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Long non-coding RNA-mediated epigenetic response for abiotic stress tolerance in plants

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ABSTRACT

Plants perceive environmental fluctuations as stress and confront several stresses throughout their life cycle individually or in combination. Plants have evolved their sensing and signaling mechanisms to perceive and respond to a variety of stresses. Epigenetic regulation plays a critical role in the regulation of genes, spatio-temporal expression of genes under stress conditions and imparts a stress memory to encounter future stress responses. It is quintessential to integrate our understanding of genetics and epigenetics to maintain plant fitness, achieve desired genetic gains with no trade-offs, and durable long-term stress tolerance. The long non-coding RNA >200 nts having no coding potential (or very low) play several roles in epigenetic memory, contributing to the regulation of gene expression and the maintenance of cellular identity which include chromatin remodeling, imprinting (dosage compensation), stable silencing, facilitating nuclear organization, regulation of enhancer-promoter interactions, response to environmental signals and epigenetic switching. The lncRNAs are involved in a myriad of stress responses by activation or repression of target genes and hence are potential candidates for deploying in climate-resilient breeding programs. This review puts forward the significant roles of long non-coding RNA as an epigenetic response during abiotic stresses in plants and the prospects of deploying lncRNAs for designing climate-resilient plants.

1. Introduction

In an era characterized by rapidly changing environmental conditions and an ever-growing global population, agriculture faces the daunting challenge of ensuring food security and sustainable crop production. Abiotic stresses, such as drought, salinity, nutrient deficiency, heavy metal toxicity, and heat stress, exert considerable pressure on crop yields, making it imperative to unravel novel mechanisms that enhance plant resilience. Plants develop tolerance by altering several molecular signaling, physiological, and biological pathways (Lamaoui et al., 2018). With the advent of next-generation sequencing (NGS) technologies, along with homology-based experimental approaches, vital progress has been made in the discovery of non-coding RNA (ncRNAs) in plants. The ncRNAs are crucial components of stress response adaptation associated with distinct gene regulatory networks on epigenetic, transcriptional, and post-transcriptional levels (Cech and Steitz, 2014; Peschansky and Wahlestedt, 2014). The ncRNAs are categorized into housekeeping ncRNA (transfer RNAs (tRNAs), small nuclear RNAs (snRNAs), ribosomal RNAs (rRNAs), small nucleolar RNAs (snoRNAs) and regulatory ncRNA (microRNAs (miRNAs), short interfering RNAs (siRNAs), piwi-interacting RNAs (piRNAs), and long non-coding RNAs (lncRNAs) (Morris and Mattick, 2014). The long non-coding RNAs (lncRNAs) are transcripts of >200 bp that do not or rarely produce proteins (D'Ario et al., 2017; Kapranov et al., 2007). The lncRNAs are major emerging players in the quest for imparting stress tolerance enabling plants to adapt and thrive in changing environmental

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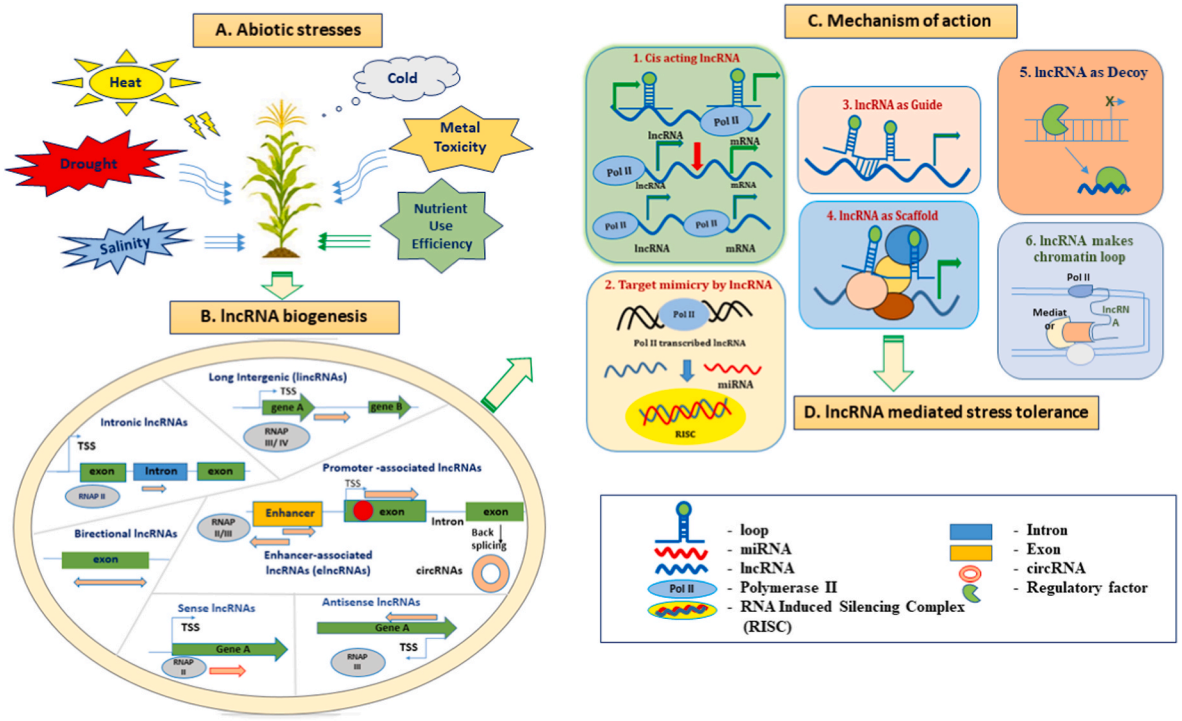

Fig. 1. Biogenesis and molecular mechanism of lncRNA action in response to abiotic stress tolerance in plants.

conditions. These intriguing molecules, once considered "junk" in the genome, have emerged as pivotal regulators of gene expression, orchestrators of epigenetic modifications, and responsive components to environmental stimuli in plants. The lncRNAs are expressed spatiotemporally with a lower magnitude as compared to the protein-coding genes as has been observed from human and animal studies (Ulitsky, 2016; Pang et al., 2019; Xu et al., 2017). The lncRNAs can either function in close proximity to the RNA synthesis site, impacting genes on the same strand, or they can operate from a distance, acting as trans-acting factors. To adapt to the terrestrial environment, plant lncRNAs are conservatively evolving and developing stress memories for improving the response of plants to abiotic stresses (Yang et al., 2023). The lncRNAs play a pivotal role in epigenetic memory, where plants retain and transmit stress-induced epigenetic changes to subsequent generations. The lncRNAs have also been reported to play a major role in controlling alternative splicing, plant hormone production and signal transmission (e.g., ABA and ethylene) (Zhang et al., 2022). The interconnectedness of these lncRNAs with various aspects of plant biology hints at their potential to revolutionize our approach to crop improvement and environmental resilience. From exploring stress-responsive lncRNAs to uncovering their intricate regulatory networks, the study of lncRNAs is poised to open new horizons in the realm of plant science. In this comprehensive exploration of the subject, we aim to illuminate the growing significance of lncRNAs in plant science and their potential to unlock new avenues for comprehending plant development, stress responses, and adaptation to a dynamic and challenging environment.

2. Discovery of lncRNAs

Earlier in the 1990s and 2000s, to study the function of lncRNAs, classical gene targeting and genetic approaches were utilized. The first lncRNA discovered in the plant was the EARLY NODULIN 40 (*ENOD40*) which was identified from nodule primordia of *Medicago trunculata* (Crespi et al., 1994). This lncRNA has been found to induce the MtRBP1 which is a cytoplasmic localization of nuclear RNA binding protein, during nodule formation (Campalans et al., 2004). Later, several lncRNAs associated with the diverse biological processes and physiological functions were demonstrated in plants *GmENOD40* in soybean, *MtENOD40* in Medicago, *TPS11* in tomato, *OsPI1* in rice, *LDMAR* in rice (Cech and Steitz, 2014; Crespi et al., 1994; Liu and Muchhal, 1997; Wasaki et al., 2003; Yang et al., 1993). With the immense increase in the study of diverse biological roles of plant lncRNAs, focus has been made on discovering the genetic and epigenetic effects associated with the lncRNAs in different biological processes.

3. Biogenesis and classification of lncRNA

The lncRNAs are classified into seven different classes based on their biogenesis, functional mechanism and the effects caused on the targeted DNA sequences viz. long intergenic non-coding RNAs (lincRNAs), intronic, exonic or sense or overlapping, natural antisense transcript (NAT), and bidirectional lncRNAs, enhancer lncRNAs (eRNAs), promoter-associated lncRNAs (Budak et al., 2020) (Fig. 1). Based on the biogenesis, lncRNAs are classified as cis-natural antisense (cis-NATs), trans-natural antisense transcripts (trans-NATs), pseudogenes (Nie et al., 2012), sense or antisense (a strand of origin) (Nam and Bartel, 2012), divergent, or convergent (orientation of transcription), and as intronic or intergenic (location) (Derrien et al., 2012). The sense lncRNAs are transcribed from protein-coding transcripts in the sense as well as antisense directions by alternative splicing while the intronic lncRNAs are synthesized from the intronic region and sometimes include exonic sequences. These lncRNAs are transcribed in both the sense and antisense directions of their corresponding transcripts. The intergenic lncRNAs are transcribed from intergenic regions of protein-coding transcripts in either of the direction, sense, or antisense between two protein-coding genes, whereas the lncRNAs that are generated antisense to the corresponding protein-coding gene are designated as natural antisense lncRNAs. The biogenesis of lncRNAs has been extensively reviewed (Ariel et al., 2014; Datta and Paul, 2019; Jha et al., 2020; Quinn and Chang, 2016; Wierzbicki et al., 2008).

The promoter and enhancer region of the protein-coding gene results in the transcription of the bi-directional lncRNAs and enhancer lncRNAs, respectively. The bi-directional lncRNAs are synthesized in the opposite direction and control the transcriptional regulation of the associated

genes, while the latter are generated with or without 3′-poly (A) tail modification. Different RNA polymerases such as RNA pol II, III, IV, transcribe lncRNA and these riboregulators are positioned in both the cytoplasm and nucleus. The RNA pol II transcribes genomic regions that include enhancer or intron splicing regions and the transcribed lncRNAs possess a 5′-cap and poly-adenylation at the 3′ tail, whereas the RNA pol IV and V are reported to produce the lncRNAs via RNA-dependent DNA methylation (RdDM), that serve as precursors for small interfering RNAs (siRNAs) (Ariel et al., 2014; Datta and Paul, 2019; Jha et al., 2020; Quinn and Chang, 2016; Wierzbicki et al., 2008). The distinct lncRNAs have been detected to have a defined role in controlling the target regulatory networks by multiple mechanisms that include chromatin remodeling, transcriptional repression, mimicry, RNA splicing, and transcriptional enhancer.

Based on the functional regulation mechanism, the lncRNAs are classified into transcriptional regulation, post-transcriptional regulation and other functions. In transcriptional regulation, lncRNAs have been found to play an important role in chromatin reconstitution and interfering with transcription. In post-transcriptional regulation, lncRNAs have a role in regulating the process of splicing and translation. Furthermore, lncRNAs regulate via several mechanisms which include telomere replication, transcription, and translation (Ma et al., 2013). The mechanism of regulation of gene expression at both transcriptional and post-transcriptional levels varies for these different lncRNAs. The lncRNAs interact with the chromatin regulatory protein as miRNA decoys as well as are involved in epigenetic silencing by acting as mediators (Wang et al., 2018). It has been reported that exonic lncRNAs evolve at a slower rate than lincRNAs and intronic lncRNAs. Nevertheless, these exonic lncRNAs have been detected to possess a faster-evolving rate than the protein-coding sequences or mRNA UTRs (Cabili et al., 2011).

According to the targeting mechanism, the functional lncRNAs are categorized into five mechanisms viz. scaffold, guide, signal, sponge, and decoy (Wang and Chang, 2011). The lncRNA regulates gene transcription through specific pathways by acting as scaffolds and also guides the ribonucleoprotein complexes at specific sites (Campalans et al., 2004; Spitale et al., 2011). In the regulation of gene transcription, lncRNAs function as signaling molecule and helps in determining the spatial, temporal, and expressional state of the regulatory factor (Di et al., 2014a). Further, when considered as decoy molecules, lncRNAs have been identified in the expressional regulation of target genes by recruiting some RNA-binding proteins that are unique to them (Vrbsky et al., 2010).

The non-polyadenylated lncRNAs join their heads with tails covalently in a process called back-splicing mediated by spliceosome machinery and are termed circRNAs (Chen, 2016). The circRNAs regulate the splicing of their cognate mRNAs such as *circ-SEP3* in *Arabidopsis* regulates the splicing of its target SEPALLATA3 (*SEP3*) (Conn et al., 2017).

