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REVIEW ARTICLE

Regulation of gene expression in plant growth and metabolism: A review

Sansuta Mohanty[1], Subrat Kumar Mahapatra[2], Madhumita Dasgupta[1], Madhusmita Panigrahy[1], Dhaneswar Swain[1], Gyana Ranjan Rout[1,*]

[1] *Department of Molecular Biology and Biotechnology, Faculty of Agricultural Sciences, Siksha 'O' Anusandhan Deemed to be University, Odisha751003, India*

[2] *Department of Agricultural statistics, Faculty of Agricultural Sciences, Siksha 'O' Anusandhan Deemed to be University, Odisha 751003, India*

*** Corresponding author:** Gyana Ranjan Rout, grrout@rediffmail.com; gyanaranjanrout@soa.ac.in

ABSTRACT

In higher eukaryotes, the genes' architecture has become an essential determinant of the variation in the number of transcripts (expression level) and the specificity of gene expression in plant tissue under stress conditions. The modern rise in genome-wide analysis accounts for summarizing the essential factors through the translocation of gene networks in a regulatory manner. Stress tolerance genes are in two groups: structural genes, which code for proteins and enzymes that directly protect cells from stress (such as genes for transporters, osmo-protectants, detoxifying enzymes, etc.), and the genes expressed in regulation and signal transduction (such as transcriptional factors (TFs) and protein kinases). The genetic regulation and protein activity arising from plants' interaction with minerals and abiotic and biotic stresses utilize high-efficiency molecular profiling. Collecting gene expression data concerning gene regulation in plants towards focus predicts an acceptable model for efficient genomic tools. Thus, this review brings insights into modifying the expression study, providing a valuable source for assisting the involvement of genes in plant growth and metabolism-generating gene databases. The manuscript significantly contributes to understanding gene expression and regulation in plants, particularly under stress conditions. Its insights into stress tolerance mechanisms have substantial implications for crop improvement, making it highly relevant and valuable to the field.

Keywords: gene expression; gene complexity; transcription factors; abiotic and biotic stress

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1. Introduction

Gene expression is the process in which genetic instructions are used to produce functional end products in the form of proteins or non-coding products, which are governed by complex biological environments. Genetic regulation controls the activity of genes in response to the physiological requirements of a specific cell type, evolutionary phase, or environmental factor. Although it delivers the fundamental stage at which the genotype of a species results in different genetic traits, the information from a gene synthesizes a functional gene product, i.e., protein or non-coding RNA, which ultimately affects a phenotype. The manifestation of phenotypes is by changing the effects of the proteins that regulate the structure and growth of the organism, which function as enzymes catalyzing particular metabolic processes. However, genetic changes such as DNA methylation, histone modification, and DNA directions for coding and non-coding RNA affect gene expression differently[1]. The exceptional genetic variation describes the changes in DNA and chromatin-associated protein modifications that modify gene expression and cell function without altering the DNA sequence. Even though they may be reversible and thus regulatory, such alterations are inherited through mitosis and, in rare cases, meiosis. However, transcription factors (TFs) are unique proteins that can bind to DNA sequences and regulate gene expression by promoting or suppressing transcription. The regulation and expression of plant genes by transcription factors (TFs) in response to different stresses have been illustrated[2]. The function and management of TFs are emerging as a critical issue in the context of molecular mechanisms. The transcription, RNA splicing, translation, and translational modification of a protein are the few controlled phases in the gene expression process. The location and amount of a particular gene product (protein or ncRNA) are governed by gene regulation, which can significantly impact cellular structure and function. The basis for cellular differentiation, development, morphogenesis along with flexibility and versatility of any organisms is due to the regulation of gene expression. Therefore, gene regulation may be a foundation for evolutionary shifts[3]. All known eukaryotic and prokaryotic life exhibits gene control and expression. Prokaryotes mainly control the expression of genes at the level of transcription (though a few epigenetic as well as post-translational regulations are applicable). On the other hand, the cells of eukaryotes regulate genetic expression at the epigenetic, transcription, post-transcription, translation, and post-translation stages. Epigenetic gene regulation is the study of how natural and environmental behavior can change effect of genes. Since the interaction between the surroundings and ecological chemical modification can result in genetic change, it is easy to find the connection between genes and environmental mutations[4]. Unlike genetic changes, epigenetic expression is reversible and does not change the DNA sequence but can change how the species reads a DNA sequence. For instance, plants also show the epigenetic level of gene expression defense control against a pathogen. Alteration of genetic changes depends on the protein, while epigenetic changes affect gene expression to turn genes "on" and "off". However, the changes may have occurred due to stress-responsive genes that facilitate adaptation to several stresses.

A distinct form of eukaryotic plant gene has higher genome diversity rates. Exploring the quantitative traits is necessary to understand the involvement of the resistant gene, a single major gene from the whole genome sequence. Targeted markers through genome-wide association and mapping using genome editing techniques have been used[5]. Plant genomes have interfered with natural complexity and expressional dataset heterogeneity under natural stress conditions. Developed over 3,000,000 expressional functional gene data sets to understand how genes evolve under environmental conditions and visualized the gene regulation in several essential crops to construct effective adaptation for the evolutionary aspects[6]. Over 27,000 genes have been identified in *Arabidopsis thaliana*, while 41,000 have been reported for rice (*Oryza sativa*). A recent genome study confirmed more than 35,000 genes in plants such as chickpeas (*Cicer arietinum*), 45,000 genes in barley (*Hordeum vulgare*), and 30,000 genes in pearl millet (*Cenchrus americanus*). Only 232 out of the 59,000 expressed genes in maize are elevated in root cells under stress conditions[7]. Thus, we emphasize the gene-regulating pattern of plants/crops under different stress conditions (**Table 1**). Nevertheless, a recent understanding of how genes function in adverse conditions opens a door for building a well-adapted functional gene. This review will outline the fundamental ideas underlying plant gene regulation and give instances of regulated plant genes and some TFs. Thus, improving gene expression prediction helps define a potently tolerant plant species/crop for further breeding.

