

Suppression of Ethylene Responses Through Application of 1-Methylcyclopropene: A Powerful Tool for Elucidating Ripening and Senescence Mechanisms in Climacteric and Nonclimacteric Fruits and Vegetables

Donald J. Huber¹

Horticultural Sciences Department, Institute of Food and Agricultural Sciences, University of Florida,
P.O. Box 110690, 1213 Fifield Hall, Gainesville, FL 32611-0690

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Abstract. The discovery of 1-methylcyclopropene (1-MCP) as an inhibitor of ethylene action has provided yet another effective tool for understanding the role of this hormone in the development of higher plants. In the nearly 12 years since the description of the effects of this growth regulator on ethylene action, the subsequent introduction of stable formulations has resulted in an explosive increase in 1-MCP-targeted research, particularly, although not exclusively, in the discipline of postharvest science. The vicinal relationship between 1-MCP and postharvest biology is understandable in view of the established roles of ethylene, both beneficial and detrimental, in the handling and storage behaviors of a vast majority of harvested fruit and vegetative organs. The use of 1-MCP is proving to be supplemental to molecular approaches for identifying and understanding the spectrum of senescence and ripening processes under the direct control of ethylene perception. Climacteric fruits have served as the predominant target for investigations of 1-MCP, and the responses of these fruits have confirmed that the antagonist operates in opposition to ethylene. Studies of nonclimacteric fruits challenged with 1-MCP and other ethylene action inhibitors have identified both ethylene-dependent and ethylene-independent ripening processes and have posed interesting questions regarding the canonical distinctions between climacteric and nonclimacteric fruits.

Nearly 12 years have passed since the discovery of 1-methylcyclopropene (1-MCP) as a specific inhibitor of ethylene action (Serek et al., 1994). Preceded in use by silver ion (Beyer, 1976), the anionic silver complex, silver thiosulfate (STS) (Veen and van der Geijn, 1978), and the cyclic olefins, 2,5-norbornadiene (Sisler et al., 1985) and diazocyclopentadiene (DACP) (Sisler and Blankenship 1993), 1-MCP presents the advantages of high efficacy at relatively low concentrations and short exposure periods for prolonged periods after a single exposure and low phytotoxicity (Sisler, 2006). The development of stable, easily applied formulations of the chemical (Daly and Kourelis, 2000) was arguably a major factor in the widespread emergence of 1-MCP research. As gases under physiological conditions, cyclic olefins including 1-MCP offer the possibility of facile, uniform delivery to even bulky fruit organs. The capacity for uniform delivery of 1-MCP to intact organs constitutes a major advantage over STS that required vascular access for uniform delivery, limiting its use to cut flowers (Veen, 1983) and, in a few instances, to intact fruits (Atta-Aly et al., 1987; Iannetta et al., 2006; Perkins-Veazie et al., 1996). Although other cyclopropenes exert more persistent antagonism of ethylene action than the methyl derivative (Buanong et al., 2005; Kebenei et al., 2003; Sisler et al., 2001, 2003), for ease of use, 1-MCP remains the cyclopropene of choice for suppressing ethylene responses (Sisler, 2006). Clearly, 1-MCP has provided postharvest scientists

with a powerful and versatile means of probing the diverse roles of ethylene during ripening and senescence of harvested fruits and vegetables (Blankenship and Dole, 2003; Watkins, 2006).

A number of thorough reviews addressing the effects of 1-MCP on harvested fruits and vegetables have appeared in recent years (Blankenship and Dole, 2003; Lurie, 2005a, 2005b; Watkins, 2006), including one addressing specifically the effects of 1-MCP on fruit softening (Huber et al., 2003). A well-maintained and comprehensive literature base for responses of horticultural crops to 1-MCP is also available (Watkins and Miller, 2005). Accordingly, this article takes a selective course, focusing on 1-MCP responses in ripening-initiated fruits, non-climacteric fruits and vegetables, and features of recovery from the effects of the ethylene inhibitor.