The lncRNAs possess a secondary structure that might have a role in their functionality. The lncRNAs generally have two types of functional site, one is the interacting site where the sequence-specific interaction with RNA binding proteins occurs, and the other is the structural site that aid in the identification of secondary and/or tertiary structures directing interacting partners (Fabbri et al., 2019). In the Brassicaceae family, *COOLAIR* lncRNA has a role in vernalization, consisting of conserved secondary structures, and a multi-way junction motif along two right-hand turn motifs (Hawkes et al., 2016). In *Arabidopsis*, almost 40,000 candidate lncRNAs were identified (>30,000 NATs and >6000 lincRNAs) (Jin et al., 2013; Liu et al., 2012; Wang et al., 2014). Similarly, several lncRNAs have been identified in plant species such as *Setaria italica, M. trunculata, Solanum tuberosum, S. lycopersicum, Triticum aestivum, O. sativa, Populus trichocarpa, Zea mays*, *M. sativa, Sorghum bicolor, Brassica rapa, etc.*

4. Epigenetic memory and lncRNAs: The abiotic stress response in plants

A crosstalk of interconnecting signaling mechanisms operates in plants which are generally inducible in nature. The stress signaling pathways operate in a cascade through secondary messengers (calcium, reactive oxygen species, reactive nitrogen species, etc.), sensory kinases (protein kinases, mitogen-activated protein kinases, etc.), phospholipids, hormones (abscisic acid (ABA), salicylic acids, etc.) (Chinnusamy et al., 2004). In order to maintain ion homeostasis and cellular stability, the plants reprogram the gene expression patterns for genetic gains. The epigenetic mechanisms are uniquely customized in the plants based on their genome structure and composition. RNA-directed DNA methylation (RdDM) is a major factor in the regulation of methylation that generates small regulatory RNAs (Erdmann and Picard, 2020). The stress-response mechanisms are generally first observed as physiological responses wherein the plasticity in traits varies as per the duration, magnitude, and degree of individual or combined stresses. When chronic stress is perceived by plants, stress memory is recorded in the form of methylation, and repeated exposure builds an adaptation. The physiological level of stress response acts as a buffer zone in a generation. Once the stress response overcomes the physiological buffer zone, it manifests at the genetic and epigenetic levels (trans-generational response). The epigenetic responses act as a link between environmental stress and genetic mechanisms (Srikant and Drost, 2021). The stress response activates the silenced loci, modulates the expression of the genes, and is manifested as an epigenetic response (Kumar and Mohapatra, 2021). Such epigenetic signatures get fixed over time and emanate as a stable stress response. The epigenetic response to stress prepares the plants for other stresses through a strong stress memory (Mladenov et al., 2021; Shanker et al., 2020). The mechanism of how this memory is fixed is being unraveled in many recent studies (García-Campa et al., 2022; Lukić et al., 2023; Nair et al., 2022; Sharma et al., 2022) and it is now known that this memory is imprinted via modifications in chromatin, changes in metabolism, modifications in small RNAs in the reproductive parts of the plants. Storage proteins, lipids and other secondary metabolites are also implicated in transgenerational memory transfer in plants (Villagómez-Aranda et al., 2022). There are studies that have found that structural and functional variations in a genome can be transmitted genetically. Novel transgenerational structural genome variants have been identified in *Brassica*. There can be structural rearrangements that are manifested in the F_1 generation in plants and can have deletions, changes in gene copy numbers, differences in methylation patterns and these can possibly contribute to abiotic stress tolerance in the successive generations (Orantes-Bonilla et al., 2022a). Recent studies have shown the role of chloroplast-mediated transgenerational memory transfer in plants. Signaling in chloroplast can be of crucial importance in memory transfer to future generations in plants (García-Campa et al., 2022).

The lncRNAs play a significant role in plant development, hormone responses, and stress reactions through interactions with various epigenetic elements. While these epigenetic components can influence lncRNA functions, lncRNAs are also intricately linked with processes steered by epigenetic modifiers (Yang et al., 2023). They might play a part in the regulation of small RNAs (sRNAs). An instance of this is how long-day-specific male-fertility-associated RNA LDMAR's function in rice relies on phasiRNA-driven DNA demethylation, hinting that sRNAs might target lncRNAs. Furthermore, lncRNAs can act as forerunners to sRNAs, like siRNAs and miRNAs, and influence the transcription of subsequent genes by managing sRNA production. The intricate interplay between lncRNAs, sRNAs, and epigenetic factors likely affects specific genetic locations in a highly structured way, warranting further research. This intricate web underscores the multifaceted and challenging nature of lncRNA-driven regulatory systems. Recent studies have significantly advanced our understanding of the role of long non-coding RNAs (lncRNAs) in epigenetic silencing through the

RNA-directed DNA methylation (RdDM) pathway (Chen et al., 2018; Chen et al., 2019a). Numerous findings indicate that in plants, lncRNAs are intricately linked with DNA methylation, influencing various developmental processes including embryogenesis (Chen et al., 2018), root formation (Chen et al., 2019a), and reproductive processes (Ding et al., 2012).

Furthermore, there's growing interest in the role of stress-responsive lncRNAs in modulating DNA methylation in response to environmental changes. A notable example is the AUXIN REGULATED PROMOTER LOOP (APOLO) in *Arabidopsis*, which is induced by auxin (Ariel et al., 2014). This lncRNA's dual transcription by both Pol II and V forms a chromatin loop, influencing the promoter of the adjacent gene PINOID (PID). This subsequently leads to a reduction in its transcript levels. Furthermore, APOLO's potential to identify distant unrelated loci through R-loop formation has been proposed. This mechanism might modulate local chromatin structures, influencing auxin-responsive genes (Ariel et al., 2014). An exhaustive research work on drought stress memory in rice identified the coordinated responses of lncRNAs, DNA methylation and phytohormones for the activation of transcripts involved in drought stress tolerance. The lncRNA, TCONS_00028567, a precursor to miRNA, osa-MIR1428e displayed treatment-specific upregulation under drought stress (Li et al., 2019a). Along similar lines, lncRNAs role in drought stress response has been demonstrated by regulating the transcription and co-expression network of lncRNA, miRNA, and protein-coding genes (Ding et al., 2019b; Pang et al., 2019; Zhang et al., 2019) or by utilizing the mechanisms like endogenous target mimics (eTMs), chromatin modulation, and antisense transcription-mediated modulation (Jha et al., 2020).

In a comprehensive methylome study, DNA methylation alterations in *Populus simonii* under various stresses were examined, suggesting a cooperative role of miRNAs and lncRNAs in responding to environmental challenges (Song et al., 2016a). Moreover, a study on soybean roots exposed to high salinity showed that a significant proportion (over 75%) of detected lncRNAs were either activated or identified in transcriptome sequencing (Chen et al., 2019a). The RdDM pathway, a primary epigenetic route mediated by siRNA in plants, showcases the remarkable transcriptional potential of eukaryotic organisms (Matzke and Mosher, 2014). This pathway involves a series of complex processes, from the transcription of single-stranded RNAs by Pol IV to the eventual *de novo* methylation. Notably, non-canonical RdDM pathways bridge the gap between post-transcriptional gene silencing of transposon transcripts and their DNA's *de novo* methylation.

Recent experiments in *Arabidopsis* mutants have provided insights into the RdDM pathway, revealing that DNA methylation at many RdDM target sites did not necessarily correlate with 24-nt siRNAs and was independent of Dicer-like proteins (DCLs) (Yang et al., 2016). The RdDM pathway's biological functions have been extensively studied, highlighting its role in various processes, from transposon suppression to plant development and biotic interactions. There's also increasing focus on DNA methylation's potential roles in plant responses to diverse abiotic stresses, including nutritional shortages, temperature fluctuations, salinity, and drought. While significant strides have been made in understanding the RdDM pathway and the role of lncRNAs, many aspects, including its mechanisms, biological significance, and evolutionary relevance, remain to be fully explored. Despite the increasing literature and research, systematic studies on the molecular mechanisms of epigenetic modifications in adaptation to abiotic stresses need further attention (Varotto et al., 2020).

5. Long non-coding RNA: Exemplary regulatory players in stress responses

The last decade has witnessed accelerated research based on the characterization of these lncRNAs in several regulatory mechanisms in plants. From transcriptional noise to a lead singer in the gene regulatory epigenetic network orchestra, long non-coding RNAs are regulatory

Table 1
Databases available for plants long-non coding RNAs.

Sr. No	Database	Description	Weblink
1	NON CODE (v.5.0)	Complete collection and annotation of all kinds of lncRNAs >500,000 (except tRNAs and rRNAs) from 16 species, including Arabidopsis as the only plant species; 3853 lncRNA transcripts and 2477 lncRNA. Provides genes expression profile of lncRNA genes by graphs Provides an ID conversion tool from RefSeq or Ensembl ID to NONCODE ID and service of lncRNA identification.	http://www.noncode.org/
2	GREENC (v2.0)	wiki-based plant lncRNA database comprised of >120,000 annotated lncRNAs with 37 plant species and algae. Enables the user to predict lncRNA, access the coding potential and folding energy for each lncRNA	http://greenc.sciencedesigners.com/
3	lncRNAdb	Comprehensive functions of lncRNAs from nine species including Arabidopsis, rice, and others Annotation information of lncRNAs such as evolutionary conservation, gene expression data, genomic context, structural information, functional evidence, subcellular localization, transcript sequence, their experimentally verified biological functions sequence analysis tools	http://lncrnadb.org
4	PLncDB	*Arabidopsis* specific intergenic transcripts lncRNAs; >13000 lincRNAs Genome browser of lncRNAs along with information regarding the associated numerous epigenetic markers.	http://plncdb.tobaccodb.org/
5	PNRD	Repository of >25,000 ncRNAs of 11 different types and from 150 plant species Provide information of both sRNAs and lncRNAs Multiple analytical tools - miRNA predictor, coding potential calculator, and customized genome browser	http://structuralbiology.cau.edu.cn/PNRD
6	CANTATAdb 1.0	lncRNAs from 10 model plant species; 45117 lncRNAs. Evaluate each lncRNAs based on potential roles in splicing regulation and miRNA modulations, along with tissue-specific expressions and coding potential.	http://yeti.amu.edu.pl/CANTATA/
7	PLNlncRbase	Repository of 1187 lncRNAs experimentally verified plant lncRNAs in 43 species	http://bioinformatics.ahau.edu.cn/PLNlncRbase.
8	PLncPRO	Prediction of lncRNAs in plants Abiotic stress-responsive lncRNAs in rice and chickpea	http://ccbb.jnu.ac.in/plncpro/

(*continued on next page*)

Table 1 (*continued*)

Sr. No	Database	Description	Weblink
9	PlaNC-TE	Provide insights into the relationship between ncRNA and transposable elements in plants	http://planc-te.cp.utfpr.edu.br/
10	CRISPRlnc	Database for validated CRISPR/Cas9 sgRNAs for lncRNAs	http://www.crisprlnc.org
11	PLncRNAdb	Plant-specific lncRNAs NATs of 70 plant species; information lncRNAs and various RNA-binding proteins (RBPs) and relationships between them as lncRNA-protein networks; prediction of NATs; deposits networks formed by NATs; GO annotation and gene set analysis available, consists of 5000 lncRNAs from Arabidopsis, Z. mays, and Populus, serving as a reference database for lncRNA prediction and evaluating the coding potential of protein transcripts.	http://bis.zju.edu.cn/PlncRNADB/index.php
12	EVLncRNAs	Annotated and experimentally validated lncRNAs, 428 plant lncRNAs from 44 plant species.	https://ngdc.cncb.ac.cn/databasecommons/database/id/3781
13	The Arabidopsis Information Resource (TAIR)	Structural and functional annotation of the Arabidopsis genes Comprehensive data repository; multiple analysis tools available	https://www.arabidopsis.org/
14	Araportll	Database on Arabidopsis Col-0 version 11 (Araport11) includes additional coding and noncoding annotations compared to TAIR10, such as lincRNAs, NATs, and other ncRNAs	https://www.araport.org/
15	Plant Natural Antisense Transcripts DataBase (PlantNATsDB)	Database for natural long noncoding antisense transcripts (NATs) from 70 plant species, associated gene information, small RNA expression, and GO annotation	https://openebench.bsc.es/tool/plantnatsdb

players in environmental stress response. The lncRNAs upon stress response, regulate the target gene expression through methylation by recruiting DNA methyl transferases or demethylases, histone modifications in addition to regulating the binding of transcription factors to the gene promoter regions (Zhang et al., 2019b). The lncRNAs influence the regulatory protein expression by acting as decoys and mimicking the targets. This target mimicry mechanism is generally used for the inhibition of miRNA activity. In *Arabidopsis*, the lncRNAs *IPS1* and alternative splicing competitor *ASCO*-lncRNA interact and compete with miRNAs and act as miRNA target mimics (Bardou et al., 2014). The lncRNAs also interact with the chromatin-modifying complexes by lncRNA-mediated chromatin modifications (lncR2Epi) regulation pathway (Wang et al., 2016). The best-known example of these types of plant lncRNAs associated with such pathways are *COLDAIR* (intronic lncRNA that is transcribed from the first intron of *FLC*) and *COOLAIR* (cold-induced FLOWERING LOCUS C (*FLC*) antisense lncRNA transcripts from the end of *FLC* gene) lncRNAs in cold-stressed *Arabidopsis* (Sun et al., 2013; Swiezewski et al., 2009). The process of vernalization is the most common phenomenon of epigenetic regulation by lncRNAs. Based on the nature of the lncRNA-chromatin complex, the activation and repression of the selective gene can be promoted (Gendrel and Heard, 2014; Meller et al., 2015). In the process of activation, lncRNAs recruit the enzyme histone H3K4 methyltransferases. Conversely, during transcription repression, lncRNAs promote DNA methylation by binding to DNA methyltransferases, such as *DNMT1* and *DNMT3b* (Mohammed et al., 2010; Schmitz et al., 2010).

