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Biological and postharvest interventions to manage the ethylene in fruit: a review

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Ethylene, the gaseous ripening hormone, notably influences the postharvest physiology of the fruit. The pronounced effect of ethylene on postharvest physiology ranges from beneficial to unacceptable, with substantial commercial repercussions. Climacteric fruit undergoes an ethylene burst with the onset of ripening, and this autocatalytic ethylene production leads to accelerated ripening and senescence of fruit. Thus, the fruit becomes soft, mealy, and prone to pathogen attack that ultimately leads to high postharvest losses during handling, storage, and marketing. The key to appropriate handling, storage, and marketing of fruit lies largely in the successful management of ethylene. Biological interventions such as gene silencing, gene editing and recently the gene modifications through CRISPR/Cas9 are widely accepted and being used to regulate ethylene in fruit. Nevertheless, postharvest interventions and use of novel molecules such as 1-MCP, polyamines, salicylic acid, and ozone have received commercial status for controlling ethylene action in fruit. Use of metal-based catalysts at low temperature has been considered as a safer approach. This review focuses on the history, biosynthesis, action mechanism and techniques employed for useful modulation of ethylene biosynthesis and action in harvested fruit.

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Sustainability spotlight

Ensuring safe food production with maximum quality retention through eco-friendly sustainable means is extremely important. Ethylene is a key compound hormone which accelerates the ripening process and triggers senescence. Managing the ethylene in the food supply line is crucial in order to maintain food safety and postharvest loss. Use of a single technology and approach is insufficient to combat the problems but managing ethylene using available sustainable technologies in an integrated manner could be worthwhile and provide a sustainable solution. In this context, we have presented the available biological and postharvest interventions to manage ethylene biosynthesis as well as action during handling. Use of novel biological tools such as gene editing, RNA sequencing, CRISPR/Cas9 and phytohormones could provide alternative long-term solutions. In addition to that, use of physical treatments, irradiation, oxidative materials and altering the physiology by means of certain agents are also equally important. Our work emphasizes the importance of certain sustainable technologies for food safety as mentioned in the UN sustainable goals of food safety and sustainable agriculture (SDG2) and climate change (SDG13).

1. Introduction

Ethylene ($H_2C{=}CH_2$) is a gaseous hydrocarbon. As a plant hormone, it is unique and spectacular in its structural simplicity but dramatic diverse physiological effects, especially in post-harvest ripening and senescence of fruit.[1–3] In addition, the ethylene level in the storage atmosphere is also augmented inadvertently due to rotting fruit, injured plant tissue, motor exhaust pollution, industrial activities and microbial sources.[1,4]

Ethylene action is the primary determinant of the rate of loss in quality and marketability of fruit, particularly of climacteric type. Yet, non-climacteric fruit and vegetables are also sensitive to ethylene exposure displaying quality loss and increased susceptibility to decay and physiological disorders.[5]

Ethylene plays a key role in escalating the rates of postharvest quality deterioration by affecting skin colour, cell turgor and structural changes leading to loss of texture, increasing respiration rate and cell wall degrading enzyme activities.[1,2,6–8] The physiological activities in response to ethylene sensitivity are triggered at concentrations as low as ppm to ppb levels with threshold concentrations varying among different crops.[9] However, the effects of ethylene on postharvest physiology and storage vary with several factors such as pre-harvest conditions, fruit species, cultivar, ethylene concentration, exposure duration, temperature and relative humidity of storage.[10] Ethylene detection techniques such as gas chromatography, electrochemical methods, colorimetric and luminescence methods, laser-based

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sensors, organic field effect transistors and surface-enhanced Raman spectroscopy are being used to detect ethylene.[11]

Some biotechnological tools have also received significant attention and could be utilized. Use of gene editing, modifications and some of the latest CRISPR/Cas9 for gene modification has been employed in fresh produce.[12] A novel technology to develop mutants at genome specific sites in a variety of fruit plants to regulate fruit colour, quality traits, aroma and shelf life, CRISPR/Cas9 generates novel mutants that affect RIN protein accumulation and fruit ripening phenotypes in tomato.[13] Use of biological materials such as plant extracts, plant based novel biological molecules, phytohormones, edible coatings, micro-organisms and biofiltration could be effectively practiced in perishables to combat the negative effects associated with ethylene.

In addition to that, important pivotal approaches such as ethylene biosynthesis blocking agents (aminoethoxyvinyl glycine), ethylene action blocking agent (1-methylcyclopropene), ethylene scavenging agents (potassium permanganate, biofiltration, ozone), packaging scrubbers (titanium dioxide), adsorbents (zeolite) and plant based signaling molecules (brassinosteroids, salicylic acid, polyamines, *etc.*), and storage technologies are being commercially used.[14–17]

Thus, it is imperative to look upon postharvest physiology triggered/induced by ethylene, causing postharvest deterioration, rotting and quality changes. There is a need to incorporate comprehensive, practical, easy-to-adopt solutions in storage and supply chains with renewed interest and caution to encourage better management of perishable horticultural commodities during commerce. This review aims to compile, present and discuss the effects of ethylene in fruit after harvest and discuss recent studies and postharvest approaches to delay and inhibit ethylene action on horticultural commodities to slow down and prevent their deterioration by blocking biosynthesis, perception and/or scavenging, thus lowering the postharvest losses.

2. History of ethylene

In 1886, Dimitry Nikolayevich Neljubow, a graduate student, observed that abnormal growth of etiolated pea seedlings was due to ethylene released from lamps.[18] This is referred to as 'triple response' due to ethylene causing inhibition of hypocotyl and root cell elongation, radial swelling of the hypocotyl and increased curvature of the plumular hook region. In 1910, H. H. Cousins reported that during storage, bananas senesced/overripened at faster rates due to a volatile product emanating from oranges. Notably, R. Gane in 1934, with the advent of the gas chromatography technique, identified and reported that the volatile substance was ethylene. Methionine as the precursor of ethylene was established by the pioneering work of M. Lieberman and L. W. Mapson in 1964. Later, D. Adams and F. Yang established that S-adenosyl methionine (SAM) and 1-aminocyclopropane-1-carboxylic acid (ACC) are the intermediates in ethylene biosynthesis (Fig. 1). In the following years, the research interest in ethylene rocketed with the realization of its dramatic influence on fruit ripening and senescence and the associated economic and humongous postharvest loss impacts.

3. Ethylene biosynthesis and action

Ethylene is derived from amino acid L-methionine which is converted to S-adenosyl methionine (SAM) by SAM synthetase. SAM is a key methyl donor in plants and plays an important role in other biochemical pathways such as polyamine biosynthesis.[19] SAM is then converted to the cyclic non-protein amino acid ACC (1-aminocyclopropane-1-carboxylic acid) by the ACC synthase (ACS) present in the cytoplasm.[20] ACS also produces 5′-methylthioadenosine (MTA) which is recycled to methionine *via* a modified methionine cycle.[21] In the final step, the synthesis of ethylene requires oxygen to oxidize ACC to ethylene by ACC oxidase (ACO) with subsequent production of carbon dioxide and cyanide. The produced cyanide is converted to β-cyanoalanine by the enzyme β-cyanoalanine synthase to reduce the toxic effect of the accumulated cyanide during increased ethylene production.[22]

The produced ethylene binds with the receptors embedded in cells. The receptors remain active in the absence of ethylene, allowing normal growth of fruit attached to the plant.[23] However, with the onset of ripening, the produced ethylene binds with the receptors and switches them off. It has been suggested that two systems operate for ethylene regulation in climacteric fruit. System 1 produces a small amount of ethylene during the pre-climacteric period or early fruit growth stage in climacteric fruit and throughout the development and ripening in non-climacteric fruit. However, with the onset of fruit ripening system 2 operates in climacteric fruit that produces auto-stimulated massive ethylene evolution. However, exogenous application of ethylene to non-climacteric fruit during ripening may hasten the process in some cases.[24] In tomato fruit, it has been observed that genes *ACS6* and *ACS1A* are involved in system 1 which are down-regulated by ethylene, while *ACS2* and *ACS4* genes are involved in system 2 of ethylene production. Thus, the main reason behind discrete production of ethylene in pre-climacteric and climacteric phases is involvement of certain genes at a particular stage of fruit development.[25]

The ethylene signaling pathway includes both positive and negative regulators. The perception of ethylene takes place by a family of five membrane bound receptors: *ETR1*, *ETR2*, *ERS1*, *ERS2* and *EIN4*.[26] The binding of ethylene with its receptors takes place *via* a copper cofactor delivered by copper transporter *RAN1*. *CTR1* (constitutive triple response 1) gene, encoding a Raf-like protein kinase, suppresses the positive regulator and downstream responses of *EIN2* and *EIN3*/*EIL* transcription factors. When ethylene binds with the receptors, it does not activate *CTR1* but activation of *EIN2*, *EIN3*, and *EIL* occurs, leading to the induction of the ripening signal in fruit.[27] ERFs are transcription factors encoded by large families of plant transcription factors due to which a wide variation in ethylene response in climacteric and non-climacteric fruit exists.[25] A study conducted on tomato revealed that most ERFs are ethylene inducible and show

