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Improving the ripening process after 1-MCP application: implications and strategies

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Abstract

Background: Consumers´ lifestyles demand high-quality products, requesting adequate fruit storage. Management of ethylene production is of paramount importance when planning postharvest storage, since this phytohormone is the key molecule behind the ripening and senescence process. Cold storage combined with 1-MCP has been one of the most applied postharvest treatments to extend the shelf-life of several fruit. However, 1-MCP is a potent inhibitor of ethylene action, leading frequently to the blockage of ripening denominated as 'evergreen' effect.

Scope and approach: Ethylene biosynthesis and perception pathway are described, as well as a critical review on 1-MCP inhibitory mechanisms. Technologies used to induce postharvest ripening after 1-MCP application are described with special attention to the latest and most significant published works. The most relevant 1-MCP reversion strategies are discussed, aiming to develop more innovative and effective approaches for stimulating ripening. Finally, the importance of tailoring treatments to specific cultivars is discussed, using pear as a case study.

Key findings and conclusions: Optimizing temperature and applying exogenous ethylene have been the main methods to reverse the effect of 1-MCP. Also, treatment with other phytohormones has shown promising results. However, the strategies effectiveness is dependent on the cultivar, time of application, and concentration of the applied compound. Also, since 1-MCP binds irreversibly to the ethylene receptor, the biosynthesis of new receptors may reverse the 'evergreen' behaviour. Therefore, attempts should be made to develop strategies according to each cultivar and their capacity to stimulate the expression of ethylene genes both related to its biosynthesis and perception.

Keywords: 1-Methycyclopropene, ethylene 'ever-green' effect, ripening recovery strategies

1. Introduction

Fruit are vulnerable to several postharvest losses due to their production seasonality, growing conditions, perishability, unpredictable ripening, and postharvest disorders, which affect their physiological and organoleptic quality (Li et al., 2020). Currently, the main challenge of the fruit sector is to extend storability of perishable fruits while guaranteeing the maintenance of fruit quality throughout postharvest storage and shelf-life (Zhang & Jiang, 2019). In particular, postharvest senescence of climacteric fruits can be reduced through the reduction of fruit metabolism by controlling the ethylene production and/or perception (Gwanpua et al., 2017; Hu et al., 2019; Luo, 2006).

Ethylene is the key gaseous phytohormone associated with the ripening phenomena. It is responsible for coordinating the timely expression of genes encoding a variety of ripening and senescence processes, such as the rise in respiration, autocatalytic ethylene production and changes in fruit colour, texture, aroma and flavour (Oetiker & Yang, 1995; Tucker et al., 2017; J. Zhang et al., 2017). In this way, the biological effects of ethylene in fruit can be either essential or injurious to the development of climacteric fruits. On one hand, ethylene-signal transduction pathway activates several processes responsible for the development of the natural ripening with the distinct quality attributes extremely important to make the fruit attractive to consumers, such as colour, flavour, texture, aroma and softening (Tucker et al., 2017). Moreover, some climacteric fruit are harvested unripe and are posteriorly artificially and timely ripened with exogenous ethylene to control and extend their shelf-life (Saraiva et al., 2018). On the other hand, in ripening fruits, excess ethylene triggers its autocatalytic production and increases respiratory rates, leading to more rapid senescence and spoilage. So, effective strategies for managing ethylene production and/or perception are of outmost importance to the postharvest sector, to slow down the ripening process and to prolong the shelf-life of fruit (Chiriboga et al., 2011).

Several technologies that modulate ethylene metabolism have been tested to suppress ethylene biosynthesis, such as adsorbing/scavenging/oxidising ethylene and blocking the ethylene receptor (Álvarez-Hernández et al., 2018; Natalia Falagán & Terry, 2018; Keller et al., 2013; Li et al., 2016; Pathak et al., 2017; J. Zhang et al., 2017).

Storage at low temperature is a traditional practice to decrease the senescence reactions that lead to quality deterioration and pathogen development (Karagiannis et al., 2018; Spotts et al., 2007; Stow & Genge, 1990; Aghdam et al., 2020). For long-term storage, the chambers atmosphere can be controlled by changing the level of oxygen (towards lowering) and carbon dioxide (CO_2) (towards increasing) to inhibit respiration and ethylene production (Stow & Genge, 1990). Controlled, modified, and/or ultra-low oxygen atmospheres, combined with cold temperature, can effectively control fruit quality. These type of storages decreases the metabolic and enzymatic activities associated with lower ethylene biosynthesis, diminishing the degradation of nutritional and quality parameters and prolonging the shelf-life of fruit (Hu et al., 2019). However, prolonged cold storage can result in various stress conditions to the fruit leading to the appearance of several injuries in the peel and flesh that can reduce their marketability, such as superficial scald, brown-heart and core-breakdown (Dias et al., 2020).

For about forty years, the postharvest application of DPA (diphenylamine) was an efficient strategy to protect fruit from quality degradation when kept at cold temperatures (Dias et al., 2020). Nevertheless, changes in legislation prohibited the use of DPA, and 1-methylcyclopropene (1-MCP) became a popular alternative to the postharvest sector (Dias et al., 2020; Lurie & Watkins, 2012), now widely implemented in apple, pear, tomato, blueberry, banana, kiwi, mango, peach, among others (Hu et al., 2019). 1-MCP is a cyclopropene derivative and a competitive inhibitor of the action of ethylene, since it interacts irreversibly with fruit ethylene receptors (Brasil & Siddiqui, 2018). When combined with low temperature and controlled atmosphere (CA), 1-MCP can prevent post-harvest disorders and protect fruit from ethylene effects (Gwanpua et al., 2017), potentially extending fruit´s shelf-life. However, after removal from cold storage, the irreversible interaction of 1-MCP with the fruit’s ethylene receptors continues. This oftentimes blocks the ripening process in climacteric fruit, such as bananas, pears, and tomato, preventing the natural ripening process (leading to the evergreen behaviour) and the development of the sensorial characteristics expected by the consumers (Blankenship & Dole, 2003; Li et al., 2016; J. Zhang et al., 2017). Therefore, the use of 1-MCP must be optimized and combined with post-1-MCP application strategies to reverse the evergreen behaviour. A few strategies have been investigated to induce ripening of fruits, such as the simultaneous application of 1-MCP and exogenous ethylene (Chiriboga et al., 2011); the storage of fruit treated with 1-MCP at elevated temperatures (Rizzolo et al., 2014; Xie et al., 2014); and the conditioning of fruit at higher temperatures and the exogenous application of ethylene (Chen et al., 1997; Xie et al., 2016), all with varying degrees of success, depending on several factors.

To understand how to develop new innovative strategies to reverse evergreen after 1-MCP application, a thorough understanding of the metabolic characteristics of the ethylene pathway and 1-MCP blockage currently is needed. In this review, we focus on the strategies already reported to reverse the inhibitory effect of 1-MCP, providing a broad understanding of the technological progress in this area and boosting future research aiming at inducing ripening after 1-MCP treatment. This will pave way for the development of innovative and adequate storage strategies that ensure fruit quality, while prolonging shelf life and avoiding physiological disorders development.

2. Ethylene vs 1-MCP

2.1. Ethylene biosynthesis and signalling

Most fruit undergo many changes during ripening which, in an evolutionary vision, occurs to make them appealing to eat and therefore benefit seed dispersal. Ripening involves several genetic networks where ethylene has a fundamental function, in combination with other hormones (Iqbal et al., 2017). The effect of ethylene on plant growth was first described around 1900 by Neljubov (1901). Later, Gane noticed that ethylene is a natural compound generated from apples (Gane, 1934). From then on, this hormone has been widely scrutinised. Ethylene (CH_2=CH_2) is the simplest plant hormone and is a gaseous plant ripening promoter governing the growth, development, and shelf-life of climacteric fruit even at trace levels (Hu et al., 2019). It is responsible for coordinating various biochemical and developmental mechanisms underlying the physiological changes that occur during plant life cycle, including seed germination, vegetative growth, leaf abscission, plant flowering, fruit ripening and senescence (Hoffman & Fa Yang, 1980). Ethylene may be also important in non-climacteric fruit, since ethylene biosynthesis and signalling genes are also expressed, albeit at much lower level when compared to climacteric fruit (Grierson, 2013). Its biosynthesis pathway and the mechanisms guiding metabolic processes associated with ripening have been widely investigated and understood (Figure 1) (Yang & Hoffman, 1984). In response to external stimuli (biotic or abiotic), internal signals induce the production of ethylene during development (Wang, Li, & Ecker, 2002). Methionine (MET) is its main precursor, which has its formation from the Yang cycle (Figure 1) (Tatsuki, 2010). This amino acid is converted to *S*-adenosyl-methionine (SAM) by SAM synthetase at the expense of ATP consumption (Ravanel et al., 1998). Subsequently, SAM is converted into 1-aminocyclopropane-1-carboxyl acid (ACC) by ACC synthase. From this reaction, 5’-methylthioadenosine (MTA) is also produced, which can be reconverted to MET through the sulphur recycling cycle (Bleecker & Kende, 2000; J. Zhang et al., 2017). Recycling of MTA to MET can maintain a constant concentration of cellular

MET, and therefore, guarantee subsequent rounds of ethylene production. This is one of the reasons for which ethylene production is considered an autocatalytic hormone (Villalobos-Acuña & Mitcham, 2008; Wang et al., 2002). Finally, ACC is oxidized to ethylene by ACC oxidase, which uses ascorbic acid as a co-substrate, and iron as a co-factor (Castellano & Vioque, 2000; Vioque & Castellano, 1998). This process occurs in the presence of oxygen and low levels of CO_2, both molecules needed for ACC oxidase activation (Burg & Burg, 1967; Hamilton, Lycett, & Grierson, 1990; Imaseki, Nakajima, & Todaka, 1988; Oetiker & Yang, 1995). The oxidation process generates CO_2 and cyanide, which is further detoxified to prevent its toxicity (Wang et al., 2002). The two processes (ATP break and ACC oxidase activation), are affected by the fruit´s respiration and the molecular oxygen content, respectively (Zhang et al., 2017). For example, increased respiration rates provide the ATP needed to the conversion of MET into SAM and, thus, can lead to higher rates of ethylene biosynthesis (Barry & Giovannoni, 2007).

