

Influence of initial gas modification on physicochemical quality attributes and molecular changes in fresh and fresh-cut fruit during modified atmosphere packaging

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ABSTRACT

The quality of fresh and fresh-cut (FC) fruit can be preserved by creating an optimal atmospheric condition around the product. Extensive research has been reported on the application and effects of initial gas modification on fruit quality. Active modified atmosphere packaging (MAP) is a commonly applied postharvest technology to maintain quality and extend shelf life of fresh fruit; however, the response of individual fruit types to the exposed atmosphere widely varies depending on gas composition and storage condition. Hence, as the demand for active MAP application increases, identifying and understanding the role of gases used for active MAP, their mechanism and effects on the quality of fresh and FC fruit becomes more relevant. This review examined the effects and mechanisms by which initially modified atmosphere affects the quality of fresh and FC fruit with respect to physicochemical quality, and composition of organic acids, bio-active compounds, and secondary metabolites. The review further highlighted on the application of genomic tools towards better understanding molecular changes in fruit subjected to MAP during postharvest handling.

1. Introduction

Fruit are living and respiring products that maintain active metabolism even after harvest. They are easily perishable after harvest due to their soft texture, high physiological activity, high sensitivity to microbial spoilage as well as mechanical injury, which limit the market potential and consumer access (Lu et al., 2018; Opara & Pathare, 2014; Opara, 2007; Zhang, Meng, Bhandari, Fang, & Chen, 2015). Therefore, it is necessary to seek methods to prolong the shelf life and maintain quality of fruit during postharvest handling. Changing the atmosphere around fresh and fresh-cut (FC) fruit through modified atmosphere packaging (MAP) has been reported as one innovative postharvest approach, which has positive impact on fruit quality and safety (Jo, An, & Lee, 2014; Caleb, Mahajan, Manley, & Opara, 2013; Caleb, Mahajan, Al-Said, & Opara, 2013a; Caleb, Mahajan, Al-Said, & Opara, 2013b; Caleb, Opara et al., 2013; Caleb, Opara, & Witthuhn, 2012). In this approach, fresh and FC fruit are packed in a plastic polymeric film and the atmosphere inside the package is modified to accelerate the establishment of in-package optimum gas composition and avoids high

concentration of unsuitable gases (Banda, Caleb, Jacobs, & Opara, 2015; Belay, Caleb, Mahajan, & Opara, 2018; Jouki & Khazaei, 2014). During respiration process, fresh and FC fruit consumes O₂ and produces CO₂, therefore, the concentration of O₂ and CO₂ inside the package is reduced and increased, respectively. Therefore, it is important to establish optimum gas composition at equilibrium, which is determined by the product weight and physiology (respiration rate (RR), maturity stage), environmental conditions (temperature, relative humidity), and properties of the packaging material (film thickness, permeability, perforation density, and surface area) (Caleb, Mahajan, Manley et al., 2013; Hussein, Caleb, & Opara, 2015; Hussein, Caleb, Jacobs, Manley, & Opara, 2015; Opara, Hussein, Caleb, & Mahajan, 2015; Opara, Hussein, & Caleb, 2017).

Modified atmosphere packaging, which utilizes only the natural component of the atmosphere (O₂, CO₂ and N₂), has achieved public acceptance due to the advantage that synthetic chemicals are not used and no toxic residue is left on produce. Initial modification of gas has the favourable effect to reduce the respiratory activity and prolonging the shelf life of fresh and FC fruit (Belay, Caleb, & Opara, 2017).

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Removal or exclusion of O₂ by displacing air with desired gas composition inhibits rate of oxidation, reduce respiration rate (RR), delay fruit ripening and slows the rate of degradation of valuable flavour and colour components (Fante, Carolina, & Boas, 2014; Li & Zhang, 2015; Teixeira, Júnior, Ferraudo, & Durigan, 2016). Similarly, super-atmospheric O₂ concentration has been shown to be effective to prevent anaerobic respiration, inhibiting microbial growth and effective at reducing decay of fresh produce (Belay et al., 2017; Maghouthi et al., 2014). Elevated O₂ could enhance the production of reactive oxygen species (ROS), such as superoxide, hydrogen peroxide, and hydroxyl radicals, that damage the cytoplasm and inhibit various metabolic activities, leading to deterioration of produce quality (Choudhury, Rivero, Blumwald, & Mittler, 2017).

Despite the enormous advantages of modifying these gases, the use of extremely low or high concentrations causes imminent risks as severe damage to fresh produce tissue could occur. For instance, if O₂ concentration declines below the critical limit required for sustaining anaerobic respiration and fermentation would set in, resulting in the development of off-flavour (Li, Jiang, Li, Tang, & Yun, 2014). Similarly, the presence or the accumulation of high CO₂ concentration could also have a negative effect on fruit quality by accelerating changes in colour (*h*⁺) and firmness, and increasing the solubilisation of pectic compounds (Teixeira et al., 2016). However, responses differ for each fresh produce when packaged under MAP conditions. Thus, it is necessary to quantify the effects of the applied atmosphere on specific produce (Lu et al., 2018).

The changes in quality attributed of fruit are linked to the over utilization of various substrates, as the activation and/or reduction of different metabolic pathways in response to the storage condition. In recent studies, these changes in quality parameters under MAP have been presented by determining the genomic interpretation and their transcriptional abundance as affected by the packaging condition (Blanch, Rosales, Mateos et al., 2015; Rosales et al., 2016). The importance of this approach includes identifying different genes, which acted as markers of fruit senescence, ripening or stress response to the storage atmosphere. The genomic interpretation of the results thus can be used to identify candidate gene for breeding new resistance cultivar for the packaging conditions (Liu et al., 2015). In this regard, individual fruit responded differently to the initially modified atmosphere conditions and controversial results were reported in the literature on how storage atmosphere impacts product quality and shelf life. These findings show the usefulness of detailed analysis of recent literature to understand how initial gas modification under MAP affects the quality of fresh and FC fruit. Therefore, the aim of this review was to assess the mechanisms and effects of initial gas modification on the quality attributes of different fresh and FC fruit during MAP, and elucidate the response at molecular level.

2. Effect of initial gas modification on physical quality attributes

Several naturally occurring gases such as oxygen, carbon dioxide, nitrogen as well as other gases (helium and argon) can be used for fresh and FC fruit packaging, each one having a different role in the preservation and maintaining quality as summarized in Table 1. The postharvest tolerance of different fresh and FC fruit have been reported in various literatures, with the general goal being to identify the safe and optimum concentration that will result in a maximum shelf life. Physical quality attributes are the most important criterion that consumers use to evaluate quality of fruit and vegetables. These quality attributes includes firmness, colour, antioxidants, sugars and others. Colour change or browning, dryness or shrivelling of fresh and FC fruit surfaces are the most limiting factors on the shelf life of FC products and a significant factor of quality deterioration. Active MAP system created by initial gas modification is a simple and inexpensive way of postharvest treatment (Soltani, Alimardani, Mobli, & Mohtasebi, 2015). According to Teixeira et al. (2016), it is possible to identify detrimental

quality modifications of a fruit under different storage atmosphere. The response of fresh and FC fruit to modified gas concentrations has been characterized by the profile of primary metabolite (RR) and secondary metabolite (fermentative metabolites and volatile compounds) (Blanch, Rosales, Palma et al., 2015).

As presented in Tables 2 and 3, the effects of storage atmospheres varied for different fresh and FC fruit, which is dependent on the gas concentration and tolerance limit of the fruit to the exposed atmosphere, storage temperature, and packaging material. In order to investigate the changes in the quality of fresh and FC fruit during MAP conditions, it has been recommended to consider the compatibility of the gas and water vapour permeability properties of a packaging film with the storage atmospheres and RH (Adiletta et al., 2017; Belay et al., 2018). If packaging film permeability (gas or water vapour) is not optimally matched with the RR or the transpiration rate (TR) of the fresh and FC fruit, adverse effects on quality such as loss of weight, texture, colour, bioactive compounds and microbial growth could be an avoidable (Zhang, Meng, Bhandari, & Fang, 2016).

2.1. Effects on weight loss

Fresh and FC fruit are highly susceptible to weight loss, which adversely affects the quality such as appearance, texture, flavour and nutritional value. Weight loss mostly associated with water or moisture loss is dependent on the physiological and morphological characteristics of an individual fruit (Manolopoulou & Varzakas, 2013). The moisture loss process in fresh produce involves diffusion of moisture from cells into the intercellular spaces until a level of saturation is reached in these intercellular spaces (Ngcobo et al., 2012). Substantial loss of water from a fruit lead to a significant loss of fresh weight, resulting in economic loss, if the commodity is sale by weight and further accelerates senescence, increase pathogen invasion, and increased susceptibility to chilling injury (Caleb, Mahajan, Al-Said et al., 2013a). A loss of 3 to 10% may render a wide range of horticultural crops unaccepted for sale (Caleb, Mahajan, Al-Said et al., 2013b).

Therefore, reducing the respiratory activity, which directly reduces TR is one of the favourable approach for minimizing weight loss (Belay et al., 2018). Transpiration is the process exhibited by fresh fruit that involve the transport of moisture through the skin of the commodity, the evaporation of this moisture from commodity surface and the convective mass transport of the moisture to the surroundings (Ngcobo et al., 2012). Other factors that affects TR includes in-package RH and storage temperature, these are responsible to control water vapour accumulation or transmission inside the package (Mahajan et al., 2015; Rux et al., 2016). Low in-package RH can increase TR and RR, whereas high in-package RH is associated with condensation and ultimately these two extreme conditions results in an unmarketable product (Hussein, Caleb, Jacobs et al., 2015). In addition to the above-mentioned factors, the difference in weight loss among fruit types could also be influenced by the differences in their form and structure. For instance, produce with protective membranes have lower water loss in comparison to the produce with lower or no protective membranes (Manolopoulou & Varzakas, 2013). Therefore, the challenge of controlling weight loss of produce under MAP system is recommended to start from controlling the RR and TR of the produce. This can be achieved by the integrated approach of selecting desired gas composition and package permeability that can regulate the in-package RH.