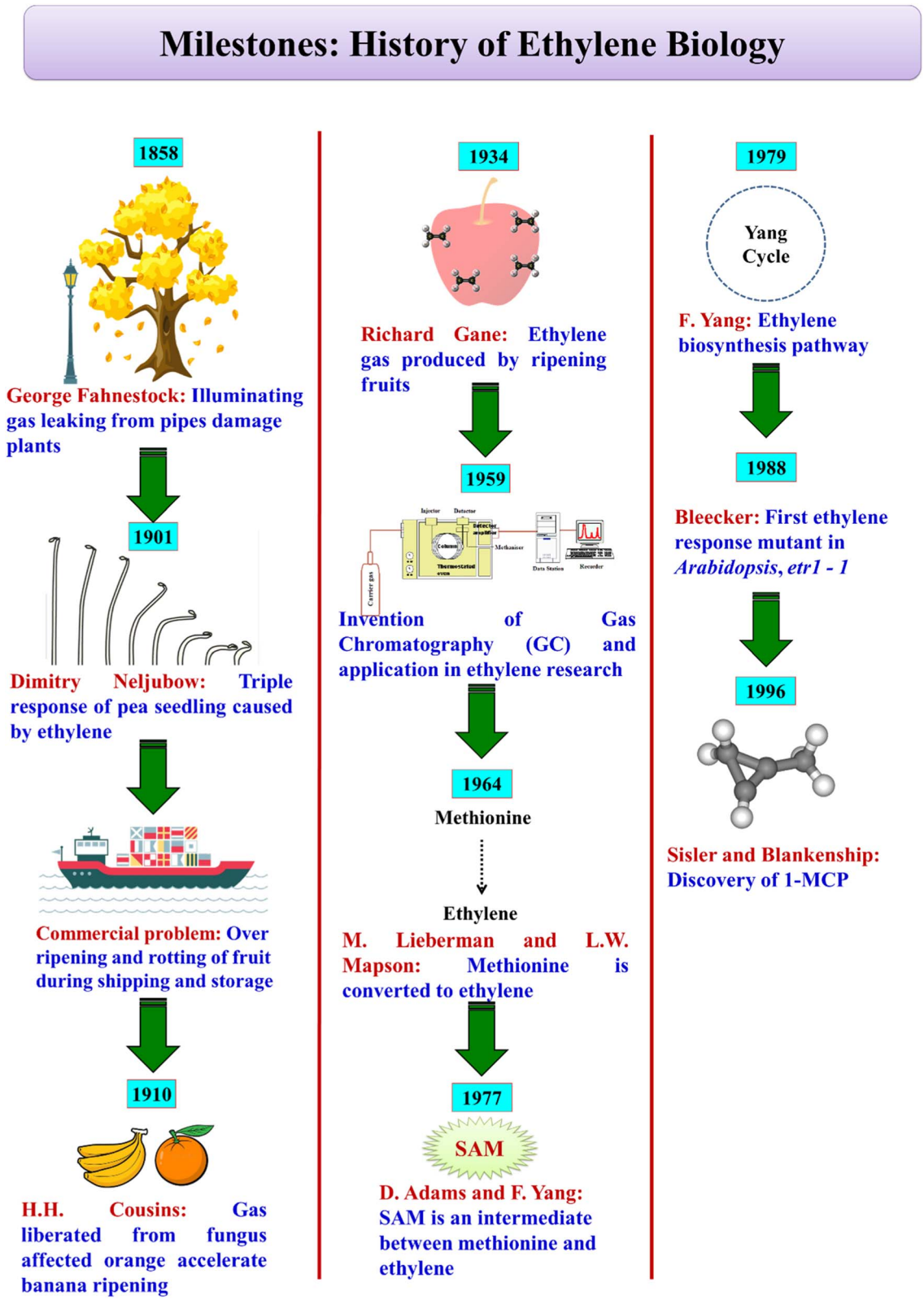

Fig. 1 History of ethylene biology.

a positive response towards ripening, which suggests that ERFs may represent the connecting link between signaling of ethylene and its regulation during fruit development and ripening. Hence, ERFs could also be used as one of the strategies to control the ethylene during fruit storage.[28] The transcriptional regulation of ethylene suggests a significant

difference between climacteric and non-climacteric signaling of ethylene by varying the number of transcription factors. A higher number of ETRs are reported in climacteric fruit while non-climacteric fruit were characterized by the earlier expression peak of ETRs.[29]

4. Management strategies for ethylene

4.1. Biotechnological approaches

Several biotechnological interventions have been made so far to suppress ethylene production in fruit. Ethylene biosynthesis involves the activity of ACC synthase (ACS) and ACC oxidase (ACO), which play a regulatory role in converting SAM to ACC and ACC to ethylene, respectively. Delay in fruit ripening can be done by incorporation of silencing genes coding for ACS and ACO or expression of genes coding for enzymes associated with breakdown of the ethylene precursor. RNA antisense technology is also an effective tool to regulate the expression of fruit ripening genes.[30,31] About 99.5% reduction in ethylene production by inhibition of ACC synthase mRNA was achieved in tomato by inserting a gene including the untranslated portions in an opposite orientation under the CaMV (cauliflower mosaic virus) 35S promoter.[32] In another study, about 87% suppression of ethylene production was achieved in tomato fruit by inserting the antisense version of ACC oxidase and overexpressing mRNA in an antisense orientation.[33] A similar approach of overexpressing an antisense ACC oxidase gene when used in Cantaloupe melon showed a 99% suppression in the ethylene level.[34] During this period in 1994, FlavrSavr® tomato was developed by Calgene Corporation which was the first genetically engineered whole food approved for commercial sale by the Food and Drug Administration (FDA).[35] In Cantaloupe Charentais melon, when antisense ACC oxidase gene was overexpressed, it showed more than 99% suppression in ethylene evolution.[36] In a similar study, Silva *et al.*[37] developed a transgenic melon that showed about 39-fold higher inhibition in ethylene production than that of wild-type by overexpression of an antisense ACC oxidase construct from apple. Application of antisense technology targeting ACC oxidase was also found to be effective in the suppression of ethylene by about 99.9% in muskmelon cv. Galia.[38] Some researchers targeted ACC deaminase to control ethylene production in tomato. Klee *et al.*[39] found 90% suppression in ethylene production and a delay in the climacteric peak by up to 3 days in tomato, in which the gene for ACC deaminase was inserted and overexpressed from *Pseudomonas chloraphis* 6G5.

Elevating the level of polyamines by biotechnological tools was also targeted by some researchers to reduce ethylene production as both the pathways are interlinked and SAM is the common precursor. The accumulation of polyamines (putrescine, spermidine and spermine) was enhanced in tomato by about 2-fold by overexpressing *ADC* (arginine decarboxylase) gene which showed about 44% reduction of ethylene production.[40] A similar approach to increase the level of polyamines in tomato was also used by overexpressing S-adenosyl methionine decarboxylase (*SAMdc*), ornithine decarboxylase (*ODC*) and spermidine synthase (*SpdSyn*) genes to suppress ethylene production.[1,41,42] Event 35-1-N in tomato was developed by Agritope Inc. in which a *sam-k* gene construct encoding SAM hydrolase was introduced leading to degradation of SAM and reduction in ethylene production.[43] Tomato event 1345-4 (trade name: Endless Summer) was developed by DNA Plant Technology Corporation by inserting an *ACS* gene construct that suppressed conversion of SAM to ACC. Monsanto developed event 8338 in tomato by inserting the ACC deaminase (*ACCd*) gene responsible for ACC metabolism. In 1995, the cultivation of tomato event 1345-4 was approved in USA by the FDA and APHIS. Nevertheless, it was cultivated for a limited period while events 8338 and 35-1-N was deregulated in 1995 and 1996, respectively. Melon events A and B were developed with delayed ripening and approved in 1999 by the FDA; however, their cultivation was not approved.[44] Likewise, tomato event Huafan No. 1 was developed in China by inserting an *anti-efe* (ethylene-forming enzyme) gene construct coding for an antisense RNA of ACO. It was approved in 1997 by the Ministry of Agriculture in China for cultivation, food and feed use.

Besides, CRISPR/Cas 9 gene editing technology has been used to regulate ripening and ethylene in climacteric fruit.[45,46] It is now widely accepted that CRISPR/Cas9 has become a popular technology for gene manipulation and complete gene modification because of its high efficiency, simplicity and low cost.[12] Many researchers used CRISPR/Cas9 for validation of functionality and inheritance of mutation of transcription factor RIPENING INHIBITOR (RIN) gene in tomato.[13] It has been observed that CRISPR/Cas9 mediated mutations at the RIN locus inhibited ripening in tomato fruit and extended its shelf life. Moreover, CRISPR/Cas9 mediated mutagenesis of RIN gene, lycopene desaturase (PDS), pectate lyases (PL), SlMYB12, and CLAVATA3 (CLV3) regulated the ripening and biochemical traits in fruit.[12]

4.2. Postharvest interventions for ethylene control

4.2.1. Physical treatments. There are several conventional and non-conventional ways to control ethylene evolution in fruit. Physical measures such as use of UV-C radiation, gamma irradiation, and hot water treatment are practiced to date in order to keep in check the ethylene evolution rate in harvested fruit (Table 1).

