

Role of internal atmosphere on fruit ripening and storability —a review

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Abstract Concentrations of different gases and volatiles present or produced inside a fruit are determined by the permeability of the fruit tissue to these compounds. Primarily, surface morphology and anatomical features of a given fruit determine the degree of permeance across the fruit. Species and varietal variability in surface characteristics and anatomical features therefore influence not only the diffusibility of gases and volatiles across the fruits but also the activity and response of various metabolic and physiological reactions/processes regulated by these compounds. Besides the well-known role of ethylene, gases and volatiles; O₂, CO₂, ethanol, acetaldehyde, water vapours, methyl salicylate, methyl jasmonate and nitric oxide (NO) have the potential to regulate the process of ripening individually and also in various interactive ways. Differences in the prevailing internal atmosphere of the fruits may therefore be considered as one of the causes behind the existing varietal variability of fruits in terms of rate of ripening, qualitative changes, firmness, shelf-life, ideal storage requirement, extent of tolerance towards reduced O₂ and/or elevated CO₂, transpirational loss and susceptibility to various physiological disorders. In this way, internal atmosphere of a fruit (in terms of different gases and volatiles) plays a critical regulatory role in the process of fruit ripening. So, better and holistic understanding of this internal atmosphere along with its exact regulatory role on various aspects of fruit ripening will facilitate the development of more meaningful, refined and effective approaches in postharvest management of fruits. Its

applicability, specially for the climacteric fruits, at various stages of the supply chain from growers to consumers would assist in reducing postharvest losses not only in quantity but also in quality.

Keywords Endogenous volatiles · Gaseous exchange · Internal atmosphere · Fruit ripening · Storage · Postharvest · Postharvest management

Introduction

Fruits are an important source of energy, vitamins, minerals, dietary fibers, pigments (carotene, xanthophylls, anthocyanins etc.), flavonoids, phenolics and other phytochemicals in human diets. Fruits are also functional foods that are a source of nutraceuticals. It is through anti-oxidizing capacity along with anti-carcinogenic and anti-mutagenic activities that the pigments and other phytochemicals present in the fruit exhibit their protective effects against chronic disease states, different types of cancers, macular and cardiac vascular diseases and other age-related problems (Rao and Agarwal 1998; Chen et al. 2001; Powell and Bennett 2002; Giovannucci 2002; Mares-Perlman et al. 2002). These health benefits emphasise the need and importance of fruits in our daily diet. Increased awareness of these health benefits has led to a significant change in the food consumption habits of people. This has resulted in an increase in the demand for high quality, fresh and nutritious fruits with almost no residue level of any toxicant. Increased demand for fruits requires not only the higher production but also improved practices in quality management, storage, transport and processing. Presently, huge losses in quality and quantity occur between harvesting and consumption of fruits. Extent of postharvest losses for few

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fruits in developing countries and India are presented in Table 1. As per an estimate by Kader (2005), about one-third of all the fruits produced are never consumed by humans. Furthermore, losses occurring between production and retail sites are higher in the developing countries in comparison with developed countries. In India, about 30% of fruits and vegetables are lost after their harvest due to mismanagement (Pulamte 2008). This therefore emphasises the need for a massive thrust to reduce the postharvest losses (Pulamte 2008).

Postharvest physiology, shelf-life and losses in fruits are interlinked and primarily governed by the last phase of fruit maturation referred to as ripening. Fruit ripening involves many physiological, biochemical and developmental changes occurring through a coordinated and genetically regulated programme (Stepanova and Alonso 2005; Barry and Giovannoni 2007; Bouzayen et al. 2010). Fruits, in general, show two distinctive respiratory patterns during the course of ripening and on this basis fruits are categorized into climacteric and non-climacteric groups (Biale 1964; McMurchie et al. 1972; Biale and Young 1981; Bufler 1986; Abeles et al. 1992; Lelievre et al. 1997; Yamane et al. 2007). Apple, mango, papaya, guava, kiwi, tomato, cherimoya, banana, pear, apricot, peach, plum, avocado and plantain etc. are climacteric fruits. On the other hand, citrus fruits (orange, grapefruit, lemon etc.), berries (cherry, strawberry, blackberry, cranberry etc.), pineapple, lychee, melon, loquat, pomegranate, cucumber and tamarillo etc. belong to non-climacteric group of fruits. Climacteric fruits show a dramatic increase in rate of respiration during ripening and this is referred as climacteric rise. The rise in respiration is either simultaneous or it is just followed after the rise in the rate of ethylene production (Burg and Burg 1962, 1965a; Lelievre et al. 1997). The process of ripening can be triggered and also accelerated by exogenous ethylene treatment in climacteric fruits (Tucker 1993). The plant hormone ethylene plays a major role in the ripening process of climacteric fruits and the presence of ethylene

and its perception is required for the expression of ripening-related genes even at advance stages of fruit ripening (Hoeberichts et al. 2002; Alexander and Grierson 2002). On the other hand, respiration rates increase at least temporarily in non-climacteric fruits when treated with exogenous ethylene. These fruits also undergo senescence more rapidly in presence of ethylene. However, they do not undergo major changes in composition as found in climacteric fruits with an exception of degradation of chlorophyll in citrus fruits and pineapples (Goldschmidt et al. 1993; Noichinda 2000). Besides this, low levels of ethylene are involved in wound healing and responses to various infections in some fruits of either climacteric group or non-climacteric group (Saltveit 1999; Pech et al. 2003; Van Loon et al. 2006). In general, perishability of climacteric fruits is more rapid and severe than the non-climacteric fruits (Mishra and Gamage 2007). This is basically due to faster rate of ripening and ripening-related changes in climacteric fruits. In this way, ripening of fruits has direct implications for human diets and nutrition as well as for the agricultural industry (Giovannoni and El-Rakshy 2005).

Postharvest metabolic changes leading to increased respiratory activity and transpirational loss of water are the two basic aspects that determine the storage life and quality of fruits. Retardation of ripening and associated physiological and biochemical changes (transpiration, respiration, ethylene production, softening and compositional changes) have been achieved by the application of controlled atmosphere (CA), modified atmosphere (MA) or modified atmosphere packaging (MAP) (Kader 1986; Leshuk and Saltveit 1990; Kanellis et al. 1993; Kader and Saltveit 2003a, b; Yahia 2009; Kanellis et al. 2009; Mangaraj and Goswami 2009). These approaches have in fact become the established methods for extending the postharvest-life of fruits (Yahia 2009; Mangaraj and Goswami 2009; Kader 2009; Sharma et al. 2011; Ramayya et al. 2011). It has been observed that CA, MA and MAP basically modify the internal gaseous atmosphere of the fruits in favour of low O₂ to CO₂ ratio (Banks et al. 1993; Elyatem et al. 1994; Klieber et al. 1996; Baldwin et al. 1999; Amarante et al. 2001; Gil et al. 2002; Kader 2009; Berry and Sargent 2009; Mangaraj and Goswami 2009; Kanellis et al. 2009; Yahia 2009; Ramayya et al. 2011; Nath et al. 2011). These methods also regulate ethylene production and its response (Scully and Horsham 2008; Yahia 2009; Mangaraj and Goswami 2009; Kanellis et al. 2009). Today, different edible coatings with wide variations in their permeability to O₂, CO₂ and water vapours are also available for practical use (Mishra et al. 2010). Since, these findings have practical relevance for above storage methods and therefore further investigations on the composition of the internal atmosphere in fruits have been undertaken by various workers.

Table 1 Estimated postharvest losses for some fruits in developing countries and India

Fruit	Postharvest losses (% of production)	
	In developing countries	In India
Apple	14	10–25
Banana	11–14	12–14
Mango	17–37	17–37
Tomato	13–16	10–20
Citrus	8–31	8–31
Grapes	27	23–30

(Chadha and Pareek 1993; Verma and Joshi 2000; Pulamte 2008)

At ambient temperature the internal atmosphere in fruits comprises a mixture of many gases and volatiles including O₂, CO₂, water vapours, ethylene, alcohols, aldehydes, acetates, esters, ketones, aromatic hydrocarbons, terpenes, carboxylic acids, sulphur compounds, ammonia, jasmonate, salicylates etc. (Speirs et al. 1998; Baldwin et al. 2000; Pesis 2005; de Leon-Sanchez et al. 2009). Several workers have suggested that these gases and volatiles as mentioned above are involved in regulating ripening, senescence and related processes (Herregods 1977; Loughheed et al. 1987; Toivonen 1997). In light of this, Saltveit (2003) posed a question—Is it possible to find an optimal controlled atmosphere for storing fruits and vegetables? He emphasized that it is not only the external but internal environment of the commodity as well that determine its storability under a given external environment. This review investigates the range of gases and volatiles including ethylene present in the internal atmosphere of fruit and the factors controlling their production and diffusion through fruit tissue. The role of some of these gases and volatiles in regulating the ripening and ripening-related changes in fruit at individual and interactive levels are discussed with special reference to climacteric fruits.

Endogenous volatiles in fruits

Higher plants and plant parts produce a large and complex mixture of volatiles. They are considered volatile because they evaporate when exposed to air at room temperature and generally have low molecular weight (<250 Da) with distinctive odour. These compounds are formed *via* several biochemical pathways and they are generally found in very small amounts (Negre-Zakharov et al. 2009; Defilippi et al. 2009). Volatiles are produced in variable amounts at different times and in different tissues (Negre-Zakharov et al. 2009; Defilippi et al. 2009). Plants use various mechanisms to regulate the production and levels of these volatiles (Negre-Zakharov et al. 2009; Defilippi et al. 2009). The timing of release of many plant volatiles is closely tied to pollination and fruit dispersal and this has ecological and evolutionary significance (Vaughn 2007; Negre-Zakharov et al. 2009). Maturity or ripening stage of the fruit also influences eating quality and sensory quality of aroma (Lalel et al. 2003).

Discovery of the plant hormone ethylene brought the realization that at least some of the gaseous compounds produced and emitted by the plants may have important physiological roles. At present, more than 1,000 organic compounds have been reported to be emitted by plants (Dudareva et al. 2004). The aroma produced by various fruits during ripening was reviewed by Defilippi et al.

(2009) and Pandit et al. (2009). Approximately 400 volatile compounds have been found in the ripening tomato fruit (Baldwin et al. 1991; de Leon-Sanchez et al. 2009). The volatiles present in fruits are as follows: ethylene, ethanol, acetaldehyde, methanol, acetone, butanol, ethane, hexanol, hexenol, 3-methyl butanal, ethyl acetate, propyl acetate, butyl acetate, propanol, acetate esters, ethyl butyrate, geraniol, octenal, octenol, citral, terpenes, carboxylic acids, sulphur compounds, ammonia, jasmonate, benzaldehyde and methyl salicylate besides other types of *iso*-, *sec*- or *tert*-alcohols, aromatic hydrocarbons, ketones, esters, aldehydes and higher carbon alcohols (Gustafson 1934; Petro-Turza 1987; Saltveit 1989; Baldwin et al. 1991; McDonald et al. 1996; Toivonen 1997; Frenkel et al. 1995; Speirs et al. 1998; Baldwin et al. 2000; Bai et al. 2003; Pesis 2005; Cadwallader 2005; Negre-Zakharov et al. 2009; Defilippi et al. 2009; de Leon-Sanchez et al. 2009).