The plant lncRNAs also utilize the RNA-directed DNA methylation (RdDM) silencing pathway for epigenetic gene silencing which involves the silencing of repetitive sequences. The RdDM pathways mainly involve the role of plant-specific RNA polymerases Pol IV, Pol V and for some instance, Pol II (Wierzbicki et al., 2021; Zheng et al., 2009). This pathway is reported to be a plant-specific *de novo* DNA methylation mechanism and requires the lncRNAs as a scaffold to determine the target genomic loci (Zheng et al., 2009). It has recently been reported that CG methylation negatively regulates the transposable element (TE)-related expression of lncRNA in rice (Li et al., 2021).

The lncRNA databases are continuously being deposited with new lncRNA sequences from various plants species. The credit to this is bestowed to the omics technologies using next-generation sequencing platforms *viz.*, genomics, transcriptomics, metabolomics, proteomics, methylomics, degradomics, etc. Since the discovery of the first lncRNA *ENOD40*, the lncRNA research has been extended to cereals, horticultural, cash crops, etc. (Crespi et al., 1994). In the last decade, enormous literature has been produced those deals with the functional characterization of lncRNAs in several biological processes found in plants. Several databases are available for lncRNA in plants. Table 1 describes the databases with the functional specifications for lncRNAs.

6. Methods for studying lncRNA

On account of its immense regulatory role in plant growth, developmental process, and responses to unfavorable environmental changes, a continuous effort has been made for high-throughput sequencing technologies, the development of several computational tools and databases. Expressed sequence tag (EST), RNA capture sequencing (RNA Capture-Seq), the lncRNA microarray technique, whole-genome tiling arrays, serial analysis of gene expression (SAGE), RNA-sequencing (RNA-Seq), degradome sequencing. The cDNA library preparation followed by sequencing is one of the traditional approaches to detect lncRNA. The most widely utilized method for discovering the lncRNAs is using RNA-sequencing or transcriptome analysis using second and third-generation sequencing platforms. The experimental identification, annotation, and functional validation of lncRNA are resource-intensive, time-consuming, and specific to the experimental setup. In contrast, *in silico* techniques to identify and annotate lncRNA are cost-effective and can be applied to any existing sequencing dataset.

The advanced wet lab assays to capture lncRNA and its interacting partners have previously been reviewed extensively (Kashi et al., 2016; Kato and Carninci, 2020). The wet lab assays include RNA-seq (second and third-generation sequencing) for identification of lncRNA, cross-linking immunoprecipitation sequencing (CLIP-seq), photoactivatable ribonucleoside enhanced CLIP-seq, RNA immunoprecipitation sequencing (RIP-Seq) for RNA-protein interaction, Chromatin isolation by RNA 261 purification (ChIRP), RNA antisense purification (RAP), Capture hybridization analysis of RNA targets (CHART) for RNA-Chromatin Interactions, cross-linking, ligation, and sequencing of hybrids (CLASH) and RAP for RNA-RNA interactions. The *in-silico* identification and annotation of lncRNA can be carried out by methods reference-based and reference-free.

In reference-based analysis, the transcript data is aligned to the reference genome to determine the coding potential of the transcript (for example a tool, lncRNA-ID (https://github.com/zhangy72/LncRNA-ID). The predicted lncRNA using these methods is restricted to known reference and new lncRNA can be omitted from the experiment. The reference-free methods (*ab-initio*) are features, fast, and suitable for less

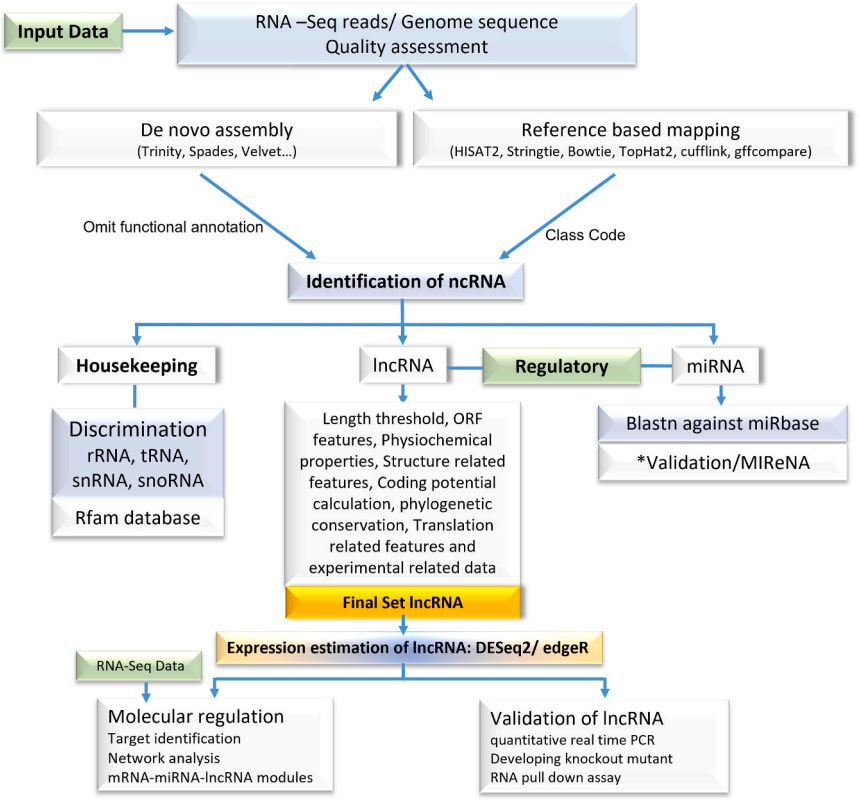

Fig. 2. *In silico* analysis of lncRNA using tools/databases.

studied or unexplored organisms with no or incomplete genome and reference transcriptome available. Efforts have been made for the prediction and functional characterization of the plant lncRNAs by using bioinformatics tools/programs (Wu et al., 2016). Fig. 2 shows the bioinformatics pipeline for the identification of lncRNAs and the co-expression network analysis. The prediction tools available for plant lncRNA along with their specifications are listed in Table 2.

7. Long non-coding RNAs in the regulation of abiotic stresses

The recent examples of lncRNAs regulating abiotic stresses in different plant species have been mentioned in this section. Their roles and the mechanism of action in plants have been depicted in Fig. 3 in response to various abiotic stresses.

7.1. lncRNAs in drought stress

In recent years, the role of long non-coding RNAs (lncRNAs) in plant responses to abiotic stresses, particularly drought, has gained significant attention (Yang et al., 2023). The lncRNAs influence both transcriptional and post-transcriptional gene regulation, thereby playing a crucial role in modulating the balance between plant growth and stress tolerance (Zhang et al., 2022). Specifically, under drought conditions, certain lncRNAs can be either induced or suppressed, thereby modulating the expression of target genes that are involved in drought response mechanisms. Chen et al., 2023 embarked on a focused exploration of a specific lncRNA, lncRNA77580, in soybean's response to drought and salinity stress. Their findings, derived from overexpression studies, revealed a dual nature of lncRNA77580, enhancing drought tolerance while simultaneously increasing sensitivity to salinity at the seedling stage. This dichotomy underscores the intricate regulatory networks that lncRNAs are involved in, suggesting that their roles may be context-dependent and multifaceted. While the study provides valuable insights into the potential of lncRNA77580 as a genetic tool for enhancing drought tolerance, the increased salinity sensitivity observed in the overexpression lines raises questions about the broader applicability of such genetic interventions, especially in environments where multiple abiotic stresses coexist. The current literature, although rich in identifying the presence and potential roles of lncRNAs, often lacks a deep dive into the specific molecular interactions and cascades triggered by these lncRNAs in response to drought stress. As the field progresses, a more detailed understanding of these mechanisms will be pivotal for harnessing the potential of lncRNAs in improving plant resilience to drought and other abiotic stresses.

Various stress-responsive lncRNAs have been discovered in crop species such as *Arabidopsis* (Amor et al., 2009), *S. italica* (Qi et al., 2013), *Populus* (Shuai et al., 2014), *Z. mays* (Zhang et al., 2014), *O. sativa* (Chung et al., 2016), *Manihot esculenta* (Li et al., 2017), and *Panicum virgatum* (Zhang et al., 2018) by utilizing genome-wide transcriptome study. RNA-seq analysis of drought-stressed leaf samples to identify the non-coding RNAs (98 lncRNAs) together with their antisense transcripts is a drought stress response (Chung et al., 2016). Similarly, drought-related down-regulated polyadenylation (DPA) lncRNA identified in rice showed a high significant nuclear retention and co-expression with protein-coding genes to cope with drought stress (Yuan et al., 2018). The regulatory mechanism of drought tolerance mediated by the lncRNA *MSTRG.28732.3* was elucidated in drought-tolerant rice. The drought-stress up-regulated miR171 induced the down-regulation of lncRNA *MSTRG.28732.3* in the chlorophyll biosynthesis pathway, by regulating the genes *Os02g0662700, Os02g0663100, and Os06g0105350* (Yang et al., 2022). Transcriptome analysis discovered 238 lncRNA involved in drought response memory under water-deficit stress in rice (Li et al., 2019b). Systematic characterization of lncRNA in Dongxiang wild rice revealed 1655 novel lncRNA transcripts of which 1092 were determined as drought-responsive (Weidong et al., 2020). In wheat, RNA seq analysis revealed the lncRNAs (c70772_g2_i1 and c90557_g1_i1) network interaction with the miRNA and target gene to regulate the drought stress

Table 2
List of commonly used tools for identification of plant lncRNA.

Tool	Algorithm	Features	Pros	Cons	Accuracy	Online(O)/ standalone (A)	Retrainable (Y/N)	Reference genome requirement (Y/N)
Coding Or Non-Coding (CONC)	Support vector machines (SVM)	Sequence related (peptide length, amino acid composition, sequence compositional entropy, number of homologs, alignment entropy) Structure related (predicted secondary structure content, mean hydrophobicity)	Integrate large numbe of features and classification model	Slow to large dataset, less accurate compared to recent tools	97%	A	Y	N
Coding Potential Calculator (CPC)	SVM	ORF features (quality, coverage, integrity), physicochemical characteristics, BLAST score	Faster runtime, give explanations behind prediction	Dependence on ORF only might lead pseudo predictions, Cannot predict from UTR region	76.2%	O/A	N	N
Coding-Non-Coding Index CNCI	SVM	Sequence related (length percentage, adjacent nucleotide triplets, sequence score, codon-bias, most like CDS, score-distance)	Enable reference free prediction, Evolution of sequential features can be studied	Low feature heterogeneity Poor prediction in weak assembly with partial transcript length	97.3%	O/A	both	N
COME COding potential calculation tool based on Multiple features	Balanced Random forest (BRF)	Sequence related (GC content, ORF score, DNA and protein sequence conservation, polyA abundance, Structure related (RNA secondary structure conservation) experimental related (expression specificity score)	Enable model Retrain, fast and robust, provide supporting evidence for its annotation	Not suitable for non-model species, restricted to five species only, integration of some feature in computational model is difficult	98.3%	A	Y	Y
PLEK (*p*redictor of *l*ong non-coding RNAs and m*e*ssenger RNAs based on an improved *k*-mer scheme)	SVM	Sequence related features, k-mer frequency (for k = [1,5])	Enable reference free prediction, Robust to indel sequencing error	Low feature heterogeneity, Limited raining dataset coverage	95.6%	A	Y	Y
Coding Potential Calculator (CPC2)	SVM	Sequence related ORF features (quality, coverage, integrity, Fickett score), physicochemical characteristics (isoelectric point)	Include physicochemical properties results good performance, Enable reference free prediction, Large scale identification of lncRNA	Comparatively slow	94.2%	O/A	N	N
PlncPRO (**P**lant **L**ong **N**on-Coding RNA **P**rediction by **R**andom fOrest)	Random forest (RF)	Sequence related (64 k-mer frequencies, ORF coverage, ORF Score, BLAST score, frame entropy)	Enable reference free prediction, Suitable for plants, suitability for both numerical and categorical data	Used pre-build model mostly, generation of a new model is time-consuming and complex	94.5%	A	Y	N
LncFinder	Logistic regression, SVM, RF, Extreme machine learning, Deep learning	Sequence related (genomic distance to lncRNA, genomic distance to protein-coding transcript, distance ratio), physicochemical characteristics (EIIP value)	Capable of large scale identification of lncRNA, present reliable results, enable reference free prediction	slow compared to CPC2	96.87%	A	Y	N
CREMA	Ensemble machine learning classifiers	Sequence related (length, GC content, hexamer score, alignment identity, ratio of alignment length and mRNA length, ratio of alignment length and ORF length, transposable elements, sequence divergence from	Enable reference free prediction, Suitable for plants, suitability for both numerical and categorical data		94%	A	Y	N