In the last few years, hot water and vapor heat treatments have drawn potential interest for reducing ethylene evolution, thus delaying the ripening and senescence of fruit and vegetables. Use of such physical treatments is growing now-a-days as it is environment friendly and does not leave any residue in the fruit and vegetable.[47] Earlier studies have shown that hot water treatment effectively reduces the production of ethylene in lime fruit by reducing the accumulation of ACC (1-aminocylocpropane-1-carboxylic acid) or eliminating the stimulation of ACS (1-aminocylocpropane-1-carboxylic acid synthase) and ACO (1-aminocylocpropane-1-carboxylic acid oxidase) involved in the biosynthesis of ethylene.[48] Moreover, heat treatment above 37 °C causes degeneration of ACS enzyme

Table 1 Recent efforts in ethylene management by using physical treatments

Commodity – cultivar	Treatments and dose	Major research output	Ref.
Tomato	Photocatalyst (TiO_2) illuminated with UV light	Complete oxidation of ethylene	89
Green lime – 'Paan'	Hot water immersion (50 °C for 5 min)	Inhibited ethylene production and respiration	48
Tomato – 'Qirui F50'	Hot water treatment at (37 °C ± 0.5 °C) for 15 min	Degenerated ACC synthase enzyme and suppressed LeERT10 and Le*EIN3*	49
Apples –'Granny Smith'	X-ray irradiation @ 310 Gy and 1000 Gy	Downregulated the ethylene biosynthesizing gene expression and reduced the ethylene evolution rate	53
Ber – 'Umran'	Gamma irradiation at 0, 0.4 and 1.0 kGy doses	Ethylene peak was delayed by 7 days at 1.0 kGy dose	52
Cherry tomato	UV-C (4.2 kJ m^{-2}) for 35 days	Inhibited ethylene production	57
Banana – 'Berangan'	UVC irradiation (0.01–0.05 kJ m^{-2})	Reduced ethylene production compared to control	56
Kiwifruit – 'Guichang'	Ozone fumigation (0, 100, 200, and 300 μL L^{-1} for 3 h)	200 μL L^{-1} ozone blocks ethylene biosynthesis by preventing ACC synthesis	175

and suppression of *LeERT10* and *LeEIN3*, thus increasing the expression of *SlERF-A1*, hence delaying the accumulation of ethylene as found in tomato fruit.[49] In contrast, vapor heat treatment (50 °C) for 5–10 min stabilized the metabolic activities of sweet orange fruit by reducing ethylene production and respiration rate, thereby retaining the fruit quality attributes.[50]

Irradiation is another physical treatment in which horticultural produce is exposed to a beam of γ rays or high energy electrons or X-rays for a stipulated time for extending the shelf life of the produce or reducing the ethylene production during storage. Irradiation treatment has been widely used to reduce the microbial load, inhibit sprouting of tubers and bulbs, delay ripening, extend shelf life and sterilize produce against insects and pests.[51] One of the major uses of this irradiation treatment is to reduce the ethylene production and delay the senescence process which has been practiced in several fruit crops such as ber and apple.[52,53] Irradiation hinders ATP production required for synthesis of ripening promoting enzymes. It also affects the carbohydrate metabolism and process of gluconeogenesis and therefore delays the action of ethylene and improves the shelf life of the commodity.[54] Two major limitations in its use are the initial capital cost and slow consumer acceptance due to the perceived association with radioactive radiation. If an adequate volume of product is available for treatment, then the cost will be minimized and maximum benefits can be incurred from the technology.[55]

Another effective physical treatment in management of ethylene is the use of UV-C radiation. It has been applied in several fruits and vegetables such as banana and cherry tomatoes.[56,57] UV-C irradiation at a wavelength of 254 nm is more effective in maintaining the physiological response by alleviating the stress responses with respect to production of defense related compounds such as malondialdehyde and proline as observed in bitter gourd fruit.[58] UV-C treatment at 4.1 kJ m^{-2} postponed the onset of the ethylene evolution peak in wounded tomato fruit when it is dropped from a 1.5 m height and stored for 12 days at 20 °C. UV-C reduced the ethylene evolution rate due to decreased activity of ACO enzyme which is responsible for the ethylene biosynthesis.[59] UV-C technology for ethylene reduction is a cost-effective and safe approach as mentioned by Pristijono *et al.*[60] The limitation in using UV-C is that it does not penetrate the surface into much deeper regions, and thereby the source of UV-C for disinfection must be placed closer to the target in the processing system.[61]

4.3. Use of biosynthesis inhibitors

4.3.1. Aminoethoxyvinylglycine (AVG). Aminoethoxyvinylglycine (AVG) impedes the conversion of S-adenosylmethionine to 1-aminocyclopropane carboxylase (ACC) by binding and thus inhibiting the ACC synthase enzyme activity hindering ethylene biosynthesis. It is a naturally occurring plant growth regulator. It is registered commercially and used for several crops like pome fruit (apple, pear), stone fruit (peach, plum and nectarine) and mandarins in both pre and postharvest stages under the trade name ReTain®.[62] It was first patented in the United States in 1973. Also, US has permitted use of AVG in organic farming.[63] Recently, it has been provided compliance with organic farming in Australia too (**https://www.sumitomo-chem.com.au/retain**). The effects of AVG, an off-white to pale yellow fine water-soluble powder, have been found to vary depending on the dose, time of application, species and cultivar.[62] It is a natural fermentation metabolite obtained from *Streptomyces* spp.[63] The remarkable effects of AVG application on delaying senescence are mainly attributed to the reduction in ethylene production and respiration rate, delaying colour change and loss of weight and texture, thus maintaining edible quality and storability over a longer period. In addition, several studies have reported a reduction in the incidence and severity of development of physiological

disorders like superficial scald, water core and internal/core browning, and stem bowl cracking.[62,64,65] Besides, beneficial influences on fruit such as delaying of tree fruit maturation and ripening often lead to better edible quality and malleable harvest management, as well as uniform ripening, leading to fewer pickings and reduced fruit drop/fall. However, some negative effects such as delay in uniform blush colour development, decrease in juiciness and lowered aroma volatiles synthesis have also been reported. Recent studies on the effects of different AVG treatments are presented in Table 2. The positive effects of AVG treatment have been reported in tomato, apple, pear, apricot, peach, nectarine and several others.[62,66]

4.3.2. Aminooxyacetic acid, norbornadiene and diazocyclopentadiene. Aminooxyacetic acid (AOA) is an ethylene inhibitor. It has similar action to AVG, *i.e.*, it inhibits ACC synthase activity. Norbornadiene (NBD), a cyclo-olefin, having structural similarity to ethylene, intercepts ethylene union to receptors, thereby suppressing the deterioration. DACP (diazocyclopentadiene) shows similar activity against ethylene. The action, however, is transient and temporary as they leave the receptors within a fortnight, allowing normal ripening henceforth.[67] Nevertheless, the use of these compounds is considered objectionable due to the associated toxicity and manufacturing issues.[68]

4.4. Use of oxidative compounds

4.4.1. Potassium permanganate. Potassium permanganate ($KMnO_4$) is a coarse purplish-black coloured powder which dissolves in water to give intensely pink to purple-coloured solutions. It is generally held onto porous inert materials such as silica (SiO_2), zeolite, montmorillonite, kaolinite, perlite, alumina (Al_2O_3), vermiculite and activated carbon to enable adsorption and oxidation of ethylene gas molecules effecting their removal from packaging and storage environments.[69] A silica support is often used for its manifold benefits such as low cost, stability, high surface area, and easy availability, while alumina and vermiculite exhibit high adsorption capacity due to their high surface area and low-cost benefits.[70] Activated carbon, particularly granular forms, produced by pyrolysis of carbonaceous materials is a non-crystalline porous support material frequently used for holding $KMnO_4$.[71] However, activated alumina and zeolite are most often used for commercial applications. Amongst powder, fibre and granular forms, frequently granular forms have been reported to show higher

Table 2 Recent efforts in ethylene management by using aminoethoxy vinyl glycine (AVG)

Commodity- cultivar	Treatments and dose	Major research output	Ref.
Persimmon – Sangjudungsi	1-MCP (1 μL L^{-1}) dipping in 75 mg L^{-1} AVG for 5 min	1-MCP maintained maximum phenolics content. Overall, treatment of persimmon with 1-MCP and AVG lowered incidence of physiological disorders	183
Apricot – Canino	1-MCP (AgroFresh® 500, 1000 μg L^{-1} at 20 ± 2 °C for 12 h); AVG (50, 100 mg L^{-1} JA (50, 100 nmol)	1-MCP at 1000 μg L^{-1} followed by AVG at 100 mg L^{-1} were reported most effective for maintaining fruit quality and delaying deterioration	109
Banana – Cavendish	AVG (1.25 ppm) and chitosan (2.5%)	Combined AVG, chitosan, and low storage temperature increased shelf-life by four days over control	184
Sweet Cherry – 0900 Ziraat	Retain (pre-harvest- 50, 100, 150 mg L^{-1})	AVG (100 mg L^{-1}) delayed colour change, softening, acidity loss and maintained sensory quality	64
Kiwifruit – Hayward	MAP; AVG (225 mg L^{-1}), AVG (225 mg L^{-1}) + MAP	Weight loss was delayed by MAP while AVG alone did not influence weight loss and quality	185
Peach – Oz delight	AVG (10 days before harvest); AVG pre and postharvest (10 μL L^{-1}) AVG + SA (pre and postharvest respectively), NO; SA (2 mM)	Pre-harvest AVG treatment with post-harvest SA reduced ethylene evolution, respiration, oxidative stress, softening and delayed changes in quality like colour, soluble solids and acids	186
Plum – Friar	AVG (0, 100, 200 and 300 mg L^{-1})	AVG deferred ripening by lowering respiration rate, chilling injury, maintained fruit quality and enhanced antioxidant capacity and shelf life over control	187
Pummelo – Tubtim siam	1-MCP microbubble, AVG – (500 ppm)	AVG significantly lowered respiration rate and ethylene evolution. AVG and 1-MCP-microbubbles maintained both external and internal postharvest quality	188

