Ethylene-induced Senescence and Physiological Disorders in Harvested Horticultural Crops

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Ethylene plays a major role in plant senescence via its direct and indirect effects on the regulation of metabolism. The known physiological and biochemical effects of C_2H_4 on harvested horticultural crops include increased respiratory activity; increased activity of enzymes such as polygalacturonase, peroxidase, lipoxidase, alpha-amylase, polyphenol oxidase, and phenylalanine ammonialyase (PAL); increased permeability and loss of cell compartmentalization; and alteration of auxin transport or metabolism (34). Nevertheless, the mechanism by which C_2H_4 promotes senescence remains unknown. Lieberman (21) stated that the action of C_2H_4 in accelerating senescence can be associated with interactions with auxins, gibberellins, cytokinins, and abscisic acid (ABA). The mechanisms involved in these interrelationships are not fully understood, but there is evidence to suggest that a general antagonism exists between the senescence promoters (C_2H_4 and ABA) and the senescence inhibitors (auxins, gibberellins, and cytokinins).

The promotion of senescence in harvested horticultural crops by C_2H_4 results in acceleration of deterioration and consequent abbreviation of postharvest life. The objective of this paper is to review briefly C_2H_4 effects on quality attributes, physiological disorders, and postharvest diseases of horticultural commodities. Emphasis is placed on information reported since Abeles' review of the role of ethylene in plant biology in 1973 (1).

Ethylene effects on quality attributes

Loss of green color. Ethylene accelerates chlorophyll degradation and induces yellowing of green tissues, thus reducing market quality of leafy, floral, and immature-fruit vegetables and foliage ornamentals. Exposure of cabbage to 10 or 100 ppm C_2H_4 during holding at 1°C for 5 weeks resulted in loss of greeness and extensive leaf abscission (32), but loss of greenness in cabbage can occur at even lower C_2H_4 levels (1 to 5 ppm) in some cultivars (15, 16). Toivonen et al. (47) reported that 4 ppm C_2H_4 increased the rates of deterioration and yellowing in cabbage, brussels sprouts, broccoli, and cauliflower kept in air at 1°C. Wang (48) concluded that senescence of broccoli is related to C_2H_4 production and effects. Olorunda and Looney (31) observed that 'Acorn' squash stored at 15° or 20° with 5 ppm C_2H_4 underwent visible degreening of peel and flesh tissues. Ethylene treatments at 0.1 to 10 ppm decreased cucumber fruit chlorophyll content and induced loss of firmness at 5 and 10 ppm (33).

Abscission. Ethylene induces abscission of leaves of cabbage, Chinese cabbage, cauliflower, and foliage plants, florets of broccoli and cut flowers, and calyces of eggplant. Exposure of eggplants to 0.8 ppm or higher concentrations of C_2H_4 for 2 days caused stem and calyx abscission, and stimulated *Botrytis cinerea* infection so that rotting was extensive after 8 days (42). Sigrist (44) found that exposure of eggplants to 1 or 10 ppm C_2H_4 for 2 days at 20°C reduced their storage-life to about 33% or 25% of that of control fruit, respectively. Symptoms of C_2H_4 damage were rapid deterioration of the calyces, calyx abscission, browning of the pulp and seeds, and accelerated decay of the fruit.

Texture. Softening of fruit exposed to C_2H_4 can reduce their storage-life shipping ability. Exposing watermelons to 5, 30, or 60 ppm C_2H_4 reduced firmness and rind thickness, accelerated deterioration, and reduced acceptability after 3 days at 18°C (38). Shimokawa (43) reported that C_2H_4 increased the activities of pectinase, cellulase, esterase, polyphenol oxidase, and peroxidase and caused tissue maceration in watermelons. Ethylene applied to fresh sweet potato roots resulted in reduced firmness after cooking, but had adverse effects on flavor and color (7).

Exposure of asparagus spears to 100 ppm C_2H_4 for 1 hr increased spear toughness, which was associated with increased activity of peroxidase isozymes and accelerated lignin biosynthesis (13). Ethylene also has been shown to stimulate PAL activity and increase lignin biosynthesis in Swedish turnip (rutabaga) roots (37).

Flavor. Ethylene promotes changes which are important to flavor quality such as starch to sugar conversion, loss of acidity, and formation of aroma volatiles in climacteric fruit (34). On the other hand, C_2H_4 can induce undesirable flavors in sweet potatoes (7) and carrots (8, 41). Bitter flavor in carrots has been associated with C_2H_4-induced isocoumarin formation (8). Sarkar and Phan (41) reported that C_2H_4 caused an increase in the total phenol content of carrots and induced formation of new compounds, including isocoumarin and eugenin. Exposure to 100 ppm C_2H_4 during controlled atmosphere (CA) storage was assoiated with development of a bitter flavor in cabbage (47).