A perusal of recent literature reveals that climacteric fruit continue to serve as the favored target for investigations of ethylene action suppression through use of 1-MCP (do Nascimento et al., 2006; Ergun et al., 2005a; Li et al., 2006; Mattheis et al., 2005; Menniti et al., 2006; Ortiz et al., 2005; Wang et al., 2006; Zhang et al., 2006). This is not unanticipated in view of the obligatory requirement of ethylene for the initiation and completion of normal ripening in climacteric fruit (Klee, 2004; Lelièvre et al., 1997). Notable responses of climacteric fruits include altered ethylene production and respiration (Ergun et al., 2005b; Golding et al., 1998; Ortiz et al., 2006; Zhang et al., 2006), delayed or suppressed softening (Adkins et al., 2005; Ergun et al., 2005b; Liguori et al., 2004; Menniti et al., 2006; Salvador et al., 2006;

Sane et al., 2005; Toivonen and Lu, 2005; Watkins and Nock, 2005), and altered or delayed volatile emissions (Defilippi et al., 2005; El-Sharkawy et al., 2005; Li et al., 2006; Mattheis et al., 2005; Pre-Aymard et al., 2005; Rizzolo et al., 2005). Evident from these and other studies is that there are no cases in which climacteric fruits have not responded significantly and dramatically to 1-MCP.

The use of 1-MCP has demonstrated that all of the primary features of ripening in climacteric fruit, including volatile production, softening, and pigment changes, are inexorably linked to competent ethylene perception and signal transduction (Adams-Phillips et al., 2004; Lelièvre et al., 1997). Consistent with heightened ethylene sensitivity in ripening competent, preclimacteric fruit (Klee, 2004), more extreme responses to ethylene action suppression have been noted before the onset of ripening. As shown for guava (*Psidium guineense* Sw.) (Bassetto et al., 2005), tomato (*Solanum lycopersicum* L.) (Hurr et al., 2005), and banana (*Musa* sp.) (Bagnato et al., 2003; Pelayo et al., 2003) fruits, application of 1-MCP, particularly at higher concentrations, to preripe fruit can result in complete inhibition of or severely compromised patterns of ripening. The inherently limited ripening capacity of immature tomato fruit is further exacerbated in response to 1-MCP (Hurr et al., 2005). Banana fruit subjected to high concentrations of 1-MCP (Bagnato et al., 2003; Pelayo et al., 2003) or when preclimacteric (Golding et al., 1998) show abnormal skin degreening, a condition circumvented to some degree using ripening-initiated fruit exposed to moderate levels of the antagonist (Bagnato et al., 2003). It seems likely that global recovery

¹To whom correspondence should be addressed; e-mail djhuber@ufl.edu

of most ripening parameters and, consequently, attainment and maintenance of optimum quality will be best achieved in instances when 1-MCP is applied after ripening initiation. Apple [*Malus sylvestris* L. (Mill.) var. *domestica* Borkh. Mansf.] appears to represent an exception to this view in that the goals of long-term storage and maintenance of firm, crisp texture in many cultivars is best achieved when 1-MCP is applied before ripening (Watkins, 2006).

That suppression of ethylene perception will interrupt the progression of ripening and senescence once initiated was first demonstrated using STS and DACP in both fruit and floral organs (Peiser, 1989; Smith et al., 1989; Tucker and Brady, 1987) and has been definitively confirmed with studies using 1-MCP. Application of 1-MCP to tomato fruit at progressively advanced stages of ripening effectively decelerated softening and red color development (Hoerberichts et al., 2002; Hurr et al., 2005) and strongly suppressed midclimacteric ethylene production when applied to turning, pink, and ripe fruit (Hoerberichts et al., 2002; Nakatsuka et al., 1997, 1998). 1-MCP-mediated suppression of ethylene production in midclimacteric tomato was accompanied by sharp declines in transcript abundance for 1-aminocyclopropane-1-carboxylic acid (ACC) oxidases (ACO) (*LE-ACO1* and *LE-ACO4*) and (ACC) synthases (*LE-ACS2* and *LE-ACS4*) (Nakatsuka et al., 1998). Transcript abundance for expansin 1 (*EXPI*), a wall-localized protein capable of destabilizing bonding between matrix polysaccharides (Cosgrove, 2000), and phytoene synthase 1 (*PSY1*), a carotenoid biosynthesis enzyme (Fray and Grierson, 1993), also declined significantly in ripening fruit treated with 1-MCP ($150 \mu\text{L}\cdot\text{L}^{-1}$) (Hoerberichts et al., 2002). Although Nakatsuka et al. (1998) did not address specifically the effects on fruit physical parameters (color, firmness, and so on), noteworthy is their observation that the significant and dramatic modulation in gene expression in both preclimacteric and midclimacteric fruit was attained using 1-MCP concentrations as low as 10 to $20 \text{ nL}\cdot\text{L}^{-1}$.

