain cellular homeostasis (33).

P uptake is mediated by the phosphate transporter (PHT/PHO/PT) family. Under drought, high-affinity PHT1 transporters are upregulated to maintain phosphate uptake through the proton/phosphate (H^+/Pi) symporter mechanism, whereas low-affinity transporters, such as PHT4, are involved in internal phosphate mobilisation (36). Mitochondrial PHT3 transporters facilitate phosphate transfer for ATP synthesis, which is crucial for reducing the oxidative damage caused by drought-induced ROS, as antioxidant systems require energy for their optimal function (37). These adjustments help sustain phosphate acquisition and the cellular energy balance during stress.

Maintaining cytosolic K^+ is vital for drought tolerance, as it supports stomatal regulation, photosynthesis and growth (38). Drought triggers the modulation of high- and low-affinity K^+ transport systems, which are often regulated by ROS signalling, to ensure efficient K^+ uptake and distribution. Enhanced K^+ transport also improves root hydraulic conductivity, supporting water uptake under drought (39). Genotypic differences in K^+ transporter expression and activity determine drought tolerance, as efficient K^+ loading into the xylem and translocation to shoots are crucial for sustaining plant growth under water deficit (40). Nutrient transporters are tightly regulated by stress-signalling pathways involving transcription factors such as DREB and myeloblastosis (MYB), as well as plant hormones including abscisic acid (ABA) and ethylene. ABA, a stress-responsive hormone, modulates the activity of the K^+ channel in *Arabidopsis thaliana* 1 (KAT1) to regulate stomatal closure during drought, preventing water loss by maintaining ionic balance (Fig. 1) (41). In summary, targeted regulation of nutrient transport is essential for drought tolerance and represents a key strategy for improving crop resilience under drought conditions.

Salinity stress and nutrient transporters

Salinity stress arises when high levels of soluble ions like sodium (Na^+), Ca^{2+}, K^+ and Mg^{2+} accumulate in the root zone, disrupting key physiological functions in plants. The primary effects of salinity stress on plant growth are osmotic stress, cytotoxicity and ionic imbalance. The degree of salt tolerance in plants is governed by their capacity for osmotic adjustment and the maintenance of ionic homeostasis (42). Osmotic adjustment involves the accumulation of osmolytes such as organic acids, sugars and amino acids, which help plants to reduce their water potential and improve their water uptake under salinity stress (43). During salinity stress, plants often take up more Na^+ than K^+, leading to a higher (Na^+/K^+) ratio and further affecting cellular functions (44). Excessive Na^+ influx disrupts ion channels, replaces essential nutrients and causes membrane depolarisation, impairing nutrient uptake and assimilation. Neither glycophytes nor halophytes can tolerate high cytoplasmic salt

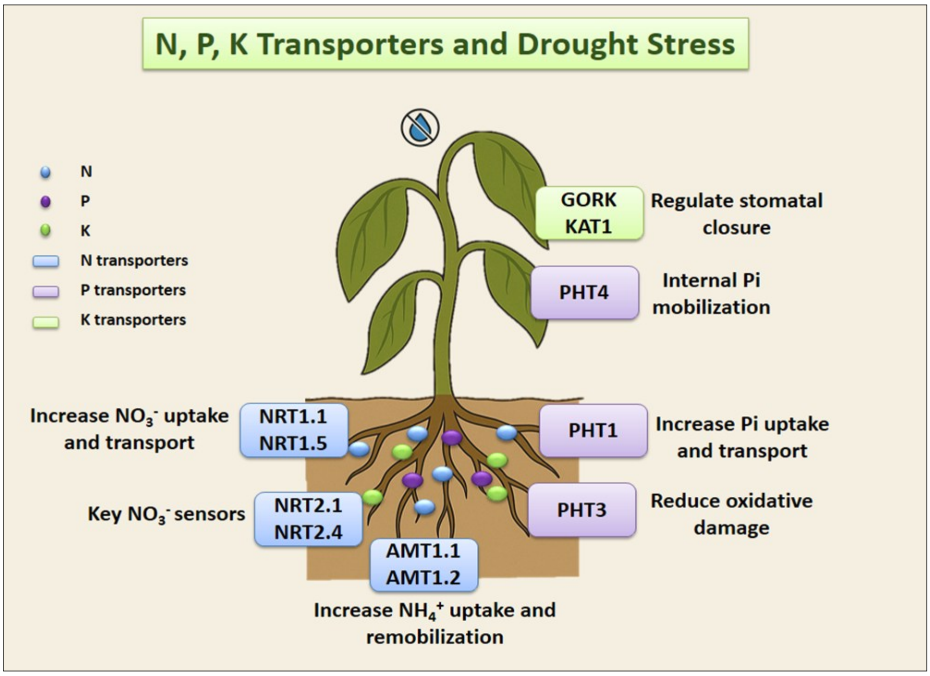

Fig. 1. N, P and K transporters involved in drought stress. NRT1.1: Nitrate transporter 1.1, NRT1.5: Nitrate transporter 1.5, NRT2.1: Nitrate transporter 2.1, NRT2.4: Nitrate transporter 2.4, AMT1.1: Ammonium transporter 1.1, AMT1.2: Ammonium transporter 1.2, PHT1: Phosphate transporter 1, PHT3: Phosphate transporter 3, PHT4: Phosphate transporter 4, GORK: Guard cell outward rectifying K^+ channel, KAT1: K^+ inward -rectifying channel 1.

concentrations, but halophytes have specialised mechanisms to sequester excess Na^+ ions, enabling them to thrive under salinity stress. Thus, maintaining a proper Na^+/K^+ balance is crucial for plant growth under salinity stress (45).

Nutrient transporters are central to salt tolerance, facilitating Na^+ exclusion and K^+ retention to preserve a high K^+/Na^+ ratio. Key cation transporters, including the high-affinity K^+ transporter 1.1 (HKT1.1) and the Na^+/H^+ antiporters 1 (NHX1) and salt overly sensitive 1 (SOS1), are crucial for maintaining ionic homeostasis under salinity stress (Fig. 2) (46, 47). These proteins mediate Na^+ exclusion from the cytoplasm and its compartmentalisation into vacuoles, which are subsequently energised by vacuolar ATPase (V-ATPase) (48). While Na^+ exclusion and compartmentalisation are vital, maintaining adequate K^+ levels is equally important for plant survival under salinity stress. HKT1 transporters, especially in the root xylem parenchyma, retrieve Na^+ from the xylem, limiting its translocation to shoots (49). Their sodium selectivity is determined by a serine residue in the first pore-loop domain (50). HKT2 transporters, which are permeable to both Na^+ and K^+, support K^+ uptake in cereals under salt stress (51). Monocots such as rice possess multiple *HKT* genes, including *OsHKT1;5* and *OsHKT2;1*, which restrict Na^+ movement from roots to shoots. (49).

Salinity stress also affects the transport of anions, particularly NO_3^-, which is vital for growth and photosynthesis (52). NO_3^- uptake is mediated by low- and high-affinity transporters (NRT1 and NRT2), which are regulated through phosphorylation.

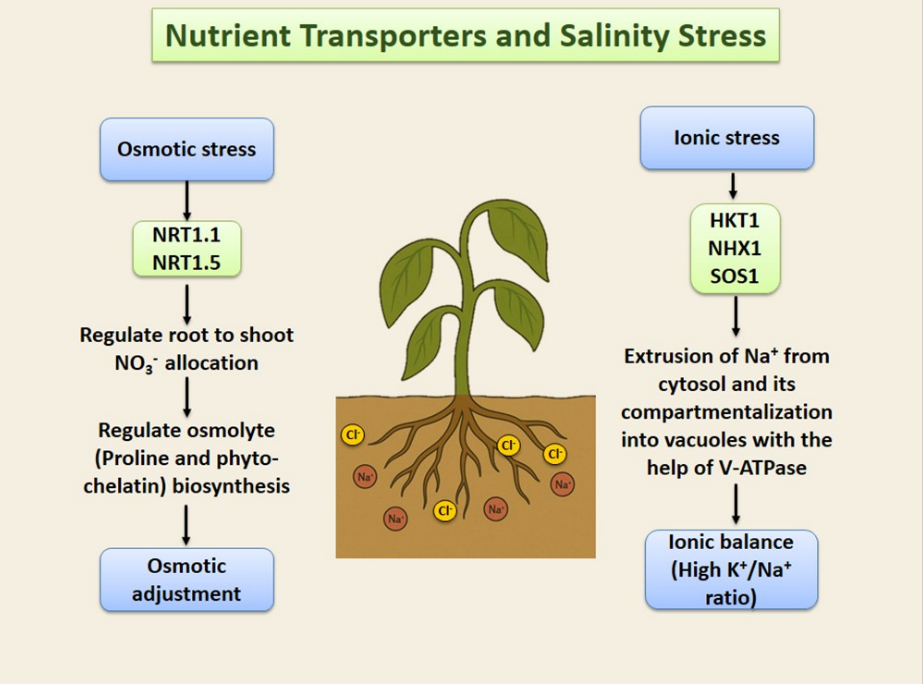

Fig. 2. Nutrient transporters involved in salinity stress. NRT1.1: Nitrate transporter 1.1, NRT1.5: Nitrate transporter 1.5, HKT1: High-affinity potassium transporter 1, NHX1: Na^+/H^+ antiporter 1, SOS1: Salt overly sensitive 1, V-ATPase: Vacuolar-type H^+-ATPase.

