16. Kopeliovitch, E., Y. Mizrahi, H.D. Rabinowitch, and N. Kedar. 1980. Physiology of the tomato mutant alcobaca. Physiol. Plant. 48:307–311.
17. Lieberman, M. 1979. Biosynthesis and action of ethylene. Ann. Rev. Plant Physiol. 30:533–591.
18. Lobo M., J.J. Augustine, and L.C. Hannah. 1981. Alcobaca tomato ripening mutant, p. 86–96. In: Proc. 3rd Tomato Quality Workshop, Univ. of Maryland, College Park.
19. Lyons, J.M. and H.K. Pratt. 1964. Effect of stage of maturity and ethylene treatment on respiration of tomato fruits. Proc. Amer. Soc. Hort. Sci. 84:491–500.
20. McGlasson, W.B. 1978. Role of hormones in ripening and senescence, p. 77–96. In: H.O. Hultin and M. Milner (eds.). Postharvest biology and biotechnology. Food & Nutr. Press, Westport, Conn.
21. McGlasson, W.B. and I. Adato. 1977. Relationship between the capacity to ripen and ontogeny in tomato fruits. Austral. J. Plant Physiol. 4:451–458.
22. McGlasson, W.B., H.C. Dostal, and E.C. Tigchelaar. 1975. Comparison of propylene-induced responses of immature fruit of normal and *rin* mutant tomatoes. Plant Physiol. 55:218–222.
23. McGlasson, W.B. and T.H. Lee. 1971. Damage and repair of protein in gamma irradiated tomato fruit. Radiat. Bot. 11:239–241.
24. McGlasson, W.B. and H.K. Pratt. 1964. Effects of ethylene on cantaloupe fruits harvested at various ages. Plant Physiol. 39:120–127.
25. McGlasson, W.B., N.L. Wade, and I. Adato. 1978. Phytohormones and fruit ripening, vol 2, p. 447–493. In: D.S. Letham, P.B. Goodwin and T.J.V. Higgins (eds.). Phytohormones and related compounds—a comprehensive treatise. Elsevier, Amsterdam.
26. McGlasson, W.B. and R.B.H. Wills. 1972. Effects of oxygen and carbon dioxide on respiration, storage life, and organic acids of green bananas. Austral. J. Biol. Sci. 25:35–42.
27. McMurchie, E.J., W.B. McGlasson, and I.L. Eaks. 1972. Treatment of fruit with propylene gives information about the biogenesis of ethylene. Nature (London) 237:235–236.
28. Mizrahi, J., R. Zohar, and S. Malis-Arad. 1982. Effect of sodium chloride on fruit ripening of the non ripening tomato mutants *nor* and *rin*. Plant Physiol. 69:497–501.
29. Ness, P.J. and R.J. Romani. 1980. Effects of aminoethoxyvinylglycine and counter effects of ethylene on ripening of 'Bartlett' pear fruits. Plant Physiol. 65:372–376.
30. Patil, S.S. and C. Tang. 1974. Inhibition of ethylene evolution in papaya pulp tissue by benzyl isothiocyanate. Plant Physiol. 53:585–588.
31. Romani, R., R. Putschmann, J. Finch, and J. Beutel. 1982. Effects of preharvest applications of AVG on ripening of 'Bartlett' pears with and without cold storage. HortScience 17(2):214–215.
32. Sakai, S. and H. Imaseki. 1973. Properties of the proteinaceous inhibitor of ethylene synthesis. Action on ethylene production and indoleacetylaspartate formation. Plant Cell Physiol. 14:881–892.
33. Saltveit, M.E., K.J. Bradford, and D.R. Dilley. 1978. Silver ion inhibits ethylene synthesis and action in ripening fruits. J. Amer. Soc. Hort. Sci. 103(4):472–475.
34. Saltveit, M.E. 1980. Effect of vitamin K5 and menadione on ripening, and ethylene and carbon dioxide production by apple and tomato fruit. J. Amer. Soc. Hort. Sci. 105(2):252–256.
35. Simpson, D.J., M.R. Baqar, W.B. McGlasson, and T.H. Lee. 1976. Changes in ultrastructure and pigment content during development and senescence of fruits of normal and *rin* and *nor* mutant tomatoes. Austral. J. Plant Physiol. 3:575–587.
36. Sisler, E.C. 1982. Ethylene binding in normal, *rin*, and *nor* mutant tomatoes. J. Plant Growth Regul. 1:219–226.
37. Su, L., T. McKeon, D. Grierson, M. Cantwell, and S.F. Yang. 1983. Development of 1-aminocyclopropane-1-carboxylic acid (ACC) synthase and polygalacturonase (PG) activities during the maturation and ripening of tomato fruits in relation to their ethylene production rates. Plant Physiol 72:206. (Suppl.)
38. Takata, M. 1981. Effect of silver ions on the ripening of Japanese persimmon fruits. J. Japan. Soc. Hort. Sci. 50:372–378.
39. Tang, C. 1971. Benzyl isothiocyanate of papaya fruit. Phytochemistry 10:117–121.
40. Tigchelaar, E.C., W.B. McGlasson, and R.W. Buescher. 1978. Genetic regulation of tomato fruit ripening. HortScience 13(5):508–513.
41. Tigchelaar, E.C., W.B. McGlasson, and M.J. Franklin. 1978. Natural and ethephon-stimulated ripening of F1 hybrids or ripening inhibitor (*rin*) and non-ripening (*nor*) mutants of tomato (*Lycopersicon esculentum* Mill.). Austral. J. Plant Physiol. 5:449–456.
42. Trewavas, A.J. 1982. Growth substance sensitivity: The limiting factor in plant development. Physiol. Plant. 55:60–72.
43. Yang, S.F. 1981. Biosynthesis of ethylene and its regulation, p. 91–106. In: J. Friend and M.J.C. Rhodes (eds.). Recent advances in the biochemistry of fruit and vegetables. Academic Press, London.

