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Effect of ethylene on quality of fresh fruits and vegetables

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Abstract

Ethylene is a naturally occurring plant growth substance that has numerous effects on the growth, development and storage life of many fruits, vegetables and ornamental crops at $\mu l\ l^{-1}$ concentrations. Harvested fruits and vegetables may be intentionally or unintentionally exposed to biologically active levels of ethylene and both endogenous and exogenous sources of ethylene contribute to its biological activity. Ethylene synthesis and sensitivity are enhanced during certain stages of plant development, as well as by a number of biotic and abiotic stresses. Exposure may occur inadvertently in storage or transit from atmospheric pollution or from ethylene produced by adjacent crops. Intentional exposure is primarily used to ripen harvested fruit. The detrimental effects of ethylene on quality center on altering or accelerating the natural processes of development, ripening and senescence, while the beneficial effects of ethylene on quality center on roughly the same attributes as the detrimental effects, but differ in both degree and direction. Care must therefore be taken to insure that crops sensitive to the effects of ethylene are only exposed to the desired atmosphere. A number of techniques to control the effects of ethylene are discussed in relation to their application with commercially important fruits and vegetables. Examples of general and specific beneficial and detrimental ethylene effects are given.

Keywords: Appearance; Aroma; Color; Ethylene synthesis and action; Flavor; Storage; Taste

1. Introduction

Both the practical agricultural use of ethylene (C_2H_4), and the basic biochemistry and physiology of C_2H_4 have been extensively studied for many decades (Abeles et al., 1992). Elucidation of the C_2H_4 biosynthetic pathway by Adams and Yang (1979) and the recent application of molecular biology to unravel the complexities of C_2H_4 biosynthesis and action have greatly stimulated research in this area (Yang, 1985; DellaPenna and Giovannoni, 1991; Grierson and Schuch, 1994; Kanellis et al., 1997). However, much of what is known about the effects of C_2H_4 on the quality of fresh fruits and vegetables has been slowly

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amassed since the 1920s, and needs constant updating. The introduction of new cultural practices, cultivars, harvest and handling methods, postharvest treatments, consumer products and packaging influence the effect C_2H_4 has on quality attributes. Continued research in these areas, though not as glamorous as in biotech. areas, provides the foundation upon which the commercial agricultural use of C_2H_4 is based. The information presented in this review has been gleaned from recent publications and from past reviews on the biochemistry and physiology of C_2H_4 (Abeles et al., 1992; Kanellis et al., 1997; Saltveit et al., 1998), its role in postharvest handling (Kader, 1985; Weichmann, 1987; Yang, 1987), and its effect on food quality (Watada, 1986; Lougheed et al., 1987).

Ethylene is a naturally produced, simple two carbon gaseous plant growth regulator that has numerous effects on the growth, development and storage life of many fruits, vegetables and ornamental crops (Table 1). This powerful plant hormone is effective at part-per-million (ppm, $\mu l\ l^{-1}$) to part-per-billion (ppb, $nl\ l^{-1}$) concentrations. Both the synthesis and action of C_2H_4 involve complicated metabolic processes, which require oxygen and are sensitive to elevated concentrations of carbon dioxide. Endogenous sensitivity to C_2H_4 changes during plant development, as does its rate of synthesis and loss by diffusion from the plant.

Table 1
Biological attributes of ethylene

Colorless gas at biological temperatures.
Naturally occurring organic compound.
Readily diffuses within and from tissue.
Produced from methionine via ACC by a highly regulated metabolic pathway.
Key enzymes are ACC synthase and ACC oxidase.
Ethylene synthesis is inhibited (negative feed-back inhibition) by C_2H_4 in vegetative and immature climacteric and non-climacteric reproductive tissue.
Ethylene synthesis is promoted (positive feed-back promotion, or autocatalytic) by C_2H_4 in reproductive climacteric tissue.
Effective at part-per-million (ppm, $\mu l\ l^{-1}$) and part-per-billion (ppb, $nl\ l^{-1}$) concentrations (1 ppm equals 6.5×10^{-9} M at 25°C).
Requires O_2 to be synthesized, and both O_2 and low levels of CO_2 to be active.

Table 2
Plant responses to ethylene

Ethylene stimulates
Synthesis of C_2H_4 in ripening climacteric fruit.
Ripening of fruit.
Pigment (e.g. anthocyanin) synthesis.
Chlorophyll destruction and yellowing.
Seed germination.
Adventitious root formation.
Respiration.
Phenylpropanoid metabolism.
Flowering of bromeliads.
Abscission.
Senescence.
Ethylene inhibits
Ethylene synthesis in vegetative tissue and non-climacteric fruit.
Flower development in most plants.
Auxin transport.
Shoot and root elongation (growth).
Normal orientation of cell wall microfibrils.

The responses to endogenously produced and exogenously applied C_2H_4 are numerous and varied (Table 2), and are only beneficial or detrimental when viewed anthropomorphicly (Table 3). For example, effects that are viewed as beneficial include the promotion of flowering in pineapple (*Ananas comosus*) and the hastening of ripening in tomato (*Lycopersicon esculentum*) and melons (*Cucumis melo*). Effects that are viewed as deleterious include the abortion of flowers and the development of russet spotting in lettuce (*Lactuca sativa*). Often the same response (e.g. acceleration

Table 3
Examples of how the same ethylene response can be beneficial in one system and detrimental in another

Example of benefit	Ethylene response	Example of detriment
Degreening of citrus	Accelerates chlorophyll loss	Yellowing of green vegetables
Ripening of climacteric fruit	Promotes ripening	Overly soft and mealy fruit
Defense against pathogens	Stimulates phenylpropanoid metabolism	Browning and bitter taste

of chlorophyll loss, promotion of ripening, or stimulation of phenylpropanoid metabolism) is viewed as beneficial in some crops (e.g. degreening of citrus, ripening of climacteric fruit, and stimulating defenses against pathogens) and detrimental in others (e.g. yellowing of green vegetables, excessive softening of fruit, or browning of lettuce; Table 3).

