



## Postharvest physiological and biochemical alterations in fruits: a review

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### ARTICLE INFORMATION

#### Article History

Submitted: 05 Jul 2020

Accepted: 18 Aug 2020

First online: 16 Nov 2020

#### Academic Editor

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### ABSTRACT

Fruits are essential components in human diet. Being a basket of nutrients, fruits contain health promoting and disease preventing vitamins, minerals and bioactive molecules like polyphenols, anthocyanins. Fruits are very perishable in nature and are very prone to microbial spoilage as well as physiological and biochemical deteriorations resulting in a shorter shelf-life with a compromised nutritional quality and huge economic loss as well. Progress in the understanding of postharvest factors commanding ripening and quality which includes tissue differentiation, respiration, transpiration and water loss, catabolic activities, color degradation and aroma biosynthesis have been examined in the current review along with challenges lying ahead. Indeed, a series of physiological events, biochemical pathways and molecular alternations are involved in fruit ripening process. During transformation of an unripe fruit into an edible ripe fruit, the above mentioned systematic changes introduce attractive color, taste, aroma and texture of the unripe fruit. Globally practicing different strategies to reduce the post-harvest losses and to enhance quality; microbial safety and shelf-life of fruits are also highlighted in this review. Finally, this review provides an update on complex physiological process and cellular metabolism during the ripening of fruits, discusses their controlling techniques to promote further improvements in fruit ripening regulation, nutritional quality, microbial safety and storage time or extend shelf life.

**Keywords:** Physiological process, fruits maturation, fruits ripening, senescence, metabolism



**Cite this article:** Hossain MA, Karim MM, Juthee SA. 2020. Postharvest physiological and biochemical alterations in fruits: a review. *Fundamental and Applied Agriculture* 5(4): 453–469. doi: 10.5455/faa.22077

## 1 Introduction

Fruits are known as a basket of nutrients needed for maintaining the body healthy. Fruits also prevent diseases since they contain health promoting and disease preventing vitamins, minerals and bioactive molecules, polyphenols. However, the problem is- fruits are very perishable that's why many physiological, biochemical and microbial deteriorations usually may be occurred resulting huge economic losses (Choudhury et al., 2019). Unfortunately, losses have been extended to 10-15% and 20-40% in developed and developing countries respectively based on the types of the produce (yearly global post-harvest food loss and waste). So it is very much clear that

the consumers are deprived to use about 25% produced fruits. Moreover, huge money, all efforts and natural resources are being used for the production, harvesting and marketing of the produce. During various post-harvest operations, some losses may not be avoided which reduces the availability of that produce. According to a study, 3–6% of cereals, 4.3–6.1% of pulses, 25-50% of fruits and vegetables are lost during harvesting and post-harvesting operations as well (Cardoen et al., 2015). Thus, a large gap is noticeable between the amount of food produced and the amount of food available to the consumers. In fact, deterioration of fruits and vegetables largely depends on some physiological aspects such as respiration,

transpiration, and ethylene production (Yahia, 2019). Regulations of these processes may contribute to prolong the post harvest life of that produce by using some technologies like cooling and storage (Saltveit, 2019).

In 2014–2016, around one in eight of the world population was suffered from chronic undernourishment or malnutrition (FAO, 2015). Poverty is the main causes for hunger in the world and it is super imposed on ever increasing of world population, food and agricultural policies and climate change (Wheeler and von Braun, 2013). Meanwhile, natural resources are being depleted with increasing rate and it is now a great concern to protect the natural resources along with a sustainable production system. Moreover, efficient handling, maintenance, storing and utilizing the produce is also very much important to feed the world's mammoth population. In fact, food security of a country could be ensured or achieved by preventing or minimizing various losses of fruits (Gutiérrez and Álvarez, 2017).

Since fresh fruits are living organs even after harvest, it continues respiration as an obligatory part of its life processes. A series of metabolic pathways is performed within the fruits to obtain the required energy to preserve their life, and therefore, physiological and biochemical processes in fruits are carried out after detaching from the plant. There are few changes including cell wall composition and structure resulted in tissue softening; chlorophyll degradation and color development (yellow/orange/red/purple) occurred concomitantly. Actually, synthesis and development of other pigments such as carotenoids and flavonoids are remarkable events during the changes in the pigments. In starchy fruits and vegetables, changes in sugar content are also an important process and sugar is presented rather than the sugar consumption by the respiratory process. Changes in flavor (taste and aroma) are also common during ripening and senescence of fruits and vegetables.

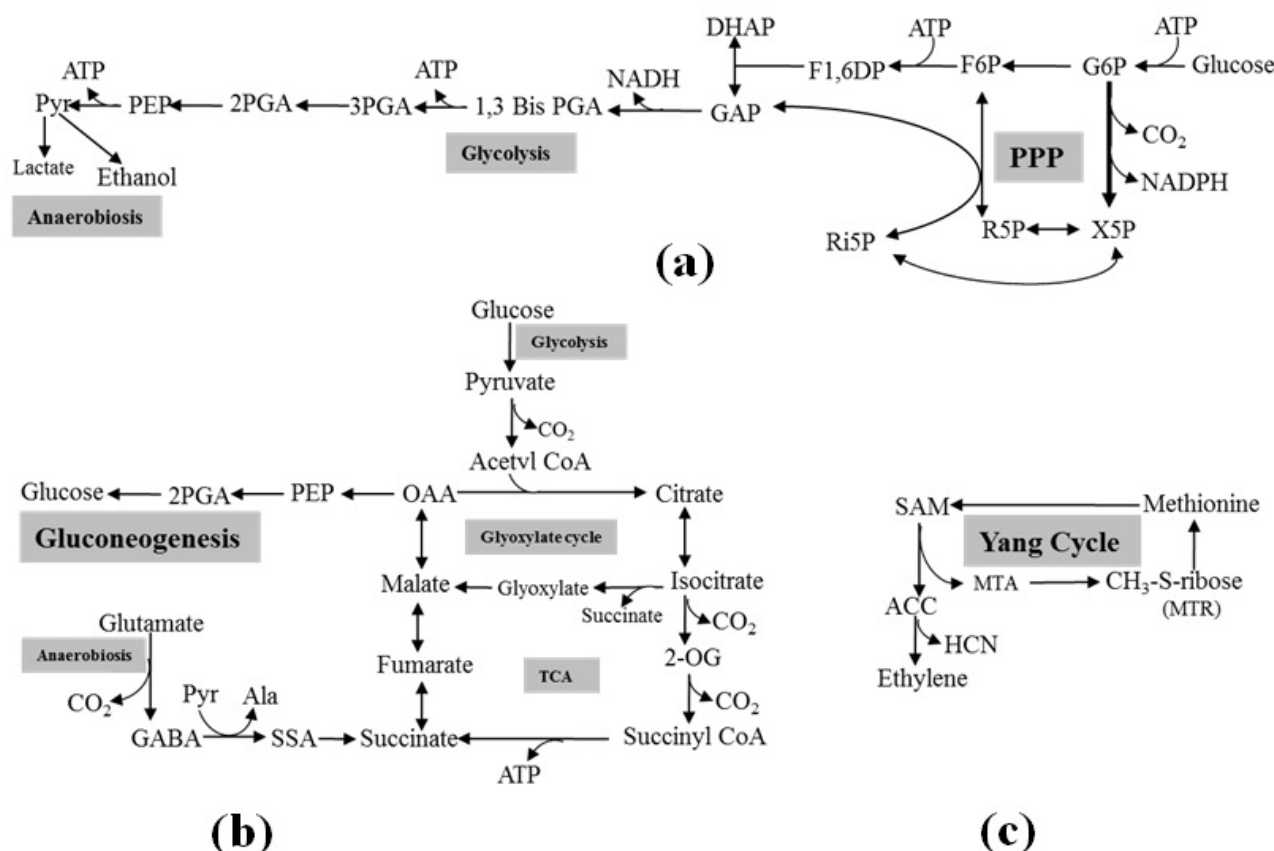
Globally, more than a half of the food produced is wasted and failed to reach consumers. Fruits and vegetables account for 45–50% of food that is lost or wasted before consumption (Choudhury et al., 2019). Deterioration of the harvested fruits is mainly caused by respiration, the basic physiological process after harvest and it largely depends on the atmospheric gas composition ( $\text{CO}_2/\text{O}_2$  ratio), temperature, ethylene and water vapor. Reduction of  $\text{O}_2$  and elevation of  $\text{CO}_2$  can delay fruit ripening by altering metabolic activities after harvest. Modified atmosphere packaging (MAP) is a useful system to regulate the composition of atmosphere in the packaging headspace whereas controlled atmosphere (CA) reduces respiration rate and other metabolic processes by lowering temperature. Recently, edible coatings and/or nanocoatings technologies are used to enhance self-life of fruits including microbial safety and quality.

