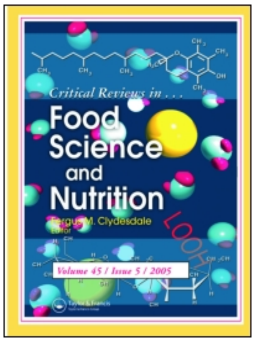

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Tools to Maintain Postharvest Fruit and Vegetable Quality through the Inhibition of Ethylene Action: A Review

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Ethylene is a plant hormone controlling a wide range of physiological processes in plants. During postharvest storage of fruit and vegetables ethylene can induce negative effects including senescence, over-ripening, accelerated quality loss, increased fruit pathogen susceptibility, and physiological disorders, among others. Apart from the endogenous ethylene production by plant tissues, external sources of ethylene (e.g. engine exhausts, pollutants, plant, and fungi metabolism) occur along the food chain, in packages, storage chambers, during transportation, and in domestic refrigerators. Thus, it is a great goal in postharvest to avoid ethylene action. This review focuses on tools which may be used to inhibit ethylene biosynthesis/action or to remove ethylene surrounding commodities in order to avoid its detrimental effects on fruit and vegetable quality. As inhibitors of ethylene biosynthesis and action, good results have been found with polyamines and 1-methylcyclopropene (1-MCP) in terms of maintenance of fruit and vegetable quality and extension of postharvest shelf-life. As ethylene scavengers, the best results can be achieved by adsorbers combined with catalysts, either chemical or biological (biofilters).

Keywords ethylene inhibitors, 1-MCP, polyamines, activated carbon, catalysis, oxidation

INTRODUCTION

Ethylene is a very simple molecule with two carbon atoms linked with a double bound and naturally occurring as gaseous form. The first indications of a gaseous compound affecting plant tissues were reported in the nineteenth century, with the observation that illuminating gas streetlights caused senescence and defoliation in neighbouring trees. In the early twentieth century (1901), Neljubov identified ethylene as the causative agent of this effect, and is recognized as the discoverer of this plant hormone. Later, Gane (1934) proved that plants produce ethylene, although only after the establishment of gas chromatography (1959) this compound could be quantified.

Ethylene is considered a plant growth regulator or plant hormone because of the large number of physiological processes that are controlled or regulated by its action, from seed germination to organ senescence. Among these processes, the effect of ethylene on fruit ripening and vegetable senescence has been of significant interest for the scientific community, due to the importance of fruit and vegetables as key components of the human diet. Fruits and vegetables provide carbohydrates, organic acids, fiber, vitamins, lipids, and minerals (nutritional properties), as well as antioxidant compounds with health-benefits (functional properties).

From the point of view of agriculture, ethylene confers both positive and negative effects during fruit ripening. Among the positive effects, ethylene stimulates the ripening process of climacteric fruits (apple, apricot, avocado, banana, peach, plum, and tomato) resulting in desirable flavors, color, and texture (quality characteristics). In these fruits, negative effects can be

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found during postharvest storage due to an acceleration of the ripening process (over-ripe fruits) leading to fruit quality loss. In contrast, in non-climacteric fruit (citrus, eggplant, grape, pepper, and strawberry), ethylene is not required for the coordination and completion of ripening of these fruit. However, in these fruits as well as in vegetables, ethylene has also negative effects since it increases pathogen susceptibility, physiological disorders, and senescence, with a net reduction in postharvest life.

Apart from the ethylene from vegetable and fruit tissues, other sources of ethylene production are biomass fermentation of some microorganisms (bacteria and fungi) and pyrolysis of hydrocarbons which release ethylene as component of air pollutant (Cape, 2003). This ethylene exerts similar effects to endogenous ethylene. Thus, in order to avoid the detrimental effects of this plant hormone on vegetable and fruit quality, and in turn prolong their storability, the inhibition of ethylene biosynthesis and/or the removal of ethylene surrounding fruit and vegetables should be achieved. To fulfil this objective, current knowledge of the ethylene biosynthesis pathway and its role in fruit ripening and vegetable senescence is reviewed. Application of ethylene inhibitors at the levels of biosynthesis and action, as well as the different tools to remove ethylene surrounding fruit and vegetable during handling, packaging, and storage, will be described.

BIOSYNTHESIS OF ETHYLENE AND ITS REGULATION

Ever since the discovery of ethylene, continuous efforts have been made to clarify its biosynthesis pathway. Ethylene biosynthesis, perception, signal transduction and its regulation at biochemical, genetic, and biotechnological levels is well-documented and covered by a number of excellent reviews (Bleecker and Kende, 2000; Deikman, 1997; Ecker, 2002; John, 1997; Sisler and Serek, 1997; Stearns and Glick, 2003). The molecular and physiological role of ethylene in fruit ripening has also been of special interest in the articles by Adams-Phillips et al. (2004), Giovannoni (2001) and Lelièvre et al. (1997). In higher vascular plants, ethylene is synthesized from the amino acid methionine, which is converted to S-adensoylmethionine (SAM) by the addition of adenine and consumption of ATP. SAM is then transformed to 1-aminocyclopropane-1-carboylic acid (ACC) by the enzyme ACC-synthase (ACS) with the generation of the by-product 5′-methylthioadenosine (MTA), which is recycled to methonine. Thus, ethylene can be produced at high rates even with a small pool of free methionine. Finally, ACC is oxidized to ethylene by ACC oxidase (ACO, formerly named as EFE, ethylene-forming enzyme). The main step controlling ethylene biosynthesis is ACS and the subsequent pool of ACC. Early studies reported the upregulation of this pathway (Fig. 1),

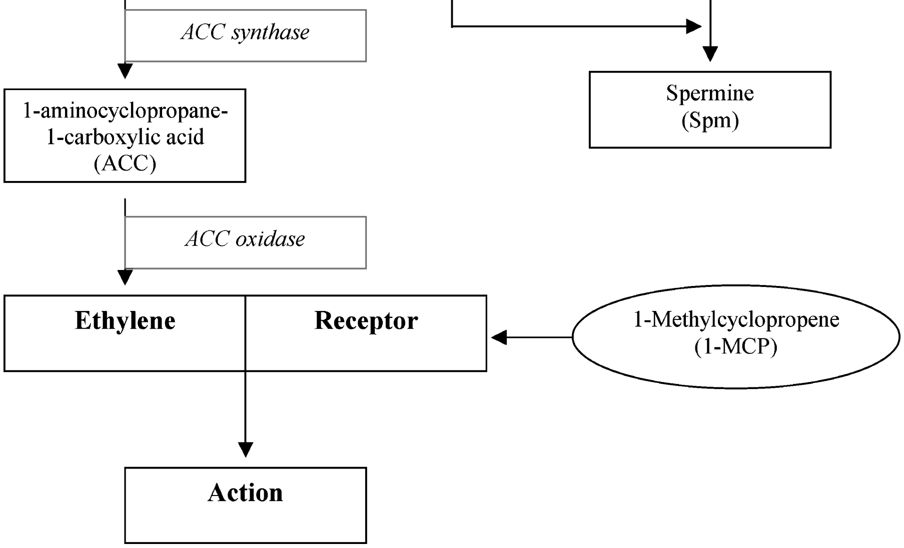

Figure 1 Partial metabolic pathway for the ethylene and polyamine biosynthesis showing SAM as the common precursor for both pathways and the binding site of 1-MCP.

by observations of ACC accumulation and increases in the activities of both ACS and ACO enzymes (Abeles et al., 1992; Kende, 1993; Yang and Hoffman, 1984). More recently, it has been reported that ACS and ACO are encoded by multigene families. The expression of ACS genes is differentially regulated by several environmental, developmental, and hormonal signals, while for ACO activity the presence of CO_2 is necessary although the exact mechanism for this is still unclear (Bleecker and Kende, 2000; Wang et al., 2002).

In climacteric fruit, once the ethylene is being synthesized at low amounts, the internal production of ethylene rapidly increase. This is very important, since the onset of the ripening process of these fruit is considered to begin at this stage, and there is a positive feedback regulation in which ethylene promotes its own synthesis. This phenomenon is the so-called autocatalytic ethylene production (Yang and Hoffman, 1984).

