

1-MCP in Post-harvest: Physiological Mechanisms of Action and Applications

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ABSTRACT

1-Methylcyclopropene (1-MCP) is an inhibitor of ethylene perception. It binds irreversibly to the ethylene receptors and inhibits downstream processes that are controlled by ethylene. In the area of postharvest this means many ripening processes of climacteric fruits, such as softening, color and aroma development, respiration increase and organic acid decrease are inhibited. However, beyond these processes, ethylene also has a role to play in responses to pathogen attack and to wounding, such as occurs during preparation of fresh-cut commodities. 1-MCP has effects on biochemical responses to these occurrences as well. In addition, 1-MCP has been used on non-climacteric commodities to determine what maturation and senescence processes are under the control of ethylene. This review will describe the current knowledge of the effect of 1-MCP on ripening and senescence, on the responses of harvested produce to pathogen infection, and responses of fresh-cut commodities.

Keywords: decay, fresh-cut, ethylene, ripening, senescence, storage disorders

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INTRODUCTION

Ethylene is one of several plant growth regulators that affect growth and developmental processes including ripening and senescence. It is a simple hydrocarbon in the class of alkenes or olefins. These are compounds with an unsaturated double bond between two carbon molecules. As a gas it can diffuse into and out of plant tissues from both endogenous and exogenous sources.

Ethylene can profoundly affect the quality of harvested products. These effects can be beneficial or deleterious depending on the product, the ripening stage, and the desired use. In some cases, such as in banana ripening or de-greening of citrus, ethylene is given to initiate uniform ripening or color change. Generally, however, commercial strategies for horticultural products are based on avoiding exposure to ethylene in order to minimize ripening processes during storage and marketing.

Burg and Burg (1967) were the first to make a compre-

hensive study of the molecular requirements of the biological activity of ethylene. In their discussion of the results of experiments on the growth of pea segments, they suggested that ethylene binds to a receptor which includes a metal atom. It is known that alkenes form complexes with metals, such as silver or copper. From the early 1970's E. Sisler and associates have worked on finding compounds that can bind to the receptor that was postulated in the Burg and Burg experiments, and possibly inhibit ethylene from binding. The first anti-ethylene compound found was another alkene, 2,5 norbornadiene (Sisler and Pian 1973). This compound interacts with the binding site and gave competitive kinetics with ethylene in a physiological response (Sisler and Yang 1984). However, the compound has an offensive odor which limited its usefulness.

In further research Sisler concentrated on cyclopropenes, which are also alkenes but with a triangular structure and instability because of the ring strain from having a three carbon ring. The first product developed was diazocyclo-

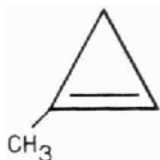


Fig. 1 Structure of 1-MCP.

prentadiene (DACP). It was found to inhibit ethylene action in mung beans (Sisler and Blankenship 1993a), ripening of tomatoes (Sisler and Blankenship 1993b) and to prolong apple storage (Blankenship and Sisler 1993). However, the drawback was that light activation was needed to cause the binding of DACP to the ethylene receptor (Sisler and Blankenship 1993a).

The second compound developed from testing of cyclopropenes as inhibitors of ethylene action was 1-methylcyclopropene (Fig. 1), and the use of cyclopropenes to inhibit ethylene action was patented by Sisler and Blankenship (1996). It was first used as a gas and tested on flowers, bananas and tomatoes (Sisler *et al.* 1996; Sisler and Serek 1997). A commercial breakthrough in 1-MCP application technology was the formulation of 1-MCP as a stable powder in which it is complexed with cyclodextran, so that 1-MCP is easily released as a gas when the powder is dissolved in water. Research is still continuing into developing and testing additional compounds with properties of ethylene antagonists, however, 1-MCP is likely to remain a primary means of controlling ethylene responses for the immediate future (Sisler 2006).

The impact of 1-MCP on postharvest science and technology has been two-fold. First, it provides the potential to maintain fruit and vegetable quality after harvest. Second, 1-MCP provides a powerful tool to gain insight into the fundamental processes that are involved in ripening and senescence. Recent reviews on the effects of 1-MCP on horticultural commodities include Blankenship and Dole (2003), Sisler and Serek (2003), Watkins and Miller (2005) and Watkins (2006). A website (<http://www.hort.cornell.edu/mcp>) that categorizes the physiological and biochemical responses for each commodity was begun in 2001 and is updated regularly.

REGISTRATION AND APPLICATION OF 1-MCP

Commercialization of 1-MCP was first undertaken for ornamental crops. This product was approved by the United States Environmental Protection Agency (EPA) in 1999, and was marketed as EthylBloc by Floralife, Inc. (Waterboro, SC, USA). Testing and registration of 1-MCP for edible crops was undertaken by AgroFresh, Inc., a subsidiary of Rohm and Haas (Springhouse, PA, USA). They determined that 1-MCP has a non-toxic mode of action, negligible residue, and is active at concentrations of parts per billion (ppb).

The safety, toxicity and environmental profiles of 1-MCP in regard to humans, animals and the environment were reported by the EPA (2002). Rat inhalation LC_{50} was greater than 2.5 mg/l (or 1.126 ppm active ingredient in air). In tests for acute toxicity of 1-MCP no death or clinical signs of systemic toxicology were seen (EPA 2002). It was approved for use by the EPA in 2002 and is sold under the trade name of SmartFresh. By 2006 it had been approved for use by over 20 countries. In each country the approval is for specific crops, and among those (depending on the country) are apple, apricot, avocado, carrot, kiwifruit, mango, melon, nectarine, papaya, peach, pear, pepper, persimmon, pineapple, plantain, plum, squash, tomato and tulip bulbs. **Table 1** gives a summary of the fruits and vegetables which have been treated with 1-MCP experimentally.

At 20°C, 1-MCP is released as a gas from a formulated cyclodextrin powder through aqueous dissolution of the cyclodextrin in approximately 20 to 30 minutes. Complete release may take longer at lower temperatures. When placed in a sealed container with plant material the 1-MCP is absorbed by the plant material over time. Peaches absorbed 80

to 90% of the 1 µl/l applied either at 20°C or 0°C when held in a closed container for 20 h (Liguori *et al.* 2004). The increase of CO₂ in closed containers due to respiration does not inhibit the effectiveness of binding of 1-MCP (Blankenship and Dole 2003). Because of the greater affinity of 1-MCP for the ethylene receptor, 100 times higher concentration of ethylene is required to compete effectively for the receptor. The highest concentration of 1-MCP that is approved for use is 1 µl/l. Once bound to receptors 1-MCP does not get released and recovery from 1-MCP treatment is due to the synthesis of new ethylene receptors in the tissue (Sisler, pers. comm.). The need for new receptors to be produced in order to relieve the inhibition by 1-MCP is supported by experiments of repeated applications of 1-MCP (Mir and Beaudry 2001; Mir *et al.* 2001; Jayanty *et al.* 2004). Weekly doses of 1-MCP helped prevent apple softening at 20°C more than at 0°C, and the interpretation was that the production of new receptors was very limited at the low temperature.