Table 1. List of genes is expressed under stress conditions.

Sl. No	Plants species	Whole gene expressed	Genes expressed in stress condition	Stress condition	References
1.	Wheat (*Triticum aestivum*)	124,000 genes	*TaMAPK3* *OsLsi6* *P5CS*, *P5CR*	Drought Salinity	[8] [9]
2.	Rice (*Oryza sativa*)	41,000 genes	*CaLG02* *Ca_18924* *OsZIP5*	Abiotic Biotic	[10]
3.	Barley (*Hordeum vulgare*)	45,000 genes	*HvZIP7*	Abiotic	[10]
4.	Pearl millet (*Cenchrus americanus*)	30,000 genes	*ZmVPP1*	Drought	[11]
5.	Thale cress (*Arabidopsis thaliana*)	27,000 genes	*AtPPRT1*, *OsHIRP1*, *miR156*	Temperature	[12]
6.	Maize (*Zea mays*)	59,000 genes	*ZmVPP1* *ZmLAZ1-4*	Drought	[13] [14]
7.	Chickpeas (*Cicer arietinum*)	35,000 genes	*Ca_20459*	Heat	[15]

2. Abiotic stress tolerance

Various abiotic stresses from nature's range adversely impact plants' growth. Extreme abiotic stress factors influencing plants include heavy metal toxicity, flooding, heat, drought, and salinity[16]. The effects of all stressors eventually limit plants' development and yield potential. Abiotic stressors are the main factor in crop failure globally since they diminish 50% of crop yields[17]. Abiotic stressors severely threaten the agricultural industry's ability to survive. Numerous stresses, either naturally or genetically, interact and compound one another, so the negative impacts are amplified under multiple stress conditions[3]. Rolly et al.[18] reported that plants react to stress in a complicated method that involves the coordinated actions and interactions of numerous genes, proteins, metabolic, and several signaling methods (**Table 2**). Plants can detect stress signals and changes in their surroundings and then react and adapt to them. One of the primary processes through which green plants respond and attempt to adapt to stress is the regulation of gene expression. The activation of the kinase cascade by abiotic stress, followed by the activation of numerous TFs, is one of the most intriguing examples of stress-induced gene regulation in plants (**Figure 1**).

Table 2. List of genes/transcription factors involved in plants.

Sl. No		Type of gene	Pathway involved	Stress	References
1.	*OSCBL8*	Calcineurin-like protein	1. Calcium-signalling pathway.	Salinity-tolerant	
	ZnCBL4	Zn interacting CBL	2. SOS signalling pathway		
	CIPK23	CBL interacting protein kinase			[19]
2.	*OsCIPK17*	Protein kinase gene	Calcium-signalling pathway.	Heat-tolerant	[12]
	CaLG02	Calcium-like protein			[15]
	OsCIPK4	Kinase cascade			
2.	*OsCIPK15*	Calcineurin-like	Calcium-signalling pathway.	Drought-tolerant	[13]
	OSCIPKI12	CBL interacting protein kinase			
	ATCBL5	Calcineurin-like protein			
3.	*SCAX1*		Membrane binding pathway	Cold-tolerant	[20]
	DREB1	Dehydration-responsive element			
	YMCE				
4.	*CCC-p1*	Ca^{2+} sensitive cross complementer	Membrane transporter pathway	Heavy metal-tolerant	[21]
	TAVTL2	Vacuolar iron transporter gene			
	TAVTL3	Vacuolar iron transporter			
5.	*AT1GO7(HL)*	Long chain base	Membrane transporter pathway	Light-tolerant	[22]
	LHCB2				
6.	*AtPPRT1*	Differentially expressed genes	MAP kinase pathway	Temperature-tolerant	[23]
	ATCAM3P				
	OsHIRP1				

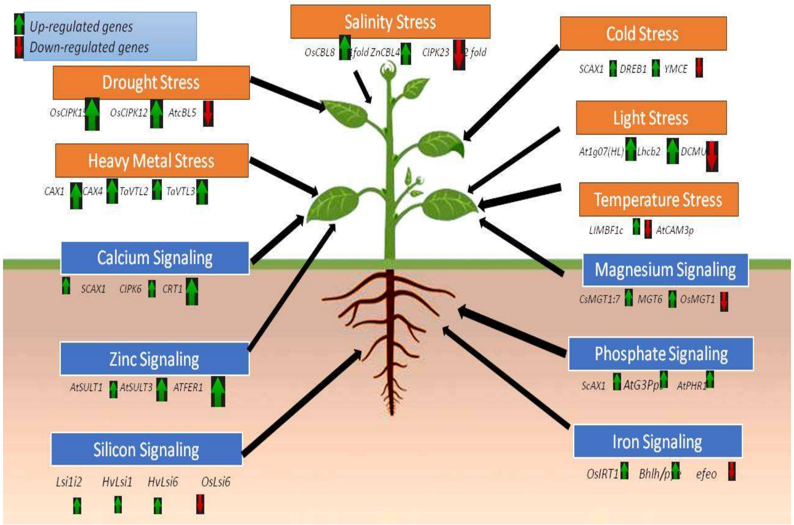

Figure 1. Plant gene regulation under abiotic stress.