As a hormone, ethylene binds to a receptor and the signal is transduced through a complex mechanism to trigger specific biological responses. Over the past decade, continuous efforts have been made to identify and isolate the ethylene receptor, using Arabidopsis as a model, although the complete set of signalling components are still unknown. Ethylene binds to its receptors using copper as a co-factor (Guo and Ecker, 2004). Tomato fruit is a good model system for the study of ethylene response, offering a number of advantages due to the well-characterized roles of ethylene in the control of its ripening. In tomato, a gene family composed of six members with major domains has been reported for the ethylene receptor (Adams-Philips et al., 2004; Klee and Tieman, 2002). Although the ethylene receptor is being well-characterized, and the use of an increasing number of transgenic plants is providing new information of ethylene control (Stearns and Glick, 2003), there are still gaps in our knowledge on the differential responsiveness of a specific tissue to ethylene.

Currently, ethylene biosynthesis and action can be blocked by chemical compounds which differ in their structure and act at different levels, such as modifying ACS and ACO activities, blocking receptor sites, diversion of SAM through polyamine biosynthesis, or through the removal of ethylene. These issues will be discussed below.

ROLE OF ETHYLENE IN FRUIT AND VEGETABLES: DETRIMENTAL EFFECT DURING POSTHARVEST STORAGE

Ripening could be defined as a physiological process that comprises several physical, chemical, and biochemical changes which renders fruit attractive and palatable (Lelièvre at al., 1997; Giovannoni, 2001). The main changes associated with ripening include color (loss of green color and the development of yellow, orange, red and other color characteristics depending on species and cultivar), firmness (softening by cell-wall degrading activities), taste (increase in sugars and decline in organic acids), and flavor (production of volatile compounds providing the characteristic aroma). All these changes are well-known to be regulated by ethylene in climacteric fruits. Additionally, fruit and vegetables are living organisms, in which transpiration, respiration, and other metabolic processes continue during the postharvest period. All these events can lead to quality losses, both external and internal, although the deterioration rate is affected by different factors, such as intrinsic characteristics of the product and storage conditions in terms of temperature, relative humidity, storage atmosphere composition, etc.

Vegetative tissues and growing fruit synthesise small amounts of ethylene ($0.1–0.2\ \mu l\ kg^{-1}\ h^{-1}$). However, ethylene production can increase markedly (up to 1,000-fold) associated with the ripening process in climacteric fruit. During the postharvest period, exposure to ethylene may occur inadvertently in storage or transit from atmosphere pollution as a by-product of human industrial activities (Chang and Bleecker, 2004) or from ethylene produced by adjacent plant products. Ethylene is biologically active at very low concentrations (nl-$\mu l\ l^{-1}$concentrations), but important differences can be found in ethylene sensitivity among the species of fruit and vegetables (Table 1), and no standard for the detrimental effects of ethylene can be set (Wills et al., 2001). Thus, climacteric fruit such as apple, cherimoya, kiwifruit, and pear, generally have high rates of ethylene production and are also highly sensitive to this plant hormone (at concentrations of $0.03–0.1\ \mu l\ l^{-1}$). Conversely, there are some vegetables (broccoli, cabbage, cauliflower, lettuce, and spinach) as well as some non-climacteric fruit (strawberry, persimmon) which produce very low amounts of ethylene but are described as extremely highly sensitive to ethylene (Wills and Warton, 2000), sometimes at lower concentrations than climacteric fruit ($0.01–0.02\ \mu l\ l^{-1}$). Finally, the majority of non-climacteric fruit (cherry, grape, berries, pepper, and pineapple) exhibit both low ethylene production and low sensitivity (over $0.2\ \mu l\ l^{-1}$). In fact, a relationship between storage life and ethylene atmospheric

Table 1 Ethylene production and sensitivity of several commodities

Commodity	Ethylene production	Ethylene sensitivity
Climacteric fruit		
Apple, Kiwifruit, Pear, Cherimoya	***	*** ($0.03–0.1\ \mu l\ l^{-1}$)
Avocado, Cantataloupe melon, Passion fruit	***	** ($>0.4\ \mu l\ l^{-1}$)
Apricot, Banana, Mango	**	*** ($0.03–0.1\ \mu l\ l^{-1}$)
Nectarine, Papaya, Peach, Plum, Tomato	**	** ($>0.4\ \mu l\ l^{-1}$)
Vegetables and non-climacteric fruit		
Broccoli, Brussels sprouts, Cabbage, Carrot,	*	*** ($0.01–0.02\ \mu l\ l^{-1}$)
Cauliflower,Cucumber, Lettuce, Persimmon.	*	***
Potato, Spinach, Strawberry	*	***
Asparagus, Bean, Celery, Citrus, Eggplant	*	** ($0.04–0.2\ \mu l\ l^{-1}$)
Artichoke, Berries, Cherry, Grape, Pineapple,	*	* ($>0.2\ \mu l\ l^{-1}$)
Pepper	*	*

* low, ** medium and *** high ethylene production or sensitivity.

Table 2 Summary of the detrimental effects of ethylene related to quality

Ethylene effect	Symptom or affected organ	Commodity	Reference
Physiological disorders	Chilling injury	Persimmon, Avocado	Salvador et al., 2003; Pesis et al., 2002
	Russet spotting	Lettuce	Manleitner et al., 2001
	Superficial scald	Pear, Apple	Bower et al., 2003; DeLong et al., 2004
	Internal browning	Pear, Peach	Soo et al., 2003
Abscission	Bunch	Cherry tomato	Beno-Moualem et al., 2004
	Stalk	Muskmelon	Lima et al., 2004
	Calyx	Persimmon	Salvador et al., 2003
Bitterness	Isocoumarin	Carrot, Lettuce	Fan and Mattheis, 2000
Toughness	Lignification	Asparagus	Hennion et al., 1992
Off-flavors	Volatiles	Banana	Imahori et al., 1998
Sprouting	Tubercle, Bulb	Potato, Onion	Wills et al., 2004; Benkeblia and Selselet-Attou, 1999
Colour	Yellowing	Broccoli	Suzuki et al., 2004
	Stem browning	Sweet cherry	Gong et al., 2002
Discoloration	Mesorcarp	Avocado	Pesis et al., 2002
Softening	Firmness	Avocado, Mango, Apple, Strawberry, Kiwifruit, Melon	Jeong and Huber, 2004; Nguyen et al., 2002; Tian et al., 2000; Johnston et al., 2002; Karakurt and Huber, 2002; Song et al. 1999

concentration has been found for fruit and vegetables, in which ethylene levels higher than 0.10 μl l^{-1} would induce important quality loss (Wills and Warton, 2000) leading to a reduction of the shelf-life by acceleration of the ripening and senescence processes. These detrimental effects depend on a number of variables, the most important being tissue sensitivity to ethylene, duration of exposure, ethylene concentration, atmospheric composition, and temperature (Saltveit, 1999). Table 2, shows a summary of some examples in which the ethylene response could be considered as detrimental for a wide range of fruit and vegetables, including acceleration of physiological disorders, abscission, bitterness, toughness, sprouting, color changes, softening, over ripening, and off-flavors. Moreover, these harmful effects of ethylene could increase in function of temperature, since fruit and vegetable sensitivity to ethylene is enhanced by increasing temperature in the range of 0–20°C (Agar et al., 2000; Nanos et al., 2002; Wills et al., 2001). In fact, using a simulation model for fruit climacteric ethylene emission, it has been recently proposed that a temperature increase as low as 5% would increase the ethylene production in more than 30% (Génard and Gouble, 2005). However, temperatures over 35°C reduced ethylene production in several commodities including apple and tomato, and the sensitivity to exogenous ethylene was reduced during heat treatments, mainly due to inactivation of ethylene receptors (Paul and Chen, 2000).

Taking into account all the adverse effects of ethylene on vegetable and fruit quality it has been recommended to keep ethylene at concentrations below 0.015 μl l^{-1} in storage areas (Wills and Warton, 2000). Then, there is a need to have available methods for delaying and/or inhibiting ethylene production or its action. Some of these tools are currently being used by industry and others with great promises, are still being investigated.

APPLICATION OF ETHYLENE BIOSYNTHESIS AND/OR ACTION INHIBITORS

Our knowledge of the ethylene biosynthesis pathway can be used to develop different ways of reducing ethylene production or inhibit its action, and in turn to maintain fruit and vegetable quality properties and prolong shelf-life. Thus, ethylene action can be counteracted at both the biosynthesis and receptor level, or through an effective elimination of released ethylene in the environment.