However, 1-MCP can be absorbed or adsorbed to sites other than ethylene receptors in plant tissue. A study of the sorptive capacity of a number of materials in storage rooms found that various plastics did not absorb the compound. However, wood or cardboard did absorb 1-MCP and moistened wood absorbed the compound at a higher rate. The data suggest that 1-MCP levels can be compromised by wooden and cardboard bin and bin liner materials, but not by plastic bin or wall surface materials used in store rooms (Vallejo and Beaudry 2006). It also suggests that 1-MCP is readily absorbed to cellulosic materials. One study suggests that boxed fruit absorbed 1-MCP better compared to bulk stored fruit, provided that the boxes were well ventilated (Valero *et al.* 2004).

1-MCP concentration in the air is measured by a gas chromatograph with a flame ionization detector. The stainless steel column (2 mm i.d. x 2 m) can contain 60/80 Chromosorb OV-103 (Alltech Associates, Deerfield, IL, USA) or 10% Carbowax – 20M on 80/100 Supelcoport (Supelco, Bellefonte, PA, USA). In both columns the lower detection rate is about 10 nl/l. There have been no methods devised to measure bound 1-MCP, and therefore, measurements have been of the disappearance of the compound in a closed container. A study comparing fruits, found faster disappearance of 1-MCP in a container with avocados than apples (Dauny *et al.* 2003). The authors suggested that the higher oil content in avocados enhanced the sorption of 1-MCP. A recent study (Nathachai *et al.* 2007) examined the capacity of a number of commodities to absorb 1-MCP including apple, asparagus, ginger, green bean, key lime, lettuce, mango, melon, parsnip, plantain, potato, and tangerine. It was found that the rate of sorption varied 30-fold among commodities. The correlation between rate of absorption and commodity characteristic was best for insoluble dry matter plus the size of the commodity. The measurements were conducted by determining the decrease of 1-MCP over time in a closed container with the commodity. In most studies measurements of 1-MCP are not performed. The amount of compound that will be released into an enclosed container is calculated, and that is reported as the concentration given to the commodity.

The company is in the process of developing a formulation of 1-MCP that can be used as a liquid spray in the field or orchard before harvest. Reports on early results of this formulation were presented at the meeting of the American Society of Horticultural Science in July of 2006 (DeEll and Murr 2006; Watkins *et al.* 2006). In addition, a recent study reported on attempts to develop a sachet release system that would supply controlled release of 1-MCP into a package containing fresh produce (Lee *et al.* 2006). An earlier attempt to develop a sustained release system utilized SmartFresh in a polyvinylchloride tubes during shipment of flowers (Macnish *et al.* 2004). These developments will give an added dimension to the use of 1-MCP to control ripening processes in the future.

Table 1 Climacteric, non-climacteric fruit and vegetables for which responses to 1-MCP have been investigated, and the range of 1-MCP concentration utilized.

	Range of 1-MCP concentrations ($\mu\text{l/l}$)
Climacteric fruit	
Apple (<i>Malus sylvestris</i> (L.) Mill. var. <i>domestica</i> (Borkh.) Mansf.)	0.01 to 1
Apricot (<i>Prunus armeniaca</i> L.)	0.3 to 1
Avocado (<i>Persea americana</i> Mill.)	0.03 to 1
Banana (<i>Musa</i> L.)	0.01 to 1
Blueberry (<i>Vaccinium corymbosum</i> L.)	0.1 to 0.4
Chinese bayberry (<i>Myrica rubra</i> Siebold and Zuccarni)	1 to 10
Custard apple (<i>Annona squamosa</i> L.)	25
Fig (<i>Ficus carica</i> L.)	0.4 to 2.5
Guava (<i>Psidium guajava</i> L.)	0.1 to 0.9
Kiwifruit (<i>Actinidia deliciosa</i>)	0.5 to 5
Jujube, Chinese (<i>Zizyphus jujube</i>) and Indian (<i>Zizyphus mauritina</i>)	0.6
Loquat (<i>Eriobotrya japonica</i> Lindl.)	0.5 to 50
Lychee (<i>Litchi chinensis</i>)	1
Mamey sapote (<i>Pouteria sapote</i> (Jacq.))	1
Mango (<i>Mangifera indica</i> L.)	25 to 100
Melon (<i>Cucumis melo</i> L.)	1
Mountain papaya (<i>Vasconcellea pubescens</i>)	0.3
Nectarine (<i>Prunus persica</i> Lindl.)	0.25 to 5
Papaya (<i>Carica papaya</i> L.)	0.05 to 2.5
Peach (<i>Prunus persica</i> L. Batsch)	0.25 to 5
Pear (<i>Pyrus communis</i> L.)	0.01 to 1
Pear, Asian (<i>Pyrus pyrifolia</i> Nakai)	0.1 to 1
Persimmon (<i>Diospyros khaki</i> L.)	0.01 to 3
Plum (<i>Prunus salicina</i> Lindl.)	0.1 to 2
Tomato (<i>Lycopersicon esculentum</i> Mill.)	0.1 to 1
Non-climacteric fruit	
Cherry (<i>Prunus avium</i> L.)	0.2 to 0.4
Clementine mandarin (<i>Citrus reticulata</i> L.)	0.1 to 1
Cucumber (<i>Cucumis sativus</i> L.)	1 to 10
Grape (<i>Vitis vinefera</i> L.)	4
Grapefruit (<i>Citrus paradisi</i> Macf.)	1
Lime (<i>Citrus latifolia</i> Tanaka)	0.25 to 1
Orange (<i>Citrus sinensis</i> L. Osbeck)	0.1 to 5
Pepper (<i>Capsicum frutescens</i> L.)	0.25 to 1
Pineapple (<i>Ananas comosus</i> L.)	0.1
Pomegranate (<i>Punica granatum</i>)	1
Strawberry (<i>Fragaria</i> \times <i>ananassa</i> Duch.)	0.01 to 1
Watermelon (<i>Citrullus lanatus</i>)	0.5 to 1
Vegetables	
Broccoli (<i>Brassica oleracea</i> L.)	0.02 to 50
Carrot (<i>Daucus carota</i> L.)	42
Chayote (<i>Sechium edule</i> Jacq.)	0.3 to 1.2
Chinese cabbage (<i>Brassica campestris</i> L.)	1
Chinese mustard (<i>Brassica juncea</i> var. <i>foliosa</i>)	1
Choy sum (<i>Brassica rapa</i> var. <i>parachinensis</i>)	1
Coriander (<i>Coriandrum sativum</i> L.)	0.1 to 10
Lettuce (<i>Lactuca sativa</i> L.)	0.5 to 1
Mibuna and mizuna (<i>Brassica rapa</i> var. <i>nipposinica</i>)	1
Mint (<i>Mentha longifolia</i> L.)	0.5
Onion (<i>Allium cepa</i> L.)	1
Pak choy (<i>Brassica rapa</i>)	1
Parsley (<i>Petroselinum crispum</i> Mill.)	10
Potato (<i>Solanum tuberosum</i>)	0.55 to 2.64
Rocket (<i>Eruca sativa</i> Mill.)	0.5
Tatsoi (<i>Brassica rapa</i> var. <i>rosularis</i>)	1

RESPONSES OF CLIMACTERIC FRUIT

1-MCP dramatically inhibits the ripening processes in most climacteric fruit. Extensive studies of the effect of 1-MCP have been conducted on apple, avocado, banana, peach and nectarine, plum and tomato.