effectiveness. It is reported to be lethal at a dose of 142.9 mg per kg body weight.[72,73] High surface area, shape and size of particles, adsorption ability, light weight, low cost, non-toxicity, stability, easy production and availability, hydrophobic nature, and $KMnO_4$ dose are desired qualities in the support material required for holding $KMnO_4$.[71,74–76] In addition, the extent of adsorption and the surface area of the supporting/holding material also influence the scavenging activity.[75,77] Ethylene is adsorbed onto the porous surface, followed by activation by moisture obtained from transpiration and respiration of fresh horticultural commodities, and oxidation of carbon–carbon double bonds by $KMnO_4$ to produce CO_2 and H_2O as end products which is visibly indicated as a colour change from purple $KMnO_4$ to brown MnO_2.[78] The colour change from purplish to brown, due to formation of MnO_2, is an indicator of the end of active usage due to saturation and removal of ethylene by the oxidative action of $KMnO_4$. It is commonly used as an effective, low-cost technology for scrubbing away ethylene and oxidizing it to carbon dioxide and water.[77,79] The concentration of $KMnO_4$ in commercial packages ranges between 4 and 6%. It is frequently used at the commercial level in active packaging in highly permeable sachets, during transportation and storage, and even at domestic levels in refrigerators for removal of ethylene from the surroundings and thus extends the storability of fresh horticultural produce.[76] Moreover, it has also been suggested that the cost of $KMnO_4$ is much less than that of ozone or irradiation and does not add additional cost to the produce.

However, Pathak[80] rightly noted that a major limitation in $KMnO_4$ embedded scrubbers is that they often need to be substituted with fresh permeable sachets to maintain effectiveness over longer storage periods. Moreover, $KMnO_4$ cannot be used directly in contact with food as it is toxic and due to possible migration of purple colour to the food at high moisture conditions.[79,81,82] Yet, due to its solubility in water (6.4 g per 100 mL at 20 °C), $KMnO_4$ can be easily washed away from the surface of fresh whole fruit and vegetables. Some recent efforts in ethylene management using potassium permanganate are listed in Table 3 and commercial products for ethylene removal are listed in Table 4.

4.4.2. Ozone. Ozone treatment is gaining popularity now-a-days as it is environment friendly, easy to use and does not leave any residue. Ozone was incorporated in 2001 in the GRAS list as a food additive by the United States Food and Drug Administration (FDA).[83] It is a strong oxidizing agent, used for ethylene removal by conversion to carbon dioxide and water.[82] Besides, it is also instrumental in the destruction of pathogenic microbes for fruit and vegetable preservation.[84] Ozone is generated on site as it is a highly reactive free radical which decomposes readily to form oxygen.[78,82] It is produced by illuminating ultraviolet (UV) radiation (285 nm wavelength) or passing a high voltage alternating current (corona discharge generator) in an oxygen or air stream. However, it can be used only with caution as the safe exposure level for human health is 0.1 μL L^{-1}.[85] Mahapatra *et al.*[86] reported that the Occupational Safety and Health Administration (OSHA), USA has suggested a worker exposure limit of 1.5 minutes at a 0.3 μL L^{-1} level, whereas exposure for a few minutes can be lethal at >1700 μL L^{-1} levels. Ozone is also used for inhibiting the expression of *ACS1* and *ACO*1 genes which further reduced the activities of ACS and ACO enzymes thereby reducing the biosynthesis of ethylene and thus delaying the ripening of fruit.[87] It has been approved for use during food processing, treatment and storage in gas and aqueous states. Notably, the usefulness of ozone is high at high relative humidity due to enhanced solubility in the condensed surface moisture of fruit and vegetables.[88]

4.4.3. Photocatalytic oxidation by metals. Recent advances in postharvest management of ethylene in fruit and vegetables include the use of photocatalytic materials such as titanium dioxide (TiO_2) illuminated with ultraviolet light. Titanium dioxide is a chemically inert, environmentally friendly, highly photo-stable and least expensive photocatalyst. When titanium dioxide comes

Table 3 Recent efforts in ethylene management by using potassium permanganate

Commodity- cultivar	Treatments and dose	Major research output	Ref.
Nectraine – Bayramiç Beyazi	Ethylene sachets (10 g $KMnO_4$) with MAP. Storage at and 90% RH for 40 days	Maintained overall fruit quality for up to 40 days at 0–1 °C and 90% RH	176
Guava – Baruipur	Moisture scavenger sachet (46 g) ethylene scavenger sachet (3 g)	Lowest chilling injury and highest L * value during 32 days storage period	177
Blueberries – Duke	$KMnO_4$ with protonated montmorillonite clay	Extended shelf life by 25 days and 14 days at 2 °C and 10 °C, respectively	79
Apricot – Mirlonaranja	$KMnO_4$ with sepiolite	No C_2H_4 concentration, reduced weight and decay loss	178
Anona – Pinha	Ethylene scavenging sachets of$KMnO_4$ (3 g)	Treatments delayed ripening and preserved food value at 13 °C for 20 days	179
Tomato	$KMnO_4$ based cotton absorber	Delayed ripening, maintained texture and extended storability of tomato at room temperature	72

Table 4 List of commercially available products for ethylene management

Product name	Manufacturer	Chemical component/description	Mode of action	Material type
SmartFresh℠	AgroFresh, Inc., USA	1-Methyl cyclopropene	Inhibition of ethylene action	Sachets and other
ReTain®	Valet BioSciences Corporation, USA	Aminoethoxy vinyl glycine	Inhibition of ethylene action	Powder
Purafil	Purafil Inc., GA, USA	$KMnO_4$ (≥8%) in activated alumina	Ethylene oxidation	Spherical pellet (3.2 mm dia.)
Purafil Chemisorbant	Purafil Inc., GEO, USA	$KMnO_4$ (≥4%) in activated alumina	Ethylene oxidation	Spherical pellet (3.2 mm dia.)
Ethysorb®	Molecular Products Ltd., UK	$KMnO_4$ (<6%) in activated alumina	Ethylene oxidation	Spherical particle (2.5–5.0 mm dia.)
Sofnofil™	Molecular Products Ltd., UK	$KMnO_4$ (<6%) in activated alumina	Ethylene oxidation	Spherical particle (2.5–5.0 mm dia.)
Multi-Mix® MM-1000	Circul-Aire Inc., Canada	$KMnO_4$ (4%) in activated alumina	Ethylene oxidation	Spherical particle (3.2 mm dia.)
BrySorb™ 508	Bry-Air (Asia) Pvt. Ltd. India	$KMnO_4$ (conc. ns) in activated alumina	Ethylene oxidation	Spherical particle (2.5–3.5 mm dia.)
Air repair™ ethylene gas absorber	Delta Track Inc., CA, USA	$KMnO_4$ (conc. ns) in activated alumina	Ethylene oxidation	Spherical particle (dia. ns)
Ozeano ETH	Ozeano Urdina S.L., Spain	$KMnO_4$ (7.5%) in alumina	Ethylene oxidation	Spherical particle (3.0–5.0 mm dia.)
Ryan®	Sensitech Inc., MA, USA	$KMnO_4$ (conc. ns) in natural clays	Ethylene oxidation	Sachets, filters
Bi-On®	Bioconservacion S.A., Spain	$KMnO_4$ (12%) in zeolite	Ethylene oxidation	Cylindrical pellet (2.3–4.0 mm dia.)
Super Fresh Media	Ethylene Control Inc., CA, USA	$KMnO_4$ (4–6%) in zeolite	Ethylene oxidation	Granule (dia. ns)
Extend-A-Life™	AgraCoTechologies International LLC., PE, USA	$KMnO_4$ (8%) in zeolite	Ethylene oxidation	Granule (dia. ns)
ETI 25, 50	Fruit Control Equipentssrl, Italy	ABSOTIL/purafil alumina pellets	Ethylene oxidation	Absorption system
EC-3+	Ethylene Control Inc., USA	Zeolite impregnated with $KMnO_4$	Ethylene oxidation	Sachets, filters, filtration system
Air repair ethylene absorbers	DeltaTRAK, Inc., USA	Sachet of $KMnO_4$	Ethylene oxidation	Packet, blankets, tube
Bio-Turbo	Miatech, Inc., USA	Ozone	Ethylene oxidation	Air filtration equipment
Kuraray Coal™	Kuraray Co. Ltd., Japan	Activated carbon/$KMnO_4$	Ethylene oxidation	Sachets
Hatofresh	Honshu Paper, Japan	Activated carbon impregnated with bromine	Ethylene oxidation	Paper bag or corrugated fiber board
Air-repair	Cal Agri Co., USA	$KMnO_4$	Ethylene oxidation	Sachets/blankets
Bio-Kleen	Kes Irrigations Systems, USA	$KMnO_4$	Ethylene oxidation	Sachets/blankets
Green Pack®	Rengo Packaging Systems Co., Ltd. Japan	KMnO4/silicon oxide	Ethylene oxidation	Sachets
Delta Track®	Delta Track Inc., USA	$KMnO_4$	Ethylene oxidation	Sachets/blankets
CJS®	CJS Ethylene Filters, USA	$KMnO_4$	Ethylene oxidation	Sachets, filters
Retarder®	Retarder S.R.L, Italy	A mix of clays and $KMnO_4$	Ethylene oxidation	Sachet
GKZ4	Greenkeeper Iberia, Spain	Zeolite loaded with $KMnO_4$	Ethylene oxidation	Sachet/sheet
BE fresh	Befresh Technology, Spain	Natural clays impregnated with $KMnO_4$	Ethylene oxidation	Sachet
Purethyl	Isolcell Spa, Italy	Activated alumina granules with $KMnO_4$	Ethylene oxidation	Machine
Mrs Green extra life	Dennis Green Ltd., USA	$KMnO_4$	Ethylene oxidation	Cartridge for refrigeration
Extend-A-Life™, Produce Saver™	AgraCo Technologies International LLC, USA	$KMnO_4$ based absrober	Absorption/adsorption	Filters, sachets
It's Fresh!	It's Fresh! Ltd., UK	Palladium impregnated zeolite	Absorption/adsorption	Sheet
Prime Pro®	DeltaTRAK, Inc., USA	LLDPE plastic film	Absorption/adsorption	Sheet
Peakfresh	Peakfresh, Australia	LDPE film impregnated with a naturally occurring mineral	Absorption/adsorption	Bags
Green Bags™	Evert-Fresh Corporation, USA	Clay	Absorption/adsorption	Bags
KEEPFRESH®	Teck Blue Systems, SL Keepfresh, Spain	Zeolite and $KMnO_4$ sachets/sheets	Absorption/adsorption	Sheets, bags
Bi-On®, ETHYL STOPPER	Bioconservacion S.A., Spain	Porous clay and $KMnO_4$	Absorption/adsorption	Filtration system, sachets

