Long non-coding RNAs: emerging players regulating plant abiotic stress response and adaptation

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Abstract

Background: The immobile nature of plants means that they can be frequently confronted by various biotic and abiotic stresses during their lifecycle. Among the various abiotic stresses, water stress, temperature extremities, salinity, and heavy metal toxicity are the major abiotic stresses challenging overall plant growth. Plants have evolved complex molecular mechanisms to adapt under the given abiotic stresses. Long non-coding RNAs (lncRNAs)—a diverse class of RNAs that contain > 200 nucleotides(nt)—play an essential role in plant adaptation to various abiotic stresses.

Results: LncRNAs play a significant role as ‘biological regulators’ for various developmental processes and biotic and abiotic stress responses in animals and plants at the transcription, post-transcription, and epigenetic level, targeting various stress-responsive mRNAs, regulatory gene(s) encoding transcription factors, and numerous microRNAs (miRNAs) that regulate the expression of different genes. However, the mechanistic role of lncRNAs at the molecular level, and possible target gene(s) contributing to plant abiotic stress response and adaptation, remain largely unknown. Here, we review various types of lncRNAs found in different plant species, with a focus on understanding the complex molecular mechanisms that contribute to abiotic stress tolerance in plants. We start by discussing the biogenesis, type and function, phylogenetic relationships, and sequence conservation of lncRNAs. Next, we review the role of lncRNAs controlling various abiotic stresses, including drought, heat, cold, heavy metal toxicity, and nutrient deficiency, with relevant examples from various plant species. Lastly, we briefly discuss the various lncRNA databases and the role of bioinformatics for predicting the structural and functional annotation of novel lncRNAs.

Conclusions: Understanding the intricate molecular mechanisms of stress-responsive lncRNAs is in its infancy. The availability of a comprehensive atlas of lncRNAs across whole genomes in crop plants, coupled with a comprehensive understanding of the complex molecular mechanisms that regulate various abiotic stress responses, will enable us to use lncRNAs as potential biomarkers for tailoring abiotic stress-tolerant plants in the future.

Keywords: Abiotic stresses, Long non-coding RNAs, Gene regulation, Target mimicry
Background

The immobile nature of plants means that they can be frequently confronted by various biotic and abiotic stresses during their lifecycle. Plants have evolved several complex mechanisms to recognize various stress factors, generate appropriate signaling pathways, and respond accordingly by reprogramming the expression of multiple genes at the transcriptional, post-transcriptional, and epigenome level to adapt under harsh environment conditions [1, 2]. The research community has successfully identified several complex mechanisms that plants use at the genetic, physiological, biochemical, and molecular levels to maintain ‘cellular homeostasis’ under unfavorable environments [2, 3]. The discovery of miRNAs (21–24 nt)—a novel class of non-coding RNAs (ncRNAs)—and their regulatory mechanisms for controlling genes involved in various developmental, biological, and stress responses has advanced our understanding of gene regulation in plants [4, 5]. The technical innovations of genome sequencing, especially next-generation sequencing, RNA-sequencing (RNA-seq), and advanced bioinformatics tools, have improved the functional elucidation of various genes at the transcription, post-transcription, post-translation, and epigenetic level [6]. These innovations have enabled the discovery of novel ncRNAs, including lncRNAs, and their role in regulating various biological processes, development, and stress responses in mammals and plants (for details, see [7, 8]). LncRNAs are a diverse class of RNAs, and the largest class acting as ‘biological regulators’ that control transcriptional regulation and genome imprinting [9, 10]. Numerous noteworthy instances of lncRNAs regulating plant development, disease resistance, nutrient acquisition, and other biological processes through chromatin remodeling, histone modification, pri-mRNA alternative splicing, or acting as ‘target mimics’ have been recorded [11–15]. However, few studies have undertaken genome-wide exploration of lncRNAs, their complex regulatory molecular mechanisms, or functional annotation [16]. Here, we explain the types and functions of IncRNAs and update the roles of various lncRNAs, their target gene(s), and the complex operational molecular mechanisms involved in acclimating plants to the challenging environments of various abiotic stresses.

Biogenesis, type, and functions of IncRNAs

Among the various classes of ncRNAs, IncRNAs are a heterogeneous class of RNA transcripts > 200 nt that are incapable of coding proteins, act as ‘riboregulators,’ are located in the nucleus or cytoplasm, and are transcribed by RNA polymerase II or III and polymerase IV/V [17–19]. Pol IV lncRNAs serve as precursors for small interfering RNAs (siRNAs) [19]. Pol V-dependent IncRNAs assist in modulating the local chromatin loop [20], are transcribed from either strand of the protein-coding locus, may or may not have 5’ cap and poly-adenylation at 3’ tail, and are expressed in a ‘tissue-specific’ manner [21–23]. IncRNAs can be broadly classified as (i) long intergenic ncRNAs (lncRNAs), (ii) intronic ncRNAs (incRNAs), (iii) natural antisense transcripts (NATs), and (iv) circular long non-coding RNAs (circRNAs) based on their location and neighboring protein-coding genes [22, 24–26]. LncRNAs originate from intergenic regions, featuring weakly spliced, polyadenylated tissue-specific expression, and execute trans (distant gene) regulatory function [27–29], while IncRNAs are transcribed from intronic regions. NATs originate from complementary DNA strands of sense coding regions [26] and feature cis- and trans-regulatory action [30]. However, circRNAs are in low abundance, originate from the ‘back-splicing reaction of internal exons in pre-mRNA’ [29, 31], feature a covalently closed structure, and display higher sequence conservation than linear IncRNAs [29, 32]. Various types of IncRNAs and their possible biogenesis are illustrated in Figs. 1 and 2. They act functionally as ‘decoy’ or ‘sponge molecules,’ ‘signal molecules,’ ‘backbone molecules,’ and ‘guide molecules’ [25, 34, 35]. Moreover, IncRNAs can be precursors of miRNAs and siRNAs, regulate alternative splicing of pre-mRNAs, and serve as endogenous target mimics (eTM) competing for various miRNAs [20, 36, 37].

Sequence conservation, diversity and phylogenetic features of plant IncRNAs

The highly evolved nature of IncRNAs has resulted in lower sequence conservation across plant and animal species and, thus, fewer phylogenetic relationships [38, 39]. Marques and Ponting [40] reported that <2% of IncRNAs in Arabidopsis thaliana were evolutionarily conserved across the plant kingdom, which explains the rapid evolution of IncRNA sequences. Conservation analysis of IncRNAs from five monocot and five dicot species demonstrated high sequence conservation at the intra-species and sub-species level [41]. At the interspecific level, IncRNAs remain highly diverged at the nucleotide level and have shown a diverse regulatory role [41, 42]. Mohammadin et al. [43] also supported positional sequence conservation of IncRNAs in Aethionema arabicum and Tarenaya hassleriiana at the nucleotide level using a phylogenomics approach. Likewise, Golicz et al. [44] confirmed the sequence homology of four IncRNAs in soybean, chickpea, and Medicago truncatula. Despite sequence dissimilarity, IncRNAs were similar in terms of their low expression capability, short length, and fewer exons and splice variants across numerous plant species, including Arabidopsis, cucumber, maize, chickpea, and soybean [43–47]. Likewise, the conserved
function of lncRNAs in both animal and plant species has been investigated [38]. The growing database of lncRNAs and comparative genomics analyses could provide new impetus into the functional conservation of lncRNA genes and their modes of action and function across various plant species [38].