The advantage of initial gas modification during MAP has been reported by various studies. Brackmann, Thewes, Anese, Ceconi, and Júnior (2013) reported low RR and low mass loss for 'Fuyu' persimons fruit stored under 1.0% O₂ and 0.0% CO₂. Similarly, prickly pear stored in active MAP at 4 and 10 °C did not lose significant weight compared to unpacked pear, which lost 26% of its initial weight at 10 °C (Ochoa-Velasco & Guerrero-Beltrán, 2014). The study further associated the lowest weight loss of prickly pear with the high moisture barrier property of polyethylene packaging film. According to Giuggioli,

Table 1
Major gases applied for modified atmosphere packaging and their role.

Type of gas	Role in fresh and FCF	Mechanism	References
Carbon dioxide	Antimicrobial characteristics, Delaying inhibition of microbial spoilage (extension of the lag phase of growth and a decrease in the growth rate during the logarithmic growth phase) Most pronounced effect against gram negative bacteria	Causes a decrease on the product's pH value can also act as hurdle of microbial growth Ability to access bacterial membranes and alter the interior pH of cells, thus changing the cellular metabolic processes Inhibition of substrate uptake by microorganisms Direct impact on enzymes as well as the alteration on the properties of proteins	Blanch, Rosales, Mateos et al. (2015), Cortellino et al. (2015), Li et al. (2018), Maghoumi et al. (2014), Teixeira et al. (2016)
Oxygen	At low O ₂ concentration, it maintain desirable colour, reduce respiration rate, and ripening or senescence High-oxygen environments can inhibit the growth of certain bacteria and fungi, prevent anaerobic fermentation reactions, and reduce the decay Maintain and texture	stimulation of lactic dehydrogenase When O ₂ is not available, fruits degrade glucose anaerobically by glycolysis to generate energy. In the glycolysis pathway, aldehydes, alcohols and lactates are produced Accumulation of anaerobic byproducts produces off-flavours associated with physiological disorders, leading to an unacceptable eating quality	
Nitrogen	Nitrogen used to replace O ₂ to slow oxidation Act like a filler and prevent package collapse Indirectly influence microorganisms by retarding the growth of aerobic spoilage organisms	Low solubility in both water and fat Un- reactive gas	

Table 2
Recent publications on effect of active modified atmosphere packaging on quality and shelf life for fresh and fresh-cut (FC) fruit.

Product	Gas composition	Main effects on quality	Reference
FC papaya	5% O ₂ and 10% CO ₂	Better firmness, lightness decreased, decreases in sensory scores Shelf life 25 days	Waghmare and Annappure (2013)
Pomegranate	low barrier BOP polymeric film (5% O ₂ , 10% CO ₂); (30% O ₂ , 40% CO ₂) high barrier polymeric film Polyid (5% O ₂ , 10% CO ₂); (30% O ₂ , 10% CO ₂); (100% N ₂)	TSS values of arils in low barrier BOP film (experiment 1) reduced significantly (P < 0.05) with storage Total anthocyanin concentration fluctuated with storage in both atmospheres Slightly higher initial TSS:TA than those packaged in the low barrier BOP film Sensory analysis for arils in low O ₂ atmospheres (5% O ₂ + 10% CO ₂) and 100% N ₂ were below the acceptance limit by day 9	Banda et al. (2015)
Cherry tomato	5% O ₂ + 5% CO ₂ and air	For both atmospheres, weight loss increased throughout the storage period No significant change in the content of fructose and glucose for samples stored in MAP was observed Highest ethylene emission observed in air stored samples	Fagundes et al. (2015)
Table Grape	PET1 (5% O ₂ + 15% CO ₂) PET2 (20% CO ₂ + air)	No significant changes occurred, between treatments, in total phenols and total anthocyanins content TSS was slightly higher in PET1 packages than in PET2, but difference was significant only at the last sampling date.	Liguori et al. (2015)
Guava	5% O ₂ and 1, 5, 10, 15 and 20% CO ₂	CO ₂ concentration accelerated changes in colour (h*) and firmness CO ₂ injury observed at 5% O ₂ with 15 and 20% CO ₂ with increase in pH value and soluble pectin content	Teixeira et al. (2016)
Prickly pear	Air, 6.25% O ₂ + 0.1% CO ₂	Delayed weight loss and total colour change No significant difference have showed on Phenolic content across the atmospheres	Ochoa-Velasco and Guerrero-Beltrán (2014)
Blood orange	Air 76% O ₂	Super-atmospheric O ₂ atmosphere increased the anthocyanin content three times higher than those stored under air Increase in phenolic content under super-atmospheric O ₂ atmosphere Decrease of sugars (glucose, fructose and sucrose)	Molinu et al. (2016)
Pomegranate	MA1 (5% O ₂ + 10% CO ₂), MA2 (10% O ₂ + 5 % CO ₂); MA3 (70% O ₂ + 10% CO ₂) and air	Highest C* and slight increase in hue angle were observed for MA1 at the end of storage day 12 Texture was not significantly (p > 0.05) affected Ascorbic acid showed marked decrease in samples stored under air and (MA3) conditions	Belay et al. (2017)
Strawberry	MA1 (90% O ₂ + 10% N ₂), MA ₂ (3% O ₂ + 5% CO ₂ + 92% N ₂), air	No significant difference was observed on the overall quality between treatments Significantly higher flavour score observed at MA1 Control fruit have higher off flavour score than MA1 and MA2 MA1 and MA2 had significantly lower astringency scores than control both MA1- and MA2-stored strawberries were significantly firmer than control but no significant difference was observed between MA1 and MA 2 After 10 d of storage, the total phenol content in MA1 was significantly higher than in MA2 and air	Lu et al. (2018)

Table 3

Recent applications of different gas compositions for packaging fresh and fresh-cut (FC) fruit.

Adopted from Zhang et al. (2015).

Product	Gas mixture			Storage temperature (°C)	Shelf life (days)
	O ₂ (%)	CO ₂ (%)	N ₂ (%)		
Strawberry	2.5	15	82.5	4 ± 0.5	8-10
FC apple	5	15	80	5-6	7
FC pear	2.5	7	90.5	4	14
Blueberry	100	0	0	5	35
Raspberry	3	5	92	7	7
Papaya	3-5	6-9	86-91	10	25
FC melon	70	0	30	5	10-14
FC jackfruit	3	5	92	6	35

Girgenti, Baudino, and Peano (2015), the weight loss of raspberries under MAP were ranged from 0.0 to 0.2%. This has shown the advantage of MAP treatments to maintain a good state of hydration of the fruit during packaging. Low weight loss at reduced RR could be associated with the consecutive decline in TR, due to low respiratory heat and low water vapour pressure deficit (WVPD), that affects the rate of water evaporated from the product (Bovi, Caleb, Linke, Rauh, & Mahajan, 2016). The rate of loss of moisture from fresh fruit is largely dependent on the humidity and temperature of the surrounding air, as well as on the heat and mass transfer properties of the fruit such as thermal conductivity, thermal and moisture diffusivity, interface heat and mass transfer coefficients (Ngcobo et al., 2012).

Liguori, D'Aquino, Sortino, De Pasquale, and Inglese (2015) reported weight loss of 'Red Globe' grape packaged under non-micro-perforated polyethylene sealed boxes (20% CO₂ and air; 5% O₂ and 15% CO₂) increased sharply during storage, reaching values of 8% and 14%, respectively, than those measured at the beginning of the shelf-life. According to Chaudhary, Jayaprakasha, Porat, and Patil (2015) active MAP (microperforated Xtend bag; 3.5% CO₂ and 18% O₂), macroperforated Xtend bag and air showed no significant weight loss of grape (cv. Star Ruby) fruit, but in the control fruit, weight loss gradually increased during the postharvest storage. The study associated the weight loss of grape fruit with RH, temperature, and storage duration. Belay et al. (2018) applied a gas composition of 4.67% O₂ and 12.67% CO₂ for pomegranate (cv. Wonderful) arils under different packaging material design at 10 °C. The study reported lower mass loss for arils packaged under PropaFilm and NatureFlex window films after 9 days of storage. On the contrary, significantly higher mass loss was observed of arils packed under NatureFlex films (NF). The most probable explanation of highest moisture loss in NF package is due to high WVTR of the film (based on Innovia films, UK for NatureFlex) and the presence of significantly lower RH inside the package.

Although different packaging materials and storage conditions are established to control the weight loss of fresh produce, the effect varies due to the difference in fruit type, cultivar, and responses to the storage environment; determining optimum in package gas composition for individual fruit is unavoidable. Furthermore, humidity packaging may provide an alternative to conventional plastic packaging material in terms of reducing accumulation of moisture in the package. However, further applied research for fresh and FC fruit packaging is required to provide scientific evidence on the compatibility between optimal atmosphere and humidity package techniques.

2.2. Effects on loss of colour attributes

Fruit colour is the first perception for consumer acceptability and it can be influenced by maturity, genotype and cultivar (Giuggioli et al., 2015; Pathare, Opara, & Al-Said, 2013). Fruit colour commonly associated with breakdown of cellular chloroplasts, chromoplasts and change in natural pigments (chlorophylls, anthocyanins, carotenoids,

flavonoids) (Yin et al., 2016). Almost all of these pigments can be affected by packaging and storage conditions. Furthermore, change in colour is the potential indicator of change in shelf life and maturity of fresh and FC fruit (Fagundes et al., 2015). For instance, FC papaya (Waghmare & Annapure, 2013), "Eva" apple (Fante et al., 2014) and strawberry (Giuggioli et al., 2015) were shown to be affected by active MAP. High CO₂ concentrations was shown to protect shredded vegetables from browning, because they limit the action of polyphenol oxidase (PPO) and the concentration in phenolic substances (Manolopoulou & Varzakas, 2013).

