

# Transcriptomics in fruit crops: present status and future prospects

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#### ABSTRACT

To meet the emerging challenges, there is a need to evolve improved genotypes in fruit crops having higher productivity, better quality and tolerance to emerging biotic and abiotic stresses. However, genetic improvement of the fruit crops using traditional breeding approaches is very time consuming due to various reasons including their perennial nature, long juvenile phase, higher heterozygosity and complex genetic makeup, self-incompatibility, seedlessness, polyploidy, higher linkage drag etc. The advent of biotechnological tools and omics science especially transcriptomics offers several ways to fulfil the above needs in a short time period. Amongst various fruit crops, transcriptomics has been widely used in crops like apple, banana, citrus, grape etc. to explore the transcriptome changes during different metabolic processes and induced changes, *i.e.* fruit development and ripening, application of exogenous plant growth regulators or chemicals, response to biotic and abiotic stresses etc. Similarly, the minor fruit crops are needed to be analysed for their transcriptome under various stress conditions. RNA-Seq is a recently developed approach for transcriptome profiling that uses deep-sequencing technologies to provide more precise measurement of levels of transcripts and their isoforms. The present review reports various significant achievements of transcriptome analysis, RNA-Seq and their future prospects in fruit crops.

Key words: Differentially expresses genes, molecular mechanism, omics, RNA-Seq, transcripts.

## INTRODUCTION

Fruit crops play an important role in human diet due to their higher vitamins and mineral content (Klee, 55). Owing to these properties there is continuous increase in demand for quality fruits amongst the consumers. However, the shrinking per capita land availability accompanied with threats of climate change and erratic weather patterns, there is an urgent need to develop improved fruit genotypes including rootstocks having higher productivity and tolerance to emerging biotic and abiotic stresses. However, genetic improvement of fruit crops using traditional breeding approaches is very time consuming due to various factors including pereniality, long juvenile phase, higher heterozygosity nature, self-incompatibility, higher linkage drag etc. (Limera et al., 66; Yamamoto, 131). The development of biotechnological tools and emergence of Omics science can offer several ways to fulfil the current needs in a short time period, along with solving the above problems of traditional breeding. Amongst the various types of Omics, 'transcriptomics' have emerged as a powerful tool, which can assist both the traditional and non-conventional approaches to fasten the process of genetic enhancement (Yamamoto, 131). At present, India is the second largest fruit producer in the world after China, though in the terms of fruit productivity, it is guite low than the

other major fruit producing countries. Several factors affect the lower fruit productivity of the fruit crops like occurrence of biotic and abiotic stresses; besides several inherent problems like alternate bearing, physiological disorders, lack of ideal rootstock genotypes *etc.* (Singh *et al.*, 103). 'Transcriptomics' can be used to unravel complexity of different metabolic pathways like resistance or susceptibility mechanism(s) to various biotic or abiotic stresses, which would not only help in efficient management of stress but also to breed improved genotypes with desired traits (Fig. 1). Current status of applications of transcriptomics, RNA-Seq and their future prospects in fruit crops is discussed hereafter in this review.

#### Transcriptomics

Transcriptomics is the study of the 'transcriptome'. The word 'transcriptome' used previously to signify an entire set of transcripts, has been attributed to Charles Auffray (Martin and Wang, 77). However, this term transcriptome now refers to complete set of all the RNA molecules expressed in some given entity, such as a cell, tissue, or organism (Martin and Wang, 77; Wolf, 124). Transcriptomics includes all kind of transcripts, including messenger RNAs (mRNAs), microRNAs (miRNAs) and different types of long noncoding RNAs (IncRNAs). It is also an extended form of RNAs transcription and expression levels, functions, locations, trafficking, and degradation (Wang *et al.*, 121). Northern blotting is the classical

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technique for analyzing the molecular size and abundance of selective RNAs in a mixture of RNAs. This technique is based up on the nucleic acid hybridization between a probe and the complementary sequence in a population of RNAs. Thus, it can be used for identification of novel splice variants, preprocessed RNAs, and non-coding RNAs, and their relative abundances. However, modern day tools like microarray and RNA-Seq offer a high-throughput alternative to Northern blotting (Lovatt and Eberwine, 71; Wang et al., 121). Present day transcriptome studies based on different high-throughput methods for analysis of expression of multiple transcripts under various growing conditions including biotic and abiotic stresses, stages of maturity etc. (Milward et al., 81). Amongst fruit crops, transcriptomics studies have been applied in crops like grape, apple, citrus etc., to study the change in transcriptome during fruit development, effect of exogenous application of plant growth regulators or chemical, response to biotic and abiotic stresses etc. (Table 1). However, its potential application is still in the nascent stage in minor and underexploited fruit crops, which need to be explored in the coming times. Comparative transcriptomics can be further used to expand our understanding of relationships between transcriptomes, and transcriptome and phenotype across the fruit crops under different agro-climatic situations.

## **Application in Fruit Crops**

# Apple

Using the microarray analysis, Lee *et al.* (60) observed that 138 genes were highly expressed in young 'Fuji' fruits (21 DAA) as compared to mature ones (175 DAA), leaf or floral tissue. However, microarray analysis of 'Royal Gala' fruit development revealed that nearly 2,000 genes that showed significant changes in expression over a 146-day post-anthesis time course (Janssen *et al.*, 48). Through the EST occurrence approach in 'Royal Gala', Wisniewski *et al.* (123) observed up-regulation of various defence/ stress-related and energy-related genes in plants subjected to water or temperature stress and down-regulation of general metabolism, photosynthesis- and transport-related genes.