**lncRNAs controlling drought stress tolerance**

Globally, episodes of drought stress-related events are increasing due to the erratic pattern of rainfall, which affects plant growth and poses a serious challenge for global food security [48]. Plants have a variety of physiological, biochemical, and complex molecular networks, including cascades of various signal transduction pathways, to adapt under drought stress [49]. Advances in molecular biology have uncovered the underlying gene(s)/QTLs and various complex regulatory gene networks and molecular signaling cascades controlling the drought stress response in plants [48, 50]. Subsequently, the discovery of drought-responsive miRNAs and their candidate target genes in various plants has shed light on the molecular mechanisms involved in drought stress adaptation (see [51]). Likewise, emerging evidence has revealed a participatory role of lncRNAs in response to drought stress in plants, capitalizing on the co-expression network based on lncRNAs, miRNAs and protein-coding genes, and transcription factors [52–54]. Notable instances of drought-responsive lncRNAs have been reported in various plant species—six in *Arabidopsis* [55], 504 in *Populus* spp. [56], 98 in rice [57], 664 in maize [58], 19 in foxtail millet [59], 185 in cassava [60], and 1597 in switchgrass [52]. LncRNAs could affect the
drought stress response by recruiting complex mechanisms based on eTM, antisense transcription-mediated modulation, chromatin modulation, or directly regulating the transcription of various drought-responsive genes [60–63]. Deep sequencing of foxtail millet provided an opportunity to explore 584 lncRNAs [59], of which 17 lincRNAs and two NAT lncRNAs exhibited differential expression under drought stress. Concurrently, the authors found 20 similar lincRNAs and one NAT lncRNA responding to drought stress in sorghum [59]. Only one drought-responsive lncRNA in foxtail millet exhibited sequence co-linearity with the drought-responsive lncRNA in sorghum, demonstrating the low conserved nature of lncRNAs [59]. In Populus trichocarpa, a systematic RNA-seq analysis explored a comprehensive landscape of >2500 lncRNAs [56], of which 504 were drought-responsive. Functional validation of eight drought-responsive lncRNAs from the 504 drought-responsive lncRNAs using RT-qPCR revealed the up-regulation of six lncRNAs and down-regulation of two lincRNAs under water stress. To survey drought-responsive lncRNAs in the cassava genome, strand-specific RNA-seq data served to identify a set of 318 lncRNAs and 153 NAT lncRNAs responding to cold and drought stress [60]. Of the 51 drought-specific differentially expressed lncRNAs (DElncRNAs), 40 showed up-regulatory action under drought stress. Functional validation of selected lncRNAs using qRT-PCR revealed the up-regulation of lincRNA101, lincRNA391, and lincRNA356 and down-regulation of lincRNA64, lincRNA350, lincRNA182, and lincRNA392 under drought stress. Furthermore, relying on the target mimic mechanism increased the expression of lincRNA340 under drought, which reduced the activity of target miR169 and ultimately increased NUCLEAR FACTOR Y (NF-Y) gene expression [60] see Fig. 3. Ding et al. [53] recovered 124 DElncRNAs under drought stress in cassava, of which 11 worked as target mimics for miR156, miR164, miR169, and miR172. Functional validation revealed that TCONS_00068353 lncRNA acted as a target mimic for miR156k and miR172c that control various abiotic stress-responsive genes, while TCONS_00060863 and TCONS_00097416 lncRNAs participated in the ABA and ethylene signaling pathways, respectively, under drought stress [53].

Considering the regulatory mechanism of NAT lncRNA, 98 drought-responsive lncRNAs were recovered in rice using RNA-seq analysis, along with two important drought-responsive lncRNAs NAT Os02g0250700–01 (targeting late embryogenesis abundant protein gene) and NAT Os02g0180800–01 (targeting cinnamoyl-CoA reductase gene) [57]. The expression of these two lncRNAs and their corresponding target genes remained inversely correlated. A study on genome-wide drought-responsive lncRNAs in maize identified 1535 lncRNAs at various developmental stages [54]. The lncRNAs captured at the R1 stage (siliation stage) had a critical role in drought stress tolerance. Furthermore, the V-ATPase encoding gene (vpp4) was unearthed as a possible target gene for lncRNA MSTRG.6838.1; vpp4 and the identified lncRNA may work as cis-acting pairs.

Apart from acting as eTM or NAT, lncRNAs could regulate the transcription of various drought-stress-responsive genes [52, 62]. The possible role of lncRNAs in regulating drought stress tolerance has been explored in Arabidopsis, with the identification of a novel lncRNA DROUGHT INDUCED lncRNA (DRIR) localized in the nucleus, containing a 755 nt long lincRNA that controls several drought-stress-responsive genes, including ABA-signaling genes (ABI5, P5CS1, RD29A, and RD29B), aquaporin genes (NIP1, TIP4), annexin gene (ANNAT7), FUCOSYL TRANSFERASE4 (FUT4) gene, and transcription factor genes (NAC3, WARKY8) at the transcription level [37]. The drirP(T-DNA insertion mutant) and DRIR-overexpressing Arabidopsis lines had higher drought tolerance than wild-type seedlings, as revealed in the higher-fold expression of these genes. Thus, the lncRNA DRIR conferred water-deficit stress tolerance by serving as a positive regulator.

Likewise, lncRNAs regulating various drought-stress-regulatory genes participating in ethylene and ABA synthesis and signaling, calcium signaling, starch and sucrose synthesis, and various metabolic processes have been reported in rice [63], switchgrass (Panicum virgatum L.) [52], P. betulifolia [70], cassava [53, 71], and Cleistogenes songorica [62] (see Table 1). Of the 441 DElncRNAs identified in switchgrass under drought stress imposed at various growth stages, lncRNAs XLOC_053020, XLOC_014465, and XLOC_033252 controlling ABA synthesis, XLOC_074836 contributing to ethylene signaling, and XLOC_005809 involved in trehalose phosphate synthase metabolism were up-regulated, suggesting their significant role in drought-stress tolerance [52]. Various lncRNAs and their possible target gene(s) and working mechanisms contributing to drought stress and other abiotic stress responses in various crops have been identified (see Table 2). Collectively, the various lncRNAs play a role in controlling drought stress by acting as target mimics for various miRNAs that control the expression of various drought-responsive target genes or transcription factors through up- or down-regulation. These emerging lncRNAs could act as a regulatory hub for controlling various drought-responsive hormonal signaling pathways at the transcription, post-transcription, and epigenome level.
IncRNAs controlling heat stress tolerance