ACC synthase is the rate-limiting enzyme for ethylene biosynthesis and since it is transcriptionally regulated, its expression is quite dependent on endogenous and exogenous signals (Cruz-Hernández & Paredes-lópez, 2012; Kende, 1993; Tatsuki, 2010). A good understanding of these processes is essential to designing new or improve effective control strategies of ethylene-mediated responses that could extend the postharvest shelf-life of climacteric fruit (Fabi & do Prado, 2019).

A particular feature of climacteric fruit is the presence of two systems regulating ethylene biosynthesis. System 1 (Figure 1), occurs during normal vegetative growth, producing basal levels of ethylene and inhibiting its own production (autoinhibition) (Grierson, 2013; Tatsuki, 2010). This system is responsible for the basal levels of ethylene that are synthesized by all plant tissues, including non-climacteric fruit. System 1 ethylene production is generally found in vegetative tissues, in non-climacteric fruit and in pre-climacteric fruit where the rate of ethylene production is low (Chang et al., 2008; Oetiker & Yang, 1995). Physiological evidence indicates that the low level of ethylene in system 1 plays an essential role in fruit ripening. In fact, Drouet and Hartmann (1982), suggested that low temperature storage of climacteric fruits activates system 1 and, upon warming these trace levels of ethylene induce system 2. System 2 produces a major burst of ethylene enhancing ACC synthase activity and resulting in an autocatalytic increase of ethylene (Lelievre et al., 1997; McMurchie, McGlasson, & Eaks, 1972). It requires the induction of new isoforms of ACC synthase and ACC oxidase (Barry, Llop-Tous, & Grierson, 2000; Inaba, 2007; Lelievre et al., 1997). In climacteric fruit, such as apple, tomato, and peach, the increase of ethylene production in system 2 co-occurs with a burst in respiration, which is necessary for normal fruit ripening and senescence (Arshad & Frankenberger, 2002; Tatsuki, 2010). After its biosynthesis, ethylene is perceived by ethylene receptors (ETRs) that span the membrane of the endoplasmic reticulum (Chen et al., 2002; Zhong, Lin, & Grierson, 2008) (Figure 2A). This activates its transduction pathway, which is responsible for triggering the specific biological responses associated with ripening (Fabi & do Prado, 2019; Xie et al., 2014). This complex ethylene signal transduction pathway involves a signalling cascade intermediated by downstream components such as constitutive triple response 1 (CTR1), ethylene insensitive 2 (EIN2), EIN3, and multiple transcription factors named Ethylene Response Factors (ERFs) that are involved in quality changes during ripening (Bapat et al., 2010; Li et al., 2013; Li et al., 2016). All ETRs are negative regulators of ethylene, meaning that in the presence of ethylene the receptors are inactivated, leading to ethylene signalling to occur (Hua & Meyerowitz, 1998; Tieman et al., 2000) (Figure 2A). Ethylene binds to the receptor at its N-terminal transmembrane domain in the presence of copper as a co-factor (Rodriguez et al., 1999; Schaller & Bleecker, 1995). This attachment deactivates the downstream Raf-like kinase, CTR1, functioning as a negative regulator in the phytohormone ethylene signalling pathway, and resulting in receptor degradation (Chen et al., 2007; Kamiyoshihara et al., 2012; Kevany et al., 2007; Zhong et al., 2008). When active (i.e. in the absence of ethylene) (Figure 2B), CTR1 physically interacts with the ETRs via its N-terminal domain (Ju et al., 2012; Lee & Yoon, 2017; Qiao et al., 2012; Wen et al., 2012). Particularly, CTR1 causes the phosphorylation EIN2, blocking the proteolytic cleavage of EIN2 needed for its activation. EIN2 is another endoplasmic reticulum spanning protein, and an essential positive regulator of ethylene transduction, whose proteolytic cleavage is responsible for liberating its C-terminal domain, which migrates into the nucleus activating EIN3, responsible to regulate gene expression (Ju et al., 2012; Qiao et al., 2012; Wen et al., 2012). In summary, binding of ethylene inactivates the receptors resulting in the offsetting of CTR1, which allows EIN2 to continue the downstream signalling to EIN3. EIN3 binds to the promoter of ERFs family genes inducing its transcription and the transcription factors of ERFs activate the downstream ethylene responses [57, 67–69]. The ERFs activate the expression of genes encoding ripening quality-degrading enzymes, such as polygalacturonase, pectinase and chlorophyllase, leading to the synthesis of enzymes that break down cell-wall pectin and chlorophyll (Gwanpua et al., 2017). Also, the expression of genes encoding enzymes that catalyse the transformation of starch into sugars, formation of aroma volatiles and vitamins is regulated by these ERFs (Iqbal et al., 2017; Tucker et al., 2017).

2.2. 1-Methycyclopropene

As referred above, ethylene is indispensable for the correct ripening of fruit, promoting several fruit attributes such as colour, flavour, texture and nutritional qualities. However, over-ripening reduces the shelf-life of fruit by the development of physiological disorders, senescence and increased pathogen susceptibility (DeLong, Prange, & Harrison, 2004; Kader, 1985). Several postharvest tools have been used to affect ethylene biosynthesis and/or action and enhance the shelf-life of various commodities. Inhibiting ethylene biosynthesis and perception by its receptor can minimize ethylene effect (Tiwari & Paliyath, 2011).

The ethylene-mediated response can be repressed using 1-MCP through a range of transcriptional regulators (Gwanpua et al., 2017). 1-MCP enhances the list of options for extending the shelf-life and quality of plant products (Sisler & Serek, 1997). It permanently binds to the receptors preventing ethylene from binding. This reduces the number of free receptors for ethylene, thereby inhibiting ethylene from eliciting action (Blankenship & Dole, 2003; Valero et al., 2016). When 1-MCP binds to the receptors (Figure 2B) the expression of genes related to ethylene signalling, such as, ETR, CTR, ERF´s, e.g. are suppressed (Tatsuki, 2010). Thus, it has been widely demonstrated that the postharvest treatment with 1-MCP can effectively delay fruit ripening and senescence process, and prolong the shelf-life of various fruit (Bulens et al., 2012; Pereira, Sargent, & Huber, 2015; Rizzolo, Grassi, & Vanoli, 2015). CO_2, silver thiosulfate (STS), aminoethyoxyvinylglycine (AVG), 2,5-norbornadiene (2,5-NBD) and DACP (5-Diazo-1,3-cyclopentadiene) are other compounds capable of turning off ethylene responses, however at higher concentrations (Goren et al., 2001; Sisler et al., 2001).

The finding that cyclopropenes such as 1-MCP block ethylene action through competitively binding to receptors represented a significant advance in controlling ethylene side effects (Blankenship & Dole, 2003). The affinity of 1-MCP for the receptor is ten times greater than that of ethylene, making 1-MCP more active at much lower concentrations than ethylene (Blankenship & Dole, 2003).

1-MCP emerged as a derivative from DACP products with biological use, as it is less volatile than cyclopropene itself. 3-MCP is another effective inhibitor, although higher concentrations are needed, when compared to 1-MCP (Sisler et al., 1999). 1-MCP is extremely favourable in terms of safety, toxicity and environmental issues, as it does not leave harmful residues (Lafer, 2006; Luo et al., 2008). This feature turned 1-MCP approved for use as food product in 2001 and was further registered as a safe active ingredient by FDA in 2004. Nowadays, the most applied products with 1-MCP as the active ingredient are SmartFresh^{TM} and EthylBlock^{TM} and Fysium$^{®}$ (Rademacher, 2015). In the European Union, 1-MCP was included in Annex I of the Directive 91/414/EEC (2005), conceding its use on commercially important fleshy fruit, especially climacteric fruit, including apples and pears (Falagán & Terry, 2020; Sozzi & Beaudry, 2007) at an admissible daily ingestion established at 0.0009 mg. kg^{-1} body weight per day (EFSA, 2014).

Effectiveness of 1-MCP varies widely and depends on many factors, including fruit cultivars (Pan et al., 2016), harvest maturity (Rupavatharam, East, & Heyes, 2015), concentration (Manganaris et al., 2007) and exposure (Cao et al., 2009) and temperature (DeEll et al., 2002). Also, the technology used to apply 1-MCP contributes to its effectiveness. Fumigation is the technique more widely used by the postharvest sector to apply 1-MCP (Blankenship & Dole, 2003; DeEll et al., 2016). Preparation of 1-MCP for aqueous solutions is also a practice to overcome some commercial scale issues of the fumigation technique, although it is difficult because of the low solubility of 1-MCP (Elfving et al., 2007). Microbubble technology have been an innovative system used to delivery 1-MCP gas in a more effective way than fumigation (Pongprasert & Srilaong, 2014; Nguyen et al., 2019; Xu et al., 2020).