Apple

In apples, 1-MCP delays the increase in ethylene production and internal ethylene concentration associated with climacteric ripening stage (Fig. 2). Effective concentrations are between 0.5 and 1 $\mu\text{l/l}$. This response had been studied on many apple cultivars and the results are dependent on the cultivar, type of storage, and length of storage (Fan *et al.* 1999; Rupasinghe *et al.* 2000; Watkins *et al.* 2000; Dauny and Joyce 2002; Jiang and Joyce 2002; Pre-Aymard *et al.* 2003; Saftner *et al.* 2003; Mattheis *et al.* 2005; Moran and McManus 2005; Toivonen and Lu 2005; Watkins and Nock 2005). Fruit respiration is also inhibited by 1-MCP (Fig. 2), but not as dramatically as the ethylene rise (Fan *et al.* 1999; Fan and Mattheis 1999a; Jiang and Joyce 2002; Pre-Aymard *et al.* 2003; Saftner *et al.* 2003; Defilippi *et al.* 2004; Mattheis *et al.* 2005; Toivonen and Lu 2005).

Softening is prevented or delayed by 1-MCP (Fan *et al.* 1999; Rupasinghe *et al.* 2000; Watkins *et al.* 2000; Mir *et al.* 2001; Dauny and Joyce 2002; Pre-Aymard *et al.* 2003; Saftner *et al.* 2003; Zanella 2003; Defilippi *et al.* 2004; Bai *et al.* 2005; Mattheis *et al.* 2005; Moran and McManus 2005; Toivonen and Lu 2005). The fruit texture has been reported to be tougher in treated fruit than in untreated fruit (Baritelle *et al.* 2001). However, this has also been reported as increased crispiness in treated fruit (Pre-Aymard *et al.* 2005). Firmness retention also occurs when fruit is held at ambient temperatures after treatment, rather than being put in cold storage (Fan *et al.* 1999; Mir *et al.* 2001). Toivonen and Lu (2005) found that 1-MCP did not affect firmness of an early ripening summer apple when the fruit were held below 15°C. However, another summer apple, 'Anna', responded well to 1-MCP when stored at 0°C (Pre-Aymard *et al.* 2003).

Loss of greenness of the peel background color is inhibited by 1-MCP (Fan and Mattheis 1999a, 2001; Dauny and Joyce 2002; Jiang and Joyce 2002; Pre-Aymard *et al.* 2003; Saftner *et al.* 2003; Zanella 2003). This loss generally is considered a negative change which indicates over-ripening in the fruit.

In general, 1-MCP delays loss of titratable acidity (TA), but does not affect soluble solids content (SSC) in any consistent manner (Fan *et al.* 1999; Fan and Mattheis 1999a; Watkins *et al.* 2000; DeEll *et al.* 2002; Pre-Aymard *et al.* 2003; Saftner *et al.* 2003; Zanella 2003; Defilippi *et al.* 2004; Bai *et al.* 2005; Moran and McManus 2005; Pre-Aymard *et al.* 2005; Toivonen and Lu 2005). However, mixed responses depending on whether the fruit were held in CA or in air have been reported (Watkins *et al.* 2000). Total volatile contents are reduced by 1-MCP treatment, although individual volatiles are affected differentially (Rupasinghe *et al.* 2000; Lurie *et al.* 2002; Saftner *et al.* 2003; Defilippi *et al.* 2004; Bai *et al.* 2005; Kondo *et al.* 2005). As fruits ripen alcohols decrease and esters increase, and this conversion is inhibited by 1-MCP. The apple alcohol transferase gene (*MdAAT2*) controls ester generation and the expression and enzyme activity of this enzyme was low in 1-MCP treated apples after storage (Li *et al.* 2006). The rapidly ripening summer apple 'Anna' had less fruity, ripe and overall aromas, which gave a perception of a less ripe apple after treatment with 1-MCP and shelf life (Lurie *et al.* 2002). This was due to inhibition of synthesis of esters and maintenance of alcohol levels in the treated fruit, and less total volatiles, preventing an over-ripe aroma.

There are conflicting reports on the effect of 1-MCP on apple antioxidants. Shaham *et al.* (2003) with 'Granny Smith' and Vilaplana *et al.* (2006) with 'Golden Smoothie' apples found that total antioxidant activity and ascorbate levels of apples in storage were not affected by 1-MCP. Both studies also found that the 1-MCP treated apples were under lower oxidative stress, with lower levels of hydrogen peroxide, lower levels of peroxidative markers and antioxidant enzyme activity. However, another study found that the total oxyradical scavenging capacity of both 'Delicious' and 'Empire' apples was higher in storage when treated

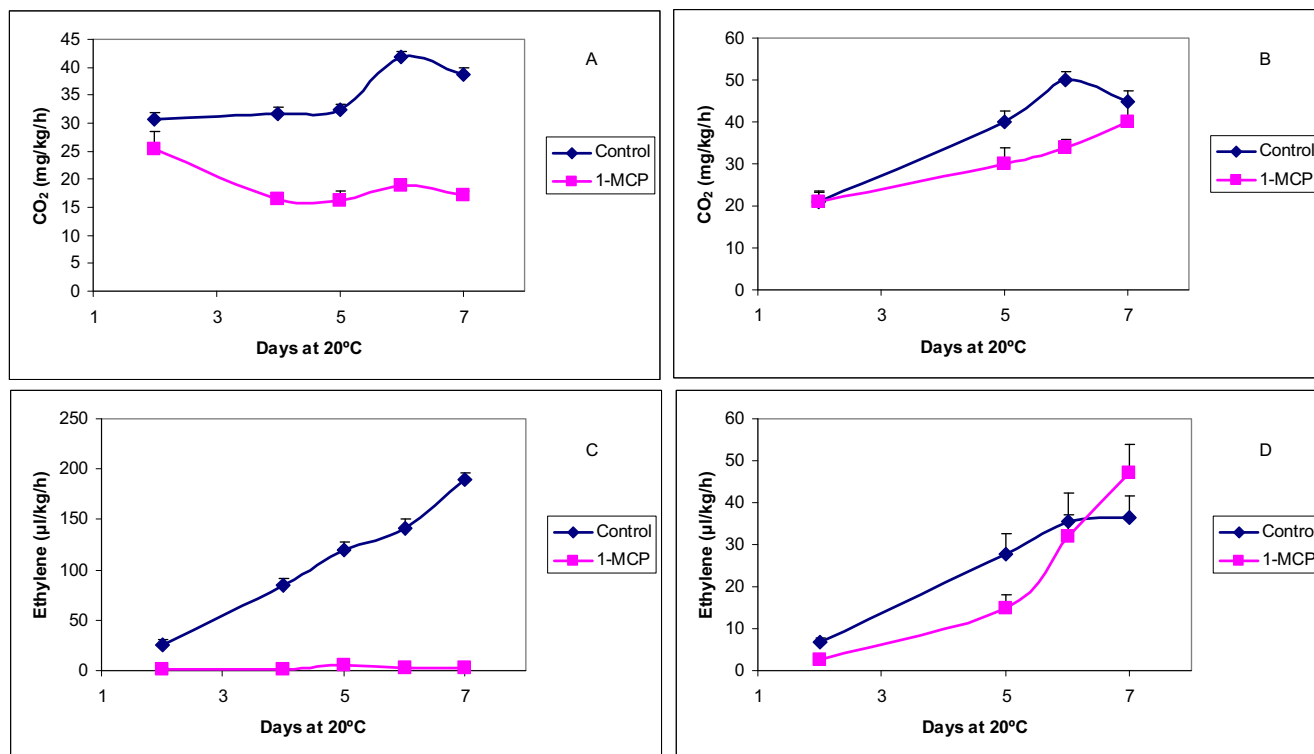


Fig. 2 The differing responses of apple and nectarine ethylene production and respiration to 1-MCP. A and C, respiration and ethylene production of 'Anna' apples, and B and D, respiration and ethylene production of 'April Glow' nectarines.