Heat stress is a major abiotic stress that significantly affects plant growth, physiology, metabolic activity, development, and yield performance [2]. With the current rise in global temperatures, changes in plant phenology and adaptation processes are negatively affecting crop yield, which is challenging global food security [107]. Plants recruit a variety of mechanisms, including adaptive, biochemical, and molecular, to cope with heat stress [2, 108]. Plants produce different phytohormones, heat shock proteins (HSPs)/chaperones, antioxidant enzymes, and metabolites that play a critical role in adjusting to heat stress [108, 109]. At the molecular level, the activation of regulatory pathways plays a role in plant adaptation to heat stress [2]. There is evidence for miRNAs regulating the heat stress response in various plants [110]. The accumulating evidence for IncRNAs acting as an important molecular regulatory layer offers insight into the regulatory mechanism of the heat stress response in crop plants. To explore the role of IncRNAs in conferring a heat stress response, 54 putative heat stress-responsive IncRNAs were identified in wheat using the wheat Affymetrix Gene Chip-based microarray and Solexa sequencing [75]. Among the identified IncRNA transcripts, four and 26 were precursors of miRNAs (viz., miR2004, Ta-miR2010, miR2066) and siRNAs, respectively. Up-regulation of IncRNAs TahlnRNA27 and TahlnRNA5 and their corresponding miR2010 and miR2004 was confirmed by qRT-PCR analysis, indicating their significant role in the heat stress response in wheat. However, the heat stress response remained tissue-specific/dependent with TahlnRNA5 displaying relatively...
| Name of stress | Crop | No. of lncRNAs identified | Number of lncRNAs expressed under stress | Platform and technique used for lncRNAs identification and their function | Function | Reference |
|----------------|------|--------------------------|------------------------------------------|---------------------------------------------------------------------|---------|----------|
| Drought        | Foxtail millet | 19 lncRNAs | 19 | Illumina HiSeq 2000, qRT-PCR | Control drought stress response | [59]  |
| Drought        | Populus trichocarpa | 2542 lincRNAs | 504 | HiSeq™ 2000, RT-qPCR | Drought- stress response | [56]  |
| Drought        | Rice | 98 lncRNAs | 98 | Illumina HiSeq 2500, qRT-PCR | Regulatory role in drought response | [57]  |
| Drought        | Arabidopsis | DROUGHT INDUCED lncRNA (DRL) | DROUGHT INDUCED lncRNA (DRL) | HiSeq 2000, RT-qPCR | Participate in regulating set of drought responsive genes | [37]  |
| Drought        | Rice | 3714 | 21 | RT-qPCR, P LncPRO | Differentially expressed under drought stress | [72]  |
| Drought        | Wheat | – | 59,110 | Illumina HiSeq 2000, qRT-PCR | Differential expression under drought stress response | [73]  |
| Drought and cold | Cassava | 682 lncRNAs | 318 | HiSeq 2500,qRT-PCR, CNCI, CPC | Hormone signal transduction, sucrose metabolism pathway etc. | [60]  |
| Drought        | Pyrus betulifolia | 14,478 | 251 | Illumina HiSeq 4000, CNCI, CPC, qRT-PCR | Various metabolic processes | [70]  |
| Drought        | Panicum virgatum L | 16,551 novel lncRNAs | 1597 | HiSeq2500, qRT-PCR | Regulating drought-stress response | [52]  |
| Drought        | Maize | 3488 | 1535 | Illumina HiSeq 2500, qRT-PCR | Oxidoreductase activity, water binding, and electron carrier activity | [54]  |
| Drought        | Cleistogenes songonica | 3397 lncRNAs | 468 | HiSeq2500, CPC, CNCI, CPATqRT-PCR | Regulating drought-stress response | [62]  |
| Drought        | Cassava | 833 | 124 | Hiseq 4000, qRT-PCR, CNCI, CPC | Cell-related metabolism, Calvin cycle, hormone metabolism etc. | [53]  |
| Drought        | Cassava | 1405 | 185 | qRT-PCR | Melatonin responsive controlling drought-stress response | [74]  |
| Drought        | Cassava | 1379 | 194 | qRT-PCR | ABA signaling regulation | [71]  |
| Heat stress    | Wheat | 12S putative | 77 | Solexa sequencing technology wheat Affymetrix GeneChip, qRT-PCR | Heat responsive | [75]  |
| Heat stress    | Brassica rapa ssp. chinensis | 4594 putative lncRNAs | 1686 | Illumina HiSeq 2500, qRT-PCR CPC,CNCI | Differential expression of these RNA suggested involvement of various phytohormones in heat stress tolerance. | [64]  |
| Heat stress    | Brassica juncea | 7613 putative lncRNAs | 1614 | qRT-PCR | Associated with enzymatic and non-enzymatic antioxidants under drought and heat stress | [76]  |
| Cold and heat  | Chinease cabbage | 10,001 | 2236 | Illumina HiSeq™ 2000 qRT-PCR, CPC | Total of 67 and 192 target genes for cold and heat were regulated | [77]  |
| Cold stress    | Banana | 12,462 lncRNAs | 20 | Illumina HiSeqTM 4000, qPCR, CPC | Cold stress response | [78]  |
| Cold stress    | Arabidopsis | 379 | 135 | Illumina HiSeq 2500, RT-qPCR | Cold or freezing acclimation | [79]  |
| Cold stress    | Arabidopsis | SVALKA | SVALKA | Repress CBF1 expression and freezing tolerance | Related to cold stress response | [80]  |
| Cold stress    | Grapevine | 2088 | 466 | HiSeq 2500, qRT-PCR, CNCI, CPC | Related to cold stress response | [81]  |
| Cold stress    | Chinese cabbage | 2088 | 549 | Illumina HiSeqTM 2000, qPCR | Controlling vernalization | [82]  |
| Name of stress | Crop                  | No. of lncRNAs identified | Number of lncRNAs expressed under stress | Platform and technique used for lncRNAs identification and their function | Function                                                                 | Reference |
|----------------|-----------------------|---------------------------|------------------------------------------|---------------------------------------------------------------------------|--------------------------------------------------------------------------|-----------|
| Cold stress    | Rice                  | 1485 lncRNAs             | 566                                      | Illumina HiSeq 2500 platform, qRT-PCR                                     | Controlling cold stress response                                        | [83]      |
| Cold stress    | *Medicago truncatula* | 24,368 unique lncRNAs    | 983 and 1288                             | Illumina HiSeq 4000,Q-PCR                                                 | Controlling cold stress response                                        | [84]      |
| Salinity       | *Arabidopsis*         | DROUGHT INDUCED lncRNA (DRIR) | DROUGHT INDUCED lncRNA (DRIR)          | HiSeq 2000, RT-qPCR                                                       | Participate in regulating set of salinity responsive genes              | [37]      |
| Salinity       | Chickpea              | 3457                      | 13                                       | RT-qPCR, PLncPRO                                                         | Differentially expressed under drought and salinity stress              | [72]      |
| Salinity       | Barley                | CNT0018772 and CNT0031477 | 2                                        | qPCR                                                                      | Both up- and down- regulatory role in salinity stress                    | [85]      |
| Salinity       | Cotton                | 1117 unique lncRNAs      | 44                                       | Illumina HiSeq 4000, RT-qPCR                                             | Controls salinity stress genes                                          | [86]      |
| Salinity and boron | Maize                | 48,345                   | 1710                                     | Illumina MiSeq, RT-qPCR, AgriGO                                          | Nicotianamine biosynthetic and metabolic processes, gene regulation    | [87]      |
| Salinity       | Poplar                | 10,646 and 10,531 lncRNAs | 8592 and 3425                           | HiSeq 2500                                                               | Regulating osmotin 34, NHX7, RARE-COLD-INDUCIBLE 2B, and WRKY 33 genes | [73]      |
| Cadmium stress | Rice                  | 3558                      | 69 lncRNAs were up-regulated and 75 lncRNAs were down-regulated | Illumina HiSeq 2000,CPC, RT-qPCR                                         | Genes related to photosynthetic pathways are involved in response to Cd stress | [88]      |
| and salinity   | Wheat                 | 44,698                    | 2064 and 2278                           |                                                                            | Regulatory roles in numerous biological processes                       | [89]      |
| Ca\(^{2+}\)-channel blocker | Wheat            | 6309                      | 177                                      | HiSeqTM2000, qRT-PCR                                                     | Affects various biological processes                                    | [90]      |
| Oxidative stress | Rice                  | 7000 lncRNAs             |                                          | Hiseq2000, DEGSeq                                                        | Down-regulated poly adenylation lncRNAs participate in abiotic stress tolerance | [91]      |
| Waterlogging   | Maize                 | 6099                      | 3190                                     | Illumina HisSeq 4000, qRT-PCR                                           | Metabolic pathways, such as glycolysis and methionine metabolism in response to water logging | [92]      |
| Phosphate starvation | *Arabidopsis*    | 1212 novel lncRNAs       | 309                                      | Illumina HiSeq 2000/2500, qRT-PCR                                       | Phosphate starvation signaling and regulation                            | [93]      |
| Phosphate deficiency | *Medicago truncatula* | 10, 785                  | 358 and 224                             | Illumina HiSeq2000, qRT-PCR, PCRC,CNCI                                  | Cell wall organization and photosynthesis                                | [61]      |
| Phosphorus use efficiency | barley             | 188 and 209              | –                                        | Illumina sequencing, qRT-PCR                                             | Related to phosphate starvation                                         | [94]      |
| Nitrogen deficiency | Poplar              | 388                       | 126                                      |                                                                            | Low nutrition adaptation                                                 | [95]      |
| Nitrogen deficiency | Maize               | 7245                      | 637                                      |                                                                            | Nitrogen metabolism, oxidative phosphorylation                           | [96]      |
| Nitrogen deficiency | Rice                 | 2588 novel putative lncRNA | 2588                                     |                                                                            | Regulatory role in N-starvation-response                                 | [14]      |
| Nitrogen deficiency | Barley               | 498 lncRNAs              | 56                                       |                                                                            | Regulatory role in N-starvation-response                                 | [97]      |
higher expression in seed tissue than other tissues [75]. Most lncRNAs are weak in sequence conservation; their expression varies from tissue to tissue, developmental stages, and even species to species [65]. Tissue/development-specific expression of lncRNAs has been reported in maize [54, 87] and cassava [53] under drought stress, and species-specific expression was noted for Populus euphratica and Populus alba var. pyramidalis under salinity stress.