The long-distance NO_3^- transporters NRT1.5 and NRT1.8 play a key role in root-to-shoot NO_3^- translocation (53, 54). Under salinity stress, the expression of these transporters is downregulated, reallocating NO_3^- to roots and reducing shoot NO_3^- availability (52). *NRT1.5* mutants show altered expression of salt-responsive genes, including those involved in Na^+ regulation (such as *HKT1* and *SOS1*) and osmolyte biosynthesis [such as *P5CS1* (Δ^1-pyrroline-5-carboxylate synthase 1) and *AtPCS1* (phytochelatin synthase 1)], suggesting that NO_3^- transporters play an integrated role in coping with salt stress (52). Overall, this regulatory mechanism underscores the importance of nutrient transporters in maintaining ionic balance and reducing salt-induced nutrient imbalances.

Heat stress and nutrient transporters

Heat stress occurs when plants are subjected to temperatures beyond their optimal range for extended periods, resulting in irreversible disruptions to key physiological processes. It causes multiple cellular disturbances, including membrane destabilisation, protein denaturation, enzyme inactivation and diminished activity of enzymes essential for photosynthesis and respiration. These cumulative effects ultimately hinder water and nutrient uptake in plants. One of the primary consequences of heat stress is the overproduction of ROS and malondialdehyde (MDA), which damage cell membrane structures and affect nutrient uptake pathways (55). Among physiological processes, photosynthesis is especially sensitive to heat stress. Damage to the photosynthetic apparatus inhibits the electron transport chain and carbon assimilation, processes critical for nutrient uptake and assimilation (56).

Heat stress adversely impacts root system architecture (RSA) by reducing root biomass, the number of lateral roots and the root-to-shoot ratio, leading to reduced nutrient uptake (57). These structural changes also impair plasma membrane function. The plasma membrane H^+ ATPase, which is essential for generating the H^+ gradients required for active transport, shows increased activity as a compensatory response under moderate heat stress. However, prolonged stress reduces transporter proteins essential for nutrient uptake (58). At the molecular level, heat stress interferes with nutrient uptake by modulating gene expression and alternative splicing and inhibiting the synthesis of transporter proteins (59). Within 24 hr of exposure to heat stress above 35 °C, key transporters for NO_3^- (*NRT1, NRT2*), NH_4^+ (*AMT1*), P (*PHT1*), Fe^{2+} [ferric reductase oxidase 1 (*FRO1*)] and boron [boron transporter 1 (*BOR1*)] are downregulated, limiting the uptake of these essential nutrients and disrupting ionic homeostasis (Fig. 3) (60, 61). Further integrative studies are needed to elucidate the regulatory networks linking heat stress responses to nutrient transporter functions to improve tolerance to heat stress.

Cold stress and nutrient transporters

Cold stress occurs when plants are exposed to suboptimal temperatures, which can be classified into chilling stress (temperatures above 0 °C but below optimal growing conditions) and freezing stress (temperatures below 0 °C) (62). Cold stress disrupts cellular functions, including photosynthesis, nutrient absorption and essential metabolic activities. Cold stress reduces photosynthetic efficiency by impairing electron transport in the thylakoid membranes and disrupting carbon fixation processes (63). This inhibition is partially due to a reduced availability of free phosphate in the chloroplast, which is related to the reduced expression of the vacuolar phosphate transporter PHT4. As cold stress decreases phosphate utilisation, triose-phosphate accumulates, limiting phosphate availability for the Calvin cycle, a critical photosynthetic process (64). Cold stress also lowers plant water potential, resulting in reduced water uptake. In response, plants undergo osmotic adjustments to maintain their osmotic potential (65). Another significant effect of chilling temperatures is a reduction in membrane fluidity. As temperatures decrease, fluid-crystalline lipid components transform to a rigid solid-gel state, causing functional impairments such as increased permeability, loss of intracellular solutes and inactivation of transport and channels (66).

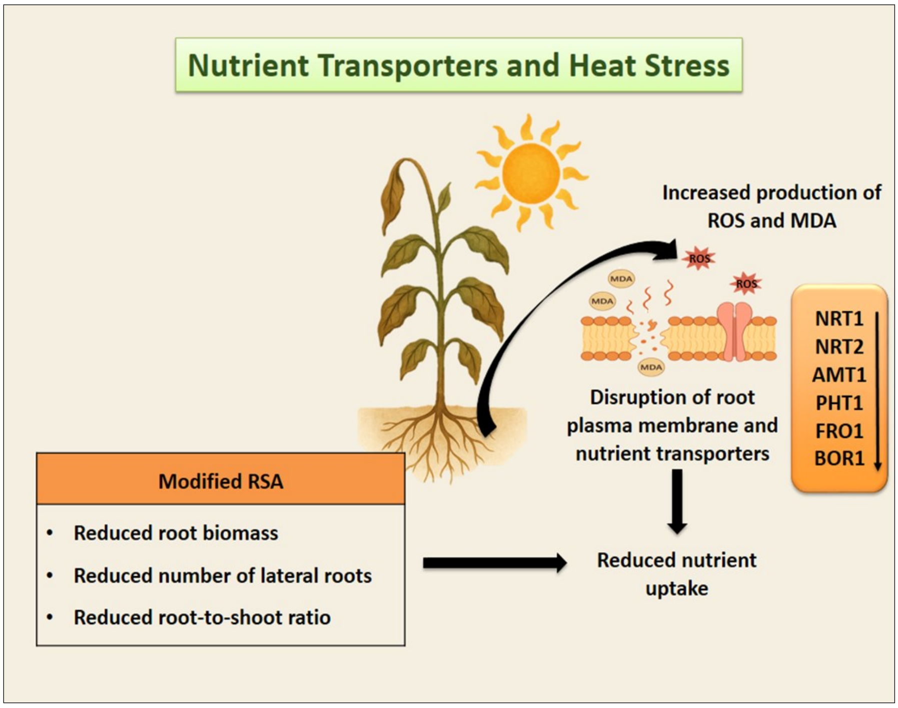

Fig. 3. Nutrient transporters involved in heat stress. NRT1: Nitrate transporter 1, NRT2: Nitrate transporter 2, AMT1: Ammonium transporter 1, PHT1: Phosphate transporter 1, FRO1: Ferric chelate reductase 1, BOR1: Boron transporter 1, ROS: Reactive oxygen species, MDA: Malondialdehyde, RSA: Root system architecture.

Root systems are especially sensitive to cold stress, leading to reduced nutrient acquisition (67). NO_3^- and NH_4^+ uptake both decline under chilling, with cold-sensitive varieties showing slower recovery after stress. Cold stress also affects soil N availability by inhibiting nitrifying bacteria, increasing the ammonium-to-nitrate (NH_4^+/NO_3^-) ratio and further limiting N uptake. The expression of key N transporters (*NRT1.1*, *NRT1.2*, *NRT1.4*, *NRT1.5*, *NRT1.8*, *NRT2.1*, *AMT2*) is downregulated under cold, as observed in *Brassica juncea* (Fig. 4) (34). Micronutrient uptake is also affected by cold stress. For instance, cold stress decreased the expression of the natural resistance-associated macrophage protein 1 (*AtNRAMP1)* transporter in *A. thaliana*, impairing the uptake of divalent cations such as Fe^{2+} and manganese (Mn^{2+}) (68). Additionally, intracellular nutrient transport mechanisms could be altered, such as the vacuolar Cation/H^+ Exchanger 1 (CAX1), whose upregulation by ABA signalling increases cytosolic Ca^{2+} levels, influencing various cellular processes (69). Overall, cold stress affects the expression of key nutrient transporters, such as N and micronutrient transporters, leading to reduced nutrient uptake.

Heavy metal stress and nutrient transporters

Heavy metals are metals with an atomic number greater than 20 or an atomic density above 5 g cm^{-3} that can be toxic to plants at high concentrations. Heavy metal stress arises when plants are exposed to excessive levels of heavy metals in the soil, negatively affecting growth and development. Heavy metals such as cadmium (Cd^{2+}), lead (Pb^{2+}) and copper (Cu^{2+}) compete with essential nutrients for transport pathways, disrupting nutrient uptake in contaminated soils (70). In general, heavy metals broadly impair the uptake and transport of Fe^{2+}, Mn^{2+}, Mg^{2+}, N and P. Specifically, Cd^{2+} inhibits zinc (Zn^{2+}) uptake and Pb^{2+} disrupts Ca^{2+} absorption (71).

Heavy metals bind to root plasma membranes, affecting the activity of nutrient transporters and reducing nutrient absorption in plants. In some cases, this stress can lead to heavy metal toxicity. Cd^{2+} toxicity specifically inhibits K^+ transporter activity through the overproduction of ROS, resulting in lipid peroxidation, which leads to plasma membrane damage and the disruption of membrane-bound nutrient transporters (71). Despite these challenges, nutrient transporters also play crucial roles in reducing heavy metal toxicity. They help plants cope by sequestering heavy metals into vacuoles, thereby reducing their availability in the cytosol and minimising cellular damage. For instance, members of the heavy metal ATPase (HMA) family, zinc/iron-regulated transporter-like protein (ZIP) family and natural resistance-associated macrophage protein (NRAMP) family, which collectively contribute to metal detoxification and homeostasis (Fig. 5) (72). Overall, heavy metal stress imposes significant challenges on nutrient transport by impairing transporter functionality and disrupting cellular integrity. Moreover, the adaptive role of nutrient transporters in reducing heavy metal toxicity through metal sequestration highlights their critical contribution to plant resilience under stress conditions.

