

Transcriptomes and its role in Plant development as well as under Stress Conditions

Satyesh Chandra Roy

Head of Botany, Emeritus Professor and Co-Ordinator, Centre of Advanced Study, University of Calcutta, Kolkata, India

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Corresponding Author: Satyesh Chandra Roy | E-Mail: (scroyind@yahoo.com)

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ABSTRACT

With the advancement of Genomic studies, different types of -OMICS have been developed like Genomics, Proteomics, Transcriptomics, Metabolomics and lastly DNA-Adductomes. These are used to understand complex biological processes as well as to identify different problems in growth, development, stress conditions and diseases in all organisms. One of the important disciplines, Transcriptomes or Transcriptomics has been discussed here. In this discipline, all transcripts (messenger RNA/mRNA) having both coding and non-coding mRNA originating from DNA are dealt with. The analysis of the entire collection of RNA sequences (coding and non-coding sequences) of cell is very important as it will show when and where each gene is turned on or off under different conditions. Transcriptome analysis is generally done through special technique called Single Cell RNA Sequencing (scRNA seq) that has been discussed in detail. The role of Transcriptomics in plant development has been studied in the Shoot and Root Meristems of different plants. Its importance has also been discussed in plants under different stress conditions (both external and internal) such as biotic, abiotic, drought, salinity etc. This study will help to identify Stress-responsive and Stress-tolerance genes (Priming Genes) having important applications in adaptation. Thus transcriptomic studies have wide applications in plants to identify genes and their expressions in the development of Shoot Apical Meristems and Root Apical Meristems. This technique can also be applied to understand differentially expressed genes under different environmental stresses.

Keywords: Transcriptomics, Types of Transcriptomics, Development of Shoot and Root Meristems, RNA-seq, Stress Conditions, KEGG pathway, Gene Ontology.

Introduction

Transcriptomes are the complete set of messenger RNAs derived from DNA and the study of transcriptomes falls under the discipline Transcriptomics. With the advancement of Genomics, several new disciplines have been developed such as Proteomics, Transcriptomics, Metabolomics, Microiomics, DNA Adductomics to understand complex biological processes leading to the identification of different problems and genes responsible for growth, development, stress conditions and several diseases in the organisms [1]. The study of whole RNA sequences or Transcriptomes will show clearly from which part of DNA sequences the transcript is originated. Its detailed analysis is important to identify when and what external and internal conditions specific gene is turned on or off to help in development and adaptation [2]. Transcriptome analysis or sequencing is a technique of highly sensitive, high throughput with high resolution.

The objective of its study is firstly to identify all transcripts of an organism for understanding the transcriptional structure of genes, splicing patterns, post-transcriptional modifications and changes in the expression levels during different conditions of growth, developmental changes and variations under different stress conditions. Thus transcriptome study has a wide application in all disciplines of research in higher organisms. These are as follows i) to identify expression of new genes in certain cellular processes for

understanding the genetic basis of plant development ; ii) to understand the patterns of gene expression during growth, development and under adverse conditions; iii) to help in genetic engineering technique for developing new crop varieties ; iv) to identify changes in gene expression during growth, development and even under different environmental stresses [3]; v) to identify differentially expressed genes, splice variants and new genes. Thus the methods used in Transcriptomics studies will help to understand the function of transcripts in different cellular processes.

I) History, Types and Methods of Transcriptomics

The word Transcriptome was first used in 1990 and the study of transcriptomes was started in 1991 for the understanding of human brain function [4]

At the initial stage RNA transcripts were studied with the help of Northern Blotting and the sequencing method of Sangers but it cannot study all transcriptomes and takes long time to perform. With the development of two methods like SAGE (Serial Analysis of Gene Expression) and Microarrays the transcriptome analysis becomes easier as thousands of transcripts can be studied simultaneously. EST (Expressed Sequence Tag) method was also used in transcriptome analysis.

Next development of transcriptome study takes place with the advancement of Next Generation Sequencing Technology particularly with the use of RNA-seq technology (RNA sequencing) and Illumina/Solexa technology in 2008.

This technique has the ability to sequence billions of DNA molecules in parallel with shorter time and cost effective way than first generation sequencing (Zhang 2019) and so it can be used in RNA sequencing.