A plethora of differentially expressed lncRNAs and their corresponding protein-coding heat stress-responsive target genes and miRNAs have been identified in various crops [64, 77]. Wang et al. [64] explored the up- and down-regulation of lncRNAs and differentially expressed genes (DEGs) involved in the brassinosteroid, ABA, auxin, jasmonic acid, salicylic acid, and ethylene hormone signaling pathways, and DEGs encoding various heat shock proteins across the whole genome, using strand-specific RNA-seq in Brassica rapa under heat stress. Among the three identified heat-responsive DElncRNAs, differential expression of lncRNA TCONS_00004594 downstream at the protein-coding gene Bra021232 via qRT-PCR suggested its cis-regulatory expression [64]. Further, lncRNAs TCONS_00048391 and TCONS_00010856 acted as endogenous target mimics for bra-miR164a, which regulates the heat stress response. Consequently, under heat stress, up-regulation of bra-miR164a and down-regulation of lncRNA TCONS_00048391 and the target Bra030820 (NAC1) gene rendered heat tolerance in ‘XK’ variety ([64], see Fig. 3). Likewise, the binding of lincRNA159 with conserved miR164 decreased the expression of three miR164-targeted NAC genes (NAM, ATAF1/2, CLIC2) in cassava under cold stress [60]. Similarly, drought-responsive lncRNA MSTRG.42613.1 was identified as the target mimic of conserved miRNA164 regulating drought stress in C. songorica [62]. In the future, manipulation of the overexpression or knockout of lncRNAs targeting genes controlling the heat stress response could help us to engineer heat-tolerant crop plants.

### LncRNAs controlling cold stress tolerance

Low-temperature stress is an important abiotic stress that challenges plant growth and yield [2, 111]. Plants orchestrate several complex regulatory gene networks of C-repeat binding factors (CBFs) and cold regulated genes (COR) [112] and myriad of novel regulatory miRNAs [110] that enable them to acclimate to cold stress. Advances in genetic and genomic approaches have elucidated several QTLs and probable candidate genes contributing to cold tolerance in plants [111]. Likewise, there is emerging evidence of lncRNAs that regulate the cold stress response in plants [65, 80, 103]. The emerging role of lncRNAs regulating cold acclimation is documented in Arabidopsis [65, 82], cassava [60], Brassica rapa [15, 82], banana, grapevine [81], and Brachypodium [104].

Vernalization is a well-established phenomenon in plant species adapted to cold climates, which prevents flowering during vegetative growth in winter and allows flowering during the reproductive phase under favorable conditions in spring [113]. In Arabidopsis, FLOWERING LOCUS C (FLC) is a well-known regulatory locus that controls flowering time epigenetically [114]. FLC also acts as a suppressor of flowering during cold in Arabidopsis [115]. In this context, the participatory role of lncRNAs in inhibiting expression of the FLC locus by vernalization under cold stress through Polycomb-mediated epigenetic regulation is a well-established mechanism.

### Table 1 Various types of lncRNAs that control abiotic stress responses in plants (Continued)

| Name of stress       | Crop                  | No. of lncRNAs identified | Number of lncRNAs expressed under stress | Platform and technique used for lncRNAs identification and their function | Function                                      | Reference |
|----------------------|-----------------------|---------------------------|------------------------------------------|--------------------------------------------------------------------------|-----------------------------------------------|-----------|
| Boron deficiency     | Poncirus trifoliata   | 2101 unique lncRNAs       | 60 differentially expressed lincRNAs     | qPCR, Illumina HiSeq X Ten platform                                      | Regulatory role in Boron-starvation response | [98]      |
| Low nutrient deficiency | Arabidopsis          | 60 differentially expressed lincRNAs | 60 differentially expressed lincRNAs | HiSeq2000TM, qRT-PCR                                                    | Controlling various nutrient response          | [99]      |

CPC=Coding Potential Calculator  
CNCI=Coding-Non-Coding Index  
CPAT = Coding Potential Assessment Tool
| Stress   | Crop       | Genotype     | LncRNA                        | Target gene                        | Regulatory mechanism                                                                 | Reference |
|---------|------------|--------------|-------------------------------|------------------------------------|--------------------------------------------------------------------------------------|-----------|
| Drought | Populus    | Nisqually    | lincRNA20 and lincRNA2752     | –                                  | Control drought stress by regulating lincRNA2962 and lincRNA1039                    | [56]      |
|         |            | trichocarpa  | lincRNA2962 and lincRNA1039   |                                    | ptc-miR476 and ptc-miR169 through eTM                                                |           |
|         |            |              | LincRNA3241                   |                                    |                                                                                     |           |
| Drought | Rice       | Oryza sativa | NAT Os02g0250600–01           | Os02g0250600–01                    | Regulate drought by NAT lncRNAs                                                     | [57]      |
|         | cv. Ilmi   |              | NAT Os02g0180800–01           | (late embryogenesis abundant protein) |                                                                                     |           |
|         |            |              | Os02g0180700–01               | (cinnamyl-CoA reductase)           |                                                                                     |           |
|         | DXWR       |              | Up-regulated lncRNAs MSTRG69391 | Transcription factor, calmodulin | Regulate biological processes in response to drought stress | [63]      |
|         |            |              | MSTRG41712 and MSTRG68635 and | HSP genes, mitochondrial carrier   |                                                                                     |           |
|         |            |              | down regulated lncRNAs       | protein gene etc                   |                                                                                     |           |
|         |            |              | MSTRG27834 and MSTRG68301    |                                    |                                                                                     |           |
| Drought | Cassava    | TMS60444     | lincRNA340                    | NUCLEAR FACTOR Y (NF-Y)            | By targeting miR169 based on target mimicry                                         | [60]      |
| Drought | Wheat      | Kiziltan     | c70772_g2_i1 and c90557_g1_i1 | c69036_g1_i1 and                    | Drought stress is regulated by lncRNA-miRNA-mRNA networks                          | [73]      |
|         |            | TR39477      |                               |                                    |                                                                                     |           |
|         |            | TTD-22       |                               |                                    |                                                                                     |           |
| Drought | Panicum    | Alamo        | XLOC_053020                   | Pavir.Ia01153                      | Regulation of genes related to ethylene synthesis, ABA synthesis and signaling,      | [52]      |
|         | virgatum L |              | XLOC_014465                   | Pavir.Bb00347                      | starch and sucrose biosynthesis gene                                               |           |
|         |            |              | XLOC_033252                   | Pavir.Eb01847                      |                                                                                     |           |
|         |            |              | XLOC_090250, XLOC_016922,    | Pavir.J23169 and                   |                                                                                     |           |
|         |            |              | and XLOC_06766                |                                    |                                                                                     |           |
|         |            |              | XLOC_074836                   | Pavir.J04626                       |                                                                                     |           |
|         |            |              | XLOC_008122                   | Pavir.J05665                       |                                                                                     |           |
|         |            |              | XLOC_081155                   | Pavir.Ba00729                      |                                                                                     |           |
|         |            |              | XLOC_005809                   | Pavir.Ab03141                      |                                                                                     |           |
| Drought | Cassava    | Ku50         | TCONS_00060863, TCONS_0006833 | CYP707A1                           | Genes involved in ABA catabolism, ethylene signaling.                               | [53]      |
|         |            |              | TCONS_00097416, TCONS_00069666 |                                   | Also regulates gene by targeting miR156, miR164, miR169, and miR172                |           |
|         |            |              | CSLDS, ERL1, SPCa,            |                                   |                                                                                     |           |
|         |            |              | LAX2, HDG11, SCR              |                                   |                                                                                     |           |
|         |            |              | GRF1 and HB51, DOX1           |                                   |                                                                                     |           |
|         | Cleistogenes|              | MSTRG.43964.1                 | Genes related to                   | By regulating miRNA166, miRNA164, miRNA393, and miRNA397a/b and acting as endogenous | [62]      |
|         | songorica  |              | MSTRG.4400.2                  | abscisic acid (ABA)                | target mimics                                                                      |           |
## Table 2 Function of various lncRNAs regulating various abiotic stress in plants (Continued)