Flooding stress and nutrient transporters

Flooding stress occurs when plants experience waterlogging, leading to hypoxic or anoxic conditions that severely limit oxygen availability to the roots and impair root respiration. This stress results in restricted water and nutrient uptake, accumulation of toxic metabolites and inhibited photosynthetic activity, ultimately hindering overall plant growth and development (73). Flood-induced hypoxia impairs the activity of H^+-ATPase in the xylem parenchyma of the stele, reducing the proton gradient and causing membrane depolarisation. This disrupts energy-dependent secondary nutrient transporters, leading to decreased nutrient transport from roots to shoots. Anoxic conditions particularly affect xylem loading, further reducing nutrient delivery to aerial parts of the plant (74).

To cope with these challenges, plants initiate a range of adaptive responses. Morphologically, they develop adventitious roots, aerenchyma and hypertrophic lenticels. Adventitious roots, especially cereals, are more efficient at nutrient uptake under low-oxygen conditions because their epidermal and cortical cells maintain better oxygenation for oxidative phosphorylation and nutrient transport (75). At the molecular level, hypoxia is sensed by mitochondria or plasma membrane-localised receptors, triggering

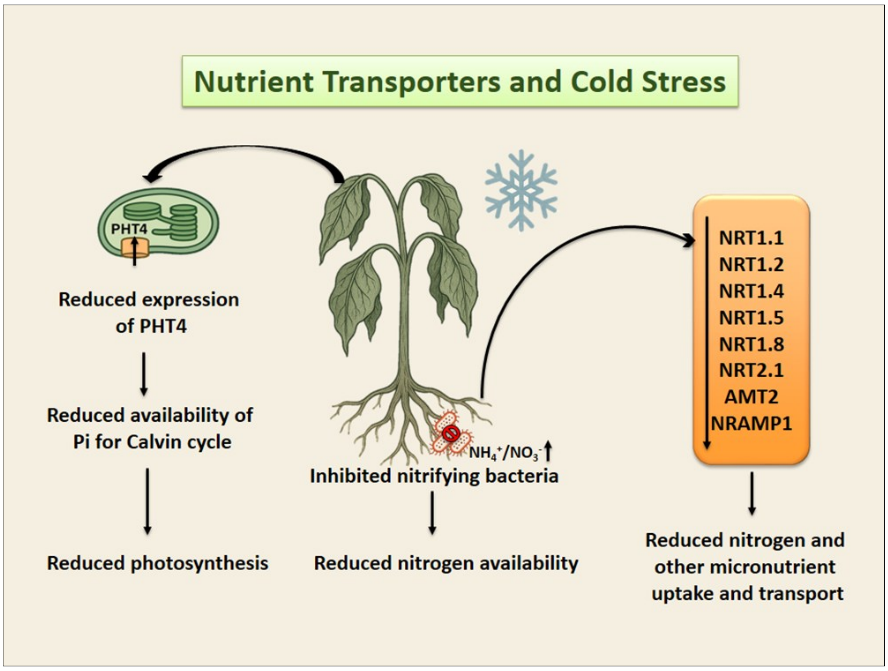

Fig. 4. Nutrient transporters involved in cold stress. NRT1.1: Nitrate transporter 1.1, NRT1.2: Nitrate transporter 1.2, NRT1.4: Nitrate transporter 1.4, NRT1.5: Nitrate transporter 1.5, NRT1.8: Nitrate transporter 1.8, NRT2.1: Nitrate transporter 2.1, AMT2: Ammonium transporter 2, PHT4: Phosphate transporter 4, NRAMP1: Natural resistance-associated macrophage protein 1.

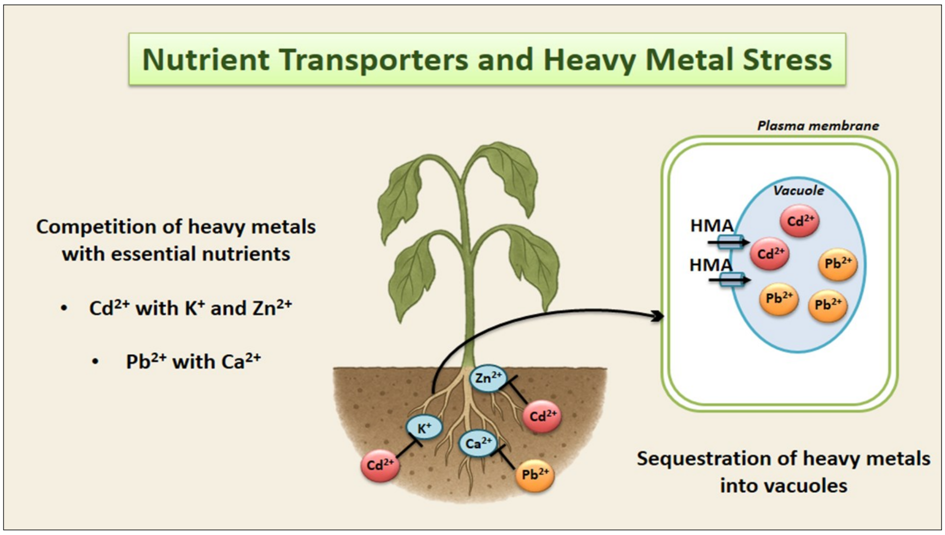

Fig. 5. Nutrient transporters involved in heavy metal stress. HMA: Heavy metal ATPase, Cd^{2+}: Cadmium ion, Pb^{2+}: Lead ion, K^+: Potassium ion, Zn^{2+}: Zinc ion, Ca^{2+}: Calcium ion.

rapid increases in cytosolic Ca^{2+} (76). This activates nicotinamide adenine dinucleotide phosphate (NADPH) oxidases, encoded by Respiratory Burst Oxidase Homolog (RBOH) genes, leading to apoplastic hydrogen peroxide (H_2O_2) production. H_2O_2 then moves into the cytosol via aquaporins, activating potassium efflux channels such as GORK and initiating programmed cell death (PCD) for aerenchyma formation (77). Ca^{2+} channels are thus crucial for this adaptive process.

Hypoxia also activates ethylene response factor VII (ERF VII) transcription factors, which increase ROS production and Ca^{2+} signalling. This cascade promotes K^+ uptake by activating Arabidopsis K^+ transporter (AKT) channels while desensitising GORK channels to maintain turgor. Mechanosensitive Ca^{2+} channels respond to root expansion and ROS-triggered GORK activity facilitates localised K^+ loss and PCD, enabling adventitious root penetration (77). Recent studies have identified key cation transporters as hypoxia stress sensors, including K^+ Channel Outward-rectifiers (KCO1, KCO4, KCO5 and KCO6), the AKT2 shaker K^+ channel and the two-pore Ca^{2+}-permeable channel 1 (TPC1) (Fig. 6) (10). These transporters are critical for maintaining nutrient uptake and ionic homeostasis during flooding stress.

Biotic stress and nutrient transporters

Biotic stress caused by living organisms such as pathogens (fungi, bacteria and viruses) and pests (insects and weeds) significantly impacts plant growth and productivity. Pathogens and pests can interfere with nutrient uptake and transport processes, leading to nutrient imbalances or deficiencies (19). Plants encounter biotic stress through interconnected morphological, physiological and biochemical responses, which include the synthesis of cuticular waxes, trichomes, secondary metabolites such as phytoalexins and protease inhibitors, as well as the activation of nutrient transporters and phytohormonal signalling pathways involving jasmonic acid, salicylic acid and ethylene. Nutrient transporters play a central role in plant defence by modulating nutrient uptake and homeostasis and influencing stress signalling, structural reinforcement and metabolic adjustments, leading to reduced pathogen and pest infestation (78).

Ca^{2+} acts as a vital secondary messenger in plant development and biotic stress responses. Biotic stress triggers a rapid influx of cytosolic Ca^{2+} and activates downstream signalling cascades, including membrane depolarisation, phytohormone

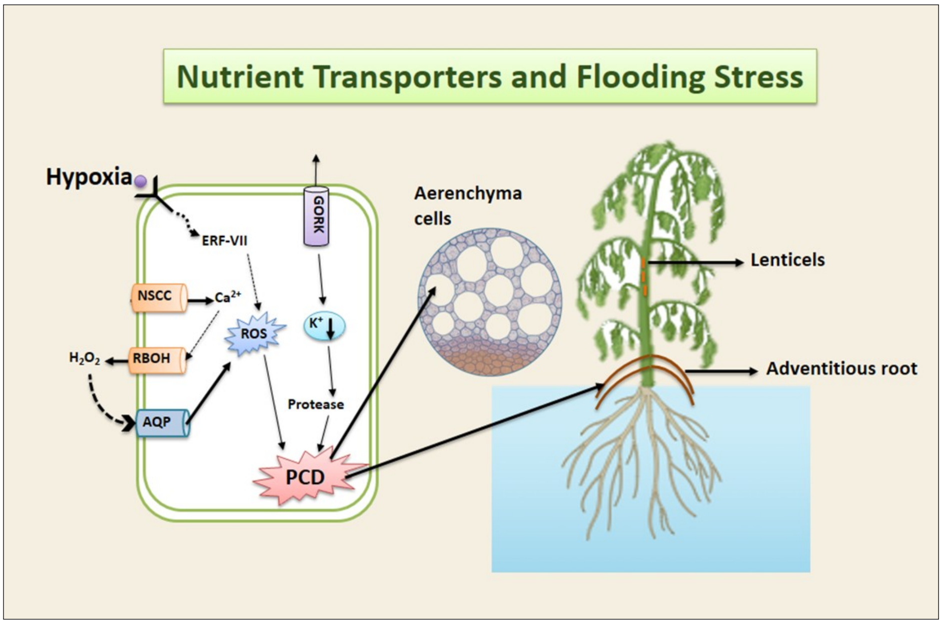

Fig. 6. Nutrient transporters involved in flooding stress. AQP: Aquaporin, RBOH: Respiratory burst oxidase homolog, NSCC: Non-selective cation channel, ERF-VII: Ethylene response factor VII, ROS: Reactive oxygen species, PCD: Programmed cell death.