This review provides an overview of physiological events (respiration, transpiration, senescence, wound healing, ethylene production) involved in ripening, especially those controlling pigment bio-synthesis and changes in the texture. We then discuss metabolic alternations which are linked with the physiological process and how this information can be used to regulate or delay ripening by means of traditional and modern technologies (MAP, CA, edible coatings and/or nanocoatings) for extending self-life and nutritional quality of ripen fruits.

## 2 Respiration

Living cells always respire for getting energy. The cells consume  $\text{O}_2$  and produce  $\text{CO}_2$  during respiration. Therefore, cellular respiration is an energy releasing process in biological system. Actually, food materials (carbohydrate, protein and lipid) use  $\text{O}_2$  for liberating energy with the concomitant release of  $\text{CO}_2$ . The ratio of moles of  $\text{CO}_2$  evolution per mole of  $\text{O}_2$  consumption is called respiratory quotient (RQ). It also indicates the types of substrates used in respiration. RQ value of sucrose is 1, fat is less than 1, organic acid is greater than 1 (Saltveit, 2019). Biochemically, cellular respiration consists of 3 major steps, i.e. glycolysis (glucose  $\rightarrow$  pyruvate), the TCA (pyruvate  $\rightarrow \text{CO}_2$ ) and oxidative phosphorylation ( $\text{NADH}$  or  $\text{FADH} \rightarrow \text{ATP}$ ) and consumed  $\text{O}_2$  is reduced to  $\text{H}_2\text{O}$ . The end product of glycolysis is pyruvate (3C) (Fig. 1a), which is completely oxidized to 3 molecules of  $\text{CO}_2$  during aerobic respiration. Out of 3, there are two  $\text{CO}_2$  releasing sites inside the tricarboxylic acid cycle (TCA) (Fig. 1b).

Rate of respiration is directly inhibited by carbon dioxide ( $\text{CO}_2$ ) at a concentration of 3 to 5% whereas  $\text{O}_2$  increases respiration rate and also increases ethylene production via Yang cycle. The conversion of amino cyclopropane carboxylate (ACC) to ethylene requires  $\text{O}_2$  which is catalyzed by ACC oxidase. A sulfur-containing amino acid, methionine is the starter point of ethylene biosynthesis pathway and the supply of methionine is continued by recycling methionine via the Yang cycle (Fig. 1c). Ethylene is well known as ripening hormone. A spike of ethylene production immediately before a climacteric rise in respiration is characterized in some fruits (so-called climacteric fruits) ripening process. However, ethylene's action is prevented by a relatively high concentration of  $\text{CO}_2$  (3 to 5%).  $\text{CO}_2$  at high concentrations (5 to 10%) also restricts many effects of ethylene. Elevated  $\text{CO}_2$  concentrations or at high  $\text{CO}_2/\text{O}_2$  ratio delayed fruits ripening during storage. In the atmosphere,  $\text{CO}_2$  is 0.035% and  $\text{O}_2$  is 21% and consequently  $\text{CO}_2/\text{O}_2$  ratio is very low. During storage of fruits and vegetables, low level of  $\text{O}_2$  (2 to 3%) is required instead of anoxia conditions to avoid low-



**Figure 1.** Biochemical events of respiration (a) glycolysis, (b) TCA and glyoxylate cycle, and (c) Yang cycle

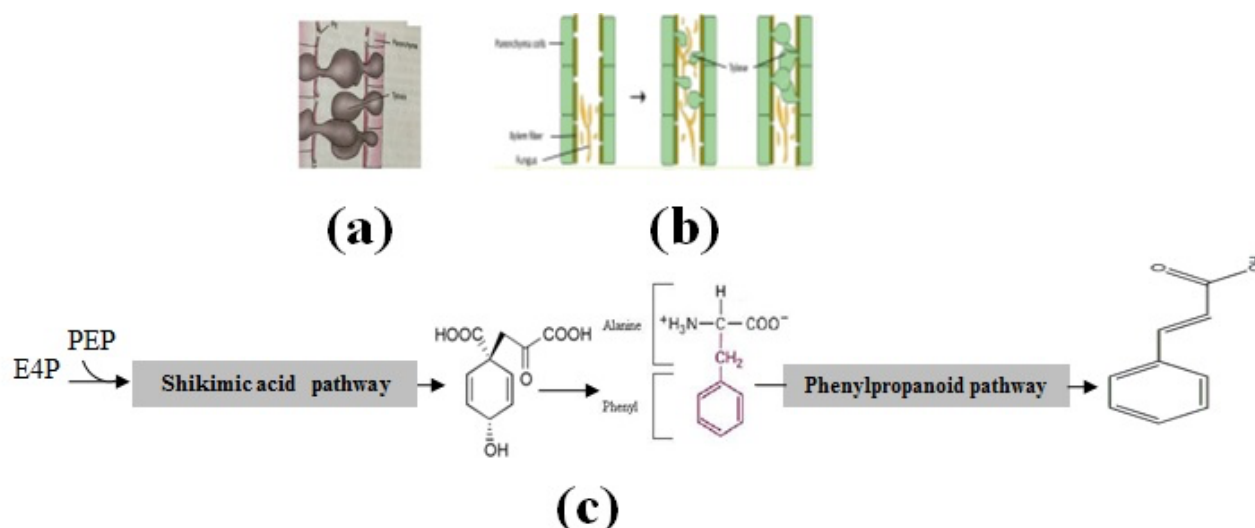
ering tissue O<sub>2</sub> tensions to the point that stimulates fermentative metabolism or anaerobiosis (Fig. 1a and Fig. 1b). Meanwhile, fermentation becomes progressively important at very low O<sub>2</sub> or high CO<sub>2</sub> atmospheres. Ethanol, acetaldehyde and lactic acids are the main fermentative metabolites that usually found in plant tissues. Therefore, gas concentration around the atmosphere of the produce is strongly influenced respiration rate and shelf-life duration (Mirdehghan and Ghotbi, 2014). Elevated CO<sub>2</sub> and low level of O<sub>2</sub> can delay the deterioration of fresh horticultural crops.

### 3 Transpiration

In plants, transpiration is helpful physiological process in which the leaves become cool and it allows the plants for water and nutrient uptake from the soil by creating the water potential gradient in the vascular system (Kramer and Boyer, 1995). It is an “unavoidable evil” because, for receiving CO<sub>2</sub> from the air, leaves have to “pay the price” of losing water. Both pre and post harvested fruits and vegetables, the losses of water through transpiration are supplied from the flow of sap that contains water, photosynthates, and minerals.

Postharvest transpiration is unexpected because

water loss along with minerals cannot be compensated by more water uptake from the soil due to detachment of the produce from the plants. Postharvest transpiration also causes a loss in cell turgor that may lead the produce to be softening, shriveling and loss of shine, epidermal color change. That’s why the losses of water and substrates used in transpiration can’t be replaced anymore and the products started to be deteriorated. Thus the process of transpiration induces wilting, shrinkage, and loss of firmness and crispness of fruits and vegetables. All the factors adversely affect the appearance, texture, flavor, and mass of the produce. Most fruits and vegetables lose their freshness after 3 to 10% mass loss. In leafy vegetables and fleshy fruits, transpiration is the main cause of postharvest losses and poor quality. It is also considered the major cause of commercial and physiological deterioration in citrus fruits. In many fruits, most of the transpiration is cuticular due to the presence of few stomata in the fruit skin. In some fruits, transpiration may occur by the calyx, as in eggplant fruit (Diaz-Perez, 1998). Since the xylem vessels of harvested fruits are probably occluded and their operation greatly impeded, water within a harvested commodity has to move through different routes via the continuum of the cell walls. Occlusion of harvested fruits may occur as a result of physiological wound healing (Williams et al., 2002), microbial colonization



**Figure 2.** Wound-induced changes (a) formation of tyloses (toppr.com), (b) xylem occlusion limits pathogen growth (adapted from Isihara 2016), and (c) activation of shikimate pathway and phenylpropanoid pathway after harvesting fruits