Reduced water and nutrient movement, changes in hormonal concentration are some of the factors, which are considered as possible canopy size control mechanism of rootstock on scion (Blake *et al.*, 19). Jensen *et al.* (49) studied the gene expression patterns in scions of the 'Gala' apple cultivar grafted to either M.7 EMLA (semi-dwarfing, reduces *Erwinia amylovora* susceptibility of the scion) or M.9 T337 (dwarfing, does not alter fire blight susceptibility of the scion). They observed that 'Gala' grafted to the M.9 T337 rootstock had higher expression of a number of photosynthesis-related, transcription/ translation-related, and cell divisionrelated genes, while showed increased stressrelated gene expression on M.7 EMLA rootstock. They accounted higher expression of *CKS1* for the dwarfing effect of M.9 rootstock.

The molecular basis of resistance or susceptibility of apple scab disease caused by *Venturia inaequalis* and fire blight disease caused by *Erwinia amylovora* has been revealed recently. Earlier, Paris *et al.* (89) identified 34 DEGs in genetically modified 'Gala' line transformed with the *HcrVf2* scab resistance gene, after 48 h of infection with *V. inaequalis*.

Penicillium expansum causing blue mould during storage is a major hindrance in commercial apple production. Using AryANE chip covering 60K apple transcripts, Ahmadi-Afzadiet al. (3) reported that, various genes including biosynthesis of flavonoids to cell-wall structure were involved in imparting the resistance or susceptibility to blue mould in apple. Worldwide, red-fleshed apples are gaining more attention due to their high anthocyanin content. The role of MdMYB10 and its homologues were explored in anthocyanin biosynthesis in apple (Espley et al., However, the roles of other transcription factors were needed to be explored. Liu et al. (69) explored the role of MdWRKY11 in anthocyanin biosynthesis in red-fleshed apple and reported that overexpression of *MdWRKY11* in apple callus could significantly increase anthocyanin accumulation. Various other researches have also reported on transcriptome analysis of apple (Table 1).

# Banana

Worldwide banana is an important fruit crop and a staple food for many nations. *Fusarium* wilt, also known as Panama disease is caused by *Fusarium oxysporum* f. sp. *cubense*. (*Foc*), affects cultivation of banana in tropical and subtropical countries. A new variant, tropical race 4 (TR4), threatens the banana trades that are based on Cavendish cultivars, and other locally important types such as the plantains (Ploetz, 93). Several attempts (Table 1) in terms of transcriptome analysis have been done to understand the disease complexity and elucidate the molecular mechanism of Foc resistance (Dong *et al.*, 34).

Based on digital gene expression, Li *et al.* (61) observed large differences in the transcriptome profiles of the Foc TR4-resistant somaclonal variant (Nongke No. 1) and its susceptible wild-type (Brazilian). A total of 5,008 genes were assigned to plant-pathogen interactions, including disease defense and signal transduction. Pathways of various

plant growth regulators like ethylene, jasmonic acid, salicylic acid *etc.* play major role in expression of plant defense related genes. Foliar pathogen *Mycosphaerella fijiensis*, causing black leaf streak disease (BLSD) commonly known as Black Sigatoka in banana is responsible for yield losses ranging from 20 to 80%. Passos *et al.* (91) infected the bananas genotypes with BLSD under *in vitro* conditions and obtained 9333 high-quality ESTs for resistant *M. acuminata* ssp. *burmaniccoides* Calcutta 4 and 3964 for susceptible *M. acuminata* cv. Cavendish Grande Naine. These EST collection was suggested to be used as a resource for further studying the functional genes, including transcripts expressed in banana and *M. fijiensis* interactions.

Musa balbisiana is a source of resistance or tolerance to several biotic and abiotic factors like drought (Vanhove et al., 113). Whole transcriptome profiling of *M. balbisiana* has been completed by ICAR-National Research Centre for Banana (NRCB), Trichy, India. The quality reads obtained from these sequencing were assembled with AA reference genome (*M. acuminata* DH Pahang). The annotated results revealed that approximately 3301 unigenes were found to be homologous to known defenserelated genes in other plants (Backiyarani et al., 14). Harikrishna et al. (45) studied the transcriptome of 'Berangan' (AAA genome) banana in response to salt stress and observed that siRNA expression patterns changed in response to salt stress. WRKY transcription factors (WRKY TFs) are involved in the regulation of various physiological processes including development, senescence and in-plant response to many biotic and abiotic stresses.

Plant growth-promoting rhizobacteria (PGPR) can be applied in banana to meet the nutrient demand along with eliminating the hazardous effect of chemical fertilizers (Vacheron *et al.*, 112). Gamez *et al.* (40) inoculated *in vitro* raised banana cv. Williams callus with *Bacillus amyloliquefaciens* strain Bs006 and *Pseudomonas fluorescens* strain Ps006 rhizobacteria. Transcriptome analysis revealed that banana gene expression profiles were influenced by bacterial colonization processes and levels that stimulate distinct groups of genes at various points in time.

## Citrus

Citrus greening orhuanglongbing (HLB) is one of the most devastating diseases caused by gramnegative, phloem-restricted bacteria *Candidatus Liberibacter asiaticus* (CaLas), *Ca. L. americanus* (*CaLam*) and *Ca. L. africanus* (*CaLaf*) (Bove, 20). Several studies showed that various gene transcripts and biological processes are significantly altered upon infection of these bacteria (Table 1). Martinelli *et al.* (78) observed down regulation for light reactions genes, while up regulation for sucrose metabolism and starch biosynthesis genes in the HLB infected leaves of 'Valencia' sweet orange.