Plants produce C_2H_4, but only ripening climacteric fruit and diseased or wounded tissue produce it in sufficient amounts to affect adjacent tissue. In all but ripening climacteric fruit tissue, C_2H_4 suppresses its own synthesis. As climacteric fruit start to ripen, this negative feedback inhibition of C_2H_4 on C_2H_4 synthesis changes into a positive feedback promotion in which C_2H_4 stimulates its own synthesis (i.e. autocatalytic C_2H_4 production) and copious amounts of C_2H_4 are produced (Yang, 1987).

Once the ripening of climacteric fruit has started, the internal C_2H_4 concentration quickly increases to saturation levels and exogenous application of C_2H_4 has no further promotive effect on ripening. Reducing the external concentration of C_2H_4 around bulky fruit (e.g. apples (*Malus domestica*), bananas (*Musa* spp.), melons and tomatoes) has almost no effect on reducing the internal concentration in these ripening climacteric fruit because of the large diffusion resistance of their skin and flesh. In these fruit, the rate of production far outstrips the rate of diffusive losses until a fairly high level is reach. Internal C_2H_4 concentration can exceed 100 μl l^{-1}, even when the external concentration is zero. Therefore, reducing the external C_2H_4 concentration by ventilation or with C_2H_4 scrubbers generally has no effect on the subsequent ripening of fruit that have progressed a few days into their climacteric. However, at the initial stages of ripening when internal C_2H_4 levels are still low, enhancing the rate of diffusion with low-pressure storage or inhibiting the synthesis or action of C_2H_4 can significantly retard ripening.

Sources of C_2H_4 not only include other plants (e.g. a ripe apple in a paper bag to promote the ripening of bananas), but also includes smoke, exhaust gases, compressed C_2H_4 gas, C_2H_4 releasing chemicals (e.g. ethephon), catalytic production of C_2H_4 from ethanol, and C_2H_4 analogues produced by a variety of processes. Other gaseous chemicals are analogs of C_2H_4 (Table 4) and can elicit the same physiological effects as C_2H_4, but often much higher concentrations are required to produce the same effect (Abeles et al., 1992). These analogs are useful in studies of C_2H_4 action when C_2H_4 production by the tissue is one of the factors being measured. The response of the tissue to C_2H_4 exposure depends on the sensitivity of the tissue, concentration of C_2H_4, composition of the atmosphere, duration of exposure, and temperature (Table 5).

Table 4
Activity of ethylene analogs in plants

Gases	Half-maximal activity μl l^{-1}
Ethylene	0.1
Propylene	10
Carbon monoxide	270
Acetylene	270
1-Butene	27 000

2. Ethylene synthesis and action

Ethylene production is promoted by stresses such as chilling (Wang, 1990) and wounding (Abeles et al., 1992), and this stress-induced C_2H_4 can enhance fruit ripening. However, these stresses also induce other physiological changes (e.g. enhanced respiration and phenylpropanoid metabolism) and it is difficult at time to deduce

Table 5
Factors governing plant responses to ethylene exposure

Tissue sensitivity: specie, cultivar, cultural practices, stage of development, prior exposure to hormones, level of past and current stress.
Ethylene concentration: like most hormones, the response to C_2H_4 is log-linear (i.e. a linear response with logarithmic increases in C_2H_4 concentration).
Atmospheric composition: adequate oxygen ($>10\%$), low carbon dioxide ($<1.0\%$).
Duration of exposure: a minimum time is usually required (the trigger effect).
Temperature: a narrow range produces optimum results.

whether it is the stress per se or one of the stress-induced changes (e.g. stimulated C_2H_4 production) that is producing the effect. In the case of lettuce, and probably in most vegetative tissue, sub-lethal levels of stress induce only transitory increases in C_2H_4 production, which have minimal lasting effects. However, in climacteric fruit tissue, stress-induced C_2H_4 can have a significant and protracted effect. For example, chilling of pears (*Pyrus communis*) and wounding of figs induce stress C_2H_4 and these techniques have been used commercially to promote fruit ripening.

Phenylpropanoid metabolism is enhanced by ethylene, and certain phenolic compounds have been associated with a reduction in certain diseases (Hertog et al., 1992; Frankel et al., 1995). However, phenolic compounds are also known to react with, bind to, and generally inactivate other nutritional components of the diet. The amount and composition of the phenylpropanoid compounds induced by C_2H_4 and their effect on health should be better characterized.

The effect of C_2H_4 on the plant's responses to stresses like chilling and wounding is quite variable. Exposing mature honeydew melons to 1000 μl l^{-1} C_2H_4 for 24 h induced ripening and eliminated chilling injury in fruit subsequently stored at 2.5°C for 2 weeks. (Lipton et al., 1979). The chilling sensitivity of citrus fruit is generally increased by exposure to C_2H_4, but C_2H_4 treatments seem to enhance tolerance of some fruit (Forney and Lipton, 1990). Avocado fruit exposed to C_2H_4 developed more chilling injury than fruit chilled without C_2H_4, whereas tomato fruit become more chilling resistant as they ripen.