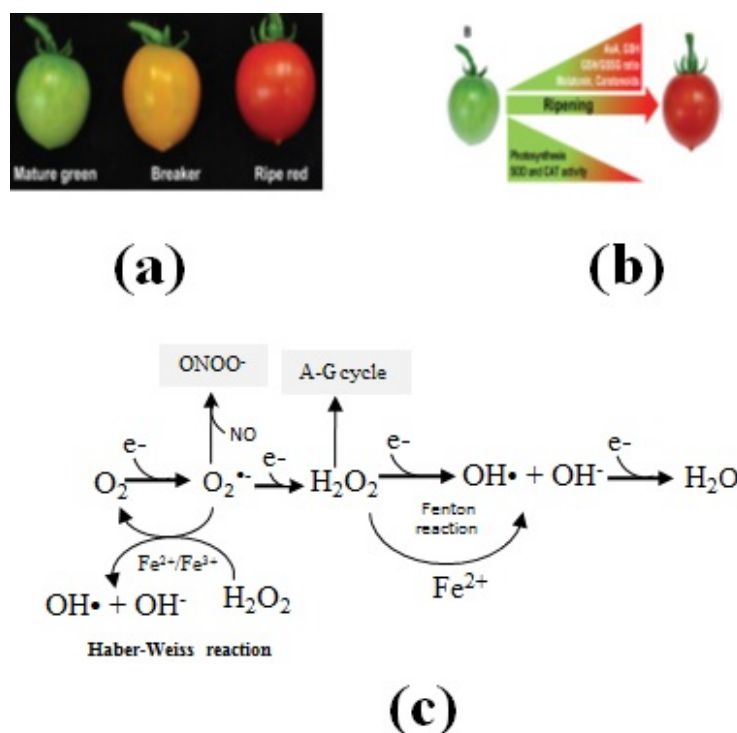
(Loubaud and van Doorn, 2004; He et al., 2006) and air embolism (van Ieperen, 2007). Tyloses are ‘balloon-shaped sacs’ and the ingrowths of parenchyma cells into the lumen of xylem vessels (Fig. 2a). It summarizes the physiological processes and occlusion in the xylem of woody plants in response to injury and/or an important event to protect heartwood from decay. To prevent the vascular wilt pathogen from spreading to near xylem vessel and to seal off a xylem vessel completely, plants naturally accumulate pectin-rich gels and gums around tyloses (Rahman et al., 1999). Additionally, the blocking of a xylem vessel or tracheid by an air bubble is called as embolism (Gr. embolus, stopper). Continuous transition from liquid to gaseous water occurred that is known as cavitation and plants experienced a huge xylem tensions during transpiration (Scholander et al., 1965; Tyree and Sperry, 1989; Holbrook et al., 1995). Cavitations caused xylem dysfunction since well accepted cohesion theory of ascent of sap has been introduced by Dixon (1914).

## 4 Wounding physiology

A wound signal is produced at the cut surface of harvested fruits and vegetables that leads the induction of many wound-induced physiological responses. To understand wounding physiology and the physiological and metabolic responses clearly, it needs to be clarified about the perception of unique ‘wound’ signals (Cisneros-Zevallos et al., 2014). Reactive oxygen species (ROS), ethylene ( $\text{CH}_2=\text{CH}_2$ ), hydraulic shock, jasmonic acid, salicylic acid, cell wall fragments, products of membrane oxidation are the main

components for generating wound signals (León et al., 2001). Fresh cut produce is alive and the cut surface may brown very fast in some cases. Oxidation of existing phenolic compounds caused this browning, that is also enhanced by polyphenol oxidase (PPO) and peroxidases (POD). It was well documented that fruits and vegetables contain various types of phenolic compounds and only a few part of these served as substrates to PPO. Moreover, the actions of PPO and POD are responsible for enzymatic browning of fresh cut fruits and vegetable meanwhile discolorations may be occurred through non-enzymatic reactions. Catechins, cinnamic acid esters (chlorogenic acid), 3, 4-dihydroxy phenylalanine (DOPA), and tyrosine are the most important natural substrates of PPO in fruits and vegetables. Biochemically, PPO and POD enzymes are associated with lignin and suberin deposition, which recognized as wound repair reactions and defense mechanism against pathogens (Hawkins and Boudet, 1996). Class III peroxidases are heme-containing enzymes that produce reactive oxygen species ( $\text{O}_2$  and  $\text{H}_2\text{O}_2$ ) in the apoplast (Daudi et al., 2012; Cosio and Dunand, 2009; Bindschedler et al., 2006). Being toxic in nature, ROS can kill vascular wilt pathogens. Moreover, peroxidases are involved in generating apoplastic  $\text{H}_2\text{O}_2$  which actively participates in polymerization of cell wall components, lignin and suberin biosynthesis as well (Hilaire et al., 2001; Passardi et al., 2005; Hossain et al., 2005). Phenylalanine synthesis is enhanced by wounding due to the stimulation of the shikimate pathway (Fig. 2). Wounding also activates the phenylpropanoid pathway via PAL (Phenylalanine Ammonia-Lyase), which leads to increased lignin synthesis and antioxidant capacity as well. In case of wound-healing of harvested





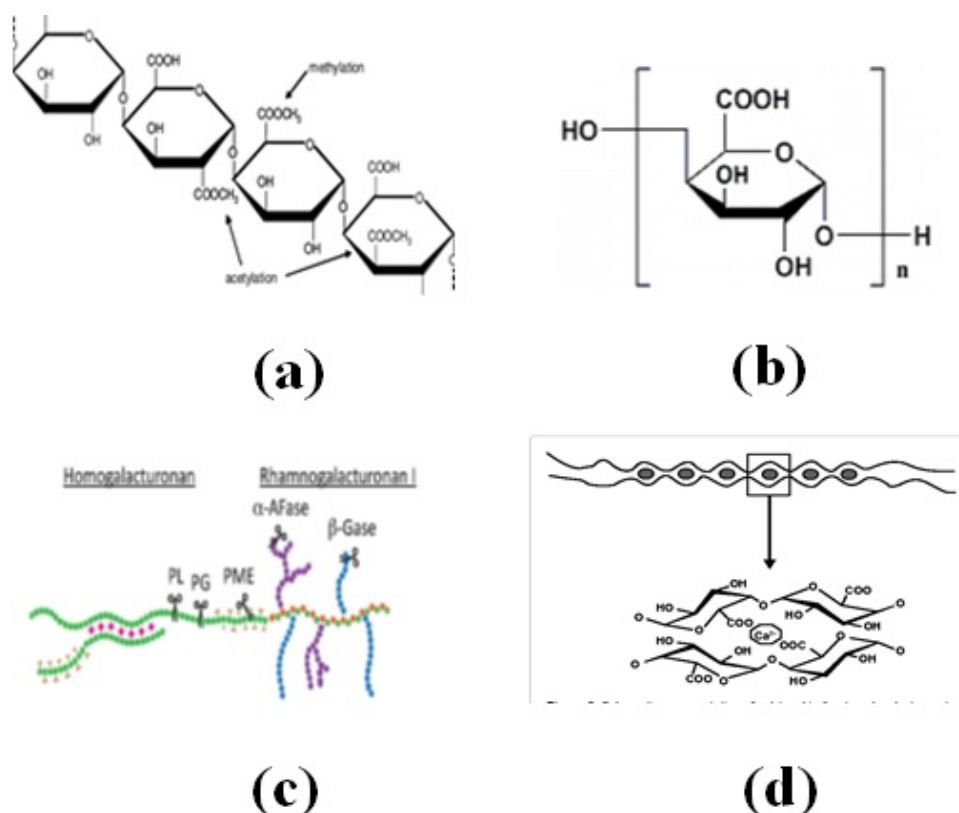
**Figure 3.** Fruit ripening events (a) colour change, (b) altering of antioxidant molecules and enzymes (Adapted from Corpas et al. (2017)), and (c) ROS generation

root crops and production of pharmaceutical compounds, the wound-induced changes are desirable while in case of lignifications of vascular tissues and browning of cut surface, the wound-induced changes are undesirable. Some of these changes are unexpected and these may reduce product quality.