with 1-MCP (MacLean *et al.* 2003). The two methods of determining antioxidant activity were different and this may explain the discrepancy. MacLean *et al.* (2006) found that flavanoid content of the apple fruit was slightly higher in 1-MCP treated fruit and anthocyanin levels were retained during storage. However, chlorogenic acid, a major apple flavonoid, was 24% lower in 1-MCP treated apples. Shaham *et al.* (2003) found no difference in flavanoid levels between control and 1-MCP treated apples during storage.

Ethylene production by apple fruit occurs both on and off the tree when the climacteric is initiated, and therefore the effectiveness of 1-MCP is affected both by the maturity/ripening stage at harvest and by the period of time that the fruit are held in cold storage before treatment. These two factors are inter-related as more mature fruit at harvest produce autocatalytic ethylene sooner than earlier harvested fruit. Cultivar effects are also important (Mir *et al.* 2001; Watkins and Nock 2005). The effect of delays between harvest and application of 1-MCP is affected by cultivar, storage type and storage length (Watkins and Nock 2005). In a study of two apple cultivars 'Orin' and 'Fuji' which differ in ethylene production, ethylene was inhibited by 1-MCP in 'Fuji' apples even when treatment was delayed for a week after storage (Tatsuki *et al.* 2007). Two ethylene receptor genes, *MdERS1* and *MdERS2* and the ACC synthase gene *MdACS1* were also inhibited in 'Fuji' apples by 1-MCP, while ACC oxidase *MdACO1* was slightly inhibited. However, in a high ethylene producing apple, 'Orin' the later 1-MCP was applied after harvest, the less was the suppression of ethylene production and the expression of these genes. In a comparison of apple peel and pulp and the responses of the ethylene pathway to 1-MCP, it was found that ACC synthase and ACC levels were decreased in both peel and pulp (Vilaplana *et al.* 2007). ACC oxidase was also inhibited but not totally. However high levels of MACC were found in 1-MCP treated tissue.

CA can prolong the impact of 1-MCP on both physical and sensory responses of apple fruit (Rupasinghe *et al.* 2000; Watkins *et al.* 2000). However, 1-MCP may be a replacement for CA storage for short term air storage, especially for maintaining quality of summer apples (Pre-Aymard *et al.* 2003; Toivonen and Lu 2005), and of other cul-

tivars that deteriorate after 2 to 3 months of storage (Watkins *et al.* 2000; Dauny and Joyce 2002; Bai *et al.* 2005). In addition, 1-MCP can be effective in many places where CA rooms are not available.

Avocado

Unlike apples, avocados do not begin to ripen until they are removed from the tree. The response of avocados to 1-MCP is concentration and time dependent (Feng *et al.* 2000; Jeong *et al.* 2002). An early study used 25 μl/l of 1-MCP (Hofman *et al.* 2001), but avocado is very sensitive to 1-MCP and most studies found that there was excessive inhibition of ripening when concentrations above 0.25 μl/l were applied (Jeong *et al.* 2003; Adkins *et al.* 2005; Woolf *et al.* 2005). The time it takes to reach both the ethylene rise and the respiratory climacteric peak is delayed and the peaks are decreased after 1-MCP treatment (Feng *et al.* 2000; Jeong *et al.* 2002, 2003; Feng *et al.* 2004; Hershkovitz *et al.* 2005). The treated fruit are firmer, slower to soften, and slower to change skin color. 1-MCP also decreases the weight loss of the fruit in shelf life (Jeong *et al.* 2003).

Two studies examined the cell wall disassembly enzymes in avocado fruit allowed to ripen after 1-MCP treatment (Feng *et al.* 2000; Jeong and Huber 2004). The earlier study found inhibition of both endo-β-1,4-glucanase and polygalacturase activity in correlation with retention of avocado firmness. Jeong and Huber (2004) found complete suppression of polygalacturonase and inhibition of endo-β-1,4-glucanase and β-galactosidase. Even without any measurable activity of polygalacturonase the 1-MCP treated fruit lost 80% of their initial firmness after 24 days at 20°C. Treating the inhibited fruit with ethylene did not reverse the inhibition by 1-MCP.

For a successful treatment of avocado with 1-MCP there is a need to find the treatment that will not overly delay ripening. A long delay of ripening and softening, particularly after removal from storage, increases decay development (Adkins *et al.* 2005; Wang *et al.* 2006). However, 1-MCP reduces the storage disorders of avocado which appear to be triggered by ethylene in storage (Pesis *et al.* 2002; Woolf *et al.* 2005), making it attractive if the proper treatment can be found.

Banana

Bananas are harvested at a mature green stage of maturity, transported and then ripened by an external ethylene treatment before being marketed. Fruit remained longer in a mature green stage when treated with 1-MCP and the response was concentration and time dependent (Jiang *et al.* 1999b; Harris *et al.* 2000; Bagnato *et al.* 2003). In addition, the length of inhibition was determined by the stage of ripening of the banana. On the one hand, if the bananas are very immature, 1-MCP does not affect ripening kinetics as much as when they are still green but more mature (Harris *et al.* 2000). On the other hand, once ripening has begun following application of propylene to mature green bananas, treatment with 1-MCP does not inhibit all ripening processes (Golding *et al.* 1998).

The 1-MCP decreased ethylene production and respiration rates, and inhibited softening (Golding *et al.* 1998; Jiang *et al.* 1999a, 1999b; Macnish *et al.* 2000; Pathak *et al.* 2003; Pelayo *et al.* 2003; Lohani *et al.* 2004). Most studies found no effect on SSC concentration, though one found a lower accumulation of SSC (Nascimento *et al.* 2006). Total volatile production of the fruit was decreased and ester concentrations were lower while those of alcohols were higher in treated fruit (Golding *et al.* 1998), similarly to what was found in apples (Lurie *et al.* 2002). A number of ripening related genes in banana were up-regulated by ethylene treatment, and the up-regulation was prevented by 1-MCP (Gupa *et al.* 2006). Two genes induced by ethylene are a fruit-specific expansin, *MaExp1*, and β -amylase, that degrades starch into sugars, and both were inhibited by 1-MCP (Trivedi and Nath 2004; Nascimento *et al.* 2006). An ethylene-responsive, ripening related expansin gene, *MiExpA1*, has also been found in mango and it too was inhibited by 1-MCP (Sane *et al.* 2005).