Table 4 (*Contd.*)

Product name	Manufacturer	Chemical component/description	Mode of action	Material type
Sendo-Mate	Mitsubishi Chemical Co. Japan	Palladium catalyst on activated carbon	Absorption/adsorption	Sachets
Orega	Cho Yang Heung San Co., Korea	PE film, filler includes pumice, zeolite, activated carbon and metallic oxides	Absorption/adsorption	Film
Sendo Mate	Mitsubishi Gas Chemical Co. Ltd., Japan	Activated carbon with a metal catalyst	Absorption/adsorption	Sachet
Neupalon	Sekisui Jushi Corp., Japan	Activated carbon with a metal catalyst	Absorption/adsorption	Sachet
Keepcool	Molina de Segura, Spain	Sepiolite mixed with $KMnO_4$ and activated carbon	Absorption/adsorption	Sachet
Profresh	E-I-A Warenhandels GmbH, Austria	Minerals	Absorption/adsorption	Film
Biofresh	Groft Plastics, Israel	Porous clay and potassium permanganate mixture	Absorption/adsorption	Zipper bag
Swingtherm-BS	Fruit Control Equipmentssrl, Italy	Air filtration	High temperature catalytic oxidation	Air filtration equipment
ECOscrub	Absorger, France	Titanium dioxide + UV light	Photocatalytic oxidation	Air filtration equipment
AiroCide®	KES Science & Technology, Inc	Air filtration	Photocatalytic oxidation	—
FRESH+™	Fresh Plus International, USA	Catalyst + UV light	Photocatalytic oxidation	—
Bo film	Odja Shoji, Japan	LDPE films extruded with finely divided crysburite ceramic	—	Film
Evert-Fresh	Evert-Fresh., USA	LDPE films impregnated with Oya- stone	—	Film

into contact with UV light it generates hydroxyl radicals and superoxide ions on its surface which act as oxidizing agents of ethylene.[83] It has been demonstrated that ethylene could be completely oxidized into CO_2 on a powdered TiO_2 surface.[89] Previous studies also showed that ethylene could be completely eliminated from tomato using TiO_2-coated glass beads.[90] Besides its advantages, some limitations such as persistent exposure of fruit to TiO_2 agglomeration decreases the ethylene degradation efficiency and hence leads to excess emission of ethylene.[91]

This is channeled by the illumination of the catalyst with ultraviolet radiation (UV-A, around 380 nm) which consequently results in generation of reactive oxygen species such as hydroxyl and superoxide radicals (OH^- and O_2^-) in the gaseous phase.[80,92] Further, these free radicals oxidize ethylene to produce water and carbon dioxide.

TiO_2 is hailed as a popular photocatalyst for ethylene degradation due to its distinct photochemical reactivity, high refractive index and resistance to colour change.[92] The embedding of TiO_2 in polypropylene film used for packaging tomatoes enhanced keeping quality.[93] Similarly, nano-composites of TiO_2/SiO_2 showed significant improvement in enhancing the shelf life of tomato fruit by ethylene scavenging action.[89] However, the ethylene degradation rate depends on the best possible process parameters, system design and proper holding material. Wei *et al.*[92] reported that photocatalysis using TiO_2 is an effective, clean and low-cost technology with potential for lowering postharvest losses. Kim *et al.*[82] also observed that shelf life of fruit can be further enhanced by using both zeolite adsorbents and photocatalytic oxidation. Yuan and Li[94] studied the effects of zeolite and $KMnO_4$ ethylene scrubbers on banana fruit. However, the drawbacks are low efficiency, possible hazardous effects of ultraviolet radiation on fruit quality, formation of toxic intermediates to human health, easy deactivation and deterring electron–hole coupling.[80,81,83]

Besides, several low temperature catalysts have been employed as a promising tool to remove volatile organic compounds. Several metals such as Pt, Au, Ag and Ti have been used by researchers.[73] Moreover, Wei *et al.*[95] found that Pt/CeO_2–O showed the highest low temperature C_2H_4 catalytic oxidation activity. In a separate study, it was noticed that CeO_2-octahedron-supported Pt catalysts could be a better tool for catalytic oxidation of ethylene at low temperature. Wei *et al.*[95] observed that a Pt/plasma-modified CeO_2 catalyst (Pt/CeO_2-P) exhibited significantly higher catalytic reactivity of ethylene oxidation at low temperature compared to Pt/pristine CeO_2.

4.5. Use of action inhibitors

4.5.1. 1-Methylcyclopropene (1-MCP). In 1973, Sisler and Pian reported that some olefin compounds (cyclopropenes) inhibit ethylene action which can be used for delaying the ripening and deterioration of fresh horticultural commodities by inhibition of ethylene perception. 1-MCP is a derivative of DACP (diazocyclopentadiene) products having biological use due to their lower volatility over cyclopropene. 1-Methylcyclopropene (C_4H_6) was identified for countering ethylene action in 1994, followed by its patenting by Sisler and Blankenship in 1996. It is a gas at standard temperature and pressure with a molecular weight of 54 which covalently binds with ethylene (C_2H_4) receptors at comparatively ten-times higher affinity levels.[96,97] 1-MCP is a very effective molecule even at very low concentrations due to its ten-fold higher affinity for ethylene binding receptors.[97] The pioneering work for

identifying 1-MCP as a potent ethylene inhibiting agent and its miraculous possibilities in extending the postharvest life of fruit and vegetables, especially climacteric ones, was done and holds the patent for its use to prevent ethylene action.[98] The binding of 1-MCP with γ-cyclodextrin gives a stable powder which readily releases 1-MCP as gas when dissolved with water. This ensured ease in providing fumigation treatment and thus gave a significant advancement for commercialization of this technology. The action of 1-MCP is due to its binding with the ethylene receptors, thus blocking ethylene action which results in delayed, suppressed or in some cases complete inhibition of ripening in such fruit. It has been found useful for lowering physiological disorder and rotting incidence and severity.[12,99] Ding *et al.*[100] reported that 1-MCP blocked AFS1 enzyme transcription by blocking α-farnesene synthesis, and thus lowering superficial scald incidence. Currently, the general notion is that 1-MCP binds permanently to receptors, and ripening at later stages as a result of ethylene action is due to development of new receptors. The binding of 1-MCP to the receptors results in suppression of ethylene biosynthetic enzymes such as ACC synthase and ACC oxidase. Besides, expression of genes associated with ethylene signaling pathways such as *ETR*, *CTR*, *ERF*, *etc.* has also been reported to be significantly inhibited.[101] It has been reported to be more effective at temperatures ranging between 20 and 25 °C and 12–24 h treatment exposure has been reported to be adequate to elicit complete response and inhibit ripening.

It is available commercially under several trade names such as SmartFresh™, EthylBlock™ and Fysium® which have 1-MCP as an active ingredient often in the form of cyclodextrin powders.[102] 1-MCP was included in Annexure I of Directive 91/414/EEC/2005 by the European Union thereby granting permission for use on commercially important climacteric fruit like apples and pears.[103] The Acute Acceptable Operator Exposure Level (AOEL/AAOEL) is noted at 0.12 mg kg^{-1}. The Acceptable Daily Intake (ADI) was increased to 0.02 mg per kg body weight over an earlier bar set at 0.0009 mg per kg body weight per day.[104]

The main advantages of using 1-MCP are its high effectiveness at very low concentrations, maintenance of firmness and quality even after removal from cold storage, and absence of hazardous or any other residues. The efficacy of 1-MCP depends on several factors such as species, cultivar, harvest stage, time of postharvest treatments, concentration, temperature, application methods and storage conditions.[105–109] Pirrung *et al.*[110] noted that the affinity of 1-MCP towards receptors is associated with chemical properties such as its strain, pyramidalization and enantiomeric selectivity.