Colour change related to the effect of an enzymatic browning under high O₂ MAP has been associated with the substrate inhibition of enzyme polyphenol oxidase (PPO) (Li et al., 2014). Molinu et al. (2016) linked the increase in *h*^{*} with PPO activity during storage of 'Sanguinello Comune' blood orange. Packaging material with high barrier properties significantly affected the evolution of PPO activity in FC apples, whereas, those packed in plastic bags with low O₂ permeability exhibited steadier inhibition (Li, Li, Fan, Tang, & Yun, 2012). In this study, storage atmosphere significantly affected the PPO depilation, where apple cubes packed in MAP were efficiently preserved from browning when O₂ is initially absent. Enzymatic browning is resulted from reactions between phenolic compounds and oxidative enzymes owing to cellular (Li et al., 2014).

Extensive literatures reported the advantage of low, high or super-atmospheric O₂ concentrations for maintaining the different colour attributes of fresh and FC fruit. Belay et al. (2017) reported that different MAP, storage time and their interaction had significant effect (*p* < 0.05) on the colour intensity (*C*^{*}) of pomegranate (cv. Wonderful) arils stored at 5 °C. In this study, highest *C*^{*} (30.14 ± 7.1) and slight increase in hue angle (*h*^{*}, 36.51 ± 8.6) were observed in arils under low O₂ atmosphere (5%), whereas, super-atmospheric O₂ (70%) maintained the initial values of *C*^{*} (14.91 ± 2.9) and *h*^{*} (30.21 ± 5.3) throughout the storage. Martínez-Romero et al. (2013) observed a reduction in hue angle of pomegranate (cv. Mollar de Elche) arils treated with A. Vera gel, citric and ascorbic acid, while *h*^{*} increased in control non-treated arils. Teixeira et al. (2016) presented the significant effect of atmospheres on *h*^{*} for guava fruit kept in 5% O₂ and (5% O₂ + 1% CO₂ and 5% O₂ + 5% CO₂). The results showed a significant (*p* < 0.05) reduction of *h*^{*} under low O₂ atmosphere than those that were stored in higher CO₂ concentration. On the other hand, Maghoumi et al. (2014) observed no significant effect of active MAP on *C*^{*} value during storage of pomegranate (cv. Malese-Saveh) arils. However, loss of colour may not be exclusively attributed to chemical reaction, but rather to a summation of many appearance defects, some of which may result from excessive loss of water (Paniagua, East, Hindmarsh, & Heyes, 2013). The tendency of a slight decreasing of *C*^{*} and increasing of *h*^{*} reflect a loss of colour intensity occurring during storage (Palma, Continella, La Malfa, Gentile, & D'Aquino, 2015). According to Bessemans, Verboven, Verlinden, and Nicolai (2016), higher *h*^{*} value indicates fresh green colour, while lower *h*^{*} indicate more yellowish background colour of the fruit.

The study conducted by Cortellino, Gobbi, Bianchi, and Rizzolo (2015) on 'Golden Delicious' apple slices under (1% O₂, 99% N₂, and 5% O₂, 90% N₂, 5% CO₂) and Ar and CO₂ combination (80% Ar, 20% CO₂) successfully maintained the initial value of browning index (BI) for 11 days of cold storage. In this study, the slices packed under Ar, N₂O mix (65% N₂O, 25% Ar, 5% CO₂, 5% O₂) showed the same behaviour as those stored in air. An atmosphere with 2.2% O₂ + 5.7% CO₂ under MAP induced significant BI development during cold storage of Bartlett' pears (Wang & Sugar, 2013). The effectiveness of super-atmospheric O₂ in preserving colour characteristics also reported by Li, Li et al. (2012). The study stated that storage under super-atmospheric greatly contributed to slow down changes in red colour of FC pears. Similar to *a*^{*} value, the increasing rate of *b*^{*} value in samples stored in high O₂ conditions was smaller than that of other packaging (low O₂ and passive atmosphere) systems. The study further illustrated that

super-atmospheric O₂ especially 80% O₂ was much effective on inhibiting discoloration. The loss of colour during active MAP can be maintained by monitoring and controlling both enzymatic and non-enzymatic activities. The enzymatic activities can be controlled by reducing the O₂ concentration, whereas, loss of colour related to water loss can be controlled by appropriately selecting packaging film, which can regulate the in-package RH (Belay et al., 2018).

2.3. Effect on textural properties

Fruit texture refers to the structural and mechanical properties of a food and their sensory perception in the hand or mouth. The complex nature of texture is associated with the diversity of tissues involved, the attributes required to describe textural properties, and changes in these attributes as the product ripens and senesces properties, such as firmness, gumminess, chewiness and resilience decreased, whereas adhesiveness, cohesiveness and springiness (Chen & Opara, 2013a, 2013b; Paniagua et al., 2013). Texture could be used to determine to produce freshness and it can be affected by traits such as cellular organelles and biochemical constituents, water content and cell wall composition (Waghmare & Annappure, 2013). The effect of active MAP on maintaining of fruit firmness is usually related to the control of weight loss, where in most studies fruit with highest weight loss have shown a higher reduction in texture. Initial gas modification can influence the textural quality and water content of fruit and vegetables by reducing the RR (Jouki & Khazaei, 2014). Postharvest softening of fruit structure occurs due to the biochemical processes that involve the direct suppression of activities of enzymes (pectin esterase and polygalacturonase enzymes) leading to deterioration in the cell structure, cell wall composition and intracellular materials (Fagundes et al., 2015). Texture softening during storage probably resulted in loss of cell turgidity due to changes in membrane permeability and breakdown of the cell wall (Paniagua et al., 2013). These biochemical processes involve the direct suppression of the activities of pectin esterase and polygalacturonase enzymes leading to postharvest softening of fruit structure or blockage of the synthesis of ethylene, which controls the activities of these enzymes especially with MAP treatment (Akbudak, Akbudak, Seniz, & Eris, 2012).

Comparing the different gas concentrations during MAP, the potential effect of high and super-atmospheric O₂ concentrations towards maintaining or improving the texture properties of fresh fruit has been widely reported than the low O₂ atmosphere. Strawberry firmness decreased by 19% during storage under modified atmosphere condition (10% CO₂, 5% O₂, 85% N₂) at 4 °C for 21 days and 68% in samples packed under air (Jouki & Khazaei, 2014). The study stated that the firmness enhancement could be associated with the different CO₂ concentrations reached inside the strawberry packages by which CO₂-induced firmness increases appear to be a common characteristic of strawberry fruits. Belay et al. (2017) have reported a similar effect of high CO₂ and super-atmospheric O₂ for pomegranate (cv. Wonderful) arils. Low RR can limit the activities of these enzymes and allow retention of firmness during storage (Fagundes et al., 2015).

Huyskens-Keil and Herppich (2013) reported that high CO₂ concentration reduces texture by inhibiting the synthesis of all cell wall components. However, CO₂ mediated effects on texture are highly dependent on cultivar, physiological age at the time of exposure, CO₂ concentration and duration of exposure. Arils stored under super-atmospheric O₂ (70%) showed a slight increase of hardness values than low O₂ (5 and 10%) treatment (Belay et al., 2017). On the other hand, Bessemans et al. (2016) stated the decreased in firmness during ambient condition due to increased RR up on removal from the storage containers.

According to Tayyari, Khazaei, Rajaei, and Jouki (2017), the firmness of pomegranate (cv. Malase-Saveh) arils stored under 4 and 8 °C was not significantly different between the low (5% O₂ and 10% CO₂) and enriched O₂ (70% O₂ and 10% CO₂) MAP treatments until day 9.

The authors observed that at the end of the storage, the highest hardness was obtained at low O₂ MAP. Similarly, Cortellino et al. (2015) reported that packaging of 'Golden Delicious' apple slices under a gas mixture of 1% O₂, 99% N₂ and 5% O₂, 90% N₂, and 5% CO₂ preserves the texture than normal air packaging. Apart from the gas concentration, the causal relationship between moisture loss and firmness responses could have an important impact on the postharvest management. Therefore, firmness retention within the commercial supply chain may be improved considering technologies (in particular packaging solutions) that limit weight loss.

3. Effect of initial gas modification on organic substrates and bio-active compounds

3.1. Effects on organic acids and sugars

As the main substrates of respiratory metabolism, sugars and acids are depleted causing corresponding changes in total soluble solid (TSS) and titratable acidity (TA) during storage (Blanch, Rosales, Mateos et al., 2015). A slight decrease of the total organic acid concentration is consistent with their use as respiratory substrates. The acidity of the fruit is determined by the concentrations of the organic acids such as citric acid, malic acid and tartaric acid (Scherer et al., 2012). Chen et al. (2015) reported that malic and citric acid in "Fuyan" longan fruit decreased due to the conversion into sugars and further utilization in the metabolic process of the fruit. Similarly, Maghoumi et al. (2013) observed a reduction of TA value of pomegranate (cv. Mollar de Elche) arils stored under UV-C treatment and super-atmospheric O₂ condition. However, the TSS content under super-atmospheric O₂ and UV-C treatment showed no changes. In another study, Maghoumi et al. (2014) observed no change on TSS content of pomegranate (cv. Malese-Saveh) arils under air, 80% O₂ and 20% N₂, 20% CO₂ and 80% N₂ at the end of storage at 4 °C, whereas, TA drastically decreased. In addition to storage atmosphere, TSS could be affected by RH, where for fruit with high water loss at lower RH (< 85%) could increase evapotranspiration which can lead to higher TSS (Beckles, 2012). The above studies associated the decrease of TA with the metabolic activity during storage, in the fact that organic acids were used as a substrate for respiratory activity and an indicator for the degree of ripeness.