Recently new technology of RNA sequencing has been further developed by Oxford Nanopore Technologies which is called Direct RNA Sequencing (DRS). This is a powerful technology in the field of Transcriptomics by sequencing of native full-length RNA molecules without using amplification methods of PCR technology. It has the ability to characterize the chemical modifications that occur in RNA transcripts of both coding and non-coding RNA, during splicing to maintain genomic stability. Some examples of chemical modifications are: N6-methyladenosine (m6A), N1-methyladenosine (m1A), Inosine, 5-Methylcytidine (m5C), 5-hydroxymethylcytidine, N4-acetylcytidine etc and other rare types (5).

Thus the analysis of all mRNA transcripts is being done easily opening a new vista in the study of cellular processes in all organisms and will also help to understand the function of plant genomes by characterizing gene expression patterns in various growth conditions.

Types of Transcriptomics

i) Bulk Transcriptomics

It is also known as bulk RNA sequencing (RNA-seq) methods showing average gene expression levels in tissues or cell population which is useful for comparative transcriptomic studies to show differences in gene expression between tissues or in a large group of cells. It will also help to understand the cellular changes during growth and development as well as in the study of biology of diseases to facilitate in the formation of biomarkers for identifying diseases including cancer.

ii) Single Cell Transcriptomics

It is a method for understanding the gene expression level by measuring RNA concentration of thousands of genes in individual cells. It can also be used to study gene expression in heterogeneous cell populations. It is known that multicellular organisms have different cell types (heterogeneous cell populations) with different gene expression levels leading to study cellular diversity in any population. It can also be used for mapping and for quantitative measurement of transcriptional activity at single cell resolution. Single Cell Transcriptomic technique is the method to observe the order and timing of gene regulatory function and gene expressions during differentiation of cells and also in developmental processes of plants. This has been studied in roots of *Arabidopsis thaliana* where the radially-symmetric root makes developmental trajectories for several cell types [6].

iii) Spatial Transcriptomics

It is a method to measure the location and the number of gene expressions occurring in tissues. It is also used in developmental biology as well as in different disciplines of medical research like neuroscience, immunology and cancer by mapping gene expression in different cell types and to know the interactions between them.

Role of Transcriptomics in Plant Development

With the help of RNA-seq technology, transcriptional activity can be measured easily; and ii) can show transcriptomic changes in the secondary metabolic pathway at different developmental changes as well as variations in gene expression

in different plant tissues and under diverse environmental stresses (7). Recently Single cell RNA sequencing (scRNA-seq) and Spatial transcriptomic studies are being used as new molecular technologies. The former technique is able to locate gene expression and its regulation at single cell level. The latter i.e., Spatial transcriptomic study shows location of genes within tissues and cell heterogeneity at the spatial level of gene expression profiles leading to know the molecular mechanism of growth, development and the effect of environmental stresses [8]. Again Direct RNA sequencing technology has an additional advantage to know the native full-length RNA transcripts without using PCR amplifications.

Importance of RNA-seq Analysis in Plants

The collection of RNA-seq data in plants helps to understand the information of full transcripts of any plant without taking the help of any reference genome leading to the development of transcriptome data bases in a short time. In this way transcriptome data bases have already been done in different plants like *Arabidopsis*, Maize, Rice, Wheat, Barley, Tobacco, Tomato and others to help further studies on gene expression, gene regulations etc [8]. With the help of transcriptomic data, different expressions patterns of ZmWRKY genes (about 125) of Maize have been noted in different developmental stages. It has also been noted that WRKY is a transcription factor which playing an important role in development of tissues and also under stress-responses. These transcriptomic methods have also been utilized to identify genes involved in plant growth, development and genes that are expressed differently under abiotic and biotic stress conditions.

i) Shoot Apex (Shoot Meristem)

Transcriptome sequencing and analysis of tissues have been done by Single cell RNA sequencing (scRNA-seq) methods to understand the relationships between cell types in space and time and the differentiation trajectories in various plant tissues of different plant species.

Transcriptomic study can also be used to study the shoot apex in understanding the cell differentiation and the development of leaves, stems and flowers. Variation of shape and organization of shoot apex have also been identified in different plant groups. Single cell RNA sequence technology (scRNA-seq) has been used to construct high resolution single cell transcriptional profiles for the study of development, differentiation of diverse cell types in plants. The transcriptional profiles of some plants have already been made in some plants like *Arabidopsis*, Rice, Maize, Cotton and Tobacco [8].