Watkins[111] has noted 1-MCP as the most significant and practical postharvest innovation in the last decade for inhibiting ethylene action. Notably, it is so effective that the "evergreen/stay green effect" due to irreversible, uneven ripening, less juiciness and/or lack of development of aroma volatiles such as alcohols and esters and incomplete sensory development have been observed in some crops like banana, pear, immature green tomato and guava. This consequently leads to hampering the commercial usage as the consumer demand wavers with non-uniform colour development, partial aroma volatiles or incomplete sensorial development. This further prompted research to induce proper ripening and revival of ethylene perception in fruit for ensuing final ripening.[106,112–118] Some recent efforts in ethylene management using 1-MCP are listed in Table 5. Thompson *et al.*[119] estimated that pre-storage 1-MCP treatment could lower the cost of fresh produce from $8.10 to $5.25 per ton by reducing the energy consumption and further meeting the challenges of reducing the CO_2 output and cost.

4.6. Use of plant signaling molecules

There are several signaling molecules that play a regulatory role in the biosynthesis and perception of ethylene in the plant system (Table 6). Association of these biomolecules like polyamines, salicylic acid, and nitric oxide with signaling responses triggered by ethylene led to interest among researchers to modulate postharvest ethylene responses in fruit by its exogenous application.[120–123]

4.6.1. Polyamines. Polyamines (PAs) are aliphatic nitrogen containing polycations of low molecular weight. The major plant polyamines are putrescine (diamine), spermidine (triamine) and spermine (tetramine). They have been known to play a significant role in the regulation of ripening and senescence due to the contention for the common limited precursor S-adenosyl methionine (SAM).[1,16,124] Moreover, endogenous polyamine levels have been observed to rise in response to injury levels. PAs have been hailed as anti-ethylene and anti-stress molecules. The polycationic nature of polyamines at cellular pH helps in stabilizing cell membranes and thus lowers lipid peroxidation. These are contained mainly in cell vacuoles.[125] Several studies have reported the down-regulation of ethylene biosynthetic enzymes, stabilization of cell membranes, higher antioxidant capacity, lowered chilling injury and severity of physiological disorders and delayed senescence. Sahu *et al.*[126] reported that guava fruits treated with spermine (1.5 mM) preserved biochemical composition and extended shelf life by 10 days. Similarly, Wang *et al.*[127] observed that spermidine treated apricot fruits delayed ethylene production by reducing ACC synthase and ACC oxidase activity.

Some recent studies related to the effects of different polyamine treatments are presented in Table 7.

4.6.2. Salicylic acid. Salicylic acid (SA) belongs to the group of phenolic compounds, is an endogenous signal molecule, and plays a crucial role in different plant physiological processes and stress responses. It is present in plant either as free phenolic acid or as a conjugate form that is produced by glucosylation, methylation or hydroxylation of the aromatic ring.[128,129] The synthesis of SA occurs in plants *via* two pathways, in which chorismate is used as a primary metabolite. In one pathway, chorismate is converted to isochorismate by isochorismate synthase that is further catalyzed by isochrismate pyruvate lyase to salicylic acid. In another pathway, chorismate is converted to L-phenylalanine, which is later converted to cinnamic acid by phenylalanine ammonia lyase. Finally, salicylic acid is produced through a series of enzymatic reactions

Table 5 Recent efforts in ethylene management by using 1-methylcyclopropene (1-MCP)

Commodity- cultivar	Treatments and dose	Major research output	Ref.
Mango – Tainong	1-MCP (1 μL L^{-1})	1-MCP treatment-maintained quality, delayed firmness, colour change (pulp and peel both), respiration and ethylene evolution rates, lowered cell wall enzyme activities, and weight loss while increasing antioxidant enzyme activity	116
Mango – Tainong 1	1-MCP (1 μL L^{-1})	Delayed ripening, firmness and maintained acidity at room temperature	117
Melon – Donatello	Gaseous 1-MCP (650 nL L^{-1}) and 1-MCP microbubbles for 10, 20 and 30 min	1-MCP microbubbles (20 m) was effective over gaseous 1-MCP treatment	180
New Queen melon – Xinmi No. 13	$CaCl_2$ (0.045, 0.09, 0.18 and 0.36 mol L^{-1}) for 25 min, along with 1-MCP fumigation (1.25, 0.5, 1.0, 2.0 μL L^{-1}) at 20 °C for 24 hours	The respiration rate, ethylene release and activities and gene expression of polygalacturonase, pectin methyl esterase and pectatelyase were significantly reduced in melons treated with 0.18 mol L^{-1} $CaCl_2$ + 1 μL L^{-1} 1-MCP	106
Papaya- Golden	Ethylene and 1-MCP	Combined application retained firmness and chlorophyll content	105
Pear – Blanquilla	CA + 1-MCP	1-MCP treated fruit completely inhibited ethylene production and fruit softening. The superficial scald disorder was totally controlled in fruit treated with 1-MCP	113
Pear – D'Anjou	1-MCP	1-MCP inhibited ethylene production, respiration rate and scald development	181
Pear – Bartlett and D'Anjou	1-MCP (320 μL L^{-1}) applied during pre-harvest stage	Ethylene evolution, respiration, and disorder incidence were lowered, higher retention of flavonoids and antioxidants	116
Pear – Nanguo	1-MCP (0.5 μL L^{-1})	Alleviated peel browning, maintained higher firmness, glutathione content, ATP concentration and energy charge value while lowering ethylene evolution, respiration rate, electrolyte leakage and malondialdehyde content in 'Nanguo' pear	114
Pear – Laiyang	1-MCP (fumigation with 0.5 μL L^{-1} 1-MCP at 20 ± 1 °C for 12 h in sealed container)	1-MCP treated fruit-maintained fruit firmness, lowered respiration and ethylene production and maintained storage quality of pear	115
Pear – Huangguan	1-MCP (1.0 μL L^{-1})	1-MCP treatment lowered browning, malondialdehyde accumulation, electrolyte leakage, hydrogen peroxide content, PPO enzyme activity and enhanced total phenol, flavonoids, ascorbate peroxidase and phenylalanine ammonia lyase activities	12
Pear – Wonhwang	1-MCP (1 μL L^{-1})	Higher firmness, delayed colour change, cortex and core browning	108
Pear – Comice	1-MCP (0.15 μL L^{-1}, 0.3 μL L^{-1})	Ethylene evolution and respiration were significantly inhibited by 1-MCP treatments	107

Table 5 (*Contd.*)

Commodity- cultivar	Treatments and dose	Major research output	Ref.
Pecan	1-MCP (1.0 μL L^{-1})	1-MCP treated unshelled pecans-maintained luminosity and showed lower internal browning. 1-MCP treated pecans showed lower acidity, peroxide value and unwanted volatiles	182

including synthesis of benzoate intermediates.[130–132] Salicylic acid received attention from researchers due to its role in imparting resistance to plants against various biotic and abiotic factors.[133] Later, investigation on harvested horticultural commodities revealed that SA also plays a regulatory role in delaying ripening by modulating ethylene production.[121,134] Salicylic acid has been reported to interfere with the biosynthesis and action of ethylene in plants.[135,136] It has been demonstrated that exogenous application of SA and acetyl salicylic acid (ASA) suppresses the activity of ACC synthase and ACC oxidase, thereby inhibiting ethylene production in fruit.[137,138] Moreover, SA also suppresses the activity of lipoxygenase and generation of reactive oxygen species.[139] This is also linked with reduced production of ethylene in fruit.[140–143] Some recent studies related to the effects of salicylic acid treatments are presented in Tables 8 and 6. Mo *et al.*[144] reported that pre-storage of SA delayed the ripening process in sugar apple. In case of tomato Mandal *et al.*[134] found that SA treated (1.2 mM) fruits exhibited an extended shelf life (32.75 days).

4.6.3. Nitric oxide. Nitric oxide (NO) is a highly diffusible, membrane permeable signaling molecule that plays a multifaceted role in various plant physiological processes involving growth, development and responses to stress. Among the different effects of NO in plants, its role in fruit ripening *via* modulation of ethylene biosynthesis has become a matter of research interest among many scientists. Another landmark research by Leshem and Haramaty[145] reports the antagonistic effect of NO on ethylene in growing plants. Inhibition of ethylene by NO involves two mechanisms, through direct stochiometric inhibition and suppressing activity of ethylene biosynthesis enzymes. NO suppresses autocatalytic ethylene production by binding with ACC oxidase and formation of an ACC oxidase–NO complex, which further combines with ACC to form stable ternary complex ACC–ACC oxidase–NO that reduces ethylene production.[146] Moreover, reaction between NO and reactive oxygen species produces peroxynitrites that affect the co-factors required for catalysis of ACC by ACC synthase and ACC oxidase. Another possible mechanism of ethylene regulation by NO involves regulation of hydrogen peroxide that affects MAP kinase mediated downstream components of ethylene biosynthesis.[147] In addition, inhibition of SAM turnover by S-nitrosylation of transcriptionally produced methionine adenosyl transferase (MAT) also suppresses biosynthesis of ethylene.[148] Some recent studies related to the effects of different polyamine treatments are presented in Tables 8 and 6. Additionally, application of NO gas in fruit and vegetables has been considered as safe also.[149] Sodium nitroprusside (SNP) is the most common commercial source of NO applied exogenously.[123,150,151] Pre-storage application of SNP (1.0 mM or 1.5 mM) significantly delayed ethylene production in mango.[123] Likewise, Sahu *et al.*[126] reported in guava that SNP (1.0 mM) treatment significantly delayed the ripening and senescence and preserved the nutritional composition of the fruits during storage. In another study, Ghasil *et al.*[151] revealed that SNP treated sugar apple fruits exhibited better nutritional properties with maximum shelf life.