(*continued on next page*)

Table 2 (*continued*)

Tool	Algorithm	Features	Pros	Cons	Accuracy	Online(O)/ standalone (A)	Retrainable (Y/N)	Reference genome requirement (Y/N)
		transposable element, ORF length) Ficket score						
Coding-Non-Coding Identifying Tool (CNIT)	XGBoost	Sequence related, Translation related (max_score of most-like CDS, standard deviation of most-like CDS scores and MLCDS lengths, frequency of 64 codons)	Fast, robust, enable reference free prediction	Used pre-trained model only	98%	O/A	N	N
LGC (ORF **L**ength and **GC** content)	Feature relationship (Maximum Likelihood Estimation)	Sequence related (GC content, ORF length, coding potential score)	Effective on wide range of species	Used pre-trained model only	96.3%	O/A	N	N
Plant LncRNA Identification Tool (PLIT)	RF	Sequence related (transcript length, GC content, Ficket-score, hexamer score, maximum ORF length, ORF coverage, mean ORF coverage, codon bias)	Suitable for plants, More accurate in RNA-seq data	Not suitable for non-model species	93%	A	Y	Y
BiologicAl Sequences NETwork (BASiNET)	Decision tree on complex networks	Clustering coefficient, motif frequency, average shortest path, average betweenness centrality, average degree, maximum and minimum degree	New feature extraction from complex network measurement, Enable reference free prediction	–	99%	A	Y	N

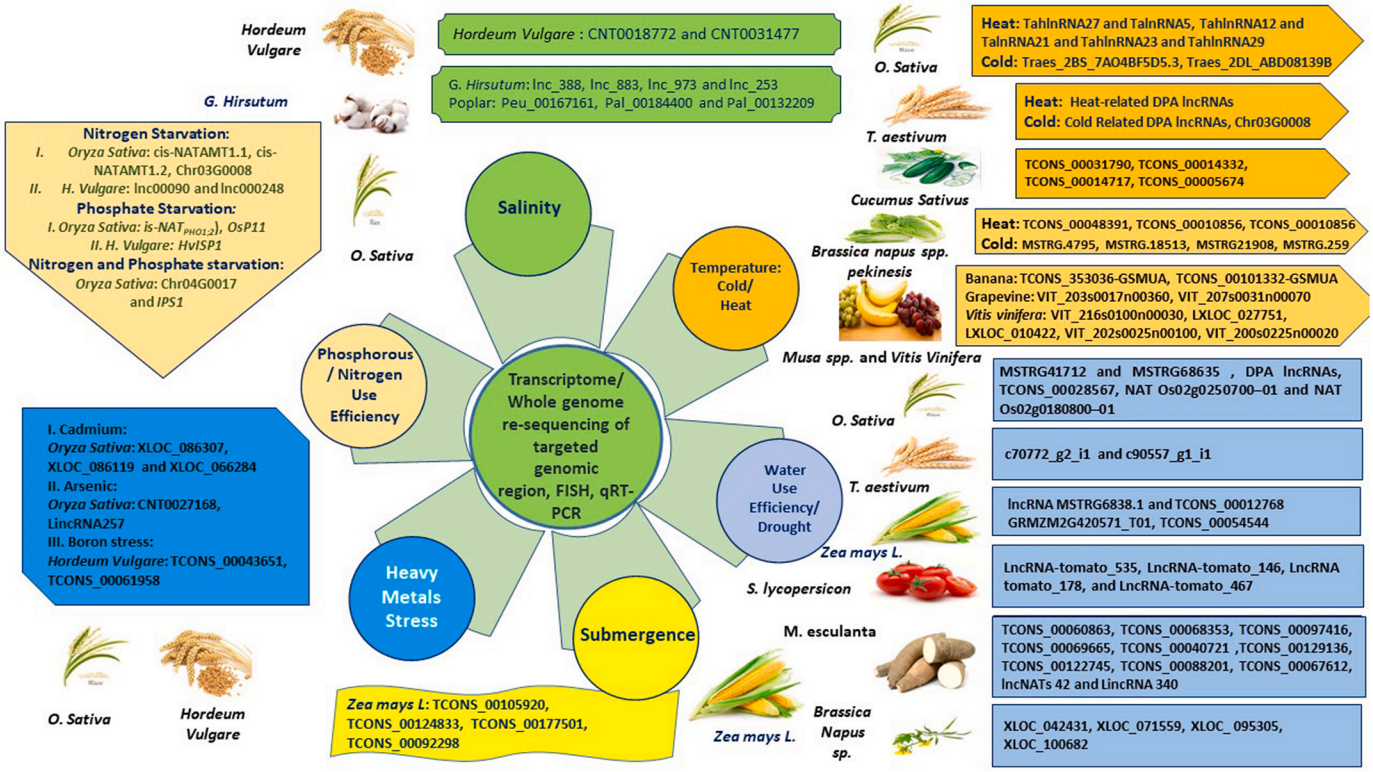

Fig. 3. Approaches for determination of lncRNA in plants and significant lncRNAs operating under abiotic stresses in major crop plants.

response (Cagirici et al., 2017). Systematic spatiotemporal transcriptional analysis at different developmental stages in maize showed the 653 potential lncRNA that plays a role in drought tolerance through mechanisms related to oxidoreductase activity, water binding, and electron carrier activity (Pang et al., 2019).

In foxtail millet, deep sequencing uncovered the ~584 lncRNAs, of which 17 lincRNAs and 2 NAR lncRNAs were drought-responsive and the lncRNA displayed collinearity with drought-responsive lncRNA in

sorghum, confirming the low conserved nature of lncRNA (Qi et al., 2013). In cassava, the first systematic study of strand-specific RNA-seq identified 682 high-confidence lncRNAs under cold and drought stress conditions. Out of that 16 lncRNAs had target mimics of cassava known miRNAs along with 153 NAT lncRNAs and 318 lncRNAs responsive to drought and cold stress which possessed the regulatory mechanism through hormone signal transduction, secondary metabolites biosynthesis, and sucrose metabolism pathway (Li et al., 2017). It has been found that 124 lncRNAs were drought-responsive among 833 high-confidence lncRNAs in cassava leaves and roots using strand-specific RNA-seq technology (Ding et al., 2019a). Drought-responsive lncRNAs induced by melatonin and polyethylene glycol (PEG) induction showed the presence of 1405 high-confidence lncRNAs, out of which 185 were differentially expressed (DE). The lncRNA regulated the expression network through calcium signaling, RNA regulation of transcription, ABA and ethylene metabolism, and redox homeostasis (Ding et al., 2019b).

Two drought stress contrasting rapeseed (*B. napus* L.) genotypes (Q2 and Qinyou8) under drought stress co-expressed lncRNAs, *XLOC_052298, XLOC_094954*, and *XLOC_012868* with plant hormone signal transduction and stress response (Tan et al., 2020). In tomato, RNA-seq analysis of tomato leaves under drought stress identified a total of 521 lncRNAs of which 244 drought-responsive lncRNAs were predicted to be putative targets of 92 tomato miRNAs (Eom et al., 2019). Drought-responsive gene expression patterns in roots of well-watered and drought-stressed alfalfa roots subjected to transcriptome sequencing revealed the involvement of lncRNAs especially *DN33069_c1g1* (Wan et al., 2022). Regulatory mechanisms of lncRNAs for drought response by ethylene and ABA synthesis, signaling, calcium signaling starch, sucrose synthesis, and various metabolic processes have been reported in rice (Weidong et al., 2020), maize, wheat, *Arabidopsis*, tomato, and cassava (Yan et al., 2019).

In addition, there has also been a report on tomato anther lncRNA transcriptome responses under drought stress using high-throughput RNA-Sequencing technology, that identified, in total, 3053 drought-responsive lncRNAs in tetrad to vacuolated uninucleate microspore (TED-VUM) and binucleate to mature pollen (BIN-MP) anthers of which 1955 and 1098 were up- and down-regulated, respectively. A large number of lncRNAs were identified to be highly co-expressed with target protein-coding genes related to phytohormone metabolism and are known to possess essential roles in pollen development. This study provides valuable insights into lncRNA function in pollen development under drought stress (Lamin-Samu et al., 2022).

The lncRNA possesses enormous potential for coping with drought stress by controlling drought-responsive hormonal signaling pathways at the transcription, post-transcriptional, and epigenome levels. These lncRNAs act as target mimics for various miRNAs possessing a regulatory role in the control of the expression of several drought-responsive target genes or transcription factors. Our group at ICAR-IIRR has deciphered the mechanism of aerobic adaptation in rice through transcriptome sequencing of aerobic-adapted and flooding-adapted genotypes at the panicle initiation stage under controlled conditions (Phule et al., 2019). The publicly available RNA-seq or transcriptome datasets can be very well utilized for mining the lncRNAs associated with the traits of interest. Such studies provide cost-effective approaches for the characterization of lncRNA under varying stress treatments in plants.

7.2. lncRNAs in cold stress

Plant growth and development are the key factors for productivity that are dependent on temperature either low or high temperature. Low temperature is one of the critical abiotic stresses that leads to a decrease in plant productivity. Several genomic regions i.e., quantitative trait loci (QTLs), complex regulatory gene networks of C-repeat binding factors (*CBFs*) and cold regulated genes (*COR*) (Amor et al., 2009), and a variety of novel regulatory miRNAs (Kang and Liu, 2015) which help to cope up in cold stress. Advancements in sequencing technologies have provided a huge information platform to elucidate the genes and QTLs involved in cold tolerance in plants (Jha et al., 2017). For example, lncRNAs including *COOLAIR*, *COLDWRAP*, and *COLDAIR* play a key role to induce flowering in *Arabidopsis* (Heo and Sung, 2011; Kim et al., 2017; Yuan et al., 2016), *M. esculenta* (Li et al., 2017), *B. rapa* (Corona-Gomez et al., 2020; Shea et al., 2019), *Musa* sp., *Vitis vinifera* (Wang et al., 2019), and *Brachypodium* (Jiao et al., 2019).

Vernalization is a well-studied phenomenon that helps to flower under favorable conditions in spring and prevents flowering during vegetative growth in winter (Kim et al., 2009). In *Arabidopsis*, the *FLC* is a regulatory locus that acts as a repressor of flowering during cold (Bastow et al., 2004) and controls flowering time epigenetically (Whittaker and Dean, 2017). In these circumstances, vernalization plays a key role in inhibiting the expression of the *FLC* gene using lncRNA under cold stress through polycomb-mediated epigenetic regulation (Q. Sun et al., 2013; Swiezewski et al., 2009). The *COLDWRAP* is an *FLC*-promoter-derived lncRNA, polycomb binding lncRNA which plays a role in stable repression during vernalization in *Arabidopsis* (Kim et al., 2009). *SVALKA* and cryptic antisense *CBF1* (*asCBF1*) lncRNA help in the cold acclimation mechanism in plants by inhibiting transcription of the *CBF1* gene (Kindgren et al., 2018). Similarly, cold-responsive lncRNAs *viz*., 4050 NAT lncRNAs and 2460 lincRNAs have been reported using strand-specific RNA-seq in *Arabidopsis* (Zhao et al., 2018). In response to cold, suppression of flowering occurred with the recruitment of WDR5a complex for epigenetic modification and consequent MAS (NAT lncRNA_2962) activated transcription of MADS AFFECTING FLOWERING4 (*MAF4)* locus (Zhao et al., 2018). Likewise, paralogs of the *FLC* locus act as a repressor of flowering in *B. rapa* (Shea et al., 2019). In *B. rapa*, NATs involved at the *FLC2* locus during cold stress have been reported (Li et al., 2016). Transcriptome data analysis of cold-treated leaves of *Brassica* showed the presence of three *BrFLC* loci that carried *BrFLC2 as* (*MSTRG.2765*), had homology with the upregulated transcript of *COOLAIR* in *Arabidopsis* under cold stress (Shea et al., 2019).

