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RESEARCH PAPER

Identification of long non-coding RNAs under nitrogen stress in maize (*Zea mays* L.)

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Abstract: Nitrogen (N) is an essential nutrient for plant growth; however, a substantial proportion of the nitrogen applied to crops such as maize (*Zea mays* L.) remains unused, contributing to environmental pollution and inefficient resource use. Consequently, improving nitrogen use efficiency is a major objective of sustainable agriculture. Although the genetic and molecular mechanisms underlying nitrogen uptake and assimilation are relatively well characterized, the role of long non-coding RNAs (lncRNAs) in regulating nitrogen responses in maize remains largely unexplored. In this study, we investigated the involvement of lncRNAs in maize responses to low-nitrogen stress. Two inbred maize lines with contrasting nitrogen stress tolerance—DMI 56 (tolerant) and DMI 81 (susceptible)—were grown hydroponically under nitrogen-sufficient and nitrogen-deficient conditions. Root and leaf tissues were analyzed for lncRNA expression, revealing a large number of differentially expressed lncRNAs, ranging from 226 to more than 1,025 across six experimental comparisons. The Gene Ontology (GO) classification and enrichment analysis helped to annotate the function of 155 lncRNAs in total. Notably, a greater number of lncRNAs were upregulated than downregulated in response to nitrogen stress, and several lncRNAs exhibited consistent expression patterns in root tissues of both genotypes. These observations suggest that certain lncRNAs may constitute a core regulatory network involved in plant adaptation to nitrogen-limited environments. Overall, this study provides new insights into the molecular responses of maize to nitrogen stress and highlights the potential of lncRNAs as targets for improving nitrogen utilization. Further functional characterization of these lncRNAs may facilitate the development of maize genotypes with enhanced performance under low-nitrogen conditions, contributing to more sustainable and efficient agricultural systems.

Keywords: Identification • lncRNAs • Maize • Nitrogen • Non-coding

Introduction

Maize (*Zea mays* L.) is one of the most important cereal crops worldwide, serving not only as a dietary staple for millions of people but also as a major source of animal feed and raw material for numerous industrial products. Like all plants, maize requires an adequate supply of essential nutrients for optimal growth and development, among which nitrogen (N) is paramount. Nitrogen plays a critical role in key physiological and biochemical processes, including protein synthesis, photosynthesis, and energy metabolism. Despite extensive use of synthetic nitrogen fertilizers to enhance crop productivity, a significant proportion of applied nitrogen remains unutilized by plants, leading to environmental pollution and inefficient resource use. Consequently, improving nitrogen use efficiency (NUE) has emerged as a major

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research priority aimed at achieving sustainable agricultural production.

Plants primarily absorb nitrogen in the form of nitrate and ammonium through specialized transport systems, including nitrate transporters (NRTs) and ammonium transporters (AMTs), respectively (Fukuda *et al.*, 2020). Nitrogen uptake, assimilation, and signaling are tightly regulated by complex genetic and molecular networks involving various transcription factors, such as NIN-like proteins and nitrate-inducible repressors (Yanagisawa, 2014; Yadava *et al.*, 2020; Singh *et al.*, 2021, 2022). Although considerable progress has been made in elucidating these regulatory pathways, several aspects of nitrogen sensing and response mechanisms in plants remain poorly understood.

In recent years, non-coding RNAs—particularly long non-coding RNAs (lncRNAs)—have emerged as an additional regulatory layer influencing gene expression. Long non-coding RNAs are transcripts longer than 200 nucleotides that do not encode proteins but play important roles in transcriptional, post-transcriptional, and epigenetic regulation (Budak *et al.*, 2020; Yadav *et al.*, 2022). In maize, lncRNAs are increasingly recognized as important regulators of growth, development, and responses to environmental stresses, including drought and nutrient deficiency. Genome-wide studies have identified numerous lncRNAs in maize, many of which exhibit stress-responsive expression patterns.