## 5 Senescence

Senescence is an important physiological phenomenon of fruit life cycles affecting the fruit quality directly. Being an oxidative process, fruit senescence is characterized by rapidly increase in reactive oxygen species (ROS) particularly  $H_2O_2$  and  $O_2^{\cdot-}$  (superoxide anion) Warm and Laties (1982); Brennan and Frenkel (1977); Frenkel and Eskin (1977). Therefore, ROS plays a vital role in the senescence process. Highly reactive molecules including free oxygen radicals, like superoxide anion ( $O_2^{\cdot-}$ ), hydroxyl radical ( $OH^{\cdot}$ ), and non-radical oxygen derivatives, like the stable hydrogen peroxide ( $H_2O_2$ ) are the members of the ROS physioma family. Hydrogen peroxides and hydroxyl radicals are formed from the superoxide radicals and may also be interconverted with reactive nitrogen species (RNS) such as  $ONOO^-$  (peroxynitrite). RNS also create similar effects of ROS (Fig. 3c). So, removal of ROS such as  $H_2O_2$  is required in fruit ripening as it is an oxidative process meanwhile there is a balance in antioxidant systems between the production and

removal of ROS (Jimenez et al., 2002). In ascorbate-glutathione cycle or A-G cycle, antioxidant enzymes eliminate  $O_2^{\cdot-}$  and  $H_2O_2$  during senescence (Fig. 3b, Fig. 3c) and thus restrict the rate of postharvest senescence (Lacan and Baccou, 1998; Lester, 2003). Fruit senescence can also be retarded effectively by lowering oxygen concentration (2–5%) in storage environment that decreases ROS generation although  $H_2O_2$  treatment in fruit enhanced senescence (Qin et al., 2006; Tian et al., 2004). Moreover, high  $O_2$  treatment in fruit is known to increase  $H_2O_2$  production in mitochondria (Turrens et al., 1982) and thereby senescence may be accelerated by affecting the activities of antioxidant enzymes (Wang et al., 2005). Now it is very much clear that oxidative stress caused the accumulation of ROS which is very much associated with fruit senescence. Fruit antioxidants can process ROS and/or RNS in different ways. Basically, antioxidants are referred to all biomolecules, including phenolics, terpenoids, thiol derivatives and vitamins,  $\beta$ -carotene, ascorbate (AsA), reduced glutathione (GSH) etc. Most antioxidants detoxify or remove ROS to avoid cell damage (Nimse and Pal, 2015). Antioxidants also engaged in recycling pathways, such as the ascorbate-glutathione (A-G) cycle, to maintain the redox state by regulating the activities of GR, DHAR and MDHAR. Thus, postharvest fruit quality, resistance to pathogen attack and environmental stress largely depends on senescence process (Tian et al., 2004). Fungal pathogens can easily attack the senes-



**Figure 4.** Cell wall metabolism (a) methylated pectins, (b) pectic acid, (c) sites of action of different cell wall metabolizing enzymes, and (d) 'Egg-box' in two antiparallel chains of homogalacturonan (HG)

cent fruits while disease caused by fungal pathogen enhances senescence process (Tian et al., 2007). During the ripening of tomato fruit, melatonin is accumulated and acts as an important antioxidant in biological systems (Arnao and Hernández-Ruiz, 2014; Huang and Mazza, 2011; Okazaki and Ezura, 2009).

## 6 Metabolic changes during ripening

Fruit ripening is a developmental process. It involves huge number of metabolic as well as physiological and biochemical changes. Some chemical parameters such as chlorophyll degradation and anthocyanin biosynthesis occurred during ripening meanwhile enzymatic degradation, ethylene production, change in sugar content, respiratory activities, and aromatic compounds also occurred in ripening of fruits (Giovannoni et al., 2017). Actually ripening occurred at the later stage of growth and development by changing physiological, biochemical and sensory attributes of fruits. Therefore, it is evident that fruit ripening is a sequential biochemical changes that leads to the breakdown of chlorophyll, new pigments formation, change in flavors and aromas, softening of the body flesh as well as abscission of the fruit and vegetables.

## 7 Cell wall metabolism

Quality fruits are usually characterized by its appearance and texture and become attractive to the consumer. It is well documented that pectins greatly influenced the texture of fruits. There are 3 major classes of pectin in cell wall polysaccharides, namely homogalacturonan (HG; polymerization of 1 → 4 α-galacturonic acid), rhamnogalacturonan I (RG-I; repeating disaccharide comprises rhamnose and galacturonic acid) and rhamnogalacturonan II (RG-II; less abundant but has a complex composition). They played an important role in cell-to-cell adhesion. Pectins may be esterified with a methyl group on carbon 6, or with an acetyl group on carbon 2 or 3 (Fig. 4a). In immature fruits, methylated polymer of galacturonic acids (HGs) are dominant species; it is insoluble in water and cannot form gels. The enzyme, pectin methyl esterase (PME) is expressed during the maturation of the fruit and it removes methyl group of carbon 6 and may increase accessibility of polygalacturonase (PG) to its pectin substrate which is necessary for ripening-related pectin depolymerization (Fig. 4c). Non-esterified pectins also exist and are known as pectic acids (Fig. 4b) and Ca<sup>2+</sup> mediated cross linking (so-called 'egg box') of two anti parallel chains of HG (Fig. 4d) is known to be necessary in

mediating cellular adhesion as the de-esterified HG, is huge in the middle lamella. In fact, cell adhesion is related to the middle lamella, the extracellular matrix that free from cellulose microfibrils. 'Egg box' are responsible for providing a structure that is resistant to PG activity but can only be hydrolyzed by the enzyme pectatelyase (PL). The products, pectins are soluble in water and able to form gels in appropriate conditions. Moreover, textural changes lead to softening of fruits along with the loss of neutral sugars (arabinose, rhamnose and galactose), de-esterification, disassembled cell wall components, solubilization and depolymerization of the polysaccharides of the cell wall, due to the combined action of several cell wall-modifying enzymes (i.e. PME, PG, PL,  $\alpha$ -AFase,  $\beta$ -Gase) (Fig. 4c). The factors responsible for softening of the fruits are degradation of the polysaccharide components of the cell wall, reduction of cell-to-cell adhesion and middle lamella degradation. Shelf life, storage, market ability and consumer acceptance of fruits can be largely affected by excessive fruit softening.

## 8 Color changes and associated metabolic pathways

Green fruits are usually unripe and it is more characterized by sour, odorless, hard and mealy conditions. With the advancement of ripening process, the fruit gets more appealing due to alterations in skin color because of chlorophyll degradation and in some cases due to synthesis of new pigments (carotenoids, flavonoids, anthocyanins, betalains, phenolics, etc.). There are several secondary metabolic pathways associated to color changes during ripening as follows.

### 8.1 Chlorophyll degradation

Fresh fruits are rich in chlorophyll and ripening of fruits involves chlorophyll degradation. In brief, it is an enzymatic process causing removal of phytol (tail) by chlorophyllase, removal of Mg by  $Mg^{2+}$  dechelataase, and the split of tetrapyrrole ring forms red chlorophyll catabolite (RCC) by pheophorbide oxygenase (Fig. 5a). In autumn, leaf senescence become highly visible with the sign of the de-greening of leaves and the emergence of the fall colors that leads to a form of programmed cell death in plants. Indeed, the products of chlorophyll breakdown, colorless tetrapyrroles known as NCCs (non fluorescent chlorophyll catabolites) were first observed in senescent leaves. The occurrence of NCCs (natural antioxidants) in ripe fruit might be very much beneficial to health (Mueller et al., 2014).