| Stress  | Crop            | Genotype | LncRNA | Target gene | Regulatory mechanism | Reference |
|---------|-----------------|----------|--------|-------------|----------------------|-----------|
| Drought | Maize           | B73      | IncRNA | V-ATPase    | IncRNA regulating transcriptional regulation by cis- and trans-acting modes | [54]      |
|         |                 |          | MSTRG.42613.1 | Genes related to starch and sucrose metabolism |                       |           |
|         |                 |          | MSTRG.25585.13 |                                                  |                       |           |
| Drought | Cassava         |          | TCONS_00129136, TCONS_00122745 | Vpp4 | Calcium signaling, ABA and ethylene metabolism | [71]      |
|         |                 |          | TCONS_00988201,TCONS_00067612 |                                                  |                       |           |
| Drought | Cassava         |          | TCONS_00003360, TCONS_00015102 | BnaC06g05090D | IAA, Cytokinin and ABA signalling | [74]      |
|         |                 |          | TCONS_00149093 | BnaA01g17750D | alpha-trehalose-phosphate synthase | [100]     |
|         |                 |          | TCONS_00149029 | BnaC07g44670D |                                                  |           |
|         |                 |          | TCONS_00003350, TCONS_00015102 | BnaC02g25020D, BnaC02g25150D |                                                  |           |
|         |                 |          | XLOC_042431, XLOC_071559 | BnaC06g05090D |                                                  |           |
|         |                 |          | XLOC_095305, XLOC_108682, XLOC_019521 and XLOC_042894 | BnaC07g44670D |                                                  |           |
|         |                 |          | XLOC_075476 and XLOC_074677, XLOC_074677, XLOC_093758 | BnaC02g25020D, BnaC02g25150D, BnaC02g25200D |                                                  |           |
|         |                 |          | XLOC_044363 and XLOC_076449 | BnaC02g25200D |                                                  |           |
|         |                 |          | XLOC_052298 | BnaC06g05090D |                                                  |           |
| Heat    | Wheat           | TAM107   | TahlnRNA27, TahlnRNAs, TahlnRNA12, TahlnRNA21 | – | Histone acetylation of TahlnRNAs | [75]      |
|         |                 |          | TahlnRNA23 and TahlnRNA29 | – |                                                  |           |
| Heat    | Chinese cabbage | GHA and XK | TCONS_00048391, TCONS_00010856, TCONS_00004594 | VAC1 (Bra030820) | By targeting bra-miR164a based on target mimicry mechanism | [64]      |
|         |                 |          | TCONS_00004594 | Bra021232 | target mimicry mechanism |           |
| Heat    | Cucumis sativus | Improved Jinchun 2 | TCONS_00031790, TCONS_00014332, TCONS_00014717, TCONS_00005674 | – | Interact with miR9748 plant hormone signal transduction pathways | [101]     |
| Heat    | Brassica juncea | TCONS_00051908 | – | By acting as targets and eTMs for the miRNAs | [76]      |
| Cold    | Cassava         | TMS60444 | lincRNA159 | NAM, ATAF1/2, CUC2 | Regulate cold tolerance targeting miRNA164 based on target mimicry mechanism | [60]      |
| Cold    | Arabidopsis     | Col-0    | SVLAKA   | CBF1 | SVK represses CBF1 and increase cold acclimation | [80]      |
| Cold    | Arabidopsis     | Col-0    | COLDWRAP | FLC | COLDWRAP reinforces stable repression of FLC under cold stress | [102]     |
| Stress | Crop            | Genotype       | LncRNA/Target gene          | Regulatory mechanism                                | Reference |
|--------|----------------|----------------|----------------------------|-----------------------------------------------------|-----------|
| Cold   | Arabidopsis    | Col-0          | TAS1a                      | By alternative splicing of lncRNA                    | [79]      |
| Cold   | Arabidopsis    | Col-0          | MAS                        | Histone modification and role of NAT-IncRNAs         | [103]     |
|         |                |                | MAF4 gene                  | regulating gene expression                          |           |
| Cold   | Brachypodium   | –              | BdCOOLAIR1, BdCOOLAIR2     | BdCOOLAIR transcript represses                      | [104]     |
| Cold   | Grapevine      | Cabernet Sauvignon | VIT_203s0017n00360        | Upregulation of the following target genes           | [81]      |
|         |                |                | VIT_207s0031n00070         |                                                     |           |
|         |                |                | VIT_201s0011n00530         |                                                     |           |
|         |                |                | VIT_209s0002n00340         |                                                     |           |
|         |                |                | VIT_213s0158n00020         |                                                     |           |
|         |                |                | VIT_213s0067n00110         |                                                     |           |
|         |                |                | VIT_200s0225n00020         |                                                     |           |
| Cold   | Chinese cabbage| RJKB-T24        | MSTRG.4795, MSTRG.18513, MSTRG21908, MtCBF genes | Epigenetic modification at BrFLC2as locus, epigenetic modification at Bra024350 and Bra031888, Bra024351 and Bra031884 loci | [82] |
| Salinity | Medicago truncatula | Jemalong A17 | IncRNA MtCOR1, Medr6g006990 | By regulating various genes | [68] |
| Salinity | Medicago truncatula | Jemalong A17 | TCONS_00046739, cytochrome P450 genes | related to ROS activity, secondary messenger molecules, |           |
|         |                |                | TCONS_00100258             |                                                     |           |
|         |                |                | TCONS_00116877             |                                                     |           |
|         |                |                | TCONS_00047650             |                                                     |           |
|         |                |                | Medr3g069280, Medr1g081900 and | carbonic anhydrase gene etc. |           |
| Salinity | Arabidopsis    | –              | DRIR                       | Affecting fucosyltransferase or NAC3 transcription factor | [37] |
| Salinity | Cotton         | SN91–11        | Inc_388, Inc_883, Gh_A09G1182, Gh_D03G0339 genes | Regulating ghr-miR399 and ghr-156e by eTM | [86] |
| Salinity | Poplar         | P. euphratica  | Pex_00167161, Pal_00184400, HKT1 | – |           |
|         |                | Pal_00132209, Pal_00132409 | Pal_00132209, Pal_00132409 | fucosyltransferase or NAC3 |           |
mechanism for controlling cold acclimation in *Arabidopsis* [65, 67, 116]. Repression of the FLC locus during the early onset of cold stress is controlled by **COLD INDUCED LONG ANTISENSE INTRAGENIC RNAs** (COOLAIR), an alternatively spliced NAT lncRNA transcribed from the antisense orientation of FLC gene by
chromatin modification (reducing active histone mark H3K36me3 and enhancing repressive histone mark H3K27me3) of the FLC locus during vernalization [65–67]. Interestingly, Castaings et al. [117] demonstrated the evolutionarily conserved role of class I antisense COOLAIR that controls FLC repression during vernalization in *Arabidopsis thaliana*, *Arabis lyrata*, and *Arabis alpina* species.