2.1. Salinity stress-tolerant gene regulation

Soil salinity is one of the leading factors influencing worldwide agricultural crop production, resulting in colossal crop losses annually. High salinity in the root area seriously impedes average plant growth, leading to decreased agricultural yield or crop failure, regardless of the underlying reason, be it ion toxicity, water scarcity, or nutritional imbalance. Creating salt-tolerant cultivars is an appealing and cost-effective solution to this issue. Although several salt-tolerant plant genotypes were developed using transgenic methods, they frequently failed or showed only sporadic success when grown in saline fields[24]. The occurrence of stress is due to various environmental pressures and genetic factors (TFs or genes), which frequently interact to influence plant survival in saline area circumstances. The vast family of TFs encoded by the gene (*bZIP*) controls numerous plant cellular functions[2]. During salinity stress, monitoring the transcript accumulation of the SOS signaling pathways is essential for genes, including *SOS1-2*, *SOS13*, and *Atbzip62*. The SOS pathway regulates the signaling mechanisms during salt stress to mediate ion homeostasis. *Atbzip62* regulates Salt Overlay Signaling (SOS)-mediated salt-stress signaling by suppressing the SOS pathway genes such as *Atbzip18* and *Atbzip62* and modulating antioxidant responses in *Arabidopsis*[18]. According to Chaudhry et al.[19], the function of tolerant genes like *bZIP62*, *AP2/ERF1*, *WRKY2*, *NACt*, and *bHLH1* in the control of the salinity stress tolerance mechanism is found to be up-regulated in several species. The *AP2/ERFs* in *Arabidopsis* are found to be associated with stress regulatory mechanisms of salinity and drought. These *TFs* are implicated in stress tolerance by modulating growth and developmental programs controlled by various plant growth regulators such as gibberellic acid, cytokinin, brassinosteroid, ABA, and ethylene[25].

2.2. Heat stress-tolerant gene regulation

The growing regions with high global warming suffer heat stress during the growth season of several crops. Wheat yield and quality are significantly affected by high temperatures. Global wheat yields have decreased by 7% due to heat stress during the past two decades (2000–2020)[26]. As a result, it is becoming more crucial to conduct research on the molecular basis of thermal tolerance and to create novel varieties of wheat that are tolerant to heat using conventional breeding and biotechnological methods. Plants, which are sessile organisms, have developed various defense mechanisms to cope with abiotic stress, particularly chemical reactions, to sustain everyday life processes. Some resistant crops regulate the expression of potential TFs that can act under unfavorable growth conditions to withstand heat stress. Heat shock transcription factors (HSFs) play a crucial role in heat stress tolerance by associating TFs of other families, including MYB, WRKY, NAC, or bZIP, and modulating the expression of other genes. Thus, HSFs are favorably exploited for heat stress tolerance in many crop plants[26]. Heat shock transcription factors (HSFs) play a crucial role in heat stress tolerance by associating TFs of other families, including MYB, WRKY, NAC, or bZIP, and modulating the expression of other genes. HSFs are thus favorably exploited for attaining heat stress tolerance in many crop plants[26]. Some potential TFs produce resistant crops that can react to unfavorable growth conditions to withstand heat stress. The heat stress-responsive transcriptome investigation of a heat-tolerant wheat cultivar (TAM107) revealed a new ferritin gene, *TaFERr.* According to the expression pattern, the *TaFER-5* gene in chromosome 5B is induced by heat polyethylene glycol (PEG). Transgenic Arabidopsis overexpressing wheat TaFER-5 conferred enhanced thermo tolerance, drought tolerance, and excess iron stress tolerance by protecting cells against heat stress, ROS, and improved leaf iron content[8]. The heat-tolerant gene *TaFERr-5B* in wheat Jimai565 (JM565) confirmed its role in the plant[8]. The trans-genic species proved to have improved thermo-tolerance. According to Jha et al.[15], heat stress in the reproduction phases of chickpeas (*Cicer arietinum)* causes substantial output losses. An inbred population of chickpeas was produced from DCP-92,3 (heat sensitive) and ICCV-92944 (heat tolerant) by sequencing processes to discover the genetic areas for identifying essential heat stress tolerance genes. The identified high heat-tolerant genotype with significant heat shock protein encodes for genes such as *CaLG02 (Ca_06915, Ca_20459)* and other genes like HSP24 (*Ca_18924*) showed expression at the reproduction stage[15]. Expressed genes such as *AtPPRT1, OsHIRP1, miR156*, and *ERF* are up-regulated in temperature stress tolerance in Arabidopsis (*Arabidopsis thaliala*) and rice (*Oryza sativa*)[23]. Large-scale screening programs in major crops such as rice, including field level screening for heat tolerance and mapping of yield traits, identified constitutive expression of ribulose bisphosphate carboxylase (RUBISCO) large chain precursor (EC 4.1.1.39) in the heat tolerant rice mutant[27].