Inhibition at Biosynthesis Level

ACC formation is probably the limiting step for ethylene production, although production can be suppressed by inhibition of both ACS and ACO enzyme activities. Thus, inhibitors have been studied and developed over recent years. Some examples for ACS inhibitors are aminoethoxyvinylglycine (AVG) and aminooxyacetic acid (AOA), while Co^{2+}, α-aminoisobutyric acid (AIB), and ethanol and acetaldehyde vapors, are examples of compounds which depress ACO activity. High rates of CO_2 have been shown to be effective in inhibiting both enzymes, and as an antagonist of ethylene action. Thus, reduction of the autocatalytic ethylene production in climacteric fruit can be achieved with high CO_2, resulting in a net extension of postharvest storage life (Abeles et al., 1992; Bleecker and Kende, 2000; Mathooko, 1996; Yang and Hoffman, 1984). Consequently, accumulation of CO_2 under modified or controlled atmospheres has been shown to improve the shelf-life of fruit and vegetables (Kader et al., 1989). In addition, heat treatments applied prior to storage have been shown to inhibit ethylene synthesis, acting on both ACO and ACS activities, although ACS is less heat-sensitive than ACO (see reviews by Lurie, 1998; Paull and Chen, 2000).

ACS Inhibitors

AVG has been the most investigated in recent years. The commercial product ReTain$^{®}$ (Valent BioSciences Corp., Libertyville, Illinois, USA), which contains 15% w/w AVG, is registered for use on apple in USA and is likely to be soon available for use in Europe. AVG has been demonstrated to be effective in both pre-harvest and postharvest applications.

For pre-harvest use, AVG is usually applied a few weeks before harvest (1–4 weeks) and has been found to be useful for apples, plums, nectarines, peaches, and pears, among others. For these commodities, a delay and/or inhibition of ethylene production has been reported on the tree and during storage, this in turn delaying softening, starch degradation, accumulation of soluble sugars, the decrease in acidity, and generation of ester volatiles related to flavor (Bregoli et al., 2002; Clayton et al., 2000; Jobling et al., 2003; Mir et al., 1999; Silverman et al., 2004; Torrigiani et al., 2004). The same effects have been observed when AVG has been applied as postharvest treatments (Byes, 1997; Garner et al., 2001; Palou and Crisosto, 2003; Saltveit, 2005). The ethylene biosynthesis inhibition by AVG in both pre- and postharvest treatments could induce an increase in fruit shelf life, although the net extension in shelf life for each particular commodity was not addressed in the available literature and deserves further research.

ACO Inhibitors

The aroma volatile synthesis during fruit ripening on tree is associated to the production of anaerobic metabolites, such as acetaldehyde and ethanol (Knee and Hatfield, 1981), which was the first evidence that the application of these metabolites could induce some beneficial effects on postharvest fruit quality. In fact, accumulation of acetaldehyde and ethanol during the fruit ripening on tree enhances color, odor, and flavor of several commodities such as apple, strawberry, and table grape, although at high concentration can result in the generation of off-flavors (Pesis, 2005). Moreover, postharvest application of acetaldehyde and ethanol to several types of fruit has shown a reduction and/or delay of softening, chlorophyll breakdown and lycopene synthesis by suppression of ethylene biosynthesis through the inhibition of ACO activity (Pesis et al., 1998; Simpson et al., 2003; Suzuki et al., 2004). However, acetaldehyde has been recently added to the list of known carcinogenic materials, and thus its use at commercial postharvest application is limited. Therefore, as an alternative, more studies with ethanol treatments (a GRAS compound) are being carried out (Pesis, 2005). Thus, for practical purposes, formulations based on an alcohol powder that gradually releases ethanol vapor are currently being tested. The application of ethanol vapor by vacuum infiltration has been effective on increasing tomato storage life (1.5–2-fold) as judged by color change (Ratanachinakorn et al., 1999). Accordingly, appropriate ethanol vapor treatments have been shown to be effective delaying yellowing in broccoli florets through the retardation of the changes from chloroplasts to chromoplasts in sepal parenchyma cells, leading to 2-fold increase in shelf life depending on the applied concentration (Suzuki et al., 2004; 2005). In addition, ethanol application was able to inhibit superficial scald on apple, which is a maturity-related disorder (Scott et al., 1995). However, ethanol application failed on delaying banana ripening since it did not penetrate into the pulp (Bagnato et al., 2003). Thus, no general conclusions can be withdrawn from ethanol treatments, since fruit response depends on a wide number of variables (specie, cultivar, ripening stage, concentration, and duration of treatment, among others), and would limit its commercial use.

Other inhibitors, such as cobalt (Co^{2+}) are known to block the autocatalytic production of ethylene by inhibition of ACO activity (Dunkley and Golden, 1998; Riov and Yang, 1982). Thus, some experiments have been conducted in several fruit crops resulting in effective delays of the ripening process, e.g. bananas (Dominguez et al., 1998), apples (Tian et al., 1994), and tomatoes (Atta-Aly et al., 2000). However, these compounds are toxic heavy metals and are not allowed to be used in the food industry. Nevertheless, Ag^{+}, formulated as silver thiosulfate, is usually the active component of preservative solutions for cut flowers, for which an extension of flower longevity by ethylene inhibition is achieved (Staby et al., 1993).

Competition by SAM

Other means of altering ethylene production have been the use of exogenous treatments with polyamines (PAs): putrescine (Put), spermidine (Spd), and spermine (Spm). Unlike the inhibitors described above, PAs are naturally-occurring compounds in most living organisms (both plant and animals) where they fulfil a wide array of physiological roles. Since there is a demonstrated competition between PAs and ethylene, as shown in Fig. 1, through their common precursor SAM (Valero et al., 2002), the balance between these two opposite growth regulators is critical in retarding or accelerating the ripening process (Pandey et al., 2000).

Several experiments have shown that exogenous application of polyamines during the growing season (pre-harvest) can delay fruit softening and decrease ethylene production in apricot (Paksasorn et al., 1995), peach (Bregoli et al., 2002), and nectarine (Torrigiani et al., 2004). These results confirm the capacity of PAs to control ethylene production during fruit ripening on the tree, and to exert their anti-senescence effects (Pandey et al., 2000) under field conditions.

However, the main application of polyamines has been carried out under postharvest conditions. PA levels decrease during fruit ripening along with an acceleration of senescence and paralleling the climacteric rise in ethylene production (see review by Valero et al., 2002). PAs applied exogenously increase levels of endogenous PAs during storage, and in turn extend shelf-life. Moreover, postharvest application of PAs can lead to an inhibition of ethylene production in avocado, pear and tomato fruit (Kakkar and Rai, 1993; Saftner and Baldi, 1990), although Wang et al. (1993) found no ethylene inhibition after Put treatment in apples. It is interesting that in conditions which are accompanied

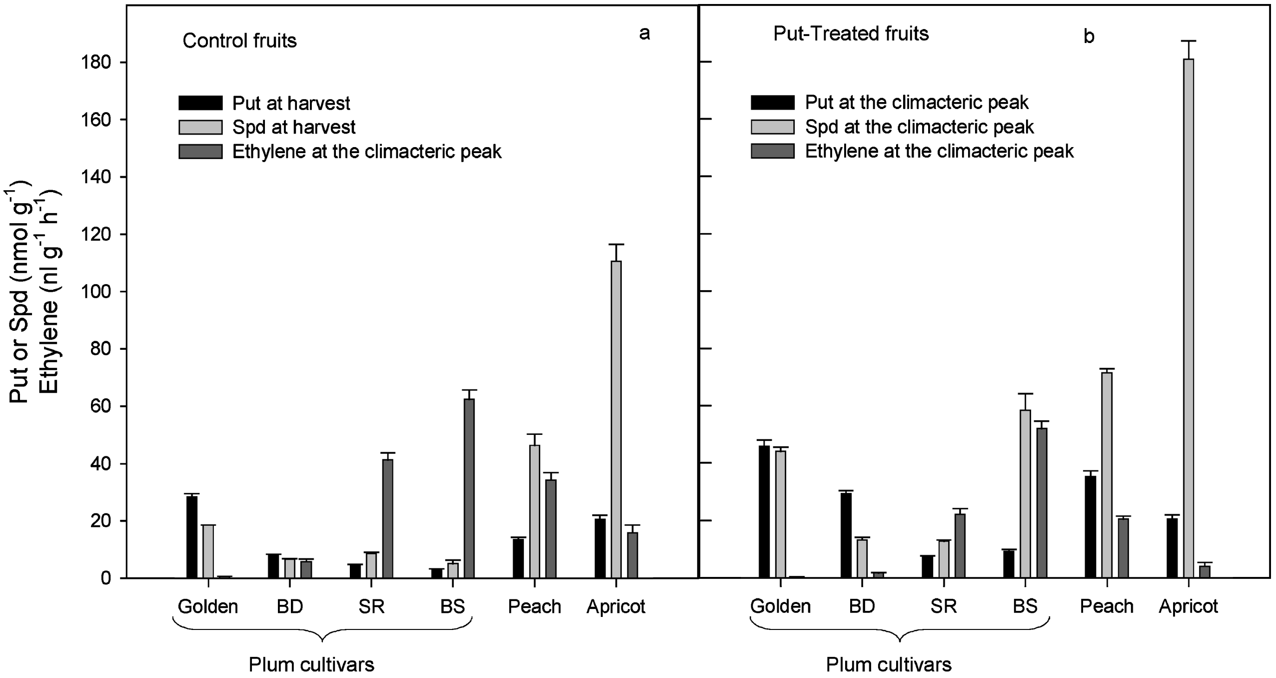

Figure 2 Levels of Putrescine (Put) and Spermidine (Spd) at harvest and ethylene production at the climacteric peak (a) during storage at 20°C and Put, Spd, and ethylene production at the climacteric peak in Put-treated fruit during storage at 20°C (b). BD ("Black Diamond"), SR ("Santa Rosa") and BS ("Blackstar") plums.

by increased levels of ethylene, such as mechanical damage during handling (wound ethylene), postharvest PA applications have been also shown to inhibit such ethylene production in several fruit crops (Martínez-Romero et al., 2004).