Likewise, COLD ASSISTED INTRONIC NONCODING RNA (COLDAIR) [116], transcribed from intron1 of the FLC gene, recruits the Polycomb Repressive Complex 2 (PRC2) that helps in chromatin modification (increase H3K27me3) of the FLC locus and thus represses expression of the FLC locus (see Fig. 3). Subsequently, Kim et al. suggested that “Polycomb-binding IncRNA, COLD-WRAP” could further cooperate in the stable repression of the FLC locus during vernalization in *Arabidopsis*.

Recently, Kindergren et al. [80] advanced our understanding of the cold acclimation mechanism in *Arabidopsis* by illustrating the novel role of SVALKA and cryptic antisense CBF1 (asCBF1) IncRNAs induced by cold stress. These IncRNAs regulate cold acclimation by suppressing transcription of the CBF1 gene by RNA polymerase II (RNAPII) collision derived from IncRNAs SVALKA and asCBF1. Likewise, to explore the role of IncRNAs controlling the cold stress response in *Arabidopsis*, strand-specific RNA-sequencing (ssRNA-seq) identified 4050 NAT IncRNAs and 2460 lincRNAs as cold-responsive IncRNAs [103]. Among these, the authors substantiated the novel role of MAS (NAT IncRNA_2962), a cis-acting NAT IncRNA induced under cold stress, which activated transcription of the corresponding cold-responsive MADS AFFECTING FLOWERING 4 (MAF4), an FLC family member, by involving WDR5a complex that deposits H3K4me3 at MAF4 gene for its activation. Thus, the activated gene eventually suppresses flowering under cold stress. Likewise, in *Brassica rapa*, three FLC paralogs that act as a floral repressor during vernalization have been reported [118, 119]. The involvement of NATs at the FLC2 locus of *Brassica rapa* under cold stress has been reported [120]. RNA-seq driven transcriptome analysis of control and cold-treated leaves of *Brassica rapa* identified 2088 IncRNAs [82], of which three BrFLC loci contributed to cold stress regulation—only BrFLC2, harboring NAT BrFLC2as (MSTRG.2765), had homology to the COOLAIR transcript of *Arabidopsis thaliana* and displayed up-regulation under cold stress [82]. Functionally, COOLAIR acts as “cis-NAT with respect to the AtFLC locus” [67]; however, the action of BrFLC2as as cis- or trans-acting mode needs further investigation. Likewise, considering the role of the MAF gene, the Bra024350 locus (homologous to AtMAF1)—with a NAT known as MSTRG.14523—was down-regulated under cold stress. However, the Bra024351 locus (homologous to AtMAF4)—with a NAT known as MSTRG.14524—was not down-regulated under cold stress in *Brassica rapa*, suggesting that the working mechanism of the IncRNAs mentioned above differed from the IncRNAs involved in vernalization in *Arabidopsis thaliana* [82]. Furthermore, among the plethora of differentially expressed lincRNAs, NAT IncRNAs identified IncRNAs MSTRG.4795, MSTRG.18513, and MSTRG21908 as up-regulated and MSTRG.259, MSTRG.491, and MSTRG.17153 as down-regulated under cold stress imposed at various stages in *Brassica rapa* [82].

A genome-wide survey for cold-responsive IncRNAs in grapevine using RNA-seq analysis recovered 284 novel up-regulated IncRNAs, 182 novel down-regulated IncRNAs, 242 DElncRNAs targeting 326 protein-coding genes, and various stress-response genes including CBF4 transcription factor genes, late embryogenesis abundant protein genes, and WRKY transcription factor genes [81]. Functional validation of selected IncRNAs through qRT-PCR confirmed up-regulation of IncRNAs VIT_200s0179n00030, VIT_207s0141n00070, and VIT_207s0005n0048 and down-regulation of VIT_201s0010n00070, VIT_208s0007n00270, and VIT_209s0002n00020, suggesting their important role in regulating cold stress tolerance in grapevine [81]. In casava, to unveil cold and drought-responsive IncRNAs genome-wide, 318 IncRNAs were captured [60]. Considering their contributory role in cold stress tolerance, functional validation of lncRNA419, 207, and 234 revealed their up-regulated activity under cold stress. To decipher the regulatory network of miRNAs, IncRNAs, and the stress-responsive gene controlling cold tolerance, lncRNA159 acting as target mimic for miR164 decreased the expression of NAC genes under cold stress [60]. Apart from these mechanisms, alternative splicing (AS) of IncRNAs and pri-miRNAs could participate in controlling the cold stress response in *Arabidopsis* [79]. Of the 135 IncRNAs identified with cold-dependent differential expression and differential alternative splicing, induction of TAS1a IncRNA regulated by AS under cold stress was uncovered in *Arabidopsis*. The unspliced intron-containing transcript AT2G27400.1 produced from TAS1a contained “miR173 binding site and tasiRNAs generation site” while the spliced transcript AT2G27400_1D1 remained intronless. Given the decrease in temperature, AT2G27400_1D1 transcript decreased rapidly in the first 6 h after cold treatment, whereas unspliced AT2G27400.1 increased in the first 3 h. Subsequently, it declined over the next 12 h [79]. Thus, AS of IncRNAs plays an important role in
regulating cold stress tolerance. LncRNAs could regulate cold tolerance through chromatin modulation/remodeling, AS mechanisms, and transcriptional regulation of genes contributing to cold tolerance. Further understanding of the working mechanism of IncRNAs controlling cold stress may provide opportunities for engineering cold-tolerant crops.

**IncRNAs as new players in plant acclimation under salinity stress**

The indiscriminate practice of excessively irrigating farmland and the rapid depletion of groundwater are major factors associated with the increase in salinity-related problems worldwide [121]. Globally, 45 Mha of irrigated land and 32 Mha of hardy land are challenged by salinity stress [122, 123]. Thus, soil salinization remains an increasing constraint to global food production. Under salinity stress, plants suffer from an excessive load of toxic ions, which reduces plant growth and development and grain yield [124].

Plants have evolved several cellular and physiological mechanisms to adapt to salinity stress (see [124]). At the molecular level, a plethora of ion transporter proteins encoded by gene(s)/QTLs and other regulatory genes play a crucial role in controlling salinity stress in various plants (see [121, 124]). Likewise, evidence of regulatory roles of IncRNAs enabling plants to tolerate salinity stress has advanced our understanding of the molecular mechanisms controlling the salinity stress response in plants [37, 55].