### 8.2 Isoprenoid Pathway

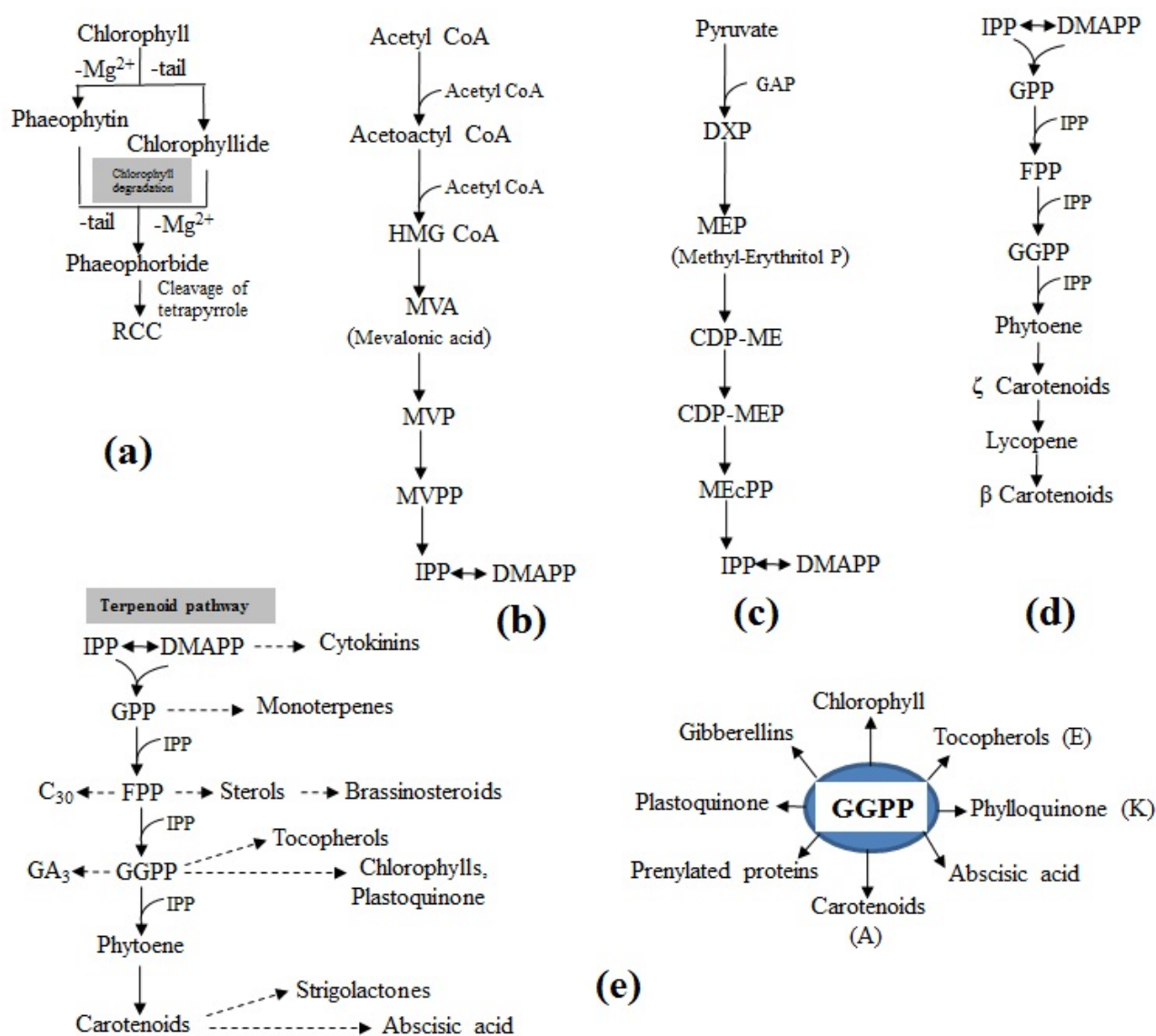
It is subdivided as MVA (mevalonic acid) and MEP (methyl-erythritol phosphate) pathways, operating in different cell organelles (Vranová et al., 2012). The MVA and MEP pathways are associated for the formation of the isoprenoid precursors IPP (isopentenyl pyrophosphate) and DMAPP (dimethylallyl pyrophosphate) in plant cells (Fig. 5b and Fig. 5c). The MEP pathway enzymes are situated in the stroma. Some special types of isoprenoids, including chlorophylls, carotenoids, and prenylquinones such as plastoquinone, phyloquinone, and tocopherol are produced in this pathway (Joyard et al., 2009) (Fig. 5e). However, the MVA pathway enzymes are located in different sub-cellular organelles, such as, cytoplasm, peroxisomes, endoplasmic reticulum and mitochondria.

### 8.3 Carotenoids biosynthetic pathway

Onset ripening, fruit carotenoid biosynthesis may alter fruit quality and nutrient content. Carotenoids ( $\beta$ -carotene and lycopene) are synthesized in harmonization with chlorophyll degradation (Fig. 5a). Carotenoids are necessary pigments in photosynthetic machinery and also an important part of human diet (Apel and Bock, 2009). Moreover, carotenoids provide  $\beta$ -carotene, the precursor of vitamin A (Fig. 6c) and act as an antioxidant. The developmental conversion of chloroplasts to chromoplasts leads the green tomato fruits to red. Actually more diversified carotenoids, represented by secondary carotenoids are found in ripe fruit than in unripe fruits and green leaves as well. The carotenoids/chlorophyll ratio is an index of ripeness and quality of fruits. As carotenoids fall into a subgroup of terpenoids, the former are derived from IPP and its allylic isomer DMAPP (Fig. 5d). Head-to-head condensation of two GGPP (Geranylgeranyl pyrophosphate) generates carotenoid. In this biosynthetic route, the first colorless carotenoid, phytoene (C40) is generated by phytoene synthase. It undergoes a series of desaturations for producing lycopene,  $\beta$ -carotene and lutein etc (Fig. 5d and Fig. 6).

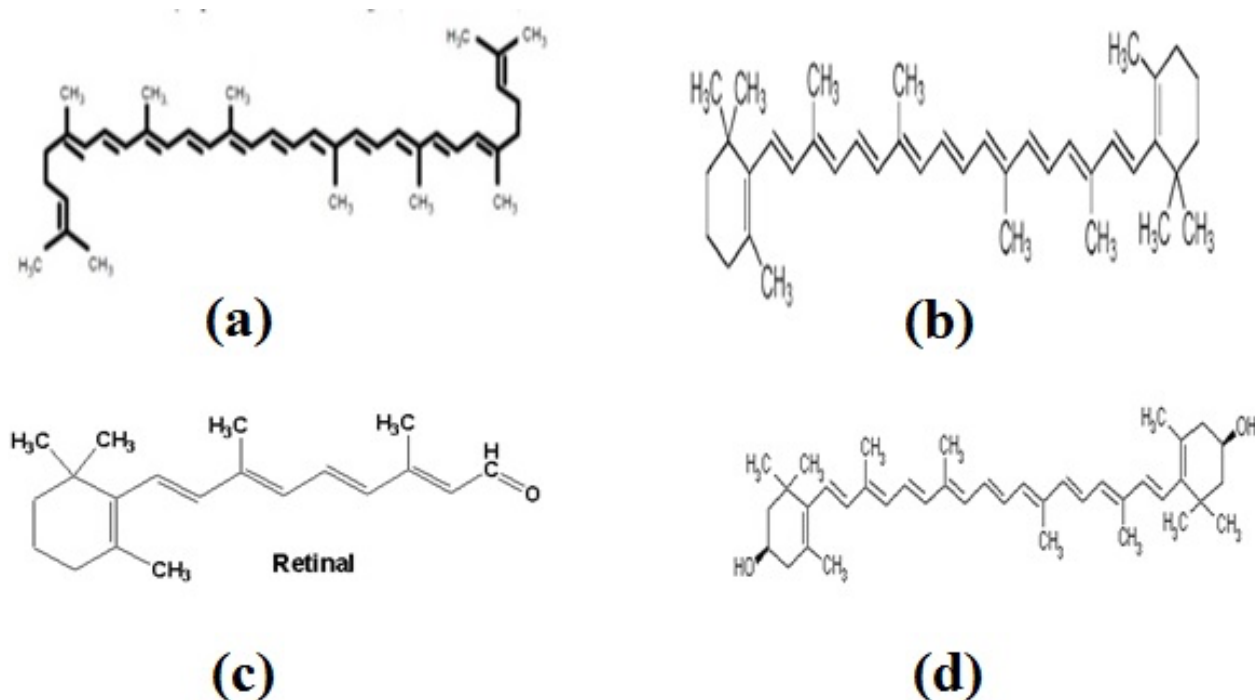
### 8.4 Phenylpropanoid biosynthetic pathway

The phenylpropanoid metabolism is unique to plants. Structurally, it is C6-C3, having a phenyl propane unit. The shikimic acid pathway (absent in animals) is the only route for biosynthesis of C6-C3 unit, the aromatic building blocks of phenyl propane derivatives. Accordingly, the shikimates can be grouped by C6-Cn classification: (i) C6: phenols and quinines, (ii) C6-C1: benzoic acid, benzaldehyde, benzyl alcohols, (iii) C6-C2: phenylethyl amines, styrenes, acetophenones, (iv)