1-MCP impacts several molecular and genetic mechanism underlying ripening, such as carbon metabolism, plant hormone signal transduction, biosynthesis of amino-acids, starch, sugar and cell wall metabolism (Serek et al., 2006; Watkins, 2006; Zhu et al., 2019). Postharvest 1-MCP treatment suppresses the expression of cell-wall related genes, reducing the activities of cell wall-degrading enzymes (pectinesterase, polygalacturonase, cellulase and β-galactosidase) of several fruit species (apple, pear, tomato, plum, banana, avocado, etc.) (Fan et al., 2018; Lin et al., 2018). Also, loss of greenness or yellowing is inhibited by 1-MCP as demonstrated by Lv et al., (Cheng et al., 2012; Lv et al., 2020). These authors showed a down-regulation expression of *MdRCCR2*, *MdNYC1*, *MdNYC3* and *MdNOL2* genes involved in chlorophyll degradation in apples (Lv et al., 2020). Another fruit quality parameter, acidity, is clearly maintained during postharvest storage after 1-MCP application (Valero & Serrano, 2010;Watkins, 2006). Fruit weight loss is also prevented by 1-MCP application (Watkins, 2006) as well as starch degradation, by inhibition of phosphorylase activity, blocking sugar formation (Mainardi et al., 2006). Conversely, 1-MCP delays the increase in total phenolics occurring during ripening of strawberry (Jiang, Joyce, & Terry, 2001). Zhu et al., (2020) showed that 1-MCP decreases the production of important flavour volatile esters like isoamyl isobutyrate, isoamyl acetate and trans-2-hexenal and hexanal, in banana. Also, it was demonstrated that 1-MCP inhibits the expression of ethylene receptors genes. *MdETR1*, *MdERS1*, and *MdERS2* were expressed in ripening fruit, and levels of *MdERS1* and *MdERS2* transcripts increased after harvest, but their expression was delayed in 1-MCP-treated fruit (Tatsuki, 2010). The 1-MCP inhibition of glycolytic metabolism, starch degradation and the repression of ACC synthase and ACC oxidase protein was previously reported (Hao et al., 2018; Li et al., 2017; Li et al., 2020). Interestingly, it was also observed that the 1-MCP artificial interference on ethylene receptors has an influence in several genes usually expressed in pre-mature stages (Tadiello et al., 2016). The most important potential benefit of 1-MCP application is the delay of ripening and senescence to extend fruit storage and marketing periods without the appearance of physiological disorders. In fact, 1-MCP blocks the transcription of AFS1, the key enzyme for α-farnesene synthesis, thus not allowing α-farnesene and conjugated trienol's to form, which are responsible for the occurrence of superficial scald (Ding et al., 2020).

Besides the effect on delaying ripening, 1-MCP can also serve as a compound reducing postharvest diseases of fruit and vegetables, such as the grey mould of apples, browning heart of pear, among others (Blankenship & Dole, 2003; Xu et al., 2020). Also, 1-MCP treatments reduces chilling injury, such as internal browning and mesocarp discoloration (Blankenship & Dole, 2003;Watkins, 2006; Zhang et al., 2020).

However, several problems regarding the application of 1-MCP persist. 1-MCP is so effective that, in some cases, the irreversible inhibition of the ripening process can be detrimental (Chiriboga et al., 2011; Li et al., 2016), since the development of natural organoleptic quality parameters does not occur. For example, 1-MCP blocks the formation of important aroma volatiles such as alcohols and esters and unsuitable treatment of the cyclopropene may cause some fruit, like banana, to stay evergreen [7,93]. These constraints have created a need to identify treatments to be applied pos-1-MCP, capable of reactivating the adequate ripening capacity when fruit are removed from storage.

3. How to reboot ripening after 1-MCP?

In fact, the commercial use of 1-MCP requires the application of a concentration, which delays the ripening process and, more important, avoids the appearance of superficial scald, and still allow the proper ripening after removal from storage. Ekman et al. (2004) identified the ideal concentration of 1-MCP applied to 'Bartlett' pear, which effectively avoided superficial scald, and did not allow the pear to ripen. However, this is not necessarily the best concentration when factoring in other characteristics such as cultivar, ripening stage, time and temperature of application (Watkins & Miller, 2004). In this way, to avoid or reverse the evergreen behaviour caused by the treatment with 1-MCP, several strategies have been evaluated. Table 1 lists the methodologies already tested to induce ripening after the application of 1-MCP. Most of the research thus far has focused on the manipulation of temperature and application of exogenous ethylene or a combination of both. Some of the treatments are applied before and others are applied after 1-MCP application, and effects vary within cultivars of the same species, demonstrating the genotype significance.

3.1 Temperature

Many metabolic and transcriptomics studies have shown that temperature induces ethylene production mainly by activating ACC synthase - the rate limiting enzyme on ethylene production (Figure 1)(Barry & Giovannoni, 2007). Ngamchuachit et al., (2014) tested the application of a hot water treatment (HWT) at 46 °C prior and post 1-MCP application in mangoes. HWT prior to 1-MCP led to faster fruit ripening compared with the application of HWT post 1-MCP. According to the authors, HWT induced an accelerated softening, probably due to the breakdown of mesocarp cells, which was delayed in part when 1-MCP was applied first. Also, the application of 1-MCP after HWT led to a reduced penetration of the gaseous 1-MCP due to the cuticle breakdown during HWT and therefore reduced its effect on delaying ripening.

In the study using with bananas, the storage at 38 °C after 1-MCP treatment allowed the normal ripening of bananas instead of abnormal ripening with temperature treatment alone or repression of ripening with 1-MCP only. The temperature exposure induced the expression of ACC synthase, ACC oxidase and ERFs, promoting ripening process (Yan et al., 2011). Transcriptome profiling of nectarine also demonstrated that storage at 20 °C for 48 h after 1-MCP prompted the expression of an ethylene receptor and three ERFs, which resulted in the restart of ripening, namely decrease of firmness, increase of ethylene production and colour modification (Ziliotto et al., 2008).

Tomato at different harvest stages showed different responses to storage at 18 °C and

13 °C after 1-MCP application. Tomato harvested at green mature stage had an increase in internal red colour, soluble solids, titratable acidity, and volatile emission. Immature green fruit did not ripen after 1-MCP treatment followed by temperature storage (Baldwin et al., 2011). This reveals the importance of having into consideration the time of 1-MCP application after harvest. Villalobos-Acuña et al. (Villalobos-Acuña et al., 2011) also hypothesized that the induction of ripening throughout storage of 1-MCP treated fruit might be greater in fruit harvested at higher maturities. Equally, Cliff et al. (2009) showed that tomatoes harvested at the 'pink' maturity stage treated with 1-MCP and exposed to 15 °C for 5 days, had visual and textural differences from the control, but differences regarding flavour attributes were not found.

Candan e Calvo (2011) tried to induce the ripening of 'Packham's Triumph' pear using several methods (temperature, exogenous ethylene and CO_2) (Table 1). The ethylene production and maturity indexes were evaluated after 160 and 230 days. They demonstrated that all treatments reversed the ripening inhibition, although depending on time of storage. For example, treatment with 5 % CO_2 was only effective after 230 days of cold storage. CO_2 is known to activate ACC oxidase, thus it could be one of the factors contributing for the ripening reboot (Figure 1)(Bleecker & Kende, 2000). They also realized the importance of temperature exposure length in the intensity of reversion, since temperature exposure for 3 weeks generated more ripening responses. This indicates that the expected storage time should be considered when establishing the reversion period. In the attempt to reverse the evergreen effect of 1-MCP on 'Abate Fetel' pears, Rizzolo et al. (2018) studied the increase of storage time, temperature and transfer of fruit from controlled (CA) to normal atmosphere (NA). They discovered the beneficial effect of rising the storage temperature from - 0.5 to 1 °C on the improvement of an edible texture. However, fruit stored under CA were less able to recover ripening than NA fruit. Ekman et al., (2004) demonstrated that the concentration of 1-MCP applied to 'Bartlett' pears, which effectively avoids superficial scald, did not allow the pear to ripen properly. Interestingly, Eccher Zerbini et al. (2005) tested the effect of 1-MCP (25 and 50 $\mu g.L^{-1}$), applied every two months on 'Conference' and 'Abbé Fétel' pears, and the results were distinct. 'Conference' pears treated with 25 $\mu g.L^{-1}$ 1-MCP and ripened at 20 °C for 7 days recovered the ripening capacity similar to control (i.e., pears not treated with 1-MCP), in contrast with the application of 50 $\mu g.L^{-1}$, which blocked the maturation process. However, 'Abbé Fétel' pears were not influenced by 1-MCP treatment. The authors concluded that 'Abbé Fétel' pears naturally produced more ethylene than 'Conference' pears and that 1-MCP treatment could be more effective in fruit with lower intrinsic ethylene production. The same conclusion was made by Bai et al. (Bai, Mattheis, & Reed, 2006). In ‘Barlett’ and ‘d’Anjou’ pears, pre-conditioning at 10 °C for 20 days or at 20 °C for 10 days after 1-MCP application allowed reaching an edible softness, but 1-MCP had no effect on ‘d’Anjou’ pears ripening. However, in another study using ‘Abbé Fétel’ pears, the fruit treated with 1-MCP and stored in air at -1 and 1 °C for 17 and 34 weeks had lower ethylene production compared to the control (Folchi, Bertolini, & Mazzoni, 2015). This suggests the role of storage time on the quality of stored pear. However, in concordance with Rizzolo et al., (2018; 2014) the increase of temperature to 1 °C permitted to recover from 1-MCP blockage (Folchi et al., 2015). Likewise, a study with ‘Rocha’ pear indicated that the elevation of storage temperature from 0 °C to 2.5 °C could overcome the retention of ripening process. But the authors also denoted that CA storage is necessary to avoid over ripening, and suggest the storage of this cultivar under CA at 2.5 °C (Gago et al., 2015). Xie et al. (2014) using ‘d’Anjou’ pear also proved that the ripening capacity was recovered increasing storage to 1.1 °C, since expression of ethylene-synthesis enzymes was higher.

Another strategy investigated to recover the ripening capacity is the use of intermittent warming. ‘Nanguo’ pear treated with 1-MCP and stored at 0 °C were exposed to 20 °C every 20 days and significant higher ester content and improved aroma quality, were found (Zhou et al., 2015).

However, from an industrial point of view, the increase of temperature in storage chambers is costly and time consuming because of chambers’ dimension, thus limiting its broader utilization.

3.2 Exogenous ethylene application

Considering that 1-MCP blocks ethylene production, several authors have been testing the application of gaseous ethylene (fumigation) or the application of the ethylene-releasing compound ethephon (2- chloroethylphosphonic acid) to reactivate ripening after 1-MCP. Few studies showed that small amounts of exogenous ethylene may rapidly accelerate the ripening process, even at low temperature (Fan et al., 2018). Balaguera-López et al. (2017) tested the immersion of cape gooseberry in an ethephon solution. An intermediate response was obtained, since the application of ethylene overcome the 1-MCP effect, with an ethylene production and respiration similar to the control fruit, though not accompanied by fruit softening. The authors justified this increase in ethylene production as a possible *de novo* biosynthesis of ethylene receptors, thus partially recovering ripening after ethylene application.