The shoot apical meristem generates all aerial parts of plants except hypocotyls and cotyledons. The Shoot Apical Meristem contains meristematic tissues containing pluripotent stem cells. In Transcriptomic studies of *Arabidopsis*, (single cell RNA sequencing methods) in shoot apex showed that it is made of heterogeneous cells that can be divided into 23 transcriptionally distinct cell clusters (Fig.1). This study has also identified developmental trajectories for epidermal cells, vascular tissues and leaf mesophyll cells. In the shoot apex of *Populus*, the transcriptome study has identified 18 cell clusters. This study has been done by Single Cell RNA sequencing and Whole Transcriptome Shot gun Sequencing (WTSS) technologies.

It is well known that the maturation of Shoot Apical Meristem (SAM) shows with the development of lateral organs as well as the increasing activity of pluripotent stem cells that can

differentiate into different cell and tissue types. With the morphological development there occurs some internal activation of some genes like CLAVATA 3 and WUS in the organizing center. The regulation in the development of SAM is done by controlling the distribution of auxin and cytokinin and signaling pathway to activate WUS gene expression. WUS gene has a function of keeping stem cells in an undifferentiated state and the CLAVATA gene stops the stem cells to proliferate in the transition phase. Another heterodomain Transcription factor has been isolated from *Zea mays* mutant known as KNOTTED 1 (KN1). Again in *Arabidopsis thaliana*, it has been found another mutant gene known as Shoot Meristem less which has a role in preventing premature differentiation of meristem cells [10]. Detailed plant developmental studies have been done in some important leguminous plants like pea, lentil and soybean. Transcriptomic studies have been done to know the gene expression profiles in the shoot apical meristem of the garden pea. It helps to identify genes that regulate SAM activity [11]. With the help of RNAseq technology the analysis of whole transcriptional profiles has been done between dwarf and non-dwarf pea plants to identify genes for understanding morphological changes and endogenous hormone levels in the shoot meristem tissues. It has been possible to find out the regulatory relationships between auxin concentration and cell patterns and the activity of genes at the transcriptional level. These studies can also help in identifying genes involved in the regulation of plant architecture. The plant architecture is referred to as the spatial arrangement of individual organs particularly in crop plants. Plant architecture study is important as it has a great economic and ornamental value in orchards and nurseries [11].

However most of the work on SAM comes from the model plants *Arabidopsis thaliana*. It is known that SAM in plants is divided into three layers such as L_1 , L_2 and L_3 . L_1 layer gives rise to the epidermis of leaves, shoots and flowers; L_2 layer produces mesophyll tissue and germ cells and L_3 layer gives vascular tissues and pith. Detailed studies have been done in the SAM of *Arabidopsis* plant. SAM can also be divided into distinct zones such as Central Zone and Organizing Center. The first zone contains stem cells and the second zone is responsible for organ initiation where frequency of cell division is more [12]. The Central Zone of SAM is characterized by anticlinal divisions while the Organizing Centre has both periclinal and anticlinal divisions.

With the help of Single Cell RNA-sequencing methods, complete transcriptome analysis helps to characterize the novel cell subpopulations in heterogeneous tissues in plants and it also shows that developmental trajectories are found in SAM proliferating cells during the formation of organs. This transcriptome analysis also helps to understand the transition from vegetative apex to flower initiation and root development from root meristem as well as the cell lineages that determine the plant form. In an experiment the transcriptome profile was made by isolating nuclei from protoplasts of the hybrid Poplar (*Populus tremula* X *alba*) vegetative shoot apex at single cell resolution and the developmental trajectories were noted during the occurrence of new tissues in the SAM [13]. Conde et al 2021 They also analysed the development of primary vascular tissues in woody plant *Populus* using the same method.

In *Arabidopsis thaliana* it has been found that the central zone is regulated by the expression of the gene CLAVATA 3 in the epidermal cells. The internal layers of organizing centers are developed by the expression of both CLAVATA 3 and the transcription factor of WUSCHEL (WUS) genes.

In addition other marker genes are noted to demarcate various cell types in SAM such as the Boundary domain between the floral primordial and SAM, Auxin-responsive domain separating leaf and floral initiation. The peripheral zone surrounding the organizing center and the Rib zone below the organizing center give rise to stem pith. Besides this, there are other domains having pro-cambial strands during primordial formation. With the help of Single cell RNA sequencing methods, cellular heterogeneity in the shoot apex has been noted in many plants like *Arabidopsis*, Rice, Poplar, Maize and others [13].

