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# Genome-Wide Identification and Characterization of Long Non-Coding RNAs in Litchi

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## Abstract

Long non-coding RNAs (lncRNAs) play key regulatory roles in different developmental processes and responses to stress. However, the bioinformatic identification of lncRNAs in litchi are largely unknown. To explore the lncRNA profiles and functions in litchi different tissues, we performed RNA sequencing of litchi leaves, pericarp, seeds, flowers fruitlet, and carpopodium, with varying biological replicates for each. We identified 2229 lncRNAs including average 293 lncRNAs were significantly differentially expressed (DE) in all the tissues used in this study. The Gene Ontology (GO) and Kyoto Encyclopedia of Genes and Genomes (KEGG) analyses were carried out to identify the cis target gene of DE lncRNAs. The results showed that the lncRNAs might play an important role in the immune response, response to abiotic stress, and metabolic processes related to fatty acids and glucose. Moreover, we identified lncRNAs associated with miRNAs, including lncRNAs acting as precursors for *miR156, miR171, miR172, miR319, miR393, miR396,* and *miR482*, as well as lncRNAs targeted by these miRNAs. The results suggest that the lncRNAs can regulate the expression of mRNA during litchi growth and development by forming competitive endogenous RNA, and further regulate various biological metabolism pathways in litchi.

**Keywords:** Litchi; lncRNA; Transcriptome; Target mimics; Regulation

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## Introduction

Until last decade, the central dogma of molecular biology considered RNA molecules as a mere intermediary for flow of genetic information from DNA → RNA → protein [1]. The advent of next generation sequencing (NGS) technologies [2] challenged this dogmatic view and discovered a range of different types of RNAs. It is now widely accepted fact that only 1–2% of the transcribed genome is required for orchestrating the module for protein synthesis. Whereas the remaining 98–99% RNAs do not code for any functional protein and are regarded as non-coding RNAs (ncRNAs) [3]. Long non-coding RNAs (lncRNAs) are one of the types of ncRNAs that are generally >200 nucleotide (nt) long and indiscernible coding potential [4]. LncRNAs can be broadly classified into different

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categories based on their genomic position or their mechanism of action [3]. Antisense transcripts (lncNATs), natural intronic RNAs (incRNAs), bidirectional lncRNAs (BI-lncRNAs), long intergenic ncRNAs (lincRNAs), and overlapping lncRNAs (OT-lncRNAs) are included in former category [5]. While later include scaffolds, decoys, signals, guides, and precursors for small interfering RNAs (siRNAs) [3]. Therefore, plant lncRNAs can be considered as indispensable elements of gene expression regulation and key player as a potential resistant gene resource [6].

Currently, plethora of studies shown that lncRNA in plants are emerging as a key regulatory molecules in range of diverse plant biological regulatory processes including floral and reproductive development, sexual differentiation, Vernalization (*COLD ASSISTED INTRONIC NONCODING RNA (COLDAIR* and *COOLAIR*), root organogenesis, photomorphogenesis, reproduction (*LONG-DAY-SPECIFIC MALE-FERTILITY-ASSOCIATED RNA, LDMAR*), nutrient homeostasis (*INDUCED BY PHOSPHATE STARVATION1, IPS1/At4*), innate plant immunity, salinity, drought (*DROUGHT INDUCED lncRNA, DRIR*), cellular localization, and defense against pathogenic infections [3, 7, 8]. lncRNAs are not involved in transcriptional regulation and epigenetics in the nucleus but do involved in mRNA stability and translocation from nucleus to cytoplasm [9, 10]. However, the regulatory mechanism of these plant lncRNAs remains largely scarce. Therefore, systematic identification of lncRNAs at specific genome level and specific function is certainly crucial to plant diversity, adaptation, and speciation.

Over the past decade, advancement in bioinformatic techniques assist large-scale transcriptomics studies that have documented a large number of plant lncRNAs in different plant tissues and responsive to different biotic and abiotic stresses [3]. lncRNAs have been predicted in various plant species, such as Arabidopsis*, Solanum lycopersicum, Zea mays, Medicago truncatula, Oryza sativa, Glycine max, Vitis vinifera, Solanum tuberosum, Triticum aestivum, Populus trichocarpa, Setaria italica, Camelina sativa,* and *Brassica rapa* [3]. For instance, in Arabidopsis, more than >6000 intergenic lncRNAs were reported [11] under various stress stimuli [12]. In rice, lncRNAs associated with sexual reproduction [13] while candidate lncRNAs functioned in fibre initiation and elongation in *Gossypium* spp. were identified [14]. In addition, 318 cold/drought responsive cassava lncRNAs associated with hormone signalling, sucrose metabolism, and secondary metabolites biosynthesis [15]. These studies mainly focused on lncRNAs identification and their expression pattern analysis.