To elucidate the functional role of IncRNAs in *Medicago truncatula* under salinity stress and osmotic stress, several IncRNAs have been identified, including TCONS_00046739 (regulating cytochrome P450 in roots), TCONS_00097188 (regulating photosynthesis by up-regulating Medtr6g006990 gene), TCONS_00047650 (up-regulating expression of the Medtr3g069280 gene encoding phosphatidylinositol-specific phospholipase C), TCONS_00116877 (up-regulating the Medtr7g094600 gene encoding glutathione peroxidase in roots), and TCONS_00020253 (up-regulating expression of Na⁺/H⁺ exchanger gene Medtr1g081900 in roots) ([68], see Fig. 3). Likewise, the presence of IncRNA DRIR regulates higher expression of *PSC51*, *RD29A*, *RD29B*, *AtrbohB*, *FLU4*, *ANNAT7*, and *NAC3* genes that confer salinity stress tolerance in the *drir* mutant and *DRIR*-overexpressing lines in *Arabidopsis* [37]. In cotton, deep transcriptome sequencing of salt-treated leaf facilitated the identification of 44 differentially expressed lncRNAs from 1117 unique IncRNAs [86]. Functional validation of selected lncRNAs via RT-qPCR revealed the up-regulatory role of *Inc_388* on *cis-acting* target leucine-rich repeat 8 (*Gh_A09G1182*) gene and *Inc_883* lncRNA targeting on *Gh_D03G0339MS_channel protein-coding gene under salinity stress (Table 2). The authors also confirmed the role of IncRNAs *Inc_973* and *Inc_253* acting as target mimics for ghr-miR399 and ghr-156e under salinity stress [86]. Likewise, 1710 IncRNAs that were responsive to combined salinity and boron stress were explored in the Lluteño landrace of maize using deep transcriptome analysis of leaf and root tissue-derived RNA libraries [87]. Interestingly, a comparison of the genome sequences of three popular maize cultivars (B73, Mo17, and Palomera) and the Lluteño landrace identified the presence of 955 conserved lncRNA transcripts; however, 755 were exclusive to the Lluteño landrace, which may explain its salinity and boron stress tolerance [87]. To gain insight into the salinity and boron response of IncRNAs, functional validation of 12 trans-NAT IncRNAs from 848 differentially expressed trans-NAT IncRNAs suggested their significant role in controlling various stress regulatory gene expression, including combined salinity and boron stress and the nicotinamide metabolic process [87]. Thus, the identified IncRNAs conferred salinity stress tolerance by controlling oxidative stress through modulating genes encoding for antioxidant enzymes and regulating various Na⁺/H⁺ exchanger genes and other regulatory genes related to salinity stress.

**IncRNAs regulating nutrient deficiency in plants**

Nutrient acquisition from soil remains one of the essential physiological processes for regulating plant growth and development [125]. Several molecular mechanisms, including many nutrient transporters, are actively involved in plant nutrient homeostasis [126, 127]. Among the various non-coding regulatory RNAs, evidence of miRNAs and IncRNAs regulating nutrient acquisition has been found in various plants [11, 14, 61].

Among the major nutrients, phosphorus (P) serves as a fundamentally important element contributing to plant growth and development; it also acts as a P source for ATP production [128]. The availability of soil inorganic phosphate (Pi) to plants is constrained by several factors that limit overall plant growth and development [129]. Little information is available on the complex regulatory network of P homeostasis in plants [127, 130]. Several molecular and biochemical mechanisms are activated by plants to improve soil inorganic phosphate availability and increase phosphorus use efficiency (PUE) [127, 129, 130]. In this context, the role of miRNAs controlling phosphate availability has been reported in various plants [110]. Likewise, the emerging role of IncRNAs regulating phosphate content in plants is well-established in *Arabidopsis* [11, 93], rice [14, 131], and the model legume *Medicago truncatula* [61]. The working mechanism of miR399 and its target gene PHOSPHATE2 (PHO2) is well-recognized for regulating
phosphate content in *Arabidopsis* [132, 133]. Subsequently, Franco-Zorrilla et al. [11] revealed the inductive mechanism of IncRNA INDUCED BY PHOSPHATE STARVATION 1 (IPS1) that works as an eTM or decoy for miR399 and regulates the target PHO2 gene expression and phosphate homeostasis in *Arabidopsis*. Thus, given the abundance of phosphate, IncRNA IPS1 binds to miR399 and prevents it from acting on target gene PHO2, which presumably abolishes the functional role of phosphate transporters by the ubiquitination pathway, thereby restricting root uptake of excessive phosphate ([69], see Fig. 3). Under phosphate-deficient conditions, the PHO2 gene is suppressed as miR399 degrades the transcript of PHO2 and eventually allows phosphate transporters to accumulate phosphate [132].

Furthermore, the phosphate regulation mechanism—based on the “PHRI–miR399–PHO2” pathway in association with phosphate deficiency-responsive IncRNAPDIL1, a paralog of Mt4—has been demonstrated in *Medicago truncatula* [61]. The authors established a negative regulatory role of the IncRNAsPDIL2 and PDIL3 controlling the expression of the phosphate transporter gene Medtr1g074930. Likewise, the working mechanism of cis-NATPHO1;2 IncRNA functioning as a translational enhancer of the PHO1;2 gene for phosphate homeostasis has been reported in rice [131].

Like P, nitrogen (N) is an essential nutrient for plant growth and development, and also serves as an N source for amino acids, ATP, and N metabolism in plants [134]. Several QTLs in various crops of agricultural importance reportedly improve nitrogen use efficiency (NUE) [134]. Advances in functional genomics approaches have identified several regulatory gene(s) and transporter genes controlling NUE in crop plants [135]. However, the entire molecular mechanism of N assimilation is not understood in plants [136]. State-of-the-art deep transcriptome sequencing via RNA-seq has further advanced our understanding of N-responsive IncRNAs contributions to N homeostasis in plants. Numerous N-responsive IncRNAs have been uncovered in various plant species viz., rice, maize, poplar [14, 95, 96]. The operating mechanism of IncRNAs cis-NATAMT1,1 and cis-NATAMT1,2 targeting the AMT1 gene for N homeostasis, is well-recognized in rice [14]. A study on IncRNAs in the *Arabidopsis* genome under various nutrient-deficient conditions uncovered the role of trans-acting siRNA3 (TAS3) as an important IncRNA targeting the nitrate transporter 2 gene, thereby regulating N transport in N-starved environments [99].

Among the various micronutrients, boron (B) is an essential micronutrient for plant growth and development, membrane integrity, and cell wall synthesis [137–139]. Genome-wide exploration of IncRNA regulating B deficiency response in *Poncirus trifoliata* through strand-specific deep transcriptome analysis detected 2101 unique IncRNAs [98]. Further, expression profiling analysis identified 729 up-regulated and 721 down-regulated IncRNAs under B deficiency stress. Functional validation of selected IncRNAs shed light on the target genes involved in the calcium signaling and plant hormone signal transduction pathways under B deficiency stress in *Poncirus trifoliata* [98].

The above findings have laid the foundation for future in-depth research on the regulatory role of various IncRNAs controlling nutrient deficiency in plants.

**Role of IncRNAs under heavy metal toxicity**

The outcome of rapid industrialization, application of heavy doses of chemical fertilizers, and indiscriminate contamination of heavy metals in irrigation water and arable land have posed a serious challenge for crop yields and human health [140], particularly cadmium. To minimize heavy metals moving from the soil into plants, plants use several regulatory molecular mechanisms [140]—IncRNAs may play a crucial role in controlling the uptake of heavy metals into the plant system.

RNA-seq profiling identified 301 cadmium-responsive IncRNAs in *Brassica napus*, of which 67 were eTMs for 36 Cd-responsive miRNAs [141]. Functional validation of TCONS_00091906, TCONS_00033487, and TCONS_00097191 IncRNA under Cd stress using qRT-PCR analysis indicated their significant role as target mimicry for EL628609, TC182597, and TC203372 mRNAs involved in Cd uptake and detoxification [141]. Likewise, Chen et al. [88] undertook a genome-wide survey of IncRNAs using RNA deep transcriptome sequencing that provided evidence of both up- and down-regulation of IncRNAs involved in the Cd response. Furthermore, functional analysis of DELinCnRNA provided insight into the role of IncRNAs regulating target genes associated with cysteine and methionine metabolism under Cd stress (see Fig. 3). Considering the mounting evidence of arsenic (As) toxicity in rice, Tang et al. [142] provided novel insights into As-responsive IncRNAs along with other non-coding RNAs regulating the As toxicity response in rice. However, the mechanisms involved in the regulatory role of IncRNAs controlling heavy metals is unknown and needs further research.