Citrus fruit ripening is accompanied by the synthesis of several proteins along with up and down regulation of many genes. Various plant growth regulators like ethylene, jasmonates, ABA play key roles in fruit development and ripening (Kumar et al., 57). Zeng et al. (137) analysed the differences in gene expression in peel of Mingliutianju (Citrus reticulata Blanco cv. Mingliutianju), a novel late ripening spontaneous bud mutant and its wild type Chuntianju (C. reticulata Blanco cv. Chuntianju) at 12 and 23 weeks after flowering. They identified 395 differentially expressed genes, which included 132 up-regulated and 263 down-regulated ones. Study of single cell transcriptome is gaining immense importance as several plant products are synthesized in specialized cells and tissues (Buchanan et al., 22). Voo and Lange (117) standardised a protocol for the isolation of epithelial cells that surround secretory cavities in grapefruit peel, which can be suitably used for RNA isolation and downstream transcriptome analyses.

Citrus stem rot disease caused by *Phytophthora nicotianae* is a worldwide problem causing severe yield loss. Comparative transcriptome analysis of the *P. nicotianae* tolerant sour orange and susceptible sweet orange cv. Madam Vinous showed that necrotrophic phase is a decisive turning point, since it included stronger modulation of a number of genes involved in pathogen perception, signal transduction, hypersensitive response-like response, hormone signalling, and cell wall modifications (Ajengui *et al.*, 4).

Boron deficiency causes corky split vein disorder in citrus. DEGs analysis of boron deficient 'Newhall' Navel orange (Yang et al., 132) and 'Xuegan' sweet orange (Lu et al., 73) showed that cytokinin signal transduction pathway might have played an important role in initiation of symptoms related to corky split vein disorder. Citrus shoot tips abscise at an anatomically distinct abscission zone that separates the top part of the shoots into basal and apical portions (commonly known as citrus self-pruning). This cell separation occurs only at the abscission zone, which suggests its cells have distinctive molecular regulation (Nakano and Ito, 87). Zhang et al. (139) observed that the various DEGs at three stages of self-pruning were related to programmed cell death (PCD), cell wall biosynthesis or metabolism. Transcriptomics of various other aspects have also been attempted (Table 1) in citrus.

## Grape

Amongst the various fruit crops, grapevine (Vitis sp.) is one of the most widely studied for transcriptome (Table 1). Using 54 samples of grapevine cv. Corvina from various plant parts including green and woody tissues, pollen, senescent leaves etc., a genomewide transcriptomic atlas was developed (Fasoli et al., 37). These samples expressed nearly 91% of the predicted grapevine genes. Grapevine is vulnerable to various pathogens, which cause significant economic losses. Accordingly, several transcriptome studies on grapevine were conducted on various diseases, viz. phytoplasma (Abba et al., 1), downy mildew (Li et al., 65), powdery mildew (Amrine et al., 8) etc. Although chemical control is available, but use of elicitors to enhance the tolerance or resistance can overcome the harmful agro-ecological concerns of the chemical. Almagro et al. (7) reported that combined treatment of elicitors (cyclodextrins and methyl jasmonate) to the grapevine cell cultures resulted in a crosstalk between the signalling cascades activated by both, which in turn, triggered various regulatory pathways involving the up-regulation of NAC, MYB15 and WRKY transcription factors, protein kinases and calcium signal transducers.

Gauthier et al. (42) reported that sulfated derivative (PS3) and ß-glucan laminarin (Lam) shared a common stress-responsive transcriptome profile that partly overlapped with the salicylate (SA) and jasmonate-dependent ones. They observed that PS3 primed the SA- and ROS-dependent defense pathways leading to induced resistance of grapevine against Plasmopara viticola causing downy mildew. Phenotypic plasticity refers to the ability of a single genotype to produce a range of phenotypes as a function of its environment (Bradshaw, 21). Dal Santo et al. (27) studied the plasticity of the grapevine cultivar Corvina berry transcriptome through 3 consecutive growth years in 11 different vineyards in the Verona area of Italy. They observed that most of the berry transcriptome clustered by year of growth rather than common environmental conditions or viticulture practices, and transcripts related to secondary metabolism showed high sensitivity towards different climates, which was confirmed also by metabolomic data obtained from the same samples. Sun et al. (107) also compared the transcriptome of Cabernet Sauvignon grape berries from two regions with distinct climate.

Apart from the transcriptome analysis under various biotic and abiotic stresses (Table 1), several reports showed that it has been well studied in topics related to various stages of berry development (Balic *et al.*, 17; Guo *et al.*, 44). Dramatic increase of ABA in the later berry growth is a trigger of ripening and this stage is called "veraison" (Pilati *et al.*, 92). Several studies have reported the relationship between ABA, ripening and anthocyanin accumulation (Koyama *et al.*, 56; Wheeler *et al.*, 122). Content of pro-anthocyanidins, anthocyanins and other volatile compounds lead to the specific flavour, colour and taste of various grape berries (Shiratake and Suzuki, 100). The transcriptomics changes associated with synthesis of ripening related secondary metabolites, such as proanthocyanidins (Huang *et al.*, 47), anthocyanins (Wu *et al.*, 125) *etc.* were also investigated.