production and secondary metabolite synthesis. Furthermore, Ca^{2+}-mediated ROS production and the activation of antioxidant enzymes, including superoxide dismutase (SOD) and catalase (CAT), enhance plant defence mechanisms. These Ca^{2+} fluxes during biotic stress are mediated by calcium channels such as cyclic nucleotide-gated channels (CNGCs), glutamate receptor-like receptors (GLRs) and two-pore channels (TPCs) (78). In addition to Ca^{2+}, K^+ levels directly influence plant resistance to biotic stress. Higher K^+ levels improve nutrient allocation, support repair mechanisms and enhance defence through increased phenolic biosynthesis (79). Biotic stress often triggers the ROS-induced activation of K^+ efflux channels, such as GORK, leading to K^+ loss and the initiation of PCD. This mechanism facilitates pathogen defence and stress tolerance (23). Interestingly, studies highlight K^+ flux as more critical than Ca^{2+} flux during viral infections. Fe^{2+} availability and transport are dynamically regulated during biotic stress. Pathogen attacks induce apoplastic Fe^{2+} accumulation, triggering oxidative bursts that activate defence genes. The translocation of Fe^{2+} to the apoplast induces intracellular Fe^{2+} deficiency, which in turn upregulates Fe^{2+} uptake transporters. This dynamic regulation, facilitated by Fe^{2+} transporters, enables plants to either restrict Fe^{2+} availability to pathogens or locally increase Fe^{2+} levels to initiate a toxic oxidative response, thereby limiting pathogens (80). Mn^{2+}-dependent enzymes, such as oxalate oxidase, play a critical role in generating ROS for pathogen defence. Manganese (Mn) transporters such as the NRAMP, ZIP, Yellow Stripe-Like 9 (YSL) and Cation Diffusion Facilitator (CDF) families ensure Mn homeostasis, enabling the lignification of cell walls to strengthen physical barriers against pathogen entry (81).

In addition to various micronutrients, silicon (Si) contributes to biotic stress tolerance by reinforcing structural defences and reducing susceptibility to pathogens and pests. Passive and active silicon transporters, including Lsi1 (low silicon 1), Lsi2, Lsi3 and Lsi6, facilitate Si uptake, distribution and deposition. This accumulation strengthens cell walls, making them less palatable to pathogens and pests (Fig. 7) (82). Overall, nutrient transporters are essential for maintaining plant resilience under biotic stress. By regulating the uptake and distribution of key nutrients such as Ca^{2+}, K^+, Fe^{2+}, Mn^{2+} and Si, these transporters enhance defence responses, strengthen structural barriers and facilitate effective stress management. This dynamic interplay ensures improved stress tolerance and promotes overall plant health in the face of biotic challenges. A comparative analysis of nutrient transporter responses under different stress conditions is summarised in Table 2 and Fig. 8. Fig. 8 represents the schematic representation of plant responses to different abiotic and biotic stresses through the regulation of nutrient and ion transporters. Under unstressed conditions, transporters support nutrient uptake, ionic balance, turgor-driven growth and signalling. Under various stresses, specific transporters are activated to mitigate damage and maintain cellular homeostasis. For example, drought induces K^+ transporters leading to stomatal closure, while salt stress activates Na^+/K^+ exchangers to promote Na^+ efflux. Heat stress enhances plasma membrane H^+-ATPase activity to maintain ion gradients. Cold stress triggers Ca^{2+} channel activation, serving as a signal for tolerance. Heavy metal stress alters the expression of cation transporters like Natural Resistance-associated Macrophage Protein (NRAMP), ZIP (ZRT, IRT-like protein), Iron-Regulated Transporter (IRT) and Yellow Stripe-Like (YSL) to regulate metal uptake. Flooding promotes K^+ and Ca^{2+} transporter activity to aid in root adaptation and biotic stress stimulates Ca^{2+} channels and transporters for Fe, Mn and Si, strengthening plant defence against pathogens and pests. These coordinated responses enhance plant tolerance across a range of stress conditions.

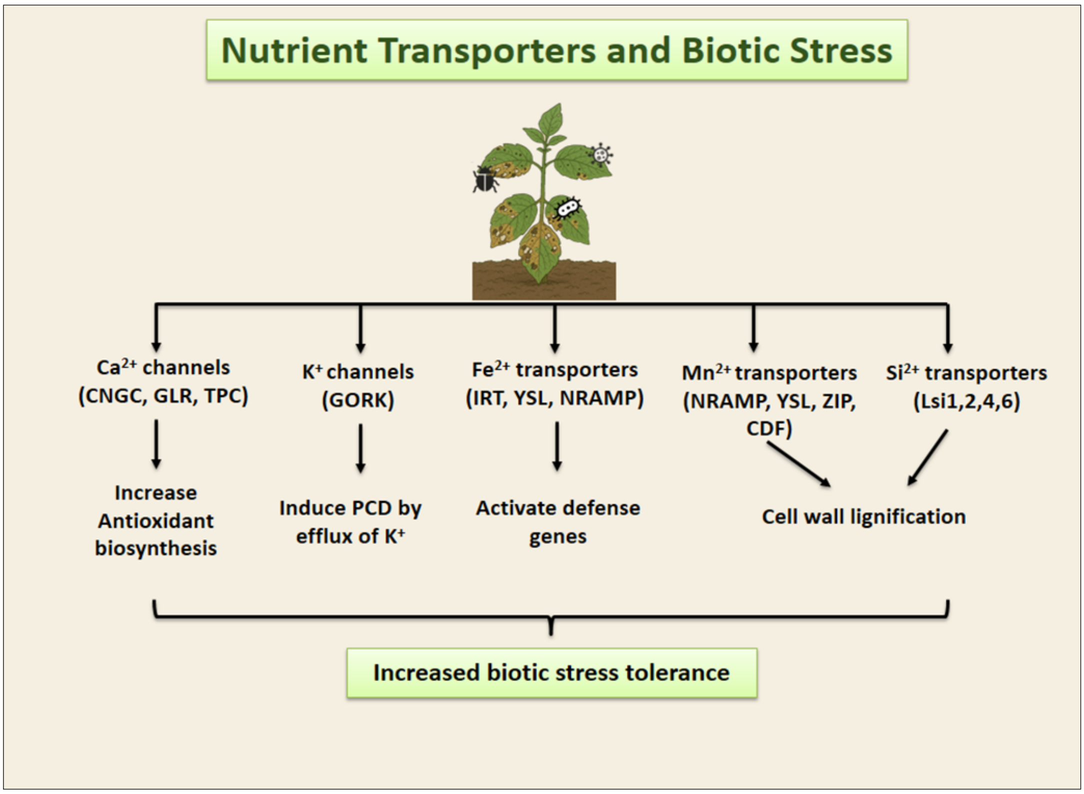

Fig. 7. Nutrient transporters involved in biotic stress tolerance. CNGC: Cyclic nucleotide-gated channel, GLR: Glutamate receptor-like channel, TPC: Two-pore channel, GORK: Guard cell outward rectifying K^+ channel, IRT: Iron-regulated transporter, YSL: Yellow stripe-like transporter, NRAMP: Natural resistance-associated macrophage protein, ZIP: Zinc-iron permease, CDF: Cation diffusion facilitator, Lsi1, 2, 4, 6: Silicon transporters.

Table 2. Overview of stress-induced regulation of nutrient transporters under stress conditions