Xiao et al. (2013) isolated *MaERFs* genes from bananas and 1-MCP treated bananas exposed to exogenous ethylene had higher expression of *MaERFs* genes, promoting ripening. Sañudo-Barajas et al., (2009) tested the application of ethephon before and after 1-MCP in papayas. The application of ethephon prior to 1-MCP did not avoid ripening blockage. Nevertheless, fruit soaked in ethephon after 1-MCP developed some ripening characteristics, not accompanied by softening. They demonstrated that uronic acid and cellulose (related will cell firmness loss) in the fruit cell walls treated with 1-MCP and ethephon showed low variation.

With the objective to avoid the ripening blockage effect of 1-MCP on bananas before the treatment with ethylene, Botondi et al. (2014), applied 1-MCP in combination with 'CD ethylene' (ethylene-cyclodextrin complex) in the gas formulation. The application of 1-MCP effective delayed ripening during storage but the presence of 'CD ethylene' did not compromise the ripening after storage, demonstrating that 'CD ethylene' could have competed with 1-MCP for the receptors. Inaba et al. (2007) also reconfirmed that 1-MCP has a strong preventive effect of banana ripening, but they realized that fruit exposed to propylene, a well-known ethylene analogue, prior to 1-MCP, increased the ripening related processes, while increasing ethylene production and ACC synthase.

Da-Peng et al. (2006) also tested the regeneration of esters after 1-MCP by immersion of 'Golden Delicious' apple in ethephon. Additionally, based on the information that methyl jasmonate (MeJA) and salicylic acid (SA) induced internal ethylene biosynthesis, these authors also verified the impact in ester production of immersion of apples in these components after 1-MCP application once or twice. They observed that ethephon and SA significantly increased the apple acyltransferase gene (*MdAAT2*) expression, which they found to control ester regeneration and to be ethylene dependent. MeJA was less effective since it did not regenerate esters production after 1-MCP treatment.

Ripening induction of tomato by exogenous ethylene application has also been investigated. Zhang et al. (2009), applied 100 $\mu L.L^{-1}$ of ethylene gas in tomatoes before treatment with 200 $\mu g.L^{-1}$ 1-MCP. The application of ethylene prior to 1-MCP clearly decreased the sensitivity of tomato to 1-MCP, which was reflected in terms of softening, ethylene and respiratory responses and hue angle decline. The authors proposed that the internal ethylene levels can lead to divergent sensitivities of some climacteric fruit to 1-MCP after the initiation of ripening, which should be taking into account when trying to reinduce the ripening.

As mentioned before, Villalobos-Acuña et al. (2011) demonstrated that cold storage influences the capacity of 'Bartlett' pears treated with 1-MCP to ripen, since ethylene treatment after 1-MCP only stimulated ethylene production, including ACC synthase and ACC oxidase activity after 180 days. However, this does not happen in all fruit. For example, inhibition of kiwi ripening by 1-MCP was not possible to reverse by the application of exogenous ethylene even after 180 days of cold storage (Minas et al., 2018). Likewise, in a study performed by Mitalo et al. (2019) kiwi treated with propylene after 1-MCP application did not register internal ethylene production, but an increase in softening, sugar, total soluble solids and carbohydrate metabolism was observed.

Chiriboga et al. (2011) tried to overcome the 'evergreen' effect of 1-MCP in 'Conference pear' with external ethylene fumigation. In his study, the simultaneous exposure to 1-MCP and exogenous ethylene affected fruit ripening, namely significant firmness loss and stimulation of ACC synthase and ACC oxidase enzymes. They also defended that the recovery of ripening capacity should be due to new formation of receptors. Contrasting results were obtained by Trinchero et al. (2004), where the external ethylene exposure to 'Bartlett' pears did not significantly induce ripening. Also, in 'd'Anjou' pears treated with 1-MCP, exogenous ethylene just had effect after 8 months when fruit began to ripen, but little impact on firmness was observed (Argenta, Fan, & Mattheis, 2003). Equally, in another study performed with 1-MCP treated 'd'Anjou' pear, although at a different concentration (Table 1), external ethylene application only revealed impact after 6-7 months of storage. After this time, post-storage ethylene exposure enhanced the up-regulation of *PcACO* and *PcETR* (Xie et al., 2016). A decrease in ACC synthase and ACC oxidase occurred also in papayas stored at low temperatures, but levels were restored after exogenous ethylene treatment (Fan et al., 2018).

Opposing results to Trinchero et al. (2004), were obtained by Eckamn et al. (2004) in 'Bartlett' pears. Although the authors applied a lower 1-MCP concentration (Table 1), ethylene application was successful at inducing ripening. The authors concluded that 1-MCP concentration used and the period that fruit were stored before ripening is quite important in the response of fruit (Ekman et al., 2004).

Cucchi et al. (2011), applied 1-MCP in the ratio of 1:0.5 to 1:2 with ethylene to 'Conference' and 'Packham's Triumph' pear, and this delivered fruit with quality according to the market requirements.

Bai and Chen (2005) tried a pre-conditioning with ethylene in 'd'Anjou' pear for 0, 1, 2, 3 and 4 days before 1-MCP application. From the results obtained for firmness, the pre-conditioning for 4 days allowed a proper ripening of the pear even after treatment with 1-MCP, allowing a shelf-life of up to14 days.

However, ethylene fumigation method is expensive and complex, requiring longer application time, hampering its broad utilization. Just recently, Pongprasert et al. (2020), developed a new technology consisting in the use of a liquid solution with ethylene microbubbles (C_2H_4-MBs). This allowed the acceleration of postharvest ripening of bananas. In just 10 min the ethylene microbubbles satisfactorily ripened the bananas similarly to the fumigation technique. This technology demonstrated to be very convenient for commercial application without the complication of airtight and cooling facilities.

3.3 Hormones/Chemicals

Studies on the physiology of climacteric fruit have found that some hormones, namely auxins, can also modulate ripening in combination with ethylene (Lohani, Trivedi, & Nath, 2004). This class of plant hormones are widely known for regulating ethylene biosynthesis (Karppinen et al., 2018). Considering this effect, there are several studies aiming at inducing ripening after 1-MCP application with the application of plant hormones or other chemicals.

Abscisic acid (ABA) is widely acknowledged to induce the ACC synthase biosynthesis, accelerating the ripening process (Mou et al., 2016). In a study performed by Mou et al. (2016), injection of ABA in tomato facilitated ethylene production by regulating crucial genes like *LeACS4*, *LeACO1* and *LeETR6*. Although post- treatment with 1-MCP blocked the early ripening induction prompted by ABA, the positive impact of ABA was found 15 days post treatment. The authors believed that the blockage of ethylene downstream process triggers the nullification of ABA effect. This synergy between ethylene and ABA was also verified by Sun et al. (2010), were grapes treated with ABA relieved the block promoted by 1-MCP by inducing ethylene and accelerate ripening.

In a separate study, although 1-MCP was not applied, the authors demonstrated that the induction of ripening is ABA dependent (Siebeneichler et al., 2020). Additionally, to the demonstration of ABA ripening inducing effect, the authors also studied the effect of the application of sucrose. This compound led to an increase of anthocyanins content and up-regulation of genes related with the maturation process in strawberry (Siebeneichler et al., 2020). Lohani et al. (2004), also tested the application of ABA alone or in combination with exogenous ethylene. ABA alone was responsible for enhancing cell wall hydrolases, which led to firmness loss. These findings support the results of Jiang et al. (2000), which observed a decrease on firmness in bananas treated with ABA. However, ABA treatment of fruit pre-treated with 1-MCP had no significant effect on ripening progress.

Another synthetic auxin, 1-Naphthaleneacetic (NAA) is known to promote ethylene production in many horticultural crops (Yue et al., 2020). 1-MCP treatment of 'Golden delicious' apple blocked ethylene production, but the application of NAA rebooted ethylene biosynthesis, particularly, the expression of *MdACS3a*, *MdACS1 and MdACO1.* The authors concluded that this auxin could induce ripening even when fruit are not able to do it naturally. The application of NAA in strawberry also induced the expression of ethylene receptor genes and ACC oxidase enzyme (Trainotti, Pavanello, & Casadoro, 2005).

Just recently, it was found that alternative oxidase 1 (AOX1), a key protein in the cyanide resistant alternative respiratory pathway, may have an impact at the pear pre-climacteric stage. Genomics approaches targeting this protein found that glyoxylic acid (GLA), the key metabolite in the glyoxylic cycle, could be a promoter of ripening in 1-MCP treated pear. Based on this information, Hewitt et al. (2020), treated pears with GLA after 1-MCP application (Table 1). This resulted in a decrease of firmness, increase of internal ethylene production and sugars production.

Cui et al. (2018) tested the immersion of grape in ABA, and genomic analysis of miRNAs showed higher expression of several genes related with ripening. In another study with grape.

Jia et al. (2016), tested the application of methyl jasmonate (MeJA), a JA derivate, in the promotion of ripening. The authors found that JA plays an important role in grape ripening by increasing the transcription levels of colour-related genes *PAL1, DFR, CHI, F3H, GST*, and *UFGT*; softening-related genes *PG, PL, PE, Cell, EG1*, and *XTH1*; and aroma-related genes *Ecar, QR* and *EGS* (Jia et al., 2016). In fact, the application of MeJA promoted the colouring, softening and aroma of grape. Also, several plant defence-related genes were induced. Similar results were obtained by Karppinen et al. (2018) with the application of ABA in bilberry. Exogenous ABA also induced the expression of several cell wall and anthocyanin biosynthesis genes.