*Litchi chinensis* L., an important evergreen economic fruit tree in southern China. Litchi floral initiation is triggered by low winter temperature and enhanced by drought. It usually suffers serious fruit abscission before harvest, leading to a low yield. Litchi lncRNAs remain poorly characterized, and no systematic screening of potential lncRNAs in the litchi genome has been reported. To identify and characterize genome-wide lncRNAs in litchi, taking the advantage large scale published RNA sequencing data, including 54 litchi samples from seven different tissues. A total of 2229 lncRNAs were identified from all unknown transcripts. We analyzed the tissue/organ specific expression profile of lncRNA in the litchi leaves, fruitlet, flowers, pericarp, seeds, and carpopodium by deep sequencing. We identified differentially expressed (DE) lncRNAs; predicted potential function of lncRNAs and their cis-acting targets; and acquired GO and KEGG information. We also predicted lncRNA-miRNA interaction and as source of miRNA biosynthesis.

## Materials and methods

### Data sets sources used in this study

RNA sequencing data sets of *Litchi chinensis* were retrieved from the Sequence Read Archive (SRA) of the National Center for Biotechnology Information (NCBI). These RNA data sets were related to seven major organizations from 54 RNA-seq experiments, including leaf, flower, fruitlet, seed, ovary, carpopodium, and pericarp (Table S1).

**Transcriptome assembly**

Firstly, the quality of RNA-sequencing data analyzed through FASTQC (https://www.bioinformatics.babraham.ac.uk/projects/fastqc/). The low-quality reads including low quality bases, adaptor sequences, and undetermined bases were filtered to obtain clean data (clean reads) with high quality using Trimmomatic version 0.40 (http://www.usadellab.org/cms/?page=trimmomatic) with default parameters. The clean reads for each library were mapped on the reference litchi genome (http://litchidb.genomics.cn/page/species/index.jsp) using Bowtie2 (http://bowtie-bio.sourceforge.net/bowtie2/index.shtml) and HISAT2 (https://daehwankimlab.github.io/hisat2/). The program was set at the maximal intron length as 5000 (--max-intronlen), and other settings were at default. Only uniquely aligned reads were assembled individually using the Cufflinks 2.0 (http://cole-trapnell-lab.github.io/cufflinks/). Cuffmerge was used to combine the transcripts with coverage higher than 2 in each library and reference litchi genome gff was used to assign the class_code to each transcript using Cuffcompare. Finally, differentially expressed genes (q-value < 0.01, fold change >2) were filtered by Cuffdiff. CummeRbund R package was used to obtain the gene expression level at FPKM (Fragments Per Kilobase of exon per Million fragments mapped).

**lncRNA identification**

The assembled transcriptome of litchi contained transcripts belong to various transcript class_codes including partially overlapping with intron (class_code "j"), old transcript or completely overlapping (class_code "="), unknown intergenic transcript (class_code "u"), intronic transcript (class_code "i"), and natural antisense transcript (NAT, class_code "x"). Among these assembled transcripts class_code "j" and class_code "=" representing the protein coding transcripts in existing genome annotation were excluded from further analysis. However, protein coding potential calculation using Coding Potential Calculator (CPC) [16]. Class codes 'j' and '=' were excluded because they represent known or annotated protein-coding transcripts, whereas class codes 'u', 'i', and 'x' were retained for coding potential analysis because they represent intergenic, intronic, and antisense transcripts. The transcripts length longer than 200 bp, both orientations possess no coding potential, and CPC < −1 were selected. Furthermore, The remaining transcripts were blasted (BlastX) against Pfam database (http://pfam.xfam.org/), Rfam database (http://rfam.xfam.org/), rRNA database (http://ssu-rrna.org/), tRNA database (http://gtrnadb.ucsc.edu/), and miRbase (http://www.mirbase.org/) to remove any known transcripts (E-value < 0.001). Only single-exon transcripts with FPKM ≥ 2 or multiple-exon transcripts with FPKM ≥ 0.5 were retained.

**Gene ontology analysis**

GO enrichment analysis of target genes correlated with differentially expressed lncRNAs was implemented by *in-house* Perl script.