According to Tayyari et al. (2017), the TA value of pomegranate (cv. Malase-Saveh) arils packaged under the modified atmosphere of 5% O₂, 10% CO₂ and 70% O₂, 10% CO₂ has shown no significant difference. However, storage time had significant effect on TA at all MAPs. Therefore, TA significantly decreased in all MAPs especially at day 12. The author associated the decrease in acidity of pomegranate with relative solubility effect of CO₂ in water molecules surrounding the freshly packed pomegranate arils. Similar result was observed for TSS, where there was no significant difference on the TSS content. Fagundes et al. (2015) studied the effect of low O₂ atmosphere (5% O₂ and 5% CO₂) and normal air on cherry tomato. The authors showed that, all organic acids decreased throughout the storage under both atmospheric treatments. However, significant effects of gases were observed only for tartaric acid. The study associated the reduction of organic acids with ripening from utilization of acids in respiration and physiological process together with carbohydrate.

Belay et al. (2018) reported an increase in sugar concentration (fructose, glucose and sucrose) of pomegranate (cv. Wonderful) arils stored under 4.6% O₂ and 12.65 CO₂. In this study, arils packed under similar gas concentration but different packaging types have different sugar content at the end of the storage. However, packaging types showed no significant effect in individual sugars; rather storage duration had a significant impact on the observed changes. In this study, organic acids (malic, citric and acetic) concentration decreased in all MAP conditions; however, the effect of MAP treatment was insignificant. On the other hand, TSS content of pomegranate significantly affected by MAP types. The study associated the progressive reduction

in acidity with the advancement of storage period might be due to the increased catabolism of organic acids present in the fruit due to respiration process.

According to Blanch, Rosales, Palma et al. (2015), the sucrose content of strawberry fruit under CO₂ (0%) concentration decreased after 3 and 6 days of storage at 0 °C. On the other hand, fruit exposed to 20% CO₂ for 3 days had the lowest values of malic acid. These results reveal that without added CO₂ fruits deplete their energy reserves, leading to a decrease in sucrose and lower levels of TSS after 6 days storage. Conversely, fruits saved energy reserves when exposed to CO₂ and had more abundant sucrose than fruits stored at low temperature without added CO₂. Furthermore, increasing pH and decreasing TA in strawberry tissues were more marked in fruit stored in high CO₂ atmospheres. Grape (cv. Star Ruby) fruit stored under active MAP (3.5% CO₂ and 18.2% O₂) and normal air showed a constant TSS content during postharvest. By contrast, acidity levels slightly decreased between harvest and prolonged storage. Overall, the observed changes in juice TSS and acidity levels resulted in a slight increase in ripening ratio from 6.5 at harvest to 8.0 after 16 weeks of storage (Chaudhary et al., 2015).

Fagundes et al. (2015) studied the change in sugar concentration of cherry tomatoes stored under MAP (5% O₂, 5% CO₂, and 90% N₂) and air. In this study, the concentration of sugar decreased with the storage time progressed. Fructose content was 0.07 g/L for the control and 0.02 g/L for the samples packaged in MAP, while glucose ranged between 0.13 and 0.05 g/L for the control and MAP, respectively. However, the change in the content of fructose and glucose for samples stored in MAP was not significant. Consistence with sugars, organic acids showed reduction during storage for samples stored under MAP as well as for the control. However, except for tartaric acid, samples stored under an atmosphere of 5% O₂, 5% CO₂, and 90% N₂, did not experience significantly reduction of organic acid over the storage time. Glucose, fructose and sucrose content of orange packaged under a regular air has shown no significant changes except a slight decrease in sucrose content, whereas, the concentration of these sugars decreased in orange stored under super-atmospheric oxygen (70%) concentration (Molinu et al., 2016).

The above-mentioned studies described that, the decrease in TSS is caused by a decline in the amount of carbohydrates and pectin, partial hydrolysis of protein and decomposition of glycosides into sub-unit during respiration. The effect of active MAP on organic acids and sugars varies in different fruit type and storage conditions, therefore monitored by controlling RR and TR could be vital to maintain both TA and TSS. Furthermore, it is possible to highlight that the higher the metabolic rate could accelerate the consumption of the acid; however the variation of the results for the same type of fruit could be cultivar dependent. Therefore, it is important to correlate between fruit and in package conditions to reduce consumption of sugars and acid with time.

3.2. Bioactive compounds

3.2.1. Total anthocyanin and phenolic concentration

Various factors affect total anthocyanin and phenolic contents, including temperature of packaging and storage, atmosphere composition, chemical nature of anthocyanin (acylation or glycosylation), and pH (Turfan, Turkyilmaz, Yemis, & Ozkan, 2011). For instance, storage under super-atmospheric O₂ concentration dramatically enhanced the anthocyanin concentration of blood orange fruit, resulting in three times higher than the fruit stored at normal air (Molinu et al., 2016). On the other hand, 'Honey' pomelo slices underwent a marked depletion of total phenolic compounds under super-atmospheric O₂ throughout storage (Li, Ban, Li, Wang, & Guan, 2012). These studies associated the increase of anthocyanin concentration with the physiological response to oxidative stress during storage, whereas, the depletion and increase of phenolic compound could be due to that phenolic are involved in the synthesis of lignin and the lignification in fruit in the phenolic

metabolism after wounding, respectively. On the contrary, Banda et al. (2015) reported the lowest anthocyanin concentration under high O₂ atmospheres (30% O₂ and 10% CO₂) for pomegranate (cv. Wonderful) arils. The decline of anthocyanin concentration under super-atmospheric O₂ condition could be due to the ascorbic acid oxidation, delay of fruit ripening process or could be due to damage during fruit peeling (Ghasemnezhad, Sherafati, & Payvast, 2011; Maghoumi et al., 2014).

Maghoumi et al. (2013) reported increase in phenolic concentration of pomegranate (cv. Malese-Saveh) arils exposed to high O₂ compared to samples stored under air. The reduction of phenolic concentration could be due to cell structure breakdown as part of senescence during storage and oxidation of phenolic compounds with PPO and POD activities (Ghasemnezhad, Zareh, Rassa, & Sajedi, 2013), which results in the synthesis and accumulation of phenolic compounds. However, the effect of super-atmospheric O₂ concentration on the total phenolic content may vary depending on commodity, genotypes, oxygen concentration, storage time and temperature (Ghasemnezhad et al., 2011). The accumulation of phenolic compounds could be a physiological response to stress or injuries, wounding may stimulate phenylalanine ammonia lyase (PAL) activity during minimally processing with the consequent further production of the phenolic compounds. From the above studies, a clear observation could be dawned that, the effect of low or high O₂ atmosphere on phenolic concentration may vary depending on the commodity and O₂ concentration.

Maghoumi et al. (2014) demonstrated that elevated O₂ in the first days of storage may increase the antioxidant activity but prolonged storage at that condition may cause reduction in the main antioxidants including anthocyanins and other phenolic compounds due to O₂-promoted oxidation. Liguori et al. (2015) studied the effect of PET1 (5% O₂ and 15% CO₂) and PET2 (20% O₂ and air) for ready to eat grape stored at 5 °C and 90% RH for 21 days. The study observed no significant changes in total phenols and total anthocyanins content between treatments. The overall trend of total phenols seemed more stable or even stimulated in PP packages, with the exception on results of day 14 at 5 °C. On the other hand, phenolics content was lower in PET1 and PET2 packages. Marked stimulation of anthocyanins production for blood orange fruit stored at super-atmospheric O₂ (70%) was reported by Molinu et al. (2016). The study associated this stimulation with exposure to super-atmospheric O₂ and a physiological response to oxidative stress. It is known that anthocyanin concentration in fruit can be enhanced by different postharvest abiotic stresses induced by physical or chemical elicitors (Baenas, García-Viguera, & Moreno, 2014).

The phenolic content of Pear fruit stored at 4 °C for 12 days under low O₂ (5% O₂ and 5% CO₂) and control significant decreased (51%) and (32%), respectively, whereas, the reduction under super-atmospheric O₂ (80%) treated samples (12.4%) was lower (Li, Li et al., 2012). In this study, the total anthocyanin value exhibited a similar pattern of change, as did the total phenolic during storage in response to high O₂ atmosphere. Significantly, higher levels of anthocyanin level was detected in 80% O₂-packaged pear than 30% O₂ packed fruit. However, no significant differences in total anthocyanin content were found between the two samples at the end of the storage. The study associated the inhibitory effect of high O₂ on the loss of anthocyanin could be due to a lower phenylalanine ammonia lyase (PAL) enzyme activity.

Studies summarized above demonstrated that, modified atmospheres and storage conditions, which leads to oxidation or accelerate ripening, cell breakdown and tissue damages could prevent depletion of antioxidant properties in fruit and FC fruit. Thus, there is still a scope to improve the capability of MAP. This could be achieved by incorporating real time physiological response, gas concentration, storage time and temperature as well as in package RH, and packaging material.

3.2.2. Ascorbic acid

Ascorbic acid (AA) is one of the most sensitive materials to be destructed when fruit subjected to adverse handling and storage

conditions (Li & Zhang, 2015). In addition to the effect of storage atmosphere, the nature of the fruit by itself has an effect on ascorbic acid concentration during storage, where for climacteric fruit; the increase of ascorbic acid during storage associated with the postharvest dehydration and ripening. The higher AA found in the advanced stages of ripening related to increased level of glucose, which is a precursor of AA (Maghoumi et al., 2014). Therefore, in order to control reduction of AA in fruit under MAP, emphasis should be given to both the storage atmosphere and the type of the fruit. Silveira, Araneda, Hinojosa, and Escalona (2014) observed higher AA concentration in watercress leaves under low O₂ and CO₂ atmosphere. The study stated that, the effect of CO₂ on AA content is due to stimulated oxidation by increasing ascorbate peroxidase activity or inhibiting monodehydroascorbate and dehydroascorbate reductase with NADP/NADPH and glutathione as electron donors, which also increased dehydroascorbic acid levels. Molinu et al. (2016) found out, storage of blood orange in super-atmospheric O₂ (70%) decreased the AA content by 20% while in regular air its change was not statistically significant.

