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Molecular Basis of Shelf-life in Fruit Crops - A Review

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ABSTRACT

Fruits play an important role in healthy diet. Due to high perishable nature, it is subjected to microbial decay, mechanical injury and senescence. These factors drastically increase the losses during postharvest storage. Fruit softening is a complicated developmental process that necessitates the coordinated action of various genes and proteins involved in metabolic processes. The enzymes that are involved during fruit softening are polygalacturonase, pectate lyase, pectin methyl esterases, pectate lyase etc. A series of bio-chemical reactions significantly increase respiration during ripening. Fruit postharvest life improvements are required on urgent basis. Therefore, enhancing the shelf-life, maintaining quality, and reducing waste through advanced research on fruit physiology is primary goal to meet out the consumer demand. Genes engaged directly in cell wall metabolism or in the mechanism governing ripening can be identified as candidate genes for shelf-life extension. This will significantly reduce the post-harvest losses. With the use of molecular approaches like marker assisted breeding (MAB), genomics and transcriptomics with traditional breeding it would be possible to silence the genes which enhance the ripening.

Keywords : Candidate genes, Ethylene, Fruit softening, Ripening, Shelf-life

FRUITS are rich source of nutrients as they include minerals, proteins, carbohydrates, fibre, vitamins, antioxidants and phytochemicals, which include flavonoids, carotenoids and other phenolic compounds (Benichou *et al.*, 2018). Unfortunately, due to deterioration, over 30 per cent of fruits are lost after harvest (Porat *et al.*, 2018; Rajapaksha *et al.*, 2021). Fruits mainly consist of water (85 to 95% of their total fresh weight) and prone to continue respiration resulting into short postharvest storage life (Asrey *et al.*, 2021). Identification of the metabolites involved in fruit ripening is important prerequisite in improvement of quality and shelf-life of fruits (Khabbazi *et al.*, 2020). Ripening of fleshy fruits is a genetically determined programme of tissue differentiation (Giovannoni, 2001; Gapper *et al.*, 2013 and Tohge *et al.*, 2013). It is essential phenomenon to provide nutritive properties to the fruits, making it suitable for human consumption. Fruit ripening is accompanied by series of biochemical events, including changes in sugar, colour, acidity, aroma, texture and volatiles that are crucial for the sensory quality (Ampomah-Dwamena *et al.*, 2002; Giovannoni, 2004 and Goff & Klee, 2006). Although, temperature and packaging material also influence the shelf-life (Nirmala and Venkatesh, 1993).

Cell wall remoulding is one of the most important visible changes that occur during ripening, and it results in a shift in texture in fleshy fruits, making them more palatable (Fabi *et al.*, 2007). Although, 'Extremeness of everything is bad' is old proverb and here this is well suited for over ripening. Fruit over softening resulted into increased disease susceptibility, development of unpleasant flavour, skin colour; diminish fruit quality as ripening advances, resulting in huge postharvest fruit losses (Mercado *et al.*, 2011). Nutritional quality is measured by a fruit's content of minerals, vitamins, carbohydrates, dietary fibers, proteins etc. Fruit ripening and softening are important features that influence food supply, fruit nutritional content and human health. Because ethylene causes climacteric fruit to ripen, it is one of the factors for controlling fruit over ripening, which causes softness and degradation (Costa and Ramina, 2014, Fig. 1).

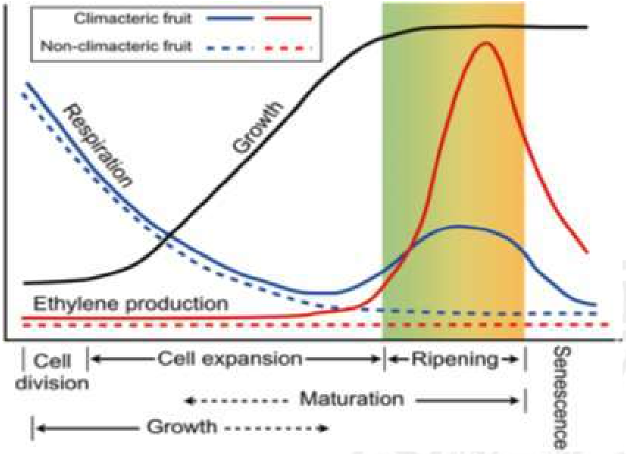

Fig. 1: Ethylene biosynthesis in climacteric and non-climacteric fruits, with respect to respiration and growth rates (Costa and Ramina, 2014)