Gibberellic acid (GA) is used commercially to induce the parthenocarpic fruit set and berry elongation in grape. The transcriptome changes associated with exogenous application of GA in grape berries is well studied (Wang *et al.*, 118; Wang *et al.*, 119). Chai *et al.* (23) provided the first sequential transcriptomic atlas of exogenous GA<sub>3</sub>-induced berry enlargement. It revealed the complexity of GA<sub>3</sub>'s effect on berry size. The exogenous GA<sub>3</sub> application induced multipoint cross talk with other plant growth regulators like auxin, cytokinin, brassinosteroid, ABA and ethylene.

# Mango

In mango (Mangifera indica L.) most of the transcriptome analyses are focused to unravel the molecular mechanism or changes associated with the fruit development, ripening process and flavour development (Table 1). Wu et al. (126) provided the first report of mango transcriptomics from using cultivar Zill and identified 7,536 peptides, which matched with 2,754 proteins. They provided extensive transcriptomics profiling from pulp and skin tissues of four fruit developing stages using pooled RNA. Similarly, Srivastava et al. (105) and Deshpande et al. (33) also unravelled various ripening associated genes in Dashehari and Alphonso fruit. Various transcripts associated with ethylene, starch, sucrose, amino acids, terpenes, lactones, furanones and secondary metabolite biosynthesis pathways were identified in Alphonso fruit (Deshpande et al., 33).

Mango fruits are given a thermal quarantine treatment to kill larvae of Mexican fruit fly (Singh *et al.*, 104) before export to the United States. Hot water treatment of Kent fruits enhanced the expression of genes related to hydrolase activity and these transcripts belong to sucrose, starch, and cell wall polysaccharide metabolic processes (Dautt-Castro *et al.*, 29). Recently, Sharma *et al.* (99) analysed the transcriptome profiling of regular (Neelam) and alternate (Dashehari) bearing mango cultivars and revealed novel insights into the regulatory mechanisms underlying alternate bearing. Amongst various genes identified, three

genes, viz. SPL-like gene, Rumani GA-20-oxidaselike gene and LOC103420644 were significantly differentially expressed, while, only single gene (gbGBVW01004309.1) related with flowering was found to be differentially expressed. There is dearth of information about the gene expression profile during flower development in mango. Yadav et al. (130) performed transcriptome analysis of Amrapali, from different stages of bud development in healthy and malformed tissues. Higher differential expressions copy numbers of seven flowering genes (FTIP1, MYB30, ATH1, TPL, CDKC2, CPK33 and bHLH) were observed in both the healthy bud and panicle development stages as compared to malformed bud development stages. The DEGs, GA<sub>20</sub>OX3, AGL24 and LDL2 were observed as the key genes regulating floral transition and differentiation.

### Papaya

World-wide papaya (*Carica papaya* L.) is grown in various tropical and sub-tropical regions. Only a few number of transcriptome studied has been reported in papaya. Porter *et al.* (94) studied the papaya root-specific gene expression and observed cDNAs for genes, which were associated with defense, beneficial plant-microbe interaction, abiotic stress, and plant development. They identified novel non-protein-coding RNAs (npcRNAs), which have no database sequence homology and are proposed to be new genes.

It is trioecious in nature and prediction of sex type at seedling stage is a major concern. Moreover, lack of reliable biochemical and molecular marker is also a major hindrance. For identification of the candidate genes for sex determination, Urasaki et al. (111) conducted the transcriptome analysis of flower samples from male, female and hermaphrodite plants using high-throughput SuperSAGE for digital gene expression analysis. They obtained short sequence tags from the transcripts. The majority of tags on the sex chromosomes were located on the X chromosome, and only 30 tags were commonly mapped to both the X and Y<sup>h</sup> chromosome. This information on sex chromosome-specific expressed genes will help elucidating sex forms in early stage of seedling. Sex reversal during high summer or low winter temperatures is also common phenomenon (Arkle and Nakasone, 11). Lin et al. (67) reported 1756 DEGs between normal male and male-tohermaphrodite sex reversal flowers under influence of low temperature. Based on the findings, they suggested that male-to-hermaphrodite sex reversal was likely caused by silencing the gynoecium suppression function on the sex determination pathway through epigenetic modification.

Fang *et al.* (36) studied the transcriptomics of PRSV resistant transgenic papaya SunUp and its PRSV susceptible progenitor SunSet to compare the transcriptional changes in young healthy leaves prior to infection with PRSV. Several known and novel stress-induced and disease-resistance genes including *MYB*, *WRKY*, *ERF*, *NAC*, nitrate and zinc transporters, and genes involved in the abscisic acid, salicylic acid, and ethylene signalling pathways, were highly expressed in SunUp. However, they did not note any detrimental pathways and allergenic or toxic proteins induction on a genome-wide scale in transgenic SunUp.

Papaya plants have been considered relatively tolerant to drought, which can be attributed towards a desiccation postponement mechanism. However, water scarcity may limit the physiological performance of papaya. It has been reported that papaya plants accumulated proline, plant growth regulators like ABA, jasmonic acid under drought stress (Mahouachi et al., 75, 76). However, there is dearth of information about the change in transcriptomics in papaya plant under drought stress. The reference and de novo transcriptomic analyses identified 8,549 and 6,089 drought-responsive genes and unigenes, respectively; in drought stress imposed three-monthold 'Maradol' papaya plants (Gamboa-Tuz et al., 39). It was observed that under moderate drought stress, various processes related to cell cycle and DNA repair were up-regulated in leaves and sap whereas under severe drought stress hormone signalling, and oxidation-reduction were up-regulated in all tissues.