Gaseous exchange and factors affecting the composition of the atmosphere in harvested fruit

Gaseous exchange across the fruit surface Gaseous exchange occurring between a plant organ and its environment usually follows a specific path. Gas-filled intercellular spaces are considered as the predominant pathway for gas transport through bulky organs such as fruits (Ho et al. 2009). The rate of movement of a gas depends on the properties of that gas molecule, the concentration gradient and the physical attributes of the intervening barriers (Kader 1987). In general, the rate of release of a compound is a function of its volatility and the properties of cellular and intracellular membranes through which the compound has to diffuse (Dudareva et al. 2004). Comparative analysis of volatile compounds (emitted and present within the plant tissues) revealed that the emission of volatiles is not merely a function of their differential volatility but it also involves a cytologically organized excretory process (Gershenzon et al. 2000). The membranes of the storage compartment (where the compound exists) or epidermal cell wall might be differentially permeable to different volatile compounds. Little is known about metabolite trafficking between various subcellular compartments, the mechanism of the release process and how these processes contribute to the regulation of volatile emission (Dudareva et al. 2004). Usually, emission of a particular volatile compound into the atmosphere depends on the rate of its biosynthesis and the rate of its release (Dudareva and Pichersky 2000). Formation of volatile compounds is regulated at spatial (Pare and Tumlinson 1997) and developmental levels (Bouwmeester et al. 1998; Dudareva and Pichersky 2000). Further, environmental factors such as; light, temperature and moisture status can greatly influence the emission of

volatiles (monoterpenes) from the leaves of plant (Staudt and Bertin 1998; Gershenzon et al. 2000).

In natural ecosystems, evolution of volatiles by the plant tissue is influenced to a larger extent by evapotranspiration (Charron and Cantliffe 1995). Emission rate of volatile organic compounds (VOCs) in Norway spruce (*Picea abies*) increased exponentially with increase in the temperature and temperature itself had a direct effect on the rate of transpiration (Filella et al. 2007). In the above study, correlation analysis indicated very clearly that the rate of emission of VOCs such as; acetic acid, acetaldehyde, methanol, acetone, ethanol, hexanal, hexanol, monoterpenes and methyl salicylate is directly associated with the rate of transpiration. This study also emphasised the role of partitioning of specific VOC between the gas and liquid phases (as described by the Henry's law constant) in determining the rate of emission of volatiles from the plant surfaces. The release of volatiles from the plant organs with lower rates of transpiration (such as bulky fruits with well-developed diffusion barriers on the surface/peel/pericarp) will be less and therefore, the volatiles can accumulate in the tissues of such organs. Keeping in view the varietal variation in diffusion barriers and their characteristics for different plants and plant parts, the accumulation of volatiles would also be different and thereby their effect on various physiological processes.

In general, there are three major routes through which gaseous exchange take place for a harvested commodity 1. Outermost layers (cuticle, cuticular cracks and periderm), 2. Apertures (stomata and/or lenticels) and 3. Stem scar region (Solomos 1987; Ben-Yehoshua and Rodov 2003). In view of the presence of cracks on cuticular layer, exchange of gases and volatiles was reported through cuticular layer and it is primarily determined by extent of cracks present on cuticular layer (Ehret et al. 1993). For most of the horticultural produce, the skin represents the major barrier to gas exchange (Solomos 1987; Kader 1987). The diffusivity of gases for the fruit flesh is 10–20 times higher than the diffusivity from the skin (Solomos 1987; Banks and Nicholson 2000). In tomato, the stem scar (the place where the pedicel along with sepals connects the fruits to the stem) is the predominant site for gas exchange (Cameron and Yang 1982). It was also demonstrated that 85–90% of ethylene exchange occurs through this region of tomato fruit (de Vries et al. 1995).

Basis of gaseous exchange across the fruit boundary Gas diffusion in fruits follows Fick's law (Burg and Burg 1965b). This law states that the flux of a gas, diffusing normally through a barrier, is dependent on the diffusion coefficient and concentration gradient. Burg and Burg (1965b) and then Solomos (1987) developed relationships between rates of ethylene production by fruit and the

internal concentrations and these relationships were surprisingly found similar across many fruit species. There is morphological and anatomical basis for gaseous exchange across the boundaries of harvested fruits (Cameron and Yang 1982; Solomos 1987; Kader and Saltveit 2003a, b). As per Kader and Morris (1977) anatomical features and not any alterations in biochemical pathways are the reasons for differences in the diffusion resistance. External (morphological) and internal (anatomical) features were reported to determine the keeping quality of grapes (Uys 1974), storability of tomato berries (Niemirów-Krizesai and Csillag 1994), firmness or mechanical resistance of tomato (Wann 1996) and olive fruits (Mulas 1994), O₂ to CO₂ ratio in tomato fruits (Yang and Shewfelt 1999; Kader and Saltveit 2003a, b; Pech et al. 2003) and ripening index, physiological loss in weight and rate of respiration in tomato fruits (Paul and Srivastava 2006). In a study by Bai et al. (2003), it was shown that 'Granny Smith' apples have relatively very few open pores (lenticels) in their peel surface and therefore they suffer from low rates of gas exchange and as a result these fruits are prone to develop off-flavours after they have been coated with waxes. In contrast, 'Delicious' apples have many open lenticels and they retain sufficient gas exchange even when coated with waxes. So, waxed 'Delicious' apples accumulate only low concentrations of ethanol and off-flavours (Bai et al. 2003). Likewise, it was reported that 'Murcott' mandarins are much more sensitive to anaerobic stress conditions than 'Star Ruby' grapefruit when exposed to N₂ enriched atmosphere because they showed much more rapid and greater increase in respiration rates, internal CO₂ concentrations, production of ethanol and acetaldehyde and development of off-flavour (Shi et al. 2005). When mandarin and grapefruits were compared by Shi et al. (2007), it emerged out that during postharvest storage or after exposure to anaerobic atmospheres, mandarin develops off-flavour much more rapidly than grapefruit. The occurrence of off-flavour was associated with increase in the levels of ethanol and acetaldehyde. Anatomical observations revealed that although the total thickness of the peel [comprising the albedo, the white inner layer and the flavedo (the coloured outer layer)] was greater in grapefruit but it was more condensed in mandarins. So, it was concluded that mandarins accumulate larger amount of acetaldehyde and ethanol after harvest than grapefruit because of higher activity of enzyme alcohol dehydrogenase (ADH) in the juice vesicles and lower permeability of their peel to gases (Shi et al. 2007). The extent of diffusibility of gases across the fruit boundaries therefore determines the internal atmosphere of the fruit in terms of the levels of O₂ and CO₂ (Nuevo et al. 1984; Ben-Yehoshua et al. 1983). Thus, the composition of the internal atmosphere of the fruit is always different to the external atmosphere in which it is kept (Dadzie et al. 1993).

Peel of the fruit acts as a barrier due to different layers of plant tissues including aqueous, cuticular and waxy layers. Exchange of gases in fruits through the peel *via* diffusion from the openings (stomata and lenticels) is proportional to difference in the concentrations of gases across the barrier, total area of the peel, solubility of a gas in peel, solid state diffusion coefficient and total hole area available on the peel surface (as contributed by openings of stomata and/or lenticels) (Hagenmaier 2004, 2005). Gas transport in fruit tissue is governed by diffusion as well as by permeation. The permeation is basically caused by overall pressure gradient of a given gas (Ho et al. 2006b). So, permeation-diffusion–reaction model was applied to study gas transport in intact pear. Permeation was found to be minimum across skin and it gradually increased for cortex and vasculature tissues of pear fruit (Ho et al. 2006b).

Gas transport properties of fruits are important in understanding the internal atmosphere of fruits specially during their controlled atmosphere storage. Temperature had stronger effect on diffusivity of CO₂ when compared with O₂ (Ho et al. 2006a). For pear fruit, gas diffusibility in vertical axis was higher than the equatorial radius axis. Diffusivity was also found to be lesser in brown tissues of brown heart disorder of pear than the healthy tissue (Ho et al. 2006a). Gas exchange to a large extent depends on the arrangement pattern of cells and intercellular spaces (Mendoza et al. 2007). In view of this, a very comprehensive model of gas exchange of pear fruit was proposed for explaining the development of physiological disorder such as core breakdown and its role in long-term storage of this fruit (Franck et al. 2007). In the above study, the effect of the actual 3-D tissue structure of plant organs has been put forward but this could not be quantified for explaining gas exchange in plant tissues. Later on, Verboven et al. (2008) used high-resolution phase tomography (making use of synchrotron radiation) to explore the 3-D structure and cellular arrangements of pome fruit tissues in their natural state (i.e., with high water content) up to sub-micrometer resolution. For this study, pome fruits like; apple and pear were selected because their gas exchange properties have been shown to be very different and closely related to their storage lives (Schotsmans et al. 2004; Ho et al. 2006a, b; Franck et al. 2007; Ho et al. 2008). Results obtained by Verboven et al. (2008) revealed very clearly that the apple fruit had more voids than pear. The differences in void fraction (23% for apple cortex and only 5% for pear cortex) along with the extent of network architectures of voids explained the better ability of tissues to facilitate the gas exchange in apple fruit. This lower void volume in pear fruit compared to apples as shown by Verboven et al. (2008) was able to explain the earlier findings where pear fruit was found to be more sensitive to physiological disorder such as internal browning and its relation to gas

exchange and the availability of internal O₂ by Lammertyn et al. (2003), Franck et al. (2007) and Ho et al. (2008). Likewise, there is risk of developing physiological disorders in pear fruit during the course of ripening. This was shown to be due to increase in respiration resulting in anoxia at and near the center of the fruit even under the recommended storage conditions (Ho et al. 2010). Very recently, quantification of microporosity in apple and tomato fruits was done by magnetic resonance imaging (MRI) for the better understanding of relationship between gas transfer and various disorders in fruits during their postharvest-life (Musse et al. 2010).

Variability and causes of differences in internal atmosphere of fruits

There exists a large variability in the internal atmosphere of fruits belonging to different species, variety/cultivar and developmental stages. Resistance to diffusion of CO₂ was found to vary with fruit, variety of a fruit and also size and maturity stage of fruit (Kader and Morris 1977; Zagory and Kader 1988). There is varietal variability in outer surface morphology as well as in internal anatomical features (distribution of trichomes, stomata and lenticels, thickness of cuticle and extent of cuticular cracks etc.) (Kader and Morris 1977; Zagory and Kader 1988; Paul and Srivastava 2006; Paul et al. 2007, 2010b). It is the combinations of all these features that determine the permeance or resistance of gaseous movement across the fruit (Saltveit 1999; Paul et al. 2007). Variations in the amount, composition and ultrastructure of cuticular/epicuticular wax among several apple cultivars were documented by Belding et al. (1998). Apart from this, morphological and mechanical properties of the cuticle as well as the epidermis were subjected to considerable change during growth and ripening of tomato fruit (Bargel and Neinhuis 2005). Number of stomata show significant difference among the cultivars of pear fruit (Kovacs et al. 1994) and sweet cherry (Peschel et al. 2003). Likewise, varietal variations in the number of lenticels, deposition pattern of cuticular/epicuticular wax, amount of cuticle and wax and internal anatomy of peel and exocarp regions were reported in mango fruits (Dietz et al. 1988; Paul et al. 2007). In tomato fruit, cuticle appeared to provide an excellent barrier (Thompson 2003) and as a result it may not contribute significantly for overall gaseous exchange across the fruit. However, instead of stomata, trichomes were observed on the surface of tomato fruits and trichome base cells are transformed into lenticels during maturation of the fruit (Clendenning 1941; Blanke 1986; Paul and Srivastava 2006). There are varietal differences in the number of trichomes, tendency of trichomes to get

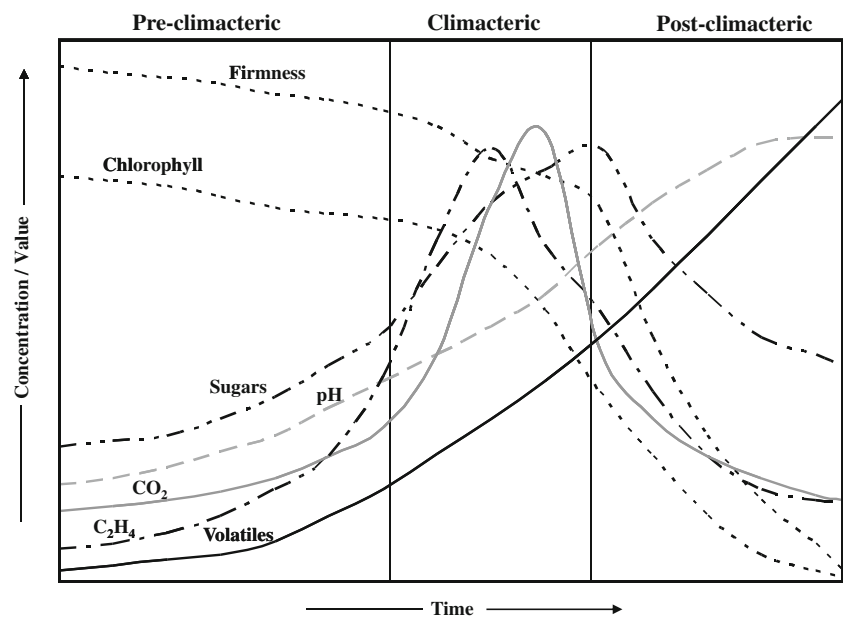
transformed into lenticels, density of lenticels and the dimension of stem scar portion of tomato fruits (Paul and Srivastava 2006).