Ethylene-induced Senescence and Physiological Disorders in Harvested Horticultural Crops

Adel A. Kader
Department of Pomology, University of California Davis, CA, 95616

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.

Literature Cited

1. Abeles, F.B. 1973. Ethylene in plant biology. Academic Press, N.Y.
2. Arpaia, M.L., F.G. Mitchell, A.A. Kader, and G. Mayer. 1982. The ethylene problem in modified atmosphere storage of kiwifruit, p. 331–335. In: D.G. Richardson and M. Meheriuk (eds.). Controlled atmospheres for storage and transport of perishable agricultural commodities. Timber Press, Beaverton, Ore.
3. Barmore, C.R. and G.E. Brown. Effect of ethylene on stem-end rot (*Diplodia natalensis*) of citrus fruit. HortScience 18(4):563. (Abstr.)
4. Brown, G.E. 1978. Hypersensitive response of orange-colored tangerines to *Colletotrichum gloeosporioides* after ethylene treatment. Phytopathology 68:700–706.
5. Brown, G.E. and C.R. Barmore. 1977. The effect of ethylene on susceptibility of 'Robinson' tangerines to anthracnose. Phytopathology 67:120–123.
6. Buescher, R.W. 1977. Hardcore in sweet potato roots as influenced by cultivar, curing, and ethylene. HortScience 12(4):326–327.
7. Buescher, R.W., W.A. Sistrunk, and P.L. Brady. 1975. Effects of ethylene on metabolic and quality attributes in sweet potato roots. J. Food Sci. 40:1018–1020.
8. Chalutz, E., J.E. DeVay, and E.C. Maxie. 1969. Ethylene-induced isocoumarin formation in carrot root tissue. Plant Physiol. 44:235–241.
9. DeClement, R., J.L. Frecon, and N.F. Childers. 1979. Ethylene gas damages fruit stock. Amer. Nurserym. 149(2):12,72,74,78.
10. El-Kazzaz, M.K., A. Chordas, and A.A. Kader. 1983. Physicological and compositional changes in orange fruit in relation to modification of their susceptibility to *Penicillium italicum* by ethylene treatments. J. Amer. Soc. Hort. Sci. 108(4):618–621.
11. El-Kazzaz, M.K., N.F. Sommer, and R.J. Fortlage. 1983. Effect of different atmospheres on postharvest decay and quality of fresh strawberries. Phytopathology 73:282–285.
12. El-Kazzaz, M.K., N.F. Sommer, and A.A. Kader. 1983. Ethylene effects on *in vitro* and *in vivo* growth of certain postharvest fruit-infecting fungi. Phytopathology 73:998–1001.
13. Haard, N.F., S.C. Sharma, R. Wolfe, and C. Frenkel. 1974. Ethylene induced isoperoxidase changes during fiber formation in postharvest asparagus. J. Food Sci. 39:452–456.
14. Halevy, A.H. and S. Mayak. 1981. Senescence and postharvest physiology of cut flowers—part 2. Hort. Rev. 3:59–143.
15. Hicks, J.R. and P.M. Ludford. 1981. Effects of low ethylene levels on storage of cabbage. Acta Hort. 116:65–73.
16. Hicks, J.R., P.M. Ludford, and J.F. Masters. 1982. Effects of atmosphere and ethylene on cabbage metabolism during storage, p. 309–316. In: D.G. Richardson and M. Meheriuk (eds.). Controlled atmospheres for storage and transport of perishable agricultural commodities. Timber Press, Beaverton, Ore.
17. Hyodo, H., H. Kuroda, and S.F. Yang. 1978. Induction of phenylalanine ammonia-lyase and increase in phenolics in lettuce leaves in relation to the development of russet spotting caused by ethylene. Plant Physiol. 62:31–35.
18. Iiker, Y., A.A. Kader, R. Ilker, and L.L. Morris. 1977. Anatomy of lettuce tissue affected by three physiological disorders. J. Amer. Soc. Hort. Sci. 102(4):426–428.