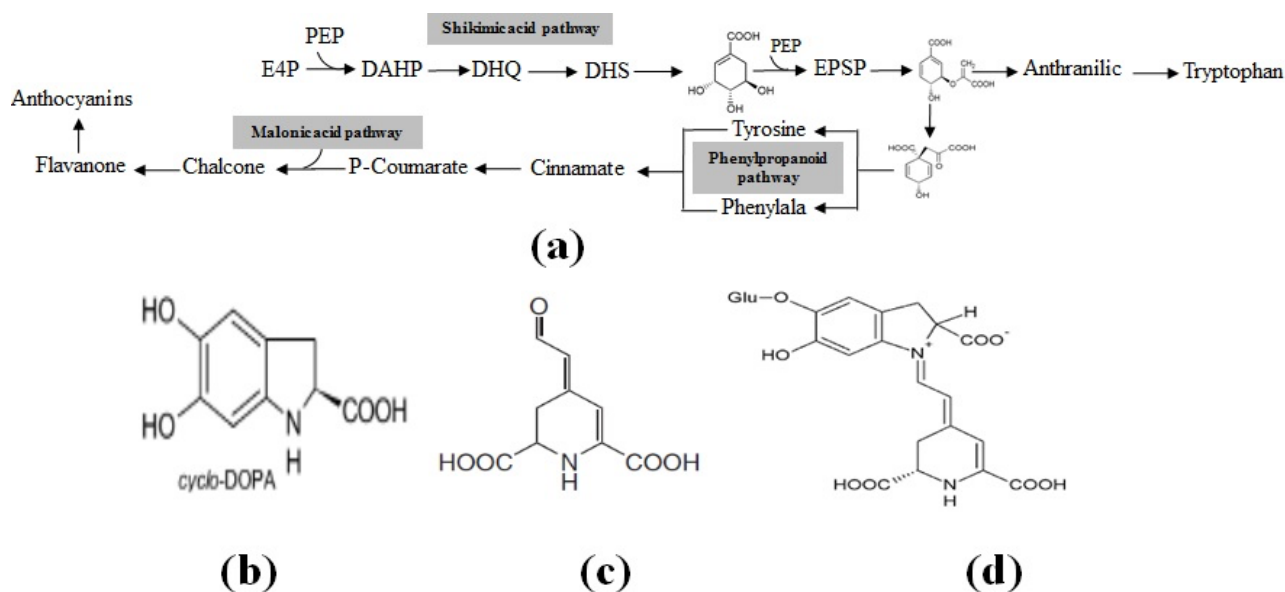


**Figure 5.** Metabolic pathways for color changes during ripening of fruits (a) Chlorophyll degradation (b) MVA pathway (c) MEP Pathway (d) Carotenoid biosynthesis (e) Terpenoid and its related biosynthetic pathways





**Figure 6.** Color-producing carotenoids during ripening of fruits (a) lycopene, (b)  $\beta$ -carotene, (c) Vitamin A, and (d) lutein



**Figure 7.** Biosynthetic pathways for secondary metabolites (a) shikimic acid and phenylpropanoids pathway, and 20 metabolites, (b) cyclo-DOPA, (c) Betalamic acid, (d) Betacyanins [Adapted from Jahan (2019)]

C6-C3: phenyl propanoids, cinnamaldehydes, aryl propanes, lignins, lignans, (v) C6-C3-C6: flavonoids, isoflavonoids, catechins, anthocyanins. The precursors of the shikimic acid pathway are phosphoenol pyruvate (PEP; a 3 carbon intermediate from glycolysis) and erythrose 4-phosphate (E4P; a 4-carbon intermediate of the pentose phosphate pathway) (Fig. 1). The end products of shikimate pathway are phenylalanine and tyrosine (Fig. 7), and acts as the starting point for the biosynthesis of nutritionally important color producing phenylpropanoid derivatives like flavonoids, anthocyanins and betalains. Anthocyanins belong to flavonoid family having a C15 skeleton (C6-C3-C6) with sugar molecule(s) in the basic structure.

### 8.5 Betalains biosynthesis

Betalains are structurally different from anthocyanins. Betalains and anthocyanins never found together in plants. It is a secondary metabolites and necessary natural food colorant derived from the amino acid, L-tyrosine. Tyrosine undergoes hydroxylation and formed L-3,4-dihydroxy phenylalanine (DOPA). Actually, simultaneous hydroxylation and oxidation of tyrosine by tyrosine hydroxylase is the first step in betalain synthesis to form DOPA and thereby oxidation and split of the aromatic ring of DOPA by DOPA-dioxygenase producing 4, 5-seco-DOPA, that exhibits a spontaneous cyclization to be betalamic acid (Fig. 7).

## 9 Ripening index and associated metabolic pathways

The ratio between total soluble solids (TSS %) and titratable acidity (TA) is termed as the ripening index. It is resulting from starch degradation and conversion of organic acid to sugar during ripening of fruits.

### 9.1 Starch degradation

Starch is a naturally occurring biopolymer in which glucose is polymerized into amylose ( $\alpha$ -1-4 glycosidic bonds), an essentially linear polysaccharide and amylopectin ( $\alpha$ -1-4 and  $\alpha$ -1-6 glycosidic bonds), a highly branched polysaccharide. During ripening of fruits and maturation of vegetables, starch degradation is a common and essential process and that actually is mediated by  $\alpha$ -amylase and  $\beta$ -amylase. Another enzyme, starch phosphorylase acts repeatedly by producing glucose-1-phosphate (G1P) and a polymer one glucose unit shorter (n-1). G1P is converted to glucose-6-phosphate (G6P), which enters various metabolic routes (Fig. 8a) during fruit maturation and ripening. In addition, during ripening of fruit, consequently starch concentration decreases and sugar concentration increases. Meanwhile, translocation of carbohydrates occurred from leaves to fruit in the

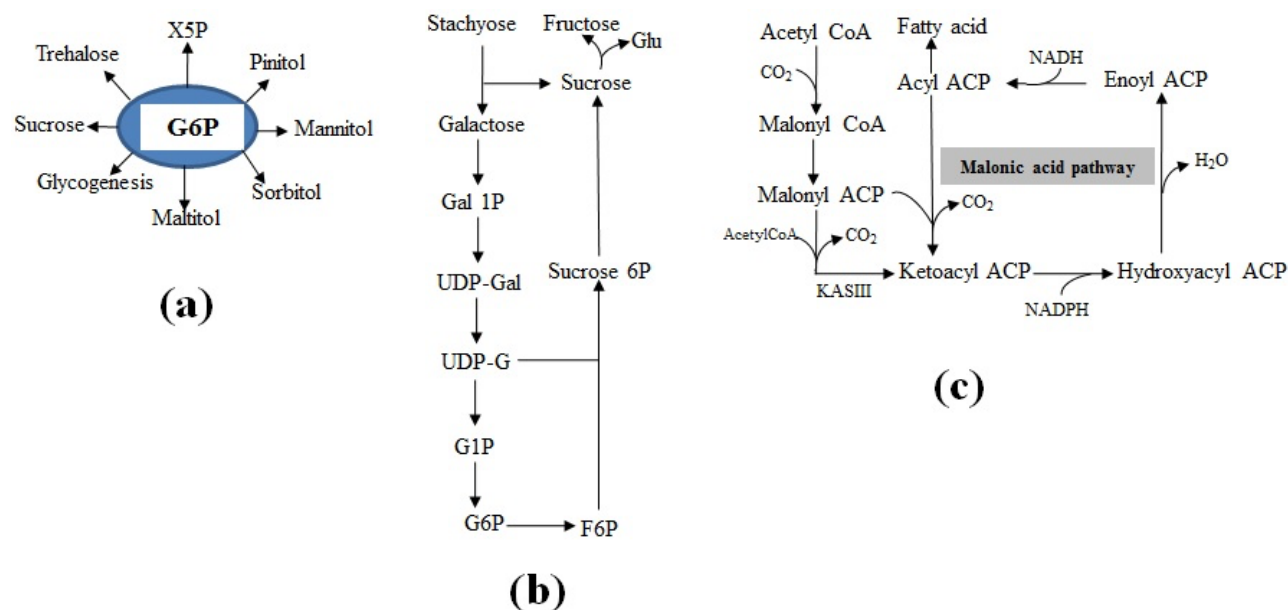
form of sucrose known as fruit sugar, an abundant disaccharide contained glucose and a fructose molecule. Stachyose occurs naturally in unripe and green fruits. It is converted to simple sugar after harvest (Fig. 8b).