During the development, maturation and ripening—fruits undergo changes in texture, firmness, skin colour, composition of aroma and flavour volatiles, chemical composition (sugar content, acidity etc.), respiration and ethylene production (Fig. 1). Ratio of O_2 to CO_2 also gets altered with the growth/development/maturity of the fruit (Burg and Burg 1965a, b; Burg 1968; Kader and Morris 1977; Zagory and Kader 1988; Saltveit 1999). Gas exchange properties (specifically due to skin resistance) are not found to be consistent with the growth and maturity of the fruit. The reason for this may be the changes that occur in the anatomical properties and anatomical features of the fruit itself during its development and maturation (Zagory and Kader 1988; Longhurst et al. 1994; Kader and Saltveit 2003a; Bargel and Neinhuis 2005; Paul and Srivastava 2006; Paul et al. 2007; Ho et al. 2008; Paul et al. 2010b). In another study, selected dose of 1-methylcyclopropene (1-MCP) delayed the ripening of tomato fruits in a variety dependent manner (Paul et al. 2010a). Earlier, similar results were demonstrated in apple by Rupasinghe et al. (2000) and Watkins et al. (2000). Such differential effect might be due to the differences in the diffusion/absorption/retainability of 1-MCP by different varieties in view of the differences in surface morphology, anatomical features, contents of lipids and other cellular constituents of fruits (Kader and Saltveit 2003a, b; Dauny et al. 2003; Paul and Srivastava 2006; Nanthachai et al. 2007; Paul et al. 2010a). Physiological and biochemical differences and also the variations in the levels of ethylene, CO_2 and O_2 etc. for the plant-attached and plant-detached

fruits for both the categories of fruits i.e., climacteric and non-climacteric were described along with their roles on the process of fruit ripening and in explaining the existing varietal variability in the rate of fruit ripening by Paul et al. (2011a).

Volatile composition of fruits and vegetables often shows wide range of variation. Such variations can partly be explained due to differences in the experimental procedures but, much of the variation is likely due to the varietal differences only. For example, wide differences in the concentrations of volatile were recorded in different varieties of apricot (Guichad and Souty 1988). The levels and proportions of different volatiles were also found to be responsible for the characteristic differences in flavour among the varieties of apricot (Guichad and Souty 1988). Similarly, Larsen and Poll (1990) found differences in flavour among the 10 raspberry cultivars due to variation in production of aroma volatiles. In apple cultivars, wide differences in susceptibility to scald were associated with the α -farnesene content (Huelin and Coggiola 1968). Gran and Beaudry (1993) observed wide variability in the threshold levels of oxygen required (at 0 °C) for the induction of anaerobic respiration in three apple varieties (0.7% for ‘Red Delicious’, 1.4% for ‘Red Fuji’ and about 1.9% for ‘McIntosh’). In this way, variety and storage condition can influence the degree of accumulation of products of anaerobic respiration such as; acetaldehyde and ethanol in tissues. Likewise, out of two varieties of raspberries (‘Meeker’ and ‘Qualicum’), when harvested at red-ripe stage and stored at 1 °C with 90% RH for 7 days, variety ‘Qualicum’ was found to be more susceptible to the accumulated acetaldehyde, ethanol and ethyl acetate in the MAP with high CO_2 i.e., 10% CO_2 with 5% O_2 in

Fig. 1 Changes in various parameters during climacteric fruit ripening (Source: Nath et al. 2006)



comparison with other MAP conditions (6% CO₂ with 10% O₂ and 3% CO₂ with 15% O₂) (Toivonen et al. 1999). On the basis of available literature, it was concluded by Toivonen (1997) that conditions for induction of anaerobic metabolism were not consistent because factors such as; commodity characteristics, variety and temperature etc. are the important determinants of above said metabolic shift. In tomato fruit, differences in flavour among different varieties were in part due to the variation in production levels of aroma volatiles (Brauss et al. 1998). For mango fruits, volatiles (in different varieties and at different maturity stages) have been used as marker for identification of different maturity stages in different varieties. So, volatiles can thereby be used in determining the most optimum maturity stage for harvesting of mango fruits as this can result in attaining the best quality of harvested fruits on ripening (Lebrun et al. 2008; Pandit et al. 2009). In another study, discrimination of 28 apricot cultivars into four distinguishable aroma groups was achieved by analysing their volatile constituents (Aubert and Chanforan 2007).

Influence of the internal atmosphere on ripening and ripening-related changes

Ripening During ripening of tomato fruits, rise in endogenous concentrations of CO₂ and ethylene were reported along with the decrease in the concentration of O₂ (Lyons and Pratt 1964). Significance of stem scar region as a major site for gaseous exchange of tomato fruit was exploited by Calbo et al. (1988) and Yang and Shewfelt (1999). They observed drastic reduction in the rate of ripening and thereby extension in the storage life of tomato fruits by sealing the stem scar region of fruits. The relationship between ripening behaviour and stem scar region of tomato fruit in different varieties was studied by blocking the stem scar region either completely or to different degrees (Paul et al. 2010b). In comparison to control, complete blockage of stem scar region of tomato fruits at green mature stage showed three-fold reduction in ripening index% (from 78.9 to 26.2 and from 45.3 to 15.1 in varieties ‘Pusa Ruby’ and ‘Pusa Gaurav’, respectively) at 14 days after treatment but with increased decay. It was also made clear in this study that it is the degree of blockage of the stem scar region that determines the extent to which the rate of respiration and ripening were suppressed. The extent of climacteric rise was reduced significantly in treated fruits. Suppressive effects of these treatments were however found to diminish with the advancement in the ripening stage of tomato fruits that were being treated (Paul et al. 2010b). Besides the major role of stem scar region, the lenticels on the surface of the tomato peel also appear to control the respiration and ripening by determining the overall exchange of gases and

volatiles depending upon the developmental stage (green mature stage and onward) and variety of tomato (Paul and Srivastava 2006). In all the above studies, the basic change causing the delay in ripening or suppression of respiration was primarily due to the lower levels of ethylene and O₂ to CO₂ ratio within the fruit.

Role of ethylene in regulating the process of ripening, senescence and postharvest aspects of fruits and vegetables has been extensively reviewed by Kader et al. (1989), Abe and Watada (1991) Bouzayen et al. (2010) and Paul et al. (2011b). Earlier, Toivonen (1997) had reviewed the accumulation of non-ethylene and non-respiratory volatiles (alcohols, aldehydes, jasmonates, terpenes, carboxylic acids, sulphur compounds and ammonium) and discussed them in terms of their biological activity in harvested fruits and vegetables. It was pointed out by Toivonen (1997) that besides removing the ethylene, ethylene removing/absorbing agents can also remove the other organic volatiles from storage or package atmosphere (Kader et al. 1989; Matsumoto and Ogawa 1995). Therefore, at least some effects that were attributed due to the removal of ethylene may in fact be related to the removal of other volatiles which have not been measured or identified. So, there is a strong reason to evaluate the potential role and significance of volatiles other than the ethylene and their interaction with ethylene in postharvest situations and under different storage conditions (Lougheed et al. 1987; Toivonen 1997). Different factors and conditions affecting the exchange of volatiles (as already described and discussed above) can influence the accumulation and release of some important volatiles such as; ethylene, alcohols (mainly the ethanol), aldehydes (mainly the acetaldehyde) and methanol. These volatiles may be accumulated or released differentially and thereby influence the ripening process in fruits (Cadwallader 2005; Pesis 2005, 2006). This has been demonstrated for the ripening of climacteric fruits like; tomato (Kelly and Saltveit 1988; Saltveit and Sharaf 1992; McDonald et al. 1996) and apple (Pesis et al. 1994; Pesis 1995). Besides this, levels of volatiles are also found to be associated with storage disorders of apple fruit like; scald (Huelin and Coggiola 1968) and internal browning (Mendoza et al. 2007). The ripening and quality of non-climacteric fruits such as; grapes, orange and strawberries were also influenced by these volatiles (Saltveit and Ballinger 1983; Ke and Kader 1990; Ke et al. 1991).

Flavour and aroma In tomato fruit, 17 volatiles have a significant impact on characteristic tomato-like aroma (Buttery 1993). Hexanal, *cis*-3-hexenal, *trans*-3-hexenal, *trans*-2-hexenal, *cis*-3-hexenol, 6-methyl-5-hepten-2-one, beta-ionone, 2-isobutylthiazole, 3-(methylthio)-1-propanol and 3-(methylthio)-1-propanal were important in imparting flavour to fresh red tomato (Tandon et al. 2000, 2001;

Lewinsohn et al. 2001; Baldwin 2004). Hayata et al. (2002) reported that tomato-like flavour was correlated strongly with geranyl acetone, 2-methylbutanol, 3-methylbutanol and 6-methyl-5-hepten-2-one. Distinctive volatile components responsible for aroma and flavour in some important fruits are presented in Table 2.

Quality of the aroma is related to concentration and composition of volatiles present in the fruit. Negative effects of some of the above volatiles produced under anaerobic condition have been perceived on the quality of aroma (Forney et al. 1991; Hansen et al. 1992) but, positive effects of accumulation of some volatiles were also found to be influenced by volatiles such as; acetaldehyde and ethanol (Paz et al. 1981; Pesis et al. 1986, 1998; Saltveit and Mencarelli 1988; Frenkel et al. 1995). These positive or negative effects were largely found to be dependent on the concentrations of ethanol and acetaldehyde in strawberries and persimmon fruits (Prasad and Stadelbacher 1974; Pesis et al. 1986). Sweetness of tomato fruit was correlated not only with sucrose equivalents and pH but also with the volatiles including *cis*-3-hexenal, *trans*-2-hexenal, *cis*-3-hexanol, geranyl-acetone, 2-methylbutanol, 3-methylbutanol *trans*-2-heptenal, 6-methyl-5-hepten-2-one and 1-nitro-2-phenylethane. Likewise, sourness was corre-

lated with soluble solids and pH along with the volatiles including acetaldehyde, acetone, 2-isobutylthiazole, geranyl-acetone, beta-ionone, hexanal and ethanol (Saltveit 2005).