A subset of lncRNAs, known as long intergenic non-coding RNAs (lincRNAs), has been shown to modulate gene expression through interactions with microRNAs (miRNAs). Some lincRNAs may function either as direct miRNA targets or as molecular decoys that sequester miRNAs away from their target mRNAs, a mechanism described by the competing endogenous RNA (ceRNA) hypothesis (Fan *et al.*, 2015; Yadav *et al.*, 2023). LncRNAs can exert their regulatory effects in cis or trans through diverse mechanisms, including RNA–RNA or RNA–DNA interactions, modulation of chromatin structure, and epigenetic regulation via DNA methylation and histone modifications (Chekanova, 2015; Kornienko *et al.*, 2013; Wang *et al.*, 2017). Due to the complexity of these mechanisms, the functional characterization of plant lncRNAs remains limited, with only a few having been studied in detail.

A well-known example of lncRNA-mediated regulation is the *INDUCED BY PHOSPHATE STARVATION 1* (*IPS1*) lncRNA in *Arabidopsis thaliana*, which acts as a target mimic for miR399 under phosphate-deficient conditions. By sequestering miR399, *IPS1* prevents the degradation of *PHO2*, a key regulator of phosphate homeostasis (Franco-Zorrilla *et al.*, 2007; Kumar *et al.*, 2022). Although lincRNAs have been implicated in various abiotic and biotic stress responses, including drought and pathogen resistance, their role in nitrogen metabolism—particularly in maize—remains largely unexplored. However, emerging evidence suggests that maize lincRNAs can function as miRNA targets or decoys associated with nitrogen-related pathways, thereby protecting key regulatory genes from miRNA-mediated silencing (Fan *et al.*, 2015).

Studies in model plants such as *Arabidopsis* have demonstrated that lncRNAs are responsive to environmental stresses and regulate key metabolic and developmental processes (Chen *et al.*, 2020). In crops, lncRNAs have been shown to participate in responses to abiotic stresses (Jha *et al.*, 2020), biotic stresses (Zhang *et al.*, 2021), and various biological processes (Zhang *et al.*, 2014). Advances in high-throughput RNA sequencing technologies, coupled with the availability of comprehensive maize genomic resources, now provide unprecedented opportunities to investigate the regulatory roles of lncRNAs in crop stress responses. Despite these advances, the involvement of lncRNAs in nutrient-related stresses—particularly low-nitrogen stress—has not been systematically explored in maize. Therefore, the present study aims to identify lncRNAs associated with low-nitrogen stress by comparing two contrasting maize inbred lines differing in their tolerance to nitrogen deficiency.

Materials and methods

Plant material and RNA sequencing

The experiment was conducted using two contrasting maize inbred lines, the nitrogen stress–susceptible line DMI 81 and the nitrogen stress–tolerant line DMI 56, at the ICAR–Indian Institute of Maize Research, Delhi Unit, Pusa Campus, India. Seeds were grown hydroponically in triplicates, under nitrogen-sufficient and nitrogen-deficient conditions as described previously (Singh *et al.*, 2022). After 21 days, fresh leaf and root tissues were harvested and immediately stored at –80 °C for further analysis.

Total RNA was isolated from 100 mg of leaf and root tissues using the Spectrum™ Plant Total RNA Kit (Sigma-Aldrich, USA) following the manufacturer's protocol. RNA concentration and purity were assessed using a NanoDrop spectrophotometer (Thermo Scientific, USA). High-throughput RNA sequencing of RNA samples derived from leaf and root tissues of both tolerant and susceptible inbred lines was performed on the Illumina sequencing platform by NxGenBio Life Sciences, Delhi, India.

Prediction of differentially expressed lncRNAs

Annotated lncRNA sequences for *Zea mays* were downloaded from the GreeNC database (http://greenc.sciencedesigners.com/wiki/Species:Zea_mays). Quality-filtered reads were mapped to lncRNA reference sequences using the BWA-MEM algorithm (version 0.7.17), and mapped read counts were generated using SAMtools (version 0.1.19). Differential expression analysis was performed using DESeq (version 1), and volcano plots were generated using the ggplot2 package in R. Significantly differentially expressed lncRNAs were identified based on a p-value ≤ 0.05 and a log, fold change ≥ 2 for upregulated and ≤ -2 for downregulated transcripts.