**Target gene functional analysis of lncRNAs**

The lncRNA may play *cis* or *trans* role acting on adjoining or distant transcripts in genome [17]. To explore this possible function of lncRNAs, we first predicted the *cis*-target genes of lncRNAs based on genome location of the protein coding and lncRNAs. We searched for protein-coding genes 10kb upstream and downstream of all predicted lncRNAs using Bedtools (https://bedtools.readthedocs.io/en/latest/). To classify lncRNA *trans*-target genes, the BLAST (e < 1E − 5) software was used to assess the impact of lncRNA binding on protein-coding genes.

**lncRNA acting as target, precursor, and endogenous target mimics of miRNAs**

psRNA Target (https://plantgrn.noble.org/psRNATarget/) was used to identify lncRNAs as probable target of miRNAs. To identify the lncRNAs function as precursors of miRNAs, the precursor sequences of known litchi miRNAs were BLAST against lncRNAs identified in this study using. A lncRNA harbouring a miRNA precursor sequence with 100% query identity and E-value < 0.01 was defined as precursor of that miRNA.

## Results

### Global identification of litchi lncRNAs

RNA seq libraries of litchi plant tissues such leaves, fruitlet, seeds, ovary, pericarp, carpopodium and flower libraries were downloaded from NCBI SRA shown in table 1 for identification of lncRNAs. Total of 565,866,923 reads were obtained after trimming using trimmomatic program. The high-quality reads were then mapped against the reference genome of litchi using TopHat2 and Bowtie. Further we used Cufflink's software to estimate the abundance of the transcripts in terms of FPKM. The transcripts having length ≥ 200 bases, FPKM ≥ 0.5 and containing atleast one exon were filtered. Coding potential analysis of the remaining sequences was done via CPC program resulting in 3368 sequences with CPC score ≤ 0. Further screening of the filtered sequences to remove the transcripts containing potential ORFs (sequence length more than 100 amino acid), protein domain, non-coding RNAs like tRNA, snRNA, snoRNA, r-RNA, using an in-house script. Cuffdiff analysis revealed 2229 transcripts were expressed differentially in the bud and leaf tissues during flower development. Finally, 2229 potential lncRNAs were identified and were carried forward for further analysis.

### Classification of identified lncRNAs

For systematic identification of lncRNAs in litchi, the cleaned read was mapped against litchi reference genome. A total of and 41756 mRNA and 2229 lncRNA