2.3. Drought stress-tolerant gene regulation

The transcription factors (TFs) with *cis*-elements shared by the specific regulatory areas of the genes and expression are regulated during stress inter-relatedly. The rise in ROS in cellular structures like the mitochondria or chloroplasts undoubtedly leads to distinct transcriptional patterns[22,28]. The varied presentation of a vast number of proteins drives a variety of morpho-physiological responses. Drought tolerance in pearl millet (*Cenchrus americanus*) is a perfect plant model to examine how cereal crops respond to drought. The primary part of a plant that suffers from drought stress is the root system, which can detect and adapt to such stressful situations. Research on the mechanisms underlying the molecular responses of essential genes for drought resistance is now making some progress. Plants under drought stress depend on their roots, which can sense the situation and react accordingly. Drought stress results in a decline in RWC, stomatal conductance, deterioration of water relation parameters, root growth, and photosynthetic rate, leading to stomatal closure, membrane damage through lipid peroxidation[29]. Recent studies compared transcriptome data from normal conditions and drought treatment to investigate the process of pearl millet tolerance to drought. Some differentially expressed genes (DEGs), such as i2_LQ_LWC_c3719/f1p0/2678 and i1_HQ_LWC_c37349/f3p10/1291, were analyzed to discover some essential genes related to drought resistance[11]. The study identified the significance of root traits and the importance of the hormone signaling pathway and the oxidoreductase activity pathway for drought tolerance in pearl millet[11]. The up-regulated gene *ZmVPP1* in the tolerant genotype of maize was reported at photosynthetic and root-growing stages. Out of 355 genes discovered from the transgenic lines, *ZmVPP1* showed significantly altered expression in inbred lines of maize grown under drought conditions[13]. *ZmVPP1* encoded a vacuolar-type H(+) pyrophosphatase, which contributes to drought tolerance in maize by boosting photosynthetic efficiency and root development[30]. Investigating the mechanism underlying resistance to drought has revealed that the relationship among the genes depends on a wealth of natural understanding, which is utilized in predicting the genetic data that may shed light on future complex processes. Several genes, such as Zeaxanthin epoxidase (ZEP), 9-cis-epoxy carotenoid dioxygenase (NCED), ABA-aldehyde oxidase (AAO), β-carotene hydroxylase

(DSM2), arginine decarboxylase (ADC), aspartic protease gene (APA1), C-5 sterol desaturase (FvC5SD), and Caffeoyl-CoA O-methyltransferase have been shown to confer drought tolerance in different crops, including rice, Arabidopsis, maize, tobacco, etc.[31]. However, more validation studies are required to clarify the connections between these several genes and point out the precise functions they perform in drought resistance.

2.4. Cold stress-tolerant gene regulation

Effective and efficient crop improvement through genetic traits depends on integrated genes and highly controlled expression, which are predictable across various freezing backgrounds. However, the regulation of a gene is not only regulated by the temperature and cold that are linked; it can also be impacted by the regulatory elements of neighboring genes or by transcriptional interference between genes. Cold-tolerant genes are one method for enhancing the predictability of gene expression by protecting it from environmental interference. The cold signal is long known to be primarily sensed due to the alteration of cytosolic Ca^{2+} levels, which affect membrane fluidity and result in membrane rigidification and the production of cryoprotectants. The pioneering gene regulations under cold stress include those due to cold-responsive COR genes and ABA-dependent or independent modules[32]. The inducer of the C-repeat binding factor/dehydration-responsive element binding (ICE1-CBF/DERB1) regulation is known to be the most prominent pathway for cold acclimation in plants[33]. The up-regulation of a responsive gene named *DREB1B1* in soybeans (*Glycine max*) boosted the face of many genes activated by various cold stimuli. Different cold-stress-inducible genes, namely *GmDREB1B1* and *GmPYL21*, were down-regulated[20]. A thorough analysis of gene expression and the *cis*-elements in regulating genes can resist cold stress, ultimately improving plant growth under freezing temperatures. In general, the gene regulatory model will significantly aid the framework for determining the genetic and biological processes in the plant system. Traditional methods of attaining cold stress tolerance in crops included cloning and isolating cold tolerant genes such as COR, DREB, CBF, and LEA, followed by the generation of transgenic plants. Several field-level screening programs followed by forward genetic characterization approaches have been conducted in various crops. Improved knowledge of plant genetic resources in recent decades has made it possible to expand the genetic base for breeding for cold tolerance. Conventional QTL-mapping, global transcriptome profiling, or genome-wide association mapping and allele-mining with diverse omics approaches have broadened the possibilities to understand mechanisms of freezing tolerance in crops[34].

2.5. Heavy metal stress-tolerance gene regulation

Several metal transporters are reported in aspects that characterize the functionality of crops. Apart from metal toxicity, the identification of metal transporter genes also performs in clustering the gene regulation investigation. Metals like zinc and iron are essential for plant growth and metabolism[35,36]. Zinc is a key structural motif in many proteins, including the DNA-binding Zn-finger protein. Therefore, zinc and iron uptake and homeostasis networks have evolved in plants. Zinc-regulated transporters, or iron-regulated transporter-like proteins (ZIP), are capable of uptaking and transporting divalent metal ions and play critical roles in balancing metal uptake and homeostasis[37]. *Thlaspi caerulescens* and *Arabidopsis halleri* are reported as heavy metal hyperaccumulators, particularly Ni, Zn, and Cd. They accumulate in the soil through a bulk flow of the metal from root to shoot. The metals are translocated from the root symplast into the xylem apoplast; in many cases, the transporter proteins are involved in this process[38]. At the tissue level, metal may accumulate in the epidermis and trichomes, while at the cellular level, these excess metals accumulate in the vacuole or cell wall. Chelators often bind the metals and play a significant role in the detoxification of the metals[39]. Talke et al.[40] identified a set of candidate genes through cross-species transcript profiling expressed in *A. halleri* more than in *A. thaliana*. These genes were further analyzed using RT-PCR, and it was observed that 29 of them encoded putative metal homeostasis proteins. Four of the genes having the highest transcript