Immersion of winter jujube fruit (*Ziziphus jujuba*) in ABA, also promoted fruit ripening via acceleration of colouring, increased polyphenol-oxidase activity, lower peroxidase activity, and higher starch degradation into sugars (Kou et al., 2019). Injection of ABA in tomato also boosted the expression of genes related to pigment metabolism, including carotenoid biosynthesis, chlorophyll degradation and flavonoid biosynthesis. ABA also enabled the transcription of genes related with antioxidant capacity, such as Superoxide dismutase, catalase, ascorbate peroxidase, glutathione S-transferases, glutathione peroxidase and thioredoxin reductases. The authors propose that ABA regulates several biological processes via multi-hormonal interactions responsible for fruit ripening (Mou et al., 2015).

Sun et al. (2013), injected ABA in melon and verified the up-regulation and expression of the *CmACS1* and *CmACO1* genes and a cell wall catabolic enzyme gene *CmPG*. But the authors also found that ABA levels should be strictly regulated, since concentrations higher than 500 μmol. L^{-1} could be harmful. In mango, application of ABA promoted the activity of the ethylene biosynthesis enzymes (ACC synthase and ACC oxidase) and accelerated ethylene production. ABA also induced softening and sugar accumulation (Zaharah et al., 2013).

Besides ABA, also indole-acetic acid (IAA) stimulates ethylene production. It does so by inducing the synthesis or activation of ACC synthase (Yu & Yang, 1979).

There is enough evidence to support these phytohormones can induce ripening in several pant species. In this way, their efficient application after 1-MCP treatment could be a promising approach to reboot ripening capacity. However, different fruit show distinct responses to 1-MCP (Tucker et al., 2017; Valero & Serrano, 2010), as well as to different ripening strategies as can been more comprehended in the next section.

Table 1. Ripening induction strategies after the application of 1-MCP

Fruit commodity	Induction strategy	1-MCP treatment	Ripening induction method	Main result	References
'Keitt' mangos	Temperature	1-MCP at 1.0 μL.L^{-1} at 20 °C for 24 h	HWT prior and post 1-MCP at 46 °C for 75 min and allowed to ripen at 20 °C	HWT prior to 1-MCP resulted in a faster rate of ripening reducing the days to full ripeness to 7 days compared with the 9 days of HWT after 1-MCP or with 13 days of 1-MCP alone.	(Ngamchuachit et al., 2014)
Banana		1-MCP at 0.5 μL.L^{-1} at 22 °C for 16 h	1-MCP + storage at 38 °C and 90 % RH for 14 days	Delay of fruit abnormal ripening, in contrast to high temperature treatment alone.	(Yan et al., 2011)
Nectarine		1-MCP at 1.0 μL.L^{-1} at 20 °C for 24 h	1-MCP + storage at 20 °C for 48 h	Rapid decrease in firmness and increase in ethylene production; Storage reactivated the 1-MCP inactivated genes related to a receptor ad three ethylene-responsive factors.	(Ziliotto et al., 2008)
Tomato		1-MCP at 0.2, 0.3 and 0.4 μL.L^{-1} at 13 °C for 12 h	1-MCP + storage at 18 °C or 13 °C for 6 days + 18 °C for ripening	Storage at 18 °C instead of 13 °C resulted in an increase of internal red colour, soluble solids and volatiles emission.	(Baldwin et al., 2011)
Tomato		1-MCP at 0.25 μL.L^{-1} at 15 °C for 8 h	1-MCP + storage at 15 °C for 5 days and allowed to ripen at 22 °C for 5-8 days	Storage at 22 °C resulted in differences in textural and visual attributes compared to the untreated fruit, but not in flavour attributes.	(Cliff et al., 2009)
Tomato		1-MCP at 50,200,400 and 600 μg.L^{-1} at 20 °C for 1 min	1-MCP + storage at 20 °C for 18 days for ripening	Storage was able to induce ripening in all treatments after 18 days, although, 50 μg.L^{-1} started to ripen normally after 8 days.	(Choi & Huber, 2008)
'Packham's Triumph' pears		1-MCP at 300 or 600 μg.L^{-1}	300 μg.L^{-1} 1-MCP + 2 weeks at 17 °C and 600 μg.L^{-1} 1-MCP + 2 weeks at 17 °C; 600 μg.L^{-1} 1-MCP + 3 weeks at 17 °C before cooling again; storage at -0.5 °C for 160 and 230 days	2 weeks at 17 °C were enough when storage extended up to 230 days; 17 °C for 3 weeks was effective to reverse 1-MCP after 160 days of cold storage.	(Candan & Calvo, 2011)
'Abate Fetel' pear		1-MCP at 0.3 μL.L^{-1} at 1 °C for 24 h	1-MCP + storage for 18, 27 and 35 weeks at -0.5 and 1 °C under NA, CA and CA for 18 weeks followed by NA after shelf-life for 7 days at 20 °C	The best results to obtained marketable fruit were achieved by fruit stored in CA+NA up to 27 weeks	(Rizzolo et al., 2018)
'Barlett' pear		1-MCP at 0.01, 0.1, 0.5 or 1 μL.L^{-1} at 0 °C for 12 h	1-MCP + ripening at 20 °C for at least 8 days after storage at -1 °C for 6,12, 18 or 24 weeks	Only 1 μL.L^{-1} 1-MCP totally inhibited superficial scald, however blocked the ripening.	(Ekman et al., 2004)
'Conference' and 'Abbé Fétel' pear		1-MCP at 25 or 50 μg.L^{-1} at – 0.5 °C for 24 h	1-MCP + ripening at 20 °C for 7 days	Fruit treated with 25 μg.L^{-1} 1-MCP after ripening at 20 °C behaved similarly to control fruit, while treatment with 50 μg.L^{-1} 1-MCP delayed the shelf-life. However, 'Abbé Fétel' ripened regardless of the 1-MCP dose.	(Eccher Zerbini et al., 2005)

‘Barlett’ and ‘d’Anjou’ pear	**Temperature**	1-MCP at 0.3 $\mu L.L^{-1}$ at 20 °C for 24 h	1-MCP + pre-conditioning temperature (10, 15 or 20 °C) for 5, 10 or 20 days	The best combination for ripening recovering was of 20 °C for 10 days or 10° C for 20 days.	(Bai et al., 2006)
‘Abbé Fétel’ pear		1-MCP at 0.32 $\mu L.L^{-1}$ at 2 °C for 24 h	1-MCP + storage at -1 and 1 °C for 17 and 34 weeks, respectively + 7 days at 20 °C	Ripening occurs easily on fruit kept at 1 °C without superficial scald development.	(Folchi et al., 2015)
‘Rocha’ pear		1-MCP at 0.312 $\mu L.L^{-1}$ at 1 °C for 20 h	1-MCP + storage at 0 and 2.5 °C in NA or CA for 14, 26 and 35 weeks, respectively + 7 days at 22 °C	1-MCP blockage can be counteract by elevating temperature from 0 to 2.5 °C, but CA is necessary to avoid over ripening	(Gago et al., 2015)
‘Nanguo’ pear		1-MCP at 0.75 $\mu L.L^{-1}$ at 20 °C for 24 h	1-MCP + exposure to 20 °C for 1 day every 20 days of storage at 0 °C (intermittent warming)	Higher aroma production increase levels of ACS and ACO genes expression, ethylene production in treated pear with intermittent warming compared to control.	(Zhou et al., 2015)
‘d’Anjou’ pear		1-MCP at 0.15 $\mu L.L^{-1}$ at 0 °C for 24 h	1-MCP + storage at -1.1, 1.1 or 2.2 °C for 8 months, followed by 7 days at 20 °C	Only pears treated with 1-MCP and stored at 1.1 °C produced ethylene and developed ripening capacity without over softening as happened at 2.2 °C	(Xie et al., 2014)
‘Abbé Fétel’ pear		1-MCP at 0.3 $\mu L.L^{-1}$ at 1 °C for 24 h	1-MCP + storage at -0.5 and 1 °C in NA, CA, DCA for 20 and 28 weeks followed by 7 days at 20 °C	7 days at 20 °C was not sufficient to reboot ripening in all conditions. However, increase of temperature demonstrated to induce better flavour quality in pear.	(Anna Rizzolo et al., 2014)
Cape gooseberry	**Exogenous ethylene**	1-MCP at 1.0 $\mu L.L^{-1}$ at RT for 16 h	Immersion in ethephon solution (1 $mL.L^{-1}$) for 10 min after 5 days of 1-MCP application and allowed to ripen at 20 °C and 75 % RH for 11 days	Fruit treated with 1-MCP + C_2H_4 partially recovered the ripening capacity compared to the control group and 1-MCP treated fruit.	(Balaguera-López et al., 2017)
‘Maradol’ papaya		1-MCP at 0.3 $\mu L.L^{-1}$ at 20 °C for 12 h	Immersion in ethephon solution (2.5 $g.L^{-1}$) for 3 min at 20 °C; 12 h after 1-MCP or 24 h after ethephon application 1-MCP-treated fruit were treated with ethephon and v.v. and allowed to ripen at 20 °C and 85 % RH	Expose to ethephon followed by 1-MCP treatment inhibited the subsequent ripening; ethephon after 1-MCP induced some ripening aspects, like increase in ethylene production and respiration, chlorophyll degradation, but it was not accompanied with fruit softening.	(Sañudo-Barajas et al., 2009)
Banana		1-MCP at 0.3 $\mu mol.mol^{-1}$ at 14 °C for 16 h at 90 % RH	0.3 $\mu mol.mol^{-1}$ 1-MCP + 1.2 or 2.4 or 4.8 $\mu mol.mol^{-1}$ of ‘CD ethylene’	1-MCP + 1.2 or 2.4 $\mu mol.mol^{-1}$ of ‘CD ethylene’ effective delay ripening during storage, but do not compromise the regular ripening following overseas shipping.	(Botondi et al., 2014)