The capacity of 1-MCP to interrupt the progression of ripening, once initiated, varies among different fruits and with the ripening parameters selected for study. Softening of avocado (*Persea americana* Mill.) was recalcitrant to 1-MCP ($500 \text{ nL}\cdot\text{L}^{-1}$, 18 h) applied beyond 48 h after ripening initiation (Adkins et al., 2005), whereas the abundance of ethylene biosynthesis and receptor transcripts *PA-ACSI* (*Persea americana* ACC synthase), *PA-ACO* (ACC oxidase), and *PA-ERSI* (ethylene response sensor) mRNAs declined to nearly trace levels within 2 d of 1-MCP application (Owino et al., 2002). Discontinuing 1-MCP treatment was followed within 2 d by hyperinduction of *PA-ACSI*, *PA-ACO*, and *PA-ERSI* transcripts. The effects of 1-MCP ($45 \mu\text{L}\cdot\text{L}^{-1}$) on several ripening parameters in banana fruit were significantly diminished when applied 24 h after initiation of ripening (Golding et al., 1998) and eliminated if delayed 3 or 5 d (Jiang et al., 1999).

Data from Golding et al. (1998) are striking in that differences in skin color, volatile production, and climacteric ethylene and CO_2 production in response to 1-MCP exposure either 6 or 12 h after ripening initiation persisted through the 30+ d required to reach the postclimacteric phase. This indicates that despite the global recovery from the effects of 1-MCP, the consequences of suppressing ethylene responses during early ripening can persist for prolonged periods. 1-MCP was also effective at suppressing softening, electrolyte leakage, and delaying overripening when applied to ripe papaya (*Carica papaya* L.) (Ergun and Huber, 2004) and 'Galia' melon (*Cucumis melo* var. *reticulatus* L.) (Ergun et al., 2005a) fruits. Softening of apple fruit exposed to 1-MCP after initiation of the climacteric was strongly suppressed, and more persistent effects were obtained with multiple applications of the inhibitor (Mir et al., 2001). The variability in responses of several cultivars of apple to 1-MCP, applied at harvest or after periods of delay, was attributed in part to whether the climacteric was initiated (Watkins and Nock, 2005).

Suppression of ethylene action using 1-MCP has lent support to results from molecular studies indicating that ethylene dependency of some ripening processes changes during ripening. Selected studies of banana (Zhang et al., 2006), papaya (Ergun and Huber, 2004), tomato (Hoerberichts et al., 2002), and 'Booth 7' avocado (Jeong and Huber, 2004; Jeong et al., 2003) reveal that softening is unaltered relative to controls in the short term (several days) after 1-MCP treatment but becomes increasingly suppressed as ripening proceeds. Although the apparent increasing suppression of softening with ripening could reflect a delay in the ability of 1-MCP to engage and affect signal output of ethylene receptors, or the time required for depletion of preexisting pools of specific enzymes and transcripts, molecular studies are supportive of the idea that ethylene dependency of softening in some fruits does change during the course of ripening. Analysis of softening of ACO-antisense 'Charentais' melons (*Cucumis melo* var. *cantalupensis*) in response to increasing dosages of ethylene revealed both ethylene-dependent and -independent components (Flores et al., 2001a, 2001b). 'Galia' melon (*Cucumis melo* L.) expressing an antisense ACO construct and exhibiting strongly suppressed ethylene production softened normally through the half-slip stage, thereafter remaining significantly firmer than wild-type lines (Nuñez-Palenius et al., 2007). Similarly, softening of ACO (EFE)-antisense tomato fruit was significantly more impaired during the later stages of ripening (Murray et al., 1993). Softening of papaya (Ergun and Huber, 2004) and 'Galia' melon (Ergun et al., 2005a) treated with 1-MCP was proportionally more impaired during the late stages of ripening. Detailed genomic analysis of the temporal sequence of softening of peach fruit has demonstrated participation of ethylene-dependent (both upregulated and downregu-