(HMA4, ZIP9, ZIP6, and ZIP3) level in *A. halleri*. The genes ZIP9, ZIP6, and ZIP3 are members of the ZIP family of metal transporters and candidates for cytoplasmic metal influx in roots, while HMA4 has been characterized as a P1B-type heavy metal ATPase in *A. thaliana* and is suggested to have a role in root-to-shoot Zn transport[41]. Wang et al.[42] identified that OsNramp5 is a crucial gene involved in the control of the uptake of Cd, Mn, and other metal ions by rice root cells. Toxicogenomic is assigned to gather, analyze, and interpret data from changes in gene expression. However, gene expression also has a definite role in classifying compounds related to the toxicological level, describing a comparative toxicogenomic study. Conventional breeding approaches and transgenic technology are being suitably used for attaining heavy metal tolerance in crops. Vacuolar iron transporter-like protein (*VTL*) genes from hexaploid wheat suggest that the quantitative expression of metal tolerant genes in root (*TaVTL-2, TaVTL-3*, and *TaVTL-5*) is upregulated. The up-regulatory gene also significantly enhanced Fe content in cereal crops like wheat and rice. Formerly, investigators studied the regulation of *VTL* genes, which have been shown to play an essential role in balancing Fe in an optimum range, utilizing the minimal toxic effects of metal. The diverse sets of *VTL* genes exhibit a high similarity within the nodulin protein *CCC-p1* (Ca^{2+} sensitive cross complementary like domain as an iron transporter)[21]. Palladium (Pd) is another heavy metal vital for industry, mainly when it is present as a nanoparticle. Due to its distinct catalytic capabilities, it has been used in morphine pharma-manufacture and electrolytic systems for automobiles. Pd harms bacterial cells and leads to oxidative stress, making it difficult for bacteria to generate Pd nanoparticles effectively. In addition, the heavy metal stress of Pd can affect alternatively in the form of homeostatic cellular disruption of transporting elements like Zn, Cu, and Fe. Interestingly, inorganic transporters' observed responses/expression changes to the side effects of heavy metal toxicity. To further understand the mechanism of the regulating genetic factor involved, observed some differentially expressed genes (DEGs) from clusters of orthologous groups (COG), such as *recQ*, which was down-regulated to 4-fold and *smbC1* up-regulated to 8-fold[43].

Furthermore, other genes like *efeO*2 and *efeB* expressed in the membrane periplasm export inorganic ions through micro-organisms (*E. coli*)[43]. Alternate strategies include microbe-assisted heavy metal tolerance, which applies beneficial microorganisms to crop management practices. These microbes help plants acclimatize to the metalliferous soil environment, reduce metal bioavailability, and decrease metal accumulation in plant tissues[44]. More likely, the study of gene regulation observes that *E. coli* exhibits some behaviors that appear to be Pd-specific, and more investigation is required to clarify its fundamental signaling mechanisms. The findings of regulating genes are crucial for remediating heavy metal contaminants using microbes in a genetic approach.

3. Micronutrient transporter gene regulation in plants

The plants can absorb micronutrients from the soil and deliver them to the aerial part of the plant, including seed formation, so that the aerial part has the resources it needs to function effectively. But plants must control the various steps during the expedition from soil to seed, including uptake, transport, remobilization, and several genes involved, including the major and trace elements. Although this phenomenon is complex and has different characteristics for different species, it has become commonplace due to various anthropogenic practices. To address the issue, a plant develops various proteomic and genomic strategies. Metallic stress sets off a multigene reaction that modifies several proteins, directly affecting almost every biological process in a living cell. Proteomic and genomic approaches can be beneficial in understanding the molecular responses to heavy metal stress. The inadequate supply of fertilizers for agricultural use has decreased crop productivity. Sustainable agricultural output depends on soil residues containing the correct number of micronutrients. The importance of genetic foundations in metal uptake involves understanding cellular and morphological mechanisms in plants. However, additional metal uptake genes like Zn-Induced Faciliatory Family (ZIFL) gene transporters have also been investigated[45]. The micronutrient transport pathways include iron chelators, nicotinamide, phytosiderophores from the muriatic acid family, citrate, and other chelator transporters, iron-chelate complexes, or free iron ions. Plants have evolved systems for controlling gene expression in response to iron availability to maintain iron homeostasis. Regulatory factor pathways in iron deficiency stimulate the encoding of numerous genes involved in iron absorption and translocation, while the ubiquitin ligase HRZ/BTS negatively regulates this expression.

3.1. Phosphate transporter gene regulation

Phosphorus is one of the most essential macronutrients for plant growth and development. Pi, the primary inorganic phosphate, can be easily assimilated by soil microbes, ultimately affecting availability and plant uptake. Therefore, the phosphate transporter requirement is essential for fulfilling the macronutrient requirement for plant developmental stages. The phosphate starvation response is initiated due to phosphate use efficiency and includes the expression of high-affinity phosphate transporter genes for enhancing phosphate uptake. Several genes, including PHO2, PHR1, and miR399, whose expression is regulated by the systemic root-born signal (SRS), mediate the phosphate starvation response. The miR399, as a mobile signal, transmits the signal to the systemic shoot signal (SSS) from shoot to root through phloem sap, leading to enhanced phosphate uptake and translocation[46]. Alternately, by analyzing expressed genes, it would be feasible to evaluate the biological Pi state of a plant utilizing transcriptome profile technologies. Nevertheless, recent researchers have characterized the transcriptome patterns of genes in plants throughout growth and during various natural stresses, particularly Pi deprivation. Therefore, knowing the gene responsible for regulation or expression will be executed by changing or modifying the enzymes and metabolites for the rhizosphere's advantage or by substituting Pi in cellular forms with microbes. Some investigators found it interesting to examine the gene AtG3Pps in mediating the uptake of organic P from the surrounding plant system[46]. According to the specificity of the principal controller of Pi, the AtPHR1 gene has a signaling function in Arabidopsis, possibly concerned with preserving sulfate, iron, and zinc[45–47].