In our laboratory, comprehensive research on the effects of putrescine treatments on fruit quality during storage has been carried out on several Prunus species, such as apricots (Martínez-Romero et al., 2002), peaches (Martínez-Romero et al., 2000), and several cultivars of plums (Pérez-Vicente et al., 2002; Serrano et al., 2003). From these papers, it can be observed that the levels of both Put and Spd at harvest were significantly different among the cultivars, as well as the ethylene production rate at the climacteric peak (Fig. 2a). Following exogenous application of 1 mM Put, concentrations of Put and also biosynthesis of Spd (from Put using DC-SAM, as shown in Fig. 1) significantly increased, while ethylene production was inhibited for all fruit (Fig. 2b), the percentage of ethylene inhibition being negatively correlated ($r^2 = 0.94$) with the production of ethylene at the climacteric peak. Thus, the diversion of DC-SAM through PA biosynthesis could explain the significant reduction in ethylene production found in Put-treated fruit, since a smaller pool of DC-SAM would be available to synthesize ACC and consequently ethylene.

Moreover, when parameters related to fruit quality following storage were determined, a reduction in color changes, maintenance of fruit firmness, and delayed ripening were observed in Put-treated fruit compared with control ones. Thus, for peach, apricot, and plum cultivars, the chroma index decreased over storage, but in those fruit treated with 1 mM Put the percentage of color retention with respect to the value at harvest was significantly higher than in control fruit (Fig. 3). The same effect was shown for firmness retention, which was significantly higher in Put-treated fruit than in control ones (Fig. 4). Reduced softening after Put treatments could be due either to an inhibition of polygalacturonase and pectinmethylesterase activities or to the polyamine capacity to cross-link pectic substances in the cell wall producing rigidification (Martínez-Romero et al., 2000, 2002; Pérez-Vicente et al., 2002; Serrano et al., 2004). As time in postharvest storage advances, soluble solids concentrations increase while a net decrease in acidity is observed, leading to an increase of the ripening index during storage (Fig. 5), which was significantly reduced in Put-treated fruit. The net result of these changes in fruit quality together with the reduction in ethylene production leads to an extension of the shelf-life of these climacteric fruit. On average, this extension was estimated as 2–3 fold more in treated than in controlled fruit.

Inhibition at the Receptor Level

Silver ions (applied as silver thiosulfate) or irradiated diazocyclopentadiene have both been shown to be inhibitors of ethylene action. However, neither can be used in foods, since silver is a heavy metal and a potential pollutant, and the latter highly explosive at high concentrations (Sisler and Serek, 1997). The most potent ethylene antagonist, amongst different organic olefins and synthetic cyclopropenes, is 1-methylcylopropene (1-MCP) (Fig. 1). 1-MCP binds to the ethylene receptor with 10 times more affinity than ethylene itself, being more active at much lower concentrations (Blankenship

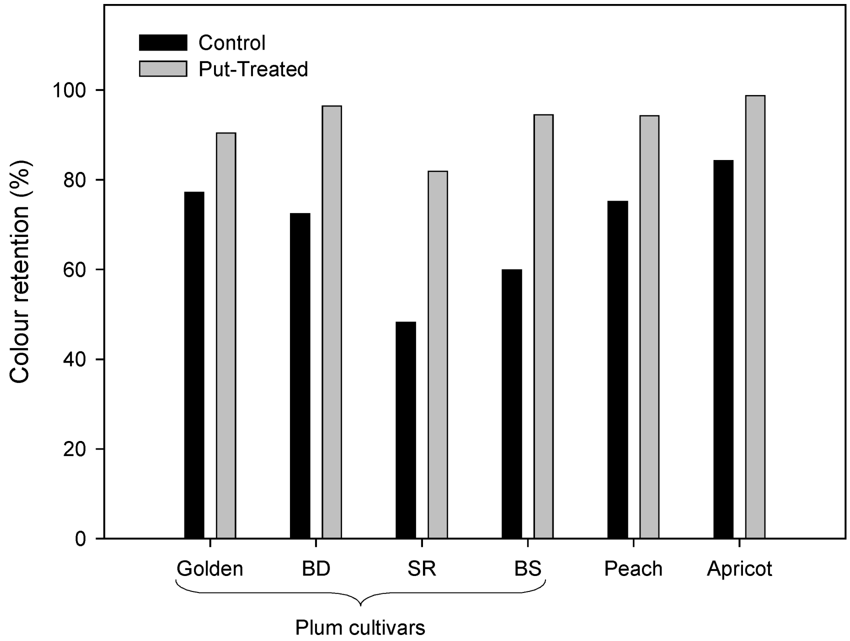

Figure 3 Percentage of color retention (chroma index) in control and Put-treated fruit at the climacteric peak during postharvest storage at 20°C. BD ("Black Diamond"), SR ("Santa Rosa") and BS ("Blackstar") plums.

and Dole, 2003; Serek et al., 1995; Sisler and Serek, 1999). This compound has attracted great interest world-wide as a new, non-toxic agent for humans and environment (Environmental Protection Agency, 2002) and safe postharvest chemical in the agro-food industry capable of maintaining the postharvest quality of many fresh commodities, both climacteric and non-climacterics (Blankenship and Dole, 2003; Watkins, 2002). Currently, 1-MCP is being commercially used in cut flowers and fruit such as apples, bananas, melons, and tomatoes, and it is registered (under the trade name of Smartfresh®, by Agrofresh, Inc, a subsidiary of Rohm and Haas, Spring House, PA) for use as postharvest fruit treatment in 6 EU countries and other 15 countries outside Europe including the United States and Canada.

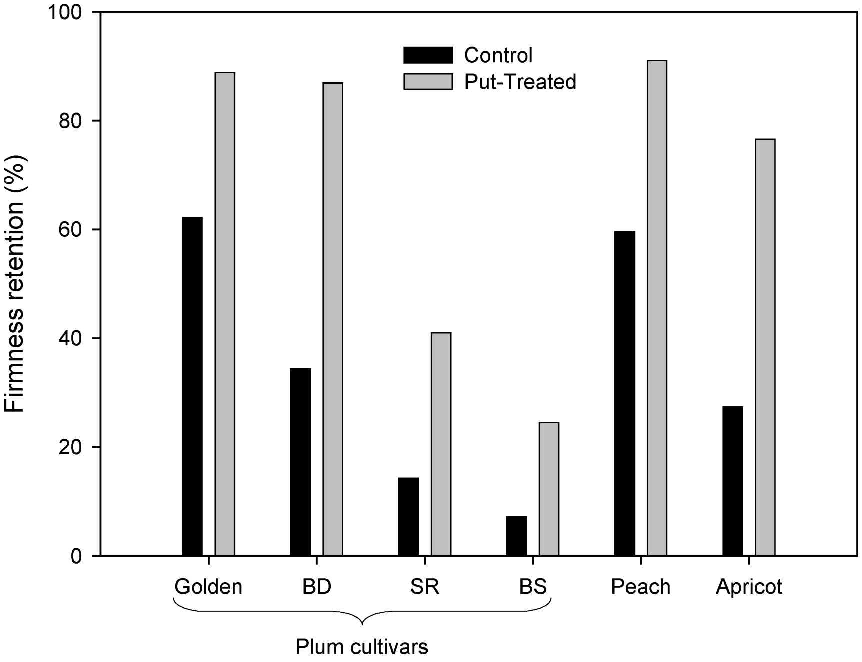

Figure 4 Percentage of firmness retention (flesh texture) in control and Put-treated fruit at the climacteric peak during postharvest storage at 20°C. BD ("Black Diamond"), SR ("Santa Rosa") and BS ("Blackstar") plums.