lated) and ethylene-independent enzymes and structural proteins, with ethylene-independent events prevailing in the early period of ripening (Trainotti et al., 2003).

In most every case, the recovery of physical and gene expression ripening responses in climacteric fruits after 1-MCP treatment can be circumvented by additional exposures to the ethylene antagonist (Hoerberichts et al., 2002; Jayanty et al., 2004; Mathooko et al., 2001; Mir et al., 2004; Toivonen and Lu, 2005). These observations are consistent with the strong upregulation of ethylene receptor transcription and translation during the climacteric (Czarny et al., 2006; Klee, 2004), and also suggest that 1-MCP receptor binding might be reversible (Jayanty et al., 2004). Apple fruit, with their potential for comparatively long storage periods over a range of temperatures, have proven useful for analysis of long-term effects of and recovery from 1-MCP exposure. In 'RedChief Delicious' apples subjected to 1-MCP ($0.7 \mu\text{L}\cdot\text{L}^{-1}$) at frequencies ranging from single (once per year) to once per week, the advantages of weekly exposure, assessed from firmness retention, were evident during extended storage at higher temperatures (Mir et al., 2001). The observation that 'RedChief Delicious' apple fruit receiving subsaturating dosages ($0.1 \mu\text{L}\cdot\text{L}^{-1}$) of 1-MCP applied weekly were unable to maintain firmness to the extent achieved at higher levels ($1.0 \mu\text{L}\cdot\text{L}^{-1}$) after ≈ 100 d in store was interpreted as evidence for a dissociation of 1-MCP from the ethylene receptor (Jayanty et al., 2004). Extended-chain cyclopropenes, including 1-octyl-, 1-nonyl-, and 1-decyl-derivatives, increased by nearly threefold the duration of chlorophyll retention compared with 1-MCP (Sisler et al., 2003). Assuming that these cyclopropenes act solely through direct interactions with the ethylene receptor, the differential recovery from the various derivatives lends support to the notion that cyclopropene receptor binding is reversible. As a result of the hydrophobic nature and low volatility of 1-octyl-, 1-nonyl-, and 1-decyl-cyclopropenes, however, they would appear to have properties conducive for partitioning into membranes, possibly providing an available pool to compensate for cyclopropene dissociation as well as receptor replenishment. Evidence for nonselective binding was the observation that 1-MCP partitioned in much higher amounts and at faster rates in the lipid-rich avocado compared with apple fruit (Dauny et al., 2003). The accumulation of internal ethylene during long-term storage (Watkins and Nock, 2005) might also contribute to the dissipation of 1-MCP responses. The effect of 1-MCP ($1.0 \mu\text{L}\cdot\text{L}^{-1}$) at suppressing ripening of tomato fruit, for example, is abolished if applied simultaneously with ethylene at $50.0 \mu\text{L}\cdot\text{L}^{-1}$ (Jeong and Huber, unpublished data). Notwithstanding the clear evidence that multiple applications of 1-MCP are more effective at suppressing ripening in general, even single applications resulted in near total suppression of polygalacturonase activity (24 d) in avocado fruit

(Jeong and Huber, 2004) and both β -amylase activity and protein (28 d) accumulation in banana fruit (do Nascimento et al., 2006), the inhibition persisting through the duration of the ethylene climacteric. Persimmon (*Diospyros kaki* Thunb.) fruit treated with 1-MCP showed only a transient delay in polygalacturonase activity but acute suppression of pectinmethylesterase and β -galactosidase activities (Ortiz et al., 2005). Treatment of avocado fruit with ethylene (100 $\mu\text{L}\cdot\text{L}^{-1}$, 24 h) at periods of up to 14 d after 1-MCP exposure did not influence time to soften (Adkins et al., 2005). Interestingly, the response of 1-MCP-treated banana fruit to subsequent ethylene exposure increased with delay between exposures to the two gases (Jiang et al., 1999), but the response was independent of ethylene concentrations from 0.1 to 100 $\mu\text{L}\cdot\text{L}^{-1}$.