3.2. Zinc transporter gene regulation

Zinc (Zn) is a major elemental micronutrient for food crops and acts as a cofactor for several physiological and biochemical reactions. Its deficiency affects rice yield (*Oryza sativa*) extensively, up to 70%. Rice is mainly grown in flooded conditions, elevating the levels of P and HCO_3 and ultimately decreasing the soil's zinc availability for the crop. Zn transporters (*OsZIP1* and *OsZIP3*) were identified from full-length gene data sets of the SLC3 (ZnT) and SLC3 (ZIP) families to express the localized gene in root[45]. Another transporter gene named *ZmLAZ1-4* controls the homeostatic level of Zn in maize and showed a negative regulation with *ZmBES1/BZR111* (yeast) on vacuolar and plasma membranes for ion transport in plant system[14]. *ZmZIP3 (Zea mays*) improved Zn accumulation in the root for better uptake. Two additional genes, *AtZIP-2* and *AtZIP2-4*, from *Arabidopsis thaliana* were observed with high Zn concentrations and have proven to contribute to increasing the Zn level in seeds. Furthermore, genes like *HvZIP7* from barley (*Hordeum vulgare*) and *OsZIP5* from rice (*Oryza sativa*) help transpose Zn from root to shoot in an appropriate ratio[31]. *OsZIP1*, *OsZIP3*, and *OsZIP4* are unregulated in the roots and over-expressed in the shoots of several genotypes of *Zea mays* when Zn is low[10]. Thus, the discovery of high-affinity *ZIPs* would be beneficial and might help to solve the issues caused by Zn deficiency in several crops. Model plants have characterized many ZIP family genes involved in Zn transport for further breeding purposes. Identification, functional analysis, and relative expression of specific transporter genes can also describe the genetically significant Zn-homeostatic level in cellular functions acting in mammalian health disorders[48].

3.3. Silicon transporter gene regulation

Silicon is an essential element for higher plants; however, its beneficial effects on plant growth are well-reported in several crops[49]. The plants generally take up Si in silicic acid form, which is later transported to shoots and polymerized as silica gel on the leaves and stem surfaces[49,50]. It supports plant growth by enhancing resistance to both abiotic (water stress, salinity, temperature stress, etc.) and mineral stresses and biotic (disease and insect damage) stresses. Si has excellent potential for alleviating mineral stress like Mn and Al toxicity. Si also acts as a fertilizer for greater productivity by evaluating and increasing the yield through its uptake. Few genes encoding for Si uptake, like *Lsi1*, *Lsi2*, and *Lsi6*, are linked with high accumulation in plant tissues, causing increased strength and rigidity in rice, a distinctive Si accumulation[51–56]. Notably, the successful practices of Si uptake depend on the influx series (*Lsi1*, *Lsi2*) of the Si transporter gene in an expressional and regulated manner. However, the general genetic mechanism understands the response of Si translocation through plant root and shoot systems. Investigating different expressional patterns of Si uptake and translocation revealed the two genes' (*Lsi3, Lsi2*) involved in rice genotype[52]. However, in barley (*Hordeum vulgare*), maize (*Zea mays*), and pumpkin (*Cucurbita moschata*), the Si transporter gene is owned by several nod-like proteins (*NIP2-nod26*) localized in the endo and exodermis of the root cells[56]. Recent researchers found the expression of *OsLsi6* for improved rice efficiency, enhancing stress resistance, as a good Si fertilizer[9]. In Si-deficient vegetational crops that undergo extreme Zn stress, up-regulated genes such as *Os08g2630* (*PsbY*), *Os5g48630* (*PsaH*), *Os7g37030* (*PetC*), *Os3g57120* (*PetH*), and *Os4g38410* are expressed. According to recent findings, the Si-upregulated genes also have a variety of roles in regulating transpiration, secondary metabolic processes, production, and water absorption. The Si transporter gene can assume the boost of water and ion uptake. However, it will benefit genetically from modifications of the gene, especially *Lsi2*, through breeding programs and a cisgenic approach to enhance nutrient and osmotic balance[54]. Hence, studying the Si gene expression gives an overview of the physiological enhancement of plant growth and stress recovery correlated with the molecular variations under stressful conditions[57].