Many reports confirm the fact that fruit maturity is a factor in chilling sensitivity. However, some of these results may be confounded by the way chilling is evaluated. If ripening is used as the major criteria to evaluate the extent of chilling injury, then the riper the fruit is, the more chilling tolerant it would appear. When the delay of red coloration is used to measure the level of chilling injury in tomatoes, chilling tolerance increases as the fruit ripens. However, if other criteria are used to evaluate chilling injury (e.g. induced respiration and C_2H_4 production, and increased solute and ion leakage), then the level of injury induced by a given level of chilling stress appears to be relatively unaffected by the stage of ripeness at chilling.

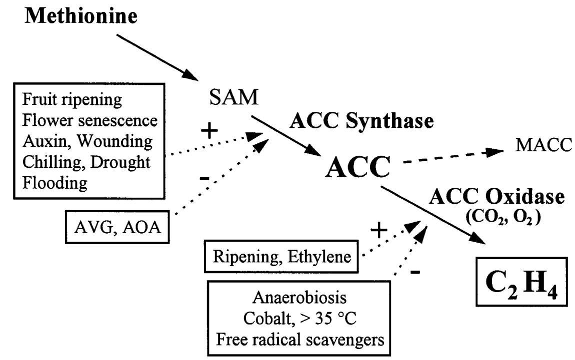

Fig. 1. Biosynthesis of ethylene in higher vascular plants. Some of the intrinsic and extrinsic factors that promote (+) or inhibit (−) ethylene (C_2H_4) synthesis in higher vascular plants.

In higher vascular plants, a relatively simple biosynthetic pathway produces C_2H_4 (Fig. 1). The amino acid methionine (MET) is the starting point for synthesis. It is converted to *S*-adenosyl methionine (SAM) by the addition of adenine, and SAM is then converted to 1-amino-cyclopropane carboxylic acid (ACC) by the enzyme ACC synthase. The production of ACC is often the controlling step for C_2H_4 synthesis. A number of intrinsic (e.g. developmental stage) and extrinsic (e.g. wounding) factors influence this pathway (Yang, 1987).

The pool of ACC available for C_2H_4 production can be increased by factors which increase ACC synthase activity, reduced by application of growth regulators (e.g. daminozide), or reduced by a side reaction which forms the relatively biologically inert MACC (Fig. 1). In the final step, ACC is oxidized by the enzyme ACC oxidase to form C_2H_4. This oxidation reaction requires the presence of oxygen, and low levels of carbon dioxide activate ACC oxidase. While the level of ACC oxidase activity is usually in excess of what is needed in most tissues, it can show a dramatic increase in activity in ripening fruit and in response to C_2H_4 exposure.

There are some significant interactions between the plant and its environment that are important in understanding how C_2H_4 effects plants (Fig. 2). Removing the source of C_2H_4 from these enclosed spaces is the best way to eliminate C_2H_4 as a problem. If this is impossible or uneconomical, dilution of C_2H_4 by adequate ventilation with clean outside air can minimize its effects. When the storage atmosphere cannot be exchanged, as in controlled atmosphere storage, chemicals can be used to remove C_2H_4 from the atmosphere. Various solid and liquid formulations of potassium permanganate are commonly used to oxidize C_2H_4. Ozone is also an effective oxidizer, but it is technically more difficult to use. Inert absorbers of C_2H_4 have yet to prove their effectiveness.

Since C_2H_4 exerts its effects through metabolic reactions, keeping the exposed tissue at their lowest recommended storage temperature will reduce the response. Similarly, reducing metabolism by reducing the oxygen concentration will mitigate the effects of exposure, as will keeping the duration of exposure to a minimum and adding C_2H_4 antagonists like carbon dioxide to the atmosphere (Lougheed, 1987). Although low oxygen reduces respiration, its inhibition of ethylene action, rather than its inhibition of respiration appears to be the basis by which low oxygen extends the storage life of many crops. However, in those crops in which oxidative browning limits shelf-life, inhibition of the browning reaction by removal of oxygen will extend shelf-life. But here again, reduced respiration is relatively unimportant and could more easily be accomplished by lowered temperatures than by controlled or modified atmospheres.

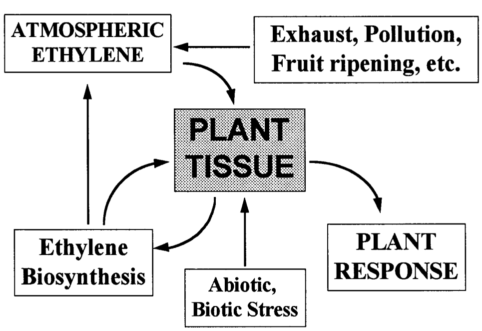

Fig. 2. Ethylene interactions with the plant and its environment.