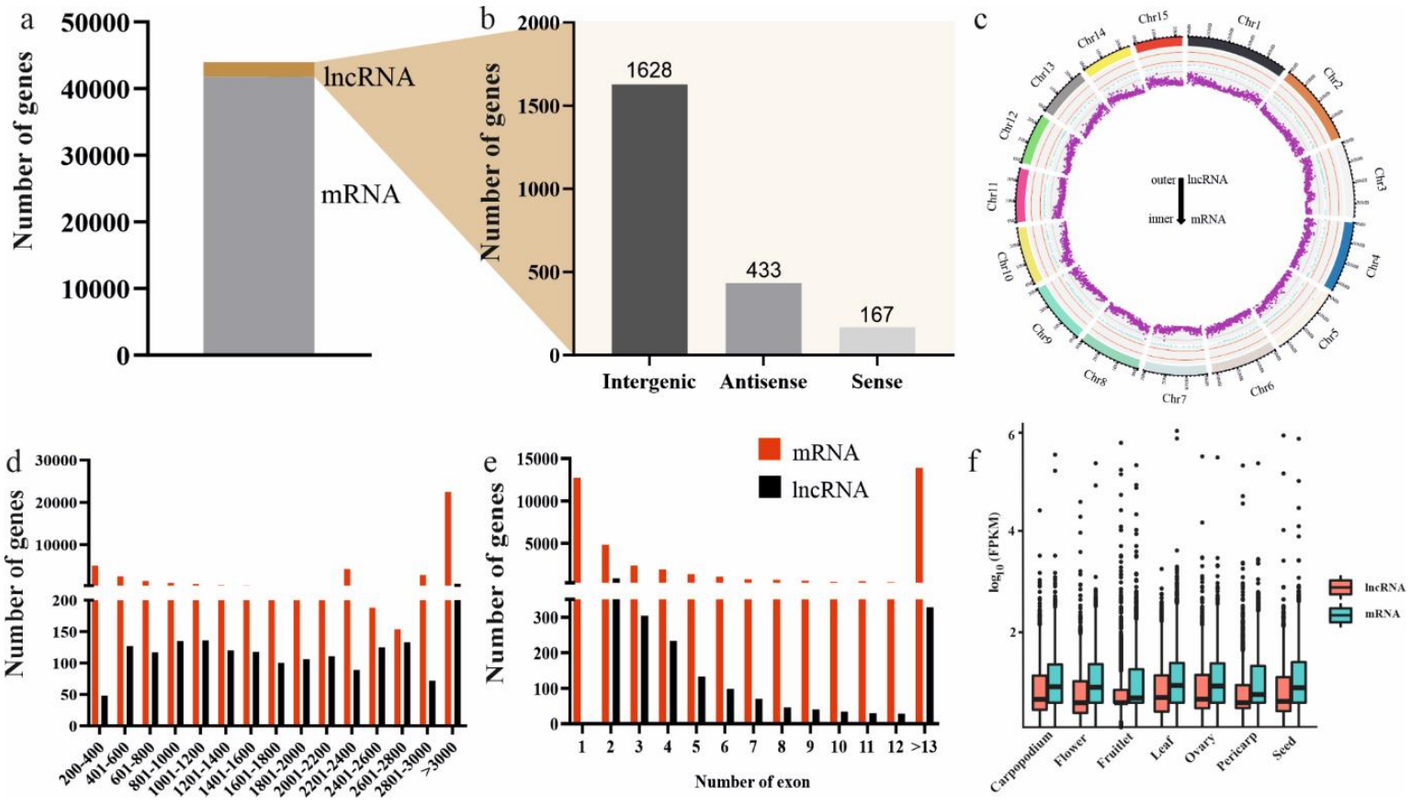


Figure 1. Long non-coding RNAs (lncRNAs) features in litchi. (a) Total number of coding and lncRNAs in lichi genome (b) numbers of different types of lncRNAs such as intergenic, antisense, and sense lncRNAs. (c) Chromosomal distribution of mRNA and lncRNAs. The inner ring represents density of mRNA and outer ring represents density of lncRNAs on different chromosomes. (d) number of genes with different length of nucleotides. (e) number of genes containing different number of exons ranging from 1 to more than 13. (f) expression density plot of lncRNAs and mRNA in different tissues of litchi.

(length ≥ 200 bp, potential coding scores < 0.5) were obtained from whole assembly (Figure 1a). For screening 2229 lncRNAs, the procedure applied to prediction of lncRNAs in litchi involves their proximity to class_code using cuff-compare. We obtained 1628 intergenic transcripts (class code: "u"), 167 sense transcripts (class code: "o"), and 433 antisense transcripts (class code: "x") (Figure 1b). The chromosome distribution of lncRNAs revealed that the highest number of lncRNAs (250) were anchored on chromosome 4 while 228 lncRNAs remained mapped in chromosomes 1. (Figure 1c). The length of lncRNAs identified in this study ranging from 200 to more than 3000 nucleotides. Among the analysed lncRNAs from our study, up to 30.57% were in the range of 200–1400 bp. Up to 69.67 %, lncRNAs were in range of number exon from 2-5. lncRNAs from our analysis, 883 lncRNAs were found to be di-exonic while no mono-exonic lncRNAs found. The range of exon number was found between 2 to more than 13 (Figure 1e). Moreover, there was considerable diversity in the distribution, number of exons, and length of mRNA and lncRNA (Figure 1). Moreover, the expression of lncRNA in different tissues is lower than mRNAs in corresponding litchi tissues (Figure 1f).

**Tissue specific expression pattern of lncRNAs**

The tissue specific expression pattern of all lncRNAs showed that few lncRNAs were expressed in more than one tissues, whereas most of lncRNAs exhibited tissue specific expression pattern in litchi. Nearly 20% lncRNAs were expressed in seeds, flower, and leaf while very less were expressed in fruitlets and ovary (Figure 2). This indicated their putative role in plant growth.

**Differential expression analysis of lncRNAs**

The differential expression of lncRNAs were analysed at between different tissues. Herein, study proved, a total of 453 were differentially expressed between flower and fruitlet. Among these lncRNAs, 329 were upregulated and 124 were downregulated. Meanwhile, 5127 (up-regulated) and 3797 (down-regulated) mRNAs were differentially expressed in same tissue combinations. The number of upregulated and downregulated lncRNAs in the various comparisons were respectively as follows: 327 and 113 in the flower vs ovary, 140 and 200 in the fruitlet vs pericarp, 164 and 300 in the fruitlet and seed, and 114 and 117 in the ovary vs fruitlet (Figure 3). Additionally, compared with flower, a total of 8924 mRNAs were differentially expressed, including 5127 upregulated and 3797 were down regulated (Figure 3). The number of upregulated