S. No.	Transporters	Plant species	Function and effects of transporters under stress	Reference
Drought stress				
Nitrogen				
1.	NRT1.1, NRT1.5 and NRT2.1	*Brassica napus* L.	The expression of all these nitrate transporters is downregulated after 24 hrs of exposure to drought stress	(34)
2.	NRT1.1	*Arabidopsis thaliana* L.	Plays a role in stomatal opening under drought stress	(83)
3.	NRT2.4	*Malus domestica* (Suckow) Borkh.	High-affinity nitrate transporter whose transcript levels increase under prolonged drought, indicating a potential function as a drought stress sensor	(84)
4.	AMT1.2	*Oryza sativa* L.	The expression of AMTT1.2 increased in drought-resistant rice, facilitating ammonium remobilisation under drought stress	(85)
5.	AMT1.2	*Triticum aestivum* L.	High-affinity ammonium transporter; upregulated under drought stress	(86)
Phosphorus				
6.	PHO9 and PHT1.2	*Populus simonii* Carr.	PHO9 is involved in phosphorus transport to shoots and maintaining phosphate homeostasis during stress, while PHT1.2 is a high-affinity transporter that enhances inorganic phosphate (Pi) uptake under drought stress	(87)
7.	PHT1.5, PHT1.7, PHT4.7, PHT3.7 and PHT4.3	*Malus domestica* (Suckow) Borkh.	The expression of MdPHT1.5, MdPHT1.7 and MdPHT4.7 is upregulated in roots, whereas the expression of MdPHT3.7 and MdPHT4.3 is upregulated in leaves	(36)
8.	PT11, PT34 and PT38	*Brassica napus* L.	H$^+$/Pi symporters; upregulate in the root and facilitate Pi uptake under stress	(88)
Potassium				
9.	AKT1	*Arabidopsis thaliana* L.	Its overexpression enhances K$^+$ accumulation in root tissues, which helps in osmotic and drought stress tolerance	(89)
10.	HAK1, HAK5, KUP1, KUP2, AKT1 and SKOR	*Hordeum vulgare* L.	HAK1, HAK5, KUP1 and KUP2 are high-affinity K$^+$ transporters; AKT1 is a K$^+$ Channel; SKOR is a K$^+$ Efflux Transporter. All these gene expressions were affected by drought in a genotype-specific manner	(41)
Salinity stress				
1.	NHX1, NHX2, NHX3 and NHX4	*Arabidopsis thaliana* L.	Plasma membrane and tonoplast-localised H$^+$ antiporters mediate Na$^+$/H$^+$ or K$^+$/H$^+$ exchange, ensuring ionic homeostasis under salinity stress	(90)
2.	SOS1	*Arabidopsis thaliana* L.	Plasma Membrane Na$^+$/H$^+$ antiporters, which extrude Na$^+$ from the cell under salinity stress	(90)
3.	HKT1	*Arabidopsis thaliana* L.	Facilitate the removal of Na$^+$ from the xylem stream, thereby limiting its accumulation in shoots and mitigating sodium toxicity	(90)
4.	KEA	*Gossypium arboretum* L., *G. raimondii* Ulbr., *G. hirsutum* L. and *G. barbadense* L.	Helps in K$^+$ homeostasis within endomembrane systems and confers tolerance to salinity stress	(91)
5.	CHX17 CHX20 CHX21	*Arabidopsis thaliana* L.	Involved in K$^+$ homeostasis and regulates Na$^+$ concentration in leaves	(92)
6.	MGT1	*Oryza sativa* L.	MGT1 mediates magnesium transport in the root maturation zone and enhances HKT1.5 activity, thereby restricting sodium uptake and promoting salinity tolerance	(93)
7.	Low affinity cation transporter1 (LCT1)	*Oryza sativa* L.	Mediate low-affinity uptake of cations, thereby enhancing salinity stress tolerance	(94)
Heat stress				
1.	NRT1, NRT2, AMT1, AMT2, BOR1, NIP5.1 and PHT1	*Solanum lycopersicum* L.	Heat stress reduces the levels of transporter protein, thereby impairing the uptake of nitrate, ammonium, boron and phosphate	(60)
2.	FRO1	*Pisum sativum* L.	Heat stress decreased FRO1 enzyme activity, which is primarily involved in iron uptake by reducing ferric iron (Fe^{3+}) to ferrous iron (Fe^{2+})	(58)
3.	PM H$^+$ ATPase	*Pisum sativum* L.	Moderate heat stress increases activity to maintain ion gradients for nutrient uptake	(58)
Cold stress				
1.	NRT1.1, NRT1.2, NRT1.4, NRT1.5, NRT1.8 and NRT2.1	*Brassica juncea* L.	Cold stress reduces the expression of key nitrate transporters, resulting in decreased nitrate uptake	(34)
2.	CAX1	*Arabidopsis thaliana* L.	Cold stress upregulates CAX1, which elevates cytosolic free Ca^{2+} concentration and affects various cellular processes	(69)
3.	NRAMP1	*Arabidopsis thaliana* L.	Cold stress suppresses the expression of NRAMP1 transporters, resulting in reduced uptake of Fe and Mn	(68)
Heavy metal stress				
1.	NRAMP	*Spirodela polyrhiza* L.	Transports divalent cations such as Fe^{2+}, Mn^{2+}, Zn^{2+} and Cd^{2+}; Heavy metals like Cd^{2+} compete for NRAMP transporters, reducing Fe^{2+} and Mn^{2+} uptake and causing nutrient imbalances	(95)
2.	ZIP	*Oryza sativa* L.	Responsible for uptake of Zn^{2+}, Fe^{2+} and Mn^{2+} and their translocation to shoots; Cd^{2+} and Pb^{2+} inhibit ZIP function, leading to deficiencies in Zn^{2+}, Fe^{2+} and Mn^{2+}	(96)
Flooding stress				
1.	CAX1	*Arabidopsis thaliana* L.	CAX1 is transiently autodownregulated during anoxia to regulate calcium signalling and improve stress tolerance	(97)
Biotic stress				
2.	CNGC9	*Oryza sativa* L.	Play a critical role in resistance to *Magnaporthe oryzae*	(98)
3.	Lsi	*Oryza sativa* L.	Mediate silicon accumulation, which helps in the reduction of lesions caused by *Magnaporthe grisea* (rice blast fungus)	(99)

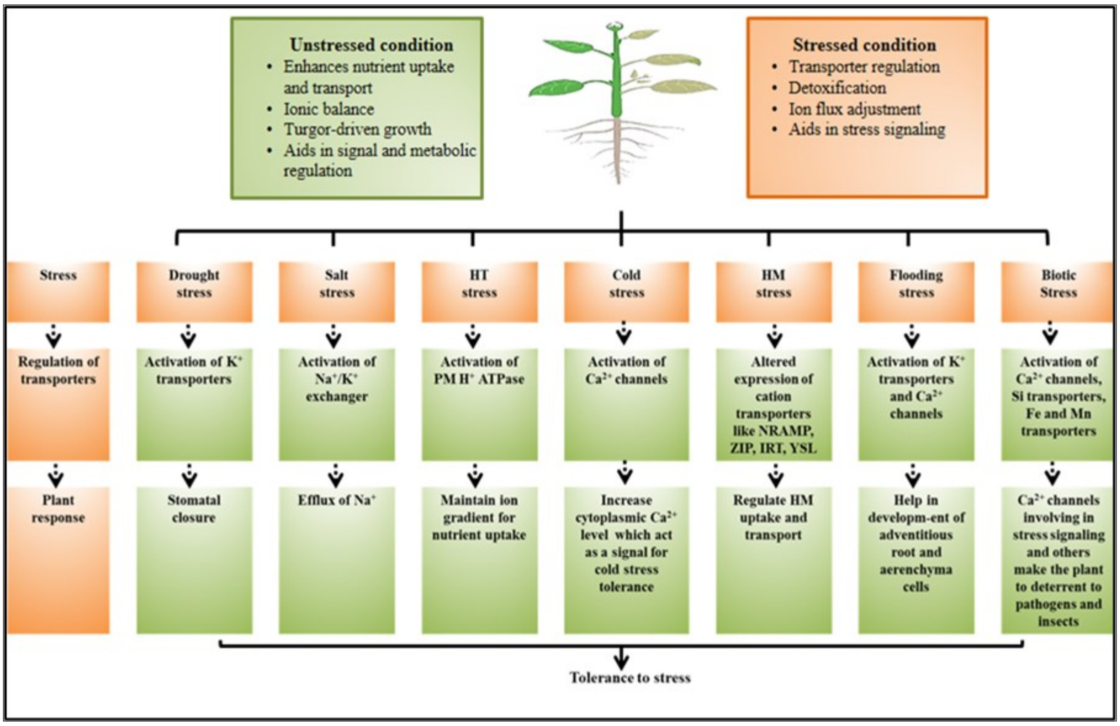

Fig. 8. Transporter-mediated plant responses under stressed and unstressed conditions.

Conclusion and prospects

Nutrient transporters are central regulators of plant adaptation to both abiotic and biotic stresses. They not only mediate the uptake, translocation and redistribution of essential nutrients but also act as key modulators of stress perception, signalling and defence responses. Under abiotic stresses such as drought, salinity, temperature extremes, flooding and heavy metal toxicity, nutrient transporters maintain ionic and osmotic balance, regulate stomatal function and protect cellular structures through coordinated transcriptional and post-translational control. Similarly, during biotic stresses, transporters of calcium, potassium, iron, manganese and silicon reinforce structural defences, modulate redox signalling and activate secondary metabolite biosynthesis to restrict pathogen invasion and pest damage.

Integrative studies combining omics approaches, functional genomics and CRISPR/Cas-based genome editing have deepened our understanding of transporter regulation and revealed novel targets for improving nutrient use efficiency and stress tolerance (Fig. 9). Under stress conditions, plants experience reduced photosynthesis, hormonal imbalance and ROS production and nutrient imbalance. To mitigate nutrient imbalance, plants trigger a cascade of stress responses, including changes in gene expression, transcription and regulation of nutrient transporters. These adaptive responses help to maintain nutrient homeostasis and improve stress tolerance. Thus, genetic engineering of nutrient transporters offers additional potential for enhancing plant resilience. However, most functional studies have focused on individual stress conditions, while plants in natural environments often encounter multiple, interacting stresses simultaneously. Therefore, future research should focus on multi-stress interactions, cross-talk among transporter networks and hormonal and signalling integration to develop a holistic understanding of nutrient transport under complex environments. Overall, elucidating the regulatory

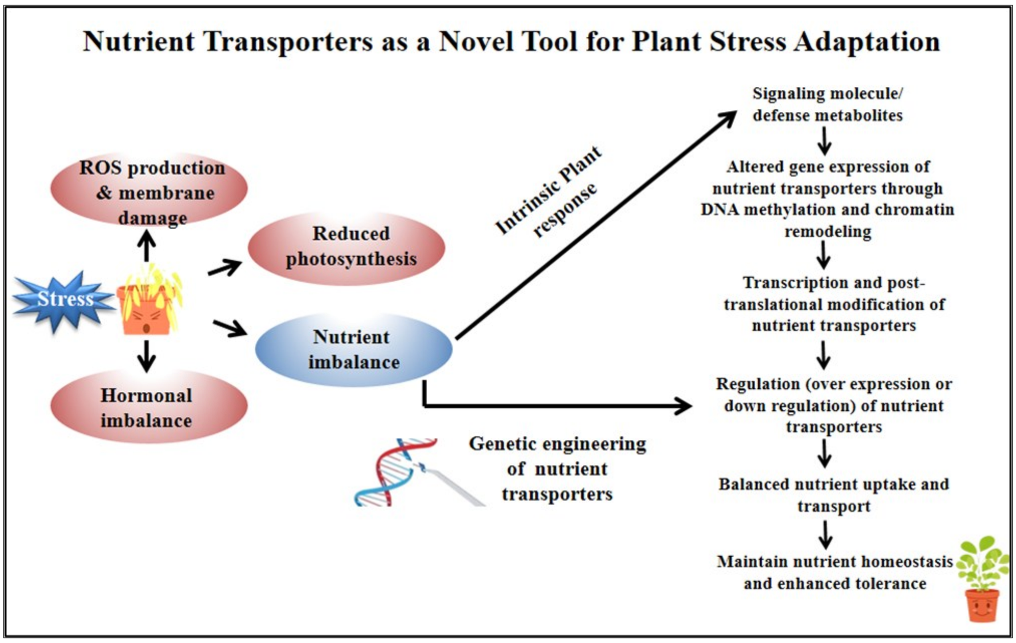

Fig. 9. Overview of the role of nutrient transporters in plant stress adaptation.

mechanisms governing nutrient transporters and harnessing them through advanced breeding and biotechnology offer promising strategies to engineer climate-resilient, nutrient-efficient crops, ensuring sustainable productivity and food security under changing environmental conditions.