### 9.2 Changes organic acid composition

Fleshy fruit acidity occurred due to presence of predominant organic acids such as malic and citric acid in the ripe fruits which is an essential component of organoleptic quality and may varies from species to species. Sourness of fruits is mainly characterized by the presence of these organic acids which usually stored in the cell vacuoles. Most of the cases, the fruits remain sour at the early ripening stage because of these organic acids however this acidity starts to decrease at later stages due to their utilization in the respiratory process. Malic acid and oxaloacetic acid (OAA) transformed into tricarboxylates, mainly citric acid and this citric acid again converted into dicarboxylic acids in different pathways: TCA cycle, glyoxylate cycle,  $\gamma$ -aminobutyrate (GABA) shunt, and cytosolic Acetyl-CoA catabolism to secondary metabolites (Fig. 1b). Degradation of organic acids can also occur through decarboxylation of malate and OAA. Phosphoenol pyruvate (PEP) is produced through the decarboxylation of OAA and malate and activates gluconeogenesis (Sweetman et al., 2009) which occur at ripening of fruits as the sugars are stored rapidly at this stage (Fig. 1b). As a result, total sucrose increased because of gluconeogenesis of organic acids. Thus acidity of fruit cells is reduced or altered due to all of these conversion reactions. The glyoxylate cycle enables acetyl-CoA to be transformed into malate and acetyl-CoA generated by  $\beta$ -oxidation of fatty acids. The glyoxylate cycle generates succinate, which is converted to malate through the TCA cycle (Fig. 1b). On the contrary, during fruit ripening this accumulation of organic acids may be specific to some fruits because since no isocitrate lyase proteins have been identified in some soft fruits (Famiani et al., 2015). In fact, citrate is converted to succinate or OAA through GABA shunt or cytosolic citrate lyase respectively (Fig. 1b). This is happening for most of the fruits.

### 9.3 Changes in fatty acids composition

In general, while the fruit are maturing, the degree of unsaturated fatty acids becomes greater. As fruit ripens, a decrease in linoleic acid (18:2,  $\omega$ 6) and an increase in linolenic acid (18:3,  $\omega$ 3) as well as reciprocal distribution of palmitic acid (16:0) and palmitoleic acid (16:1) were observed in mango pulp (Bandyopadhyay and Gholap, 1973). The changes in FAs composition are remarkably important for developing aroma and flavor of fruits. Avocado contains high amount of unsaturated fatty acids. This unique fea-



**Figure 8.** Biochemical changes during fruits maturation and ripening (a) Glucose-6-P, (b) starch degradation, (c) fatty acid biosynthesis

ture is related to its high caloric value. Acetyl-CoA is the precursor for de novo fatty acid biosynthesis in biological system (Fig. 7c) and chloroplastic acetyl-CoA carboxylase actively participates for the production of long chain fatty acids from acetate in avocado tissues. The products of fatty acid syntheses are mainly C16 or C18 saturated acyl chains via malonic acid pathway (Fig. 8c).

#### 9.4 Changes of flavor and aroma

The odor and aroma of fruits are induced by biochemical compounds, generated during all phases of growth and fruit maturation. Among the secondary metabolites, terpenoids belong to the largest family. Terpenoids are not only important for the quality of fruits but also have commercial interest because of their use as flavorings and fragrances in foods and cosmetics. An isopentane skeleton (5-carbon unit) is the root of all terpenoid derivatives (Fig. 4). The fruit aromatic characteristics are associated with alcohols, aldehydes, esters, ketones, furanones, and terpenes. They are volatile compounds derived from different chemical families.

Consumer's choice and acceptance depends on flavor and aroma of fruits. Sweet, sour, and bitter are the main tastes found in fruits and vegetables. Sweet and sour taste are associated with soluble sugars and organic acids respectively, while bitterness in fruits and vegetables is linked to poly phenols content. The most common organic acids in fruits are malic, citric, tartaric, quinic, benzoic, oxalic, fumaric, and succinic acid. In contrast, phenolic acids (hydroxybenzoates and hydroxycinnamates) and flavonoids are under polyphenolic compounds found in fruits

(Fig. 9). The aromatic amino acid, L-phenylalanine acts as the main precursor of most fruit phenolic compounds and the shikimate (Fig. 2 and Fig. 7) pathway is the well known biosynthetic route of phenylalanine in plants. Astringency is due to chemical compounds producing a sensation of dryness in the mouth caused by the precipitation of salivary proline-rich proteins. Some of the most common astringent phenols are caffeic acid (cocoa), catechin (tea), kaempferol (onion), ferulic acid (cocoa), gallic acid (tea), luteolin (cocoa), quercetin (tea), etc (Fig. 9c-g). During preharvest and postharvest ripening, the polymerization of tannins reduces astringency. Flavonoids consist of two aromatic rings (A ring and B ring) connected by a three-carbon bridge, generally expressed as C6-C3-C6 (Fig. 9b). Interestingly, this structure originates with two separate biosynthetic pathways; A ring is from malonic acid pathway and B ring is from phenylpropanoid pathway. Anthocyanins are members of flavonoid group having a C15 skeleton (C6-C3-C6) and one or more sugar molecules bonded at different hydroxylated positions of the basic structure.

## 10 Changes in controlled and modified atmospheres

Fruits remain alive after harvest. Improvement of storability and extend shelf life of fresh products would be possible by regulating respiration of these living tissues. Because, living tissues always respire by absorbing O<sub>2</sub> and releasing CO<sub>2</sub> along with energy (ATP and heat) and vapor. All these factors are related to handling, storage, transportation, shelf-life exten-

sion and quality regulators. Alternatively, several physiological and biochemical changes such as respiration rate, ethylene production, ripening, and senescence processes can be controlled in post-harvested fruits by controlling the atmospheric gas composition (in particularly  $O_2$ ) in the storage room. There are various ways to control respiration and ethylene production as well. They are as follows:

**$CO_2/O_2$  ratio** Gas composition of normal air is 21%  $O_2$ , 78%  $N_2$ , 0.038%  $CO_2$  and 0.93% argon. Therefore,  $CO_2/O_2$  ratio is very low. Excess  $O_2$  accelerates ethylene production via enhancing the activity of ACC oxidase. In contrast, the elevated  $CO_2$  (5–20%) decreases ACC synthase and ACC oxidase activities and consequently curtails ethylene production in climacteric fruits. Again very low  $O_2$  (hypoxia/anoxia condition) accelerates anaerobic respiration, which deteriorates fruits quality. So,  $CO_2/O_2$  ratio should be maintained by the reducing  $O_2$  concentration coupled with an increase in  $CO_2$  levels during postharvest handling of fruits. Indeed, high  $CO_2/O_2$  ratio is maintained for extending shelf life and quality of specific fruits.

**Controlled Atmosphere (CA)** In CA, the atmospheric conditions and/or gas composition in storage rooms or transportation containers is continuously monitored and adjusted.

**Modified Atmosphere (MA)** In an MA, the changes of gas composition (especially  $CO_2/O_2$  ratio) inside the package are the result of the metabolic activity (respiration) of the produce. Here, the gas composition is not closely monitored and could not be adjusted. In fact, MAP technology provides an atmosphere for increasing the shelf-life and maintaining the quality of the food by modifying or altering gas composition or  $CO_2/O_2$  ratio around the products in food packages. When actively respiring produce is placed in sealed plastic bags, atmospheric gas composition (<2%  $O_2$  and >10%  $CO_2$ ) modifies or alters in the bags (Kays and Paull, 2004). Better understanding of physiological responses to low  $O_2$ /high  $CO_2$  atmospheres makes possible the successful application of CA/MA for extending shelf-life and decreasing postharvest losses of fruits. Since fresh fruits remain alive after harvest, respiration and transpiration occur during storage and consequently, water loss and texture change are remarkable Kader (2005). To minimize the metabolic activities of the fruits and vegetables, low temperature and specific barrier/permeability to gas are required.

**Coatings** A modified atmosphere is created after applying coatings on the fruit surface and it provides a barrier to oxygen, moisture and the movement of solutes (Gutiérrez and Álvarez, 2017; Tapia-Blácido

et al., 2018). The functions of coatings are similar to controlled and modified storages, depending on their formulations (Fig. 10a). It increases  $CO_2$  level and decreases  $O_2$  concentration internally since coatings reduces gas permeability significantly (Ansorena et al., 2018).

**Edible coatings** Microbial spoilage as well as food oxidation, enzymatic browning and oxidative rancidity are of major concern regarding food quality deterioration, and are the greatest challenges in the food industry. Edible coatings application could be an alternative to reduce food deterioration in some extent (Álvarez et al., 2017; Alvarez et al., 2017). Edible coatings consist of biopolymer (chitosan/starch) and antimicrobial or antioxidant properties enriched bioactive compound (anthocyanins) which act as a barrier against physical, chemical, and biological contaminants, as well as against water vapor, oxygen and moisture (Eça et al., 2014).