Gene Ontology (GO) enrichment analysis

The predicted target genes of differentially expressed lncRNAs were used for functional analysis. Since lncRNAs lack direct functional annotation, their roles were inferred based on associated protein-coding genes. All gene IDs (GRMZM) were mapped to updated Zm IDs using the MaizeGDB (www.maizegdb.org). Due to annotation differences, unmapped or unannotated genes were excluded, and only valid genes were used for further analysis. Gene Ontology (GO) classification was performed using PANTHER (https://pantherdb.org) to categorize genes into biological process, molecular function, and cellular component. GO enrichment analysis was conducted using ShinyGO (https://bioinformatics.sdstate.edu/go/), with significance determined based on false discovery rate (FDR < 0.05). Enrichment results were visualized using dot plots based on fold enrichment and FDR values. Only biological process and molecular function categories showed significant enrichment.

Results and discussion

The present study aimed to identify lncRNAs involved in plant adaptation to nitrogen-related stress. Maize plants grown hydroponically under nitrogen-deficient conditions exhibited typical deficiency symptoms, including stunted growth, leaf chlorosis, and reduced biomass. To investigate the role of lncRNAs in nitrogen stress responses, transcriptomic analyses were performed on two contrasting maize inbred lines—the nitrogen stress–tolerant line DMI 56 and the susceptible line DMI 81—grown under nitrogen-sufficient and nitrogen-deficient conditions.

To capture tissue-specific responses, both root and leaf tissues were analyzed for lncRNA expression under the different treatments. In total, six experimental comparisons were examined (Table 1). A total of 17,100; 16,732; 17,101; 16,897; 16,418; and 16,549 differentially expressed (DE) lncRNAs were identified in comparisons 1, 2, 3, 4, 5, and 6, respectively. These results provide insights into the potential regulatory roles of lncRNAs in maize adaptation to nitrogen stress.

Table 1. List of combinations used to identify significantly differentially expressed lncRNAs under nitrogen stress*

Comparison	Total lncRNAs	DE lncRNAs at logFC2	DE lncRNAs at (log_2FC ≥ 2 and $P_{adj} \leq 0.05$)
56_RN-_81_RN-	17100	2984	978
56_SN-_81_SN-	16732	3272	1025
56_RN+_56_RN-	17101	2474	700
81_RN+_81_RN-	16897	2582	811
56_SN+_56_SN-	16418	2104	525
81_SN+_81_SN-	16549	1669	226

*Letters S, R, N^+, and N^- represent leaf, root, nitrogen-sufficient, and nitrogen-deficient conditions, respectively. The numbers 56 and 81 correspond to the maize inbred lines DMI 56 and DMI 81, respectively

After further filtering to retain only lncRNAs with statistically significant differential expression, the final counts were reduced to 978, 1,025, 700, 811, 525, and 226 for combinations 1, 2, 3, 4, 5, and 6, respectively. Overall, the number of significantly differentially expressed lncRNAs ranged from 226 to 1,025, which is considerably higher than that reported in previous studies, where fewer lncRNAs were identified (Lv *et al.*, 2016; Ma *et al.*, 2021). Moreover, the number of differentially expressed

lncRNAs observed in the present study exceeds those reported under other abiotic stresses in maize, such as salt and heat stress (Liu *et al.*, 2022; Hu *et al.*, 2022).

This higher number of differentially expressed lncRNAs may be attributed to the greater complexity of nutrient-related stress responses compared with other abiotic stresses, which likely involves more intricate regulatory networks. Additionally, most previous studies have focused on a single maize line, whereas the present study employed two contrasting inbred lines with differential nitrogen stress tolerance. This comparative approach enables a more comprehensive understanding of lncRNA-mediated regulatory mechanisms by allowing direct comparison across multiple experimental combinations.