Fruit decay Fruit decay means any condition or sign, either physiological or pathological in origin, that makes the fruit unacceptable (Wills and Ku 2002). The role of low O₂ to CO₂ ratio or anaerobic condition is well known in determining the overall decay of fruits and vegetables (Banks 1984). Such situations were reported to suppress not only the biosynthesis but also the action of ethylene (Kanellis et al. 1989a, b). Ethylene is known to be involved in defense against pathogen as it stimulates phenylpropanoid pathway, synthesis of pathogenesis-related proteins and induces systemic resistance (Saltveit 1999). These findings explain the higher decay under the influence of blockage of stem scar region of tomato fruit as observed by Paul et al. (2010b). In tomato fruits, decay was up to 50% or more when the stem scar portion of fruits was sealed by coconut grease and it was primarily due to the anaerobic conditions (Calbo et al. 1988; Yang and Shewfelt 1999). Fruits of highbush blueberry, on the other hand, produce antimicrobial volatiles such as *trans*-2-

Table 2 Distinctive components of aroma for some fruits

Fruit	Compound
Apple	β-Damascenone, butyl hexanoate, isoamyl hexanoate, hexyl hexanoate, ethyl butanoate, propyl butanoate, hexyl butanoate, butyl acetate, hexanal, 2-hexenal, ethyl 2-methylbutyrate
Banana	2-Hexenal, Eugenol, Isopentanol, decan-1-ol, 2-phenylethanol, 3-oxy-pentanoic acid, 3-methylbutanoic acid, 3-methylbutyl acetate, butanoate, 3-methylbutanoate, 5-methoxyeugenol, eugenol-methylether, elemicin
Mango	Ethyl butanoate, ethyl-2-butanoate, hexanal, <i>cis</i> -3-hexenal, <i>trans</i> -2-hexenal, γ-octalactone, γ-dodecalactone, furaneol, α-pinene, β-pinene, 3-carene, myrcenelimonene, <i>p</i> -cymene, terpinolene, α-copaene, caryophyllene
Tomato	Hexanal, <i>trans</i> -2-hexenal, <i>cis</i> -3-hexenal, <i>cis</i> -3-hexenol, β-ionone, β-damascenone, 1-penten-3-one, 3-methylbutanal, 3-methylbutanol, 2-isobutylthiazole, 3-(methylthio)-1-propanol, 3-(methylthio)-1-propanal, 1-nitro-phenylethane, <i>trans</i> -2-heptenal, phenylacetaldehyde, 6-methyl-5-hepten-2-one, methyl salicylate, geranylacetone
Peach	Benzaldehyde, benzyl alcohol, nonanol, linalool, ethyl hexanoate, 3-methylbutanoate, α-terpineol, γ-hexalactone, δ-decalactone, γ-undecalactone, δ-dodecalactone, α-pyrone, 6-pentyl-α-pyrone
Orange	Geranial, neral acetaldehyde, decanal, octanal, nonanal, ethyl acetate, ethyl propionate, ethyl butanoate, methyl butanoate, ethyl-2-methyl butanoate, ethyl-3-hydroxy hexanoate, linalool, α-terpineol, limonene, myrcene, α-pinene, valencene
Lemon	Citral
Grapefruit	Acetaldehyde, decanal, ethyl acetate, methyl butanoate, ethyl butanoate, 1- <i>p</i> -menthene-8-thiol, nootkatone, limonene, naringin
Strawberry	Hexanal, <i>cis</i> -3-hexenal, <i>trans</i> -2-hexenal, furaneol, mesifuran, ethyl hexanoate, ethyl butanoate, methyl butanoate, ethyl-2-methyl propanoate,
Grape	Methyl anthranilate, <i>o</i> -aminoacetophenone, furaneol, methyl furaneol, β-damascenone, β-phenylethanol, butyl alcohol, hexyl alcohol, hexanal <i>trans</i> -2-hexenal, isoamyl alcohol, acetaldehyde, isobutyraldehyde, ethyl acetate, ethyl propionate, butyl acetate, propyl acetate, 2-methylbutanol Linalool, geraniol, methoxyisobutylpyrazine
Raspberry	1-(π -Hydroxyphenyl)-3-butanone, α-ionone, β-ionone, geraniolinalool, benzyl alcohol, ethyl hexanoate, ethyl butanoate, methyl butanoate, γ-decalactone, 2-heptanone, <i>cis</i> -3-hexenal, β-damascenone

(Salunkhe and Do 1977; Tandon et al. 2000, 2001; Lewinsohn et al. 2001; Baldwin 2004; Hui 2010)

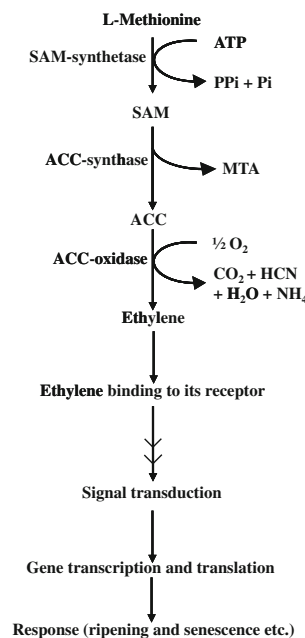
hexenal that conferred resistance to anthracnose fruit decay (Polashock et al. 2007). Likewise, preharvest spray treatment of volatile compound like ethanol with calcium also reduced the gray mold development in table grapes (Chervin et al. 2009).

Role of some important endogenous volatiles in regulating fruit ripening

I. Ethylene

Ethylene is the main regulator of ripening in climacteric fruits Ethylene (C₂H₄) is a naturally produced gaseous plant growth hormone with numerous effects on growth, development and storage-life of many fruits. As already stated earlier, this plant hormone plays a major role in the ripening process of climacteric fruits (Theologis et al. 1992; Yang 1995; Nagata et al. 1995; Lelievre et al. 1997; Saltveit 1999; Barry et al. 2000; Atta-Aly et al. 2000; Klee 2002; Alexander and Grierson 2002; Hoerberichts et al. 2002; Bouzayen et al. 2010; Paul et al. 2011b). Ethylene is thought to start a cascade of events leading to many interactive signaling and metabolic pathways for the progress of ripening in climacteric fruits (Fig. 2). The production of aroma during ripening of fruits also depends strongly on production and action of ethylene (Golding et al. 1998, 1999; Rupasinghe et al. 2000; Alexander and Grierson 2002; Lurie et al. 2002; Flores et al. 2002; Dandekar et al. 2004; Pech et al. 2008; Defilippi et al. 2009). But, Zhu et al. (2005) made it clear that production of aromatic volatiles may or may not be totally dependent on ethylene.

Fig. 2 Ethylene biosynthesis, perception and response. SAM: S-Adenosyl-L-methionine, ACC: 1-Amino-cyclopropane-1-carboxylic acid, MTA: 5-Methylthioadenosine, HCN: Hydrogen cyanide



Regulation of ethylene production It is known that the rate of ethylene production in fruits undergoing ripening is controlled by the ability of the fruit to synthesize 1-aminocyclopropane-1-carboxylic acid (ACC) and to convert ACC to ethylene (Fig. 2). The two key enzymatic controls are at the levels of expression and activity of ACC-synthase and ACC-oxidase (Tucker 1993) as shown in Fig. 2. Two systems of ethylene production have been defined in plants (McMurchie et al. 1972). The first one is designated as system 1. System 1 operates and functions during normal growth and development and in response to various stresses. System 1 is responsible for the basal level of ethylene production in vegetative tissues and unripe fruits. This system is regulated in an auto-inhibitory manner (Fig. 3). This means that even the treatment of exogenous ethylene will not trigger any further synthesis of ethylene. The second system is system 2 and this operates during floral senescence and fruit ripening. This system is responsible for the large auto-inductive (auto-catalytic)

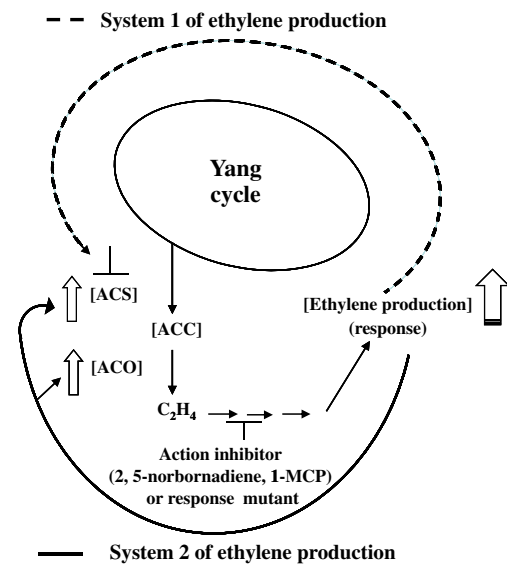


Fig. 3 Simplified pathway of ethylene biosynthesis in plants showing auto-inhibition (inhibiting its own production) and auto-induction of ethylene (inducing its own production). These two systems are referred as system 1 and system 2 of ethylene production respectively. In system 1, ethylene inhibits its own production by inhibiting (⊥) ACS (ACC-synthase) expression/activity. It may be noted that the ACO (ACC-oxidase) activity is enhanced during system 1 but due to the absence of any enhancement in the activity of ACS there is no auto-induction. In system 2, ethylene induces more of its own production by stimulating (⌆) the expression/activity of both of the enzymes (ACS and ACO) simultaneously and this thereby enhances the overall ethylene production (⌆). 2, 4- norbornadiene and 1-MCP (1-methylcyclopropene) [action inhibitors of ethylene] and response mutants of ethylene block (⊥) the action/response of the ethylene and thereby inhibit the system 2 of ethylene production (Source: Adapted and modified from Srivastava 2001)

increase in ethylene production during fruit ripening, specially in the climacteric fruits (Oetiker and Yang 1995; Lelievre et al. 1997; Nakatsuka et al. 1998; Inaba 2007) (Fig. 3). High genetic variability in the rate of production of ethylene has been reported for fruits such as; muskmelon, melon, peach and kiwifruit by Kendall and Ng (1988), Miccolis and Saltveit (1991), Klozenbucher et al. (1994) and Xu et al. (1998) respectively. It has been demonstrated that both these enzymes i.e., ACC-synthase and ACC-oxidase are encoded by multigene families in various plants and they are regulated by a number of regulating factors (Fluhr and Mattoo 1996; Lelievre et al. 1997; Nakatsuka et al. 1998; Barry et al. 2000; Alexander and Grierson 2002). Both of these enzymes are also regulated by the final product of the reaction i.e., ethylene (Lelievre et al. 1997) (Fig. 3). Lower ethylene production due to lower activity of ACC-oxidase was assigned as the cause for the formation of spongy tissue disorder in ‘Alphonso’ mango (Nagamani et al. 2010). The O₂ and CO₂ concentrations in the fruit play important role in the biosynthesis of ethylene and its action as well. This aspect has been described and discussed in detail in the subsequent part of this review.

Besides the levels of ambient and internal concentrations of ethylene, production of ethylene is also governed by abiotic and biotic stresses. The interactive nature of ethylene at plant and at the level of its immediate environment is shown in Fig. 4. Plants and plant parts are not the only source of ethylene but; smoke, exhaust gases, ethylene releasing chemicals, catalytic production of ethylene from ethanol and analogs of ethylene (as produced by variety of processes within the plant system itself) are also important sources of ethylene or the other chemicals with

ethylene-like activities. Such sources of ethylene and ethylene-like chemicals are common under storage/cold storage conditions. Although different analogs of ethylene (as listed in Table 3) have reduced activity or efficiency but, these analogs can elicit the same physiological effects as that of ethylene. So, presence of analogs of ethylene can also influence the fruit ripening specially under the storage conditions.

Ethylene-diffusibility, its internal concentration and fruit ripening In general, there is an inverse relationship between ethylene production and postharvest-life (Gussman et al. 1993; Zheng and Wolff 2000). Diffusion of ethylene to the external atmosphere follows Fick’s law from flat surfaces and it has often been applied to study the gas exchange in bulky organs such as fruits (Ben-Yehoshua and Cameron 1989). According to Lescourret et al. (2001), skin permeability can vary with fruit size. Permeability and skin area are highly variable among different species and also within the same species (Cameron and Reid 1982). Ethylene is diluted in fruit tissues and diffuses into the atmosphere and therefore according to Ben-Yehoshua and Cameron (1989), fruit volume and gaseous permeability of skin are important biophysical traits of fruits that need to be considered when analysing emission of ethylene.