1-MCP has been of immense value for detailing the diverse roles of endogenous and exogenous ethylene in the postharvest metabolism of fruits and vegetables exhibiting nonclimacteric ripening and senescence patterns. Responses of nonclimacteric fruit and vegetative organs to 1-MCP include delayed chlorophyll and protein degradation in coriander (*Coriandrum sativum* L.) (Jiang et al., 2002) and parsley (*Petroselinum crispum* Mill.) (Ella et al., 2003); delayed yellowing of broccoli (*Brassica oleracea* L.) (Fan and Mattheis, 2000b; Forney et al., 2003) and rocket leaves (*Eruca sativa* Mill.) (Koukounaras et al., 2006); firmness retention in cucumber (*Cucumis sativus* L.) (Lima et al., 2005) and watermelon (*Citrullus lanatus* Thunb. Matsum and Nakai) (Mao et al., 2004); delayed vivipary in chayote (*Sechium edule*) (Cadena-Iniguez et al., 2006); suppressed pigment accumulation and softening of strawberry (*Fragaria* \times *ananassa* Duch.) (Jiang et al., 2001); suppressed degreening of 'Shamouti' orange (*Citrus sinensis* L.) (Porat et al., 1999), grapefruit (*Citrus paradisi*) (McCollum and Maul, 2007), and 'Tahiti' lime (*Citrus latifolia* Yu. Tanaka) (Jomori et al., 2003); reduced disorders in carrot (*Daucus carota* L.) (Fan and Mattheis, 2000a) and 'Iceberg' lettuce (*Lactuca sativa* L.) (Fan and Mattheis, 2000a); and delayed lignin deposition and firmness increases in loquat (*Eriobotrya japonica* Lindl.) (Cai et al., 2006a, 2006b). In general, the effects of 1-MCP on nonclimacterics are dramatically more evident when these commodities are exposed to exogenous ethylene. In a survey of six leafy Asian vegetables, for example, only mizuna (*Brassica rapa* var. *nipposinica*) and tatsoi (*Brassica rapa* var. *rosularis*) benefitted from 1-MCP treatment when subsequently stored in an ethylene-free environment (Able et al., 2003). Nevertheless, because ambient ethylene levels in retail settings are often sufficient to affect significant reductions in postharvest shelf life (Wills et al., 1999, 2000), 1-MCP perhaps has some potential for application to high-value nonclimacteric commodities with low-threshold ethylene sensitivity.

Features of ethylene biosynthesis in vegetative and other nonclimacteric organs are

consistent with system 1, negative feedback regulation (Kende, 1993; McMurchie et al., 1972). Accordingly, both coriander (Jiang et al., 2002) and parsley (Ella et al., 2003) showed significantly enhanced ethylene production in the short term after 1-MCP exposure. Particularly noteworthy are parsley (Ella et al., 2003) and 'Marsh' grapefruit (McCollum and Maul, 2007) that, in response to 1-MCP (10 $\mu\text{L}\cdot\text{L}^{-1}$ parsley, 300 $\text{nL}\cdot\text{L}^{-1}$ grapefruit), exhibited hyperproduction of ethylene to levels as high as 20 and 50 $\mu\text{L}\cdot\text{kg}^{-1}\cdot\text{h}^{-1}$, respectively.