Fruits can be divided into two different sections according to the regulatory mechanisms of the ripening process. Climacteric fruit, like apple, mango, pear, papaya, banana, etc. are characterized by a ripening-associated increase in ethylene production and respiration (Desai & Dashpandey, 1975 and Hiwasa *et al*., 2003a). In contrast to, non-climacteric fruits, like pineapple, grape, orange, lime, litchi, are characterized by the absence of ethylene-associated respiratory peak (Table 1). When climacteric fruit begins to ripen, it experiences a surge in respiration and a burst of ethylene production (Bouzayen *et al*., 2010). During fruit development, respiration decrease steadily until it reaches its lowest levels during senescence. Climacteric fruit have a distinct behaviour, with a peak in respiration that decrease in the post-climacteric phase, indicating the onset of senescence. The increase in climacteric respiration occurs in tandem with the attainment of maximum fruit size and the primary changes that occur during ripening. Ethylene production follows the same pattern as climacteric respiration and regulates the majority of the ripening process (Giovannoni, 2004 and Barry & Giovannoni, 2007). To reduce the postharvest losses, fruits need to be harvested at the right stages and could be a major contribution to satisfying higher global food demand (Teferra *et al.,* 2022). Therefore, present review highlights the methodological problems and research gaps during postharvest storage. Further, advanced molecular tools to delay the ripening and to improve the shelf-life of fruits.

Major Research Gaps in Fruit Breeding for Enhanced Shelf-life

Perennial fruit crops are considered to be a difficult plant species to handle in breeding programmes due to inherent problems of long juvenile phase, high level of heterozygosity, lack of knowledge about the genetic nature of important agronomic traits and lack of availability of co-dominant markers towards marker assisted screening. Many of the problems also associated with postharvest loses (Hesami *et al*., 2021 andTaher *et al*., 2022). Conventional breeding approaches thus, rely on field screening and needs long period for evaluation and identification of new suitable genotypes. To increase the shelf-life of fruit crops requires understanding ripening phenomenon at biochemical and molecular levels, cloning of gene(s) related to softening and studying its features and tailoring of gene to make it available for genetic control of ripening process itself (Sharma *et al*., 2020). Recently, important advances have been made in understanding the various ripening characteristics of mango at the molecular level. Candidate genes related to ethylene biosynthesis, cell wall modification, aroma production and stress response have been cloned and characterized for future use in crop improvement. Efforts are also being made for establishment of a suitable transformation and plant regeneration system so that a transgenic crop can be developed with various added value and increased shelf life for long distance transportation could be developed (Singh *et al.,* 2013).

Molecular Basis of Fruit Softening

Fruit ripening is a complex phenomenon and with the available methodology especially physiological parameters like respiration rate, physiological loss in

Table 1

List of climacteric and non-climacteric fruit crops

Climacteric fruits	Non-climacteric fruits
Banana (*Musa acuminata* L.)	Lime (*Citrus aurantifolia* Swingle)
Mango (*Mangifera indica* L.)	Mandarin (*Citrus reticulata* Blanco)
Papaya (*Carica papaya* L.)	Grapefruit (*Citrus grandis* Osbech)
Fig (*Ficus carica*L.)	Cherry (*Prunus avium* L.)
Guava (*Psidium guajava* L.)	Litchi (*Litchi sinensis* Sonn.)
Avocado (*Persea americana* Mill.)	Strawberry (*Fragaria* sp.)
Sapota (*Manilkara achras*Fosb.)	Raspberry (*Rubus idaeus*L.)
Apple (*Malus domestica* Borkh.)	Pomegranate (*Punica granatum* L.)
Kiwifruit (*Actinidia sinensis* Planch.)	Pineapple (*Ananas comosus* Merr.)
Apricot (*Prunus armeniaca* L.)	Carambola (*Averrhoa carambola* L.)
Cherimoya (*Annona cherimola*Mill.)	Cashew (*Anacardium occidentale* L.)
Durian (*Duriozibethinus*Murr.)	Limon (*Citrus limonia*Burm.)
Feijoa (*Feijoa sellowiana*Berg.)	Mangosteen (*Garcinia mangostana*L.)
Peach (*Prunus persica* Batsch)	Olive (*Olea europaea* L.)
Passion fruit (*Passiflora edulis* Sims.)	Rambutan (*Nephelium lappaceum*L.)
Pear (*Pyrus communis* L.)	Tamarillo (*Cyphomandrabetacea*Sendtu)
Persimmon (*Diospyros kaki* Thunb.)	