1-MCP also inhibits the color change from green to yellow. However, the color changes sometimes were problematical after 1-MCP treatment, with disrupted or incomplete and uneven yellowing (Golding *et al.* 1998; Harris *et al.* 2000; Macnish *et al.* 2000). This may limit the use of 1-MCP on bananas. Applying 1-MCP to fruit after an ethylene treatment in order to circumvent the uneven color change was not successful (Pelayo *et al.* 2003). There was large variability in responses of the fruit because different bananas in the same bunch were at different stages of ripening. In another study where propylene was used instead of ethylene to induce ripening, 1-MCP applied 24 h after propylene treatment inhibited color and volatile production but not ethylene or respiration (Golding *et al.* 1998).

Pear

1-MCP has been tested with summer and winter pears. The fruit requires exposure to chilling temperatures to begin the ripening, with winter pears requiring as long as 8 weeks at low temperature. Winter pears soften and develop a buttery texture, while summer pears retain more crispiness when they ripen. 1-MCP delayed or prevented softening, the degree of response depended on the cultivar and the concentration of 1-MCP applied (Baritelle *et al.* 2001; Argenta *et al.* 2003; Hiwasa *et al.* 2003; Kubo *et al.* 2003; Calvo and Sozzi 2004; Ekman *et al.* 2004; Trincherro *et al.* 2004). An effective concentration that delays ripening but does not prevent it was 0.2 $\mu\text{l/l}$ (Calvo and Sozzi 2004; Moya-Leon *et al.* 2006). Peel color change from green to yellow was inhibited and ethylene and respiration were lower (Argenta *et al.* 2003; Hiwasa *et al.* 2003; Kubo *et al.* 2003; Ekman *et al.* 2004; Larrigaudière *et al.* 2004; Trincherro *et al.* 2004; Mwaniki *et al.* 2005). As in other fruit SSC was not affected, while TA changes were inconsistent, sometimes TA was retained in fruit treated with 1-MCP and sometimes there was no effect (Argenta *et al.* 2003; Calvo and Sozzi 2004; Larrigaudière *et al.* 2004; Trincherro *et al.* 2004). In a sensory study with 'Packham's Triumph' pears the flavor and aroma profile of 1-MCP treated fruit stored

in air were preferred over CA stored fruit (Moya-Leon *et al.* 2006).

The concentrations that delay but do not prevent pear ripening appear to be variable. Application of 0.2 $\mu\text{l/l}$ resulted in normal ripening with no over-ripening (Calvo and Sozzi 2004; Moya-Leon *et al.* 2006), while concentrations as high as 10 $\mu\text{l/l}$ resulted in maintenance of optimal eating firmness for extended periods to fruit where ripening had been initiated by chilling temperatures (Kubo *et al.* 2003). The efficiency of giving ethylene after storage to initiate ripening on fruit treated with 1-MCP depended on the concentration of 1-MCP applied and the length of time the fruit had been stored (Argenta *et al.* 2003; Calvo and Sozzi 2004; Ekman *et al.* 2004).

Peach and nectarine

Responses of fruit to 1-MCP are affected by concentration and exposure period, but not treatment temperature (Liguori *et al.* 2004). Inhibition of fruit ripening was transitory in all published studies, but repeated 1-MCP applications helped maintain suppression of ripening (Liu *et al.* 2005). The transitory effect of 1-MCP was not related to diffusion limitations within the flesh (Hayama *et al.* 2005). One explanation for the transient effect of 1-MCP is rapid turnover of ethylene receptors in the fruit tissue (Dal Cin *et al.* 2006), so that the receptors with 1-MCP bound to them disappear and new receptors are synthesized allowing ethylene to bind and initiate ripening. This turnover was not found in apples which may help explain the prolonged effect that 1-MCP has on apple fruit, but not on peach (Dal Cin *et al.* 2006).

Ethylene production can be inhibited in 1-MCP treated peaches and nectarines, not affected, or enhanced (Mathooko *et al.* 2001; Fan *et al.* 2002; Rasori *et al.* 2002; Liguori *et al.* 2004; Bregoli *et al.* 2005; Girardi *et al.* 2005). Recovery from 1-MCP induced inhibition resulted in higher ethylene production than in untreated fruit (Rasori *et al.* 2002), and the transcript levels of ACS and ACO were higher in treated fruit (Bregoli *et al.* 2005). Similar to ethylene, respiration rates are sometimes lower or not affected by 1-MCP (**Fig. 2**) (Dong *et al.* 2001b; Fan *et al.* 2002; Liguori *et al.* 2004). Softening is slower in 1-MCP treated fruits, but fruit reach the same level of firmness as untreated fruit (Dong *et al.* 2001b; Mathooko *et al.* 2001; Liguori *et al.* 2004). SSC is not consistently affected, but TA loss is slowed in high acid (Fan *et al.* 2002; Liguori *et al.* 2004; Bregoli *et al.* 2005; Liu *et al.* 2005) but not low acid cultivars.

Plum

Plums are much more responsive to 1-MCP than are peaches and nectarines. Japanese type plums can be either climacteric or suppressed climacteric types. The suppressed climacteric fruit have a lower climacteric rise in respiration and ethylene and it comes later in the ripening of the fruit. Suppressed climacteric cultivars did not ripen when treated with 1 $\mu\text{l/l}$ 1-MCP unless they were subsequently treated with propylene (Abdi *et al.* 1998). However, in another study with a suppressed climacteric cultivar with 0.1 $\mu\text{l/l}$ 1-MCP, the fruit eventually ripened and softened (Dong *et al.* 2001a).

1-MCP prevented or delayed the climacteric increase in ethylene production and respiration of plums (Dong *et al.* 2002; Martinez-Romero *et al.* 2003; Salvador *et al.* 2003; Valero *et al.* 2003, 2004; Kahn and Singh 2007). Softening was delayed as were skin color changes, and weight loss was less (Dong *et al.* 2001a, 2002; Menniti *et al.* 2004; Kahn and Singh 2007). The SSC was not affected by 1-MCP treatment (Dong *et al.* 2002; Salvador *et al.* 2003; Menniti *et al.* 2004), but its ripening associated increase was (Valero *et al.* 2004). Loss of acidity was generally reduced (Dong *et al.* 2002; Salvador *et al.* 2003), except in one study (Menniti *et al.* 2004).

Postharvest softening and susceptibility to mechanical injury and pathogens are major problems limiting shipping and shelf life of plums. The response of plums to 1-MCP varies by cultivar and harvest maturity, but there are reports of large extension of storage and shelf life periods of treated fruit, due to decrease in mechanical damage and decay (Abdi *et al.* 1998; Martinez-Romero *et al.* 2003; Kahn and Singh 2007). Moreover, 1-MCP is effective on mature fruit which have better organoleptic quality (Salvador *et al.* 2003; Valero *et al.* 2003). Studies on climacteric and suppressed-climacteric cultivars indicate that concentrations may be different for different cultivars.