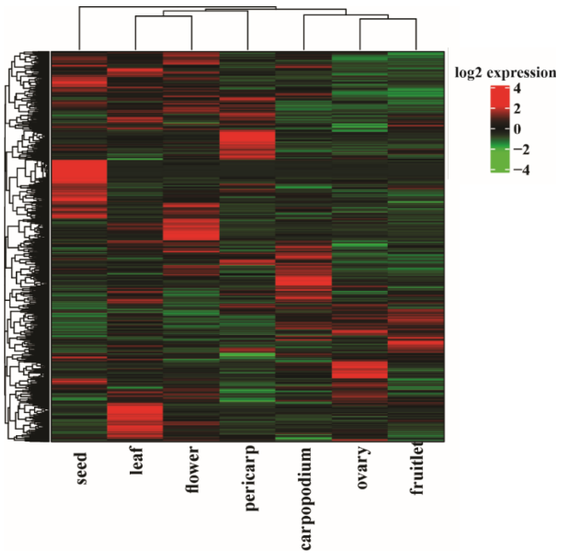


Figure 2. Tissue specific expression pattern of lncRNAs in litchi

and downregulated mRNAs in the various comparisons were respectively as follows: 3989 and 4179 in the flower vs ovary, 4312 and 4339 in the fruitlet vs pericarp, 4092 and 5574 in the fruitlet and seed, and 3884 and 2697 in the ovary vs fruitlet (Figure 3). Next, we used the differentially expressed lncRNAs only to perform a clustering analysis. The expression patterns of the samples in the one group were distinguished from their expression patterns in the other group for lncRNAs (Figure 4).

**LncRNAs predicted as precursor of miRNAs**

For identification of lncRNAs that can act as miRNA precursors, first miRNA precursor sequences were blasted against the identified lncRNAs transcripts. Then the sequences which had an Evalue less than $10^{-6}$ were used for the prediction of the hairpin in the aligned region with mature miRNA sequence in the stem-loop. lncRNAs could act as a precursor various