weight, peel thickness etc. are not sufficient to improve the varieties with enhanced shelf-life. Therefore, to understand the molecular basis of fruit softening of climacteric and non-climacteric fruits model species like tomato and strawberry have been studied extensively (Alexander and Grierson *et al*., 2002 and Fuentes *et al*., 2019). The decline in production is attributed not only due to the incidence of pests and diseases, but also because of others factors like poor germination percentage, lack of efficient rootstocks, irregular bearing habit, short shelf-life etc. Detailed study of post-harvest changes indicated that this mechanism cannot be completely stopped but can be regulated up to certain limits. Ripening in climacteric fruit is closely linked to its softening which in turn is associated with structural changes in the cell wall including reduction in size of hemicellulose, loss of galactose side chains and solubilisation and depolymerisation of pectin. The enzymes that are involved during fruit softening are polygalacturonase, pectin methyl esterases, pectate lyase, cellulose etc. (Brummnell & Harpster, 2001a; Gapper *et al*., 2013 and Tohge *et al*., 2013). Mechanism of ripening *via* different enzymes with intermediate product is well explained in Fig. 2. A series of bio-chemical reactions resulted into increased respiration during ripening. Further, ethylene production change in structural polysaccharides causing softening, degradation of chlorophyll, developing pigment by carotenoides, biosynthesis change in carbohydrates or starch conversion into sugars, organic acid, lipid, phenolics and volatile compounds. It leads to ripening of fruit with softening of texture to acceptable quality (Rathore *et al*., 2007). Expression of ethylene biosynthesis genes such as *ACC synthase* (*ACS*) and *ACC oxidase (ACO)* are predicted to change during ripening. In tomato, *LeACS2* and *LeACO1* dominate gene expression was reported during climacteric ethylene production (Dautt-Castro *et al*., 2015). *Expansin* gene also plays an important role in ripening process. The expression of *expansin* gene during various stages of fruit ripening in peach (Hayama *et al.,* 2003 and Obenland *et al.,* 2003), pear (Hiwasa *et al.,* 2003b), banana (Harrison *et al.,* 2001) and strawberry (Trivedi and Nath, 2004) suggested their important role in regulating the textural changes mainly at stage of fruit senescence.

Molecular Approaches for Increased Shelf-life

There are different possible ways to reduce ethylene production and extend the shelf-life of fruits (Ebrahimi *et al*., 2021). Fruit genetic manipulations are primarily based on the genes involved in these changes (Goulao and Oliveria, 2007; Vicente *et al*., 2007 and Matas *et al*., 2009). Since, this gene is rapidly triggered by ethylene; it may be a good candidate for manipulation of softening in mango *via* recombinant DNA technology (Reddy *et al*., 2017). Two cDNA homologues of the ethylene receptor gene *ETR-1* (Ethylene Receptor 1), referred to as *MiETR1*and *MiERS1* (Shalom *et al.,* 2011) have been isolated in mango. During ripening and wounding, the *MiETR1* transcript increases, whereas the *MiERS1* transcript does not alter. There are likely to be more ETR homologues in mango. Mango fruitlet abscission is aided by *MiERS1*(Singh *et al*., 2013). The majority of the molecular technologies aim to reduce gene expression, such as RNA inhibition (RNAi), co-suppression (CS), antisense, virus-induced gene silencing (VIGS), or chimeric repressor gene silencing technology (CREST), which uses the EAR amphiphilic repression domain to silence transcription factors (SRDX), TILLING (Targeting Induced Local Lesions IN Genomes), clustered regularly interspaced short palindromic repeat (CRISPR) / Cas9 system. Further, genetic transformation of the plants with any of the genes that control ethylene production so that mRNA in the antisense configuration is produced has been demonstrated to be an effective strategy for blocking fruit ripening. An increase in the availability of genome sequences of tropical fruits further aided in the discovery of single nucleotide polymorphism (SNP) variants / Indels, quantitative trait loci (QTLs) and genes that can ascertain the genetic determinants of fruit characters. Through multi-omics approaches such as genomics, transcriptomics, metabolomics and proteomics, the identification and quantification of transcripts, including non-coding RNAs, involved in sugar metabolism, fruit development and ripening, shelf life, and the biotic and abiotic stress that impacts fruit quality were made possible (Mathiazhagan *et al*., 2021)