4.6.4. Novel phytohormones. In the past couple of years, use of melatonin and brassinosteroids showed their significant impacts on altering ethylene production. Previous studies on jujube and blueberry have shown delayed ethylene production during storage (Table 6).[152,153] Exogenous application of melatonin has been found to be crucial in delaying ethylene production through decreased expression of *MdACO1*, *MdACS1*, *MdAP2.4* and *MdERF10* genes in apple.[17] Moreover, Medina-Santamarina *et al.*[154] reported delayed ethylene evolution in melatonin treated cherimoya fruits. In case of pear, ethylene biosynthesis genes *PcACS1* and *PcACO1* were significantly downregulated by the exogenous melatonin treatments and enhanced the shelf life.[155] Likewise, application of brassinazole significantly delayed ripening and senescence by suppressing biosynthesis genes in tomato.[14]

4.7. Edible coatings

Edible coatings create a semipermeable membrane over the fruit surface, thus altering the physiology of the fruits. Several starch-based coatings such as carboxymethyl cellulose, guar gum, gum arabic, sago starch, chitosan, *etc.* have been reported to be fruitful in delaying ethylene content in fruits during storage.[156,157] Nowadays, edible coatings based on polysaccharides are gaining commercial importance and have been found to be highly effective in extending shelf life (Table 6). In peach and plum fruits, Guillén *et al.*[158] found that an aloe vera coating can significantly delay the ethylene evolution, thus reducing the harmful effects of ethylene on the fruits. Zapata *et al.*[159] found delayed ethylene formation in tomato fruits during storage when coated with alginate and zein based coating materials.

4.8. Use of packaging technology

The postharvest quality is influenced mainly by storage temperature, relative humidity and gaseous composition.[160,161]

Table 6 Effects of various treatments on ethylene evolution and shelf life of fruit during storage

Postharvest treatments	Crop	Major findings	Ref.
Hot water treatment (HWT)			
HWT at 50 °C for 5 min + ethylene vapour pad	Lime	Ethylene production reduced up to 15 days and extended shelf life without impairing quality	48
HWT (50 ± 1 °C) for 10 min	Mango	Reduced ethylene production at low temp storage as well as room temp with elevated catalase activity	198
HWT at 50 °C, for 2 min	Mandarin	Suppressed ethylene evolution, decreased chilling injury, maintained high CAT activity	199
HWT at 40 °C for 20 min	Tomato	Delayed ethylene, reduced chilling injury and extended shelf life about 3 days more than the control	200
Gamma irradiation			
Gamma irradiation doses (0, 0.4, and 1.0 kGy)	Jujube	Extended storage life of jujube with higher nutritional value	201
0.5, 1.0 or 2.0 kGy	Raspberry	Did not alter ethylene production but extended storage life by 8 days	202
Gamma irradiation (0.08 kGy)	Papaya	Enhanced storage up to 13 days with reduced ripening rate	203
$KMnO_4$			
$KMnO_4$ levels (0, 10, 20, 30, 40, and 50 g)	Mango	30 g $KMnO_4$ significantly extended shelf life with maximum biochemical parameters	204
$KMnO_4$ (20 g)	Papaya	Reduced about 2.2% ethylene	205
Nano zeolite-$KMnO_4$	Banana	Extended shelf life of banana up to 23 days	206
$KMnO_4$ (0, 2, 4, 6 and 8 g)	Banana	Maximum shelf life (13.50 days) was recorded in 6 g $KMnO_4$	207
Ozone			
Ozone (0.3 μL L^{-1})	Kiwifruit	Ethylene biosynthesis due to inhibited *adacs1* and *adaco1* expression	208
Ozone fumigation (0, 1.5, 2.5, 3.5 and 5.0 μL L^{-1})	Papaya	Ozone (<5.0 μL L^{-1}) also potently delays the papaya ripening with lower respiration rate and ethylene production	209
Ozone concentrations (100 μL L^{-1}, 200 μL L^{-1}, 300 μL L^{-1}	Kiwifruit	200 μL L^{-1} delayed fruit senescence, ethylene concentration at 1 °C	210
0.05 μmol mol^{-1}	Tomato	Reduced the expression of ethylene biosynthesis related enzymes	211
1-MCP			
Immersion treatment in 0, 10, 25 or 50 μg L^{-1} 1-MCP	Banana	1-MCP (25 μg L^{-1}) delayed ripening up to 12 days	212
1-MCP treatment	Pear	Downregulated ripening related genes and reduced enzymatic activity	213
1-MCP treatment (0.14%)	Apricot	Slowed down the fruit senescence process and favored antioxidant activity	214
1-MCP (500 ppb)	Guava	Reduced ethylene (5.02 μL kg^{-1} h) and extended shelf life	215
1-Methylcyclopropene (1-MCP) (500 nl L^{-1})	Mango	Delayed the skin and flesh colour development with delayed ethylene formation	216
Polyamines			
Spermidine (spd)	Apricot	Spd reduced ACC synthase and ACC oxidase activity. Reduced ethylene production	127
Putrescine, spermidine and spermine 1 and 10 mm	Kiwifruit	Putrescine at 1 mM suppressed ethylene production	217
Spermine (0.5, 1.0 and 1.5) mm] and spermidine (1.0, 1.5 and 2.0) mm	Kiwifruit	Spermine at 1.5 mM and spermidine at 2.0 mM showed extended shelf life and reduced ethylene amount	218
Putrescine (1 mM)	Plum	Exogenous putrescine inhibited and delayed ethylene and CO_2 production rates	219
Salicylic acid (SA) and NO_2			
SA (0.5, 1.0, 1.5, 2.0, 2.5 mM)	Plum	Delayed the onset of the climacteric peak of respiration and inhibited the ethylene	121
SA (0.2–1.2 mM)	Tomato	SA treated (1.2 mM) fruits exhibited maximum shelf life (32.75 days)	134
SA (1, 2, 3 and 4 mmol L^{-1})	Plum	Delayed ripening with enhancing antioxidants	122
SA at 0.4, 0.8 and 1.2 mmol L^{-1}	Sugar apple	Delay in the fruits ripening process was achieved after 10 days of storage	144
Sodium nitro prusside (SNP) (1.0, 5.0 and 10.0 μmoL l^{-1})	Strawberry	Inhibited ethylene production, activity of ACC synthase	150
SNP at 0.5 mM, 1.0 mM, 1.5 mM, and 2.0 mM	Custard apple	SNP (2.0 mM) extended the shelf life with maintain bioactive compounds	151
SNP (0.5, 1.0, and 1.5 mM	Guava	SNP (1.0 mM) delayed ripening and senescence with minimum weight loss, MDA content and decay	126

Table 6 (*Contd.*)

Postharvest treatments	Crop	Major findings	Ref.
Sodium nitroprusside (at 1.0 mM or 1.5 mM)	Mango	Enhanced shelf life by downregulating softening enzymes and delayed ripening	123
Novel phytohormones			
Brassinosteroids (BRs)	Pear	Suppressed fruit ripening *via* delaying ethylene biosynthesis	220
24-Epibrassionolide (EBR) 5 μM	Jujube	Delayed senescence by reducing ethylene production	152
24-Epibrassionolide (EBR) (0.25, 0.5, 0.75, and 1 mg L^{-1}	Blueberry	EBR (0.75 mg L^{-1}) significantly delayed senescence and enhanced shelf life with maximum quality	153
Melatonin (1 mmol L^{-1})	Apple	MT treated apples reduced ethylene production (28 days–56 d) by decreased expressions of *MdACO1*, *MdACS1*, *MdAP2.4* and *MdERF109*	17
MT solution (100 μM)	Pear	Ethylene biosynthesis genes *PcACS1* and *PcACO1* completely inhibited by the MT and delayed the senescence and ripening process	155
MT (0.5 mM)	Mango	Delayed ethylene biosynthesis and reduced ethylene production	221
Edible coatings			
Chitosan/alginate based layer bilayer coating	Japanese pear	Reduced ethylene with preservation of food value	222
Carboxymethyl cellulose (CMC) (1%), guar gum (GG) (2%) and gum acacia (GA) (2%)	Mango	Delayed senescence and maintained antioxidants properties with better shelf life	156
Chitosan (CH) and guar gum (GG) based composite edible coating enriched with different starch	Kinnow	GG + TAM coating enhanced the shelf life of kinnow fruits without losing desirable traits	223

An ideal packaging needs to be tailored to the specific horticultural produce as they vary largely in respiration and ethylene production rates, with varying sensitivities to ethylene and CO_2. Active packaging films with modified permeability have been developed with addition of zeolite and montmorillonite mineral powders and bromine type inorganic chemicals for ethylene scrubbing.[78,92,162] The ethylene is held by physical adsorption and bound to activated carbon or zeolite structure by van der Waals force.[163] The functionality is based on the removal of ethylene by absorption as well as by allowing higher diffusion rates outside. This reaction is aided by moisture released by transpiration and respiration of fresh commodities. The commercially available ethylene scrubbing films are mostly based on zeolite mineral due to its highly porous 3D structure with high adsorption. Ethylene scavenging using zeolite is being frequently used at the domestic scale in refrigerators with the aim of extending the keeping quality of fresh fruit and vegetables. However, the use of packaging films is limited by the film opacity and limited efficiency due to lower mineral concentration, decline in efficacy with the increase in saturation, incomplete decomposition, possible escape of ethylene and need for regular replacement.[78,92] Zeolite incorporated with finely dispersed palladium was found more efficacious over $KMnO_4$ based zeolite at lower concentrations.[164] The use of a platinum catalyst heated to 250 °C and ultraviolet radiation (184 and 254 nm) to form reactive oxygen species (ROS) and oxidize ethylene to CO_2 and H_2O has also been reported. The use of different ethylene scrubbing agents depends on scavenging potential, degree, possible hazardous intermediates and/or final derivatives, mechanism of action and possible migration. In addition, cost, safety and acceptance among buyers are of paramount importance.