Saltveit (1999) described that once the ripening of climacteric fruits has started, the internal ethylene concentration increases quickly to a much higher levels (even up to 100 $\mu\text{l l}^{-1}$). This is due to the stronger diffusion resistance specially at later stages of fruit development. Ethylene concentration in tomato fruit was reported to surpass a threshold value of 4.9 ppm in order to induce ripening (Knegt et al. 1974). Work carried out by Sawamura et al. (1978) indicated that during the ripening of tomato fruits average ethylene concentration was unusually high in plant-attached fruits (5.4 ppm; on an average with a range from 2 to 13 ppm depending upon cultivars and seasonal conditions) in comparison to plant-detached tomato fruits (where the values for ethylene dropped to a lower level i.e., 1.4 ppm on an average). Since, such lower levels of ethylene are more commonly found in ethylene-induced processes and therefore the results suggested the possibility of presence of ethylene antagonizing factor in the plant-attached fruits (Sawamura et al. 1978). This concept might be true but, drastic reduction in the levels of ethylene in plant-detached fruits in comparison with plant-attached fruits might also be because of more effective gaseous exchange across the stem scar region of the harvested tomato fruits in comparison with the fruits that are still attached with the mother plant where the stem scar region is not exposed (as it is linked with pedicel). This explanation appears to be more relevant in view of the report by de Vries et al. (1995) where it was

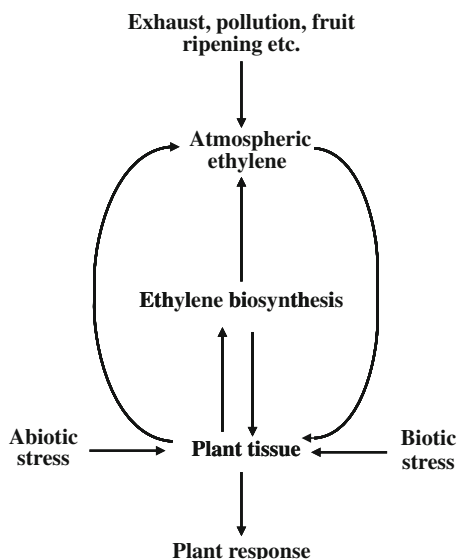


Fig. 4 Interaction of ethylene with plant/plant parts and its immediate environment (Source: Adapted and modified from Saltveit 1999)

Table 3 Relative activity of ethylene and its analogs in pea straight growth bioassay test

Gases	Formula	ppm ($\mu\text{l l}^{-1}$) in gas phase for half-maximum activity
Ethylene	C_2H_4	0.1
Propylene	C_3H_6	10
Vinyl chloride	$\text{C}_2\text{H}_3\text{Cl}$	140
Carbon monoxide	CO	270
Acetylene	C_2H_2	280
Vinyl fluoride	$\text{C}_2\text{H}_3\text{F}$	430
Methyl acetylene (Propyne)	C_3H_4	800
Vinyl bromide	$\text{C}_2\text{H}_3\text{Br}$	1,600
Allene (Propadiene)	C_3H_4	2,900
Vinyl methyl ether	$\text{C}_3\text{H}_6\text{O}$	10,000
Ethyl acetylene (1-butyne)	C_4H_6	11,000
1-Butene	C_4H_8	27,000
Vinyl ethyl ether	$\text{C}_4\text{H}_8\text{O}$	30,000
Carbon dioxide	CO_2	30,000
1, 3-Butadiene	C_4H_6	500,000

(Burg and Burg 1967; Abeles and Gahagan 1968; Abeles et al. 1992; Saltveit 1999)

found that 85 to 90% of ethylene released by tomato fruit takes place through this stem scar region only.

Basic studies on the effect of ethylene on respiration have been done in climacteric as well as in non-climacteric fruits. Application of propylene (an analogue of ethylene) was reported to initiate an increase in respiration in climacteric fruits as well as in non-climacteric fruits but, this propylene-mediated induction or rise in the endogenous ethylene production occurred only in climacteric fruits (McMurchie et al. 1972; Yamane et al. 2007). In climacteric fruits like; banana, mango and tomato a substantial proportion of rise in rate of respiration is reported to be contributed by cyanide-insensitive or cyanide-resistant respiration (Kumar and Sinha 1992; Pandey et al. 1995; Reddy and Srivastava 1999). In contrast to climacteric fruits, cyanide-resistant respiration is present only to a limited extent in non-climacteric fruits. In these fruits, the upsurge in respiration and ethylene is either not observed or it is only transitory even after the application of exogenous ethylene (Lurie and Klein 1989; Kays and Paul 2004). A definite ethylene-mediated stimulation of respiration was however noticed in the peel of citrus fruits (non-climacteric) during their ripening (Goldschmidt 1997). Recently, it was pointed out by Paul et al. (2011a) that more information on the interactive and regulatory aspects of ethylene on the respiration (specially at biochemical and molecular levels) are required.

The concept of binding of ethylene to its receptor in plant system is widely accepted (Sisler and Yang 1984) and has also been proven beyond doubt (Sisler and Serek 1997; Sisler et al. 2006). But, usually, this aspect has not been taken into consideration in the studies dealing with resistance of the fruits to diffusion and exchange of gases

(Ben-Yehoshua et al. 1985). So, more has to be learned about the retention and release of bound ethylene in plant tissues in relation to physiological activity of ethylene (Goldschmidt et al. 1993). In this direction, a theory of ethylene emission by tomato fruit was developed and used as a base to develop simulation model called 'ETHY' by Genard and Gouble (2005). This model was found to be highly sensitive to the parameters like; permeability of skin surface, internal concentration of O_2 , CO_2 and ACC, change in fruit growth and temperature, activities of ACC-oxidase and ACC-synthase, concentration of ethylene itself and ATP production status. Besides this, changes in the levels of ethylene receptors and/or sensitivity towards the ethylene with the development and ripening have been reported not only in climacteric fruits like; tomato (Kevany et al. 2007, 2008), banana (Golding et al. 1999) and apple (Johnston et al. 2009) but also in non-climacteric fruits like; citrus (Goldschmidt 1997) and melon (Bower et al. 2002; Pech et al. 2008) and in *Arabidopsis* plant as well (Yoo et al. 2009).

II. Oxygen and carbon dioxide

Low oxygen From outer to inner parts of plant organs (roots, tubers, seed and fruit etc.), levels of oxygen (O_2) showed decreasing trend (Lammertyn et al. 2003). For fruits in general, same is being presented in Fig. 5. Difference in the depletion of internal O_2 levels in different kind of fruits under MA condition was observed (Sornsri-vichai et al. 1998). Yip et al. (1988) claimed that 50% reduction in ethylene production could be obtained at 1% level of O_2 . This is primarily because of the fact that O_2 is

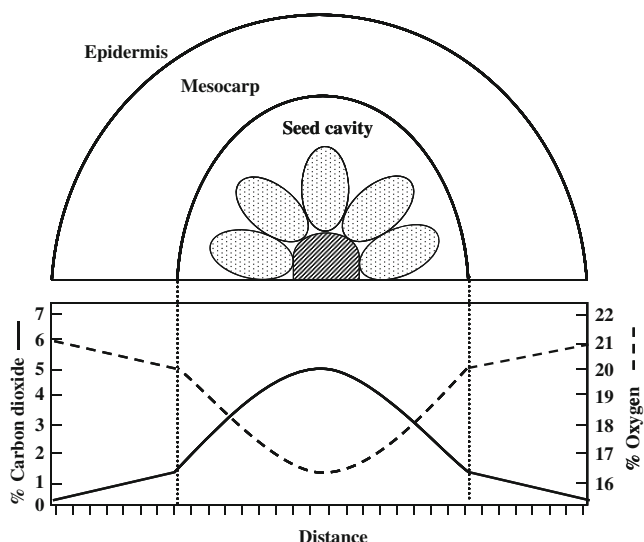


Fig. 5 Cross section passing through a fruit showing how the concentration of O_2 and CO_2 can vary within different tissues of the fruit due to respiration and external and internal barriers to gas diffusion (Source: Kader and Saltveit 2003b)

itself a substrate for the reaction catalysed by the enzyme ACC-oxidase (Fig. 2). It has already been reported that O_2 is required for the synthesis as well as the action of ethylene in fruits including tomato (Burg and Burg 1967). Fruits show reduction in respiration with lowering of O_2 in the surrounding atmosphere and at specific reduced level of O_2 there is induction of anaerobic respiration which leads to fast breakdown of sugars and this is named as the Pasteur effect (Kader 1986; Boersig et al. 1988). The Pasteur effect has practical importance in the modified atmosphere storage of fruits (Weichmann 1986). Oxygen concentrations must be managed so that aerobic respiration is minimised but anaerobic respiration, which leads to fast breakdown of sugars, is avoided (Kader 1986; Weichmann 1986; Boersig et al. 1988; Kubo et al. 1996). It was reported by Saltveit (2003) that the optimum level of O_2 concentration needed to maintain the aerobic respiration is not only different for different commodities but it also shifts for a given commodity over a period of time during storage. In tomato fruits, low O_2 caused not only an increase in the production of ethanol and acetaldehyde but it also delayed the ripening in comparison to control (Klieber et al. 1996). In bulky and dense storage organs (such as; apple fruit, potato tubers and legume seed pods), internal O_2 concentration may fall to low levels of 8–10% near the surface and even to a very low levels of 2–5% in the center. Such conditions may enhance anaerobic respiration and trigger the accumulation of acetaldehyde and ethanol (Magness 1920; Rolletscheck et al. 2002). In tomato and pear fruits, hypoxia [the term loosely applies to any partial pressure of O_2 that is less than 21 kPa Chervin et al. (1996)] can also result in increase in activity of pyruvate decarboxylase (PDC) and ADH (Nanos

et al. 1992; Chen and Chase 1993). The activities of isoenzymes of ADH were found to be inversely related to the levels of O_2 (Kanellis et al. 1991). Below a certain level of O_2 , the rise in CO_2 production indicates a switch to fermentative metabolism. This O_2 level has been called as the anaerobic compensation point (ACP) (Leshuk and Saltveit 1990). The ACP may vary for different fruits and for the same fruit at different maturity and at different storage temperatures besides being affected by different varieties of a given fruit (Boersig et al. 1988; Gran and Beaudry 1993; Kubo et al. 1996). McGlasson and Wills (1972) suggested that storage of green banana fruits at low O_2 (3%) limits the operation of Krebs cycle at two steps 1. Between, either oxaloacetate or pyruvate and citrate and 2. Between 2-oxoglutarate and succinate. Besides this, this condition also caused the reduction in the activity of enzyme malate synthase which is involved in glyoxylate cycle.

Susceptibility of apple fruit to low O_2 injury in CA storage was found to be positively correlated with resistance of the fruit towards the diffusion of gases. For a given strain/cultivar, resistance to gas diffusion was found to be affected by fruit's maturity, duration of storage and whole fruit volume (Park et al. 1993). It was noticed that, 'Marshall' strain of McIntosh apple had higher resistance and thereby it showed more susceptibility to low O_2 injury as this strain accumulated ten times higher ethanol when compared with 'Rogers' (another strain of McIntosh apple) (Park et al. 1993). This demonstrates the extent of varietal variability among the fruits for response towards their internal atmosphere and specially for the lower concentrations of O_2 .

Modified atmospheres with low concentrations of O_2 can slow down the deterioration of fruits by decreasing respiration, ethylene production and tissue sensitivity to the ethylene (Kader et al. 1989). The extent of decrease in ethylene production therefore depends not only on the O_2 concentration which is present in the fruit's internal atmosphere but also on the sensitivity of ethylene production system under a prevailing concentration of O_2 . Sanders and de Wild (2003) reported lower partial pressure of O_2 (lower than the external partial pressure of O_2) due to rapid consumption of O_2 by the tomato fruit and higher resistance of fruit to the diffusion of O_2 . Reduced O_2 or elevated CO_2 decreased the respiration rate (Smith et al. 1987a). In bulky storage organs such as fruits (where the length of the diffusion path may be considerable), hypoxia conditions have been demonstrated (Ho et al. 2008). So, low O_2 stress may occur within the fruit as it grows and the resistance to the entry of O_2 from the atmosphere into the fruit (*via* diffusion process through the skin and thickened cell layers of the cortex) becomes significant.