Presently, C_2H_4 action can be blocked by a variety of compounds including carbon dioxide, silver, and a number of unsaturated cyclic olefins (Abeles et al., 1992). Carbon dioxide is currently used to reduce C_2H_4 activity in controlled atmosphere storage. Silver is used to promote the longevity of cut flowers sensitive to C_2H_4, in the breeding and seed production of cucumbers, and in research. However, silver is incompatible with food crops. Basic studies of C_2H_4 binding have resulted in the identification of a number of unsaturated cyclic olefins that effectively inhibit C_2H_4 action. A comparison of three of these compounds showed that exposure to 1-methylcyclopropene (1-MCP) for 6 h at 0.5 nl l^{-1} made bananas insensitive to C_2H_4 for 12 days and carnations for 24 h, while 5 nl l^{-1} was needed to make mature-green tomatoes insensitive to C_2H_4 for 8 days (Sisler et al., 1996). If shown to be compatible with food crops, these compounds offer a convenient way to modify C_2H_4 action in currently used cultivars.

Considerable progress has been made during the past decade in understanding the physiology, biochemistry, and molecular biology of the induction and regulation of genes involved in C_2H_4 synthesis and action (Bleecker and Schaller, 1996; Fluhr and Mattoo, 1996; Lelievre et al., 1997; Saltveit et al., 1998). A highly diverse multigene family encodes ACC synthase, the key regulatory enzyme in C_2H_4 biosynthesis (Zarembinski and Theologis, 1994). Wounding, ripening, senescence, C_2H_4, and other factors induce members of this gene family. Identifying, characterizing and isolating the inducers for these genes should allow the genetic engineering of transgenetic plants with anti-sense constructs to nullify specific developmental changes. This technology has been used to produce tomato lines with fruit that have reduced rates of C_2H_4 synthesis during ripening and reduced ability to perceive and react to C_2H_4 (DellaPenna and Giovannoni, 1991; Picton et al., 1994). Similar molecular and genetic research should soon describe the mode of C_2H_4 action, identify the genes involved, and characterize their induction and regulation (Kanellis et al., 1997). These discoveries will provide additional strategies to control the biological action of C_2H_4.

Table 6
Beneficial effects of ethylene on the quality of fresh fruits and vegetables

Promotes color development in fruit.
Stimulates ripening of climacteric fruit.
Promotes de-greening of citrus.
Stimulates dehiscence in nuts.
Alters sex expression in the cucurbitaceae.
Promotes flowering in bromeliaceae (e.g. pineapple).
Reduces lodging of cereals by inhibiting stem elongation.

3. Beneficial effects of ethylene

The beneficial effects of C_2H_4 are realized by its application to growing plants in the field and orchard, to plants in the greenhouse, and to harvested commodities (Table 6). Field application of C_2H_4 became practical with the development of C_2H_4 releasing chemicals like ethephon; (2-chloroethyl)phosphonic acid. Ethylene has been used in this liquid form to effect seed germination and bulb sprouting, to retard growth, to reduce apical dominance, to initiate or inhibit root initiation, to stimulate latex and other secretions, to induce, promote, or delay flowering, to alter sex expression, to thin flower and fruit, to enhance color development, to aid in harvest, to defoliate plants, and to assist in the cultural control of insect pests (Abeles et al., 1992). For example, flowering is promoted in pineapple and sex expression altered in cucumbers. Color development is enhanced through stimulation of pigment synthesis in apples and tomatoes or chlorophyll destruction in bananas and citrus. Ethephon has been used on apples, cereals, cherries, citrus, coffee, cotton, cucumbers, grapes, guava, olives, peaches, peppers, pineapple, rice, rubber, sugarcane, sweetpotatoes, tobacco, tomatoes and walnuts (Watada, 1986; Abeles et al., 1992). It is also used on many ornamentals and small fruit. However, not all these uses are registered or approved for food crops.

Postharvest applications of C_2H_4 are predominantly in the gas phase and come from cylinders of compressed C_2H_4 gas that is diluted with air, or from the catalytic decomposition of ethanol (i.e. C_2H_4 generators) and are used primarily to promote fruit ripening. There is usually no significance difference in the effectiveness of these two methods of applying C_2H_4 to ripen fruit. However, the catalytic method does introduce small amounts of ethers and alcohols into the atmosphere. These gases may have accounted for the ability of a taste panel to distinguish between tomato fruit ripened by these two methods. Although the flavor of the tomatoes was different, the taste panel did not express a preference of one treatment over the other (Blankenship and Sisler, 1991).

The best quality fruit are produced when the concentration of C_2H_4, carbon dioxide and oxygen in the atmosphere, and the duration of exposure, temperature, and humidity are carefully controlled and maintained at optimum levels. Since even marginally mature fruit can be forced to ripen if given sufficient stimulation (i.e. high C_2H_4 concentrations for an extended duration), the ripening promotive effects of C_2H_4 should not be abused since inferior quality ripe fruit will be produced from fruit that are less than fully mature when harvested or fruit improperly handled after harvest.

Although the half-maximal response for most C_2H_4 effects is 0.1 $\mu l\ l^{-1}$ air, concentrations from 10 to 1000 $\mu l\ l^{-1}$ are used commercially to promote the ripen of avocados, bananas, mangos, honeydew melons, kiwifruit, mango, stone fruit and tomatoes. After exposures for 12–24 h at 15–25°C in a ‘shot’ system to ‘trigger’ ripening, the gassing rooms are opened and the product moved to other storage rooms or shipped to market. This method can be used to initiate ripening of some fruit (e.g. avocados) before marketing. More commonly, C_2H_4 is applied at 10–150 $\mu l\ l^{-1}$ for 2–3 days in a flow-through system at elevated temperatures (15–25°C) in specially constructed ripening rooms at regional distribution centers. Bananas, mangos, and tomatoes are ripened in this way. The flow-through method is best accomplished with forced-air circulation to maintain the optimum temperature, humidity, carbon dioxide and C_2H_4 concentration uniformly throughout the packaged product. The stimulation of respiration and heat production by C_2H_4 in either system requires more refrigeration capacity and better air circulation to maintain optimal conditions than is commonly found in storage rooms. There are exceptions to these commonly used ripening conditions. For example, citrus are degreened at C_2H_4 concentrations below 5 μl l^{-1} and temperatures around 20°C to reduce the incidence of decay.