In *V. vinifera*, RNA-Seq analysis potential identified 284 novel up-regulated lncRNAs, 182 novel down-regulated lncRNAs, 242 differentially expressed lncRNAs that targeted 326 protein-coding genes, and different stress-responsive genes such as *CBF4* transcription factor genes, *LEA* (Late Embryogenesis Abundant) protein genes, and *WRKY* transcription factor genes (Wang et al., 2019). In *M. esculenta*, 318 lncRNA were reported under cold stress, and *lincRNA419, 207,* and *234* were upregulated during functional validation under drought stress (Li et al., 2017).

To unravel the role of miRNAs, lncRNAs, and the stress-responsive gene in regulatory mechanism under cold stress, *lincRNA159* was used as a target mimic for miR164 which decreased the expression of the *NAC* gene (Li et al., 2017). In *Arabidopsis*, *TAS1a* lncRNA was regulated by an alternative splicing mechanism under cold stress. There are two different forms of transcript *TAS1a* i.e. unspliced *AT2G27400.1* which contains miR173 binding site and *tasiRNAs* generation site and intro less spliced transcript *AT2G27400_ID1*. As the temperature decreased, down-regulation of spliced *AT2G27400_ID1* and upregulation of unspliced *AT2G27400.1* transcript were observed. Thus, alternative splicing, chromatin remodeling, and transcriptional gene regulation play a key role in cold tolerance (Calixto et al., 2019).

With a crop-specific perspective, Li et al. (2023) offered a view on the regulatory roles of ncRNAs in tomato's response to a spectrum of stresses, including cold. The authors highlight the recent discoveries of a plethora of ncRNAs, including miRNAs and lncRNAs, identified under various stress conditions in tomato. For instance, specific miRNAs have been identified in response to infections by *Phytophthora infestans*, while others have been observed in pollen under heat-stress conditions. The authors emphasized that these ncRNAs, particularly lncRNAs, play critical roles in tomato's defense mechanisms against both abiotic and biotic stresses. This research also provided insights into the biogenesis of

these ncRNAs and their regulatory roles, offering a foundation for future research aimed at enhancing tomato's resilience against environmental stresses.

7.3. lncRNA in salinity stress

Salinity is also one of the major abiotic stresses that lead to decrement in plant growth and productivity. Due to saline condition, plants especially legume production has been reported to be more affected (Jha et al., 2019). In order to survive the high salinity stress, plants have adapted several biochemical and molecular mechanisms, that includes ncRNAs (Chen et al., 2019b; Sun et al., 2016; Tian et al., 2020; Wang et al., 2015). The ncRNAs have been reported to target the genes for photosynthesis, TFs regulating growth, salinity-responsive hormone signaling genes, genes that lower the uptake of toxic ions, viz., Na^+, and genes that limit ROS activity (Khandal et al., 2017; Sun et al., 2016; Wang et al., 2015).

Salinity stress is one of the major abiotic challenges that plants face, affecting their growth, development, and productivity. In recent years, long non-coding RNAs (lncRNAs) have emerged as pivotal regulators in the plant's response to salinity stress (Yang et al., 2023b). Explicitly, under salinity conditions, certain lncRNAs can be either induced or suppressed, thereby modulating the expression of target genes involved in salinity response mechanisms. A study on tomato, a model plant species, highlighted the significant roles of lncRNAs in response to various abiotic stresses, including salinization (Li et al., 2023). However, while the involvement of lncRNAs in salinity response is evident, the precise molecular mechanisms and pathways through which they exert their regulatory roles remain to be fully elucidated. The current literature, although rich in identifying the presence and potential roles of lncRNAs, often lacks a deep dive into the specific molecular interactions and cascades triggered by these lncRNAs in response to salinity stress. As the field progresses, a more detailed understanding of these mechanisms will be pivotal for harnessing the potential of lncRNAs in improving plant resilience to salinity and other abiotic stresses.

Another study in salinity stress by Luo et al. (2022) sheds light on the intricate dynamics of lncRNAs in *Chenopodium quinoa*, a crop renowned for its salinity resilience. Leveraging state-of-the-art high-throughput RNA-seq technology against a high-quality quinoa reference genome, the study meticulously identified an impressive array of 153,751 high-confidence lncRNAs. Intriguingly, under salinity stress conditions, a subset of 4,460 lncRNAs exhibited differential expression, underscoring their potential regulatory roles. The study further delineated a robust correlation between salt-responsive lncRNAs and their proximal genes, hinting at intricate regulatory networks. Through the construction of a weighted co-expression network, Luo et al. (2022) unveiled seven modules significantly correlated with salt treatments, encompassing pivotal hub genes, including transcription factors and lncRNAs. This intricate interplay between lncRNAs and transcription factors offers a novel perspective on the molecular mechanisms underpinning quinoa's salinity tolerance. While Luo et al.'s findings provide a robust foundation, they also pave the way for future studies, emphasizing the functional validation of these lncRNAs and their broader implications in enhancing agricultural resilience in saline-prone environments.

In soybean, 3030 lincRNAs and 275 lncNATs have been reported in salt-stressed roots (Chen et al., 2019b). The lncRNAs have been reported to accumulate during salt stress in plants viz. *Arabidopsis* (Di et al., 2014b) and *M. trunculata* (Wang et al., 2015). In groundnut, transcriptomic analysis for a genome-wide survey of lncRNAs uncovered 1442 lncRNAs. Down-regulation of *TCONS_ 00292946* lncRNA in roots was observed within 12 h of salinity stress and then up-regulation after 24 h was noted. Another *TCONS_00176941* lncRNA was up-regulated in roots within 12 h during salinity stress and down-regulated in leaves, while *TCONS_00011551* was up-regulated slowly with salinity stress (Tian et al., 2020). Differential expression was studied in grapevine and *C. sinensis* roots under salt stress, 1661 lncRNAs, and 172 lncRNAs were found to be expressed respectively (Jin et al., 2020; Wan et al., 2020). In *M. truncatula*, *TCONS_00116877* lncRNA induces the expression of the *Medtr7g094600* gene (glutathione peroxidase) which alleviates ROS-related stress in roots during salinity stress (Wang et al., 2015). Similarly, ROS scavenging activity was observed to regulate salt stress-responsive genes by *lncRNA973* in cotton (Zhang et al., 2019a). In sorghum, the differential study was performed under salt stress, 26 lncRNAs in salt-tolerant *M-81E* and 133 lncRNAs in salt-sensitive Roma strains were observed (Sun and Chen, 2020). Two closely related poplars (*P. euphratica* and *P. alba* var. *pyramidalis*) were studied under salt stress using strand-specific RNA-seq which uncovered 10,646 and 10,531 lncRNAs (Ma et al., 2019). The interaction of miRNA and lncRNA in soybean root and leaf tissues under salinity stress was studied using comprehensive small RNA transcriptome analysis at six data points. Under salinity stress, tissue-specific expression patterns of miRNA interaction with lncRNA were recorded for two pairs *viz. miR166-i-5p*-lncRNA Gmax_MSTRG.35921.1 and *miR394a-3p*-lncRNA *Gmax MSTRG.18616.1* (C. Li et al., 2022). Such interaction-specific miRNA-lncRNA interaction can be explored under varying abiotic stresses in plants.

Differentially expressed root-specific lncRNAs induced upon salinity stress in salinity tolerant and salinity sensitive chickpea genotypes were mined from NCBI publicly available transcriptome datasets (Kumar et al., 2021). The identified lncRNAs regulated the salt stress-responsive genes for the potassium transporter, transcription factors (*AP2, NAC, bZIP, ERF, MYB, WRKY*), and aquaporins (*TIP1-2*, *PIP2-5*). The simple sequence repeats markers (SSRs) molecular markers based on lncRNA i.e., lncRNA-SSRs were also identified. This type of lncRNA-based SSRs is a new generation of highly efficient molecular marker systems that have the potential for molecular breeding and characterization deployment. Transcriptome datasets generated from salt-treated and untreated leaves of the *M. truncatula* ecotype presented differential expression and interaction co-relation networks between mRNAs, lncRNAs, circRNAs, and miRNAs. A significantly higher expression of *novel_circ_000001* (from *MTR_1g116947* gene) was recorded upon salt treatment in addition to salinity-responsive regulatory lncRNAs, miRNAs, and ceRNAs mRNA. It was noted that lncRNA *MSTRG.15691.1-SPL* transcription factors-novel miRNA interacted in response to salt stress through differential patterns of expression (An et al., 2022). In response to salinity stress, seedlings of two maize inbred lines with contrasting salt tolerance displayed differential expression of lncRNAs and target genes of transcription factor families. Through a gene network co-expression analysis, a salt-tolerant module of five lncRNAs, 18 TFs, and 56 functional transcripts was constructed. The lncRNA *MSTRG.8888.1 via* altering the *bHLH* protein level regulated the upregulation of salt-tolerant transcripts by binding their promoters (trans-acting) (P. Liu et al., 2022). In barley root and shoot samples, the expression levels of maize (*CNT0018772*) and rice (*CNT0031477*) lncRNAs were evaluated under salt stress in roots and shoots. It was found that there was no significant statistical difference between barley varieties for the expression level of *CNT0018772* ($p > 0.05$). However, the expression level of *CNT0031477* ($p < 0.05$) showed a statistically significant difference between barley varieties (Karlik and Gozukırmızı, 2018).

Transcription factors such as DREB (dehydration responsive element binding factors), bZIP (basic leucine zipper), MYB (v-myb avian myeloblastosis viral oncogene homolog) sense and transduce early responses to salt stress in plants. MYB transcription factors, one of the most important TSs have been known to possess a role in abiotic stress tolerance (Yao et al., 2022; Yu et al., 2017). In wheat, alkalinity stress-responsive lncRNAs were identified in alkaline-tolerant and sensitive bread wheat cultivars through lncRNA sequencing. Wei et al., 2022 demonstrated virus-induced gene silencing (VIGS) for understanding the regulatory function of lncRNA under salinity stress. The transient knock-down of differentially expressed lncRNAs *viz*. *L0760* and *L2098* displayed sensitivity to alkaline stress while lncRNAs *viz*., *L6247*, *L0208*, and *L3065* displayed increased tolerance to alkalinity.

Strand-specific transcriptome sequencing depicted under salinity stress lncRNAs *viz*. *lncRNA13472*, *lncRNA11310, lncRNA2846* were up-regulated in the salinity tolerant sweet sorghum, and *lncRNA26929* and *lncRNA14798* were down-regulated upon salt treatment in the salt-sensitive genotype. The lncRNAs regulated the expression of target genes related to ion transport, protein modification, transcriptional regulation, and material synthesis and transport (Sun et al., 2020). In wild tomato *S. pennellii* and cultivated tomato M82, the high-throughput sequencing led to the identification of the 1044 putative lncRNAs. Among them, 154 and 137 lncRNAs were identified to show the differential expression in M82 and *S. pennellii*, respectively. The functional analysis of target genes of these differentially expressed lncRNAs (DE-lncRNAs), led to the observation that some genes respond positively to salt stress by being involved in various pathways such as the ABA signaling pathway, brassinosteroid (BR) signaling pathway, ethylene (ETH) signaling pathway, and anti-oxidation process. The study identified the role of salt-induced lncRNAs in tomato roots at the genome-wide levels by constructing a salt-induced lncRNA-mRNA co-expression network and this finally contributed to understanding the molecular mechanisms of salt tolerance in tomatoes from the perspective of lncRNAs (Li et al., 2022). Understanding such expression networks can reflect on the target for further functional validation.

7.4. lncRNAs in nutrient use efficiency

Nutrient availability in the soil can have an immense effect on plant growth and development which ultimately helps to increase yield. Various membrane transporters are involved in the nutrient uptake from the soil. Majorly, 70% of agricultural lands are deficient in inorganic phosphates (Pi), which requires external phosphates as input or else reduction in productivity and yield. Phosphate is one of the essential mineral nutrients contributing to plant growth and development (Jabnoune et al., 2013; Lv et al., 2016). Phosphate-starvation-inducible lncRNAs *At4* and *AtIPS1* regulate the phosphate balance and phosphate starvation and act as target mimics of miR399 and compete with PHOSPHATE2 (*PHO2*) mRNA for interacting with miR399 and thereby act as non- cleavable miRNA target. It also leads to the sequestration of *miR399* to reduce *miR399*-mediated cleavage of *PHO2* (Franco-Zorrilla et al., 2007; Shin et al., 2006). The *PHO2* has been reported to possess a critical role in phosphate signaling and is one of the targets of *miR399* (Shin et al., 2006).