In avocado fruit, synthesis of cellulase and polygalacturonase was found to be directly related to the levels of O_2 . Insufficient availability of O_2 can decrease the activities of cellulase and polygalacturonase (Knee 1982; Kanellis et al. 1989a, 1991). These two enzymes are involved in causing softening of fruits during ripening. In general, it has been observed that treatment to the fruits just prior to their storage with the condition like anaerobic or even exposure to the metabolites which are produced under such condition (like; acetaldehyde and/or ethanol) lead to improvement in fruit quality (Pesis 2006).

High carbon dioxide There is a decreasing gradient in CO_2 concentrations from the inner parts of the fruit to the surface, in reverse to the gradients observed for O_2 (Fig. 5). High CO_2 was reported to reduce the activity or synthesis of various enzymes of respiratory metabolism (Kerbel et al. 1988; Lange and Kader 1997a) including oxidative phosphorylation (Shipway and Bramlage 1973). Activation of enzymes of glyoxylate cycle was noticed in cucumber fruits when fruits were exposed to the environment of 60% CO_2 (Yang et al. 1998). As per Lange and Kader (1997b), elevated CO_2 could influence the respiration negatively by changing the intercellular pH. Studies on respiration and the factors influencing the respiration become important because the potential shelf-life of harvested plant parts (including fruits) was found to be closely related to the rate of respiration of the plant part (Uys 1974; Kader 1987; Varoquaux and Ozdemir 2005; Kader and Saltveit 2003b). Bufler (1984) reported that CO_2 at high concentrations competitively inhibits the effects of ethylene by preventing the auto-induction of ACC-synthase, as shown in Fig. 6. The inhibitory effect of CO_2 on auto-induced ethylene production in climacteric fruits could be due to competition between CO_2 and ethylene for the same active site (Burg and Burg 1967; Mathooko et al. 1995). As per Burg and Burg (1967), the amount of CO_2 in the intercellular spaces of fruits at pre-climacteric stage is low but this may approach to higher levels of around 10% during ripening and post-climacteric phase. This higher endogenous level of CO_2 probably raises the threshold concentration of ethylene to higher levels for its action in fruits. It has been demonstrated that elevated CO_2 (5–20%) inhibits ethylene production in climacteric fruits by inhibiting activities of ACC-synthase (Bufler 1984; Chavez-Franco and Kader 1993; Mathooko et al. 1995) and ACC-oxidase (Chavez-Franco and Kader 1993; Mathooko et al. 1995). CO_2 -mediated regulation of ACC-synthase and ACC-oxidase has also been reported by Kader (1986) and Yang (1987). In tomato, high CO_2 induces the expression of stress-related genes and suppresses the transcription of ethylene-dependent and ethylene-independent ripening-associated genes (Rothan et al. 1997).

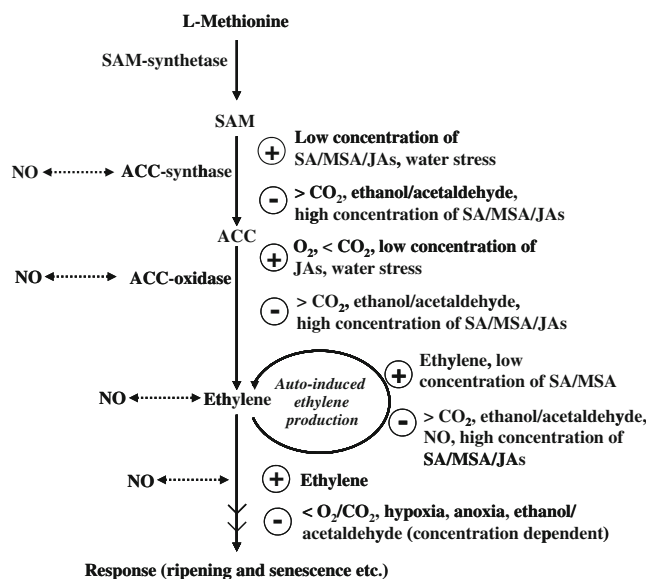


Fig. 6 Different endogenous volatiles and other factors that play regulatory role in determining the production as well as the response of ethylene. The symbols \oplus , \ominus , $>$, $<$ and \blacktriangleleft indicate inducers, suppressors, higher, lower and possible interaction respectively. SAM: S-Adenosyl-L-methionine, ACC: 1-Aminocyclopropane-1-carboxylic acid, SA: Salicylic acid, MSA: Methyl salicylic acid, JAs: Jasmonates, NO: Nitric oxide

Work carried out by Chaves and Tomas (1984) suggested that CO_2 interferes with ethylene metabolism through a mass action effect. Besides this, displacing ethylene from its receptor site has also been proposed (Yang and Hoffman 1984). In comparison with control, production of ethylene in tomato and activities of ACC-synthase and ACC-oxidase were found to increase upon withdrawal of CO_2 gas from the storage environment (Kubo et al. 1990; Mathooko et al. 1995). Levin et al. (1993) reported that CO_2 concentration up to 10% stimulated *in vivo* activity of ACC-oxidase but, CO_2 at 20% concentration had an inhibitory effect. Using a continuous flow through gas system, it has been demonstrated that 20% CO_2 markedly decreases ethylene biosynthesis in ripening peaches by delaying and suppressing ACC-synthase at transcriptional level however, recovery occurs upon withdrawal of CO_2 (Mathooko et al. 2001). At low concentrations (of about 1%), CO_2 may promote ethylene production in climacteric fruits (Bufler 1986; Chavez-Franco and Kader 1993). At low levels, stimulatory effect of CO_2 on the production of ethylene could be due to a balance between its stimulatory effect on the activity of ACC-oxidase and inhibitory effect on the activity of ACC-synthase wherein the contribution by the former being more significant (Mathooko 1996). All elevated levels of CO_2 inhibit the activity of ACC-synthase while the activity of

ACC-oxidase is differentially regulated by CO₂ (it is stimulated at low CO₂ levels but inhibited at high CO₂ levels) (Mathooko 1996).

Tolerance of a commodity to elevated levels of CO₂ depends on its physiological condition, maturity status, CO₂ concentration within the tissue, duration of exposure, internal O₂ concentration and storage temperature (Zagory and Kader 1988). It was reported by Mathooko et al. (1995) that CO₂ itself could also act as an inducer of ACC-synthase depending on the commodity. Since the effect of CO₂ was rapid and reversible so Kao and Yang (1982) proposed that CO₂ exerts its effect by directly activating the ACC-oxidase (in vivo) rather than stimulating its synthesis. Later, Tian et al. (1994) proposed that the mechanism of CO₂ stimulation of ACC-oxidase may be direct and probably through interaction with a non-substrate binding site on ACC-oxidase. They further stated that CO₂ might combine reversibly with an ACC-oxidase-ACC complex to increase V_{max} of the reaction. In tomato, interestingly, there are at least three forms of ACC-oxidase i.e., *eth1*, *eth2* and *eth3*. These different forms of ACC-oxidase could probably be induced and/or synthesized in different tissues and at different developmental stages besides being a strong possibility that CO₂ can also affect each of these forms of ACC-oxidase differentially (Bouzayen et al. 1993).

Ratio of O₂ to CO₂ As early as in 1936, Wardlaw and Leonard reported that respiratory climacteric is an anaerobic type of respiratory shift. Later on, climacteric rise was considered as a type of anaerobiosis because fruits naturally ripen from inside to outward (Leonard and Wardlaw 1941). Diagrammatic representation of fruit in Fig. 5 shows that how the concentrations of O₂ and CO₂ vary within the fruit. Respiration by the fruit tissues and barriers of diffusion/exchange of gases as posed by anatomical/morphological/physical/biochemical components (present either on surface or inside the fruit) are the responsible factors for the gradual lowering of O₂ to CO₂ ratio from outside to inside of the fruit.

As described above, conditions like; hypoxia or low O₂/CO₂ reduce the synthesis as well as the action of ethylene (Kanellis et al. 1991; Blanke 1991; Kanellis et al. 1993; Gorny and Kader 1996; Mathooko 1996). At the same time, hypoxia was also reported to reduce the expression of genes involved in the maturation process, which are regulated by ethylene (Kanellis et al. 1993). Production of volatiles has been shown to get altered in high CO₂ or low O₂ conditions (Mattheis et al. 1991; Ke et al. 1994; Larsen 1994). Besides this, high CO₂ and/or low O₂ within the atmosphere of the fruit can induce anaerobic metabolism resulting in enhanced accumulation of ethanol and acetaldehyde (Kader 1987). Ethanol and acetaldehyde were in fact reported to delay the ripening of tomato fruit (Kelly and Saltveit 1988;

Beaulieu et al. 1997). This thereby explains the reason behind the retardation of ripening process due to short period of anaerobiosis treatment prior to the storage of tomato fruits as observed by Kelly and Saltveit (1988), Pesis and Marinansky (1993) and Paul and Srivastava (2006). CO₂ at the level of 10 kPa in combination with 6 kPa of O₂ was suggested to be suitable for cold storage for late and early harvested grapes up to 12 weeks and 4 weeks, respectively as this limits the losses due to gray mold (Crisosto et al. 2002).

Model based *in silico* analysis for the exchange of O₂ and CO₂ in pear fruit showed that O₂ exchange takes place mainly through the intercellular spaces and the cell wall network and marginally through the intracellular liquid (cytoplasm). On the other hand, CO₂ exchange occurs at similar rates through each of these phases (Ho et al. 2009). The biological variation in the apparent diffusivity of gases in tissue was related to the natural and random distribution of cells and pores in the cortex tissue (Ho et al. 2009). This thereby can have strong influence in deciding the available O₂/CO₂ ratio and subsequently the metabolic shifts and conditions created due to this. In this way, anatomical features can be considered to be responsible for already existing differences in the tolerance to reduced O₂ and/or elevated CO₂ levels among various fruits and vegetables. Promotive or inhibitory effects of O₂ and/or CO₂ levels, O₂ to CO₂ ratio, conditions like; hypoxia, anoxia and various volatile metabolites are being summarized for their effect on different steps of ethylene biosynthesis and ethylene response (or action) in Fig. 6. Regulatory role of above factors on the production of acetaldehyde and ethanol by modulating the expression and activities of PDC and ADH is presented in Fig. 7.

III. Ethanol

Ethanol production in plants/fruits Ethanol production (through anaerobic metabolism) generally results from low concentrations of O₂ which can either be caused by reduced levels of external O₂ or due to enhanced resistance to the diffusion of O₂ into the plant parts/fruits (Jackson et al. 1982). Fruits undergoing the developmental/ripening process exhibit changes in the levels of O₂ and CO₂ inside them. These changes are usually in a direction that leads to a net reduction in O₂ to CO₂ ratio within the fruit and results in the accumulation of ethanol (Bufler and Bangerth 1982).