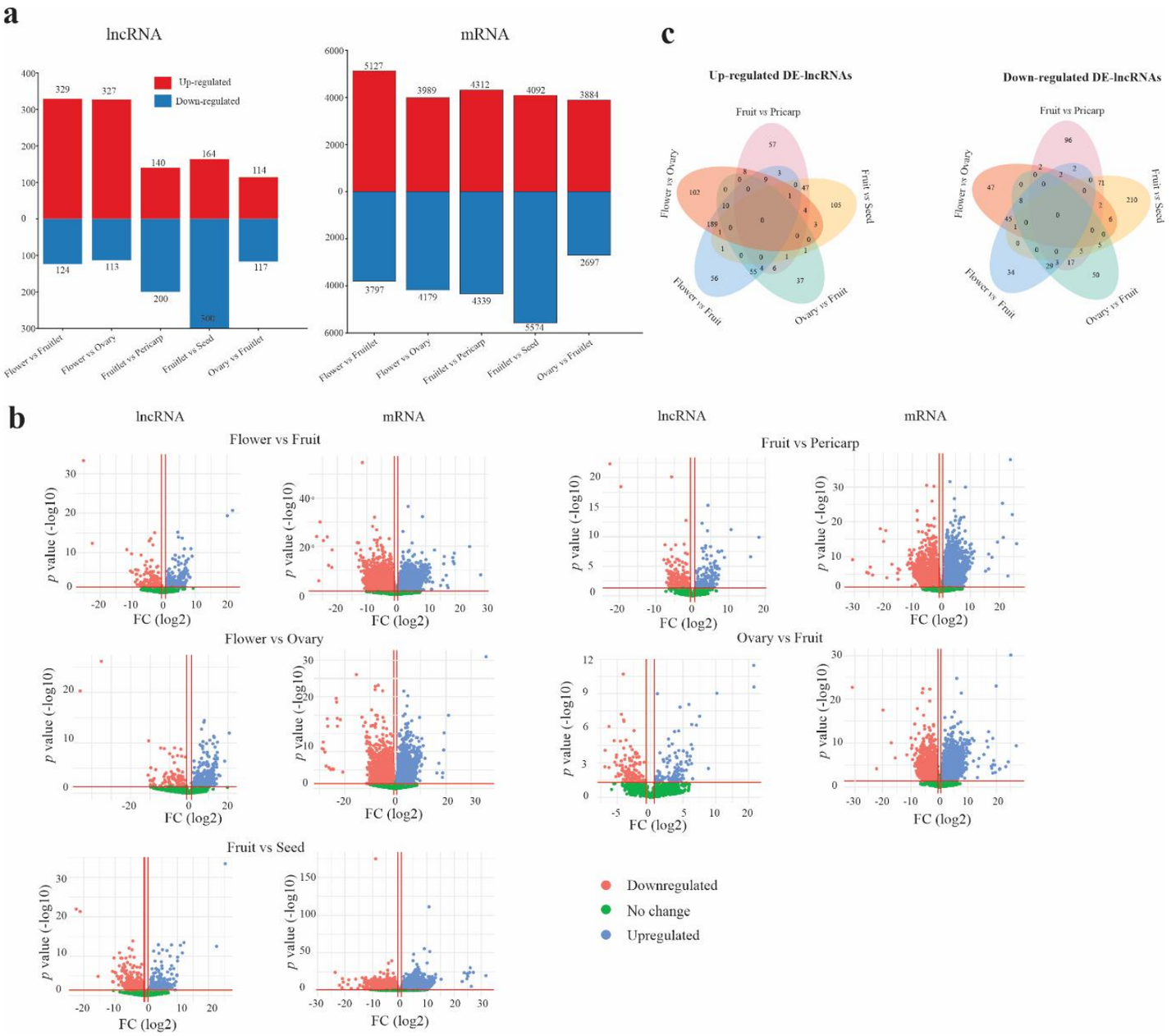


Figure 3. Number of differentially expressed genes for different litchi tissues. (a) number of differentially expressed genes (b) the volcano plots of the differentially expressed lncRNAs and mRNAs (c) The Venn diagram presents the upregulated and downregulated lncRNAs among five comparison groups (flower vs fruitlet, flower vs ovary, fruitlet vs pericarp, fruitlet vs seed, and ovary vs fruitlet).

litchi miRNAs are shown in Table 1.

**LncRNAs as endogenous target mimics for miRNAs**

Non-coding RNAs including both lncRNAs and miRNAs play pivotal role in various developmental processes of plants. All 2229 lncRNAs were submitted to psRNAtarget for checking their potential targets in litchi miRNAs. In present study, forty miRNA targets were identified in the litchi lncRNA including, miR156 targeting *XLOC_015354, XLOC_033976, XLOC_024401, XLOC_042072, XLOC_006537, XLOC_027742, XLOC_015354*. *miR2275* and *miR482* target include *XLOC_024408, XLOC_035742,*

*XLOC_037346* and *XLOC_003573, XLOC_010958, XLOC_021443, XLOC_027107, XLOC_029983, XLOC_031307, XLOC_033024, XLOC_034122, XLOC_034176, XLOC_034220, XLOC_034591, XLOC_036598,* and *XLOC_039169,* respectively (Table 2).

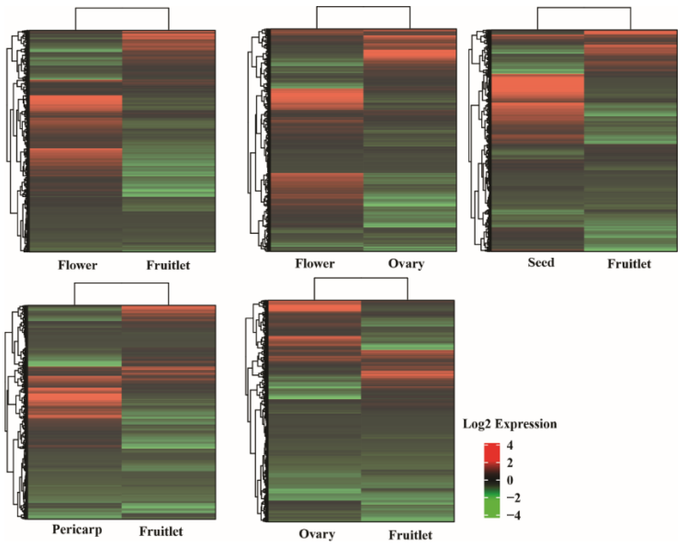


Figure 4. Heatmap showing the expression profile of differentially expressed lncRNAs