Belay et al. (2017) reported a significant effect of storage atmospheres, low O₂ (5 and 10% O₂, 10% CO₂), super-atmospheric O₂ (70% O₂, 10% CO₂) and air on AA content of pomegranate (cv. Wonderful) arils at 5 °C. This study associated the ascorbic acid oxidation by the presence of oxygen and thus, AA content marked decrease in samples stored under air and super-atmospheric conditions. Similarly, Maghoumi et al. (2014) also reported reduction of AA concentration of pomegranate (cv. Malese-Saveh) arils stored at 4 °C for 14 days under super-atmospheric O₂ (70%). The gradual decrease of ascorbic acid concentration was observed for arils stored under super-atmospheric condition despite the high concentration of CO₂. High CO₂ level could lead the oxidation of ascorbic acid by ascorbate peroxide or inhibition of dehydroascorbic acid (DHH) reduction to ascorbic acid or by ethylene production.

Li, Li et al. (2012) stated that the packaging atmospheres significantly affected the AA content during storage. On the study done by Chaudhary et al. (2015), active MAP (microperforated Xtend bag; 3.5% CO₂ and 18% O₂), macroperforated Xtend bag and air retained AA content of grape (cv. Star Ruby) fruit during postharvest storage. Ascorbic acid increased in all three treatments at 8 weeks after storage; nevertheless, at the end of the 16-week storage period, fruits in all three treatments had AA concentration similar to the initial. Ascorbic acid is a major antioxidant present in citrus fruits and acts as a first defence response against oxidative stress. The study associated the increase in ascorbic acid up to 8 weeks with the de novo biosynthesis and regeneration due to increase in stress after harvest and during initial storage weeks of the fruits.

In another study by Li, Ban et al. (2012), ascorbic acid content in honey pomelo slices underwent a substantial depletion under super-atmospheric O₂ (75%), whereas, it remained higher value and decreased slightly during storage under passive and low O₂ atmosphere. The magnitude of AA content degradation related to the O₂ concentration inside the packages. The study further associated the different changes of ascorbic acid content under different atmospheres may be explained through the low O₂ and / or high CO₂ concentration, contributing to increase oxidative stress and, in turn, peroxidase activity and ascorbic acid oxidation. Critical evaluation of the above studies showed that the application of super-atmospheric O₂ can causes a substantial reduction of AA concentration due to oxidation. However, super-atmospheric O₂ showed beneficial effects towards other quality parameters. By taking this in to consideration, further investigation is unavoidable for the practical application of super-atmospheric O₂ atmospheres by using different packaging material.

4. Volatile organic compounds

The increase in the synthesis and formation of volatiles organic compounds (VOCs) can be explained by an acceleration of metabolism

as a response to storage atmosphere, which could lead to stress and disrupt enzyme systems (Amaro, Beaulieu, Grimm, Stein, & Almeida, 2012; Giuggioli et al., 2015). Excessively low O₂ atmospheres may trigger anaerobic metabolism in fresh and FC fruit resulting in an increase of fermentation (Cortellino et al., 2015), initiate the development of hazardous anaerobic conditions, membrane damage or further it could cause cell injury and senescence (Li & Zhang, 2015). In this condition, accumulation of alcohol that leads to the production of ethyl esters and the reduction of other esters could be accelerated (Giuggioli et al., 2015). The increase of VOCs at low O₂ could be associated with exceeding the range of tolerance induced anaerobic metabolism, which can stimulate the production of fermentative compounds (Zhang et al., 2013).

On the other hand, elevated and super-atmospheric O₂ concentration could affect the synthesis and accumulation of some VOCs (acetaldehyde, ethanol and ethyl esters) associated with respiratory metabolism. Accumulation of acetaldehyde is the first indicator of fermentative metabolism and the most harmful, which can rapidly convert into ethanol by the enzyme alcohol dehydrogenase (ADH) (Thewes, Both, Brackmann, Weber, & de Oliveira Anese, 2015). A significant increase in ethanol and acetaldehyde concentrations may affect the sensory properties of the products (Manolopoulou & Varzakas, 2013). Giuggioli et al. (2015) reported the possible retention or increase of these VOCs under MAP using low-O₂ atmosphere for raspberry fruit. On the contrary, Teixeira et al. (2016) characterized super-atmospheric O₂ concentration (100%) with a higher relative concentration of Limonene.

Cortellino et al. (2015) reported the progressive ethanol concentration increase in apple under different MAP treatments. Samples packaged under 80% Ar, 20% CO₂ atmosphere showed the highest production of ethanol throughout the storage time. At the end of shelf-life (11 days) apples under 80% Ar, 20% CO₂ and 65% N₂O 25% Ar, 5% CO₂, 5% O₂ alternative MAPs were characterized by higher values of ethanol content than samples under 99% N₂, 1% O₂ and 90% N₂ 5% O₂ 5% CO₂ conventional MAPs, while apple slices packed under normal air developed limited quantity of ethanol. The overall results underlined that the production of ethanol is greatly influenced by the packaging atmosphere.

Belay et al. (2017) observed highest VOCs composition for arils stored under super-atmospheric O₂ and enriched CO₂ (70% O₂, 10% CO₂) concentrations, while the lowest composition was found in arils stored under air at the end of storage (day 12). The increase in the synthesis and formation of VOCs can be explained by an acceleration of metabolism as a response to wounding (Amaro et al., 2012), or due to high CO₂ concentration which leads to disrupt enzyme systems, such as the lipoxygenase pathway (Giuggioli et al., 2015). These findings clearly show the effect of CO₂ on the production of alcohol volatile compounds, with a progressive increase in alcohol production as CO₂ level increased under super-atmospheric O₂. Furthermore, the results indicated that the production of volatile compounds during storage was directly proportional to the CO₂ production and inversely proportional to O₂ consumption. For VOCs the production of fermentative metabolites has been described by the presence of extreme atmospheric conditions, which normally triggered by stress, accelerated metabolism, and disruption of enzyme. Hence avoiding unfavourable atmospheres is important to prevent the emission of fermentative metabolites.

5. Molecular changes related to fruit metabolomics and transcriptional responses under MAP

During molecular changes, cells undergo a major functional transformation from carbon assimilation and other anabolic reactions to degradation of macromolecules such as proteins, lipids, and nucleic acids that results in cell dysfunction, structural disintegration and cell death (Yun et al., 2012). These dynamic processes involve a series of molecular changes under gene regulation (Tang, Deng, Hu, Chen, & Li,

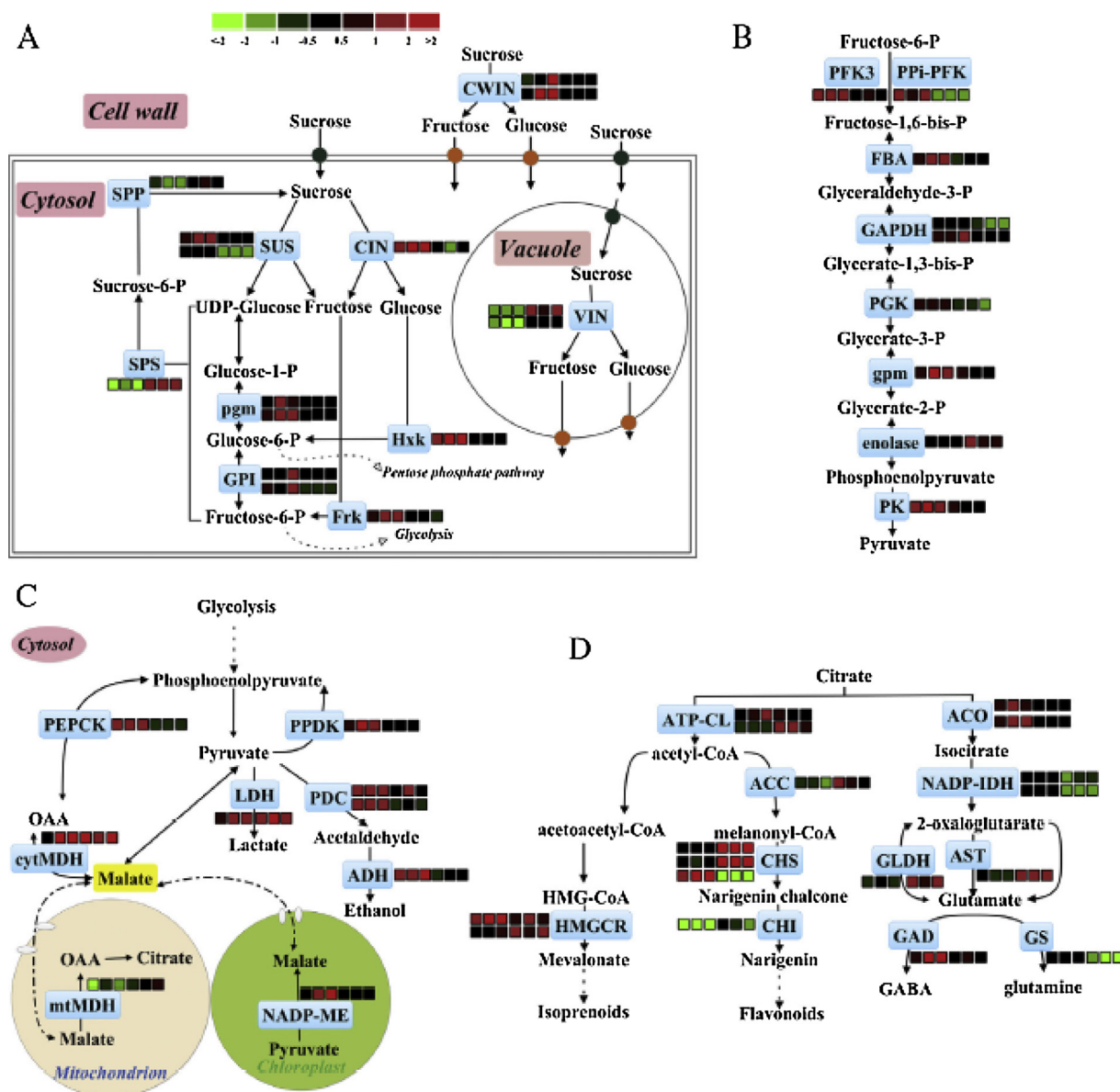


Fig. 1. Transcriptomic mapping of genes associated with primary metabolism during postharvest storage of Powell orange fruit.