Application of ethylene can be done to promote papaya fruit ripening, whereas 1-methylcyclopropene (1-MCP) can delay ripening via the inhibition of ethylene receptor. However, inappropriate treatment of 1-MCP can lead to fruit ripening disorders like "rubbery" textured fruits (Thumdee et al., 109). Transcriptome analysis revealed that longterm treatment of 1-MCP (400 nl l-1, 16 h) could severely inhibit the ethylene signalling and cell wall metabolism pathways, which might result in the failure of cell wall degradation and fruit softening causing "rubbery" texture (Zhu et al., 144). However, short-term treatment of 1-MCP (400 nl l<sup>-1</sup>, 2 h) significantly delayed the papaya fruit ripening with normal ripening characteristics. 1-MCP treatments accelerated the lignin accumulation and delayed cellulose degradation during fruit ripening.

Papaya sticky disease is due to a combined infection of papaya meleira virus (PMeV) and papaya meleira virus 2 (PMeV2), the only laticifers-occurring viruses (Sa Antunes *et al.*, 97). Papaya sticky disease symptoms appear only after flowering, indicating a host stress response associated with sticky disease

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Fig. 1. Possible areas of transcriptome studies on fruit crops. Apart from the above, the other transcriptome studies are related to post-harvest management, *in vitro* experiments, trans-/ cisgenics, *etc.* 

tolerance at the pre-flowering stage (Ventura *et al.*, 114). This suggests that a tolerance mechanism to papaya sticky disease symptom development operates before flowering. Global gene expression analysis indicated that a host stress responses, mainly mediated by salicylic acid was associated to the tolerance to sticky disease symptoms at pre-flowering stage in *C. papaya* (Madronero *et al.*, 74). Later on, transcriptomic and proteomic of symptomatic papaya plants by Antunes *et al.* (9) revealed the modulation of protein turnover, suggesting the involvement of the ubiquitin/ proteasome system (UPS) in this pathosystem. Analysis of microRNAs modulated during the infection showed that microRNAs predicted to target *UPS* genes were specially altered.

#### Strawberry

It has been shown that anthocyanin biosynthesis is controlled by a series of key structural genes that encode for important enzymes in biosynthesis pathway (Allan *et al.*, 6). Xu *et al.* (129) observed that light can promote anthocyanin accumulation in mature fruit, and also increased the expression of aroma-related genes and stabilized FvMYB10 protein, a key regulator of anthocyanin biosynthesis, in woodland strawberry. Grey mould caused by *Botrytis cinerea* is amongst the most devastating diseases causing economic losses worldwide (Dean *et al.*, 31). Mehari *et al.* (80) studied the transcriptome profiles of *F. vesca* fruit at different ripening stages with interaction to *B. cinerea* infection. In general, unripe fruits exhibited a stronger defense response than red fruits. However, they observed that a broad transcriptional reprogramming in both unripe and ripe fruits, involving in particular receptor and signalling, secondary metabolites, and defense response pathways. Various membrane-localized receptor-like kinases genes were mostly down-regulated in white and up-regulated in red fruits. Later, Badmi (15) also identified the genes which were common between different tissues (leaf, white berries, red berries) upon pathogen infection. Genes involved in MAP kinase signalling, pathogenesis-related, allergens, cell-wall defences, detoxification and secondary metabolites were common responsive and up-regulated between *F. vesca* infected leaf, white berries and red berries.

#### Other fruit crops

Except the fruit crops mentioned here to fore, *viz.* apple, banana, citrus, grape, mango, papaya and strawberry, transcriptomics have been explored in a limited scale in most of the other fruit crops (Table 1). In apricot,Grimplet *et al.* (43) studied the transcriptomics during various stages of ripening (immature, half-ripe and ripe stages). About 15,000 EST were generated from three  $\lambda$ zap cDNA libraries of apricots at these three ripening stages yielding 5,212 (35%) unigenes.

Alternaria alternata is one of the major challenges to postharvest storage of jujube (*Ziziphus jujuba* Mill.) fruit (Mirzaee, 82). Typical phenotype of 'green ring' and 'red ring' is produced in jujubes in response to the infection by *A. alternata*. Global transcriptomic profiling of the tissues from these rings revealed a