‘Packham’s Triumph’ pear	1-MCP at 300 or 600 µg.L^{-1}	300 µg.L^{-1} 1-MCP + 300 µg.L^{-1} C_2H_4 and 600 µg.L^{-1} 1-MCP + 600 µg.L^{-1} C_2H_4; storage at -0.5 °C for 160 and 230 days and allowed to ripen before 7 and 14 days at RT	300 µg.L^{-1} 1-MCP + 300 µg.L^{-1} C_2H_4 completely reversed 1-MCP blockage; 600 ppb 1-MCP + 600 µg.L^{-1} C_2H_4 was only effective after 230 days of storage plus shelf-life.	(Candan & Calvo, 2011)
Banana	No treatment with 1-MCP	Dip in C_2H_4-MBs with 0.3 g. L^{-1} of ethylene for 10 min and 20 min; fumigation with 1 g. L^{-1} of ethylene at 25 °C for 12 h	C_2H_4-MBs for 10 min is sufficient to accelerate ripening compared to fumigation.	(Pongprasert et al., 2020)
‘Golden Delicious’ apple	1-MCP at 0.75 µL.L^{-1} at 20 °C for 20 h	Immersion into 2 mM ethephon in 0.02 % (v/v) Tween 20 and 1 % (v/v) ethanol for 2 min; allowed to ripen at 20 °C	Effective regeneration of total esters production treated once or twice with 1-MCP.	(Li et al., 2006)
Tomato	1-MCP at 0.516 µL.L^{-1} at 20 °C for 9 h; aqueous 1-MCP at 200 µg.L^{-1} for 1 min	1-MCP + 100 µL.L^{-1} of C_2H_4 for 3 or 6 h at 20 °C; 100 µL.L^{-1} or 10 µL.L^{-1} of C_2H_4 for 5 min + 1-MCP at 20 °C; 100 µL.L^{-1} for 6 h at 20 °C + aqueous 1-MCP	Ethylene exposure after 1-MCP treatment minimally affected fruit softening and hue angle; Simultaneous application of ethylene followed by 1-MCP blocked the 1-MCP capacity to inhibit fruit ripening; sensitivity of fruit to 1-MCP treated with ethylene followed by aqueous 1-MCP was reduced in the short-term (0-1h) of ethylene exposure.	(Zhang et al., 2009)
Banana	1-MCP at 1 µL.L^{-1} at 22 °C for 24 h	1-MCP + 100 µL.L^{-1} of C_2H_4 for 24 h at 22 °C and allowed to ripen for 7 days at 22 °C	Ethylene treatment followed by storage at 22 °C was not able to reboot ripening blocked by 1-MCP	(Lohani et al., 2004)
Banana	1-MCP at 20-40 µL.L^{-1} at 20 °C for 6 h	1-MCP + 500 µL.L^{-1} with propylene for 18 h and allowed to ripen at 22 °C	1-MCP treatment avoided the ripening-induced effect of propylene in pre-climacteric banana, but treatment with propylene stimulated ripening after its onset.	(Inaba et al., 2007)
‘Barlett’ pear	1-MCP at 0.3 µL.L^{-1} at 20 °C for 12 h	1-MCP + 100 µL.L^{-1} of C_2H_4 for 24 h at 20 °C; storage at -1 °C for 120 and 180 days	Fruit only recovered the capacity to ripen after 180 days of storage plus ripening at 20 °C	(Villalobos-Acuña et al., 2011)
Kiwi	1-MCP at 0.6 µL.L^{-1} at 0 °C for 24 h	1-MCP + 100 µL.L^{-1} of C_2H_4 for 24 h at 20 °C after 4 months of cold-storage and allowed to ripen for 8 days at 20 °C	Ethylene treatment was not effective in reverse the ripening induction promoted by 1-MCP.	(Minas et al., 2018)
Banana	1-MCP at 0.5 µL.L^{-1} at 22 °C for 18 h	1-MCP + 100 µL.L^{-1} of C_2H_4 for 18 h and allowed to ripen at 22 °C	Ethylene treatment was able to induce ERF’s contributing to ripening process to occur.	(Xiao et al., 2013)
‘Conference’ pear	1-MCP at 0.3 or 0.6 µL.L^{-1}	0.3 µL.L^{-1} 1-MCP + 0.3 µL.L^{-1} C_2H_4; 0.6 µL.L^{-1} 1-MCP + 0.6 µL.L^{-1} C_2H_4; storage at - 0.5 °C for 90 and 180 days	Ethylene treatment allowed the ripening to occur after 90 and 180 days, although at a lower rate compared to control.	(Chiriboga et al., 2011)

‘Barlett’ pear	Exogenous ethylene	1-MCP at 0.4 $\mu L.L^{-1}$ at 20 °C for 10 h	1-MCP + 400 $\mu L.L^{-1}$ of C_2H_4 for 6 h and allowed to ripen at 20 °C	The climacteric ethylene peak was delayed by 15 days compared to the control and did not achieve the same ripening pattern of untreated fruit.	(Trinchero et al., 2004)
Kiwi		1-MCP at 2 $\mu L.L^{-1}$ at 22 °C for 12 h	1-MCP + 5000 $\mu L.L^{-1}$ of propylene for 9 days at 22 °C	Application of polypropylene did not induce softening, ethylene production, aroma volatiles and expression of associated genes. However, it was noticed an increase in sugar production, namely sucrose, glucose and fructose.	(Mitalo et al., 2019)
‘dAnjou’ pear		1-MCP^1 at 0.00042, 0.0042, 0.042 $\mu mol.L^{-1}$ at 20 °C for 18 h; 1-MCP^2 at 0.042 $\mu mol.L^{-1}$ at 20 °C for 20 h	1-MCP^1 + 0.45 $\mu mol.L^{-1}$ of C_2H_4 for 7 days at 20 °C following 2,4,6 and 8 months of storage at 1 °C; 1-MCP^2 + 4-18 $\mu mol.L^{-1}$ of C_2H_4 for 7 days at 20 °C following 3,8,16 and 24 months of storage at 1 °C	Exposure of 1-MCP treated pears to C_2H_4 after storage did not fully reverse the effect of 1-MCP, but when fruit begin to ripen (after 8 months) it occurs similar to untreated fruit.	(Argenta et al., 2003)
‘dAnjou’ pear		1-MCP at 0.15 $\mu L.L^{-1}$ at 0 °C for 24 h	1-MCP + 100 $\mu l.L^{-1}$ of C_2H_4 for 48 h at 20 °C after 5,6, and 7 months of storage at -1°C; treatment applied to green and red fruit	Ethylene exposure of green fruit did not reactivate the ripening in 7 days but rendered red fruit to develop ripening after 6-7 months of cold storage.	(Xie et al., 2016)
‘Barlett’ pear		1-MCP at 0.01, 0.1, 0.5 or 1 $\mu L.L^{-1}$ at 0 °C for 12 h	1-MCP + 100 $\mu l.L^{-1}$ of C_2H_4 for 42 h at 20 °C for up to 19 days	Ethylene exposure induced ripening in all 1-MCP treated pears.	(Ekman et al., 2004)
Abbé Fétel’, ‘Conference’ and ‘Blanquilla’		1-MCP in the ration of 1:0.5 to 1:2 with ethylene at – 0.5 °C for 24 h	1-MCP + C_2H_4 simultaneously; after storage at - 0.5 °C pear was allowed to ripen at 15-20 °C	The results obtained on firmness showed that fruit softened at a slower rate compared to control but achieving the consumer quality.	(Cucchi & Regiroli, 2011)
‘d’Anjou’ pear		1-MCP at 1 $\mu L.L^{-1}$ at 20 °C for 24 h	Pre-conditioning with 100 $\mu l.L^{-1}$ of C_2H_4 for 1,2,3 and 4 days at 20 °C + 1-MCP	1-MCP treated fruit only softened as the control if the pre-conditioning occurs for 4 days.	(Bai & Chen, 2005)
‘Packham’s Triumph’ pear	**CO_2**	1-MCP at 300 or 600 $\mu g.L^{-1}$	600 $\mu g.L^{-1}$ 1-MCP + 5 % CO_2; storage at -0.5 °C for 160 and 230 days and allowed to ripen before 7 and 14 days at RT	Only effective after 230 days of storage plus shelf-life.	(Candan & Calvo, 2011)
Golden Delicious’ apple	**Other chemicals/hormones**	1-MCP at 0.75 $\mu L.L^{-1}$ at 20 °C for 20 h	Immersion into 2 mM salicylic acid in 0.02 % (v/v) Tween 20 and 1 % (v/v) ethanol for 2 min; Immersion into 2 mM methyl jasmonate in 0.02 % (v/v) Tween 20 and 1 % (v/v) ethanol for 2 min: allowed to ripen at 20 °C	Effective regeneration of total esters production treated once or twice with 1-MCP in salicylic acid treated apples. Methyl jasmonate resulted in regeneration of total esters after a single 1-MCP application.	(Li et al., 2006)
Tomato		1-MCP at 2 $\mu L.L^{-1}$ at 20 °C for 8 h	Injection of 25 μL of 10 $mmol.\ L^{-1}$ of ABA + 1-MCP (4 days after) and allowed to ripen at 20 °C	ABA induced ripening was not found with the subsequent treatment with 1-MCP.	(Mou et al., 2016)
Grape		1-MCP 5 $\mu L.L^{-1}$ for 24 h	1-MCP + 100 $mmol.\ L^{-1}$of ABA (after 5 days of 1-MCP treatment)	Treatment with ABA restores fruit ripening course.	(Sun et al., 2010)
Strawberry		No 1-MCP treatment	Immersion of fruit in a 100 $\mu mol.\ L^{-1}$ of ABA or 50, 270, 500 $mmol.\ L^{-1}$ of sucrose for 5 min; storage at 20 °C and 80 % RH for 5 days	The application of ABA and sucrose improves the content of anthocyanin and vitamin C and induce the expression of maturation genes.	(Siebeneichler et al., 2020)