19. Kamerbeek, G.A. and W.J. DeMunk. 1976. A review of ethylene effects in bulbous plants. Scientia Hort. 4:101–115.
20. Klaustermeyer, J.A., L.L. Morris, and A.A. Kader. 1974. Some factors affecting the occurrence and severity of russet spotting in harvested lettuce. HortScience 9(3):274. (Abstr.)
21. Lieberman, M. 1979. Biosynthesis and action of ethylene. Annu. Rev. Plant Physiol. 30:533–591.
22. Lipton, W.J. and Y. Aharoni. 1979. Chilling injury and ripening of 'Honey Dew' muskmelons stored at 2.5° or 5°C after ethylene treatment at 20°C. J. Amer. Soc. Hort. Sci. 104(3):327–330.
23. Liu, F.W. 1977. Varietal and maturity differences of apples in response to ethylene in controlled atmosphere storage. J. Amer. Soc. Hort. Sci. 102(1):93–95.
24. Lockhart, C.L., F.R. Forsyth, and C.A. Eaves. 1968. Effect of ethylene on development of *Gloeosporium album* in apple and on growth of the fungus in culture. Can. J. Plant Sci. 48:557–559.
25. Marousky, F.J. and B.K. Harbaugh. 1979. Ethylene-induced floret sleepiness in *Kalanchoe blossfeldiana* Poelln. HortScience 14(4):505–507.
26. Marousky, F.J. and B.K. Harbaugh. 1981. Influence of temperature, light, and ethylene on seedlings of geranium (*Pelargonium* × *hortorum* Bailey) during simulated shipping conditions. J. Amer. Soc. Hort. Sci. 106(5):527–530.
27. Marousky, F.J. and B.K. Harbaugh. 1982. Responses of certain flowering and foliage plants to exogenous ethylene. Proc. Fla. State Hort. Soc. 95:159–162.
28. Maxie, E.C., D.S. Farnham, F,G. Mitchell, N.F. Sommer, R.A. Parsons, R.G. Snyder, and H.L. Rae. 1973. Temperature and ethylene effects on cut flowers of carnation (*Dianthus carophyllus* L.). J. Amer. Soc. Hort. Sci. 98(6):568–572.
29. Meadows, S.E. and D.G. Richardson. 1983. Interactive effects of ethylene concentration and storage temperature on budbreak and viability of dormat 'Viva' roses. HortScience 18(4):453–454.
30. Morris, L.L., A.A. Kader, J.A. Klaustermeyer, and C.C. Cheyney. 1978. Avoiding ethylene concentrations in harvested lettuce. Calif. Agr. 32(6):14–15.
31. Olorunda, A.O. and N.E. Looney. 1977. Response of squash to ethylene and chilling injury. Ann. Appl. Biol. 87:465–469.
32. Pendergrass, A., F.M.R. Isenberg, L.L. Howell, and J.E. Carroll. 1976. Ethylene-induced changes in appearance and hormone content of Florida-grown cabbage. Can. J. Plant Sci. 56:319–324.
33. Poenicke, E.F., S.J. Kays, D.A. Smittle, and R.E. Williamson. 1977. Ethylene in relation to postharvest quality deterioration in processing cucumbers. J. Amer. Soc. Hort. Sci. 102(3):303–306.
34. Pratt, H.K. and J.D. Goeschl. 1969. Physiological roles in ethylene in plants. Annu. Rev. Plant Physiol. 20:541–584.
35. Prince, T.A., R.C. Herner, and A.A. Dettertogh. 1981. Low oxygen storage of specially precooled 'Kees Nelis' and 'Prominence' tulip bulbs. J. Amer. Soc. Hort. Sci. 106(6):747–751.
36. Reid, M.S. and H.K. Pratt. 1972. Effects of ethylene on potato tuber respiration. Plant Physiol. 49:252–255.
37. Rhodes, M.J.C. and L.S.C. Wooltorton. 1973. Changes in phenolic acid and lignin biosynthesis in response to treatment of root tissue of the Swedish turnip (*Brassica napo-brassica*) with ethylene. Qual. Plant. 23:145–155.
38. Risse, L.A. and T.T. Hatton. 1982. Sensitivity of watermelons to ethylene during storage. HortScience 17(6):946–948.
39. Rylski, I., L. Rappaport, and H.K. Pratt. 1974. Dual effects of eth-