Sprouting of potatoes. Sprouting is promoted by short (up to 72 hr) exposures to 2 ppm C_2H_4 (39). Ethylene exerts a dual effect on potato tubers: it shortens the duration of rest markedly, but inhibits elongation of the sprouts. Although these effects are desirable for seed potatoes, they are undesirable for table and processing potatoes. Ethylene also causes a rapid increase in the respiration rate of potato tubers (36, 39).

Black spot in potatoes. Timm et al. (46) found that the severity of black spot in potatoes, in most instances, was lowered by exposure to C_2H_4 for 24 to 48 hr. Ethylene did not prevent black spot development after bruising, but it reduced the area of tissue showing visible damage. Ethylene induced healthy cells to develop callus rapidly around injured cells, confining the area of damaged tissue.

Physiological disorders induced by ethylene

Ethylene has been implicated in several postharvest physiological disorders of horticultural crops. The incidence and severity of these disorders depend upon the physiological age of the commodity, temperature, C_2H_4 concentration, and duration of exposure to C_2H_4.

Russet spotting of lettuce. Ethylene is the primary factor determining the incidence and severity of russet spotting (RS) on lettuce; 0.1 ppm C_2H_4 is sufficient to cause commercially important damage during a normal transit period of 5–8 days at 5°C (20, 30). RS produces well-defined, localized, spot-like lesions that may start either in the epidermis or in the mesophyll. In advanced stages of RS, the vascular tissue may show discoloration, and the mesophyll cells collapse, resulting in pit-like depressions (18). Ilker et al. (18) observed thickening of the cell walls and granulation of the cytoplasm in C_2H_4-treated lettuce tissue. Hyodo et al. (17) found a close relationship among increased PAL activity, content of phenolic compounds, and development of RS in lettuce tissue.

Physiological disorders of cut flowers. The effects of C_2H_4 on flower longevity were reviewed recently by Halevy and Mayak (14). They reported that C_2H_4 causes inrolling of petals, fading, wilting, and abscission of many flowers. Ethylene at about 0.5 ppm or higher induced "sleepiness" (closure of open flowers) in carnations (28) and *Kalanchoe blossfeldiana* (25); "sleepy" flowers or florets failed to reopen. Extensive research on carnations aimed at understanding the mechanism of C_2H_4 action has revealed many physical, anatomical, and biochemical changes (14), but the sequence of events leading to senescence of cut flowers is still unknown.

Physiological disorders of flowering bulbs. Kamerbeek and DeMunk (19) reviewed C_2H_4 effects in bulbous plants and listed the following responses to C_2H_4 at 0.1 ppm or higher:

- Inhibition of shoot and root elongation in several bulb species.
- Induction of physiological disorders, such as gummosis, bud necrosis, and flower-bud blasting in tulips.
- Promotion of flower-bud abscission in lily and leaf abscission in hyacinth.
- An increase in the respiration rates of iris and tulip bulbs that was proportional to C_2H_4 concentration. Prince et al. (35) reported that storage of tulip bulbs for 3 weeks in air with 5 ppm C_2H_4 caused flower abortion upon forcing; abnormal flowers had dried, papery petals.

Physiological disorders of nursery stock. Exposure of dormant nursery stock to C_2H_4 may cause injury, with symptoms of damage not appearing until several days to weeks after planting. As little as 1 ppm C_2H_4 during cold storage damaged dormant apple and pear trees (9). Meadows and Richardson (29) found greater cane mortality and less budbreak in rose plants which had been exposed to C_2H_4 when dormant and in storage at 0° or 5°C than in those kept in C_2H_4-free air. The extent of the injury was greater at 5° and increased with C_2H_4 concentration. Geranium seedlings exposed to C_2H_4 for 2 days developed more chlorotic leaves and did not grow as well as seedlings kept in air (26).

Physiological disorders of ornamental plants. Ethylene induces epinastic responses (downward curvature of leaves) in many plant species (1). However, plants recover normal appearance in 3 to 5 days after C_2H_4 is removed from the environment. Mechanical stress has been shown to induce C_2H_4 production and epinasty in poinsettia cultivars (40). Marousky and Harbaugh (27) held various flowering and foliage plants in light for 3 days at 23.5°C in chambers ventilated with air contianing 0, 1, 5, or 10 ppm C_2H_4. They found that exposure of most foliage plants to 5 or 10 ppm C_2H_4 caused leaf abscission, chlorosis, and epinasty. Most flowering plants exposed to 1 ppm C_2H_4 or higher exhibited flower abscission or flower closure (sleepiness or wilting).