The combinations showed the upregulation and downregulation of the lncRNAs when compared with each other (Figure 1). In the combination 1, the upregulated lncRNA were 568 whereas the downregulated are 410. Similarly in the combination 2 the 597 lncRNA were upregulated compared to 428 downregulated lncRNAs with significant differential expression. In the N-stress tolerant line grown under normal and stress conditions, the upregulated lncRNAs in the root and leaf tissue were 476 & 324, respectively whereas the downregulated ones were 224 & 207 in root and leaf tissue, respectively. The similar trend also reported for the stress susceptible line grown under control and stress condition, where more number of upregulated lncRNAs (643 & 150) were reported than the downregulated (168 & 76) ones in the root and leaf tissue (Figure 1). The results are similar to the previous studies where more number of lncRNAs are found to be upregulated than the downregulated ones (Lv *et al.*, 2016; Ma *et al.*, 2021). However, the leaves tissues have been reported to have more downregulated lncRNAs than the ones that were upregulated (Ma *et al.*, 2021).

In all the combinations, top thirty upregulated and downregulated lncRNAs from root and leaf tissues of tolerant and susceptible lines were shortlisted (Figure 2). The differences in their expression pattern signifies their role in the adaptation of the plants towards the nitrogen stress. Also, there were lncRNAs that were common in the combinations but in all upregulated or downregulated lncRNAs, the common were few. In the leaf tissue there was no common lncRNA which was upregulated or downregulated in all combinations. However in the root tissue two lncRNA were common in upregulated and one in downregulated in all the root tissue combinations. The previous studies lack the comparison in between two or more contrasting lines to study the expression pattern of lncRNAs against the N-stress, therefore the common lncRNA found in different lines has not been reported before this study. However the lncRNAs expression has been studied in the contrasting lines against the drought stress in maize (Tang *et al.*, 2023). The study revealed that the differentially expressed lncRNAs were more common in the contrasting lines than the plants under control and water-stressed conditions. These results are in contrast to our present study where the common lncRNAs were fewer in number than the unique ones expressed specifically in the one line. Also when the differential expression of the lncRNAs was compared in the root tissues of the two lines in three combinations (1, 3 & 4), the results showed presence of common lncRNAs in all cases. The Venn diagram (Figure 3) shows that the number of upregulated lncRNAs are higher in number as compared to the downregulated ones. Further there were higher number of common upregulated lncRNAs in all the three combinations compared with their counterpart. Further there were two upregulated and one downregulated lncRNAs that were common in all three combinations showing their key role in nitrogen stress management in maize plant.

The exact role of these lncRNAs was not identified but it has previously been reported that the lncRNAs play significant role in regulating the expression of other mRNAs that are associated with different functions such as chlorophyll biosynthesis, nitrogen accumulation, nitrogen utilization, etc (Ma *et al.,* 2021). The Gene Ontology (GO) classification and enrichment analysis of the predicted target genes of differentially expressed long non-coding RNAs (lncRNAs) revealed their involvement in diverse biological functions associated with nitrogen stress responses in maize. Of the total 4265 lncRNAs that were differentially expressed in both tissues, only 155 were annotated with their functions **(Supplementary 1)** by using different tools. GO classification indicated that the majority of genes were associated with cellular processes (31.3%), metabolic processes (21.3%), and biological regulation (16.3%) in the biological process category, highlighting their roles in fundamental cellular activities and regulatory mechanisms. In the molecular function category, genes were predominantly enriched in