ylene on potato dormancy and sprout growth. Plant Physiol. 53:658–662.
40. Saltveit, M.E., Jr., D.M. Pharr, and R.A. Larson. 1979. Mechanical stress induces ethylene production and epinasty in poinsettia cultivars. J. Amer. Soc. Hort. Sci. 104(4):452–455.
41. Sarkar, S.K. and C.T. Phan. 1979. Naturally-occurring and ethylene-induced phenolic compounds in the carrot root. J. Food Prot. 42:526–534.
42. Schouten, S.P. and H.W. Stork. 1977. Ethylene damage in eggplants. Do not keep with tomatoes! Groenten en Fruit 32:1688–1689.
43. Shimokawa, K. 1973. Maceration of watermelon by ethylene evolved by the 'Prince' melon. Bul. Fac. Agr., Miyazaki Univ. 20:365–375.
44. Sigrist, J.M. 1981. Physiological studies of harvested eggplant, *Solanum melongena* L. MS Thesis, Univ. of California, Davis.
45. Stahmann, M.A., B.G. Clare, and W. Woodbury. 1966. Increased disease resistance and enzyme activity induced by ethylene and ethylene production by black rot-infected sweet potato tissue. Plant Physiol. 41:1505–1512.
46. Timm, H., M. Yamaguchi, D.L. Hughes, and M.L. Weaver. 1976. Influence of ethylene on black spot of potato tubers. Amer. Potato J. 53:49–56.
47. Toivonen, P., J. Walsh, E.C. Lougheed, and D.P. Murr. 1982. Ethylene relationships in storage of some vegetables, p. 299–307. In: D.G. Richardson and M. Meheriuk (eds.). Controlled atmospheres for storage and transport of perishable agricultural commodities. Timber Press, Beaverton, Ore.
48. Wang, C.Y. 1977. Effect of aminoethoxy analog of rhizobitoxine and sodium benzoate on senescence of broccoli. HortScience 12(1):54–56.

Control of Ethylene in the Postharvest Environment

Mark Sherman
Vegetable Crops Department, Institute of Food and Agricultural Sciences, University of Florida, Gainesville, FL 32611

The beneficial and harmful effects of ethylene (C_2H_4) on harvested horticultural products are well documented. The purpose of this presentation is to outline the technologies currently available in commercial horticulture for both the application of C_2H_4 to harvested horticultural crops, and the protection of these crops from the undesirable effects of C_2H_4. The research base for this topic cuts across many areas of considerable postharvest research, including temperature effects, atmospheric modification, and regulation of C_2H_4 synthesis. A complete review of any of these topics is beyond the scope of the presentation, and, in most instances, the reader is referred to recent research reports or comprehensive reviews of the specific subject.