Again RNA-seq analysis of transcripts showed Differentially expressed gene expressions in germinating shoots and young leaves of Shoot Apical Meristem of Chick pea (*Cicer arietinum*) where 882 up- and 1031 down-regulated genes were identified (Fig. 1). In the second stage gene expressions were compared with first stage of flower development showing 1143-up and 1008 down-regulated genes. When all the tissues were compared in one set, then 546 up and 354 down-regulated genes were identified. Differentially expressed genes were identified using DEseq (differentially Expressed- sequences) followed by other analyses [14]. In other studies they have also identified regulatory networks, specific pathways and active genes during development of shoot apex and flower development in Chick pea. It has also been found that the development of mature chloroplasts from immature chloroplast takes place in the shoot apical meristem. Transcriptome analysis showed that genes encoding chloroplast proteins are found in the stem cells of the proplastid located in the central zone of Shoot Apical Meristem. The expression of gene starts in the Shoot apical meristem and then progressively goes to the primordial leaves. Their expressions are correlated with thylakoid proliferation and chloroplast development [15]. In the study of transcriptome profiles in the shoot apex of Pea plants, some genes were identified showing differential expressions between Shoot apical meristem and non-meristematic tissues leading to identify specific genes responsible for controlling the activity of Shoot Apical Meristem. EST sequences derived from cDNA libraries showed that oligonucleotide array was representative of the gene content of the Shoot Apical meristem using CombiMatrix Custom Array methods [10]. The data shows that transcripts are associated with cell division, proliferation, epigenetic regulation, auxin-mediated responses and microRNA regulation. These are abundant in Shoot meristem tissues than in non-meristematic tissues.

ii) Root Apex (Root Meristem)

Most of the studies in root development have been done in *Arabidopsis* species using single cell RNA-sequencing methods to identify expression features of major cell types and quiescent cells. Generally the root is organised in concentric rings of endodermis, cortex and epidermis that surrounds the stele consisting of pericycle, phloem and xylem tissues. These cells originate from some stem cells known as Quiescent Centre. It is a group of cells in the root apical meristem that maintains stem cells and send signals to initial cells for root generation as well as in plant growth and productivity. Transcriptome studies also reveal some developmental trajectories along the length of the root. Different cell clusters were identified through single cell RNA sequencing methods (scRNA-seq). It was showed that mature cells of mixed identity were present at the level of sequencing resolution. With the help of this technique, the number of genes and transcripts detected was 4276 and 14,758 per cell respectively [16].

The identification of gene expression profiles on specific cell populations of Arabidopsis roots was done using graph-based clustering on 4727 single-cell transcriptomes using Seurat Software package. They also identified 15 clusters having 81 and 596 cells in each cluster. The function of cell clusters was identified by comparing with the cell type-specific marker genes collected from root transcriptomic datasets. The expression of some root development genes such as PLT1, SCR, SHR, APL, COBL9, and GL2 were identified in some clusters leading to the importance of scRNA-seq technique in transcriptome analysis for the identification of specific genes in developmental processes.

Transcriptome Studies under Stress Conditions

Generally, plant shows response in environmental changes of nature like abiotic, biotic, drought, salinity stresses etc. Thus plants always try to adapt their growth and development under stress conditions which may be called development plasticity. Shoot Apical Meristem shows more developmental plasticity as it is the main center of growth and development. These stress conditions may be external or internal. The best example of internal stimuli is found to select the developmental stage, length of light, temperature (vernalization), hormone like GA3 etc. required for floral transition.

Several morphological changes in plants are noted under different stress conditions. In *Rosa hybrida*, drought stress shows reduced shoot growth and some defects in shoot length, weight and early floral organ formation. More shoot growth is found under Mannitol stress where the importance of EGM1/2 gene (Enhanced Shoot Growth Under Mannitol Stress 1/2) encoding putative-receptor like kinases has been noted [17].

It has been noted that adaptation to stress conditions for plant growth and development is controlled by some genes called Priming genes. Priming is also known as Epigenetic priming, a process that helps to make active some transcription factors through some specific chromatin domain when there is an external or environmental stimuli or stress. The priming may also occur through i) pre-accumulation of stress-responsive transcripts, ii) through alterations in some specific metabolites and iii) due to accumulation of stress mitogen-activated protein kinases (MPKs) and iv) through epigenetic regulation [17]. Another study showed that the expression of primary carbohydrate metabolism genes under heat-stress conditions are also involved in adapting heat stress conditions. These heat stress primed (memory) genes are already present in the Shoot Apical Meristem [17,18].