‘d’Anjou’ pear	**Other chemicals/hormones**	1-MCP 130 µL.L^{-1} for 24 h at 1 °C	1-MCP + humidify atmosphere with 3 % GLA for 16 h at 20 °C	GLA treatment resulted in a significant decrease in firmness, increase in ethylene and respiration and sugars production.	(Hewitt et al., 2020)
Banana		No 1-MCP treatment	Immersion of fruit in a 100 µmol. L^{-1} of ABA in 0.2 % Teepol for 6 h	ABA enhances the activity of cell wall hydrolases and increased the ethylene production.	(Lohani et al., 2004)
Banana		1-MCP 1 µL.L^{-1} for 12 h	1-MCP + vacuum infiltration of 10^{-3} mol.L^{-1} of ABA	ABA did not induced ripening of 1MCP treated fruit	(Jiang et al., 2000)
Grape berries		No 1-MCP treatment	Immersion of fruit in 100 mg.L^{-1} of ABA for 15 s	ABA promoted the expression on ripening inducing genes	(Cui et al., 2018)
Grape berries		No 1-MCP treatment	Immersion of fruit in 10 or 100 µmol. L^{-1} of MeJA for 10 min	MeJA application induced fruit colouring, softening and aroma release.	(Jia et al., 2016)
Bilberry		No 1-MCP treatment	Immersion of fruit in 0.5 or 2 mmol. L^{-1} of ABA for 4 and 6 days	**Effect:** ABA promoted anthocyanin synthesis and expression of several genes involved in cell wall modification during ripening.	(Karppinen et al., 2018)
Winter jujube fruit		No 1-MCP treatment	Immersion of fruit in 0.05 mg.mL^{-1} of ABA for 3 min	ABA induced the ripening and reduced the quality loss time.	(Kou et al., 2019)
Tomato		No 1-MCP treatment	Injection of 25 µL of 10 mmol. L^{-1} of ABA; storage at 20 °C for 18 days	ABA boosted the transcription of genes involved in carotenoids biosynthesis and chlorophyll degradation.	(Mou et al., 2015)
Melon		No 1-MCP treatment	Injection of 1 mL of 10, 50, 100 or 500 µmol. L^{-1}of ABA; storage at 25 °C	ABA promoted ripening and softening and the upregulation of ACS and ACO genes	(Y. Sun et al., 2013)
Mango		No 1-MCP treatment	Immersion of fruit in 1 mmol. L^{-1} of ABA for 5 min; storage at 21 °C and 56 % RH	ABA accelerated ethylene synthesis and the activity of ACS and ACO enzymes. Also, higher sugars content was found in ABA treated fruit.	(Zaharah et al., 2013)
Mung bean		No 1-MCP treatment	Incubation of fruit with 5 mL of 50 µmol. L^{-1} of IAA; storage at 27 °C	IAA stimulated ethylene production by inducing ACC synthase formation and activation.	(Yu & Yang, 1979)
Strawberry		No 1-MCP treatment	Spray of fruit with 2 mmol.L^{-1} of NAA for 12 h over a period of 48 h	Application of NAA excited the expression of ethylene receptors genes and ACO enzyme.	(Trainotti et al., 2005)
Apple		1-MCP at 1 µL.L^{-1} at 20 °C for 12 h	1-MCP + immersion of fruit in 4 mmol. L^{-1} NAA for 2 h; storage at RT for 20 days	NAA application induced ethylene biosynthesis and, therefore the onset of ripening.	(Yue et al., 2020)

Note: HTW- Hot water treatment; RT- Room temperature; RH-Relative humidity; C_2H_4 - ethylene; CD ethylene- ethylene-cyclodextrin complex; C_2H_4-MBs- aqueous ethylene micro-bubble solution; ABA- Abscisic acid; CA- Controlled atmosphere; NA-Normal atmosphere; DCA- Dynamic controlled atmosphere; GLA- Glyoxylic acid; MeJA- Jasmonic acid derivate; IAA- Indole-acetic acid; NAA- napthaleneacetic acid

4. Cultivar variability in response to 1-MCP and pos-1-MCP treatments: pear as a case study

The adverse effects of 1-MCP on the ability of fruit to ripen normally is also highly cultivar-dependent (Bai et al., 2006; Xie et al., 2016). According to the literature, each cultivar exhibits different internal ethylene concentration (IEC) and ability to develop new ethylene receptor sites. Tatsuki et al., (2010) attributed this differences to the different expression levels of ACS gene family among cultivars, which could justify the higher and lower tolerance to 1-MCP.

Pear is a climacteric fruit whose ripening behaviour is particularly cultivar-dependent, with different ripening characteristic and responses to 1- MCP. Among the genus *Pyrus*, there are two groups: European and Asian (Table 2). European pears are climacteric, requiring exposure to chilling temperature or ethylene to ripen correctly (Valero et al., 2016). On the contrary, Asian pears, with the exception of *P. ussuriensis* Maxim and *P. bretschneideri* Reld, are classified as non-climacteric, not needing a postharvest ripening (Li, 2012). Amongst European pears, their ripening behaviour varies widely (Villalobos-Acuña & Mitcham, 2008), being often divided into summer and winter pears. Winter pears are often slow-ripening and suitable for long-term storage, requiring extended chilling exposure to initiate the autocatalytic ethylene production (system 2). Summer pears have a fast ripening process, demanding minimum or no exposure to chilling temperatures in order to ripe (Lindo-García et al., 2020; Saquet & Almeida, 2017; Villalobos-Acuña & Mitcham, 2008).

Table 2. Classification of the genus *Pyrus*

Specie	Classification	Cultivar	Ripening requirements
European pear (*P. communis* L.)	**Winter pear**	‘d’Anjou’, ‘Comice’, ‘Hardy’ and ‘Flor d’Hivern’	Chilling exposure for long periods
	Summer pear	‘Bartlett’, ‘Conference’, ‘Blanquilla’, ‘Williams’, ‘Packham’s Triumph’ or ‘Spadona’	Chilling exposure for shorter periods
	Intermediate pear	‘Rocha’	Chilling exposure for short periods (15-30 days)
Asian pear	Not applicable	*P. pyrifolia* Nakai, *P. sinkangensis* Yu, Reld and *P. pyrifolia* Nakai	Non-climacteric

Furthermore, cultivars such as ‘Rocha’, can be described as intermediate between a summer and a winter pear considering the time of cold pre-conditioning. This cultivar requires a short exposure to chilling temperatures (Table 2) to induce the ripening (like a summer pear), but is suitable for long-term storage (up to 10 months) under controlled atmosphere (like a winter pear) (Almeida, Carvalho, & Dupille, 2016; Saquet, 2017; Saquet & Almeida, 2017).

The application of 1-MCP has been tested in both summer and winter pear, and the effects depend on maturity stage, 1-MCP dose, time of application, storage conditions and are highly cultivar-dependent (Saquet, 2019; Valero et al., 2016; Watkins, 2006). For example, ‘d’Anjou’ and ‘Bartlett’ exhibited a delay on ripening with 0.1 or 0.4 $\mu L.L^{-1}$ 1-MCP (Argenta et al., 2003; Trinchero et al., 2004), but similar doses (0.3 or 0.4 $\mu L.L^{-1}$) caused complete inhibition of ripening in ‘Conference’ (Chiriboga et al., 2011). Regarding the adverse effects of 1-MCP, ‘Conference’, ‘d’Anjou’, ‘Barlett’, ‘Blanquilla’ and ‘Rocha’ revealed difficulty to ripe, remaining firm, green and not attaining the desirable taste and flavour after shelf-life (Chiriboga et al., 2011; Saquet, 2019). However, ‘Packham’s Triumph’ or ‘Spadona’ pears treated with 0.2 $\mu L.L^{-1}$ 1-MCP, although with a reduction in the volatile aromatic production, reached a satisfactory consumer acceptance after 5 or 10 days of shelf-life, respectively (Gamrasni, Ben-Arie, & Goldway, 2010; Moya-León et al., 2006).

When applying 1-MCP it is challenging to identify a concentration that guarantees the reduction of physiological disorders appearance while assuring correct ripening.

As demonstrated before, the application of exogenous ethylene to induce ripening after 1-MCP application has been tested in several cultivars including ‘d’Anjou’ (Chen & Spotts, 2005; Xie et al., 2016; Yu & Wang, 2017), ‘Barlett’ (Argenta et al., 2016), ‘Abbé Fétel’, ‘Conference’ and ‘Blanquilla’ (Cucchi & Regiroli, 2011) with distinct results. In ‘d’Anjou’, only the simultaneous application of ethoxyquin (2.7 $g.L^{-1}$) together with ethylene (0.3 $\mu L.L^{-1}$or 0.6 $\mu L.L^{-1}$) and 1-MCP (0.3 $\mu L.L^{-1}$) was effective on controlling fruit scald without compromising the recovery of the ripening capacity after long term storage (Yu & Wang, 2017). On the other hand, Calvo and Candan (2015) found that ‘Packham’s Triumph’ pears treated with the same dosage of 1-MCP (0.3 $\mu L.L^{-1}$) needed lower ethylene (0.15 or 0.3 $\mu L.L^{-1}$) to induce ripening after 160 days of storage with a very low incidence of superficial scald.

Also, as stated previously there are differences between the same cultivar. The application of 100 μL.L^{-1} exogenous ethylene at 20 ºC for 48 h only ripened red 'Anjou' pears but green 'Anjou' pears (Xie et al., 2016).

Post-heat treatment was tested in the 'd'Anjou' and 'Bartlet' pears treated with 1-MCP stored under 4 months in regular atmosphere. These pears were pre-conditioned at 10-20 ºC during 10-20 days before shipping (Bai et al., 2006). In the case of the 'd'Anjou' pears, a lower 1-MCP dosage (50 nL.L^{-1}) was needed to guarantee the initiation of their ripening after 21 days at 20 °C or after 7 days using a lower dosage of 1-MCP (< 25 nL.L^{-1}). However, the scald incidence increased from < 20% to >40% with the use of < 25 nL.L^{-1}1-MCP (Bai et al., 2006). On the other hand, on 1-MCP-treated 'Bartlett' pears, higher doses of 1-MCP were used (0.3 μL.L^{-1}) without affecting the ripening recovery capacity and the combination of 10 days at 20 ºC or 20 days at 10 °C were enough to initiate fruit ripening without scald incidence.