Metabolic pathways related to sucrose degradation (A), glycolysis (B), malate degradation (C) and citrate metabolism (D) during postharvest storage in Powell fruits. Expression profile for each gene was shown in coloured blocks. The first 3 squares represent mRNA levels at 30, 60 and 90 days under room temperature, and the following squares represent mRNA levels under low temperature compared to control. The expression changes represented by red colours/green colours correspond to up-/down-regulation of these genes. Adopted from Tang et al. (2016).

2016). Hence, the knowledge of identifying of genes and quantitative profiling for these metabolites is of major importance for biomarkers discovery during postharvest has significant implications for food supply, nutrition, and health (Tang et al., 2016). Pathways related to biosynthesis and catabolism of these metabolites, such as sucrose metabolism, glycolysis, TCA cycle and other pathways, were dramatically regulated during postharvest (Ma et al., 2013). In various studies, this interconnections mostly presented by genetic mapping of differently expressed genes associated with the response to the postharvest treatments as shown in Fig. 1. Therefore, analysis of gene expression during postharvest storage can give important insights into the transcriptional regulation of metabolism (Rosales et al., 2016; Tang et al., 2016).

Liu et al. (2015) studied the effect of storage atmosphere (pure O_2) on the gene expression of litchi fruit. The study found the significant increase in *LcAtpB* gene expression after harvest, which acted as a marker of senescence. Pure oxygen treatment stimulated respiration intensity and down regulated the expression of *LcAtpB*. Treatments that

downregulated the expression of this gene could postpone the senescence process of litchi fruit. *LcAtpB* could be a good candidate gene for breeding new litchi cultivars with increased ATP supplies and longer storage lives. To determine whether high CO_2 concentration applied to maintain table grape quality modulate accumulation, and how the length of the treatment could affect these changes, Romero et al. (2018) analysed the expression of genes by qRT-PCR in the skin of non-treated and treated table grapes. The authors highlight the duration of the gaseous treatment influenced its effect on maintaining table grape quality. Furthermore, the treatment with high CO_2 concentration is an active process in which HSPs could play a role in preventing the denaturation and dysfunction of many proteins. The effect of high levels of CO_2 for activation of the expression of transcription factors also reported by (Rosales et al., 2016; Vazquez-Hernandez, Navarro, Sanchez-Ballesta, Merodio, & Escibano, 2018). Sanhueza, Vizoso, Balic, Campos-Vargas, and Meneses (2015) analysed transcriptomic data obtained from “Red Pearl” nectarine fruits. The analysis was focused on a

comparison of ripening and the effect of storage atmospheres on mealiness prevention. Because of the connection between the use of different atmospheres and the reduction in ethylene synthesis, the study identified candidate genes that could explain the positive effect of the storage atmospheres on mealiness prevention.

Blanch, Rosales, Palma et al. (2015) studied the effect of low-temperature and high-CO₂ levels on fermentative metabolism. The study analysed the expression of genes encoding using RT-qPCR for pyruvate decarboxylase (PDC) and alcohol dehydrogenase (ADH) in strawberries stored for 3 and 6 days under 0, 20, or 40% CO₂ in 20% O₂. The results showed that, the expression of PDC at 0 °C without added CO₂ induced a progressive accumulation of its transcripts. However, in fruit exposed to 20 and 40% CO₂ PDC expression was similar to that found in fruit at harvest, suggesting the application of high-CO₂ concentration prevented the increase in PDC transcription induced by low temperature. Cheng et al. (2015) studied the expression patterns of genes for Pear fruits. In this study, the authors differentiate the response of the genes at different storage atmospheres. The results of quantitative RT-PCR suggested that storage under 10-µm-thick low-density polyethylene film down regulated and storage under 30-µm-thick low-density polyethylene film up regulated the expression of *PAL1*, *PAL2* and *PbPPO1*. The expression pattern of *PAL1*, *PAL2* and *PbPPO1* was correlated with changes in core browning, phenolic contents and PPO activity, and this finding implied that these genes were involved in the core browning process under MAP storage.

Rosales et al. (2016) studied the application of high CO₂ concentration for 3 days at 0 °C in early-harvested grapes. The presence of high CO₂ significantly induced the expression of genes encoding mainly transcription factors associated with different GO terms such as “response to chitin,” “ethylene mediated signalling pathway,” “response to bacterium,” and “regulation of transcription, DNA-dependent” as well as response to salicylic acid, jasmonic and abscisic acid stimulus. These observations suggest that susceptibility to postharvest disorders such as internal browning are linked to cell wall modifications. In various studies the transcriptional responses of various fruit to temperature and gas concentrations depend on the stage of maturity, and physiological response (Liu et al., 2018; Rosales et al., 2016; Vazquez-Hernandez et al., 2018). By using transcriptional data, identifying a gene that can be regulated at a specific biochemical process and differentiating the response of the gene at different storage atmospheres and packaging materials is possible. However, gene expression studies have been extensively reported only on preharvest studies and much scientific investigation is required to understand the gene expression during postharvest treatments and handling.

6. Conclusions

This review examined the effects of active modified atmosphere packaging (MAP) for preservation of physicochemical quality attributes of fresh and FC fruit and highlighted the molecular response of produce exposed to specific atmospheres. The exposure of fresh and FC fruit to initially modified atmosphere involves several changes since the produce physiological and metabolic process continues during postharvest. Under specific conditions, the packaging atmospheres may lead to a wide of range of effects and responses including reduced respiration of produce, changes in colour, textural attributes and concentration of bioactive compounds, as the production of fermentative metabolites, which are responsible for unpleasant off-flavours and odours. However, a contradiction exists in the literature regarding the benefit of active MAPs; this demonstrates the importance of research focusing on individual fruit type under different storage conditions. Depending on MAP type and product characteristics, the literature continues to look for alternatives approaches to understand the molecular mechanisms aiming to slow down biochemical and physiological functions and degradation of macromolecules. These dynamic processes involve a series of molecular changes under gene expression and regulation through

several components of signal transduction pathways. In this regard, transcriptomic approach has gaining popularity to identifying a responsive gene that can be regulated at a specific postharvest treatment. The information from the transcriptomic analysis could be useful for biomarker discovery during modified atmosphere packaging of fruit, with the goal of slowing down senescence, ripening and reducing quality deterioration; however, there is a dearth of information in the literature in this area. Thus, further research is recommended for various fruits on the implementation of genomic tools to identify candidate genes for breeding new cultivars suitable for maintaining quality and safety of produce under packaging conditions.