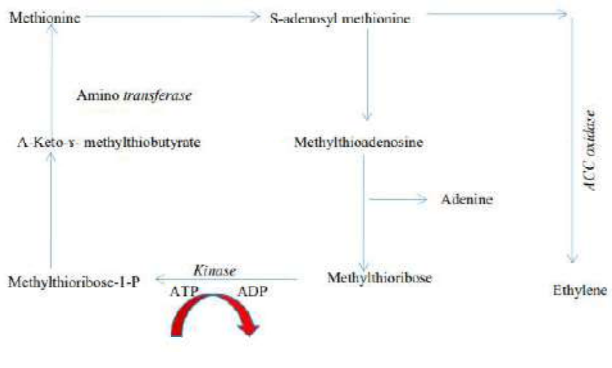

Fig. 2: Ethylene signal transduction mechanism in climacteric fruits

Molecular Markers Associated with Shelf-life

Identification of molecular markers associated with shelf-life is the utmost important for the breeding programs of high perishable fruit crops (Table 2). As the early stage and easy screening of genotypes having longer shelf-life will be of great use. Besides screening of genotypes and parentages these markers will be useful for pedigree determination in open pollinated population involving differential shelf-life properties of parentages. Silencing of genes generating cell wall disintegration proteins provides a more specialized technique of reducing fruit softening, allowing for the normal development of other ripening events such as the accumulation of sugars, volatiles, or colors (Brummell and Harpster, 2001b). Recently, there has been interest in using marker assisted breeding (MAB) to improve fruit texture and shelf-life of mango, apple and peach by the European community (Aranzana *et al*., 2010). This approach enables identifying plants that carry a specific desired trait at an early developmental stage by following a specific DNA marker. Simple sequence repeats (SSRs) or single nucleotide polymorphisms (SNPs) that are substantially

TABLE 2

Details of shelf-life specific simple sequence repeat (SSRs) markers in fruit crops

Fruit	Trait Studied	References
Banana	Sugar content and Seedlessness	Ming *et al.* (2001)
Japanese pear	Firmness of fresh, fruit size, fruit shape in longitudinal selection, acid content, total soluble solids content.	Iwata *et al.* (2013)
Peach	Total sugars & total phenols	Forcada *et al*. (2013)
Peach	Flesh colour around the stone, red pigment in the flesh, flesh texture, flesh adhesion, flesh firmness, fruit weight, ripening time, and fruit development period.	Cao *et al.* (2016)
Mango	Acidity, TSS, Fruit weight	Padmakar *et al.*(2016)
Mango	Fruit width, fruit length, TSS and yield.	Lal *et al.* (2017)

associated to a desired phenotype are found using the traditional marker assisted breeding (MAB) approach.