Acknowledgements

We sincerely acknowledge the Department of Crop Physiology, Tamil Nadu Agricultural University, Coimbatore, India, for their invaluable support and resources in facilitating the preparation of this manuscript.

Authors' contributions

ASP contributed to the drafting and editing of the manuscript. MKK contributed to the conceptualisation and supervision of the article. AS, RS, MU, RK, MP and DS contributed to editing the manuscript. All authors read and approved the manuscript.

Compliance with ethical standards

Conflict of interest: The authors declare that they have no conflict of interest

Ethical issues: None

References

1. United Nations, Department of Economic and Social Affairs, Population Division. World Population Prospects: The 2017 Revision. New York: United Nations; 2017. https://population.un.org/wpp/
2. Godoy F, Olivos-Hernandez K, Stange C, Handford M. Abiotic stress in crop species: Improving tolerance by applying plant metabolites. Plants. 2021;10(2):186. https://doi: 10.3390/plants10020186
3. Vishwakarma K, Mishra M, Patil G, Mulkey S, Ramawat N, Pratap Singh V, et al. Avenues of the membrane transport system in adaptation of plants to abiotic stresses. Crit Rev Biotechnol. 2019;39 (7):861–83. https://doi: 10.1080/07388551.2019.1616669
4. Yadav B, Jogawat A, Lal SK, Lakra N, Mehta S, Shabek N, et al. Plant mineral transport systems and the potential for crop improvement. Planta. 2021;253(2):45. https://doi:10.1007/s00425-020-03551-7
5. Mishra G, Mohapatra SK, Rout GR. Plant membrane transporters function under abiotic stresses: A review. Planta. 2024;260(6):125. https://doi:10.1007/s00425-024-04548-2
6. Du B, Haensch R, Alfarraj S, Rennenberg H. Strategies of plants to overcome abiotic and biotic stresses. Biol Rev. 2024;99(4):1524–36. https://doi:10.1111/brv.13079
7. Jarzyniak KM, Jasinski M. Membrane transporters and drought resistance–a complex issue. Front Plant Sci. 2014;5(1):687. https://doi:10.3389/fpls.2014.00687
8. Shabala S, Pottosin I. Regulation of potassium transport in plants under hostile conditions: Implications for abiotic and biotic stress tolerance. Physiol Plant. 2014;151(3):257–79. https://doi:10.1111/ppl.12165
9. Lata C, Prasad M. Role of DREBs in regulation of abiotic stress responses in plants. J Exp Bot. 2011;62(14):4731–48. https://doi:10.1093/jxb/err210
10. Aslam R, Wali Q, Sarwar M, Naeem M, Zia M. A comprehensive overview of transcription factors (WRKY, NAC and BZIP) in plants. J Biosci. 2019;14(1):495–509. https://doi:10.12692/ijb/14.1.495-509
11. Paul S, Datta SK, Datta K. miRNA regulation of nutrient homeostasis in plants. Front Plant Sci. 2015;6:232. https://doi:10.3389/fpls.2015.00232
12. Straub T, Ludewig U, Neuhäuser B. The kinase CIPK23 inhibits ammonium transport in *Arabidopsis thaliana*. Plant Cell. 2017;29 (2):409–22. https://doi:10.1105/tpc.16.00806
13. Grubb LE, Derbyshire P, Dunning KE, Zipfel C, Menke FLH, Monaghan J. Large-scale identification of ubiquitination sites on membrane-associated proteins in *Arabidopsis thaliana* seedlings. Plant Physiol. 2021;185(4):1483–88. https://doi:10.1093/plphys/kiab023
14. Singh P, Kumar K, Jha AK, Yadava P, Pal M, Rakshit S, et al. Global gene expression profiling under nitrogen stress identifies key genes involved in nitrogen stress adaptation in maize (*Zea mays* L.). Sci Rep. 2022;12:4211. https://doi:10.1038/s41598-022-07709-z
15. Sathee L, Jagadhesan B, Pandesha PH, Barman D, Adavi BS, Nagar S, et al. Genome editing targets for improving nutrient use efficiency and nutrient stress adaptation. *Front Genet.* 2022;13:900897. https://doi:10.3389/fgene.2022.900897
16. Zhang Y, Liu X, La S, Wang M, Hu X, Shi A, et al. Transcriptome analysis reveals nutrient deprivation reduces nitrate content in lettuce (*Lactuca sativa* var. *ramosa* Hort.) and enhances nitrogen metabolism. *Front Plant Sci.* 2025;16:1585955. https://doi:10.3389/fpls.2025.1585955
17. Rouphael Y, Cardarelli M, Schwarz D, Franken P, Colla G. Effects of drought on nutrient uptake and assimilation in vegetable crops. In: Aroca R, editor. Plant Responses to Drought Stress: From Morphological to Molecular Features. Berlin: Springer; 2012. p. 171–195.
18. Barzana G, Carvajal M. Genetic regulation of water and nutrient transport in water stress tolerance in roots. J Biotechnol. 2020;324:134–42. https://doi:10.1016/j.jbiotec.2020.10.003
19. Goel P, Singh AK. Abiotic stresses downregulate key genes involved in nitrogen uptake and assimilation in *Brassica juncea* L. PLoS One. 2015;10(11):e0143645. https://doi:10.1371/journal.pone.0143645
20. Orsel M, Krapp A, Daniel-Vedele F. Analysis of the *NRT2* nitrate transporter family in Arabidopsis: Structure and gene expression. Plant Physiol. 2002;129(2):886–96. https://doi:10.1104/pp.005280
21. Sun T, Li M, Shao Y, Yu L, Ma F. Comprehensive genomic identification and expression analysis of the phosphate transporter (PHT) gene family in apple. Front Plant Sci. 2017;8:426. https://doi:10.3389/fpls.2017.00426
22. Nussaume L, Kanno S, Javot H, Marin E, Pochon N, Ayadi A, et al. Phosphate import in plants: Focus on the PHT1 transporters. Front Plant Sci. 2011;2:83. https://doi:10.3389/fpls.2011.00083
23. Xu Q, Fu H, Zhu B, Hussain HA, Zhang K, Tian X, et al. Potassium improves drought stress tolerance in plants by affecting root morphology, root exudates and microbial diversity. Metabolites. 2021;11(3):131. https://doi:10.3390/metabo11030131
24. Liu C, Liao W. Potassium signaling in plant abiotic responses: Crosstalk with calcium and reactive oxygen species/reactive nitrogen species. Plant Physiol Biochem. 2022;173:110-21. https://doi:10.1016/j.plaphy.2022.01.016
25. Cai K, Gao H, Wu X, Zhang S, Han Z, Chen X, et al. The ability to regulate transmembrane potassium transport in root is critical for drought tolerance in barley. Int J Mol Sci. 2019;20(17):4111. https://doi:10.3390/ijms20174111
26. Liu H, Song S, Zhang H, Li Y, Niu L, Zhang J, et al. Signaling transduction of ABA, ROS and Ca^{2+} in plant stomatal closure in response to drought. Int J Mol Sci. 2022;23(23):14824. https://doi:10.3390/ijms232314824
27. Choudhary S, Wani KI, Naeem M, Khan MMA, Aftab T. Cellular

responses, osmotic adjustments and role of osmolytes in providing salt stress resilience in higher plants: polyamines and nitric oxide crosstalk. J Plant Growth Regul. 2023;42(2):539–53. https://doi:10.1007/s00344-022-10584-7

28. Jogawat A. Osmolytes and their role in abiotic stress tolerance in plants. In: Smith J, editor. Molecular Plant Abiotic Stress: Biology and Biotechnology. Hoboken: Wiley Online Library; 2019. p. 91–104.