The functional role of lncRNA in phosphate homeostasis has been well illustrated (Franco-Zorrilla et al., 2007; Jabnoune et al., 2013). In *Arabidopsis*, differentially expressed ~309 lncRNAs among 1212 lncRNAs were identified in Pi-sufficient (P+) and Pi-deficient (P-) plants using strand-specific RNA sequencing (Yuan et al., 2016). The lncRNA *Npc536* was induced in roots and leaves of *Arabidopsis* during drought and Pi starvation stress affected root growth during salt stress. This highlights the conserved and crosstalk nature of lncRNAs under multiple stresses. Moreover, eTM-type lncRNA *IPS1* has been directly involved in phosphate homeostasis during the phosphorous deficient condition and acts as target mimics for miR399 (Franco-Zorrilla et al., 2007). In rice, *cis-NATPHO1;2* (cis-natural antisense RNA) increases the expression of sense gene *PHOSPHATE1;2* (*PHO1;2*) which is an ortholog of *PHO1* gene in *Arabidopsis* (Hamburger et al., 2002; Jabnoune et al., 2013). Many miRNAs have a major role in regulating phosphate homeostasis (Chiou et al., 2006; Lin et al., 2013). It has been shown that *PHO2* encoding ubiquitin conjugating E2 enzyme with *PHO1*, membrane protein helps to load phosphate in the xylem and acts as an important regulator for phosphate homeostasis (Hamburger et al., 2002). Thus, the role of miRNA itself indicates the involvement of lncRNA in phosphate homeostasis. Phosphate Deficiency-Induced lncRNAs (*PDILs*) have been characterized to regulate *Pi* deficiency signaling. Regulation of signaling under Pi deficient condition by *PDIL1* suppresses the degradation of *MtPHO2* using *miR399*, whereas *PDIL2* and *PDIL3* are found to be directly involved in the transcriptional regulation of Pi homeostasis (Wang et al., 2017).

Nitrogen (N) is also one of the important macronutrients for plant growth and development. It is a major component of amino acids, the energy-carrying molecule ATP (adenosine triphosphate), and N metabolism (Hawkesford and Griffiths, 2019). Plant productivity is dependent on nitrogen uptake which is performed by various regulatory and transporter genes for nitrogen use efficiency (Chen et al., 2016). Several N-responsive lncRNAs have been reported in crops like rice (Shin et al., 2018), Populus (Chen et al., 2016), barley (Chen et al., 2020), and maize (Lv et al., 2016). In rice, homeostasis of nitrogen (N) by lncRNAs such as *cis-NAT*$_{AMT1.1}$ and *cis-NAT*$_{AMT1.2}$ targeting the ammonium transporter (AMT) gene is well studied (Shin et al., 2018). In *Arabidopsis* trans-acting siRNA3 (*TAS3*) a lincRNA plays a crucial role to target the nitrate transporter2 gene to regulate nitrogen transport in nitrogen-deficient conditions (Fukuda et al., 2019). Our group at ICAR-IIRR has observed selective down-regulation of metabolic pathways as an acclimation strategy for nitrogen use efficiency (NUE) using transcriptome analyses (Neeraja et al., 2021). Also, all-encompassing physiological responses under varying levels of soil nitrogen in the whole rice plant parts have been documented. It can be extended that such responses can have epigenetic regulation and thus need to be studied all together with lncRNA sequencing, bi-sulphite, RNA-sequencing and targeted resequencing.

Potassium is a crucial macronutrient implicated in homeostasis, osmoregulation, membrane polarization, etc. Enhancing the potassium use efficiency (KUE) is equally essential as water, nitrogen and phosphate for maintaining plant fitness. The seedlings transcriptomic analysis under low and sufficient concentrations of potassium (K) of model plant, tobacco revealed significant differential expression of 242 lncRNAs under potassium starvation. Through co-expression network analysis, module-trait analysis, module membership (MM) ranking, the lncRNAs *viz*. *MSTRG.6626.1, MSTRG.11330.1,* and *MSTRG.16041.1* were found to be associated with transcript factors *viz*. MYB, C3H, NFYC, and antioxidative stress in response to the K starvation stress (P. Chen et al., 2022). Parallel studies need to be undertaken in major cereal crops, especially rice, to understand the K nutrient physiology and molecular mechanism of KUE.

Boron (B) is a major micronutrient essential for plant growth and development, membrane integrity, and cell wall synthesis (Camacho-Cristóbal et al., 2002; Camacho-Cristóbal and González-Fontes, 2007). In *Poncirus trifoliate*, strand-specific sequencing analysis revealed 2101 lncRNA under boron (B) deficient condition with 729 up-regulated and 721 down-regulated lncRNAs. The DE lncRNA targeted the genes for calcium signaling and plant hormone signal transduction pathway (Zhou et al., 2019). The nutrient stress-responsive lncRNA can be deployed for functional studies.

There is a need to enhance the studies on nutrient uptake, and utilization efficiencies in plants for deciphering the molecular mechanism including lncRNA. Increasing nutrient efficiency has been the foremost objective in the current climate change scenario, deploying lncRNA as the target is one of the most feasible options for the same.

7.5. lncRNAs in metal toxicity

Metal toxicity is one of the major challenges for agriculture and human health. It arises because of various reasons like the outcome of rapid industrialization, heavy doses of inorganic fertilizers, and excessive use of contaminated irrigated water (Ali et al., 2019). Plants are adapting the mechanism to regulate the movements of heavy metals from the soil, this uncovers the role of ncRNA including lncRNA and miRNA in the regulation of this complex mechanism. This will be a key approach to reducing metal toxicity in plants and ultimately in human consumption (Feng et al., 2016; Zhou et al., 2012).

The lncRNAs have also emerged as pivotal molecular players, intricately modulating a myriad of cellular pathways to mitigate the detrimental effects of heavy metals. A recent study by Lu et al. (2023) delves

Table 3
LncRNA involved in abiotic stress tolerance in plants.

Sr. No	*Plants*	lncRNAs	Abiotic Stress	Regulation mechanism	Expression	References
1	*Triticum aestivum*	LncRNA_082364, LncRNA_047461, LncRNA_008977, LncRNA_061738, LncRNA_018111(Roots)	Ca^{2+}-channel blocking	Trans-acting factor	Induced	Ma et al. (2018)
		LncRNA_074658, LncRNA_000823, LncRNA_058136 (Roots)	Ca^{2+}-channel blocking	Trans-acting factor	Repressed	
		MSTRG.148484.1 and MSTRG.188250.2 (DS) MSTRG.148484.1 and MSTRG.188250.2 (DT)	Drought	It centered on novel-miR-340 and novel-miR-417 which regulated different genes and plays role in wheat drought stress response	Induced	Li et al. (2022a)
	Triticum turgidum ssp. *durum*	Traes_2BS_7AO4BF5D5.3	Cold	Targeting cold acclimation protein gene WCOR413	Induced	Díaz et al. (2019)
		Traes_2DL_ABD08139B	Cold	Targeting flower promoting factor 1 like protein 3	–	
	Triticum aestivum	TahlnRNA27 and TalnRNA5	Heat	Histone acetylation of TalnRNA5 and putative miRNA precursor	Upregulated	Xin et al. (2011)
	Triticum turgidum ssp. *dicoccoides*	c70772_g2_i1 and c90557_g1_i1	Drought	lncRNAs-miRNA-mRNA networks	Upregulated	Cagirici et al. (2017)
2.	*Zea mays*	GRMZM2G574383_T01 (Roots), TCONS_12690, TCONS_00007700, TCONS_00000649 (Leaves)	Drought	Putative miRNA precursor	Upregulated	Zhang et al. (2014)
		TCONS_00056395 (Leaves) TCONS_00037470 and TCONS_00012768 (Roots)			Downregulated	
		MSTRG.11125, MSTRG.15555, MSTRG.31362	Heat	Unknown	Induced	Lv et al. (2019)
		MSTRG.4636, MSTRG.38321, MSTRG.63799	Heat	Unknown	Repressed	
		DElncRNAs	Heat	Cis-and trans-regulation	–	Hu et al. (2022)
		MSTRG.6838.1	Drought	Cis-acting factor	Repressed	Pang et al. (2019)
		TCONS_00177501	Waterlogging	co-expression analysis revealed lncRNAs to be involved in 11 transcription modules, 10 of which were significantly associated with WS	Upregulated	Yu et al. (2020)
		GRMZM6g851663_T01 GRMZM6g320373_T01	Drought Salinity	Unknown	Upregulated	Forestan et al. (2016)
		lncRNA *MSTRG.8888.1*	Salinity	Trans-acting factor	Upregulated	(P. G. Liu et al., 2022)
3.	*Oryza rufipogon*	lncRNAs MSTRG69391 MSTRG41712 and MSTRG68635	Drought	Transcription factor, calmoduli, HSP genes, mitochondrial carrier Protein gene etc.	Upregulated	Weidong et al. (2020)
		lncRNAs MSTRG65848 MSTRG27834 and MSTRG46301	Drought	–	Downregulated	
	Oryza sativa	lncRNAs	Alkaline-salt stress	lncRNAs acting as competing endogenous RNA(ceRNAs) in the mechanisms underlying alkaline-salt resistance	Induced	Rehman et al. (2023)
		TCONS_00028567	Drought	The precursor of osa-MIR1428e might regulate ABA signaling through its critical gene SAPK10	Upregulated	Li et al. (2019)
		lncRNA.2-FL	Drought	It regulating sense and signaling, ion homeostasis and oxidative stress tolerance	Upregulated	(Mirdar Mansuri et al., 2022)
		Drought-related DPA lncRNAs	Drought	nuclear retention and co-expressed with protein-coding genes	Downregulated	Yuan et al. (2018)
		NAT Os02g0250700–01, NAT Os02g0180800–01	Drought	NAT lncRNAs	Upregulated	Chung et al. (2016)
		DRILs	Drought	Transcriptional regualtion	upregulated	Oh et al. (2022)
		Chr03G0008, Chr04G0017	Nitrogen and Phosphate starvation	Changed in response to both N and Pi starvation	Upregulated	Shin et al. (2018)
		IPS1	Nitrogen and Phosphate starvation	RHC-class lncRNA, induced in both N and Pi starvation, especially in rice roots	Upregulated	
		CNT0027168	Arsenic	Targeted by high shoot As-17275 and root-CK high 1309 which AGO1-enriched sRNAs	Repressed	Tang et al. (2019)
		LincRNA257	Arsenic	Targeted by root CK- high 13603 and root CK- high 2928 which AGO1-enriched sRNAs	Repressed	
		Chr03G0008	Cold	Induce expression under cold condition	Upregulated	
		Heat-related DPA lncRNAs	Heat	Upregulated under heat stress	Induced	Yuan et al. (2018)

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Table 3 (*continued*)

Sr. No	*Plants*	lncRNAs	Abiotic Stress	Regulation mechanism	Expression	References
		Cold Related DPA lncRNAs	Cold	Upregulated under cold stress	Upregulated	
		3714 high-reliability lncRNAs	Drought Salinity	Response to both drought and salinity stress	Upregulated	Singh et al. (2017)
		Cis-NATPHO1;2	Phosphate starvation	–	Upregulated	Jabnoune et al. (2013)
		XLOC_086307, XLOC_086119, XLOC_066284	Cadmium stress	Genes regulating cysteine and methionine metabolism and carotenoid biosynthesis	Upregulated	Chen et al. (2018)
		XLOC_058523, XLOC_104363, XLOC_059778, XLOC_122123, XLOC_125848, XLOC_098316		Genes regulating the phenylpropanoid biosynthesis Photosynthesis related activities		
4.	*Arabidopsis thaliana*	AT1G34844, AT3G26612 l	Cold stress	NAT antisense transcript	Induced	Calixto et al. (2019)
		TAS3 (trans-acting siRNA3)	Low-nitrogen stress	Trans-acting factor, Maintains cellular N homeostasis by multiple tasiRNAs targeting ARF2, 3, and 4	Repressed	Fukuda et al. (2019)
		COLDAIR (NATs/lincRNAs)	Cold stress	Histone modification	Induced	Heo and Sung (2011)
		COOLAIR (NATs/lincRNAs)		Promoter interference, Transcriptional regulation, Chromatin remodeling	Induced	Sun et al. (2013)
		SVALKA		SVK repression - *CBF1* for cold acclimation	Induced	Kindgren et al. (2018)
		COLDWRAP		COLDWRAP reinforce stable repression of *FLC* under cold stress	Induced	Kim and Sung (2017)
		TAS1a		By alternative spicing of lncRNA	Repressed	Calixto et al. (2019)
		MAS		Histone modification and role of NAT-lncRNAs regulating gene expression	Induced	Zhao et al. (2018)
		COLD INDUCED lncRNA 1(CIL 1)		Regulate the expression of multiple stress-related genes during the seedling stage	Induced	Liu et al. (2022)
		npc536, npc60	Salt	NAT antisense siRNAs	Induced	Amor et al. (2009)
		Drought Induced RNA (DRIR)	Salt	Affecting fucosyltransferase or *NAC3* transcription factor	Induced	Qin et al. (2017)
		DROUGHT INDUCED lncRNA (DRIR)	Drought	Participate in upregulation of drought responsive genes	Induced	
		lncRNA	Salt Heat	–	Repressed	Xu et al. (2015)
		Lnc-225, Lnc-173	Light	–	Induced	Di et al. (2014)
		asHSFB2a	Heat	Antisense transcription	Induced	Wunderlich et al. (2014)
		IPS1 (lincRNAs)	Phosphate starvation	Target mimicry	Induced	Franco-Zorrilla et al. (2007)
		XLOC_020833, XLOC_001691 and XLOC_013661		Regulating phosphate homeostasis by targeting miR399	Induced	Yuan et al. (2016)
		AT4G07235, AT4G09215, AT3G00800	DNA Damage	It helps to recover plants from genotoxic stress	Induced	Durut et al. (2023)
5.	*Solanum lycopersicum*	LncRNA-tomato_535,LncRNA-tomato_146, LncRNA-tomato_178	Drought	Target mimicry	Induced	Eom et al. (2019)
		LncRNA_tomato_467	Drought	Unknown	Induced	
		lncRNAs	Salt Drought	RdDM pathway	Downregulated	Huang et al. (2016)
6.	*Solanum pennellii*	lncRNAs	Salinity	Differential expression in salt stress	upregulated	Li et al. (2022b)
7.	*Vitis vinifera*	VIT_216s0100n00030, LXLOC_027751, LXLOC_010422, VIT_202s0025n00100	Cold	Cis-acting factor	Induced	Wang et al. (2019)
		VIT_200s0225n00020	Cold	Trans-acting factor	Repressed	
		VIT_203s0017n00360, VIT_207s0031n00070, VIT_201s0011n00530, VIT_209s0002n00340, VIT_213s0158n00020, VIT_213s0067n00110, VIT_200s0225n00020	Cold	Up and down-regulation of the target genes	Up and down regulated	
8.	*Cleistogenes songorica*	MSTRG.43964.1, MSTRG.4400.2	Drought	Target mimicry	Induced	Yan et al. (2019)
		XLOC_063105 and XLOC_115463	Drought	regulating two adjacent coding genes CotAD_37096 and CotAD_12502 for plant hormone pathways	Induced	(Li et al., 2016)
		LncRNA973	Salt	Trans-acting factor	Induced	Zhang et al. (2019)
		lnc_388, lnc_883, lnc_973 and lnc_253	Salt	Trans-acting factor, targeting *Gh_A09G1182, Gh_D03G0339* genes, regulating ghr-miR399 and ghr-156e by eTM	Induced	Deng et al. (2018)
		GhDAN1	Drought	Under stress, reduced GhDAN1 expression which releases the AAAG	Reduced	Tao et al. (2021)