In 1-MCP treated 'd'Anjou' pears (0.15 μL.L^{-1}), the storage temperature of 1.1 ºC during 6–8 months facilitated the initiation of the ripening capacity (Xie et al., 2014). However, in 'Abbé Fétel' pears stored for 5-7 months, only higher doses of 1-MCP (0.3 μL.L^{-1}) together with higher storage temperatures (1 ºC) showed promising results in enhancing shelf-life of this cultivar and improving the sensory profile of 1-MCP treated pears (Rizzolo et al., 2014).

Regarding 'Rocha' pear, 1-MCP has been tested in dosages between 0.1 and 1.0 μL.L^{-1} to control superficial scald and delay post-storage ripening during storage periods of 4 - 6 months (Almeida et al., 2016; Isidoro & Almeida, 2006; Saquet & Almeida, 2017; Saquet & Almeida, 2017). However, the use of higher concentrations of 1-MCP (0.5 to 1.0 μL.L^{-1}) delayed or inhibited ripening after storage and the use of lower concentrations of 1-MCP (0.1 to 0.15 μL.L^{-1}) increased the incidence of superficial scald incidence (Isidoro & Almeida, 2006).

It is clear that, it is difficult to generalise about the best combination of harvest maturity, 1-MCP concentration, application conditions (temperature, time), and storage time after 1-MCP treatment to adequately control fruit softening and development of physiological disorders, while simultaneously allowing the fruit to ripe to good quality for marketing. Thus, 1-MCP application conditions and strategies to recover ripening must be tailored to each cultivar, allowing ripening to occur, so that the final quality of the treated fruit is similar to that of the untreated product in normal consumption time.

Conclusions and future prospects

The most important advantage of 1-MCP application in combination with controlled atmospheres after harvest is to extend fruit shelf-life through suppression of ethylene action, delaying ripening and senescence and controlling the appearance of postharvest disorders. However, in most cases 1-MCP promotes the evergreen effect on fruit. Since ethylene is the central hormone associated with ripening, the understanding of ethylene biosynthesis and perception in regulating growth and senescence could support the development of new approaches to induce ripening. The majority of the studies described thus far have tested the application of temperature and exogenous ethylene or a combination of both. Recently, the application of other phytohormones, namely ABA and NAA, have also demonstrated potential to reboot ripening after 1-MCP application. Most of these methodologies were successful at rebooting ripening via stimulation of ethylene production, including modulation of ACC synthase activity, ACC oxidase activity, and expression of genes associated with these enzymes. Nevertheless, more important than stimulating the activity of the enzymes involved in ethylene production, is the capacity of the ripening recovery strategies to induce the synthesis of new receptors. Since 1-MCP binds irreversibly to the ethylene receptors, only *de novo* synthesis of these receptors will allow the ethylene downstream perception to occur. However, there is a crucial influence of cultivar, maturity at harvest, 1-MCP concentration, and storage time after 1-MCP treatment on the potential effectiveness of the tested strategies. There are several successful strategies to restart the ripening process after 1-MCP application; however, these are very dependent on extrinsic factors. The differences in ripening recovery of fruit might be associated with the abundance of ethylene receptors at the time of the 1-MCP treatment. Thus, it is still a challenge to reach a balance between a good storage with 1-MCP and eventual ripening after removal from storage. If an optimum treatment combination is found, ripening can be reactivated in a predictable manner becoming a useful tool to improve fruit supply chain management, reduce post-harvest losses, and recover consumer acceptance.

CRediT author contribution statement

Cindy Dias: Conceptualization, Writing - review & editing, Investigation; **Tânia Ribeiro:** Writing - review & editing; **Ana Cristina Rodrigues:** Validation; **António**

Ferrante: Supervision, Validation; **Marta W Vasconcelos:** Supervision, Validation; **Manuela Pintado:** Conceptualization, Supervision, Validation.

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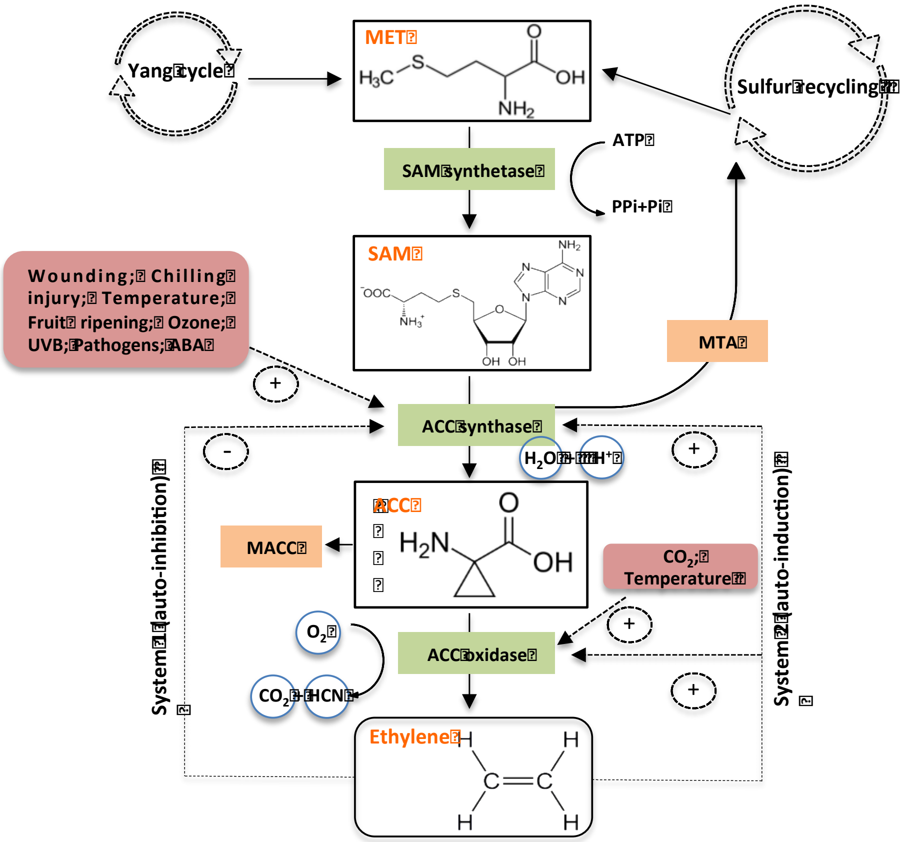
Figures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ATP
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SAM
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+
MTA
ACC synthase
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+
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ACC
H_2N O OH
MACC
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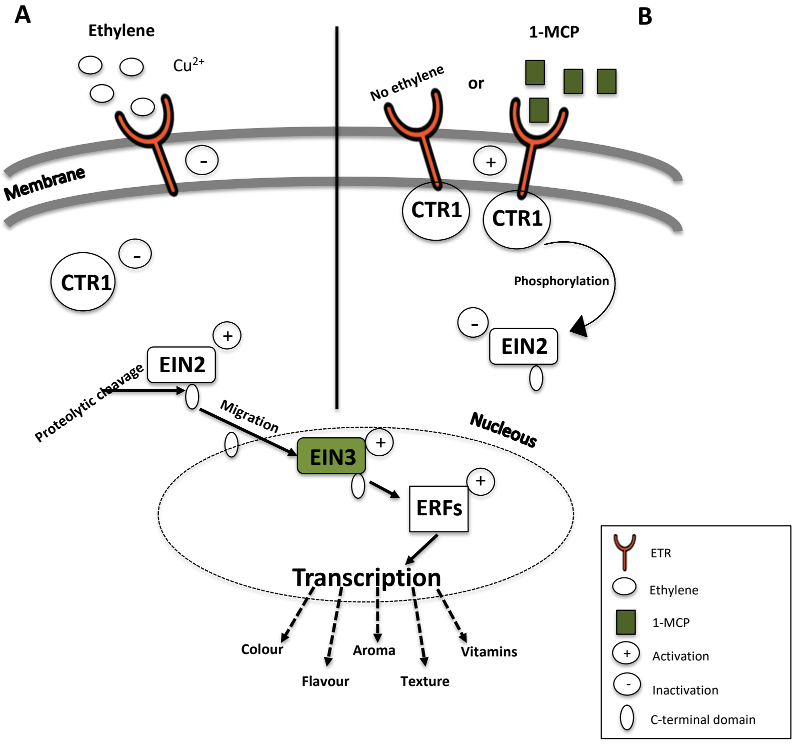
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EIN2
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Migration
EIN3
+
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Nucleous
Transcription
Colour
Flavour
Aroma
Texture
Vitamins
B
1-MCP
No ethylene
or
+
CTR1
CTR1
Phosphorylation
-
EIN2
ETR
Ethylene
1-MCP
+ Activation
- Inactivation
C-terminal domain

List of captions

Figure 1. Ethylene biosynthesis pathway. The degradation of MET (obtained from the Yang cycle) into SAM is catalysed by SAM synthethase consuming one molecule of ATP. The rate-limiting step of ethylene formation is the transformation of SAM to ACC by ACC synthase. From this conversion also results the formation of MTA, which is recycled back to MET through the sulphur cycle. ACC undergoes into oxidation by ACC oxidase in the presence of O_2 to generate ethylene, CO_2 and cyanide (HCN). Malonylation of ACC into malonyl-ACC (MACC) avoids the ACC pool and reduces the ethylene production. The dashed arrows indicate transcriptional regulation of both ACC synthase and oxidase by internal and external signals.

Figure 2. Ethylene signalling pathway. A-The binding of ethylene to the receptors inactivates them, allowing the signalling via proteolytic cleavage of EIN2. This cleavage induces the C-terminal domain of EIN2 to migrate into the nucleus binding to EIN3, which activates the ERFs responsible for the transcription of the genes encoding enzymes responsible for ripening quality changes. B- In the absence of ethylene binding, or presence of an inhibitor (1-MCP), CRT1 binds to the receptor prompting the phosphorylation of EIN2 and therefore blocking ethylene downstream signalling.