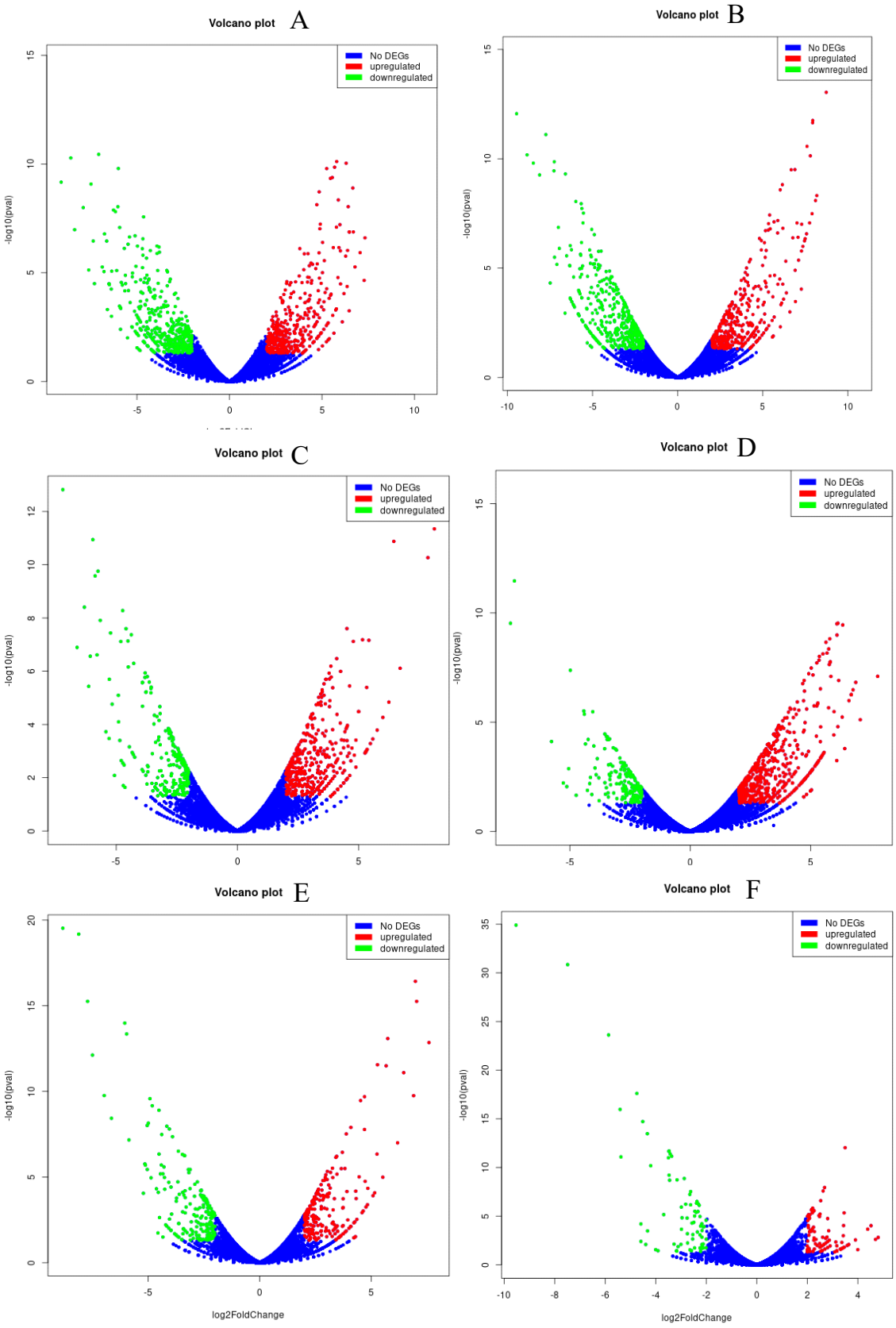


Figure 1. The volcano plot showing the all the obtained lncRNAs in following combinations. (**A**) 56_RN-_81_RN-; (**B**) 56_SN-_81_SN-; (**C**) 56_RN+_56_RN-; (**D**) 81_RN+_81_RN-; (**E**) 56_SN+_56_SN-; (**F**) 81_SN+_81_SN-. In the volcano plot, each dot represents a single lncRNA. The lncRNAs that are relatively upregulated are displayed in red, while those that are downregulated appear in green and which are not significant with p value<0.05 appear in blue.