Table 1. List of lncRNAs acting as precursor lncRNA

| miRNA | Precursor lncRNA | miRNA | Precursor lncRNA |
|---|---|---|---|
| miR1030b | XLOC_012904 | miR171 | XLOC_011697 |
| | XLOC_015354 | | XLOC_011697 |
| miR156 | LITCHI016139 | miR172 | XLOC_018610 |
| | XLOC_003371 | | XLOC_024341 |
| | XLOC_006537 | | XLOC_024408 |
| miR159a | XLOC_021947 | miR319 | XLOC_015354 |
| miR164a | XLOC_006526 | miR3627 | XLOC_007853 |
| | XLOC_018320 | | XLOC_007853 |
| | XLOC_029832 | | XLOC_007853 |
| miR166 | XLOC_005863 | miR393 | XLOC_017231 |
| | XLOC_005857 | miR394 | XLOC_025708 |
| | XLOC_021141 | miR395 | XLOC_039557 |
| | XLOC_023504 | miR396 | XLOC_016052 |
| miR167 | XLOC_005863 | miR482 | XLOC_001658 |
| | XLOC_005857 | miR536 | XLOC_003573 |
| | XLOC_024933 | miRN32 | XLOC_036809 |
| | XLOC_034722 | | XLOC_015801 |
| miR169 | XLOC_015101 | | XLOC_010408 |
| | XLOC_033412 | | |

Table 2. lncRNAs targeted by miRNAs in litchi

| miRNA | Targeted lncRNA | miRNA | Targeted lncRNA |
|---|---|---|---|
| miR156 | XLOC_015354 | miR319 | XLOC_015354 |
| | XLOC_033976 | | XLOC_020592 |
| | XLOC_024401 | miR396 | XLOC_035915 |
| | XLOC_042072 | | XLOC_001658 |
| | XLOC_006537 | | XLOC_003573 |
| miR159 | XLOC_027742 | miR482 | XLOC_010958 |
| | XLOC_015354 | | XLOC_021443 |
| | XLOC_020592 | | XLOC_027107 |
| | XLOC_031149 | | XLOC_029983 |
| miR169 | XLOC_015101 | | XLOC_031307 |
| | XLOC_033412 | | XLOC_033024 |
| | XLOC_024408 | | XLOC_034122 |
| miR171 | XLOC_011697 | | XLOC_034176 |
| | XLOC_037218 | | XLOC_034220 |
| miR172 | XLOC_003297 | | XLOC_034591 |
| | XLOC_024341 | | XLOC_036598 |
| | XLOC_024408 | | XLOC_039169 |
| miR2275 | XLOC_035742 | miR394 | XLOC_022195 |
| | XLOC_037346 | miR395 | XLOC_016052 |

**Coregulation of lncRNA and the protein coding genes and functional annotation of DEGs**

Long non-coding genes regulate the expression of coding genes in *cis* or *trans*-acting mode. In this study, 3808 and 1257 (data not provided) mRNAs were regulated by *cis*-acting and *trans*-regulating lncRNAs. To analyse the potential function of coding genes located within 100kb window away from differentially expressed lncRNAs, we performed GO and KEGG analysis. GO enrichment analysis of DEGs revealed that DEGs were related to "plastid envelope", chloroplast envelope", "immune system process", regulation of defence, abiotic process", "cell wall organization", "meristem development", "peptide transmembrane transporters activity" and "manganese ion binding" (Figure 5). The KEGG enrichment showed that these collocated DE-genes were assigned to variety KEGG pathways including, carbon fixation, energy metabolism, glycolysis,

carbohydrate metabolism and lipid metabolism (Figure 6).