# Transcriptomics in Fruit Crops

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SI. No.	Genotype(s)	Targeted trait(s)	Reference			
-		Apple (Malus × domestica Borkh.)				
01	Transgenic Gala apple	Transcriptome of <i>Hcrvf12</i> -transformed resistant line to <i>Venturia inaequalis</i>	Paris <i>et al.</i> (90)			
02	Mondial Gala	Changes during fruit maturation and ripening	Costa et al. (26)			
03	Golden Delicious	Transcriptomics of shading-induced and NAA-induced abscission	Zhu <i>et al.</i> (142)			
04	Golden Delicious	Response to inoculation to <i>Penicillium expansum</i> and <i>P. digitatum</i>	Vilanova <i>et al.</i> (116)			
05	Fuji	Resistance responses against Valsamali	Yin <i>et al.</i> (135)			
06	Starking Delicious	Response to Alternaria alternata infection	Zhu <i>et al.</i> (143)			
07	Hongyu	Hormonal regulations and anthocyanin biosynthesis	Onik <i>et al.</i> (88)			
08	Dwarfing apple rootstock 'SH6'	Response to drought, cold and high salinity	Li <i>et al.</i> (64)			
09	Nagafu No. 2	Fruit quality under long term cold storage	Zhao <i>et al.</i> (141)			
		Banana (Musa sp.)				
10	Dwarf Cavendish	Fruit ripening	Asif et al. (12)			
11	Saba and Grand Naine	Response to drought stress	Muthusamy <i>et al.</i> (85)			
12	Cavendish	Benzothiadiazole-induced genes and defense response	Cheng et al. (25)			
13	Minhou wild banana ( <i>M. itinerans</i> )	Anthocyanin biosynthesis genes	Deng et al. (32)			
14	Williams	Response to <i>Bacillus amyloliquefaciens</i> Bs006 and <i>Pseudomonas fluorescens</i> Ps006	Gamez <i>et al.</i> (40)			
15	Brazilian	Differential resistance to infection of Focrace1 and race4	Dong <i>et al</i> . (34)			
16	Rasthali	Cold stress tolerance	Tak <i>et al.</i> (108)			
	Citrus sp.					
17	C. sinensis Osbeck cv. Valencia	Responses to <i>Candidatus Liberibacter asiaticus</i> ( <i>CaLas</i> ) infection	Aritua et al. (10)			
18	C. sinensis Osbeck cv. Navel	Developing ovules during nucellar embryo initiation	Kumar <i>et al.</i> (58)			
19	<i>C. sinensis</i> Osbeck cv. 'Fengjie 72-1' and its mutant 'Fengwan'	Fruit ripening	Wu <i>et al.</i> (127)			
20	C. limon (L.) Burm. F. cv. Xiangshui	Genes associated with self-incompatibility	Zhang <i>et al.</i> (140)			
21	C. sinensis Osbeck cv. Newhall	Response to inoculation with the arbuscular mycorrhiza <i>Glomus versiforme</i>	Gao <i>et al.</i> (41)			
22	<i>C. reticulata</i> Blanco cv. Shatangju grafted on five rootstocks	Influence of rootstock on scion	Liu <i>et al.</i> (70)			
23	<i>Citrus</i> sp.	Citrus bark cracking viroid (CBCVd)	Wang <i>et al.</i> (120)			
24	Carrizo citrange	Response to Phytophthora parasitica infection	Afzal <i>et al.</i> (2)			
25	C. sinensis Osbeck cv. Fengjie 72-1	Fruit developmental stages	Feng <i>et al.</i> (38)			
26	Orlando tangelo, Algerian tangerine	Nucellar embryonic mechanism	Simsek <i>et al.</i> (102)			
27	Seedless citrus mutant	Transcriptomics during pollen abortion Grape (Vitis sp.)	Ye <i>et al.</i> (134)			
28	<i>V. vinifera</i> cv. Cabernet Sauvignon and <i>V. aestivalis</i> cv. Norton	Berry peel development and flavonoid biosynthesis	Ali <i>et al.</i> (5)			

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Table 1 contd...

SI. No.	Genotype(s)	Targeted trait(s)	Reference			
29	<i>V. riparia</i> Michx. and inter- specific hybrid 'Frontenac'	Mechanism of leaf-galling phylloxera on grapes host metabolism and morphology	Nabity <i>et al.</i> (86)			
30	Muscat of Hamburg and V. amurensis	Genome wide transcriptional profile analysis in response to cold stress	Xin <i>et al.</i> (128)			
31	Trincadeira and Touriga Nacional	Comparative transcriptomics under heat, high light and drought stress	Rocheta <i>et al.</i> (96)			
32	Ten <i>V. vinifera</i> L cultivars	Berry peel anthocyanin accumulation	Massonnet <i>et al.</i> (79)			
33	Summer Black	Berry-size effects of gibberellin (GA) on seedless grape	Wang <i>et al.</i> (119)			
34	Thompson Seedless	Transcriptome analysis of vine under salinity and identification of key genes	Das and Majumder (28)			
	Mango (Mangifera indica L.)					
35	Zill	Fruit development and ripening stages	Wu <i>et al.</i> (126)			
36	Kent	Fruit ripening	Dautt-Castro et al. (30)			
37	Dashehari	Ripening associated genes	Srivastava <i>et al.</i> (105)			
38	Langra, Zill, Shelly and Kent	Pathways involved in flavour and colour	Khan <i>et al.</i> (53)			
39	Neelam and Dashehari	Alternate bearing	Sharma <i>et al.</i> (99)			
40	Amrapali	Floral malformation	Yadav <i>et al.</i> (130)			
Other fruit crops						
41	Litchi chinensis Sonn. cv. Nuomici	Fruit maturation	Lai <i>et al.</i> (59)			
42	Actinidia chinensis Planch.	Anthocyanin accumulation	Li et al. (63)			
43	<i>Ananas comosus</i> L. cv. Smooth Cayenne	Response to ethephon induction	Liu and Fan, (68)			
44	Punica granatum L. cv. Wonderful	Changes associated with husk scald incidence on fruit peel under cold storage	Belay <i>et al.</i> (18)			
45	Ficus carica L. cv. Bojihong	Genes involved in anthocyanin biosynthesis	Li et al. (62)			
46	Olea europaea L. subsp. europaea	Transcriptomic activity of different tissues/organs of olive tree	Ramirez-Tejero <i>et</i> <i>al.</i> (95)			

higher numbers of DEGs in the 'green ring' (Yuan *et al.*, 136).