Tomato

Tomato was one of the earliest fruits examined by Sisler *et al.* (1996). 1-MCP inhibits ethylene and respiration, softening, color changes, TA decrease but has no effect on SSC. The extent of ripening inhibition of tomato fruit is affected by 1-MCP concentration, exposure time and ripening stage, and optimal treatment concentrations are also affected by cultivar (Sisler *et al.* 1996; Hoerberichts *et al.* 2002; Wills and Ku 2002; Mir *et al.* 2004; Opiyo and Ying 2005; Guillen *et al.* 2006, 2007). Fruit recover the capacity to ripen after treatment, but a second application can further delay ripening (Hoerberichts *et al.* 2002; Mir *et al.* 2004). Fruit treated at pink and light red stages ripened properly after a delay (Hurr *et al.* 2005), while red ripe fruit had a longer shelf life of only 1 day when given 1-MCP (Ergun *et al.* 2006a).

A new method of marketing of tomatoes is as bunches with the tomatoes still attached to the stem. 1-MCP has been found to inhibit the abscission of cherry tomatoes from the vines (Beno-Moualem *et al.* 2004; Lichter *et al.* 2006). The concentration to inhibit abscission may be higher than that needed to inhibit ripening, which might be a drawback in its usage for this purpose. However, in citrus plantations ethephon sprays are given to cause fruit loosening, with an undesired side effect of leaf abscission. 1-MCP was found to inhibit the leaf drop without affecting the ability of ethephon to cause fruit loosening (Poza *et al.* 2004).

Other climacteric fruit

Recent reports have investigated tropical and subtropical fruits other than avocado and banana. These fruits cannot be stored at the low temperatures necessary to slow ripening because of chilling injury development, and so 1-MCP is of great potential benefit. In addition, in many countries there are not many cool stores available and fruits are held at ambient temperature. Guava, mamey sapote and mountain papaya are three exotics that have been tested with 1-MCP. Guava could have its shelf life doubled by a treatment with 1-MCP, although if given at a high dosage (0.9 µl/l for 6 h or longer) the fruit did not ripen at all (Bassetto *et al.* 2005). This effect of over-treatment with 1-MCP was seen in other fruits as well including kiwifruit (Boquete *et al.* 2004) and papaya (Manenoi *et al.* 2006), while some fruits, such as stone fruit did not appear to have an upper limit of 1-MCP. Mamey sapote is a large fruit grown in Central America and the Caribbean which softens rapidly after harvest. 1-MCP increased the postharvest life of this fruit and also retained total TA without affecting SSC (Ergun *et al.* 2005). This effect of maintaining the soluble solids: titratable acidity ratio of freshly harvested fruits was observed in many fruits. Part of the slower loss of organic acids may be due to the delay in climacteric respiration. Mountain papaya ripens by rapid degreening followed by climacteric ethylene and flesh softening. 1-MCP prevented the increase in ethylene, and partially inhibited softening and color development (Moya-Leon *et al.* 2004). The fruit also develops a strong and characteristic aroma, due to increased production of esters and alcohols during ripening (Balbontin *et al.* 2007). The increase in esters was depen-

dent on ethylene and was enhanced by ethrel and reduced by 1-MCP. In this fruit, as in most climacteric fruits, the use of 1-MCP has demonstrated that most ripening processes are under the control both of ethylene and of other developmental signals, and that 1-MCP does not totally stop ripening processes.

Persimmon also has benefited by treatment with 1-MCP by slower ripening after de-astringification, particularly slower softening (Harima *et al.* 2003; Salvador *et al.* 2004; Luo 2007). Cultivars that are sensitive to chilling injury also had less internal gel formation, possibly because of inhibited softening (Salvador *et al.* 2004).

PHYSIOLOGICAL STORAGE DISORDERS

There has been a lot of work on the effect of 1-MCP on physiological storage disorders of apples. Much has focused on superficial scald because of the interaction between ethylene production and that of α -farnesene, and early reports that 1-MCP inhibited scald development (Fig. 3) (Fan and Mattheis 1999a, 1999b; Rupasinghe *et al.* 2000; Watkins *et al.* 2000). Superficial scald is manifested on both apple and pear as browning or blackening of the peel. The disorder occurs during low temperature storage and is a type of chilling injury (Watkins *et al.* 1995). The injury to the peel occurs because of accumulation of α -farnesene at low temperatures and its oxidation to conjugated trienols (Rowan *et al.* 1995; Whitaker *et al.* 1997), and α -farnesene production is enhanced by ethylene (Du and Bramlage 1994; Watkins *et al.* 1995; Whitaker *et al.* 2000). Superficial scald can be prevented or alleviated by inhibiting α -farnesene production or its oxidation. It has been demonstrated that inhibition of scald by 1-MCP is associated with inhibition of α -farnesene accumulation and therefore less substrate for oxidation (Fan and Mattheis 1999a; Rupasinghe *et al.* 2000; Watkins *et al.* 2000; Shaham *et al.* 2003; Arquiza *et al.* 2005; Pechous *et al.* 2005).

Other apple disorders have also been found to be affected by inhibition of ethylene signaling. 1-MCP can reduce senescent breakdown (Watkins *et al.* 2000; de Long *et al.* 2004; Moran and McManus 2005), core-flush or brown core (Fan and Mattheis 1999a; Zanella 2003; de Long *et al.* 2004), and soft scald (Fan and Mattheis 1999a). These are all disorders associated with senescence and cold storage. The development of greasiness in some apple cultivars, such as 'Granny Smith', is also a process that develops in cold storage, and this is inhibited by 1-MCP (Fan and Mattheis 1999a; Watkins and Nock 2005).

One problem that has been found as 1-MCP is used commercially is carbon dioxide injury which is higher in 1-MCP treated fruit than untreated fruit (DeEll *et al.* 2003; Zanella 2003; Watkins and Nock 2005). The disorder is associated with less mature fruit from early harvests when CA is applied quickly (Watkins *et al.* 1997; Fernandez-Trujillo *et al.* 2001). This is consistent with the fact that 1-MCP maintains the fruit in a less ripe state and therefore more susceptible to injury. The disorder can be alleviated

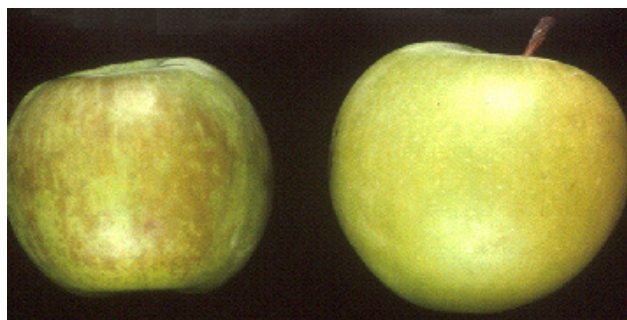


Fig. 3 Superficial scald on 'Granny Smith' apples and its prevention by 1-MCP treatment at harvest. The apples were stored for 5 months at 0°C and held 5 days at 20°C.

by maintaining low carbon dioxide in the storage room for the first few weeks (Watkins and Nock 2005). Alternatively, since 1-MCP mimics the beneficial effect of CO₂ on firmness retention, CO₂ could be eliminated or reduced in CA regimes for 'Empire' apples treated with 1-MCP (DeEll *et al.* 2005).