Ethanol-mediated inhibition of ripening Loss of ethanol from fruit occurs predominantly by evaporation process and this is mainly determined by degree of diffusion resistance posed by the fruit in view of its surface/anatomical features

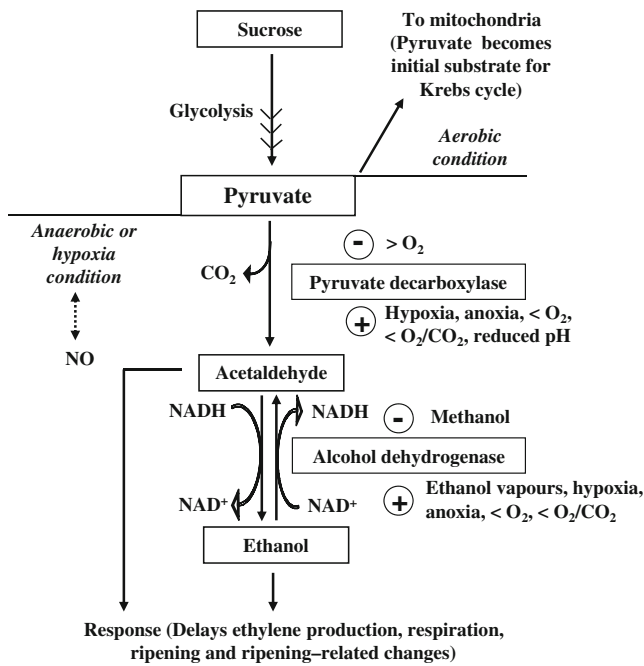


Fig. 7 Pyruvate is produced during glycolysis. Under aerobic condition, this pyruvate enters into mitochondria for Krebs cycle. But under hypoxia or anaerobic condition, pyruvate is diverted for ethanolic glycolysis [where it is initially converted into acetaldehyde by the enzyme pyruvate decarboxylase (PDC) and then acetaldehyde is converted into ethanol by a reaction catalyzed by alcohol dehydrogenase (ADH)]. ADH basically catalyses bidirectional reaction for the inter-conversion of acetaldehyde and ethanol. The symbols (+), (−), >, <, and ⇄ indicate inducers, suppressors, higher, lower and possible interaction respectively. NO: Nitric oxide

as already described above. Effective ethanol concentrations for delaying the ripening were however found to be similar to that of endogenously built-up levels of ethanol as observed in following conditions 1. During ripening of fruit (Bufler and Bangerth 1982), 2. During anoxia (Jackson et al. 1982), 3. Under few days of anaerobiosis (Kelly and Saltveit 1988), 4. Under stress (Kimmerer and Kozlowski 1982) and 5. Fruits exposed directly to ethanol vapours (Kelly and Saltveit 1988). Ethanol appears to inhibit not only the synthesis of ethylene but its action as well (Ritenour et al. 1997; Saltveit and Mencarelli 1988; Pesis 2005; Asoda et al. 2009). Ethanol was also reported to delay ripening, production of ethylene and CO₂, loss of chlorophyll and synthesis of lycopene (Kelly and Saltveit 1988; Yang and Shewfelt 1999; Podd et al. 2002; Pesis 2005). Promotive or inhibitory effect of O₂ and/or CO₂ levels, O₂ to CO₂ ratio, conditions like; hypoxia and anoxia and ethanol itself on the production of acetaldehyde (and thereby ethanol) by modulating the expression and activities of PDC and ADH are summarized in Fig. 7.

IV. Acetaldehyde

It has been proposed and demonstrated that ethanol-mediated delay in ripening is basically caused by acetaldehyde. Acetaldehyde is produced by conversion of ethanol into acetaldehyde *via* the reversible reaction catalyzed by the enzyme ADH (Pesis and Marinansky 1993; Burdon et al. 1996; Beaulieu et al. 1997; Podd et al. 2002) (Fig. 7). Since, acetaldehyde and ethanol are inter-convertible volatile compounds so they are being discussed together not only in relation to one another but also in terms of their final effect on fruit ripening.

Factors affecting the production of acetaldehyde and ethanol Anaerobiosis leads to the production of acetaldehyde besides ethanol (Cossins 1978). Both, climacteric as well as non-climacteric fruits produce a lot of acetaldehyde and ethanol (Pesis 2005). For a given fruit, genetic variability was also seen in the levels of production of acetaldehyde and ethanol and also in the ability to survive under anaerobiosis (Pesis 2005).

Acetaldehyde in regulating the fruit ripening Acetaldehyde inhibits the formation of ethylene by preventing the action of ACC-synthase and action and synthesis of ACC-oxidase (Pesis and Marinansky 1993; Burdon et al. 1996; Podd and van Staden 1998; Pesis et al. 1998). Exogenous ethanol application resulted in marked increase in acetaldehyde levels and this inhibited the ethylene production and ripening of tomato fruits (Pesis and Marinansky 1993). It was therefore suggested that it is the acetaldehyde and not the ethanol which is the causal agent for ethanol-induced inhibition of fruit ripening. Later on, it was in fact found to be true because it was only the level of acetaldehyde which was found to be associated with inhibition of ripening by Beaulieu et al. (1997). In light of above findings, it was concluded by Pesis (2005) that ethanol and acetaldehyde are natural compounds that are essential in governing the process of fruit ripening. These compounds are also associated with aroma production and removal of astringency. Various sites where acetaldehyde and ethanol can regulate the production and response of ethylene are presented in Fig. 6. Whereas in Fig. 7 regulatory effects of different gases, volatiles and conditions (that may prevail within the fruit’s internal atmosphere) are being presented on the activity of enzymes involved in the production of ethanol and acetaldehyde.

V. Water vapours/water status in fruit

Importance and diffusibility Water is the most important component of plant tissues with unique physical and

chemical properties. It plays a significant role in determining the quality of the fresh produce. Important functions of water in plant include; exchange of resources, medium for biochemical reactions, cell expansion and physical and chemical integrity of cell walls and other cellular constituents (Nilsen and Orcutt 1996). Fruit maintains vascular continuity with the mother plant and receives water till it remains attached to the plant. But, once detached, the fruit have no renewable source of water to compensate for the water that is being lost through transpiration. Detached fruit therefore experiences water stress. Water loss (transpiration) from freshly harvested fruit results in loss of salable weight, appearance (wilting and shriveling), textural quality (softening, flaccidity, limpness and crispness), juiciness and nutritional quality as well (Kader and Barrett 1996). Generally, it has been found true that fresh fruits become unacceptable when weight loss reaches more than 5% of harvest weight (Salunkhe and Desai 1984).

Transpiration rate of harvested fruit depends mainly on 1. The rate of cooling of fruit after its harvest, 2. Structure and condition of the fruit surface, 3. Surface to volume ratio of fruit, 4. Relative humidity and temperature during storage, 5. Air movement/circulation and 6. Atmospheric pressure in storage environment (Salunkhe and Desai 1984; Gamage and Rahman 1999). The main sites of transpiration in plant and its parts are the stomata, epidermal cells, lenticels, trichomes (hairs), stem scar, hydathodes and cuticular cracks (Ben-Yehoshua 1987). The surface characteristics such as; number of stomata on epidermis, type of surface, tissue underlying the skin and the structure, thickness and chemical composition of wax and cuticle play role in determining the water loss from fruit and these features vary greatly among the fruits and also with the developmental stages for a given fruit. Stem scar region is an important pathway for water loss in tomato fruit. In apple, lenticels account for up to 21% of the transpiration (Maquire et al. 2001). Complete coating of fruit was found to retard gaseous exchange by plugging the stomatal pores of citrus (Ben-Yehoshua et al. 1985). Such coatings reduced weight loss up to 20% in mandarin (Lawes and Prasad 1999), mango (Baldwin et al. 1999) and pear (Amarante et al. 2001). Variability in peel permeance, weight loss and internal atmosphere was recorded in different lines of mandarin fruit (Lawes and Prasad 1999). Size of the fruit is also an important determinant for extent of its weight loss because higher the ratio of surface area to unit volume the greater will be the loss of water by evaporation. As a result of this, a small size fruit or a tuber will lose weight faster than a bigger one (Salunkhe and Desai 1984). Likewise, under similar conditions, a leaf will lose its water (and thereby its weight) much faster than a fruit with similar surface area.

Influence of water status on ethylene production, ripening, senescence and shelf-life It was reported by Grierson and Wardowski (1978) that water loss after harvesting causes reduction in fruit mass and it may also induce senescence. Water deficit in plant tissues also stimulate ethylene production (Fig. 6) and as a consequence there is an increase in the respiration of tissues (Yang and Pratt 1978). Several authors found that water stress decreases the pre-climacteric life of many fruits such as; banana, avocado, pear and plantain (Littmann 1972; Adato and Gazit 1974; George et al. 1982). It was found by Finger et al. (1995) that increase in respiration and evolution of ethylene was significantly higher when the fruits reached 5% of loss in terms of fresh mass. The increase in respiration was 70% and ethylene production was 50% more for such fruits when compared to the control fruits in banana. The results thereby confirmed that water stress (after the harvest of fruit) might affect the shelf-life depending upon the intensity of the water stress. So, alleviation of water stress has been proposed as an additional controlling factor for reducing the deterioration of fruits (Ben-Yehoshua et al. 1983). Increased ethylene production was found when fruit was detached (Hyodo 1991) and also after having experienced water stress/deficit during its development (Gelly et al. 2003). The level of transcription for the genes of ACC-synthase and ACC-oxidase responded positively to the water deficit in a tissue-specific and coordinated manner (Nakano et al. 2002). This resulted in enhanced activities of these two enzymes under water stress (Fig. 6). However, only little is known about the interaction of altered water status with other important volatiles that also have role in fruit ripening (Smith et al. 1987a, b). In this way, water status governs not only the broad changes but also the specific changes. Further studies are therefore necessary to understand the interactions and implications of altered water status with important volatile components of fruits.

Water content alone is not sufficient to describe the water status of different parts of fruits, its movement in fruits and also the associated physiological and biochemical changes occurring in the fruits (Nguyen et al. 2004). Water activity (a_w) is considered as a more reliable parameter of water status. Water activity is defined as the ratio of the partial pressure of water in equilibrium with the food material to the partial pressure of pure water at the same temperature. It includes contribution of the pressure forces in the tissue (Nguyen et al. 2004). Water activity is important in the determination of the stability criteria for food stuffs in terms of microbial growth, browning, lipid oxidation, ripening, ripening-related changes and shelf-life. (Rockland and Stewart 1981; Labuza 1984; Joyce et al. 2002). Relationship between water content and a_w of a given fruit gives water sorption isotherm. Since, different tissues of a fruit have different water status so, a_w and water

sorption isotherm for different tissues are also different. Besides this, a_w and water sorption isotherm also change with changes in the storage conditions and storage durations (Hubinger et al. 1992; Joyce et al. 2002; Nguyen et al. 2004). In an attempt to relate the moisture distribution (water content) to the water status (water potential) for understanding the water movement in fresh fruit need was felt for a detailed modeling of cellular structural properties and intercellular spaces (Nguyen et al. 2004)

VI. Role of some other endogenous volatiles

Salicylic acid/methyl salicylate Salicylic acid (SA) and its volatile derivatives [such as methyl salicylate (MeSA)] were characterized as inhibitors of ethylene biosynthesis (Leslie and Romani 1986). These volatiles were reported to inhibit the wound-induced expression ACC-synthase (Li et al. 1992). At low concentrations, MeSA appears to enhance the ripening processes in tomato (Ding et al. 2002). Dual effects of MeSA on ethylene metabolism (inhibitory and promotive) were suggested to be dependent upon the dose and developmental stage of fruits (Ding and Wang 2003). It was clearly demonstrated by Ding and Wang (2003) that low concentrations of MeSA have the potential to up-regulate ethylene biosynthesis by increasing the expression of ACC-synthase genes *LE-ACS2* and *LE-ACS4* (responsible for auto-induced production of ethylene during ripening of tomato fruit) and eliminating the transcription of *LE-ACS6* (genes of ACC-synthase responsible for basal level of ethylene production in tomato fruit). On the other hand, high levels of MeSA in tomato fruit keep the ACC-synthase and ACC-oxidase genes repressed and thus inhibit the timely production of ethylene during ripening (Ding and Wang 2003). In this way, the endogenous concentration of MeSA could be critical in determining ethylene metabolism depending on the stage of the fruit.