Physiological disorders induced by C_2H_4 + CO_2

Arpaia et al. (2) found that the presence of C_2H_4 as low as 50 ppb under CA conditions can negate the benefits of CA storage at 0°C on kiwifruits (*Actinidia chinensis* Planch.) by enhancing flesh softening and altering the internal appearance of the fruit. The incidence and severity of white inclusions (containing large amounts of starch granules) in the fruit core resulted from an interaction between CO_2 and C_2H_4.

Physiological disorders aggravated or alleviated by C_2H_4

Ethylene at 10 ppm increased the severity of rusty-brown discoloration and CO_2-induced brown stain on lettuce (Kader et al., unpublished data). Liu (23) reported that 'Delicious' apples stored for 7 months in CA with 10 or 500 ppm C_2H_4 developed severe scald, but those kept in CA with <10 ppm C_2H_4 did not.

Ethylene alleviates some of the chilling injury symptoms on certain commodities. For example, exposure of sweet potatoes to C_2H_4 during the postchilling period did not reduce the incidence of hardcore but significantly reduced its severity. This effect may have been related to the observed stimulation of pectin methylesterase activity (6). Lipton and Aharoni (22) reported that treating 'Honey Dew' muskmelons at 20°C with 1000 ppm C_2H_4 for 24 hr before storage at 2.5° for 2.5 weeks reduced the incidence of chilling injury by about 75%.

Ethylene effects on postharvest diseases

The effects of C_2H_4 on fungal growth and disease development on harvested horticultural commodites are still unclear. Ethylene was found to stimulate rot development by some fungi, e.g., diplodia stem-end rot (*Diplodia natalensis* Pole-Evans), on citrus fruit in Florida (3, 5). This may have been due to accelerated growth of the fungus and/or increased susceptibility of fruit tissue to hyphal penetration. El-Kazzaz et al. (11) reported that the presence of 20 ppm C_2H_4 in the storage atmosphere enhanced growth of *Botrytis cinerea* Pehs, ex Fr. and disease development on strawberries. Exposure of 10 postharvest fruit-infecting fungi, in vitro, to C_2H_4 at 1, 10, 100, and 1,000 ppm stimulated germ tube elongation but had little effect on their final growth rate, as determined by colony diameter at 20°C (12). But, when glucosamine content was determined as an indicator of fungal dry weight, C_2H_4 was shown to stimulate growth of *Botrytis cinerea* Pers. ex Fr. and *Penicillium italicum* Wehmer, in vitro and in vivo on strawberries and oranges, respectively (12).

In contrast, C_2H_4 has been shown to induce resistance to certain pathogens in some harvested plant organs. Sweet potato slices exposed to 8 ppm C_2H_4 for 2 days became more resistant to infection by *Ceratocystis fimbriata* Ell. and Halst. The increased resistance was accompanied by an increase in peroxidase and polyphenol oxidase activities (45). Lockhart et al. (24) found that C_2H_4 treatment inhibited development of apple rot caused by *Gloeosporium album* Osterw. Florida 'Robinson' tangerines exhibited resistance to *Colletotrichum gloeosporioides* (Penz.) Arx that were treated with C_2H_4 for 3 days before inoculation, and then were exposed to additional C_2H_4 to complete degreening (5). Ethylene-treated tangerines accumulated more phenolic compounds and were more intensely lignified than untreated fruit (4). However, Brown and Barmore (5) reported that resistance in orange-colored tangerines was broken down by subjecting them to 100 ppm C_2H_4 for 76 hr. In contrast, El-Kazzaz et al. (10) found that California oranges developed more resistance to *Penicillium italicum* when exposed to 1000 ppm C_2H_4 for 5 or 6 days than at lower C_2H_4 concentrations or shorter treatment durations.

Both the direct stimulatory effects of C_2H_4 on postharvest fruit fungi and the indirect inhibitory effects via possible modifications of the host's metabolism have practical implications in the postharvest biology of fresh horticultural crops. Additional research is needed to evaluate the potential benefits of avoiding exposure to C_2H_4 on rate of rot development. The possible use of C_2H_4 treatment to induce disease resistance in the commodity and the biochemical basis of this response also merit further investigation.

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