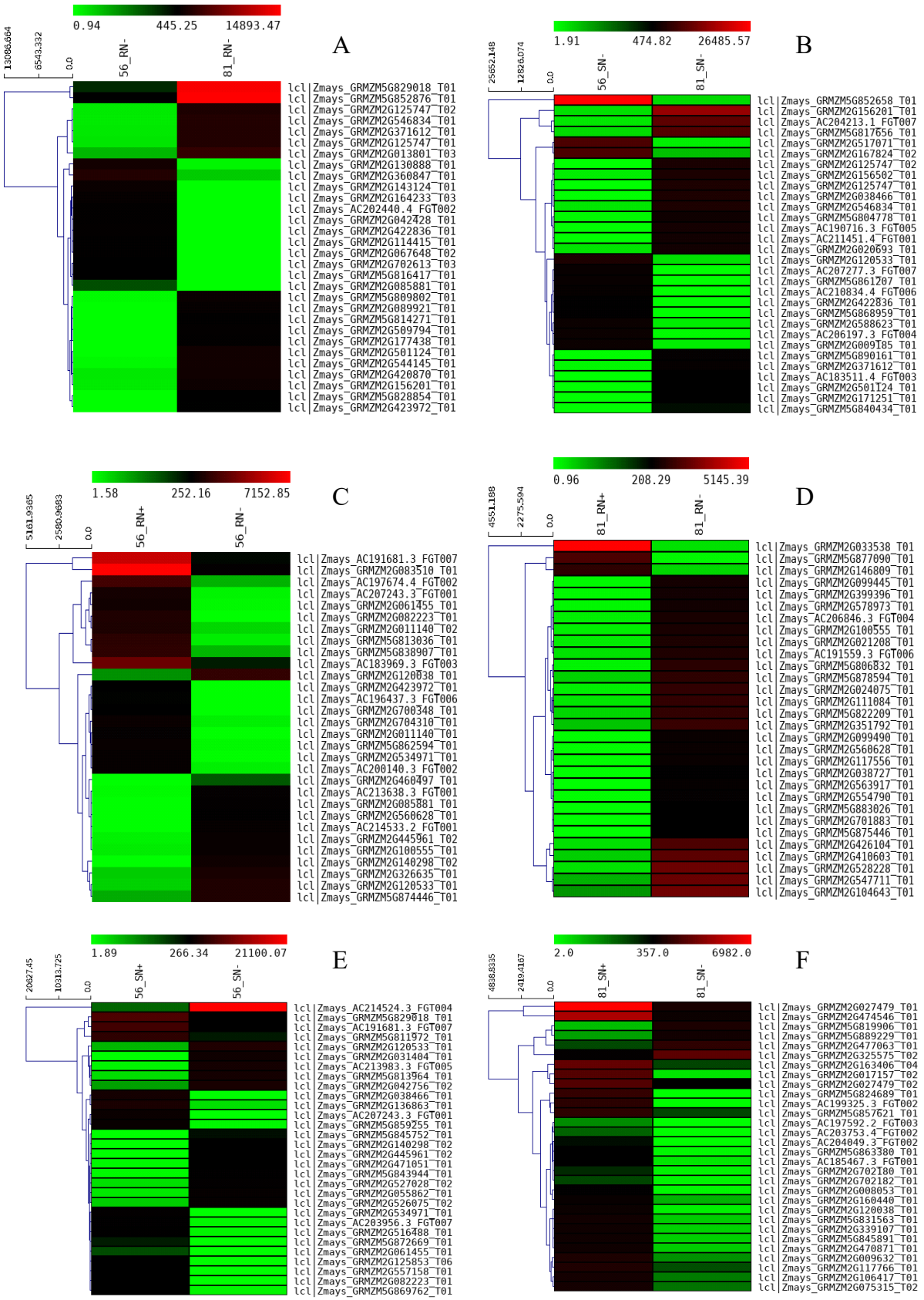


Figure 2. Heat map depicting top 30 cluster of lncRNAs with p value<0.05 in following combinations. (**A**) 56_RN-_81_RN-; (**B**) 56_SN-_81_SN-; (**C**) 56_RN+_56_RN-; (**D**) 81_RN+_81_RN-; (**E**) 56_SN+_56_SN-; (**F**) - 81_SN+_81_SN-. In the heat maps, each row represents a single lncRNA. The lncRNAs that are relatively upregulated are displayed in red, while those that are downregulated appear in green.