Jasmonic acid/jasmonates Jasmonic acid (JA), its volatile ester i.e., methyl jasmonate (MJ) and other derivatives are collectively known as jasmonates (JAs). JAs are ubiquitous signaling molecules that mediate plant responses to environmental stress such as; wounding and insect/pathogen attack (Wasternack 2007). JAs also play role during developmental processes including pollen development, seed germination, root growth, and fruit growth and ripening (Pena-Cortes et al. 2005; Wasternack 2007). Multiple interferences and interactions between JAs and ethylene signaling pathways were studied by analyzing *Arabidopsis* mutants (Devoto and Turner 2005). The exact role of JA in fruit ripening and JA-ethylene interaction are still largely unclear. Both, delaying as well as promotive

effects on ripening were recorded besides the response being the cultivar dependent.

Transient increases in concentrations of JAs occur during the onset of fruit ripening in apple and tomato suggest their involvement in modulation of the early steps of climacteric fruit ripening (Saniewski and Czapski 1983; Saniewski et al. 1987; Perez et al. 1993; Creelman and Mullet 1997). Furthermore, JAs were reported to regulate the early steps of climacteric fruit ripening by stimulating ethylene biosynthesis (Fan et al. 1998; Kondo et al. 2000). The application of exogenous JAs stimulates ethylene production and colour change in tomato (Saniewski and Czapski 1985). It was found that activities of ACC-synthase and ACC-oxidase were stimulated by JAs in a concentration range of 1–100 μ M. But, continuous exposure at higher dose i.e., 1,000 μ M inhibited both the activities (Fan et al. 1998). The convergence of ethylene and jasmonate pathways at transcriptional level of ethylene response factor 1 (ERF1) was proposed by Lorenzo et al. (2003). MJ induced the transcription of ACC-oxidase in tomato fruit (Imanishi and Nagata 2004; Imanishi et al. 2005). The mRNA levels of 81 genes were found to show elevation (by more than three-fold) in response to MJ in wild type tomato in comparison to *nor* mutant (Imanishi et al. 2005). The results indicate a strong interaction of jasmonate and ethylene and in this way endogenous status of jasmonate could regulate the ripening and ripening-related changes (Fig. 6). In a study by Ziosi et al. (2007), exogenous application of JAs led to alteration in ethylene biosynthesis, ethylene perception and polyamine accumulation. In another study involving transcriptome analysis of JAs treated peach fruit (at harvest) indicated that delayed ripening was due to interference in ripening- and stress/defense-related genes (Ziosi et al. 2008).

Nitric oxide Nitric oxide (NO) has been reported to be emitted simultaneously with ethylene and in this way it showed a stoichiometric relationship with ethylene production (Leshem and Haramaty 1996). It was shown by Leshem et al. (1998) that exogenous NO extends the postharvest-life and delayed senescence in fruits, vegetables and flowers. Later, Leshem et al. (2000) made it clear that NO is natural senescence-delaying plant growth substance acting by down-regulating ethylene production. NO affects the ethylene production through its direct regulatory effect on ACC-synthase or ACC-oxidase enzymes as well as on their genes (Wills et al. 2000). Programmed cell death, which is considered to be caused by ethylene, is rather induced by NO as per Neil et al. (2003). In this context, some studies have shown that the aerenchyma formation (which is stimulated by hypoxia and ethylene) is instead caused by NO (Igamberdiev and Hill 2004; Borisjuk et al. 2007).

Application of NO to tomato delayed the burst in ethylene production and colour development at green mature and breaker stages of fruits but not at pink and full red stages (Eum et al. 2009). The results therefore implicate that NO might control the postharvest metabolism of fruits depending on its dose and the status of the commodity that is being treated (Eum et al. 2009). Borisjuk et al. (2007) proposed a key role of NO in immediate sensing and balancing the O₂ status in seeds of the plant. NO was found to mediate reversible O₂ balancing *via* its effect on respiratory activity and enabling the seed to avoid endogenous anoxia or extreme hypoxia. In this way, NO appears to control energy availability for ongoing biochemical and physiological activities. Depletion in the level of O₂ and the conditions like; hypoxia or anoxia were already reported to prevail in fruit undergoing maturation and ripening (Lammertyn et al. 2003; Franck et al. 2007; Ho et al. 2008). So, NO-mediated sensing of O₂ and balancing its levels in fruits cannot be ruled out. NO is also found to act as a regulatory factor for embryonic dormancy break in apple by stimulating biosynthesis of ethylene (Gniazdowska et al. 2007). It has been reported that NO can function as an endogenous mediator in diverse plant physiological processes but its production, effect and associated mechanisms are not known very precisely (Besson-Bard et al. 2008). Likewise, Wills et al. (2000) and Leshem et al. (2000), Eum et al. (2009) also reported that NO affects the ethylene production through its direct regulatory effect on the enzymes of ethylene biosynthesis (ACC-synthase and ACC-oxidase) and also on their genes during ripening of tomato.

The regulatory and interactive linkages of NO with biosynthesis and response of ethylene are presented in Fig. 6 beside this, interaction of NO with the anaerobic or hypoxia condition is shown in Fig. 7. Interactions of some of the volatiles like; C₂H₄, O₂, CO₂, SA/MeSA, JAs and NO on various components of respiratory metabolism was reported by Millar and Day (1996), Fan et al. (1997), Yang et al. (1998), Ederli et al. (2006), Leakey et al. (2009) and Wang et al. (2010). This shows that different volatiles and gases can affect the status of respiration which in turn is closely linked with the potential shelf-life of plant parts (including fruits) after their harvest (Kader 1987; Kader and Saltveit 2003b; Varoquaux and Ozdemir 2005; Paul and Srivastava 2006; Paul et al. 2010b).

Practical implications of the internal atmosphere in fruit

Permeability of different volatiles or gases is governed by diffusivity of these compounds in air, water and across the cellular microstructures of fruit. Microstructures of internal

and surface tissues of fruit include their cellular details, porosity (up to micro level) and 3-D organization of cells. In this way, permeability changes in a dynamic way with changes in the metabolic activities of tissues, developmental stage, maturity and storage time. Besides this, the external factors like; temperature, relative humidity and gaseous composition of immediate storage environment also affect the permeability within and across the fruit. Fick's law, as such cannot be applied directly to predict the gaseous concentration in fruits because fruit tissue does not represent a continuum. Several researchers have described different geometrical models with mathematical equations that also take into the consideration the tissue microstructures besides other factors (Nguyen et al. 2004; Verboven et al. 2008; Ho et al. 2008, 2009, 2010).

Today, efforts are being made for more effective use of some gases such as; carbon monoxide (CO), nitrous oxide (N₂O), nitrogen (N₂), sulphur dioxide (SO₂), chlorine dioxide (ClO₂) in the storage environment to reduce the microbial, insect and pest infestation. Besides this, ozone (O₃) gas is also being exploited in delaying the ripening and improving the quality of the stored fruits (Scully and Horsham 2008; Mangaraj and Goswami 2009; Hoehn et al. 2009; Yahia 2009; Zambre et al. 2010; Rodoni et al. 2010). Ozone treated fruits are reported to show delay in ripening and decay, proper maintenance of quality, suppression in microbial contamination and reduction in the levels of ethylene in storage environment and within the fruits as well (Rice et al. 1982; Kim et al. 1999; Xu 1999; Zambre et al. 2010; Rodoni et al. 2010). Exposure of O₃ also reduced the levels of pesticide in stored apples (Ong et al. 1996). Besides the practical applicability of above gases, required levels of O₂, CO₂, ethylene, humidity and condensation levels in the storage environment can also delay ripening and improve quality and storability of fruits (Scully and Horsham 2008; Mangaraj and Goswami 2009; Hoehn et al. 2009; Yahia 2009).

Developments in the field of plant volatiles and their roles further showed that the quality and quantity of volatiles in plant/plant part may also be linked with various types of abiotic and biotic stresses (Steindel et al. 2005; Karl et al. 2008; Loreto and Schnitzler 2010). Some specific examples are 1. Hexanal, *trans*-2-hexenal and hexyl acetate improve the safety of freshly sliced apple (Lanciotti et al. 2003), 2. *Trans*-2-hexenal confer resistance to anthracnose fruit decay in highbush blueberry (Polashock et al. 2007), 3. Hexanal also reduces infection of tomatoes by *Botrytis cinerea* (Utto et al. 2008), 4. Alpha-farnesene increases the susceptibility of apple fruits to scald disorder (Huelin and Coggiola 1968; Watkins et al. 1993), 5. Different endogenous volatiles (aldehydes, alcohols and esters) and *trans*-2-hexenal exhibit antifungal properties against the *Colletotrichum acutatum* that causes anthrac-

nose in strawberry fruits (Arroyo et al. 2007), 6. Several terpenoids (sesquiterpenes like; zingiberene and curcumene and the monoterpenes like; *p*-cymene, α -terpinene, and α -phellandrene) strongly repel whiteflies that infest tomatoes (Bleeker et al. 2009) and 7. Isoprene is reported to provide thermo tolerance in *Arabidopsis* (Sasaki et al. 2007) but, its role in fruits is yet to be studied. Strawberries treated with MJ alone or in combination with ethanol showed higher antioxidant capacity, total phenolics and anthocyanins along with longer postharvest-life and better quality and aromatic properties. Combined treatment also increased total volatile compounds during storage (although there were quantitative and qualitative changes depending upon the individual volatile compound) (Ayala-Zavala et al. 2005). In view of the above reports, plant volatiles are important because fruits are reported to be accompanied by increase in the levels of reactive oxygen species during their maturation and ripening and this situation represents an oxidative stress like condition for fruits (Stanley 1991; Ferrie et al. 1994; Palma et al. 1995; Rogiers et al. 1998). These examples show that at least some of the volatiles in the internal atmosphere of fruit can provide protection against biotic and abiotic stresses during ripening and storage and reflect the potential practical applications of these volatiles in overall postharvest management of fruits.

Better understanding of the environment that prevails inside and also outside the fruit will allow us to further refine measures for improving the efficacy of storage environments for delaying the ripening and senescence, minimizing microbial or insect/pest-mediated contamination and improving the shelf-life and quality aspects of stored items. Future studies on storage technology should focus on 1. Defining and then generating optimum internal atmospheres in fruits, 2. Providing conditions which are cultivar specific, 3. Making use of high precision sensors for monitoring the levels of volatiles and gases 4. Developing and using a fruit specific and real time system to manipulate the levels of at least some of the most critical volatiles/gases during storage and 5. Exploiting the use of some of the fruit specific volatiles as exogenous treatments to tackle both a specific or a broad problems related to postharvest management.

Conclusion

Endogenous volatiles in fruits are usually known for their role in determining the flavour and aroma. Only a few studies show their importance and role in a specific plant process. It is rare that combined and interactive effects of different endogenous volatiles have been studied on postharvest physiology of fruits, ripening process and postharvest management practices that are being followed

for fruits. Both, the external and the internal gaseous environments of the fruit play crucial role in regulating the process of ripening. So far, very little is being understood about the interactive mechanisms of different volatiles (other than ethylene) in regulating the process of ripening. Ethylene is of course a major controlling factor for the ripening and related changes in climacteric fruits but its biosynthesis, perception, sensitivity and even action are being influenced either directly or indirectly by other endogenous volatiles such as; acetaldehyde, ethanol, methyl salicylate, methyl jasmonate and NO besides the O₂ to CO₂ ratio and water status of the fruit. The internal atmospheres in fruit should be analysed and understood to enable effective manipulation of ripening and control of the quality of fruits. Efforts to decipher the dynamics of internal atmospheres in relation to the progress of fruit ripening could be of great practical importance. Such information could be used to more precisely manage the storage environment and to optimize the composition of the internal atmosphere in the fruit. This will help not only in achieving the best quality, aroma, flavour and shelf-life but also in minimizing the decay, pest infestation and microbial infection of fruits during storage.

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