29. Ketehouli T, Carther KFI, Noman M, Wang FW, Li XW, Li HY. Adaptation of plants to salt stress: characterization of Na$^+$ and K$^+$ transporters and role of *CBL* gene family in regulating salt stress response. Agronomy. 2019;9(11):687. https://doi:10.3390/agronomy9110687

30. Zhang Y, Fang J, Wu X, Dong L. Na$^+$/K$^+$ balance and transport regulatory mechanisms in weedy and cultivated rice (*Oryza sativa* L.) under salt stress. BMC Plant Biol. 2018;18(1):375. https://doi:10.1186/s12870-018-1586-9

31. Ali A, Maggio A, Bressan RA, Yun DJ. Role and functional differences of *HKT1*-type transporters in plants under salt stress. Int J Mol Sci. 2019;20(5):1059. https://doi:10.3390/ijms20051059

32. Pabuayon ICM, Jiang J, Qian H, Chung JS, Shi H. Gain-of-function mutations of *AtNHX1* suppress sos1 salt sensitivity and improve salt tolerance in Arabidopsis. Stress Biol. 2021;1(1):14. https://doi:10.1007/s44154-021-00014-1

33. Mansour MMF. Role of vacuolar membrane transport systems in plant salinity tolerance. J Plant Growth Regul. 2023;42(4):1364–401. https://doi:10.1007/s00344-022-10655-9

34. Ullah MA, Abdullah-Zawawi MR, Sukiran NL, Uddin MI, Ismail I, Zainal Z. In silico approach to investigate the potential *HKT* gene responsive to salt stress in rice. CABI Agric Biosci. 2024;5:49. https://doi:10.1186/s43170-024-00256-9

35. Dave A, Agarwal P, Agarwal PK. Mechanism of high-affinity potassium transporter (HKT) towards improved crop productivity in saline agricultural lands. 3 Biotech. 2022;12(2):51. https://doi:10.1007/s13205-021-03092-0

36. Huang S, Spielmeyer W, Lagudah ES, Munns R. Comparative mapping of *HKT* genes in wheat, barley and rice, key determinants of Na$^+$ transport and salt tolerance. J Exp Bot. 2008;59(4):927–37. https://doi:10.1093/jxb/ern033

37. Chen CZ, Lv XF, Li JY, Yi HY, Gong JM. Arabidopsis *NRT1.5* is another essential component in the regulation of nitrate reallocation and stress tolerance. Plant Physiol. 2012;159(4):1582–90. https://doi:10.1104/pp.112.199257

38. Lin SH, Kuo HF, Canivenc G, Lin CS, Lepetit M, Hsu PK, et al. Mutation of the Arabidopsis *NRT1.5* nitrate transporter causes defective root-to-shoot nitrate transport. Plant Cell. 2008;20(9):2514–28. https://doi:10.1105/tpc.108.060244

39. Li JY, Fu YL, Pike SM, Bao J, Tian W, Zhang Y, et al. The Arabidopsis nitrate transporter *NRT1.8* functions in nitrate removal from the xylem sap and mediates cadmium tolerance. Plant Cell. 2010;22(5):1633–46. https://doi:10.1105/tpc.110.075242

40. Hussain HA, Men S, Hussain S, Chen Y, Ali S, Zhang S, et al. Interactive effects of drought and heat stresses on morpho-physiological attributes, yield, nutrient uptake and oxidative status in maize hybrids. Sci Rep. 2019;9(1):3890. https://doi:10.1038/s41598-019-40362-7

41. Lillo C. Signalling cascades integrating light-enhanced nitrate metabolism. Biochem J. 2008;415(1):11–19. https://doi:10.1042/BJ20081115

42. Huang B, Rachmilevitch S, Xu J. Root carbon and protein metabolism associated with heat tolerance. J Exp Bot. 2012;63(9):3455–65. https://doi:10.1093/jxb/ers003

43. Liu Y, Liu H, Pan Q, Yang H, Zhan J, Huang W. The plasma membrane H$^+$-ATPase is related to the development of salicylic acid-induced thermotolerance in pea leaves. Planta. 2009;229(5):1087–98. https://doi:10.1007/s00425-009-0897-3

44. Poidevin L, Forment J, Unal D, Ferrando A. Transcriptome and translatome changes in germinated pollen under heat stress uncover roles of transporter genes involved in pollen tube growth. Plant Cell Environ. 2021;44(7):2167-84. https://doi:10.1111/pce.13972

45. Giri A, Heckathorn S, Mishra S, Krause C. Heat stress decreases levels of nutrient-uptake and assimilation proteins in tomato roots. Plants. 2017;6(1):6. https://doi:10.3390/plants6010006

46. Tarafdar S, Chowdhary G. Translating the *Arabidopsis thaliana* peroxisome proteome insights to *Solanum lycopersicum*: Consensus versus diversity. Front Cell Dev Biol. 2022;10(1):909604. https://doi:10.3389/fcell.2022.909604

47. Raju SKK, Barnes AC, Schnable JC, Roston RL. Low-temperature tolerance in land plants: Are transcript and membrane responses conserved? Plant Sci. 2018;276(1):73–86. https://doi:10.1016/j.plantsci.2018.08.002

48. Li Y, Zhu J, Xu J, Zhang X, Xie Z, Li Z. Effect of cold stress on photosynthetic physiological characteristics and molecular mechanism analysis in cold-resistant cotton (*ZM36*) seedlings. Front Plant Sci. 2024;15(1):1396666. https://doi:10.3389/fpls.2024.1396666

49. Taiz L, Zeiger E, Møller IM, Murphy A. Plant Physiology and Development. 6th ed. Sunderland (MA): Sinauer Associates Incorporated; 2015.

50. Qian Z, He L, Li F. Understanding cold stress response mechanisms in plants: An overview. Front Plant Sci. 2024;15(1):1443317. https://doi:10.3389/fpls.2024.1443317

51. Semmar N. Temperature-linked constraints and plant protection responses. In: Secondary Metabolites in Plant Stress Adaptation: Analytic Space of Secondary Metabolites. Cham: Springer International Publishing; 2024. p. 155–219. https://doi:10.1007/978-3-031-52595-7_7

52. Mishra S, Spaccarotella K, Gido J, Samanta I, Chowdhary G. Effects of heat stress on plant-nutrient relations: An update on nutrient uptake, transport and assimilation. Int J Mol Sci. 2023;24(21):15670. https://doi:10.3390/ijms242115670

53. Ihnatowicz A, Siwinska J, Meharg AA, Carey M, Koornneef M, Reymond M. Conserved histidine of metal transporter *AtNRAMP1* is crucial for optimal plant growth under manganese deficiency at chilling temperatures. New Phytol. 2014;202(4):1173–83. https://doi:10.1111/nph.12737

54. Catalá R, Santos E, Alonso JM, Ecker JR, Martínez-Zapater JM, Salinas J. Mutations in the Ca^{2+}/H$^+$ transporter *CAX1* increase CBF/DREB1 expression and the cold-acclimation response in Arabidopsis. Plant Cell. 2003;15(12):2940–51. https://doi:10.1105/tpc.015248

55. Feng D, Wang X, Gao J, Zhang C, Liu H, Liu P, et al. Exogenous calcium: Its mechanisms and research advances involved in plant stress tolerance. Front Plant Sci. 2023;14(1):1143963. https://doi:10.3389/fpls.2023.1143963

56. Zulfiqar U, Jiang W, Xiukang W, Hussain S, Ahmad M, Maqsood MF, et al. Cadmium phytotoxicity, tolerance and advanced remediation approaches in agricultural soils: A comprehensive review. Front Plant Sci. 2022;13(1):773815. https://doi:10.3389/fpls.2022.773815

57. Veraestrella R, Gomezmendez MF, Amezcuaromero JC, Barkla BJ, Rosassantiago P, Pantoja O. Cadmium and zinc activate adaptive mechanisms in *Nicotiana tabacum* similar to those observed in metal-tolerant plants. Planta. 2017;246(3):433–51. https://doi:10.1007/s00425-017-2700-1

58. Manghwar H, Hussain A, Alam I, Khoso MA, Ali Q, Liu F. Waterlogging stress in plants: Unraveling the mechanisms and impacts on growth, development and productivity. Environ Exp Bot. 2024;224(1):105824. https://doi:10.1016/j.envexpbot.2024.105824

59. Ishikawa T, Cuin TA, Bazihizina N, Shabala S. Xylem ion loading and its implications for plant abiotic stress tolerance. Adv Bot Res. 2018;87(1):267–301. https://doi:10.1016/bs.abr.2018.09.006

60. Colmer TD, Greenway H. Ion transport in seminal and adventitious roots of cereals during O_2 deficiency. J Exp Bot. 2011;62(1):39–57. https://doi:10.1093/jxb/erq271

61. Sedbrook JC, Kronebusch PJ, Borisy GG, Trewavas AJ, Masson PH. Transgenic AEQUORIN reveals organ-specific cytosolic Ca^{2+} responses to anoxia in Arabidopsis thaliana seedlings. Plant Physiol. 1996;111(1):243–57. https://doi:10.1104/pp.111.1.243

62. Huang X, Shabala L, Zhang X, Zhou M, Voesenek LA, Hartman S, et al. Cation transporters in cell fate determination and plant adaptive responses to a low-oxygen environment. J Exp Bot. 2022;73(3):636–45. https://doi:10.1093/jxb/erab480

63. Wang F, Chen ZH, Liu X, Colmer TD, Shabala L, Salih A, et al. Revealing the roles of GORK channels and NADPH oxidase in acclimation to hypoxia in Arabidopsis. J Exp Bot. 2017;68(12):3191–204. https://doi:10.1093/jxb/erw378

64. Park CJ, Shin R. Calcium channels and transporters: Roles in response to biotic and abiotic stresses. Front Plant Sci. 2022;13(1):964059. https://doi:10.3389/fpls.2022.964059

65. Prasad D, Singh R, Singh A. Management of sheath blight of rice with integrated nutrients. Indian Phytopathol. 2010;63(1):11–15. https://epubs.icar.org.in/index.php/IPPJ/article/view/11033

66. Verbon EH, Trapet PL, Stringlis IA, Kruijs S, Bakker PA, Pieterse CM. Iron and immunity. Annu Rev Phytopathol. 2017;55(1):355–75. https://doi:10.1146/annurev-phyto-080516-035537