3.4. Iron transporter gene regulation

Iron (Fe) plays a role in several biological functions, such as respiration, chlorophyll production, and photosynthesis, making it a crucial element for plants and other creatures through the interaction of transcription factors (TFs) with cis-elements shared by the specific regulatory areas of these genes and the regulation of gene expression under stress. The rise in ROS in cellular structures like the mitochondria or chloroplasts undoubtedly leads to distinct transcriptional patterns. The varied presentation of many proteins drives various morpho-physiological responses under high Fe content[58,59]. However, plants can still absorb Fe in soil morphologically with very low iron solubility, especially in aerobic circumstances at high pH ranges. As a result, plants have developed effective methods for absorbing iron; however, Fe is an intermediate metal and a redox material that reacts. Undissolved ferric hydroxide compounds of Fe are often present in soil but are non-biodegradable to plants. Plants have evolved intricate mechanisms to maintain a sufficient supply of Fe in a changing environment. Plants can detect Fe levels and alter the expression of genes linked to Fe uptake, thus influencing the uptake of Fe from the soil to the roots. *ZmYS1*, the known YSL transporter gene, is in the plasma membrane. It is increased in both roots and leaves in response to iron deficiency, indicating that it is involved in both rhizosphere-to-plant body Fe absorption and Fe translocation. Other transporter genes co-expressionally involved are *AtSULT1-3*, *AtSULT2-1*, and *AtSULT3-4* for sulfate uptake, and the *AtFER1* gene co-expressed for regulation of iron storage[58,59]. A typical Fe deficiency-inducible gene, *AtMYB72*, has an exciting note to modulate *AtFIT-AtbHLHIb*, which controls the expression at the transcript level. The interaction of the gene *AtMYB72* with *AtFIT/AtbHLHIb* shows overexpression in the wild type of *Arabidopsis thaliana*[54]. *OsYSL16* participates in Fe allocation along the vascular bundle and transports Fe^{3+}, which is present in the xylem. *OsYSL18*, on the other hand, is another Fe^{3+} transporter that has been proposed to be associated with Fe translocation in the phloem. *OsYSL9* has recently been identified as a Fe^{2+} and Fe^{3+} transporter and directs internal Fe transport, particularly in growing seeds[59]. In the last decade, there has been a fundamental regulation of gene frameworks for Fe deficiency in response to the discovery of Fe sensors and numerous essential transcription factors. Studying each component's functioning in greater detail will significantly advance the understanding of plant biological processes, food production, and the nutritional needs of humans.

3.5. Calcium regulatory gene regulation

Plants have excellent sensing networks with the functional effects of secondary messengers, kinases, and several genetic transcription factors. The plants sense and react to environmental signals to control gene expression and adapt to the changing environment. Calcium (Ca^{2+}) is a highly significant, ubiquitous, and intracellular second messenger molecule that modulates a signaling pathway to counter diverse abiotic stress. Ca^{2+} transport is tightly regulated to maintain cytosolic fluctuation while supplying intracellular Ca^{2+} reserves for signaling and simultaneously supporting the developing cell wall and membrane structures. Various channel transporters (channel and carrier proteins) provide the genetic basis for balancing Ca^{2+} homeostasis and the production of Ca^{2+} signals to accomplish the balance. Recent studies demonstrated that various biophysical stimulations, such as pathogen elicitors, plant hormonal effects, and abiotic conditions, such as excessive salinity, cold, and drought, cause an increase in the level of cytosolic Ca^{2+} concentration (cyt[Ca^{2+}]).Nevertheless, many researchers have investigated the role of different genes in increasing the transport of Ca^{2+} to resolve the tolerance mechanism in plants[60]. The genetic approach based on the binding capacity of Ca^{2+} to the CRT1 domain has increased the tolerance capability by 30%, resulting in the overexpression of the *sCAX1* gene by 3-fold up-regulation. Other expressing genes like *RBOH1* and *RBOH2* are regulated in response to an increase in H_2O_2 accumulation, activating calmodulin and some kinases to react and withstand the stress effect. To overcom the damage through ROS signaling, another gene, SlCaM2, was expressed to control the H_2O_2-elevating concentration[61]. Thus, plants might be more capable of allocating vital resources toward sustaining a broad spectrum of diverse stressors by improving the level of response to stress without altering the mechanism. In addition, this might turn Ca^{2+} widespread availability into a benefit rather than a barrier to study. The more we know about Ca-regulating processes, the better we can modify our responses to challenging circumstances. Further investigation into the transgenic production of calcium-regulating genes can benefit agricultural outcomes, crop production, and soil management by improving productivity.

3.6. Magnesium regulatory genesin plants

In *Arabidopsis*, the *MGT6* gene (magnesium transporter) expressed in the root system has a high affinity for Mg^{2+} uptake at a specific concentration. However, with the reduction in the level of Mg^{2+}, the expression of *MGT6* is up-regulated. Under favorable conditions, plants' adaptation to low levels of Mg^{2+} is highly expressed by the gene *MRS2*, *7/MGT7*, maintaining the homeostatic mechanism in the plant's root system[62]. Furthermore, negative correlation depends on the acidic soil under low levels of Mg^{2+}, resulting in inappropriate binding of Al^{3+} and showing strong inhibition uptake. Al^{3+} accelerates the expression of the *OsMGT1* gene in the roots of rice, directly blocking the channel of Mg^{2+}[62].

Similarly, Bin et al.[63] studied the expression of the *CsMGT1* and *CsMGT7* genes, showing the beneficial effect of the Mg^{2+} deficiency response in *Citrus sinensis* as a potent Mg^{2+} transporter. Further, the Mg transporter gene can maintain the uptake of Na^+ and K^+, ultimately promoting the tolerance sensor gene in salt-resistant plant species[64]. Constructing and developing mechanisms for signaling channels that precisely control the development and functioning of these transporter gene networks can also be challenging but urgent, ultimately resulting in plants' genetic modification for precise environmental Mg concentration adaptation.