4. Detrimental effects of ethylene

The detrimental effects of C_2H_4 on quality center on altering or accelerating the same natural processes of development, ripening and senescence that are viewed as beneficial in a different context. For example, promoting chlorophyll destruction would be detrimental in lettuce, (but it would be beneficial in the curing of tobacco), or it could be beneficial in the degreening of lemons, (but it would be detrimental in the storage of limes). Unless intentionally added to the storage environment to elicit a specific response, C_2H_4 is considered a contaminant and exposure should be minimized.

Detrimental effects are often caused by unintentional exposure of the harvested commodity to C_2H_4 (Table 7). Exposure of plants in the field and orchard is rare since normal levels of C_2H_4 in the atmosphere are exceedingly low and C_2H_4 is rapidly destroyed by soil microorganisms and solar radiation. Atmospheric pollution with C_2H_4 and its analogs is much more common when plants are grown or stored in confined spaces such as greenhouses, cold storage rooms, and packages.

Table 7
Detrimental effects of ethylene on the quality of fresh fruits and vegetables

Accelerates senescence.
Stimulates chlorophyll loss (e.g. yellowing).
Enhances excessive softening of fruits.
Stimulates sprouting of potato.
Promotes abscission of leaves and flowers.
Stimulates phenylpropanoid metabolism.
Promotes discoloration (e.g. browning).
Hastens toughening of vegetables.

5. Effects of ethylene on appearance

Consumers equate the visual appearance of fresh fruit and vegetables with quality. Ethylene enhances the appearance of many fruit by stimulating their ripening. Rapid development of the characteristic color can produce a higher quality fruit since less time will have elapsed from harvest for anabolic reactions to occur.

The skin of early season citrus fruit is still green when the flesh has become edible. Treatment with C_2H_4 accelerates chlorophyll degradation and the appearance of yellow or orange colors. A similar process occurs in bananas where C_2H_4 stimulates chlorophyll loss and the appearance of yellow color; however, C_2H_4 also promotes ripening of the pulp. One of the first commercial uses of C_2H_4 was to blanch or whiten celery by enhancing chlorophyll loss (Harvey, 1925). In other crops like apples and tomatoes, pigment synthesis is stimulated by C_2H_4, as is chlorophyll loss. Treatment of peppers (*Capsicum annuum*) plants with up to 2000-ppm ethephon when two fruit on the plant were completely colored, increased the percentage of ripe fruit by 30% compared with the control (Graifenberg and Giustiniani, 1980). Higher concentrations of ethephon reduced fruit quality (dry matter, sugar and vitamin C contents), but did not increase fruit coloration.

Removal of C_2H_4 or inhibition of its action can delay color changes in storage and prolong the storage life of selected commodities. However, other ripening parameters (e.g. softening, soluble solids, organic acids, and aroma and flavor) may be less inhibited so that while an acceptable appearance is maintained, other quality parameters may decrease to unacceptable levels. For example, exogenously applied C_2H_4 (100 μl l^{-1}) stimulated the ripening of papaya fruit (*Carica papaya*), as measured by rates of skin degreening and yellowing, carotenoid synthesis and flesh softening (An and Paull, 1990). However, ethylene was unable to completely ripen slightly immature papayas. The outer portion of the flesh ripened faster in C_2H_4 treated fruit compared with control fruit, while C_2H_4 had little promotive effect on the inner mesocarp tissue because it had already started to ripen. The coefficient of variation for skin color, flesh softening, and flesh color development was reduced in fruit treated with C_2H_4.

Ethylene affects other attributes that contribute to acceptable appearance. The sprouting of seeds on the exposed surface of slices of mature-green tomato fruit during their ripening ruined the appearance of this lightly processed product (Mencarelli and Saltveit, 1988). Exposure to C_2H_4 accelerated ripening while suppressing seed germination and radical elongation, and produces an acceptable product. The bright external appearance of fresh 'Mission' figs (*Ficus carica*) was maintained longer when stored in atmospheres enriched with the C_2H_4 antagonist CO_2 than in air (Colelli et al., 1991). Other C_2H_4 sensitive changes like fruit softening and C_2H_4 production were also reduced by the elevated CO_2 content. The appearance may also be effected by the ability of C_2H_4 to stimulate the growth of some decay-causing fungi on fruit and vegetables (El-Kazzaz et al., 1983.)

Another detrimental effect of C_2H_4 is on the yellowing of green stem and leafy vegetables. Ethylene from either endogenous production or exogenous application stimulated chlorophyll loss and the yellowing of harvested broccoli florets (Tian et al., 1994). Sensitivity to C_2H_4 increased with time after harvest, with 1 μl l^{-1} giving the maximum response in 3-day-old heads.