4.9. Use of storage technology

Effective removal of ethylene from the storage atmosphere by ventilation, getting rid of exhaust gases from combustion sources and eliminating rotten and over-ripened fruit is a simple way to exclude the detrimental senescence effects of ethylene. Low temperature in the storage atmosphere helps in reducing the respiration and ethylene evolution rates. Moreover, it also reduces the sensitivity of fresh produce towards exogenous ethylene sources. Carbon dioxide prevents ethylene action, thus delaying senescence responses. However, the CO_2 inhibitory action engages till ethylene levels do not exceed 1 μL L^{-1}.[165] It works by displacing ethylene at the binding sites and inhibiting the ACC oxidase activity. Controlled atmosphere storage eliminates ethylene gas build up by enhancing CO_2 concentration, thereby initiating competition for ethylene receptors. The elevated level of CO_2 and lower level of oxygen with other gaseous compositions may be helpful in delaying ethylene biosynthesis and action of ethylene.[166] Recently, dynamic controlled atmosphere (DCA) storage has come up which involves the reduction of oxygen to the lowest endured level by the fruit to the anaerobic compensation point. This has potential in extending the shelf life of fresh produce beyond modified atmosphere and controlled atmosphere storages.

Hypobaric storage results in ethylene elimination from the storage environment and lowers internal ethylene concentration. It is effective in reducing the respiration rate to a minimum due to the lowered partial pressure of oxygen.[9]

Several scrubber systems to remove ethylene in storage using activated charcoal, ozone and catalysts such as platinum have been patented and marketed. These may be portable or fixed to scrub ethylene and provide fresh treated air circulation. These

Table 7 Recent efforts in ethylene management by using polyamines[a]

Commodity- cultivar	Treatments and methodology	Major research output	Ref.
Carambola – B10	Putrescine and spermidine (SPD) (0.1, 1.0 and 2.0 mM)	PUT (2.0 mM) reduced weight loss, delayed peel colour change and firmness loss	189
Apricot – Saimaiti	0.1 mmol L^{-1} SPD, 0.1 mmol L^{-1} D-arginine	SPD treated apricot exhibited higher firmness, lowered ACC synthase and ACC oxidase activity, inhibition of relative gene expression of *PaACS2* and *PaACO*, ethylene production and delayed senescence	127
Mandarin – Murcott	Salicylic acid (SA- 200 and 400 ppm) and PUT (50 and 100 ppm)	SA (400 ppm) delayed weight loss and decay-maintained fruit firmness, total soluble solids (TSS), acidity, and ascorbic acid during storage	190
Tomato – Pusa Ruby	*A. tumefaciens* having recombinant plasmid pBin2A11ADC was used to transform cotyledonary explants. Such tomato fruits amassed PAs by over-expression of arginine decarboxylase (*ADC*) gene. Fully developed transformants were grown under transgenic green-house and nethouse growth conditions	The AsADC over expressed transgenic tomatoes showed higher PUT, SPD and SPM content over control. These fruits showed better shelf-life due to decline in ethylene production and respiration rates	40
Mango – Langra	Chitosan solutions (0.5%, 1%, and 2%) and SPD (0, 0.5, 1, and 2 mM)	Chitosan (2%) and SPD (2 mM) treated mangoes showed delay in weight and firmness loss, and rotting	191
Peach – Florda king cultivar grafted on Peshawar local	Aqueous solution of PUT (0, 1, 2 and 3 mM)	PUT (2 mM) treatment lowered chilling injury, fruit softening, weight loss, sugars, acidity, vitamin C and delayed colour changes	192

[a] Abbreviations. – [PUT-putrescine, SPD-spermidine and SPM-spermine].

Table 8 Recent efforts in ethylene management using salicylic acid and nitric oxide

Commodity- cultivar	Treatments and methodology	Major research output	Ref.
Peach – Jinqiuhongmi	SA (1 μmol L^{-1})	Reduced ethylene production, increased sucrose content and reduced chilling injury incidence	193
Tomato – Hisar Arun, BSS-488	Immersion treatment with salicylic acid	Delayed loss of firmness, weight loss, lycopene content and loss of TSS	194
Jamun	SA (1.0 mM and 1.5 mM)	The treatment reduced weight loss, decay loss, delayed senescence and preserved higher anthocyanins and antioxidant capacity	195
Blueberry – Powderblue	Spray with 1.0 mmol L^{-1} salicylic acid	SA treatment delayed fruit softening and deterioration	196
Pistachionut cv. Ahmad Aghaei	Fruit sprayed with 15, 30, 45 or 60 μM SNP (a NO donor)	Nitric oxide treated fruit had reduced activity of polyphenol oxidase, phenylalanine ammonia lyase and peroxidase and had the maximum activity of superoxide dismutase	197
Guava – Lucknow 49	SNP (0.5, 1.0-, and 1.5 mM)	1.0 mM SNP treated fruit had lower physical quality loss, delayed loss of chlorophyll, ascorbic acid, phenolics, and flavonoids	126

generally use a swing system to first adsorb and oxidize ethylene gas from the storage, followed by its release by ventilation at higher temperature or movement of fresh air. Hydrated aluminium silicate or aluminium calcium silicate is used in such systems. The devices based on these technologies are marketed using the trade names "Swingtherm" and "Swingcat".

4.10. Use of bio-filtration and microbes

In 1998, Elsgaard reported the pioneering studies on removal of ethylene, known as biofiltration based on catalysts of biological origin. He reported adequate operational scrubbing and efficacy to remove ethylene.[167,168] This was based on isolated ethylene-oxidizing bacteria (RD-4 strain) incorporated on peat-soil. The efficiency for ethylene scrubbing was found to be 98.4% at varied temperatures (5, 10 and 20 °C). Later, Kim[169] observed that ethylene scavenging using *Bacillus* or *Pseudomonas* embedded with activated carbon could reach up to 100%. This technology may be used for removing the ethylene level in storage due to its high scavenging potential (minimum 0.017 μL L^{-1} level), stability and efficiency at low temperatures (0 to 10 °C). In addition to that, plant rhizosphere contains several microbiomes and consumes them with the help of feeding roots. This association of plants and microbes has the ability to modulate the ethylene signaling in plants.[170,171]

It has been reported that microbes can inhibit the ethylene production by producing ACC deaminase.[171] The microbiome can potentially alter the stress in direct and indirect ways, thus reducing the level of ethylene. The microbial population containing ACC deaminase is of the same magnitude as the one resulting from knocking out the *ACS* gene.[172,173] Nonetheless, the ethylene modulating microbes can transmit vertically from one generation to another, thus allowing coevolution of microbes and the host as a cohesive unit of selection.[174]

Conclusion

A perishable horticultural supply chain involves the movement of fruit and vegetables from the harvest point to the ultimate consumer through handling, transportation and storage. The likelihood to maintain postharvest quality with minimum losses and waste can be augmented by managing ethylene in the surrounding atmosphere. The effective, practical and inexpensive means are imperative to block ethylene synthesis and/or perception and its removal from packaging and storage. Use of biotechnological interventions significantly combat the problem of ethylene. CRISPR/Cas9 is a novel approach that could be utilized for gene modification. Likewise, biomolecules such as polyamines, 1-MCP, salicylic acid, NO_2, ozone, *etc.* can be applied to avoid the deleterious effects of ethylene. In summary, comprehensive solutions ranging from biosynthesis to inhibition of its action including alteration by application of efficacious cocktail postharvest technologies are the need of the hour. This shall go a long way in minimizing postharvest losses and wastage and optimize the maintenance of quality of horticultural produce. There are limited studies on stress induced deleterious cellular changes responsible for inducing the appearance of new receptor sites for effective ripening colour and aroma development. Also, there are hardly any studies on the various specific ethylene induced ripening requirements of different varieties within a crop. There is a need to develop a convenient in-packaging ethylene delivery mechanism, low-cost portable real time ethylene measuring sensors and intelligent packaging for enhancing the marketability of perishable horticultural produce.

Conflicts of interest

There are no conflicts to declare.

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