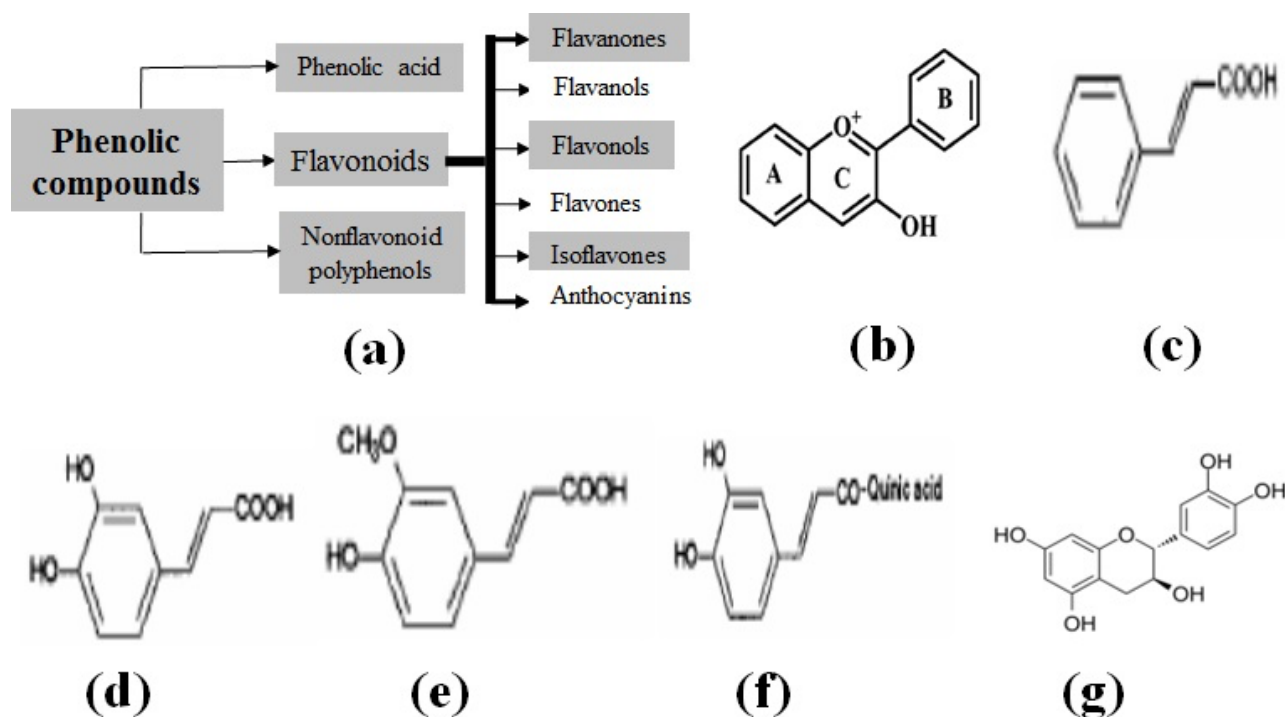
**Edible nanocoating** An edible nanocoating is specially designed for incorporating of nanoscale antioxidants, antimicrobial agents through diverse fabrication techniques that release nutraceuticals in a controlled manner (Luksiene and Buchovec, 2019).

**Smart packaging** The application of nanosensors in the food packaging system can't only control food quality but also able to monitoring food safety up to delivery to the final consumer (He et al., 2018). Nanotechnology through IP (Intelligent Packaging) tools can monitor tracking and locating product features including its authentication to avoid falsification, adulteration of the products intended for a specific market. During postharvest handling and storage, fresh produce undergoes ripening process which is controlled by ethylene ( $C_2H_4$ ). In fact, ethylene causes substantial quality degradation and shelf-life reduction of climacteric fruit (Martínez-Romero et al., 2009; Kaya et al., 2016). Therefore, controlling production or emission of ethylene is a very important factor for suppressing the detrimental process of climacteric fruit (Maneerat and Hayata, 2006; Saltveit, 2019).

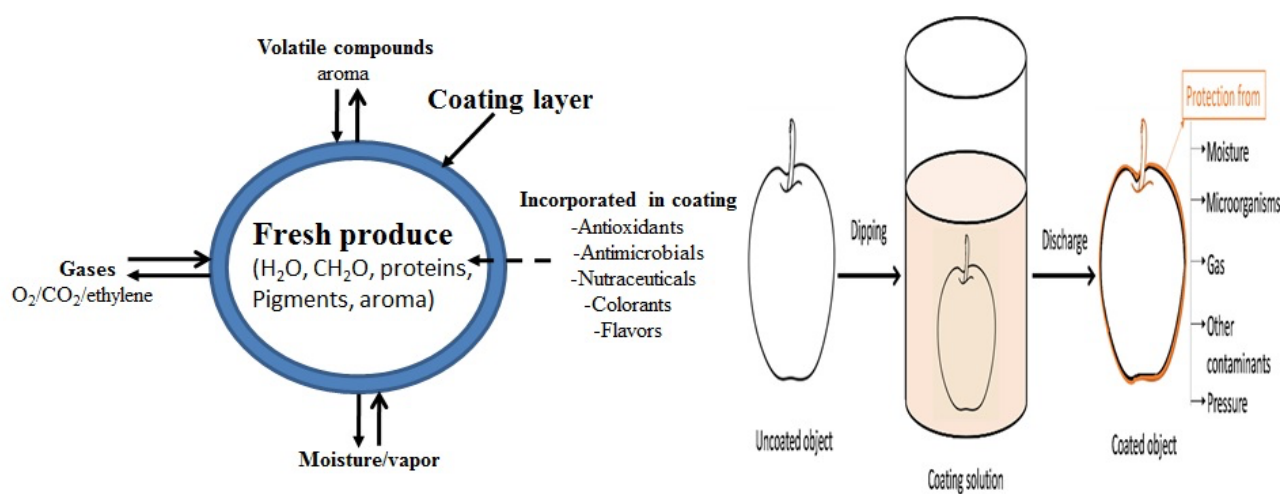
**1-Methylcyclopropene (1-MCP)** A good protection of avocado fruit against ethylene for a period of up to 13 days could be possible by applying 1-MCP, a potent inhibitor of ethylene. In fact, 1-MCP is a gas, non-phytotoxic and odorless chemical. It is effective at low concentrations which renders it a promising candidate for commercial use.

**Metabolic engineering** Inhibition ethylene synthesis and reduction sensitivity to ethylene are two important genetic engineering approaches successfully employed to delay ripening or senescence (Bleecker





**Figure 9.** Classification of the (a) polyphenolic compounds in fruits, (b) basic structure C6-C3-C6 of flavonoids, (c) cinnamic acid, (d) caffeic acid, (e) ferulic acid, (f) chlorogenic acid, (g) catechin



**Figure 10.** (a) Functional characters of coating on fruits and (b) Technology

and Kende, 2000). Antisense technology that construct of a cDNA encoding ACC oxidase can decrease ethylene formation in tomatoes (Hamilton et al., 1990). It also delayed ripening of the transgenic fruits, and prolonged their storage life. A similar approach was followed by Oeller et al. (1991), who transformed tomato plants with the antisense construct of a cDNA coding for ACC synthase. In this particular case, ripening was suppressed due to inhibition of ethylene production by 99.5% in transgenic fruits and applied ethylene restored normal ripening. By removing ACC from the precursor pool, ethylene synthesis and ripening could be inhibited significantly. It was achieved by expressing a bacterial ACC deaminase gene in tomatoes (Klee and Giovannoni, 2011). The dominant *etr1* mutation confers ethylene insensitivity in *Arabidopsis* plant while it causes significant delays fruit ripening, flower fading, and flower abscission in tomato and petunia (Wilkinson et al., 1997). Physical damages during handling and transportation induce greater susceptibility to microorganism attacks and post-harvest losses as well (Manrique and Lajolo, 2004). The loss of firmness as a result of cell wall and starch degradation in fleshy fruit is greater than others. In traditional postharvest storage technique at low temperature can slow down microbial growth and at the same time, it adversely effects on nutritional properties since reduced the antioxidant capacity and flavonoids in strawberries (Nielsen and Leufven, 2008). Widely accepted hypochlorite ( $200 \mu\text{g mL}^{-1}$ ) reduced the microbial contamination of strawberries just 0.45 log (Alexandre et al., 2014).

## 11 Conclusions

Apart from being economically important commodity, fruits are excellent dietary supplement owing to their high nutritive value and unprecedented organoleptic properties. During ripening, fruit undergoes well co-ordinated and extensive physiological, biochemical and molecular changes imparting the desired attributes to the ripe fruits and at the same time, they cause quality deterioration of the fruits. This review on various physiological, biochemical and molecular insights of fruit maturation and ripening have fortified our knowledge of the process and consequently reduction of postharvest quality losses of fruits to some extent would be possible by applying our knowledge.

## Conflict of Interest

The authors declare that there is no conflict of interests regarding the publication of this paper.

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