67. Schmidt SB, Husted S. The biochemical properties of manganese in plants. Plants. 2019;8(10):381. https://doi:10.3390/plants8100381

68. Mandlik R, Thakral V, Raturi G, Shinde S, Nikolić M, Tripathi DK, et al. Significance of silicon uptake, transport and deposition in plants. J Exp Bot. 2020;71(21):6703–18. https://doi:10.1093/jxb/eraa301

69. Hsu PK, Tsay YF. Two phloem nitrate transporters, *NRT1.11* and *NRT1.12*, are important for redistributing xylem-borne nitrate to enhance plant growth. Plant Physiol. 2013;163(2):844–56. https://doi:10.1104/pp.113.226563

70. Zoghbi-Rodríguez NM, Gamboa-Tuz SD, Pereira-Santana A, Rodríguez-Zapata LC, Sánchez-Teyer LF, Echevarría-Machado I. Phylogenomic and microsynteny analysis provides evidence of genome arrangements of high-affinity nitrate transporter gene families of plants. Int J Mol Sci. 2021;22(23):13036. https://doi:10.3390/ijms222313036

71. Hao DL, Zhou JY, Yang SY, Qi W, Yang KJ, Su YH. Function and regulation of ammonium transporters in plants. Int J Mol Sci. 2020;21(10):3557. https://doi:10.3390/ijms21103557

72. Wang Y, Wang F, Lu H, Liu Y, Mao C. Phosphate uptake and transport in plants: An elaborate regulatory system. Plant Cell Physiol. 2021;62(4):564–72. https://doi:10.1093/pcp/pcab011

73. Ragel P, Raddatz N, Leidi EO, Quintero FJ, Pardo JM. Regulation of K^+ nutrition in plants. Front Plant Sci. 2019;10(1):281. https://doi:10.3389/fpls.2019.00281

74. Bakshi A, Gilroy S. Moving magnesium. Mol Plant. 2022;15(5):796–98. https://doi:10.1016/j.molp.2022.04.002

75. Takahashi H. Sulfate transport systems in plants: Functional diversity and molecular mechanisms underlying regulatory coordination. J Exp Bot. 2019;70(16):4075–87. https://doi:10.1093/jxb/erz132

76. Khan S, Kaur K, Kumar V, Tiwari S. Iron transport and homeostasis in plants: Current updates and applications for improving human nutrition values and sustainable agriculture. Plant Growth Regul. 2023;100(2):373–84. https://doi:10.1007/s10725-023-00979-1

77. Alejandro S, Höller S, Meier B, Peiter E. Manganese in plants: From acquisition to subcellular allocation. Front Plant Sci. 2020;11(1):300. https://doi:10.3389/fpls.2020.00300

78. Printz B, Lutts S, Hausman JF, Sergeant K. Copper trafficking in plants and its implication on cell wall dynamics. Front Plant Sci. 2016;7(1):601. https://doi:10.3389/fpls.2016.00601

79. Tufino VO, Casellas MA, Flis P, Salt DE, Schat H, Aarts MGM. *Arabidopsis thaliana* Zn transporter genes *ZIP3* and *ZIP5* provide the main Zn uptake route and act redundantly to face Zn deficiency. Plant J. 2025;121(3):e17251. https://doi:10.1111/tpj.17251

80. Liu B, Yu H, Yang Q, Ding L, Sun F, Qu J, et al. Zinc transporter ZmLAZ1-4 modulates zinc homeostasis on plasma and vacuolar membrane in maize. Front Plant Sci. 2022;13:881055. https://doi:10.3389/fpls.2022.881055

81. Zhang J, Liu S, Liu CB, Zhang M, Fu XQ, Wang YL, et al. Natural variants of molybdate transporters contribute to yield traits of soybean by affecting auxin synthesis. Curr Biol. 2023;33(24):5355. https://doi:10.1016/j.cub.2023.10.072

82. Onuh AF, Miwa K. Regulation, diversity and evolution of boron transporters in plants. Plant Cell Physiol. 2021;62(4):590–99. https://doi:10.1093/pcp/pcab025

83. Ma Q, Zhao C, Hu S, Zuo K. Arabidopsis calcium-dependent protein kinase CPK6 regulates drought tolerance under high nitrogen by the phosphorylation of *NRT1.1*. J Exp Bot. 2023;74(18):5682–93. https://doi:10.1093/jxb/erad277

84. Bassett CL, Baldo AM, Moore JT, Jenkins RM, Soffe DS, Wisniewski ME, et al. Genes responding to water deficit in apple (*Malus* × *domestica* Borkh.) roots. BMC Plant Biol. 2014;14(1):182. https://doi:10.1186/1471-2229-14-182

85. Eragam A, Mohapatra A, Shukla V, Kadumuri RV, George AP, Putta L, et al. Panicle transcriptome of high-yield mutant indica rice reveals physiological mechanisms and novel candidate regulatory genes for yield under reproductive stage drought stress. BMC Plant Biol. 2023;23(1):493. https://doi:10.1186/s12870-023-04507-1

86. Duan J, Tian H, Gao Y. Expression of nitrogen transporter genes in roots of winter wheat (*Triticum aestivum* L.) in response to soil drought with contrasting nitrogen supplies. Crop Pasture Sci. 2016;67(2):128–36. https://doi:10.1071/CP15152

87. Zhang C, Meng S, Li M, Zhao Z. Genomic identification and expression analysis of the phosphate transporter gene family in poplar. Front Plant Sci. 2016;7(1):1398. https://doi:10.3389/fpls.2016.01398

88. Li Y, Wang X, Zhang H, Wang S, Ye X, Shi L, et al. Molecular identification of the phosphate transporter family 1 (*PHT1*) genes and their expression profiles in response to phosphorus deprivation and other abiotic stresses in *Brassica napus*. PLoS One. 2019;14(7):e0220374. https://doi:10.1371/journal.pone.0220374

89. Ahmad I, Mian A, Maathuis FJ. Overexpression of the rice *AKT1* potassium channel affects potassium nutrition and rice drought tolerance. J Exp Bot. 2016;67(9):2689–98. https://doi:10.1093/jxb/erw103

90. Khan IU, Ali A, Yun DJ. Arabidopsis NHX transporters: Sodium and potassium antiport mythology and sequestration during ionic stress. J Plant Biol. 2018;61:292–300. https://doi.org/10.1007/s12374-018-0244-y

91. Li Y, Feng Z, Wei H, Cheng S, Hao P, Yu S, et al. Silencing of *GhKEA4* and *GhKEA12* revealed their potential functions under salt and potassium stresses in upland cotton. Front Plant Sci. 2021;12:789775. https://doi:10.3389/fpls.2021.789775

92. Guo Y, Zhu C, Tian Z. Overexpression of *KvCHX* enhances salt tolerance in *Arabidopsis thaliana* seedlings. Curr Issues Mol Biol. 2023;45(12):9692–708. https://doi.org/10.3390/cimb45120605

93. Chen ZC, Yamaji N, Horie T, Che J, Li J, An G, et al. A magnesium transporter OsMGT1 plays a critical role in salt tolerance in rice. Plant Physiol. 2017;174(3):1837–49. https://doi:10.1104/pp.17.00532

94. Nino MC, Nogoy FM, KwonKyoo KK, Cho CY. Low-affinity cation transporter 1 improves salt stress tolerance in Japonica rice. Plant Breed Biotech. 2018;6:82–93. https://doi.org/10.9787/PBB.2018.6.1.82

95. Chen Y, Li G, Yang J, Zhao X, Sun Z, Hou H. Role of *NRAMP* transporter genes of *Spirodela polyrhiza* in cadmium accumulation. Ecotoxicol Environ Saf. 2021;227:112907. https://doi.org/10.1016/j.ecoenv.2021.112907

96. Tan L, Zhu Y, Fan T, Peng C, Wang J, Sun L, et al. OsZIP7 functions in xylem loading in roots and inter-vascular transfer in nodes to deliver Zn/Cd to grain in rice. Biochem Biophys Res Commun. 2019;512(1):112–118. https://doi.org/10.1016/j.bbrc.2019.03.024

97. Yang J, Mathew IE, Rhein H, Barker R, Guo Q, Brunello L, et al. The vacuolar H^+/Ca^{2+} transporter *CAX1* participates in submergence and anoxia stress responses. Plant Physiol. 2022;190(4):2617–36. https://doi.org/10.1093/plphys/kiac457

98. Wang J, Liu XI, Zhang AN, Ren Y, Wu F, Wang G, et al. A cyclic nucleotide-gated channel mediates cytoplasmic calcium elevation and disease resistance in rice. Cell Res. 2019;29(10):820–31. https://doi.org/10.1038/s41422-019-0219-7

99. Nakata Y, Ueno M, Kihara J, Ichii M, Taketa S, Arase S. Rice blast disease and susceptibility to pests in a silicon uptake-deficient mutant *lsi1* of rice. Crop Prot. 2008;27(3–5):865–68. https://doi.org/10.1016/j.cropro.2007.08.016

Additional information

Peer review: Publisher thanks Sectional Editor and the other anonymous reviewers for their contribution to the peer review of this work.

Reprints & permissions information is available at https://horizonepublishing.com/journals/index.php/PST/open_access_policy

Publisher's Note: Horizon e-Publishing Group remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.

Indexing: Plant Science Today, published by Horizon e-Publishing Group, is covered by Scopus, Web of Science, BIOSIS Previews, Clarivate Analytics, NAAS, UGC Care, etc
See https://horizonepublishing.com/journals/index.php/PST/indexing_abstracting

Publisher information: Plant Science Today is published by HORIZON e-Publishing Group with support from Empirion Publishers Private Limited, Thiruvananthapuram, India.