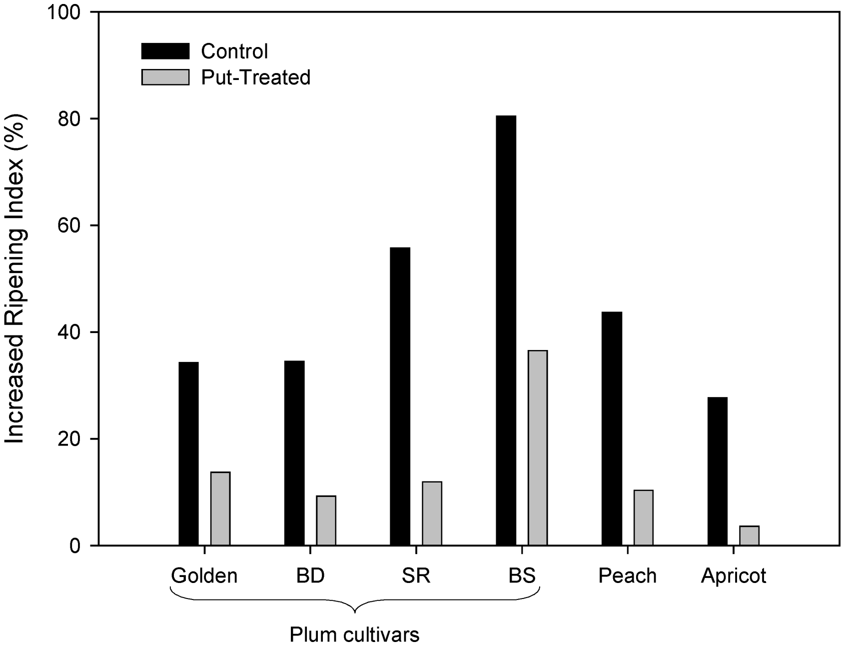

Figure 5 Percentage of increased ripening index (TSS/TA) with respct to values at harvest in control and Put-treated fruit at the climacteric peak during postharvest storage at 20°C. BD ("Black Diamond"), SR ("Santa Rosa") and BS ("Blackstar") plums.

1-MCP treatments have been carried out at different temperatures (1–20°C), concentrations (from 20 nl l^{-1} to 40 μl l^{-1}), durations (4–24 h) and ripening stages at harvest, and there is no one general rule to achieve the maximum effectiveness of 1-MCP treatment (Abdi et al., 1998; Blankenship and Dole, 2003; Dong et al., 2001a; 2001b; 2002; Fan et al., 2000; 2002; Gong et al., 2002; Martínez-Romero et al., 2003; Salvador et al., 2004; Valero et al., 2003).

In our survey of the effects on fruit quality properties following 1-MCP application at 0.5 μl l^{-1} to apricots ("Currot" and "Bulida"), early-season plums ("Golden Japan" and "Santa Rosa"), late-season plums ("President," "Reina Claudia," and "Sungold") and tomato cultivars harvested at two ripening stages ("Raf," "Cherry," "Patrona," and "Daniela"), we found that all changes that are normally accelerated by ethylene action were delayed during postharvest storage (Guillén et al., 2003; 2006a; 2006b; Martínez-Romero et al., 2003; Valero et al., 2003; 2004). The main effects observed were a significant reduction in ethylene production, a delay in color changes, and diminution of the changes in both ripening index and softening. Interestingly, a significant reduction in the weight loss during storage was observed, which has an economical benefit apart from reduction of fruit quality deterioration. These more global effects suggest that ethylene receptors were blocked by 1-MCP and the ethylene action was delayed with time, leading to maintenance of quality parameters of these climacteric fruits during a period 2–4 times higher than in control ones. It is interesting to point out that the percentage of ethylene inhibition by 1-MCP was correlated inversely to the maximum value of ethylene production at the climacteric peak of each particular fruit (Fig. 6). Thus, fruit with the lowest ethylene production ("Golden Japan" plum, <0.5 nl g^{-1} h^{-1}) showed the highest rate of ethylene inhibition (over 90%). Conversely, in "Currot" apricot which had a climacteric peak production rate of >40 nl g^{-1} h^{-1}, an inhibition below 40% was observed. After 7 days of cold storage plus 7 days at 20°C, simulating commercial conditions, all fruit treated with 1-MCP had retained firmness at more than 50% of that found at harvest, while non-treated fruit showed 2-fold lower firmness retention (Fig. 7).

In the other study, comparing several tomato cultivars which were harvested at two different ripening stages, 1-MCP inhibited the typical increase in the color parameter a* during storage (Fig. 8). Thus, following the 1-MCP application an extension of self-life could be achieved, since increase in a* (negative a* values mean green and positive values red) is a good indicator of tomato ripening. In addition, other parameters related to fruit ripening, such as softening and increase in ripening index were also lower in 1-MCP treated than in control tomatoes (Guillén et al., 2006a; 2006b).

In non-climacteric fruit and vegetables, 1-MCP treatments delayed or decreased the evolution of several parameters ethylene-induced, such as softening, loss of green colour, anthocyanin accumulation, chilling injury, decay, and loss of ascorbic acid, among others, as summarized on a web site by Watkins and Miller at Cornell University (http://www.hort.cornell.edu/department/faculty/watkins/ethylene/). However, in bananas some disturbances to the physiological and biochemical changes related to normal ripening, such as uneven peel degreening, increased chilling injury symptoms and suppressed total volatile production have been reported after 1-MCP treatment (Golding et al., 1998; Jiang et al., 2004).

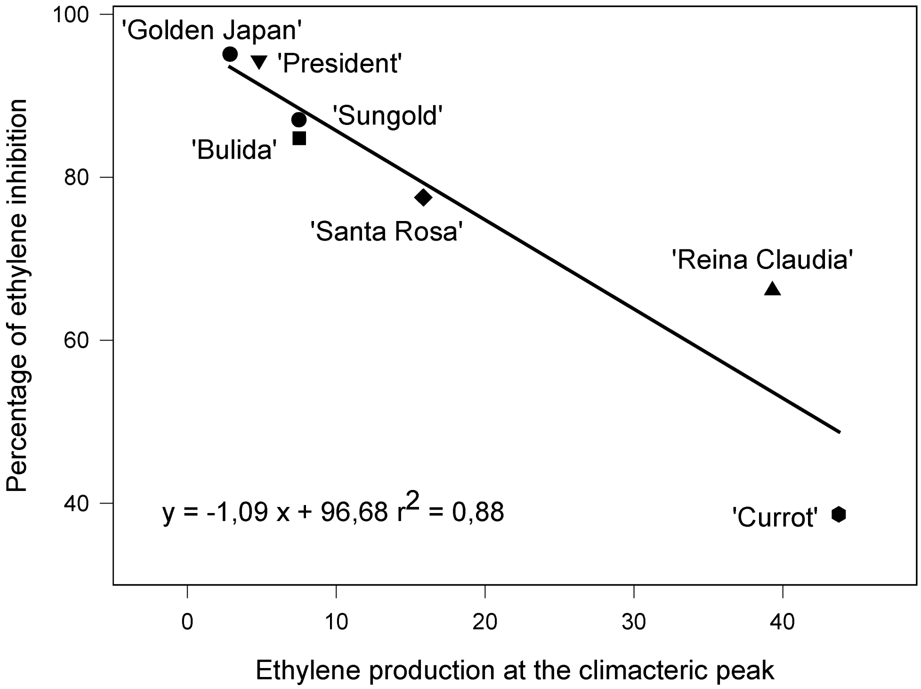

Figure 6 Ethylene production (nl g^{-1} h^{-1}) at the climacteric peak and percentage of ethylene inhibition by 1-MCP (0.5 $\mu l\, l^{-1}$) in apricot and plum cultivars.