Russet spotting is a postharvest disorder of lettuce in which small brown sunken lesions appear on the leaf. It is caused by exposure to hormonal levels of C_2H_4 at storage temperatures around 5°C (Ke and Saltveit, 1988). Many biotic and abiotic stresses stimulate phenylpropanoid metabolism and the accumulation of phenolic compounds in lettuce (Ke and Saltveit, 1989b). However, even though the level of phenolics compounds is elevated in stressed lettuce, C_2H_4 is still essential for the browning reaction which is characteristic of russet spotting to occur (Ke and Saltveit, 1989a). Interestingly, when phenlyalanine ammonia lyase (PAL, the crucial enzyme in phenylpropanoid metabolism) is inhibited, the lesions still appear, but they do not turn brown (Peiser et al., 1998). Additional experiments are needed to further dissect the direct and indirect effects of C_2H_4 in this and other systems.

6. Effects of ethylene on texture

Apart from its beneficial effect on promoting tissue softening during fruit ripening, C_2H_4 detrimentally effects the texture by promoting unwanted softening in cucumbers and peppers, or toughening in asparagus, and sweetpotatoes. The firmness of many ripening fruit and vegetables decreases with C_2H_4 treatment. This is usually beneficial when associated with ripening (e.g. apricots, avocados, melons, pears and tomatoes), but if applied for too long, ripening can progress into senescence and the flesh can become too soft. The crisp texture of cucumbers and peppers is lost upon exposure to C_2H_4. Peaches become mealy and tomatoes become grainy if improperly treated with C_2H_4. Excessive flesh softening and maceration occurred within 3 days of exposure of watermelon to 5 μl l^{-1} C_2H_4 at 18°C (Risse and Hatton, 1982).

In asparagus, C_2H_4 exposure stimulates phenylpropanoind metabolism, accumulation of phenolic compounds and lignification of the tissue (Lipton, 1990). Inhibition of the shikimic acid pathway, which produces the substrates for lignin, by glyphosate reduces the toughening, fiber content, and lignification of stored asparagus spears (Saltveit, 1988). However, C_2H_4 exposure still stimulated senescence yellowing of the asparagus spears. Cucumbers exposed to C_2H_4 develop unacceptable textural attributes (Poenicke et al., 1977). Sweetpotatoes exposed to C_2H_4 during curing or storage develops hardcore; a condition in which the flesh becomes hard and inedible when cooked (Timbie and Haard, 1977).

Even quite low levels of C_2H_4 can affect fruit firmness. Kiwifruit are very sensitive to C_2H_4, and exposure to 30 ppb can cause unacceptable softening in storage. Removal of C_2H_4 from storage rooms, even from controlled atmosphere storage, can improve quality. Melons (*Cucumis melo*, cv. Galia) stored in a controlled atmosphere of 10% CO_2 plus 10% O_2 were firmer and exhibited less decay when an C_2H_4 absorbent was included in the storage room (Aharoni et al., 1993).

7. Effects of ethylene on taste and flavor

Ethylene biosynthesis rises prodigiously in ripening climacteric fruit and is thought to coordinate many ripening phenomena (Abeles et al., 1992). In general, C_2H_4 enhances taste and flavor by stimulating fruit ripening (Watada, 1986). However, total volatile development in tomatoes picked mature-green and ripened with C_2H_4 never attained the levels produced by fruit ripened on the plant (Stern et al., 1994). For example, the most important aroma compound (Z)-3-hexenal, was 31% and 17% higher in fruit ripened on the plant compared to fruit harvested mature-green and ripened with or without C_2H_4, respectively. In this case, as with the other 31 tomato volatiles measured in their study, total volatiles were 12% higher in ripe fruit that were harvested mature-green and treated with C_2H_4 than in those ripened without C_2H_4. In contrast, in a study of the effect of prestorage heat treatments on chilling tolerance of mature-green tomatoes, the level of six of the 15 flavor volatiles analyzed were significantly lower as a result of C_2H_4 treatment (McDonald et al., 1996). However, the effect of these reduced levels of aromatic compounds on taste and flavor were not assessed.

Ethylene treatment also increases the desirable aroma in honeydew melons, in addition to stimulating flesh softening and enhancing external color. However, application of ethephon 3 days before harvest reduced the soluble solids content and sucrose concentration, and the texture and flavor ratings of muskmelon fruit harvested at the full-slip stage (Yamaguchi et al., 1977). Although the fruit from the treated plants were more aromatic than fruit from untreated plants, they softened more rapidly during 5 days of storage at 20°C. Ethylene-treated carambola fruits had lower total soluble solids concentration, higher titratable acidity and pH, and a less preferred flavor and texture than control fruits (Miller and McDonald, 1997).

The sensory qualities of fruitiness, greenness and softness of banana were evaluated by a trained analytical sensory panel (Scriven et al., 1989). Banana fruit that were harvested mature-green and naturally ripened were considered more fruity, less green and softer than fruit ripened with the aid of C_2H_4 (Fig. 3). They concluded, as have other authors, that exogenous C_2H_4 caused the peel and flesh to ripen out of phase, with the flesh ripening faster than the peel. However, much of the applicability of this work has been negated by the adoption of cultivars that do not ripen without exogenous C_2H_4 exposure.