Kaushik and Kumar (52) reported the first transcript study in *bael* (*Aegle marmelos*) leaves. They assembled 133,616 contigs into 46,335 unigenes. These transcripts were annotated based on information available in *Citrus clementina* and *C. sinensis*. The monoterpenoid biosynthesis pathway was predominant in *bael* leaves. This information on the transcriptome sequencing data can be used in future for better understanding of important pathways in the *A. marmelos* L. (Kaushik and Kumar, 51).

There was not a single database which contains the sequence information on guava (*Psidium guajava* L.) genomic or transcriptomic sequences (Sharma *et al.*, 98). However, Mittal *et al.* (83) reported the first reference transcriptome for guava consisting of 84,206 genes comprising 279,792 total transcripts from tissue (leaf, flower and fruit of cv. Allahabad Safeda) specific RNA sequencing and *de novo* transcriptome assembly using Trinity pipeline. Using transcriptomics Veto *et al.* (115)unveil potential genes involved in fruit pigmentation of *P. cattleyanum* Sabine. Genes such as the anthocyanidin synthase and UDP-glucose:flavonoid-o-glucosyltransferase were differentially regulated during fruit ripening and involved in the synthesis and pigment accumulation in red fruits.

Transcriptomic studies in litchi (*Litchi chinensis*) have been done to identify DEGs in response to reactive oxygen species (Lu *et al.*, 72), floral initiation (Zhang *et al.*, 138)*etc*. Grafting is commercial means of propagation in many of fruit crops, however, the molecular mechanism of grafting healing or graft

incompatibility is not fully understood. Chen et al. (24) studied the difference in transcriptomics between compatible and incompatible graft combination of litchi. Various DEGs were observed to be involved in metabolism, wound response, phenylpropanoid biosynthesis and plant hormone signal transduction. It was observed that 9 DEGs annotated in auxin pathway was up-regulated in compatible combination indicating role of IAA in enhancing graft compatibility. Fig (Ficus carica L.) is one of earliest domesticated fruit crops (Kislev et al., 54), however, there is scarce of information on its transcriptomics. Recently, Li et al. (62) provided new insights into the molecular mechanisms behind fig anthocyanin biosynthesis and colouration. Amongst the 6224 DEGs obtained, various anthocyanin-related genes including five CHS, three CHI, three DFR, three ANS, two UFGT and seven R2R3-MYB genes were identified. Several other attempts have been initiated recently in various fruit crops (Table 1).

# **RNA-Seq**

RNA-Seq is a recently developed approach for transcriptome profiling that uses deep-sequencing technologies to provide more precise measurement of levels of transcripts and their isoforms (Wang et al., 121). The high-throughput sequencing of cDNA fragment populations is commonly known as RNA-Seq. RNA-Seq is a powerful tool for transcriptome analysis and uses deep sequencing technologies to produce millions of short cDNA reads (Simsek et al., 101). These reads are either aligned to a reference genome or reference transcripts. These can also be assembled *de novo* (without the genomic sequence) to produce a genome-scale transcription map that consists of both the transcript structure and level of expression for each gene at any particular developmental stage (Trapnell et al., 110). RNA-Seq has been applied in fruit crops for various purposes.

To clarify self-incompatibility mechanism, Zhang et al. (140) performed RNA-seq in lemon and found a putative S-RNase gene that had not been previously reported. Asif et al. (12) sequenced the transcriptomes of the unripe and ripe stages of Musa accuminata (Dwarf Cavendish) fruit using a 454 GSFLX-Titanium platform, which resulted in more than 7,00,000 high quality (HQ) reads. They observed up-regulation of gene families related to expansin and xyloglucan transglycosylase/ hydrolase (XTH). It was evident that the purple peel formation in the Minhou wild banana (Musa *itinerans*) is due to the differential accumulation of secondary metabolites (Deng et al., 32). RNA-Seq from the epidermal cells of both the purple and green parts of peel revealed 3,640 differently expressed

unigenes most of which were involved in flavonoid or phenylpropanoid biosynthesis, plant hormone signal transduction, starch, sucrose and phenylalanine metabolism pathways. RNA-Seq has also been exploited for response of banana plants to drought (Muthusamy *et al.*, 84) and cold stress (Yang *et al.*, 133) and *Fusarium oxysporum* f. sp. *cubense* (*Foc*) inoculation (Sun *et al.*, 106).

Transcriptomics for flower colour variation in the ornamental crab apple (Malus spp.) through Illumina and PacBio Sequel sequencing revealed 603 DEGs, amongst which 449 were up-regulated and 154 downregulated (Huang et al., 46). Transcription factors related to anthocyanin synthesis and transport were highly expressed in red petals. The endogenous plant hormones also have regulatory effect on flower colour. Transcriptomic related works are often studied under open field conditions where these are exposed to various other biotic and abiotic variability except the concern one. Therefore, identification of some particular up- or down-regulated genes may not be enough to draw conclusions (Yin et al., 135). Metaanalysis is needed to validate a transcriptomic works with other similar kind of studies performed on same topics. Balan et al. (16) did the meta-analysis of transcriptome data related to fungi, virus and bacteria attacks in Malus × domestica for identification of specific and common molecular responses. The meta-analysis revealed that infection with the plant pathogens enhanced various genes involved in plant metabolic processes, viz. bacterial infection enhanced sugar alcohol metabolism genes, while fungal enhanced the brassinosteroids and Erwinia amylovora enhanced the ethylene. However, viral and fungal infections repressed the jasmonates and gibberellins.