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Table 3 (*continued*)

Sr. No	*Plants*	lncRNAs	Abiotic Stress	Regulation mechanism	Expression	References
				motif site of the drought-related genes to adapt to environmental drought stress		
		LncRNA354	Salt	Expression of LncRNA354 in is decreased under salt stress, thus impairing the binding to miR160b and it increases the expression of miR160b which inhibits the expression of GhARF17/18 to enhance salt stress tolerance.	Reduced	Zhang et al. (2021)
10.	*Spirodela polyrhiza*	TCONS_00024229 TCONS_00057092 TCONS_00018576 TCONS_00023928 TCONS_00045028	Salt	Cis-acting factor	Induced	Fu et al. (2020)
		TCONS_00033722 TCONS_00018793 TCONS_ 00045706 TCONS_00057092 TCONS_ 00045512	Salt	Target mimicry	Induced	
11.	*Brassica juncea*	TCONS_00051908	Heat	Unknown but, act as targets and eTMs for the miRNAs	Induced	Bhatia et al. (2020)
		TCONS_00088973	Drought	Unknown But act as targets and eTMs for the miRNAs	Induced	
12.	*Brassica napus*	XLOC_012868	Drought	Unknown	Repressed	Tan et al. (2020)
		XLOC_052298, XLOC_094954	Drought	Unknown	Induced	
13.	*Brassica. rapa*	MSTRG.4795, MSTRG.18513, MSTRG21908,	Cold	Epigenetic modification at *BrFLC2as* locus, epigenetic modification at *Bra024350* and *Bra031888, Bra024351* and *Bra031884* loci	upregulated	Shea et al. (2019)
		MSTRG.259, MSTRG.491, MSTRG.17153			Downregulated	
14.	*Brassica rapa* spp. *chinensis*	TCONS_00048391, TCONS_00010856	Heat	Target mimicry, by targeting bra-miR164a.	Induced	(A. Wang et al., 2019)
		lncRNAs	Cold and Heat	Role in crosstalk between cold and heat stresses	–	Song et al. (2016)
15.	*Medicago sativa*	*DN33069_c1g1*	Drought stress	Differential expression pattern	–	Wan et al. (2022)
16.	*Medicago truncatula*	MtCIR1	Cold stress	Cis-acting factor	Induced	Zhao et al. (2020)
		MtCIR2		Overexpression of MtCIR2 led to higher survival rate and lower cell membrane damage, regulate MtCBF/DREB1s expression and glycometabolism	Upregulated	Zhao et al. (2023)
		lncRNA *MSTRG.15691.1-SPL*	Salt stress	Differential expression patterns	–	An et al. (2022)
17.	*Manihot esculenta*	NcM9574	Cold stress	Cis-acting factor	Induced	Suksamran et al. (2020)
		NcP12248	Cold stress	Cis-acting factor	Repressed	
		NcP456	Cold stress	Trans-acting factor	Repressed	
		NcM17949	Drought stress	Cis-acting factor	Induced	
		NcP12197	Drought stress	Trans-acting factor	Induced	
		NcM15664	Drought stress	Trans-acting factor	Repressed	
		lincRNA159	Cold stress	Regulate cold tolerance targeting miRNA164 based on target mimicry mechanism	Downregulated	Li et al. (2017)
		LncRNAs 682, lncNATs 42, lincRNA340	Cold and drought	By targeting miR169 based on target mimicry	Up and down regulated	
		TCONS_00097416	Drought Stress	Ethylene signaling	Upregulated and co-expressed	Ding et al. (2019a)
		TCONS_00069665		Target miR156		
		TCONS_00060863, TCONS_00068353		ABA signaling regulation by targeting genes involved in ABA catabolism		
		TCONS_00040721		miR164, miR169, and miR172		
		TCONS_00003360, TCONS_00015102, TCONS_00149293		Calcium signaling, ABA, ethylene metabolism	Upregulated	Ding et al. (2019b)
		DROUGHT-INDUCED INTERGENIC lncRNA		Proline accumulation, and enhance the expression of drought-related TFs	Induced	DONG et al. (2022)
		TCONS_00129136,TCONS_0012275	Drought and ABA stress	cassava drought response *via* ABA-dependent pathways, with miRNA regulation playing a role	Downregulated	Wu et al. (2019)
18.	*Sorghum bicolor*	LncRNA13472	Salt stress	Target mimicry	Induced	Sun et al. (2020)
		LncRNA14798, LncRNA11310, LncRNA2846, LncRNA26929	Salt stress	Target mimicry	Repressed	
19.	*Hordeum vulgare*	TCONS_00043651	Boron stress	Target mimicry	Induced	Unver and Tombuloglu (2020)
		TCONS_00061958	Boron stress	Cis-acting factor	Induced	
		lnc00090 and lnc000248	Nitrogen Starvation	Target mimics for hvu-miR399	Induced	Chen et al. (2020)
		CNT0018772, CNT0031477 and AK363461 (CNT20168194)	Salt stress	Regulatory role in salinity stress	Downregulated	Karlik et al. (2018)
		AK370506	Salt stress	NAT lncRNA	Downregulated	

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Table 3 (*continued*)

Sr. No	*Plants*	lncRNAs	Abiotic Stress	Regulation mechanism	Expression	References
		CNT20168342, CNT0031477	Salt stress	Putative sno lncRNA	–	(Karlik and
		AK370814	Salt stress	Cis-acting factor	Induced	Gozukirmizi, 2018; Karlik and Gözükırmızı, 2018)
20.	*Glycine max*	miR166i-5p - lncRNA *Gmax_MSTRG.35921.1* and miR394a-3p-lncRNA Gmax *MSTRG.18616.1*	Salt stress	Tissue specific expression patterns	–	Li et al. (2022)
		lncRNA77580	Drought and salt stress	It modulates the transcription of different gene sets during salt and drought stress response	Overexpression	Chen et al. (2023)
		525 Differentially Expressed lncRNAs	Low-phosphorous stress	Differential expression	–	Zhang et al. (2021)
21.	*Cucumis sativus*	TCONS_00031790, TCONS_00014717 TCONS_00005674, TCONS_00014332,	Heat Stress	Interact with miR9748 plant hormone signal transduction pathways	Upregulated Downregulated	He et al. (2020)
22.	*Cicer arietinum*	LncRNAs	Salinity and Drought	Differentially expressed under drought and salinity stress	Downregulated	Singh et al. (2018)
		3450 lncRNAs	Salt stress	3373 lncRNAs - cis-regulate their target genes, 80 unique lncRNAs interact with 136 different miRNAs as eTM targets of miRNAs	Up and Downregulated	Kumar and Mohapatra (2021)
		DElncRNAs		lncRNAs generally acts as miRNA targets and eTMs, which plays vital roles in the competitive endogenous RNA regulatory network	–	
		894 putative lincRNAs (TCONS_00015729, TCONS_00053423, and TCONS_00071748)	Heat Stress	linRNAs and mRNA were identified from leaf and root tissues at the vegetative and reproductive stages of the plant under control and heat stress conditions	Upregulated	Bhogireddy et al. (2023)
23.	*Brachypodium distachyon*	BdCOOLAIR1, BdCOOLAIR2	Cold stress	Antisense (BdCOOLAIR) transcript represses function of BdODDSOC gene	Induced	Jiao et al. (2019)
24.	*Musa itinerans*	TCONS_353036–GSMUA, TCONS_00101332–GSMUA, TCONS_00048199–GSMUA, TCONS_00079899–GSMUA, TCONS_240541–GSMUA, TCONS_00044687–GSMUA, TCONS_00279487–GSMUA	Cold stress	NAT antisense transcript altered enzyme activity, cellular location, or associations with other proteins during post-translational modifications, signal transduction pathways, and TFs activation	Induced	Liu et al. (2018)
25.	*Musa acuminata*	363 novel HS-lncRNA	Heat stress	Differentially expressed heat stress	upregulated	Murthy et al. (2022)
26.	*Pyrus betulifolia*	LncRNAs	Drought Stress	Cis-acting factor	–	Wang et al. (2018)
27.	*Panicum virgatum* L	LncRNAs	Drought Stress	Involved in ABA biosynthesis and signal transduction, starch and sucrose metabolism	Upregulated	Zhang et al. (2018)
				Ethylene (ETH) biosynthesis and signal transduction	Downregulated	
28.	*Populus trichocarpa*	lincRNA20, lincRNA2752, lincRNA2962, lincRNA1039 and LincRNA3241	Drought Stress	Target mimicry, control drought stress by regulating ptc-miR476 and	Induced	Shuai et al. (2014)
		LincRNA1128, LincRNA2623		ptc-miR169 through eTM	Repressed	
29.	*Populus tomentosa*	lncRNA *PMAT*	Lead toxicity	lncRNA *PMAT* interact epistatically with PtoMYB46	–	Chen et al. (2022)
30.	*Arachis hypogea*	TCONS_00292946 (Roots and Leaves), TCONS_00176941 (Roots and Leaves)	Salinity	Alternative Splicing changed the target gene profiles of lncRNAs and increased the diversity and flexibility of lncRNAs	Downregulated and upregulated	Tian et al. (2020)
31.	*Nicotiana tabacum*	lncRNAs *viz. MSTRG.6626.1, MSTRG.11330.1, and MSTRG.16041.1*	potassium starvation stress	Differential expression	–	Chen et al. (2022)
32	*Chenopodium quinoa*	4,460 differentially expressed LncRNAs	Salt stress	only 54 were differentially expressed at all the stress time points	Upregulated	Luo et al. (2022)
33	*Phyllostachys edulis*	PelncRNA1	UV-B stress	Regulate the expression of transcription factors related to the UV-B signaling pathway	Upregulated	(Yu et al., 2020)
34	*Beta vulgaris* L.	TCONS_00055787 TCONS_00038334	Drought	Involved in several drought stress tolerance mechanism	Upregulated Downregulated	Zou et al. (2023)

into the role of microRNA-encoded regulatory peptides, specifically *miPEP156e*, in rice's response to cadmium (Cd) stress. The authors elucidate that overexpression of *miPEP156e* led to a marked reduction in the accumulation of reactive oxygen species (ROS) and Cd in plants under Cd stress, thereby enhancing rice's Cd tolerance. This highlights the multifaceted roles of lncRNAs, not just as regulators, but also as potential encoders of functional peptides that can modulate stress responses. Another study by Ma and Hu (2023) provides a broader perspective, emphasizing the role of microRNAs (miRNAs) as dynamic players in plant signaling pathways related to various abiotic stresses, including heavy metal stress. The authors underscore the importance of understanding the molecular mechanisms of action of miRNAs

downstream target genes, suggesting that such insights could pave the way for optimizing genetic manipulations to enhance crop resilience against heavy metal stress.