**Database and web-based resources of IncRNAs**

Advances in functional genomics, especially RNA-seq analysis, have enabled the discovery of novel IncRNAs that regulate various biological processes, including stress responses. However, the accurate prediction of IncRNAs, their structure, genomic content, conservation, and functional annotation remains a challenge (see [8]). To address these shortcomings, several web-based resources and databases have been developed, viz., NONCODE provides the comprehensive biological functions of IncRNAs [143–
145], PLNlncRbase contains information on 1187 plant lncRNAs from more than 40 species [146], and Plant Long non-coding RNA Database (PLncDB) offers information on 6480 IncRNAs in Arabidopsis [147]. Likewise, the Plant Natural Antisense Transcripts Database (PlantNATsDB) provides information on plant NATs controlling various physiological and development processes [148], Plant ncRNA Database (PNRD) maintains records of 25,739 non-coding RNAs including lncRNAs [149], CANTATAdb maintains 45,117 IncRNAs from 10 plant species [16], CANTATAdb 2.0. annotates plant IncRNAs [155] and PLncPRO provides information on abiotic stress-responsive IncRNAs in rice and chickpea [72]. A detailed list of plant IncRNA databases is in Table 3. Several important tools, such as CPPred [158], REPTree [159], Pfamscan [160], COME [161], PLIT [156], and CPC2 [162], are available to distinguish IncRNAs from mRNAs. Advances in bioinformatics tools and new algorithms could further boost our efforts in discovering novel IncRNAs and their accurate functional annotations.

**Conclusion**

The rapidly increasing number of plant IncRNAs and their multifaceted regulatory roles in governing various biological processes is becoming a hotspot in biological research [8, 12]. However, genome-wide discovery, characterization, and functional annotation of IncRNAs remain limited in plant species. The increasing availability of reference genome sequences of crop plants could offer opportunities to explore various IncRNAs and their sequence similarity and ‘functional conservation’ using comparative genome analysis [38]. Further, in-depth transcriptome sequencing, rapid advances in computational biology, and increasing databases for IncRNAs and efficient methods/tools could assist in the prediction of accurate IncRNAs and functional annotation of novel IncRNAs. The paucity of mutants corresponding to IncRNAs is another challenge for functional analysis of novel IncRNAs [17]. In this context, CRISPR/Cas9 engineered mutation in novel abiotic stress-responsive IncRNAs could shed light on the function of IncRNAs, and thus help in the design of abiotic stress-resistant crops.

| Name       | Characteristics                                                                 | IncRNA and details                                                                 | References | Link                                                                                                                                 |
|------------|---------------------------------------------------------------------------------|------------------------------------------------------------------------------------|------------|-------------------------------------------------------------------------------------------------------------------------------------|
| PLncDB     | It provides comprehensive data on Arabidopsis IncRNAs                           | Arabidopsis IncRNAs                                                               | [147]      | [http://chualab.rockefeller.edu/gbrowse2/homepage.html](http://chualab.rockefeller.edu/gbrowse2/homepage.html)                       |
| PLNlncRbase| Detailed information on experimentally identified plant IncRNAs                 | Supply information on 1187 plant IncRNAs in 43 plant species                       | [146]      | [http://bioinformatics.ahau.edu.cn/PLNlncRbase/](http://bioinformatics.ahau.edu.cn/PLNlncRbase/)                                 |
| PNRD       | It provides information on different types of ncRNAs                            | 150 plant species                                                                 | [149]      | [http://structuralbiology.cau.edu.cn/PNRD](http://structuralbiology.cau.edu.cn/PNRD)                                           |
| CANTATAdb  | Used for annotation of identified IncRNAs                                       | Covers information on IncRNA on 10 plant species                                  | [16]       | [http://cantata.amu.edu.pl](http://cantata.amu.edu.pl), [http://yeti.amu.edu.pl/CANTATA/](http://yeti.amu.edu.pl/CANTATA/)       |
| GREENC     | Used for annotate IncRNAs                                                        | Annotation of more than 120,000 IncRNAs associated to 37 plant species could be done | [150]      | [http://greenc.sciencedesigners.com/](http://greenc.sciencedesigners.com/)                                                     |
| PLncPRO    | Used for prediction of IncRNAs in plants and used for investigating abiotic stress responsive IncRNAs in rice and chickpea | 3714 and 3457 IncRNAs in rice and chickpea for drought and salinity                | [72]       | [http://ccbcb.jnu.ac.in/PLncPRO](http://ccbcb.jnu.ac.in/PLncPRO)                                                                 |
| PlaNC-TE   | Provide insights about the relationship between ncRNA and TEs in plants          | Information on overlapping of ncRNA and transposon elements from 40 plant genomes | [151]      | [http://planc-te.cp.utfpr.edu.br](http://planc-te.cp.utfpr.edu.br)                                                              |
| EVLncRNAs  | It contains IncRNA information on various species including plant               | 1543 IncRNAs from 77 species and also 428 plant IncRNAs from 44 plant species     | [152, 153] | [http://biophy.dzu.edu.cn/EVLncRNAs](http://biophy.dzu.edu.cn/EVLncRNAs)                                                       |
| CRISPRInc  | Database for validated CRISPR/Cas9 sgRNAs for IncRNAs from various species including plants | 305 IncRNAs and 2102 validated sgRNAs on eight species including plant             | [154]      | [http://www.crisprlnc.org](http://www.crisprlnc.org) or [http://crisprlnc.xtbg.ac.cn](http://crisprlnc.xtbg.ac.cn)            |
| CANTATAdb  | It provides information on annotation of plant IncRNAs                          | Covers information on IncRNA on 39 plant species                                  | [155]      | [http://cantata.amu.edu.pl](http://cantata.amu.edu.pl), [http://yeti.amu.edu.pl/CANTATA/](http://yeti.amu.edu.pl/CANTATA/)      |
| PLIT       | Used for investigating of plant IncRNAs from RNA seq data.                     | Provides information on IncRNA from 8 plant species                               | [156]      |                                                                                                                                     |
| PLncDB     | Detail information on plant IncRNAs                                             | Provides plant lncRNAs and IncNATs information                                     | [157]      |                                                                                                                                 |

The table is updated version of [17, 61, 143]
tolerant crop plants [163]. The availability of a comprehensive atlas of lncRNAs across whole genomes in crop plants, coupled with a comprehensive understanding of the complex molecular mechanisms that regulate various abiotic stress responses, will enable us to use lncRNAs as potential biomarkers for tailoring abiotic stress-tolerant plants in the future.

Abbreviations

lncRNA: Long non-coding RNA; miRNA: MicroRNA; ncRNAs: Non-coding RNAs; RNA-seq: RNA-sequencing; siRNAs: Small interfering RNAs; eTM: Endogenous target mimics; lincRNAs: Long intergenic lncRNAs; NAT: Natural anti-transcript; DElncRNAs: Differentially expressed lncRNAs; vpp4: V-ATPase encoding gene; DRIR: DROUGHT INDUCED lncRNA; DEGs: Differentially expressed genes; CBFs: C-repeat binding factors; COR: Cold regulated genes; FLC: FLOWERING LOCUS C; COOLAIR: COLD INDUCED LONG ANTISENSE INTRANIC RNAS; COLDAIR: COLD ASSISTED INTRONIC NONCODING RNA; RNApol: RNA polymerase II; P: Phosphorus; N: Nitrogen; B: Boron; IPS1: INDUCED BY PHOSPHATE STARVATION 1; NUE: Nitrogen use efficiency

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