REMOVAL OF EXTERNAL ETHYLENE

The different tools and technologies described above were found to be useful to reduce or to inhibit ethylene production and action. However, there are many situations in which considerable ethylene emission occurs along the food chain, such as inside the packages, storage chambers, during transportation, and in domestic refrigerators. This external ethylene comes from sources such as internal combustion engines, pollutants released in the atmosphere, normal emission from plant organs, and from fungal metabolism. Adequate fresh air ventilation of storage rooms of work areas has been classically used as an effective way of removing ethylene, although this procedure has enormous disadvantages in terms of losses of energy (by increasing

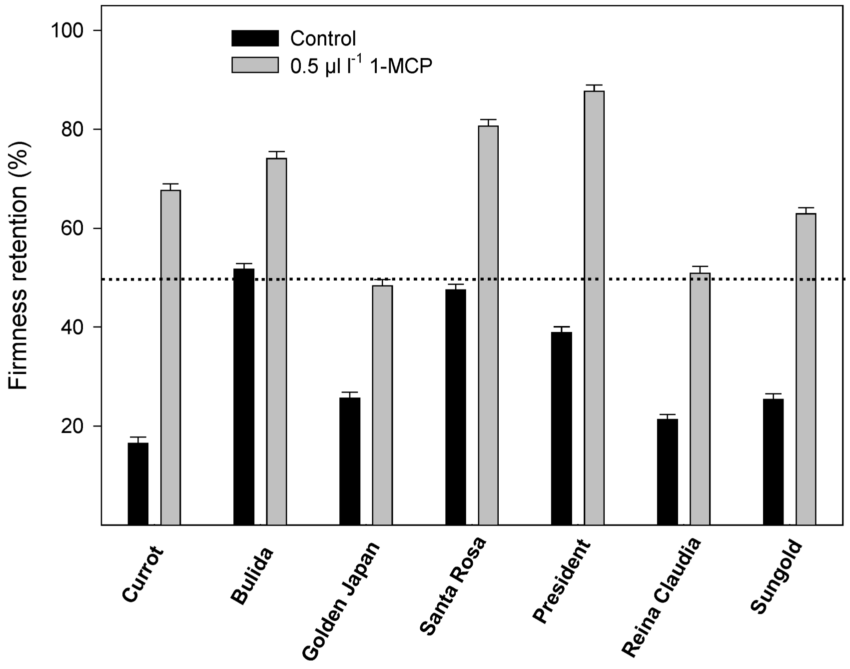

Figure 7 Percentage of firmness retention (flesh texture) in control and 1-MCP-treated fruit (0.5 $\mu l\, l^{-1}$) after 7 days of cold storage plus 7 days at 20°C.

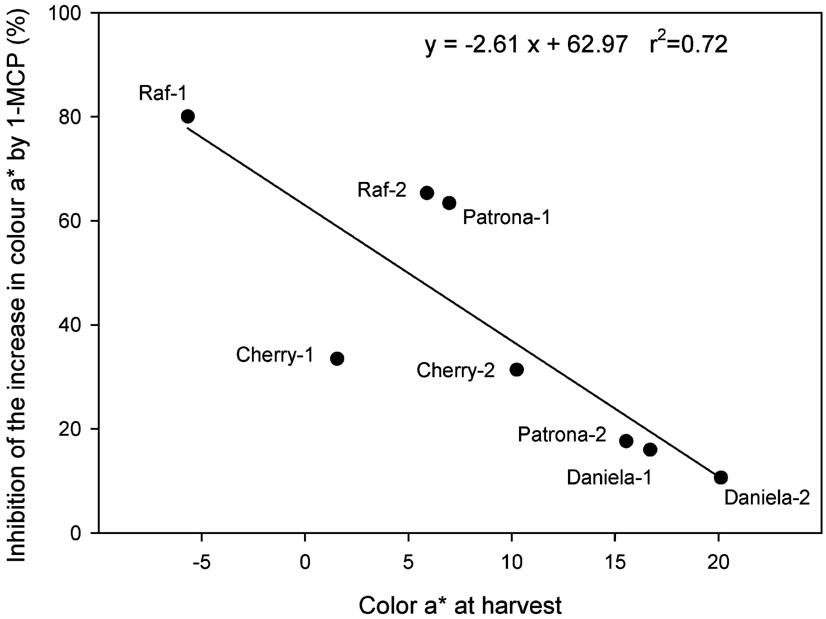

Figure 8 Color (a*) at harvest and inhibition percentage of the increase in colour a* by 1-MCP (0.5 $\mu l\, l^{-1}$) in tomato after 7 days of cold storage plus 7 days at 20°C.

the temperature of cold storage rooms) and loss of humidity, and is not practicable in controlled-atmosphere storage. Thus, additional tools to eliminate this ethylene are therefore necessary. Some of these techniques have been used for decades, although they are being modified and improved in recent years, and used under two distinct forms or devices: filters applied to trucks and storage chambers (for large volumes), and films, trays and sachets for packaging (active packaging).

Ethylene Adsorbers

Some phenomena related to adsorption are known from ancient times, although the first scientific evidences were carried out by Scheele (1773) and Fontana (1777), who reported some experiments about the efficacy of charcoal and clays on gas adsorption (Dąbrowski, 2001), these early discoveries being the origin of current applications and possibly of future developments. Adsorption is a surface phenomenon in which particles (gas or solid in solution) are held on the surface of solid material. The particles are commonly named as adsorbates and the trapping solid material as the adsorbent. Adsorption is distinguished from absorption by the fact that with the latter, the absorbate is accumulated throughout the absorber, not only on its surface. Two different patterns of adsorption can be described: physico-adsorption involving binding through van der Waals forces, or chemi-adsorption, in which chemical linkages occur (Atkins, 1991). The amount of the adsorbed material depends on temperature, pressure, and the adsorbate concentration.

The main compounds used as ethylene adsorbers are activated carbon and zeolites. The commercial application of activated carbon in the adsorption of gases and vapor started in the 1930s, although the specific use for ethylene was in the late 1950s. Any carbonaceous material may be used to make activated carbon, but the selection of the raw material should have low inorganic matter content, be easily activated, be easily available, have low cost, and low degradation during storage (Dąbrowski et al., 2005). Thus, lignocellulosic material such as wood, fruit shells, fruit stones, apple pulp, wheat, cotton stalks, viscose rayon, and coal, among others, are often used for activated carbon production (Puziy et al., 2002). There are both physical and chemical methods for carbon activation. Chemical procedures have advantages over physical ones, in terms of greater yield, no previous carbonization being necessary, lower temperatures of activation, and good development of the porous structure (Rodriguez-Reinoso, 1997).

The ability of activated carbon to act as an adsorber is dependent on a wide range of properties (Aygün et al., 2003), such as magnitude and distribution of pore volume (pore structure), surface area, and finally the type and quality of surface-bound functional groups (surface chemistry). The adsorption capacity is proportionally related to both the large surface area and the pore volume. For commercial food grade, activated carbons with surface areas ranging between 300–2000 $m^2\ g^{-1}$ are used, although some of them could achieve surface areas as high as 5000 $m^2\ g^{-1}$. Specific uses of activated carbon in foods are decolourising agents, taste-odor removing agents and purification agents (Food Chemical Codex, 1996).

Activated carbon can be granular, powdered or fiber (Ahmedna et al., 2000; Carrott et al., 2001). However, the granular type is preferred due to its easier regeneration and versatility. The adsorption process of ethylene on these adsorbers fits a model proposed by Langmuir in 1916. Using this model, it is assumed that the rate of adsorption is directly related to ethylene

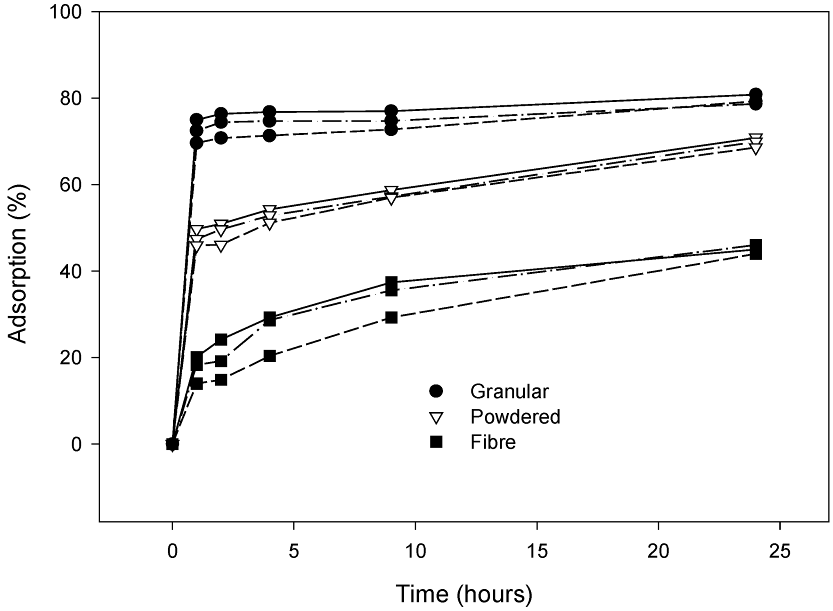

Figure 9 Ethylene adsorption percentage of several activated carbon types: granular, powdered and fiber in 24 h time-course in a closed-glass jar in which different exogenous ethylene concentrations (μl l^{-1}): 2.5 (solid line), 5.0 (dot-dash line) or 7.5 (dash line) were added.

pressure (temperature and relative humidity) and the surface of the adsorber, reaching a dynamic equilibrium between adsorption and desorption. In our laboratory, a comparative study about the ethylene adsorption capacity of three forms of activated carbon was performed (Fig. 9). The best results in terms of ethylene adsorption were obtained with granular (over 80%) followed by powered (over 70%), while fiber had the lower adsorption capacity for this gas (over 40%). Moreover, the exogenous application of ethylene at 2.5, 5.0, or 7.5 μl l^{-1} concentrations, to a constant mass of activated carbon led to the same percentage of adsorbed ethylene, independently of the concentration of the applied ethylene (Fig. 9). In addition, the adsorption capacity of these activated carbons was not affected by temperature in the range of 2–20°C.