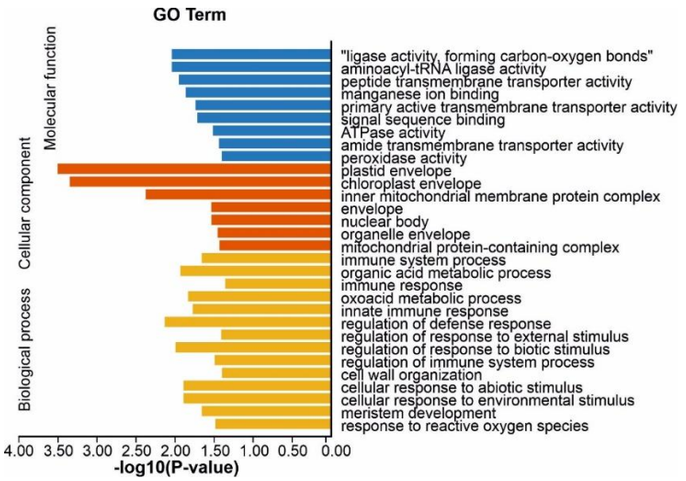


Figure 5. GO enrichment analysis of DEGs of the litchi

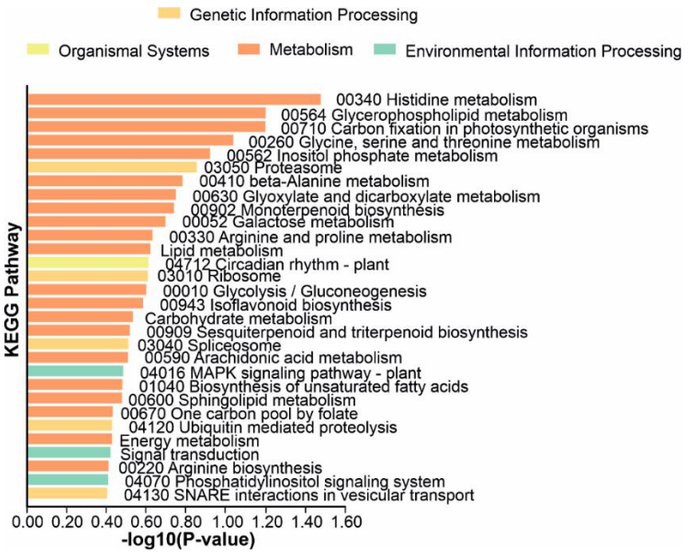


Figure 6. KEGG enrichment analysis of DEGs of the litchi

## Discussion

Recently, a plethora of studies shown the importance of lncRNAs in regulation of distinct developmental and physiological processes. lncRNAs has been identified in various model plant species, including tomato, Arabidopsis, rice, wheat, maize, and hot pepper [18], the studies in litchi has not been well reported. In this study, we identified 2229 lncRNAs in litchi different tissues, which was less than that of pepper (2505) [18], tomato (3679) [19], and rice [13]. Moreover, most of the lncRNAs were in intergenic regions, which were consistent with previous studies [18, 20, 21]. Our results Our results demonstrated that lncRNAs exhibited less conservation in sequence, type, expression patterns, and regulatory role in litchi, which would provide flexible and different regulatory mechanisms in different plant parts.

lncRNAs has been identified in various plant species, it is still difficult to characterize of lncRNAs due to lncRNAs low conservation and expressed at low levels [22]. We found that, litchi lncRNAs showed less similarity in transcript length, exon number, chromosomal distribution, tissue specific expression, and relationship among the all the tissue types used in this study compared with mRNAs. The comparison of lncRNAs conservation with lncRNAs of other species such as Arabidopsis, rice, tomato, maize, and poplar showed a negligible conservation of sequences. Global studies in different plant species demonstrated that lncRNAs indicate high tissue specificity of expression [13, 23]. Here, we decided to analyze the expression of lncRNAs in different parts of litchi using transcriptomic studies. LncRNAs showed varied expression patterns in the different tissues. Our data show that even in the same lncRNAs may be specifically expressed in a certain tissue, while the others lncRNAs remain inactive.

In this study, the function annotation of GO terms and KEGG pathways related to “plastid envelope”, chloroplast envelope”, “immune system process”, regulation of defence, abiotic process”, “cell wall organization”, “meristem development”, “peptide transmembrane transporters activity” and “manganese ion binding” or carbon fixation, energy metabolism, glycolysis, carbohydrate metabolism and lipid metabolism were reported. Several studies have suggested that lncRNA can act as a ceRNA to inhibit the function of miRNAs and compete with mRNA, pseudogenes, and other miRNA sponges for miRNA [24]. In the present study, we found that 37lncRNAs act as precursor for miRNA such as *miR156, miR172, miR319, miR393,* and *miR396*. while

38 lncRNAs have binding sites for 11 miRNAs including *miR156, miR171, miR172, miR2275,* and *miR482*. This suggests that lncRNA may be involved in litchi plant flowering. Further studies on how litchi lncRNAs act ceRNAs to regulate the development of flowering litchi are needed to verify the underlying mechanisms.

## Conclusion

In this study, we analysed the expression characteristics of lncRNA and identified a series of lncRNAs with significant expression in different litchi plant tissues. By analysing the GO and KEGG data indicated their role in different processes. Simultaneously, we also found that lncRNA might act as miRNA precursor or target of miRNAs. The results substantially improve our understanding of the lncRNAs during the litchi plant development. The study lays a foundation for further research on the lncRNA function litchi growth and development.

## Data availability

The data supporting the findings of this study are publicly available as supplementary files. All relevant information is included within the manuscript.

## Acknowledgments

Not applicable

## Conflict of interest

The authors declare that they have no conflict of interest.

## Author Contribution

The authors confirm contribution to the paper as follows: study conception and design: MN; data collection: MN, SB; draft manuscript preparation: MW, IS; manuscript revision: MN, IS. All authors discussed the content, reviewed the results and approved the final version of the manuscript.

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Not applicable

## Ethics Statement

Not applicable

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