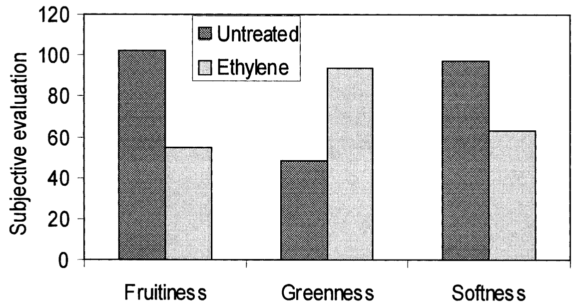

Fig. 3. Effect of ethylene treatment on the subjective quality of banana fruit harvested mature-green and left untreated or exposed to ethylene to promote ripening (redrawn from Scriven et al., 1989).

A similar observation that C_2H_4 exposure can cause differential stimulation in various parts of a fruit was made with persimmons. The astringency of persimmons is removed by treating the fruit with ethanol to reduce free tannins. Exposure to C_2H_4 after the ethanol treatment decreased tannin content and fruit firmness, and increased color, producing high-quality fruit in a shorter time (Kato, 1990). The ripening of C_2H_4-treated fruit was different from normal ripening in that softening preceded yellow or orange color development.

An untrained taste panel rated freshly harvested 'Starkrimson Red Delicious' apples that had internal C_2H_4 concentrations of 1.3–51 $\mu l\ l^{-1}$ higher in overall eating quality than fruit producing more or less C_2H_4 (Saltveit, 1983). These concentrations occurred in fruit a few days into their climacteric. In general, less mature fruit were rated superior to over-mature fruit. Interestingly, soluble solids measurements were generally high and not significantly correlated with taste panel acceptance in this 1-year study. In a later study, Blankenship and Unrath (1988) reported that the internal C_2H_4 concentration of 'Red Delicious' and 'Golden Delicious' apples was not a reliable indicator of fresh market maturity. Rather, a combination of fruit firmness, soluble solids and starch content were judged to be better indicators of minimal maturity. In their study, however, soluble solids were generally low and unexpectedly, internal C_2H_4 levels frequently did not rise into the climacteric range until after the fruit had been ranked acceptable. In a number of samples firmness decreased, soluble solids increased, and starch conversion was evident prior to the beginning of the C_2H_4 climacteric. Obviously, there may not only be differences among the ripening behavior of apples from different cultivars, growing locations and seasons, but also differences between taste panel evaluation of minimal market maturity and optimal eating quality.

The inhibition of C_2H_4 biosynthesis or action will inhibit not only ripening but also the production of characteristic aroma volatiles. A period of time is often needed after prolonged storage in which C_2H_4 action was suppressed in order for volatile production to return to normal and reestablish the characteristic aroma profile. When respiration and C_2H_4 production are greatly reduced, as they were during the storage of 'McIntosh' apples (*Malus domestica*.) for 9 months at 3.3°C under a low-C_2H_4 controlled atmosphere, the production of many odor-active volatiles are greatly diminished (Yahia, 1991). Subsequent storage in air at 20°C was necessary to significantly increased the production of the odor volatiles, but conditions that did not stimulate respiration and C_2H_4 production (e.g. air at 3.3°C for up to 4 weeks) were ineffective in enhancing volatile formation.

Ethylene is also produced in copious amounts by diseased and injured tissue and mediates the defense responses of stressed tissue (Ecker and Davis, 1987; Abeles et al., 1992). In a possible defense response, carrot and parsnip roots synthesize bitter tasting phenolic compounds when exposed to C_2H_4 in storage. Parsnip roots exposed to ~ 5 μl l^{-1} C_2H_4 for 68 days at 1°C developed higher concentrations of total phenolic compounds than air stored roots and a bitter off-flavor when cooked (Shattuck et al., 1988). In a more detailed study of the induction of the antimicrobial compound isocoumarin in carrots, Lafuente et al. (1996) found that the more rapid the respiratory rise was in response to C_2H_4, the more rapidly isocoumarin (8-hydroxy-3-methyl-6-methoxy-3,4-dihydro-isocoumarin) accumulated and the greater the respiratory response to C_2H_4 was, the higher the level of isocoumarin formed. Exposing mature carrots to 0.5 μl l^{-1} C_2H_4 for 14 days at 5°C resulted in isocoumarin contents of 40 mg/100 g peel, a level easily detected as a bitter flavor in the intact carrot. Immature carrots formed higher levels of isocoumarin than mature carrots; 180 mg/100 g peel, while freshly harvested carrots accumulated four-fold higher levels than those stored before exposure to C_2H_4. Isocoumarin levels were halved when the C_2H_4 treatments were given in 1% oxygen. Sliced, cut or dropped carrots exposed to C_2H_4 showed greater rates of isocoumarin accumulation than intact, uninjured carrots.

This enhanced level of C_2H_4 sensitivity has also been noted in mechanically wounded lettuce and sweetpotatoes. Cutting stimulates phenylpropanoid metabolism in lettuce leaves and transforms leaves from russet spot-resistant cultivars into leaves very sensitive to the inducing effects of C_2H_4 (Ke and Saltveit, 1989b). Immersion of sweetpotato roots in ethephon before bedding significantly increased the total number of transplants produced (Hall, 1990). In this case, combining the ethephon treatment with cutting or presprouting whole roots further increased the total number of plants produced.