4. Biotic stress tolerance

The plant's ability to deal with an adverse condition strongly relates to stress. In most contexts, stress is a severe deviation from the ideal conditions for the existence of a plant variety. Several reports delivered the cause, changes, and responses of biotic stress at all levels of the species functioning that are, in theory, reversible but may be permanent. However, focusing on biotic stress responsible for disease resistance poses a severe danger to worldwide agricultural production because it reduces plants' growth, development, and survival rates, which results in substantial reductions in yield. Furthermore, the cellular effect of pathogens in plants responds to hormonal changes and some significant genes in a regulating manner under biotic stress (**Table 3**). The regulation of numerous genes involved in protection against the consequences of nutrient deprivation is induced by pathogens, which raises plants' jasmonic (JA) levels. The effect of JA brings on the expression of specific genes, ultimately raising tolerance levels. Over 2000 genes are expressed during plant defense under the guidance of the master regulator *NPR1* (Nonexpresser of PR Genes 1) (**Figure 2**). Although the method is unclear, *NPR1* interacts with transcription factors to activate the expression of defense genes. While studying the biotic tolerance mechanism in *Arabidopsis thaliana*, it was found that *NPR1* recruits *CDK8* (Cyclin-Dependent-Kinase 8) and *WRKY18* (WRKY DNA binding protein 18) to the *NPR1* promoter to increase its expression when salicylic acid[12]. The presentation of transcription factors (TFs), each of which stimulates a different set of targeted genes, including those required to generate protective compounds, is one result of the signal transduction cascade of dehydration. Other tissues express TFs (*LRNAC35*, *ZMNAC41*, *VdCE11*, and *VVNACO42*) differently under stress conditions[64,65]. Numerous genes are highly expressed in dehydration, with the known late embryogenesis abundant genes (LEA) being considered the most notable genes[66].

Table 3. List of genes/transcription factors involved in biotic stress in plants.

Sl. No	Genes/transcription factors	Stress organism	Organism	Plant infected	References
1.	SMNAC	*Pseudomonas solanacearum*	Bacteria	*Solanum melongena* (Eggplant)	[65]
2.	GHATAF1, VdCE11	*Verticillium dahliae*	Fungus	*Gossypium hirsutum* (Cotton)	[66]
3.	STNACB4	*Colletotrichum graminicola*	Bacteria	*Solanum tuberosum* (Potato)	[67]
4.	LRNAC35	*Tobacco mosaic virus*	Virus	*Lycopersicon esculentum* (Tomato)	[12]
5.	ZMNAC41	*Glomerellagraminicola*	Fungus	*Zea mays* (Maize)	[67]
6.	OSNAC66, OSNAC4	*Magnaporthe grisea*	Fungus	*Oryza sativa* (Rice)	[68]
7.	VVNACO42	*Erysiphe graminis*	Fungus	*Hordeum vulgare* (Barley)	[69]

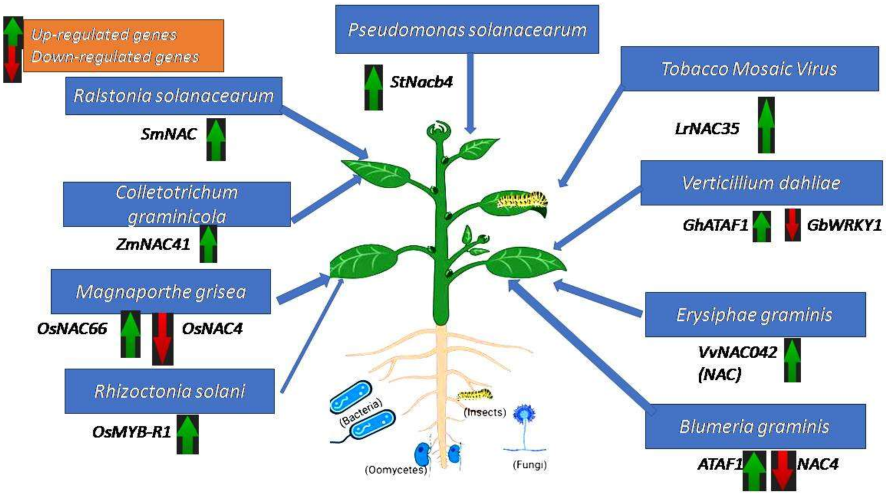

Figure 2. Plant gene expression during biotic stress.

5. Conclusion

In conclusion, plant gene regulation enables the identification of genes and the elucidation of molecular mechanisms related to physiological events, signal transduction, primary and secondary metabolism, defense mechanisms, stress response, and other genetic and physiological factors. Differential expression analysis provides an effective and efficient method for studying biological cellular pathways to examine and catalog plant model organisms' natural regulatory components. The significant impact of gene-regulating principles and design can address fundamental research issues and several plant science developmental goals, such as genetic improvement strategies, plant protein synthesis, and biosensor design. This review briefly summarizes our understanding of the gene regulators and their functions in plant cellular function, physiology, and pathology. However, many crucial issues still need to be addressed in this aspect. For instance, more research is needed to find out the biological functions of several stress-regulated genes, which provide a link in the progression of agricultural productivity. Furthermore, the molecular pathways of genes associated with the transport mechanism remain a mystery. We must still learn how genes work with other transporter factors or regulating networks to control homeostatic levels. Therefore, we can find a direct link between transporters and gene factors through different omics approaches, which have yet to confirm how these transporters affect the associated target genes or proteins. The researchers need to explore the various strategies of plant promoter editing to study gene functional diversity and evolve new genetic resources with unique traits based on the same loci through fine regulation of gene expression.

Conflict of interest

The authors declare that there is no conflict of interest.

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