Azim et al. (13) characterized the transcriptome of mango cv. Langra using RNA-Seq using Illumina HiSeq2000. The RNA-Seq output generated >12 million reads. De novo transcriptome assembly generated 30,509 unigenes with lengths in the range of 300 to  $\geq$ 3,000 nt and 67× depth of coverage. Mapping of unigenes to the reference canonical pathways in the Kyoto Encyclopaedia of Genes and Genomes (KEGG) revealed the active presence of an array of biochemical pathways involved in flavonoids, flavones and flavonols, terpenoids and lignins and plant hormone signal transduction (Kanehisa et al., 50). Similarly, using the mesocarp of mango cv. Kent, Dautt-Castro et al. (30) identified DEGs amongst, which a total of 1,178 were up-regulated, while 1,128 down-regulated. These genes were assigned to 327 metabolic pathways some of which were involved in fruit ripening such as plant hormone signal transduction, starch and sucrose metabolism, galactose metabolism, terpenoid backbone, and carotenoid biosynthesis. Alphonso is acclaimed as the "King of mangoes" due to its unique flavour, attractive colour, low fibre pulp and long shelf-life. Using Illumina sequencing, Deshpande *et al.* (33) studied the transcriptional transitions in Alphonso mango from flowering to ripening, which explained its distinct aroma and shelf-life characteristics. It revealed the involvement of 142 biological pathways including ethylene and flavour related secondary metabolite biosynthesis pathways, as well as those involved in metabolism of starch, sucrose, amino acids and fatty acids. Several novel transcripts for biosynthesis of mono-, di- and sesquiterpenes, lactones and furanones were also involved in flavour formation.

### **Future Prospectus**

Yield and quality traits in fruit crops are subjected to a various biotic and abiotic stresses under the field conditions. However, the ability to tolerate or resist these stresses vary amongst fruit crops or genotypes within the fruit species. According to the United Nations forecast world's population will reach nearly 8.1 billion in 2025 and 9.6 billion by 2050. It is major challenge for the fruit breeders to provide the nutritional security to such ever increasing population. There is a need to produce highly productive and efficient (smart) fruit crop genotytpes. However, the climate change phenomenon is another major hindrance, which necessitates the need of biotic and abiotic stress tolerant improved fruit genotypes in near future. Biotechnological tools with tools coupled with Omics science can assist the fruit breeders to achieve the need of the future. In order to breed new fruit genotypes according to the need of present or future, there is a need to understand the molecular mechanism of host-pathogen interaction, resistance, tolerance or susceptibility to a particular stress, changes in the growth and development under the influence of various environmental factors or exogenous application of hormones, chemicals, elicitors etc. However, transcriptomics has been explored only in a limited fruit crops like apple, banana citrus, grape, mango, papaya etc. The minor fruit crops are yet to be analysed for their transcriptome for studying various DEGs. Still now, there are some fruit crops, which do not have any database containing sequence information on transcriptome or genomics. These scarcities in Omics sequence resources are restricting the researchers from utilizing the new biotechnological tools for the



Fig. 2. Important targetable traits (diseases and physiological disorders), in some fruit crops which can be considered for transcriptome analysis in near future. FB: Fire blight; PM: Powdery mildew; PCR: Phytophthora crown rot; Foc TR4: Fusarium oxysporum f. sp. cubense tropical race 4; SLS: Sigatoka leaf spot; BTV: Bunchytop virus; HLB: Huanglongbing; DM: Downy mildew; HCD: Hen and chicken disorder; MMD: Mango malformation disease; PRSV: Papaya ring spot virus; PMV: Papaya mosaic virus.

improvement of fruit crops. Thus, there is a need to generate more and more Omic sequence resources especially transcriptomics. With the advent of high throughput sequencing technologies, RNA-Seq can be undertaken to sequence the cDNA fragment of expressed gene(s). In the present scenario of climate change, water scarcity and high temperature stress situations, the future of fruit crop transcriptomics involves establishing more and more transcriptomic data for important traits like disease resistance, drought and salt tolerance etc. according to the priority in various fruit crops (Fig. 2). There are still some bottlenecks in the transcriptome analysis of fruit crops. The abundant data generated is still needed to be validated. Higher meta-analysis can be done to validate the transcriptome of other similar kind of species in same or other fruit crop(s). Apart from this, the result of transcriptome analysis is needed to be incorporated in the field research for fast track breeding of the fruit crops. RNA-Seq based tissue specific expressed genomic information, de novo transcriptome assembly, functional annotation of gene(s), differential gene expression among contrasting fruit genotypes under various growing conditions, meta-analysis of the transcriptome data are some of the important avenues, which need to be explored in the coming years.

In this review, it can be concluded that the compiled information on various transcriptomics studies on fruit crops are too meagre. The transcriptome analysis in fruit crops is merely one to two decade-old, which got some momentum since 2010. Advances in transcriptomic approaches have provided a better understanding of the various regulatory gene(s)/ network(s), functional gene(s), and complex biosynthetic pathways related to fruit crops. Transcriptomics along with the RNA-Seq have not only made us understand the underlying tolerance or resistance mechanism for different insect-pests, diseases or physiological disorders but also provided usable genomic resources, which can assist the fruit breeders for bringing precision in their quest for developing elite genotypes.

# DECLARATION

The authors declare no conflict of interest.

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(Received : August, 2020; Revised : November, 2020; Accepted : December, 2020)