Pears also have superficial scald inhibited by 1-MCP, although some can develop after the inhibition of ripening wears off (Ekman *et al.* 2004). 1-MCP inhibits the accumulation of α -farnesene and conjugated trienols in pears (Isidoro and Almeida 2006). The inhibition appeared to be at the level of gene transcription since the expression of *PcAFS1* was attenuated in 1-MCP treated fruit (Gapper *et al.* 2006). Other disorders in pears, similar to those in apples are also alleviated by 1-MCP. These include senescent scald and core browning (Argenta *et al.* 2003), internal and senescent breakdown (Kubo *et al.* 2003; Ekman *et al.* 2004), and watery and core breakdown (Calvo and Sozzi 2004). The development of scratches or browning on the peel is also delayed by 1-MCP.

Other low temperature disorders on a number of fruits can be inhibited by 1-MCP. These include internal flesh browning in avocado (Pesis *et al.* 2002; Hershkovitz *et al.* 2005; Woolf *et al.* 2005), loquat (Cai *et al.* 2006a) and pineapple (Selvarajah *et al.* 2001), and chilling injury of citrus fruit (Dou *et al.* 2005). However, an early study reported that chilling injury in citrus was enhanced by 1-MCP (Porat *et al.* 1999). Scald on pomegranate can be reduced but not eliminated by 1-MCP (Defilippi *et al.* 2006). This scald is not due to α -farnesene oxidation, but it correlated with phenol levels in the peel (Ben-Arie and Or 1985). Reduced browning is associated with reduced polyphenol oxidase and peroxidase activities (Pesis *et al.* 2002; Hershkovitz *et al.* 2005). Also associated with phenol metabolism is the inhibition by 1-MCP in carrots of *iso*-coumarin which leads to bitterness development (Fan and Mattheis 2000; Fan *et al.* 2000). In loquat fruit there is an increase in fruit firmness during low temperature storage due to tissue lignification, and 1-MCP mitigated this increase (Cai *et al.* 2006b). In watermelon, exposure to ethylene induces water soaking, due to increases in lipid-degrading enzymes and phospholipid degradation (Mao *et al.* 2004), and this disorder is prevented by prior exposure to 1-MCP.

In stone fruits the development chilling injury symptoms such as internal browning, flesh wooliness and reddening (Fig. 4) were increased in peaches and nectarines by 1-MCP (Dong *et al.* 2001b; Fan *et al.* 2002; Girardi *et al.* 2005). It was found that a certain level of ethylene production by the fruit is necessary for normal ripening after storage (Zhou *et al.* 2002; Dong *et al.* 2001b). In apricots as well, 1-MCP enhanced internal browning even without storage (Dong *et al.* 2002). In plums, however, 1-MCP has been found to decrease internal browning during storage (Menniti *et al.* 2006). Also, impact injury in apricots (Martino *et al.* 2006) and in European plums (Lippert and Blanke 2004) was decreased by 1-MCP, due to its inhibition of softening.

RESPONSES TO PATHOGENS

Relatively little has been researched concerning the effects of 1-MCP on disease incidence, compared to its effects on ripening. Delayed ripening due to inhibition of ethylene action may increase the resistance of the commodity to infection. However, small amounts of endogenous ethylene may be necessary to maintain basic levels of resistance to pathogens because of its involvement in regulation of plant defense genes.

In two non-climacteric fruits, citrus and strawberry, 1-MCP has been reported to enhance decay. In citrus, 1-MCP treatment effectively inhibited the ethylene effect on the degreening process, but it increased mold rots caused by *Penicillium digitatum* and *P. italicum*, and stem-end decay caused by *Diplodia natalensis* (Porat *et al.* 1999; Marcos *et al.* 2005). However, in grapefruit inoculated with *Peni-*



Fig. 4 Internal reddening of peaches treated with 1-MCP at harvest, stored 3 weeks at 0°C and then 5 days at 20°C. Top, 1-MCP treated; bottom, control.

cillium digitatum 1-MCP did not affect the process of decay development (Mullins *et al.* 2000).

1-MCP treatment tended to maintain strawberry fruit firmness and color. However, disease development was accelerated in fruit treated at high (0.5 and 1 μ l/l) 1-MCP concentrations, though not at lower concentrations (Ku *et al.* 1999b; Jiang *et al.* 2001). In another study, exposure of strawberries to 0.01, 0.1 or 1 μ l/l 1-MCP did not affect overall fruit acceptability but did slightly increase the rate of rot development (Bower *et al.* 2003).

Apples were found to be more susceptible to bitter rot (*Colletotrichum acutatum*) and blue mold (*P. expansum*) in 1-MCP treated than untreated fruit (Janisiewicz *et al.* 2003). However, Saftner *et al.* (2003) found that 1-MCP reduced decay when fruit were inoculated at harvest with *P. expansum*, *Botrytis cinerea* and *C. acutatum* and then stored in controlled atmosphere. The interpretation was that firmness and resistance to infection was maintained due to the 1-MCP treatment. Pears developed less stem end decay after inoculating the fruit with *B. cinerea* and treating with 0.1 μ l/l 1-MCP than without treatment (Spotts *et al.* 2007). Natural infections caused by *Phacidiopycnis piri* was also reduced in 1-MCP treated fruit, and the fruit remained firmer in storage than untreated fruit.

1-MCP increased disease susceptibility of custard apple, mango and papaya (Hofman *et al.* 2001), and also of avocado (Hofman *et al.* 2001; Adkins *et al.* 2005; Woolf *et al.* 2005). Avocado has an antifungal diene compound that is present in unripe fruit and enhanced by ethylene (Leikin-Frenkel and Prusky 1998). Latent infections of *C. gloeosporioides* are inhibited from developing until the level of the diene declines during fruit ripening. 1-MCP treatment of avocado at two stages of maturity prevented further diene synthesis, but the early harvested fruit had high initial levels of diene and because of the inhibitory effect on ripening, 1-MCP decreased decay development. In the later harvest the level of diene was lower and decay developed more rapidly in treated fruit than untreated (Wang *et al.* 2006).

Most studies of stone fruit found benefit of 1-MCP in reducing decay. In two plum cultivars, 'Fortune' and 'Angeleno', 1-MCP treatment before storage at low temperature reduced decay caused by *Monilinia laxa* (Menniti *et al.* 2004). Also, decay development in apricots was decreased

by 1-MCP in a concentration dependent manner (Dong *et al.* 2002). In peaches, decay development after inoculation with *P. expansum* was slightly reduced by 1-MCP treatment (Liu *et al.* 2005). Decay of sweet cherries was also lower in 1-MCP treated fruit (Mozetic *et al.* 2006). The use of 1-MCP can help to elucidate defense pathways that include ethylene in different commodities. Currently, the data indicate that 1-MCP can lead to either increased or decreased susceptibility to pathogens. In addition, there may be a difference between natural infection and results from inoculated fruit.

RESPONSES OF VEGETABLES

Most of the research on 1-MCP has been concentrated on climacteric fruit. The dearth of research on fresh vegetables may be due to the fact that many vegetables are consumed shortly after harvest rather than being stored for extended periods. Some work has been done on broccoli, carrots, cucumbers and lettuce. Broccoli is very sensitive to ethylene, which promotes senescent processes and yellowing. This is delayed by treatment with 1-MCP (Fan and Mattheis 2000a). On the other hand, yellowing of cucumbers was delayed by 1-MCP only when ethylene was present (Nilsson 2005). Both Nilsson using cucumbers and Able *et al.* (2003) examining bok choy and broccoli found that 1-MCP had to be applied immediately after harvest, otherwise its efficacy was greatly reduced. If cucumbers were stored before applying 1-MCP the treatment was ineffective. Apparently senescent processes are activated soon after harvest, and once they begin 1-MCP cannot stop their progression.