In *B. napus*, RNA-seq analysis revealed 301 Cd-responsive lncRNAs, among them 67 lncRNAs were identified as eTM for 36 Cd-responsive miRNAs (Feng et al., 2016). Gene expression through as done under Cd stress for functional validation of three lncRNA i.e., *TCONS_00091906*, *TCONS_00033487*, and *TCONS_ 00097191*. These lncRNAs were found to be a significant player in target mimicry for *EL628609*, *TC182597* and *TC203372* mRNAs which are involved in Cd uptake and detoxification (Feng et al., 2016). In *M. truncatula* combined RNA-sequencing and degradome analysis unraveled 201 miRNAs in a comparative study of mercury-treated and mercury-free *Medicago* seedlings. The functional characterization was performed for *miR2681*, *miR2708*, and *miR2687* that targeted the *TIR-NBS-LRR* (encoding disease resistance protein), *TC114805* (encoding salinity tolerance protein), and *XTH* gene coding xyloglucan endotrans glucosylase/hydrolase contributing to cell wall development. Hence, it was concluded that the miRNAs and their putative targets have been found to possess an important role in the regulation of heavy metal toxicity (Zhou et al., 2012). In rice, systematic analysis, and characterization of root lncRNAs during an early stage in response to Cd stress emanated 120 DE lncRNAs using the RNA-sequencing approach (Chen et al., 2018). The functional analysis of lncRNAs provided the mechanism to regulate target genes in response to Cd stress using cysteine and methionine metabolism. In rice, arsenic stress-responsive novel lncRNA *CNT0*0027168 has been identified (Tang et al., 2019). In barley, six differentially expressed lncRNAs have been identified in comparative studies of both B-sensitive and B-tolerant cultivars with high B-level treatment. Notable lncRNAs such as *TCONS_00045190* and *TCONS_00056415* are overexpressed under excess boron treatment in B tolerant cultivar (Unver and Tombuloglu, 2020). The *Populus tomentosa* lncRNA *PMAT* (Pb^{2+} induced multidrug and toxic compound extrusion (MATE) antisense lncRNA) has been documented to promote the uptake of lead by interacting epistatically with *PtoMYB46*. The lncRNA *PMAT-mediated* regulatory module-controlled lead tolerance, uptake, and plant growth for phytoremediation of soil contaminated with lead (X. Chen et al., 2022). There is a need for further studies to understand the mechanism behind the regulation of heavy metal toxicity using lncRNA.

7.6. lncRNAs in heat stress

Increasing temperature is a serious threat to crop production that negatively impacts its harvest index (Piao et al., 2019). Heat stress is a limiting factor for growth, physiology, and development which ultimately affects yield (Zhang et al., 2019). Various heat shock proteins, phytohormones, antioxidant enzymes, and metabolites were expressed during heat stress (Janni et al., 2020; Jha et al., 2017). The roles of ncRNAs under heat stress regulatory response in plants have been established (Song et al., 2019; Mangrauthia et al., 2017; Xin et al., 2011). Under heat stress, 245 poly(A)+ and 58 poly(A)-lncRNAs were expressed differentially during heat stress in *Arabidopsis*. A higher expression level of lncRNA i.e., *PsiLncRNA00268512* was observed in *P. simonii*, during heat stress. Likewise, 192 target genes were also identified to be regulated by 34 differentially expressed lncRNAs which help to cope with heat stress (Song et al., 2016b). In wheat, 54 putative lncRNA were identified in response to heat stress with the help of Chip-based microarray and Solexa sequencing. These lncRNAs were reported as precursors of four miRNAs and 26 siRNAs. The heat-responsive DE lncRNA such as *TahlnRNA27* and *TalnRNA5* with their corresponding miR2010 and miR2004 were analyzed (Xin et al., 2011). In *B. rapa,* RNA-seq revealed several genes including brassinosteroid, ABA, auxin, jasmonic acid, salicylic acid, ethylene, and lncRNA were up and down-regulated during heat stress. Differentially expressed heat-responsive DE lncRNAs such as lncRNA *TCONS_00004594* expressed downstream with *Bra021232*. While, lncRNAs *TCONS_ 00048391* and *TCONS_00010856* acted as eTMs for bra-miR164a which help to cope with heat stress (Wang et al., 2019).

There has been a report on the identification of 363 novel banana HS-lncRNA expressed during heat stress in the Banana. Further, miRNAs like *miR8007b*, *miR414*, *miR2083*, and *miR847* were also predicted where lncRNAs act as precursors for target gene regulation including transcriptional and post-transcriptional changes (Murthy et al., 2022). Similarly, in *B. juncea,* lncRNAs *TCONS_00051908* and *TCONS_00088973* were identified to be involved in heat and drought responses and act as putative targets and eTMs of miRNAs (Bhatia et al., 2020). Our group at ICAR-IIRR has analyzed the expression of miRNA in roots and shoots of rice seedlings under heat stress (Sailaja et al., 2014). Furthermore, deep sequencing of small RNAs expressed during control, short, prolonged heat stress, and recovery have been extensively analyzed and candidate miRNAs are being functionally characterized (Mangrauthia et al., 2017). The differentially expressed lncRNAs have been identified under long and short heat stress treatments in rice heat tolerant and susceptible varieties through strand-specific RNA sequencing. A total of 238 lncRNA-mRNA pairs were identified in the interaction network of heat-responsive lncRNAs with target genes (Zhang et al., 2021). The lncRNA *TCONS_00092993* was induced under heat stress in both varieties and was predicted to be the precursor of *osa-miR1850*, which has been earlier reported to be down-regulated after heat treatment in a heat-tolerant variety N22 (Mangrauthia et al., 2017). Heat-responsive lncRNAs were identified by transcriptome sequencing of control and heat-treated maize inbred leaves. A lncRNA-miRNA-mRNA regulatory network-based was predicted wherein the heat-responsive lncRNAs mainly regulated the heat shock proteins, spliceosome, late embryogenesis abundant protein, and genes involved in response to stress (Hu et al., 2022). Table 3 describes regulation along with the pattern of expression of the lncRNAs in various plant species under abiotic stress conditions.

8. Prospects of deploying lncRNA for improving climate resilience of crops

The signaling molecules, transcription factors, hormones etc. have been the major targets for crop improvement and comparatively less attention has been given to the regulatory non-coding RNAs. The research on lncRNAs under a particular stress condition opens a plethora of avenues in terms of elucidation of regulatory mechanisms and interactions between the mRNA-miRNA-lncRNA. The lncRNAs along with the miRNAs are potential targets for developing plants resilient to environmental stresses. The involvement of lncRNAs in the complete mechanism of the RdDM silencing pathway before and after stress needs focused attention for developing climate-smart plants. In the direction to elucidate the mechanism of RdRM upon stress signaling, basic studies by simultaneously executing transcriptomics, lncRNA sequencing, bisulfite sequencing, chromatin immunoprecipitation sequencing ChIP-seq/methylomics in a spatiotemporal means should be addressed. The global run-on sequencing (GRO-seq), used to measure nascent RNA, can be applied to study the biogenesis, functional aspects, and mechanism of plant lncRNA.

The lncRNAs have been discovered in a few plants and should be explored in more plants under varying abiotic stresses in a spatiotemporal manner by leveraging the advances in next-generation sequencing. Several prediction tools aid in the precise identification of lncRNAs even in the absence of gold standard reference assembly. The lncRNAs can be mined from the available transcriptome datasets as well. Delineation of conserved structural motifs of stress-responsive lncRNAs will strengthen the understanding of site-specific targeting for any further functional characterization. The newly discovered or novel lncRNAs can be mapped with the already known trait-linked quantitative trait loci (QTL) for co-localization. The co-localization of lncRNAs with the known QTL region increases confidence in the involvement of lncRNAs in the trait of interest. The association between phenotype and epigenetic variants can

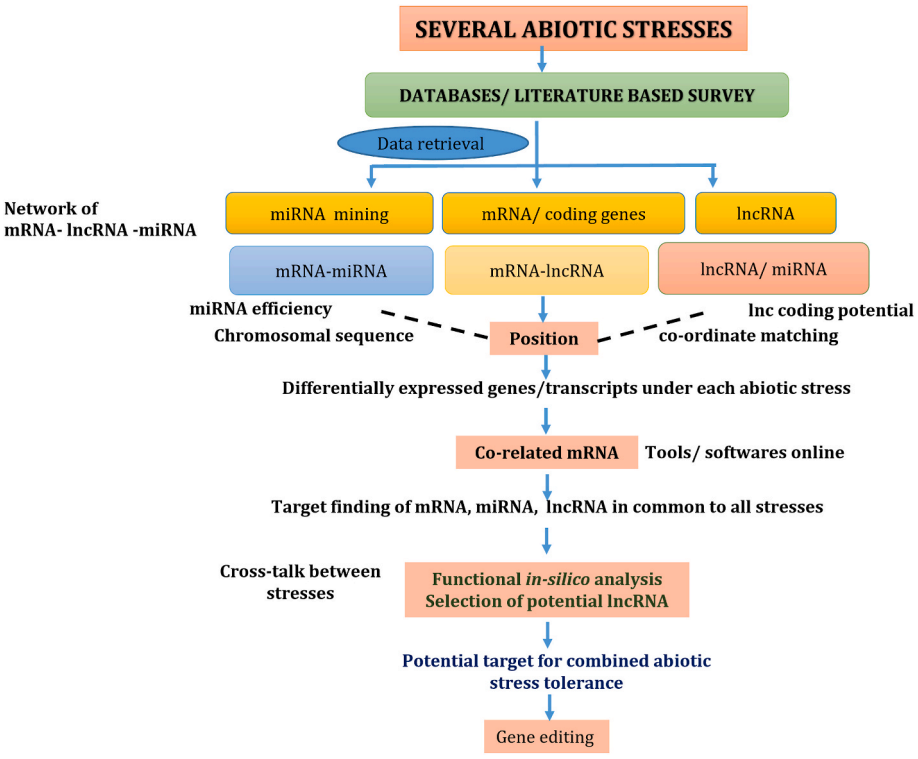

Fig. 4. Prospects of novel lncRNA for functional characterization
Cartoon representation of epigenetic mechanism mediated by lncRNA upon stress response. The broken line represents stress induction; solid lines represent signaling responses.

be investigated through Epigenome-wide association studies (EWASes) and can be co-related with the lncRNAs. The data emanating by conglomerating the omics technologies along with bioinformatics is expected to give a clear picture at the molecular level. The stress memory mechanisms and the genes responsible during the stress and after the stress recovery can be elucidated for the target genes of lncRNA. This information will be useful for understanding the epigenetic stress memory genes. A crosstalk stress signaling mechanism exists for multiple stress responses. Crosstalk or cross-adaptation mechanisms utilize the epigenetic repertoire for gene regulatory networks. A plethora of omics data sets are available in public databases and a common set of lncRNAs involved in multiple abiotic stress responses can be retrieved (Fig. 4). As the lncRNA regulates the gene expression at genetic, epigenetic, transcriptional, and post-transcriptional, translational, and post-translational stages, complete profiling of lncRNA, regulated transcripts, metabolites would yield prospective targets for editing. Such lncRNAs can be functionally characterized using accurate site-directed nucleases like CRISPR/Cas9.

9. Conclusion

The review provides insights into the intricate regulatory networks of stress-responsive lncRNAs, the mechanism of action, experimental and computational methods for studying lncRNAs highlighting the value of high-throughput sequencing technologies and bioinformatics tools. The study of lncRNAs is poised to open new horizons in the realm of plant science and hints at their potential to revolutionize crop improvement for environmental resilience. While substantial progress has been made in identifying stress-responsive lncRNAs, there remains a need for deeper investigations into the precise molecular mechanisms through which these lncRNAs exert their regulatory roles. Understanding the intricate interactions and cascades triggered by lncRNAs will be essential to harness their potential for improving plant resilience to abiotic stresses. Furthermore, functional validation of specific lncRNAs and their broader implications in enhancing agricultural resilience in stress-prone environments, enhancing nutrient use efficiency, mitigation of heavy metal toxicity, and adverse impacts of rising temperatures should be a focus for future research. Overall, the study of lncRNAs in the context of abiotic stress responses holds significant promise for advancing our understanding of plant resilience mechanisms and enhancing agricultural sustainability in a changing climate.

Contributions

KMB conceived and planned the review; NDM, PS, TCB, KMB drafted review section-wise; SKM, MKP, SS provided critical timely inputs; MSM, CNN, RMS edited the review.

Declaration of competing interest

On behalf of all authors, the corresponding author states that there is no conflict of interest.

Data availability

No data was used for the research described in the article.

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