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References

- Adiletta, G., Liguori, L., Albanese, D., Russo, P., Di Matteo, M., & Crescitelli, A. (2017). Soft-seeded pomegranate (*Punica granatum* L.) varieties: Preliminary characterization and quality changes of minimally processed arils during storage. *Food and Bioprocess Technology*, 10(9), 1631–1641.
- Akbudak, B., Akbudak, N., Seniz, V., & Eris, A. (2012). Effect of pre-harvest harpin and modified atmosphere packaging on quality of cherry tomato cultivars “Alona” and “Cluster”. *British Food Journal*, 114, 180–196.
- Amaro, A. L., Beaulieu, J. C., Grimm, C. C., Stein, R. E., & Almeida, D. P. (2012). Effect of oxygen on aroma volatiles and quality of fresh-cut cantaloupe and honeydew melons. *Food Chemistry*, 130, 49–57.
- Banda, K., Caleb, O. J., Jacobs, K., & Opara, U. L. (2015). Effect of active-modified atmosphere packaging on the respiration rate and quality pomegranate arils (cv. Wonderful). *Postharvest Biology and Technology*, 109, 97–105.
- Baenas, N., García-Viguera, C., & Moreno, D. (2014). Elicitation: a tool for enriching the bioactive composition of foods. *Molecules*, 19(9), 13541–13563.
- Beckles, D. M. (2012). Factors affecting the postharvest soluble solids and sugar content of tomato (*Solanum lycopersicum* L.) fruit. *Postharvest Biology and Technology*, 63, 129–140.
- Belay, Z. A., Caleb, O. J., & Opara, U. L. (2017). Impacts of low and super-atmospheric oxygen concentrations on quality attributes, phytonutrient content and volatile compounds of minimally processed pomegranate arils (cv. Wonderful). *Postharvest Biology and Technology*, 124, 119–127.
- Belay, Z. A., Caleb, O. J., Mahajan, P. V., & Opara, U. L. (2018). Design of active modified atmosphere and humidity packaging (MAHP) for “Wonderful” pomegranate arils. *Food and Bioprocess Technology*, 11(8), 1478–1494.
- Bessemans, N., Verboven, P., Verlinden, B. E., & Nicolaï, B. M. (2016). A novel type of dynamic controlled atmosphere storage based on the respiratory quotient (RQ-DCA). *Postharvest Biology and Technology*, 115, 91–102.
- Blanch, M., Rosales, R., Mateos, R., Perez-Gago, M. B., Sanchez-Ballesta, M. T., Escribano, M. I., et al. (2015). Effects of high CO₂ levels on fermentation, peroxidation, and cellular water stress in fragaria vesca stored at low temperature in conditions of unlimited O₂. *Journal of Agricultural and Food Chemistry*, 63(3), 761–768.
- Blanch, M., Rosales, R., Palma, F., Sanchez-Ballesta, M. T., Escribano, M. I., & Merodio, C. (2015). CO₂-driven changes in energy and fermentative metabolism in harvested strawberries. *Postharvest Biology and Technology*, 110, 33–39.
- Bovi, G. G., Caleb, O. J., Linke, M., Rauh, C., & Mahajan, P. V. (2016). Transpiration and moisture evolution in packaged fresh horticultural produce and the role of integrated mathematical models: A review. *Biosystems Engineering*, 150, 24–39.
- Brackmann, A., Thewes, F. R., Anese, R. O., Ceconi, D. L., & Júnior, W. L. (2013). Active modified atmosphere and 1-methylcyclopropene during shelf life on ‘Fuyu’ persimmons. *Bioscience Journal*, 29, 1912–1919.
- Caleb, O. J., Mahajan, P. V., Manley, M., & Opara, U. L. (2013). Evaluation of parameters affecting modified atmosphere packaging engineering design for pomegranate arils. *International Journal of Food Science and Technology*, 48(11), 2315–2323.
- Caleb, O. J., Mahajan, P. V., Al-Said, F. A. J., & Opara, U. L. (Mahajan, Al-Said et al., 2013a). Modified atmosphere packaging technology of fresh and fresh-cut produce and the microbial consequences—A review. *Food and Bioprocess Technology*, 6(2), 303–329.
- Caleb, O. J., Mahajan, P. V., Al-Said, F. A. J., & Opara, U. L. (Mahajan, Al-Said et al., 2013b). Transpiration rate and quality of pomegranate arils as affected by storage conditions. *CyTA Journal of Food*, 11(3), 199–207.
- Caleb, O. J., Opara, U. L., Mahajan, P. V., Manley, M., Mokwena, L., & Tredoux, A. G. (2013). Effect of modified atmosphere packaging and storage temperature on volatile composition and postharvest life of minimally-processed pomegranate arils (cvs. ‘Acco’ and ‘Herskowitz’). *Postharvest Biology and Technology*, 79, 54–61.
- Caleb, O. J., Opara, U. L., & Witthuhn, C. R. (2012). Modified atmosphere packaging of pomegranate fruit and arils: A review. *Food and Bioprocess Technology*, 5(1), 15–30.
- Chaudhary, P. R., Jayaprakasha, G. K., Porat, R., & Patil, B. S. (2015). Influence of