It has also been identified as R2R3-MYB family genes (abiotic stress-responsive genes) in Wheat plant through transcriptome studies by RNAseq analysis. Again various transcription factors like ERF, NAC, ARF and HD-ZIP are noted in Maize plant during abiotic stress-responses. In case of Soybean plant drought-stress responses show changes in gene expression with upregulation of genes involved in ABA signaling and activation of ABA receptor complex [19].

Salinity stress in plants affects the growth by inhibiting photosynthesis affecting agricultural productivity and sustainability. In addition to Genomic studies, Transcriptomic studies are being done in plants growing under salt stress conditions to identify the differentially expressed (DE) genes in crop plants. Lot of works on salinity tolerance were done on Sea Grasses as these plants can survive environment of high salinity in ocean. *Thalassia hemprichii* species is distributed in shallow coastal areas in the tropics and subtropics of the eastern Atlantic

and Indo-Pacific Ocean, South of China Sea, Queensland of Australia and other places of the world. Although the optimal salinity for growth of this plant is generally 25 to 35 PSU but it can survive both in high and low salinity of water. About 319 Differentially Expressed Genes were identified through transcriptomic studies (Fig.1). These genes are regulating transport mechanisms and metabolisms to give environmental adaptation through regulation of gene expression. It has been noted in an experiment of this plant under high salinity or low salinity stress that the upregulated genes were more than downregulated genes. [20]. On analysis of differentially expressed genes, eight co-repressed genes were identified as methyl transferase, putative glucose-6-phosphate 1-epimerase, putative bystin, cytochrome cl-2 etc. Many structural changes in plants were found under salt stress conditions to reduce water loss by thickening cuticle in the epidermis of leaves and mechanical tissues.

Chloroplast is the most salinity-sensitive organelles and the presence of osmiophilic granules in leaves may be the biomarkers for measuring salt tolerance in plants.

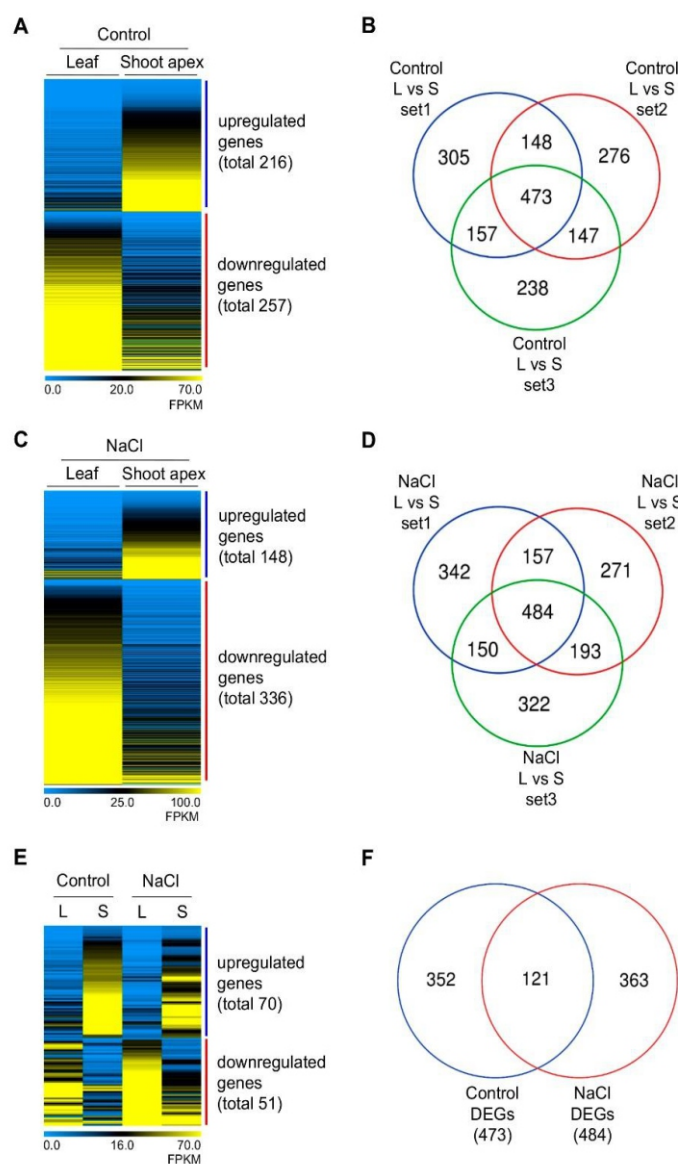


Fig.1. Explanation of Figures. Showing profiles of developmental priming genes in Shoot apex.

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