1-MCP studies with grape (*Vitis vinifera* L.) and strawberry have confirmed and extended our understanding of the role of endogenous ethylene in the development and ripening of these paradigmatic nonclimacteric fruits (Rhodes, 1980). Ethephon has long been known to promote the maturation and coloration of grapes (Weaver and Montgomery, 1974), and ACC or STS, respectively, either accelerated or suppressed growth and red color development in strawberry fruit (Perkins-Veazie et al., 1996). Application of 1-MCP to attached grapes at weekly intervals after bloom strongly reduced final berry diameter and anthocyanin levels (Chervin et al., 2004). Furthermore, the responses to 1-MCP were dependent on stage of berry development with the maximum response temporally associated with and reciprocal to internal ethylene levels, which followed a climacteric-like accumulation pattern. The expression of alcohol dehydrogenase (*VvADH2*) during grape berry ripening was inhibited in response to 1-MCP treatment of attached grape clusters (Tesniere et al., 2004) as was the accumulation of sucrose and mRNA of two sucrose transporters (*SUC11* and *SUC12*) (Chervin et al., 2006). Applied to harvested, ripe grapes, 1-MCP suppressed ethylene production, enhanced losses in terpenols and esters, and delayed loss in anthocyanins (Bellincontro et al., 2006). The responses of harvested, ripe strawberry fruit to 1-MCP include suppression of softening and anthocyanin accumulation (Jiang et al., 2001), decreased ethylene production (Bower et al., 2003; Jiang et al., 2001), and higher incidence of decay (Bower et al., 2003; Jiang et al., 2001; Ku et al., 1999). Although the effects of 1-MCP on strawberry physical attributes (firmness, color) are for the most part unremarkable, a significant effect on the expression (upregulated or downregulated in response to 1-MCP) of a number of genes strongly suggests that ethylene-dependent processes operate during both growth and ripening (Balogh et al., 2005). Analysis of strawberry fruit *in planta* demonstrated a distinct and significant rise in ethylene and CO_2 production coincident with the transition from pink through red, and ethylene production in response to STS applied through the pedicel vasculature of fruit at progressively more advanced stages of development responded in a manner indicative of a transition from system 1 regulation (STS stimulated ethylene production) during early growth and expan-

sion to system 2 regulation (STS suppressed ethylene production) during ripening (Iannetta et al., 2006). This report is supported by other studies in which 1-MCP application decreased the ethylene production of harvested ripe strawberry fruit (Bower et al., 2003; Jiang et al., 2001). Ripening strawberry fruit contain type 1 (*FaEtr1*, *FaErs1*) and type 2 (*FaEtr2*) ethylene receptor genes, the expression of which increase or persist as fruit ripen (Trainotti et al., 2005).

The responses of strawberry and grape fruits to ethylene and ethylene suppression contrast sharply with those reported for other nonclimacteric fruits, including cucumber and watermelon. Both cucumber (*Cucumis sativus* L.) (Lima et al., 2005) and watermelon (*Citrullus lanatus* Thunb. Matsum and Nakai) (Mao et al., 2004) fruits within days of exposure to ethylene exhibit accelerated softening and acute water soaking. In the case of watermelon, which can be adversely influenced by ethylene regardless of stage of maturation (Karakurt and Huber, 2004), exposure to ethylene induces significant increases in electrolyte efflux, juice leakage, lipase and LOX activities, and phospholipid catabolism (Mao et al., 2004). A single exposure to 1-MCP afforded complete protection from the effects of continuous ethylene for up to 8 (watermelon) or 16 d (cucumber). That cucumber and watermelon retain a capacity to respond acutely to ethylene is intriguing. Some semblance of climacteric behavior might have been expressed in progenitors of these highly domesticated fruit, having been outselected in efforts to improve storage properties.