- modified atmosphere packaging on 'star ruby' grapefruit phytochemicals. *Journal of Agricultural and Food Chemistry*, 63(3), 1020–1028.
- Chen, L., & Opara, U. L. (2013a). Texture measurement approaches in fresh and processed foods - a review. *Food Research International*, 51(2), 823–835.
- Chen, L., & Opara, U. L. (2013b). Approaches to analysis and modeling texture in fresh and processed foods - a review. *Journal of Food Engineering*, 119(3), 497–507.
- Chen, M., Lin, H., Zhang, S., Lin, Y., Chen, Y., & Lin, Y. (2015). Effects of adenosine triphosphate (ATP) treatment on postharvest physiology, quality and storage behaviour of longan fruit. *Food and Bioprocess Technology*, 8(5), 971–982.
- Cheng, Y., Liu, L., Zhao, G., Shen, C., Yan, H., Guan, J., et al. (2015). The effects of modified atmosphere packaging on core browning and the expression patterns of PPO and PAL genes in 'Yali' pears during cold storage. *LWT-Food Science and Technology*, 60(2), 1243–1248.
- Choudhury, F. K., Rivero, R. M., Blumwald, E., & Mittler, R. (2017). Reactive oxygen species, abiotic stress and stress combination. *The Plant Journal*, 90(5), 856–867.
- Cortellino, G., Gobbi, S., Bianchi, G., & Rizzolo, A. (2015). Modified atmosphere packaging for shelf life extension of fresh-cut apples. *Trends in Food Science and Technology*, 46(2), 320–330.
- Fagundes, C., Moraes, K., Pérez-Gago, M. B., Palou, L., Maraschin, M., & Monteiro, A. R. (2015). Effect of active modified atmosphere and cold storage on the postharvest quality of cherry tomatoes. *Postharvest Biology and Technology*, 109, 73–81.
- Fante, C. A., Carolina, A., & Boas, V. (2014). Modified atmosphere efficiency in the quality maintenance of Eva apples. *Food Science and Technology*, 34, 309–314.
- Ghasemnezhad, M., Sherafati, M., & Payvast, G. A. (2011). Variation in phenolic compounds, ascorbic acid and antioxidant activity of five coloured bell pepper (*Capsicum annuum*) fruits at two different harvest times. *Journal of Functional Foods*, 3(1), 44–49.
- Ghasemnezhad, M., Zareh, S., Rassa, M., & Sajedi, R. H. (2013). Effect of chitosan coating on maintenance of aril quality, microbial population and PPO activity of pomegranate (*Punica granatum* L. cv. Tarom) at cold storage temperature. *Journal of the Science of Food and Agriculture*, 93(2), 368–374.
- Giuggioli, N. R., Girgenti, V., Baudino, C., & Peano, C. (2015). Influence of modified atmosphere packaging storage on postharvest quality and aroma compounds of strawberry fruits in a short distribution chain. *Journal of Food Processing and Preservation*, 39, 3154–3164.
- Hussein, Z., Caleb, O. J., & Opara, U. L. (2015). Perforation-mediated modified atmosphere packaging of fresh and minimally processed produce-A review. *Food Packaging and Shelf Life*, 6, 7–20.
- Hussein, Z., Caleb, O. J., Jacobs, K., Manley, M., & Opara, U. L. (2015). Effect of perforation-mediated modified atmosphere packaging and storage duration on physicochemical properties and microbial quality of fresh minimally processed 'Acco' pomegranate arils. *LWT-Food Science and Technology*, 64(2), 911–918.
- Huyskens-Keil, S., & Herppich, W. B. (2013). High CO₂ effects on postharvest biochemical and textural properties of white asparagus (*Asparagus officinalis* L.) spears. *Postharvest Biology and Technology*, 75, 45–53.
- Jo, Y. H., An, D. S., & Lee, D. S. (2014). Active air flushing in a sensor-controlled fresh produce container system to maintain the desired modified atmosphere. *Biosystems Engineering*, 125, 122–127.
- Jouki, M., & Khazaei, N. (2014). Effect of low-dose gamma radiation and active equilibrium modified atmosphere packaging on shelf life extension of fresh strawberry fruits. *Food Packaging and Shelf Life*, 1(1), 49–55.
- Li, D., Li, L., Xiao, G., Limwachiranon, J., Xu, Y., Lu, H., et al. (2018). Effects of elevated CO₂ on energy metabolism and γ -aminobutyric acid shunt pathway in postharvest strawberry fruit. *Food Chemistry*, 281–289.
- Li, L., Ban, Z., Li, X., Wang, X., & Guan, J. (2012). Phytochemical and microbiological changes of honey pomelo (*Citrus grandis* L.) slices stored under super-atmospheric oxygen, low-oxygen and passive modified atmospheres. *International Journal of Food Science and Technology*, 47(10), 2205–2211.
- Li, T., & Zhang, M. (2015). Effects of modified atmosphere package (MAP) with a silicon gum film window on the quality of stored green asparagus (*Asparagus officinalis* L.) spears. *LWT-Food Science and Technology*, 60(2), 1046–1053.
- Li, W. L., Li, X. H., Fan, X., Tang, Y., & Yun, J. (2012). Response of antioxidant activity and sensory quality in fresh-cut pear as affected by high O₂ active packaging in comparison with low O₂ packaging. *Food Science and Technology International*, 18(3), 197–205.
- Li, X., Jiang, Y., Li, W., Tang, Y., & Yun, J. (2014). Effects of ascorbic acid and high oxygen modified atmosphere packaging during storage of fresh-cut eggplants. *Food Science and Technology International*, 20(2), 99–108.
- Liguori, G., D'Aquino, S., Sortino, G., De Pasquale, C., & Inglesse, P. (2015). Effects of passive and active modified atmosphere packaging conditions on quality parameters of minimally processed table grapes during cold storage. *Journal of Berry Research*, 5(3), 131–143.
- Liu, T., Wang, H., Kuang, J., Sun, C., Shi, J., Duan, X., et al. (2015). Short-term anaerobic, pure oxygen and refrigerated storage conditions affect the energy status and selective gene expression in litchi fruit. *LWT-Food Science and Technology*, 60(2), 1254–1261.
- Lu, H., Wang, K., Wang, L., Li, D., Yan, J., Ban, Z., et al. (2018). Effect of super-atmospheric oxygen exposure on strawberry (*Fragaria ananassa* Fuch.) volatiles, sensory and chemical attributes. *Postharvest Biology and Technology*, 142, 60–71.
- Liu, X., Wang, T., Chen, L., Li, L., Wang, Y., Li, X., & Xing, Y. (2018). Transcriptomic and gene expression changes in response to postharvest surface pitting in 'Lingwu Long' jujube fruit. *Horticulture, Environment, and Biotechnology*, 59(1), 59–70.
- Ma, Q., Ding, Y., Chang, J., Sun, X., Zhang, L., Wei, Q., et al. (2013). Comprehensive insights on how 2,4-dichlorophenoxyacetic acid retards senescence in post-harvest citrus fruits using transcriptomic and proteomic approaches. *Journal of Experimental Botany*, 65(1), 61–74.
- Maghouthi, M., Gómez, P. A., Mostofi, Y., Zamani, Z., Artés-Hernández, F., & Artés, F. (2013). Combined effect of heat treatment, UV-C and super-atmospheric oxygen packing on phenolics and browning related enzymes of fresh-cut pomegranate arils. *LWT-Food Science and Technology*, 54, 389–396.
- Maghouthi, M., Mostofi, Y., Zamani, Z., Talaie, A., Boojar, M., & Gómez, P. A. (2014). Influence of hot-air treatment, super-atmospheric O₂ and elevated CO₂ on bioactive compounds and storage properties of fresh-cut pomegranate arils. *International Journal of Food Science and Technology*, 49, 153–159.
- Mahajan, P., Rux, G., Caleb, O., Linke, M., Herppich, W., & Geyer, M. (2015). Mathematical model for transpiration rate at 100% humidity for designing modified humidity packaging. September *Acta Horticulturae*, 1141, 269–274.
- Manolopoulou, E., & Varzakas, T. H. (2013). Effect of modified atmosphere packaging (MAP) on the quality of 'ready-to-eat' shredded cabbage. *International Journal of Agricultural and Food Research*, 2(3).
- Martínez-Romero, D., Castillo, S., Guillen, F., Díaz-Mula, H. M., Zapata, P. J., Valero, D., et al. (2013). Aloe vera gel coating maintains quality and safety of ready-to-eat pomegranate arils. *Postharvest Biology and Technology*, 86, 107–112.
- Molinu, M. G., Dore, A., Palma, A., D'Aquino, S., Azara, E., Rodov, V., et al. (2016). Effect of super-atmospheric oxygen storage on the content of phytonutrients in 'Sanguinello Comune' blood orange. *Postharvest Biology and Technology*, 112, 24–30.
- Ngobo, M. E., Delele, M. A., Pathare, P. B., Chen, L., Opara, U. L., & Meyer, C. J. (2012). Moisture loss characteristics of fresh table grapes packed in different film liners during cold storage. *Biosystems Engineering*, 113(4), 363–370.
- Ochoa-Velasco, C. E., & Guerrero-Beltrán, J. A. (2014). Postharvest quality of peeled prickly pear fruit treated with acetic acid and chitosan. *Postharvest Biology and Technology*, 92, 139–145.
- Opara, U. L., Hussein, Z., & Caleb, O. J. (2017). Phytochemical properties and antioxidant activities of minimally processed 'Acco' pomegranate arils as affected by perforation-mediated modified atmosphere packaging. *Journal of Food Processing and Preservation*, 41(3), e12948.
- Opara, U. L., Hussein, Z., Caleb, O. J., & Mahajan, P. V. (2015). Investigating the effect of perforation and storage temperature on water vapour transmission rate of packaging film; experimental and modelling approaches. *Wulfenia Journal*, 22, 498–509.
- Opara, U. L., & Pathare, P. B. (2014). Bruise damage measurement and analysis of fresh horticultural produce - A review. *Postharvest Biology and Technology*, 91, 9–24.
- Opara, L. U. (2007). Bruise susceptibilities of 'Gala' apples as affected by orchard management practices and harvest date. *Postharvest Biology and Technology*, 43(1), 47–54.
- Palma, A., Continella, A., La Malfa, S., Gentile, A., & D'Aquino, S. (2015). Overall quality of ready-to-eat pomegranate arils processed from cold stored fruit. *Postharvest Biology and Technology*, 109, 1–9.
- Paniagua, A. C., East, A. R., Hindmarsh, J. P., & Heyes, J. (2013). Moisture loss is the major cause of firmness change during postharvest storage of blueberry. *Postharvest Biology and Technology*, 79, 13–19.
- Pathare, P. B., Opara, U. L., & Al-Said, F. A.-J. (2013). Colour measurement and analysis in fresh and processed foods: A review. *Food and Bioprocess Technology*, 6(1), 36–60.
- Romero, I., Casillas-Gonzalez, A. C., Carrazana-Villalba, S. J., Escribano, M. I., Merodio, C., & Sanchez-Ballesta, M. T. (2018). Impact of high CO₂ levels on heat shock proteins during postharvest storage of table grapes at low temperature. Functional in vitro characterization of VVIHSP18. 1. *Postharvest Biology and Technology*, 145, 108–116.
- Rosales, R., Romero, I., Fernandez-Caballero, C., Escribano, M. I., Merodio, C., & Sanchez-Ballesta, M. T. (2016). Low temperature and short-term high-CO₂ treatment in postharvest storage of table grapes at two maturity stages: Effects on transcriptome profiling. *Frontiers in Plant Science*, 7, 1020.
- Rux, G., Mahajan, P. V., Linke, M., Pant, A., Sänglerlaub, S., Caleb, O. J., et al. (2016). Humidity-regulating trays: Moisture absorption kinetics and applications for fresh produce packaging. *Food and Bioprocess Technology*, 9(4), 709–716.
- Sanhueza, D., Vizoso, P., Balic, I., Campos-Vargas, R., & Meneses, C. (2015). Transcriptomic analysis of fruit stored under cold conditions using controlled atmosphere in *Prunus persica* cv. "Red Pearl". *Frontiers in Plant Science*, 6, 788.
- Scherer, R., Rybka, A. C. P., Ballus, C. A., Meinhardt, A. D., Teixeira Filho, J., & Godoy, H. T. (2012). Validation of a HPLC method for simultaneous determination of main organic acids in fruits and juices. *Food Chemistry*, 135(1), 150–154.
- Silveira, A. C., Aranedo, C., Hinojosa, A., & Escalona, V. H. (2014). Effect of non-conventional modified atmosphere packaging on fresh cut watercress (*Nasturtium officinale* R. Br.) quality. *Postharvest Biology and Technology*, 92, 114–120.
- Soltani, M., Alimardani, R., Mobli, H., & Mohtasebi, S. S. (2015). Modified atmosphere packaging: A progressive technology for shelf-life extension of fruits and vegetables. *Journal of Applied Packaging Research*, 7(3), 2.
- Tang, N., Deng, W., Hu, N., Chen, N., & Li, Z. (2016). Metabolite and transcriptomic analysis reveals metabolic and regulatory features associated with Powell orange pulp deterioration during room temperature and cold storage. *Postharvest Biology and Technology*, 112, 75–86.
- Tayyari, F., Khazaei, J., Rajaei, P., & Jouki, M. (2017). Effects of modified atmosphere packaging systems, low temperature and storage time on the quality of fresh minimally processed pomegranate arils. *Carpathian Journal of Food Science and Technology*, 9(1).
- Teixeira, G. H., Júnior, L. C. C., Ferraudo, A. S., & Durigan, J. F. (2016). Quality of guava (*Psidium guajava* L. cv. Pedro Sato) fruit stored in low O₂ controlled atmospheres is negatively affected by increasing levels of CO₂. *Postharvest Biology and Technology*, 111, 62–68.
- Thewes, F. R., Both, V., Brackmann, A., Weber, A., & de Oliveira Anese, R. (2015). Dynamic controlled atmosphere and ultralow oxygen storage on 'Gala' mutants quality maintenance. *Food Chemistry*, 188, 62–70.
- Turfan, Ö., Turkyilmaz, M., Yemis, O., & Ozkan, M. (2011). Anthocyanin and colour changes during processing of pomegranate (*Punica granatum* L., cv. Hicaznar) juice from sacs and whole fruit. *Food Chemistry*, 129, 1644–1651.
- Vazquez-Hernandez, M., Navarro, S., Sanchez-Ballesta, M. T., Merodio, C., & Escribano, M. I. (2018). Short-term high CO₂ treatment reduces water loss and decay by

- modulating defense proteins and organic osmolytes in Cardinal table grape after cold storage and shelf life. *Scientia Horticulturae*, 234, 27–35.
- Waghmare, R. B., & Annapure, U. S. (2013). Combined effect of chemical treatment and/or modified atmosphere packaging (MAP) on quality of fresh-cut papaya. *Postharvest Biology and Technology*, 85, 147–153.
- Wang, Y., & Sugar, D. (2013). Internal browning disorder and fruit quality in modified atmosphere packaged 'Bartlett' pears during storage and transit. *Postharvest Biology and Technology*, 83, 72–82.
- Yin, X. R., Xie, X. L., Xia, X. J., Yu, J. Q., Ferguson, I. B., Giovannoni, J. J., et al. (2016). Involvement of an ethylene response factor in chlorophyll degradation during citrus fruit degreening. *The Plant Journal*, 86(5), 403–412.
- Yun, Z., Jin, S., Ding, Y., Wang, Z., Gao, H., Pan, Z., et al. (2012). Comparative transcriptomics and proteomics analysis of citrus fruit, to improve understanding of the effect of low temperature on maintaining fruit quality during lengthy post-harvest storage. *Journal of Experimental Botany*, 63(8), 2873–2893.
- Zhang, B. Y., Samapundo, S., Pothakos, V., de Baenst, I., Sürengil, G., Nosedá, B., et al. (2013). Effect of atmospheres combining high oxygen and carbon dioxide levels on microbial spoilage and sensory quality of fresh-cut pineapple. *Postharvest Biology and Technology*, 86, 73–84.
- Zhang, M., Meng, X., Bhandari, B., & Fang, Z. (2016). Recent developments in film and gas research in modified atmosphere packaging of fresh foods. *Critical Reviews in Food Science and Nutrition*, 56(13), 2174–2182.
- Zhang, M., Meng, X., Bhandari, B., Fang, Z., & Chen, H. (2015). Recent application of modified atmosphere packaging (MAP) in fresh and fresh-cut foods. *Food Reviews International*, 31(2), 172–193.