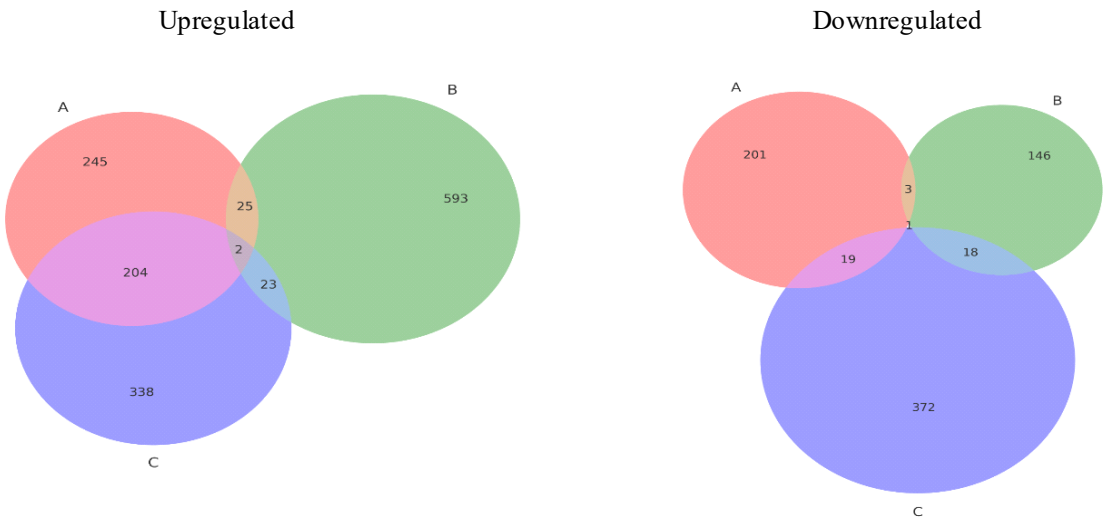


Figure 3. Venn diagram showing the number of up-regulated and down-regulated differentially expressed lncRNAs in root in various combinations. A - 56_RN+_56_RN-; B - 81_RN+_81_RN-; C - 56_RN-_81_RN-

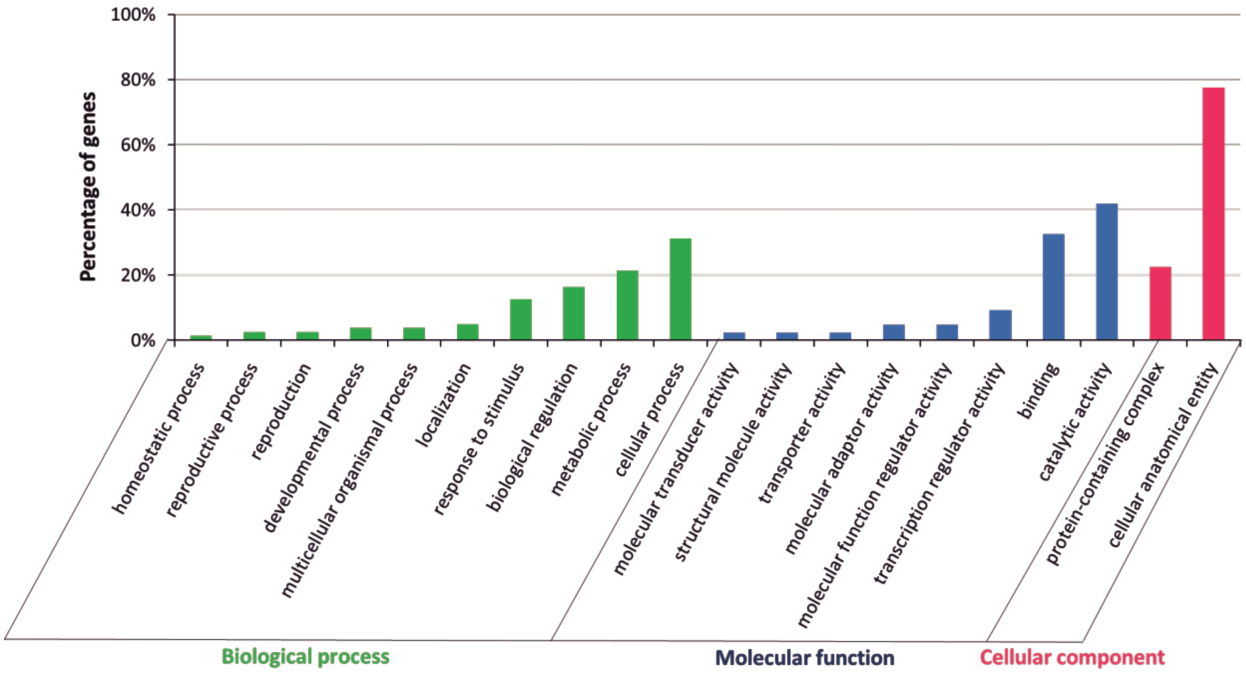


Figure 4. Gene Ontology (GO) classification of predicted target genes of differentially expressed lncRNAs in maize. The bar plot represents the distribution of predicted target genes of differentially expressed lncRNAs across three Gene Ontology categories: biological process, molecular function, and cellular component.