Other potent adsorbers are the zeolites, which are a diverse type of volcanic aluminosilicate crystalline materials. Zeolites have a three-dimensional structure with interconnected cages and channels, which can be natural or synthetic with more than one hundred characterised crystalline structures (Tscherneich, 1992). Due to their cation exchange capacity, molecular sieving and adsorption, zeolites have great potential in the agro-industry to remove ethylene (Limtrakul et al., 2001; Suslow, 1997). Different types of devices containing zeolites have been used for ethylene adsorption, such as inorganic membranes for filtration (Caro et al., 2000), polyethylene films for modified atmosphere packaging (MAP) (López-Rubio et al., 2004), or small sachets deposited inside the packages (Vermeiren et al., 1999). In plastic films, zeolite is added at approximately 5% and positive effects on ethylene removal inside the MAP have been reported. The adsorption isotherms also fitted the Langmuir model, in a way similar to that of activated carbon. The main effect of the zeolite combined with films is to extend the shelf-life of foods not only from the point of view of sensory quality (Wang et al., 1998), but also in controlling microbial spoilage (Cutter, 2002). There are several manufacturers of films filled with zeolites: BioFresh® (Grofit Plastics), PeakFresf® (Multiflex Packaging Pty Ltd) and EverFresh® bag (Everfresh AB Group). The main disadvantage of these films is opacity (Vermeiren et al., 1999), and thus most of the plastic found in the markets is coloured.

It has also been shown that activated carbon or zeolite efficacy is even greater when used in combination with oxidizers or catalysts (chemi-adsorption), which may reduce the residual ethylene. Thus, adsorption and destruction of the ethylene can be performed along the food chain.

Ethylene Oxidizers

The double bond between two carbon atoms of the ethylene molecule is vulnerable to attack from suitable reagents with the generation of saturated compounds. Thus, potassium permanganate ($KMnO_4$) with a purple color oxidies ethylene to form either ethylene glycol or acetic acid, which in the presence of more permanganate could be further oxidied to CO_2 and H_2O, and the generation of MnO_2 with a dark brown color (Ozdemir and Floros, 2004). Thus, this oxidation process could be used as a test to detect ethylene and the scavenging capacity of the permanganate, known as Baeyer's test.

However, potassium permanganate can not be used in contact with food products due to its high toxicity, and so some devices (sachets, films, or filters) have been supplied in combination with different inert substrates: silica gel, activated carbon, perlite, zeolite or alumina. Some of commercial products are: Green Pack® (Rengo Co., Japan), Fridge Friend® (Dennis

Green, USA), Purafil® (Purafil Inc., Doraville, USA), Ethylene Control® (Ethylene Control Inc.), DeltaTrack® (DeltaTrack Inc.), and CJS® (CJS Ethylene Filters). These products are being used in packages, storage facilities, or during transportation, where the substrates adsorb the ethylene and the permanganate oxidies it. These systems have been tested with different commodities, such as persimmon (Ahr et al., 2000), grapes (Yun and Lee, 1996), avocado (Zamorano et al., 1994), and mango (Illeperuma and Jayasuriya, 2002), where removal of ethylene led to a delay in the ripening process, senescence, and the occurrence of disorders, and in turn maintained quality attributes. However, in a recent study (Wills and Warton, 2004) it has been reported that with high ethylene accumulation inside large packages, the use of these systems is questionable, since large quantities of the adsorbent would be required.

The use of ozone for ethylene degradation in air has been well-documented (Dickson et al., 1992). Ozone is the product from the rearrangement of atoms when O_2 molecules are submitted to a high-voltage discharge. The final product is a gas with strong oxidizing properties. In nature, O_3 is formed by UV-radiation from the sun, but there are two possibilities for obtaining commercial O_3: one is UV-based generation using ambient or O_2-enriched air, and the other involved passing O_2-enriched air or highly purified O_2 across a high electric voltage, which is usually known as the corona discharge generator. The latter has the advantage of producing higher O_3 concentrations than the former (Suslow, 2004).

The physicochemical characteristics of O_3 in terms of solubility in water and reactivity make it useful in the food industry for food preservation and equipment sterilization (disinfectant and sanitizer) and promoting shelf-life extension (Graham, 1997; Guzel-Seydim et al., 2004; Khadre et al., 2001; Smilanick et al., 1999; Suslow, 2004). Ozone has been listed as a GRAS (generally recognize as safe) material by the FDA (2001) and approved for use during food processing (raw and processed fruit and vegetables), and for treatment and storage, both in gas or aqueous phases.

During postharvest handling and storage of fruit and vegetables, the application of ozone is a benefit in terms of maintenance of quality by slowing the ripening process through the removal of ethylene, together with the prevention of mould and bacteria proliferation and lowering decay incidence. Ozone can inhibit ethylene biosynthesis through inhibition of ACS, but the levels required to achieve this might be phytotoxic, causing rapid lesion formation and programmed cell death (Vahala et al., 2003). In broccoli, changing from 0.2 to 0.7 $\mu l\ l^{-1}$ of O_3 inside the storage chambers was enough to stimulate the respiration rate, ethylene production and increased visual damage (Forney et al., 2003). In addition, onion, citrus, cantaloupe melons, and kiwifruit remained unharmed after the application of 200 $\mu l\ l^{-1}$ O_3 during 1 hour, while stonefruit, bananas, mushrooms, leafy vegetables, mangoes, broccoli, and pears were severely harmed (Smilanick, 2003a, 2003b). Skog and Chu (2001) reported the effect of several O_3 doses on ethylene reduction and fruit quality. They observed that 0.04 $\mu l\ l^{-1}$ were enough to reduce ethylene levels in vegetable storage chambers. However, ozone is highly unstable and decomposes into O_2 in a very short time, and most times it is difficult to maintain stable concentrations in storage chambers or in water. On the other hand, ozone toxicity is the most important criterion for the use of ozone in food plants, since ozone is a toxic gas and can cause severe illness including death depending on the inhaled quantity. In this sense, the Occupational Safety and Health Administration (OSHA) of USA has recommended the limit of exposure of workers as 1.5 minute for 0.3 $\mu l\ l^{-1}$ concentration, being lethal in few minutes for >1700 $\mu l\ l^{-1}$ concentration (Mahapatra et al., 2005). In summary, the means of O_3 application (continuous or intermittent), the selection of the dose, and the commodity sensitivity are the main factors in controlling quality, while avoiding the undesirable effects of O_3 together with the safety requirements are also necessary.

Ethylene Catalysts/Photocatalysts

A catalyst increases the rate of a chemical reaction but remains unchanged afterwards. In the case of ethylene, the oxidation reaction produces carbon dioxide and water when catalysts are added. Before the final products are produced, the reactants must overtake several energy barriers, which are called activation energies. Most of the catalysts used in industry reactions are pure metallic elements associated with chemi-sorption, such as Pt, Fe, Ni, Rh, Pd, Cu, or Co, or as oxides (PdO, CoO), but high temperatures (over 100°C) are frequently needed to reach the activation energy (Conte et al., 1992). However, with the development of plasma reactors (electrode plasma), a reduction of 75% of the ethylene in a storage chamber can be achieved without significant increase of air temperature or decrease in humidity (Graham et al., 1998).

For practical ethylene removal, the most tested catalysts have been Pd and TiO_2 fixed on activated carbons, which have been recommended as suitable catalyst supports since their porosity and chemical surface composition can be controlled appropriately (Rodríguez-Reinoso, 1997). In fact, we have found that palladium under fixation on activated carbon at two different concentrations (1 or 10%) was highly efficient in adsorbing exogenous ethylene (5 $\mu l\ l^{-1}$), since after 48 h of storage at 20°C the remaining ethylene levels were 1 and 0.15 $\mu l\ l^{-1}$ for 1% and 10% Pd, respectively, compared with 1.5 $\mu l\ l^{-1}$ found in activated carbon alone (Fig. 10).