The vast majority of isocoumarin (a.k.a. 6-methoxymellein) is synthesized in the outer layers of the peel (Mercier et al., 1994). The concentration of 6-methoxymellein in the peel of UV-treated roots was ~ 200 mg/100 g tissue, while the concentration in the pulp was ~ 0.8 mg/100 g tissue. This may account for the interesting observation that peeled 'baby' carrots in which the peel had been abrasively removed had little capacity to form isocoumarin (Lafuente et al., 1996). Isocoumarin accumulation in the pulp of 'baby' carrots was less than 20 mg/100 g tissue after 20 days exposure to 0.5 μl l^{-1} C_2H_4 in air, while the pulp of whole roots contained ~ 30 mg/100 g tissue and 5-cm long root pieces contained over 120 mg/100 g tissue (Fig. 4). Induction of isocoumarin to ward off diseases during storage is certainly untenable for fresh market carrot roots, but it may have application for carrot products in which the peel is removed.

Exposure to ~ 4 μl l^{-1} C_2H_4 caused large increases in the trim loss of Brussels sprouts and cabbage (Toivonen et al., 1982). Market quality was reduced in cabbage exposed to 10 or 100 μl l^{-1} C_2H_4 at 1°C for 5 weeks (Pendergrass et al., 1976). External green color was lost and there was extensive leaf abscission. Controlled atmosphere stored cabbages were in better condition and had lower trim loss than air-stored heads after 5 months, but high levels of C_2H_4 were associated with development of bitter flavor which was reduced by scrubbing C_2H_4 from the controlled atmosphere (Toivonen et al., 1982). Off-flavors did not develop during controlled atmosphere storage of celery, cauliflower or broccoli, and the produce remained in excellent condition in spite of high concentrations of C_2H_4 in the atmosphere.

8. Effects of ethylene on nutritive value

8.1. Vitamin C

The average content of ascorbic acid in ripe tomatoes for fruit harvested mature-green and red-rip were not significantly different (Watada et al., 1976). Variations in ascorbic acid content were large, with differences among the cultivars greater than between ripe fruit harvested as mature-green or red-ripe. The ascorbic acid content of fruit harvested mature-green and ripened with the aid of C_2H_4 was higher than for untreated fruit. However, this effect was not consistent among fruit from different growers or fruit harvested at different times of the year. The content of vitamin C was significantly higher in papaya fruit ripened with the aid of C_2H_4, than in controls left to ripen on their own (Bal et al., 1992). In both cases, the effect of C_2H_4 was not directly on ascorbic acid, which decreases with ripening, but on a stimulation of the other ripening parameters so the fruit ripened quicker and there was less time for the loss of ascorbic acid.

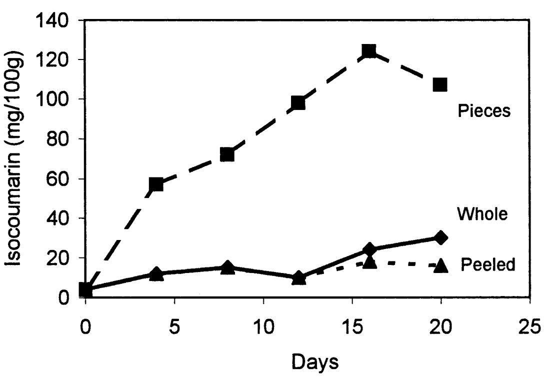

Fig. 4. Isocoumarin levels in the pulp of immature whole roots, roots cut in 5-cm pieces, or peeled cut pieces during storage at 5°C in 0.5 μl l^{-1} ethylene in air (redrawn from Lafuente et al., 1996).

Ethylene can also enhance other quality attributes without adversely affecting vitamin C content. Ethephon treatment increased the quality of mung bean (*Vigna mungo*) sprouts (i.e. they had shorter roots and hypocotyls and larger diameter hypocotyls) without significantly effecting vitamin C content (Ahmad and Abdullah, 1993).

8.2. Vitamin A

The β-carotene (provitamin A) content of ripe tomatoes varied directly with the ripeness of the fruit at harvest (Watada et al., 1976). However, the differences in vitamin A content were greater among the cultivars than among the ripeness stages at harvest. Vitamin A activity was not affected by C_2H_4, but was again slightly higher in ripe fruit that had been harvested ripe than those harvested mature-green. However, fruit harvested mature-green or breaker, the stages at which most fresh market tomatoes are harvested, did not differ in vitamin A activity among the cultivars tested.

9. Summary

A better understanding of C_2H_4 synthesis, perception and action should allow the development of postharvest strategies to enhance the beneficial effects and mitigate the detrimental effects of C_2H_4 on the quality of fresh fruits and vegetables.

But it should be kept in mind that many so-called detrimental effects of C_2H_4 are simply responses that are unwanted in certain situations, but which are beneficial in others. Their alteration should not be global, but confined to specific stages of development, responses to specific situations, or to specific tissues. Molecular biology and genetic engineering may be able to dissect the biochemistry and physiology of ethylene and to produce fresh fruit and vegetables with specifically designed responses to ethylene. However, quality depends on a number of criteria, not just a few easily manipulated genetic traits. Many of these quality criteria (e.g. taste) are only fully expressed when there is a coordinated interplay among their various components. Traditional evaluation of these quality criteria in new cultivars and postharvest practices will remain absolutely essential to provide consumers with quality fresh fruit and vegetables. Consumers are already redefining quality to include nutritive as wells as visual and organoleptic criteria. Cultivars and postharvest treatments which only maintain superficial appearance at the expense of hidden, but increasingly important criteria, will be replaced by cultivars and technology which maintains a greater level and number of quality attributes.

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