catalytic activity (41.9%) and binding functions (32.6%), followed by transcription regulator activity, indicating active involvement in enzymatic reactions and gene regulation. Cellular component analysis showed that most genes were localized to cellular anatomical entities (77.5%), with a smaller proportion associated with protein-containing complexes (Figure 4).

Further enrichment analysis provided deeper insights into the specific biological roles of these genes. In the biological process category, the most significantly enriched term was systemic acquired resistance (FDR = 4.46×10^{-7}), along with enrichment of defense response to symbiont, defense response, and response to stress, indicating activation of stress-responsive pathways under

nitrogen deficiency. Additionally, significant enrichment of processes related to the regulation of proteolysis and peptidase activity suggests an important role for controlled protein turnover in stress adaptation. The enrichment of mannose metabolic process further indicates the involvement of carbohydrate metabolism in maintaining cellular energy balance. In the molecular function category, genes were significantly enriched in fatty acid binding (FDR = 3.36×10^{-7}), monocarboxylic acid binding, and organic/carboxylic acid binding, reflecting roles in lipid metabolism and metabolite interactions. Moreover, enrichment of peptidase inhibitor and regulator activities, along with enzyme inhibitor activity, highlights the importance of enzymatic regulation and post-translational control under stress conditions (Figure 4). Collectively, these results suggest that lncRNAs may regulate genes involved in defense responses, metabolic reprogramming, and proteolytic regulation, thereby contributing to nitrogen stress adaptation and improved nitrogen use efficiency in maize.

The interaction of the lncRNA with the miRNA has also been reported to be another pathway by which these non-coding RNAs interact to control the gene expression. The interaction between the miRNA and lncRNA can be in cis form or trans form as reported in *A. thaliana* (Fukuda *et al.*, 2020) The exact function of lncRNA cannot be detected easily but has been predicted the role by adopting the coexpression system and associating them with a functional gene (Lv *et al.,* 2016). The lncRNAs not only help plant to adapt under low nitrogen conditions but also helps to counter other abiotic stress (Jha *et al.,* 2020) and also involved in various plant physiological functions (Zhang *et al.,* 2014). The many fold expression differences in the lncRNAs under normal and stress condition also signifies their role in plant's response generated towards the nitrogen deficiency stress as similar patterns were observed with the genes associated with the nitrogen related stress (Singh *et al.,* 2022). Further work on the real time expression profiling and annotating the pathways these lncRNAs follows for their action will help to precisely identify their function in combating the low nitrogen condition in maize.

Conclusion

This study provides new insight into the role of long non-coding RNAs (lncRNAs) in maize's response to nitrogen deficiency. By comparing two genetically contrasting inbred lines under nitrogen-sufficient and nitrogen-deficient conditions, a large number of differentially expressed lncRNAs across root and leaf tissues has been identified. The significant variation in expression patterns, especially the consistent upregulation of certain lncRNAs in root tissues, suggests that these molecules may play a key role in regulating nitrogen uptake and utilization. Importantly, this work highlights the power of combining transcriptomic data with contrasting genotypes to uncover molecular responses that may otherwise remain hidden. The role of many lncRNAs were identified using various tools, showing their role in various biological processes. Although the precise functions of many lncRNAs remain to be validated, our findings lay the foundation for future research into how these molecules influence nitrogen metabolism, possibly through interactions with microRNAs or other regulatory networks. Understanding and harnessing the regulatory potential of lncRNAs could open new avenues for improving nitrogen use efficiency in maize. Ultimately, this knowledge can contribute to the development of more resilient and resource-efficient crop varieties, supporting the broader goal of sustainable agriculture.

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