Postharvest application of ethylene

History and economic importance. The use of practices to hasten fruit ripening dates to antiquity (35), although it was not known until relatively recently that C_2H_4 was the causal agent. The earliest practices employed the emanations from ripe fruit or the smoke generated from burning combustible products. The use of kerosene stoves for "sweating" or "forced curing" of citrus was a well-established commercial practice by the late 1800s. It was believed that the high temperatures and high humidities in the "sweating" rooms resulted in degreening. Sievers and True (43) demonstrated that degreening was due to some unknown gaseous product from the incomplete combustion of kerosene. Denny (15) provided convincing evidence in 1924, that C_2H_4 was the effective constituent in "stove gas", and described a method for commercially degreening lemons using cylinders of compressed C_2H_4 gas.

Denny's work (15) marked the beginning of the knowledgeable use of C_2H_4 gas in commercial degreening and fruit ripening practices. Harvey (27) published the 1st comprehensive bulletin describing the commercial application of C_2H_4 for ripening bananas, pineapples, dates, Japanese persimmons, tomatoes, hard pears, apples, and muskmelons. Interestingly, one early commercial use for C_2H_4 was for blanching celery (26), a practice which has long since been discontinued.

Rosa (39) predicted that for tomatoes "the acceleration of the coloring process by low concentrations of C_2H_4 is sufficiently great to make it commercially valuable. . .". These words seem especially prophetic when considering the economic importance of C_2H_4 applications in postharvest horticulture today. Although it is not possible to assign an exact monetary value for C_2H_4 use, it is accurate to state that C_2H_4 applications play an important role in the orderly marketing of fresh citrus (excluding limes), tomatoes, bananas, mangoes, and honeydew melons. Recent reports (20, 47, 48) indicate that these products have a value of over 1.9 billion dollars in the United States alone.

Sources of ethylene. There are 3 potential sources of C_2H_4 for commercial use: liquids, gases, and ripening fruit. Liquid sources are C_2H_4-releasing chemicals such as (2-chloroethyl) phosphonic acid, commonly known as ethephon. This chemical is registered and widely used for preharvest applications to concentrate maturity or otherwise facilitate harvest of several horticultural crops. According to the label, the only presently registered use for postharvest application is for the degreening of lemons in Florida (49). Therefore, further discussion will be limited to the other sources of C_2H_4 for postharvest use.

Ethylene gas can be generated *in situ* or purchased in compressed cylinders. The gas is generated by catalytic conversion of a flammable liquid concentrate (Ethy-Gen) to C_2H_4 gas (11). This is one of the most popular commercial sources of C_2H_4 gas. The other widely used source of C_2H_4 gas is that purchased in compressed cylinders of either pure C_2H_4 or C_2H_4 diluted with an inert gas such as the product called "banana gas" (50, 3, 51).

Postharvest physiologists are aware that ripening fruit produce C_2H_4, but many commercial handlers either are unaware of or ignore this fact. If ripening room operators conscientiously monitored C_2H_4 levels in these rooms, then the use of ripening fruit might be a viable commercial alternative. However, the use of ripening fruit as a source of C_2H_4 generally is limited to home ripening recommendations.

Which source to use? The source of C_2H_4 used by handlers normally is determined by the facilities for treatment, legal considerations, cost, and safety. The use of C_2H_4 gas requires some type of enclosure. The cost of building special ripening facilities with precise temperature and humidity controls is well-justified when repeated ethylene applications are required.

Each handler also must consider the legality of C_2H_4 application (25). Ethylene gas used for plant regulation such as coloration or ripening of fruit and vegetables is regarded legally as a pesticide for regulatory purposes (52). Therefore, it must be registered with the Environmental Protection Agency (EPA) and the appropriate state agencies. Containers of C_2H_4 gas or C_2H_4-releasing liquids must bear EPA approved labeling, including EPA registration and establishment numbers, intended uses, ingredients statement, and appropriate precautionary labeling statements.

Because of the explosive nature of certain mixtures of C_2H_4 and

Florida Agr. Expt. Sta. J. Series No. 5413. Mention of vendors or products does not constitute a guarantee or endorsement of the vendor or product by the Florida Agr. Expt. Sta., and it does not imply its approval to the exclusion of other vendors or products that may also be suitable.