Gene Expression Studies for Shelf-life

Advances in sequencing technologies and bioinformatics helped a lot in generating and understanding the genomic information in fruit crops. This information will be useful to reveal the pathways influencing the shelf-life of fruit crops. Further, differential gene expression analysis in contrasting genotypes could be utilized to infer the regulatory mechanism underlying fruit ripening and shelf-life associated phenomena. RNA sequencing (RNA-sequencing) is a useful technology to measure global changes in transcription. Transcriptomics has been used to understand the molecular aspects of ripening process in fruits like banana, kiwi, blueberry, orange and tomato (Wang *et al*., 2017). Recent studies of gene expression of mango mesocarp tissues, explore the complex ripening process (Dautt-Castro *et al*., 2015 and Srivastava *et al*., 2016). RNA sequencing has advantage over DNA markers that these sequences are from transcribed region of genome thus, omits the non-expressed part of genome. These markers would be more robust in identification of genotypes for long shelf-life. The quantum of available transcriptome data would be highly useful in genomic-assisted breeding for important horticultural traits.

Differential Expression of Genes Associated with Shelf-life

Genes directly involved in cell wall metabolism or governing the ripening can be identified as candidate genes for shelf-life extension (Brummell, 2006). Although a correlation between a gene's expression and ripening is not sufficient to classify it as a candidate gene, functional investigations using several methodologies can confirm candidate genes functions in ripening.

In melon, the expression of ripening-related cell wall-associated genes and activities, such as *polyglactouranase (PGs)* (Hiwasa *et al*., 2003c), *expansin* and *EGases (Endo-1,4—D-glucanases)* had been observed. *Expansin* a new class of cell wall enzymes has been identified as the principal enzymatic agents involved in the early stages of softening. A divergent multigene family encodes *expansins*. Some ethylene-controlled components, in instance, are exclusively expressed during fruit ripening.

Expansin play a role in a plant growth and development processes, particularly during cell expansion and cell-wall extension. These are also thought to help prepare cell walls for disintegration by cell wall hydrolyses during ripening, especially in climacteric fruits. For the first time, the *MaExp1* gene, a fruit-specific *expansin*, has been identified and characterized in banana. The 1098-bp *MaExp1* cDNA encodes a 255-amino-acid polypeptide with all of the properties of an *expansin*. *MaExp1* has two short introns of 83 and 79 nucleotides, according to genomic sequence analysis. *MaExp1* might be used to manipulate banana ripening, and its promoter could be a good option for expressing foreign genes (vaccines) in transgenic banana fruit (Trivedi *et al*., 2004). *Expansin* breaks the hydrogen bond between cellulose microfibrils and the glycans that crosslink them (Brummell *et al*., 1999). *Expansin* genes are up-regulated during ripening in tomato and strawberry (Civello *et al*., 1999) and over expression of *expansin genes* cause mature green fruit to soften.

In tomato, *1-Aminocyclopropane-1-carboxylic acid synthase* (*ACS*) and *1-Aminocyclopropane-1-Carboxylic Acid Oxidase* (*ACO*) are members of a multigene family with nine and five members, respectively, whose expression is controlled differently during fruits growth and ripening (Barry *et al*., 2000). Down-regulation of *ETP1* (EIN2 TARGETING PROTEIN1) and *ETP2* (EIN2 TARGETING PROTEIN2) genes resulted in partial ethylene-insensitive phenotypes as compared to wild type phenotypes, indicating that they play a role in ripening (Qiao *et al*., 2009). *EIN2* (Ethylene-insensitive protein 2) interacts with *ETP1* and *ETP2*. *EIN2* suppression through a co-suppression mechanism or a VIGS strategy resulted in ethylene insensitivity and ripening inhibition, as well as lower expression of ethylene and ripening related genes (Fu *et al*., 2005 and Hu *et al*., 2010), Suggesting that *LeEIN2* is a positive regulator of ethylene-mediated responses during fruit ripening.*ERF6* has been shown to have a good association with carotenoids and ethylene control, and is strongly expressed in fleshy fruits. *SlERF6* expression analysis revealed that it increases at maturity, peaks at post-beaker stage, and then declines, indicating a connection with later fruit development and ripening (Li *et al*., 2013). Some genes that affect ripening-related traits including firmness, colour, fragrance, taste, and postharvest shelf-life have been discovered to be regulated by elongation factors (*EFRs*) (Ju and Chang, 2015). In *RIN* (ripening inhibitor) and *NOR* (non-ripening) mutant fruits, *ERF6* expression was reduced, suggesting that *ERF6* is involved in the positive control of ethylene responses and plays an important function in the ripening of fruits (Li *et al*., 2019). During tomato ripening, genes encoding enzymes involved in pectin degradation, such as polygalacturonase (PG), pectin methylesterase (PME), pectate lyase (PL) and galactosidase (GAL) or matrix glycan degradation, such as endoglucanase (EGase), xyloglucan endotransglycosylasehydrolases (XTH) (Han and Korban, 2011). PME gene expression or activity is induced during ripening in different fruits like peach and tomato (Brummell *et al*., 2004). PME activity or gene expression is lowered during ripening in apples (Gwanpua *et al*., 2016), and there is conflicting information about pectin methylesterase (PME) levels during ripening in strawberries (Mercado *et al.,* 2011). Pectin methylesterase (PME) in apple and strawberry softening during ripening is still unclear, and there is little evidence to suggest that pectin methylesterase (PME) plays a significant role in fruit softening. Because it was lowered when *βGAL* (β-galactosidase) was silenced, this enzyme clearly plays a part in strawberry softening. In addition to *Malus domestica* polygalacturonase (*MdPG1*), recent research has found a link between the expression of *β GAL* and fruit softening (Gwanpua *et al*., 2016). Many fruits contain *PL* (pectate lyase) (Marin-