1-MCP has proven useful for elucidating changes in ethylene-dependent and ethylene-independent events occurring in response to tissue wounding. Treatment with 1-MCP before wounding of mature green *rin* and wild-type tomato resulted in a 50% reduction in wound-induced ethylene production but did not affect wound-enhanced expression of *LE-ACS2* (*Lycopersicon esculentum* ACC synthase 1), *LE-ACS-6* (ACC synthase 6), and *LE-ACO1* (ACC oxidase 1) (Yokotani et al., 2004). Expression of ripening-related *LE-ACO1* and *LE-ACS2* genes, however, were arrested in intact (nonwounded) tomato fruit after 1-MCP treatment (Hoeberichts et al., 2002; Nakatsuka et al., 1997), indicating that wound-induced events operate to some extent independently of ethylene signaling. In contrast to tomato, 1-MCP significantly enhanced wound-induced ethylene synthesis and *PC-ACS2* mRNA levels in preclimacteric avocado fruit (Owino et al., 2002) and ethylene biosynthesis and accumulation of *PP-ACS1* in peach (Mathooko et al., 2001) fruit. Independent wound and ethylene signaling was also evident in studies of intact and fresh-cut lettuce. 1-MCP treatment (0.5 $\mu\text{L}\cdot\text{L}^{-1}$, 3 h) inhibited ethylene-induced phenol accumulation in whole heads of 'Iceberg' lettuce but did not prevent accumulation in fresh-cut (wounded) product (Saltveit, 2004). Consistent with the influence of wounding at overriding components

of ethylene signaling, it is evident that the benefits conferred on treatment of whole fruit with 1-MCP are considerably dampened in fresh-cut tissues (Calderon-Lopez et al., 2005; Ergun et al., 2006a, 2007; Mao et al., 2006, 2007).

Interruption of ethylene receptor interactions and downstream signal output through applications of 1-MCP has revealed a broad array of responses in horticultural crops. This is not unexpected. Edible fruits and vegetables represent a highly diverse group in terms of both inherent physiology and in morphological derivation. Although it is tempting to speculate that tissue-specific ethylene receptor characteristics might contribute to 1-MCP response variation, binding studies do not envision differential receptor selectivity for 1-MCP and ethylene (Binder and Bleecker, 2003; Hall et al., 2000). Analysis of yeast-expressed receptor proteins from *Arabidopsis thaliana* (L.) Heynh and tomato fruit has provided no evidence of differences in ethylene binding or dissociation kinetics between the receptor subtypes (O'Malley et al., 2005), a noteworthy observation in view of the fact that responses to ethylene in *Arabidopsis* alone can occur over 10^7 orders of magnitude in ethylene concentration (Binder et al., 2004; Chen and Bleecker, 1995). Even so, the responses of *Arabidopsis* mutants deficient in one or more ethylene receptors has revealed that quantitative compensation in functional receptor abundance is not accompanied by a parallel compensation in ethylene responses (O'Malley et al., 2005). Indeed, detailed molecular analyses of the nonripening *Green-Ripe* (*GR*) tomato mutant have led to suggestions that the ethylene responsiveness or signaling of individual receptors with differential spatial distribution might be modulated by *GR* and other, as yet undiscovered, proteins (Barry and Giovannoni, 2006).

The availability of ethylene action inhibitors in general and 1-MCP in particular has indeed provided a powerful tool for investigating the spectrum of ethylene effects in postharvest biology. The responses of horticultural crops to 1-MCP are impressively complex and varied, demonstrating both known as well as previously unrecognized responses to ethylene. Although at this writing, the chemical is used commercially with but a few crops, it has potential for broader application. A more thorough understanding of the variables controlling the responses to 1-MCP application will be required before it can be adopted routinely for harvested commodities. The importance of maturity, cultivar, and exposure variables (time, temperature, concentration) are complex and continue to be the focus of much research (Watkins, 2006). Of equal importance will be understanding the factors limiting the capacity of some commodities after 1-MCP treatment to engage fully the entire spectrum of developmental changes essential for expressing optimum quality. Irreversibility of 1-MCP effects is perhaps not problematic for the nonclimacterics in which arrested

postharvest development and suppression of ethylene effects has no overt effect on commodity quality. The benefits of 1-MCP application with other fruits, notably the climacterics, may be in imparting the flexibility for more extended "on-vine" development followed by scheduled exposure to 1-MCP and timely, predictable recovery in marketing channels. Other possible applications might be realized for fruits of exceptionally high perishability as a result of rapid ripening or those intolerant of low-temperature storage. Clearly, the widespread adoption of these practices will involve consideration of both commodity and economic issues.

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