An early report of Abe and Watada (1991) showed that the use of packages with Pd-activated carbon reduced the ethylene accumulation and retarded softening of kiwifruit and banana slices, although the Pd concentration was not provided. From this work, no information was available about the possible use of activated carbon-Pd in maintaining fruit quality until our recent paper in tomatoes stored under MAP conditions (Bailén et al., 2006). Since the main disadvantage of Pd is the high cost and would limit its practical application, in this paper the concentration of 1% Pd was used with satisfactory results in

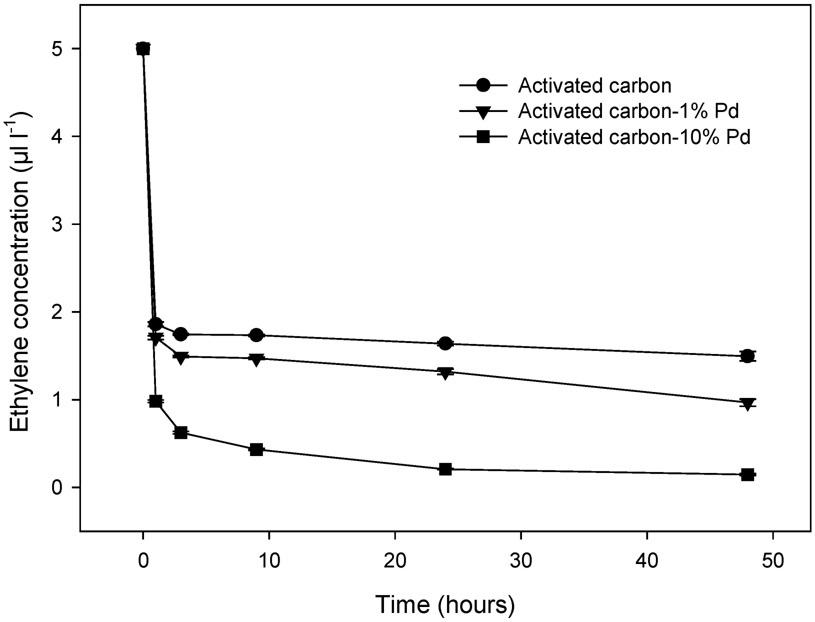

Figure 10 Adsorption kinetic following the exogenous application of ethylene (5 μl l^{-1}) in a sealed-glass jar containing activated carbon alone or combined with 1 or 10% of palladium as catalyst.

terms of reducing ethylene concentration inside the packages compared to activated carbon alone. Moreover, a reduction in color evolution, softening and weight loss was shown in tomatoes in MAP packages containing 1%Pd. Accordingly, activated carbon–1%Pd reduced ethylene accumulation inside of sealed-glass jars containing tomatoes and showed benefits in terms of tomato quality maintenance, since lower firmness loss and colour changes were observed with respect to the use of activated carbon alone (Fig. 11).

Another means of removing ethylene is the use of light-activated catalysts (photocatalysis). The main compound of this group is TiO_2 (Fujishima et al., 2000), which is activated by a source of UV light (300–370 nm wavelengths), either natural (sun) or artificial (lamps). The photocatalytic reaction of TiO_2 as a possible means of ethylene decomposition in fruit and vegetable storage rooms has been researched in recent years. The great advantages of TiO_2 are related to several facts: (a) ethylene is destroyed in the same place at which is produced, (b) titanium is cheap, photostable, and clean, (c) there is no interference with relative humidity, and (d) ethylene removal can be achieved at room temperature. However, the main disadvantage is the permanent need for UV light and thus can not be used

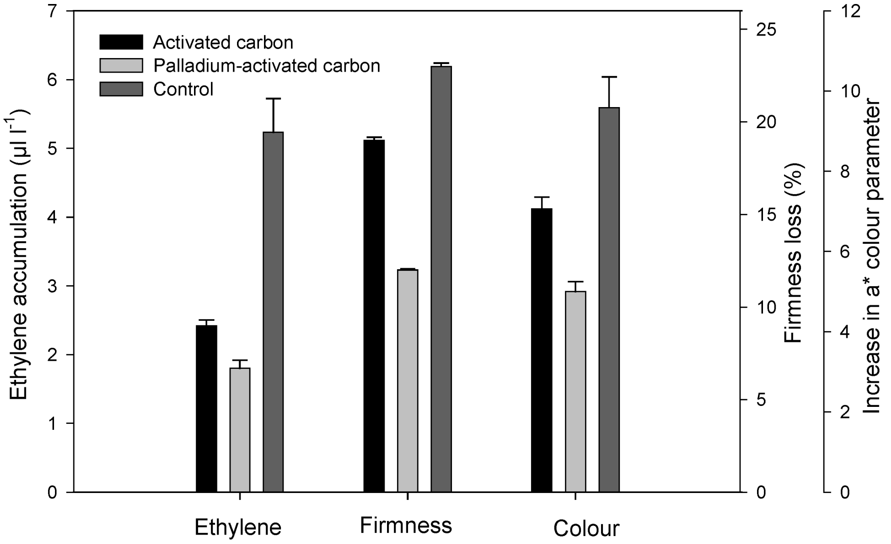

Figure 11 Quality retention of tomato (firmness and color) and levels of ethylene after 48 hours of storage at 20°C inside sealed-glass jar containing activated carbon, palladium-activated carbon, and control.

inside packages or packages which need to be continuously illuminated. The effectiveness of ethylene decomposition is directly related to increasing amounts of TiO_2 (Maneerat et al., 2003), with the maintenance of organoleptic quality and nutrition retention in tomato, and absence of disorders. Commercial devices based on TiO_2 are: BIO-KES® (Kes Science and Technology, USA) and Titan Aire® (Catalyx Technologies LLC, USA).

Biofilters

All of the above ethylene removal technologies are chemically based. However, the use of biological catalysis is being considered as an alternative in postharvest technology to reduce the detrimental effects of ethylene. Biological catalysts are able to scrub ethylene from different sources, both of plant and industrial origin, and the technology is known as biofiltration. The first studies about the use of biological systems for ethylene removal with a satisfactory operational stability and a sufficient efficiency to reduce ethylene concentration to levels near the threshold limit for the plant hormone response were reported by Elsgaard (Elsgaard, 1998, 2000). This biofilter was based on isolated ethylene-oxidizing bacteria (RD-4 strain) immobilized on peat-soil, and its efficiency for ethylene removal was over 98.4% at several temperatures (5, 10, and 20°C). Accordingly, Kim (2003, 2006) has shown that biofilter using *Bacillus* or *Pseudomonas* packed with activated carbon were capable of achieving an ethylene removal efficiency up to 100%. Thus, this technology could be applied to reduce ethylene concentration in storage rooms due to its: (a) high capacity to remove ethylene (minimum level of 0.017 $\mu l\, l^{-1}$), (b) good operational stability, and (c) efficient operation at cold temperatures, 0–10°C. However, there is a need for further research in this area, especially about the efficacy of these systems in reducing ethylene from fruit and vegetable, which is being produced continuously, and thus ethylene concentration inside the storage chambers is being accumulated over time.

CONCLUSIONS

The tools that can be used to avoid the detrimental effects of ethylene on fruit and vegetable during postharvest storage can be summarized as follows:

a) At biosynthesis level, the best results have been obtained using AVG (specially applied during pre-harvest) and with the postharvest application of polyamines, which reduce ethylene biosynthesis and delay the changes related to quality loss.
b) At receptor level, 1-MCP has been found as a potent ethylene antagonist with satisfactory results on extending shelf life and maintaining fruit and vegetable quality.
c) The ethylene surrounding fruit and vegetable storage areas can be effectively removed by the use of a combination of adsorber and catalyst, the best results being obtained with activated carbon and palladium (chemical catalysis) or using biofilters (biological catalysis).

The development of new insights about ethylene biosynthesis, perception and action will allow the development of future postharvest technologies (especially non-contaminant for human and environmentally friendly). There are many open research directions that will lead to a full elimination of ethylene surrounding fruit and vegetables. Since ethylene is the "ripening plant hormone" insufficient attention has been paid in nonclimacteric fruit, whose maturity is not regulated by ethylene but is sensible to the exogenous ethylene. The efficiency of a tool alone described in this review was not enough to completely eliminate the ethylene problem, thus the combination of some of them deserves further investigation.

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