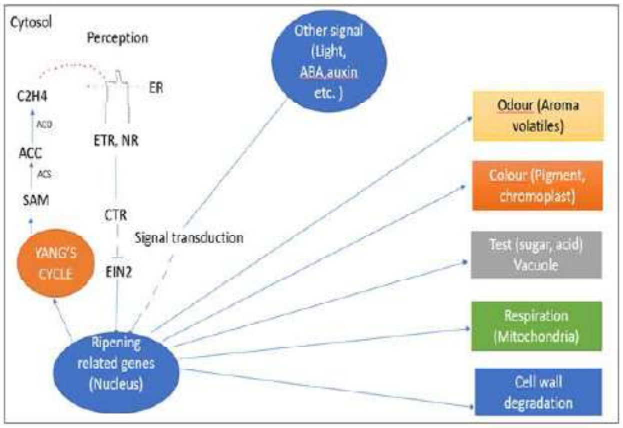

Fig. 3: This graphic depicts the molecular processes that control the ripening of climacteric fruit. Ripening-related genes are expressed, and these genes encode enzymes (proteins) involved in the various ripening mechanisms (e.g., colour development, softening). Hormonal and environmental signals control the entire process, with ethylene playing a critical role

Rodrguez *et al*., 2002) and its expression has been established in fruit with melting flesh, such as bananas and peaches (Trainotti *et al*., 2003). Furthermore, a banana *PL* (pectate lyase) gene produced in yeast showed PL (pectate lyase) activity. Expansin (*EXP*) appears to be linked to ripening in bananas, as its promoters bind to a possible banana ripening negative regulator (Friedman *et al*., 2019). How different transcription factors and genes affect the ripening well explained in Fig. 3. Transcriptional control network involved in overall ripening regulation, ethylene biosynthesis, ethylene perception, downstream ethylene response, cell wall metabolism, colour development and aroma synthesis. Expression of genes associated to ripening results in the encoding of enzymes (proteins) that are involved in the various ripening mechanisms. The entire process is governed by hormonal and environmental signal, with ethylene playing a crucial role.

Conclusion and Future Thrust

Commercial post-harvest technologies are mostly used in industrialised countries to prevent excessive softening, improving shelf-life, and reduce fresh food waste. However, these technologies raise the price of fresh fruits; they are rarely used in developing countries, where they are mostly needed. Present review discusses the potential genes that have been proven to delay softening in mango, banana, apple, peach, strawberry etc. Although, the function of selected candidate genes has been established in these crops, more research into translational research in other crops is needed. Multiple potential genes have already been discovered, which may be modified through genome editing or utilised in marker-assistant breeding to enhance the shelf-life of fruits, lowering postharvest handling expenses.

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