In carrots and lettuce, treatment with 1-MCP was found to prevent physiological disorders that were associated with ethylene (Fan and Mattheis 2000b). In carrots, the bitterness due to accumulation of isocoumarin, and in lettuce, the phenols synthesized through the shikimic acid pathway leading to russet spotting were prevented. Potatoes close wounds inflicted during harvesting by developing a layer of suberization, and during this wound healing, ethylene is produced by the tuber. Preventing the production of ethylene by 1-MCP or other inhibitors did not affect suberization (Lulai and Suttle 2004). Onion bulbs responded to 1-MCP by maintaining higher sugar and dry weight levels (Chope *et al.* 2007). Sprout growth was reduced by 1-MCP treatment at 4 and 12°C but not at 20°C. Germination of chayote (*Sechium edule* (Jacq.) Sw, a vegetable native to Middle America, was also prevented by 1-MCP (Cadena-Iñiguez *et al.* 2006).

FRESH CUT PRODUCTS

The quality of fresh cut products depends on the initial quality of the product, its maintenance between harvest and preparation, the method of preparation and the subsequent handling conditions. A major problem after preparation is a relative short post-cutting life due to excessive tissue softening and cut-surface browning. These processes are stimulated by ethylene. Vegetables are more often prepared and sold as fresh-cut, minimally processed or ready-to-eat, and lettuce is one of the major products prepared in this way. Its browning after preparation is due to increased synthesis of phenolic compounds. 1-MCP applied to lettuce before minimal processing reduced russet spotting of ribs and cut-edge browning (Saltveit 2004; Tay and Perara 2004). However, if the application was made after cutting the increase in phenolic compounds was not affected. Other vegetables and herbs can also benefit from 1-MCP. Although most vegetables are non-climacteric and are generally not stored for extended periods, it has been shown that even low levels of ethylene can significantly decrease their shelf life (Ku *et al.* 1999a). Therefore, 1-MCP may be beneficial even on these commodities.

The wound response generated during preparation of fresh-cut produce induces a transient elevation of ethylene

in the tissue. Cucumbers treated with 1-MCP before slicing had a greater retention of firmness and better surface color, even when exposed to ethylene after slicing (Lima *et al.* 2005). The response was cultivar dependent, with firmer cultivars benefiting less than those that were less firm. This has led Nilsson (2005) to suggest that cucumber may not benefit from 1-MCP unless ethylene is present.

Harvested leafy vegetables and herbs also benefit from 1-MCP with slowing of senescent processes, particularly leaf yellowing. Mint (Kenigsbuch *et al.* 2007), rocket (Koukounaras *et al.* 2006), parsley (Lomaniec *et al.* 2003) and coriander (Jiang *et al.* 2002) all had longer shelf life after treatment with 1-MCP, even when stored in the presence of ethylene. Both chlorophyll and protein degradation leading to amino acid accumulation were lower in treated leaves. Interestingly, in detached coriander, mint, and parsley leaves both ethylene and respiration were higher with 1-MCP than in control leaves, although senescence was retarded (Jiang *et al.* 2002; Lomaniec *et al.* 2003; Kenigsbuch *et al.* 2007).

Asian vegetables such as Chinese mustard, choy sum, garland chrysanthemum, mibuna, mizuna and tatsoi, are often sold in minimally processed packages. They have leaf yellowing due to senescent processes and this is prevented with pre-treatment with 1-MCP (Able *et al.* 2003). The greatest effect was when ethylene was present during the shelf life period. Without ethylene 1-MCP had a minimal effect on all the vegetables except mizuna and mibuna where natural yellowing was delayed. Pak choy also had longer shelf life after 1-MCP treatment only when ethylene was present (Able *et al.* 2002).

Tomato is climacteric and in addition to wound ethylene which develops from slicing will have the ethylene increase due to ripening. A study of the best stage of ripeness to use for fresh tomato slices found that light-red tomatoes responded to 1-MCP treatment and slices prepared from these fruit maintained firmness and did not develop waterlogging when held at 5°C, while slices from control tomatoes lost firmness (Jeong *et al.* 2004). Treating red tomatoes with 1-MCP before slicing gave no benefit or extension of shelf life.

Recent studies have examined fresh cut fruit. The 1-MCP effect on fresh-cut fruit is variable. The application of this compound in fresh-cut apples decreased the ethylene production, respiration, softening, color change and synthesis of aroma compounds (Jiang and Joyce 2002; Bai *et al.* 2004; Calderon-Lopez *et al.* 2005). In pineapple, 1-MCP decreased respiration, browning, loss of visual quality, lightness and ascorbic acid (Budu and Joyce 2003). Ergun *et al.* (2006b) reported that slices made from 1-MCP treated papayas had double the shelf life of slices made from untreated papayas. 'Galia' melon cubes had reduced water soaking and better firmness when treated with 1-MCP before slicing (Ergun *et al.* 2007). Fresh cut watermelon slices stored longer under modified atmosphere at 5°C when fruit were treated with 1-MCP before slicing (Saftner *et al.* 2006). Fresh cut banana has a short shelf life due to fast browning and softening after processing. 1-MCP treatment of slices decreased the rate of softening and respiration rate, but browning rates were not affected (Vilas-Boas and Kader 2006). To control browning a dip in antioxidants was required. In other fruit, kiwifruit, persimmon and mango, Vilas-Boas and Kader (2007) found different responses in firmness, color and respiration and ethylene production depending on the timing of the 1-MCP application. In general, giving the 1-MCP after slicing had a stronger effect than giving it to the whole fruit, and giving the 1-MCP together with a CaCl₂ dip had a synergistic effect on slice firmness. A similar study with strawberries also found a synergistic effect with 1-MCP and a CaCl₂ dip (Aguayo *et al.* 2006). In strawberry, 1-MCP by itself, either to whole strawberries or to slices had no beneficial effect on firmness or appearance. Strawberry is the only non-climacteric fruit that has been reported on so far for fresh-cut.

CONCLUSIONS

The discovery and subsequent commercialization of 1-MCP has provided exciting opportunities for postharvest scientists to gain insight into the fundamental processes that are involved in ripening and senescence of fruit and vegetables. For products such as vegetables and non-climacteric fruit where further senescence, such as yellowing, will decrease quality, 1-MCP applications that prevent change are desirable. For climacteric fruit success on a commercial scale will be based on delaying rather than preventing ripening, in order to extend shelf life but eventually achieve a full ripe product. There are many problems that will be associated with commercial applications that will need solving to develop a procedure that will yield the desired result. The application on apples is the furthest developed and solutions that have been developed in this industry can be of help for establishing protocols for other commodities. In the area of basic research, the availability of 1-MCP is likely to have a dramatic impact on our understanding of the involvement of ethylene in plant metabolism and in plant-pathogen interactions. It is an exciting tool to use and much knowledge can be gained from its application.

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