Ethylene and Fruit Ripening

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An investigator commencing work on ethylene and fruit ripening is confronted by the enormous diversity among fruit. It is necessary to identify unique characteristics that differentiate fleshy plant structures from other plant parts in order to develop new treatments successfully for extending the commercial life of fruit. Fleshy fruit are typically determinate structures genetically programmed within each species to achieve a distinctive maximum size, shape, color, texture, and taste. Botanical origins of the tissues that comprise fruit are various. The metabolism of fruit is qualitatively similar, despite their morphological and anatomical diversity, in all cases involving glycolysis, the tricarboxylic acid cycle, terminal oxidases and the biogenesis of ethylene, auxin, gibberellin, cytokinin, and abscisic acid. Genetic diversity in the patterns of ethylene production during growth, ripening, and senescence is apparent among fruit.

Fruit have been classified as climacteric or nonclimacteric depending on their respiratory behavior during ripening (5). This distinction, now almost folklore in postharvest horticulture, is nevertheless useful. Climacteric fruit at the end of growth undergo a large increase in respiration accompanied by marked changes in composition and texture, whereas nonclimacteric fruit show no change in respiration that can be associated with distinct changes in composition. Another distinguishing feature is that ripening in climacteric fruit is associated with a large increase in ethylene production. The increases in respiration and ethylene production can be induced prematurely in climacteric fruit by treating them with a suitable concentration of ethylene or other unsaturated hydrocarbon. The ripening process is irreversible once endogenous (autocatalytic) ethylene production increases to a certain level. In contrast, an unnatural climacteric-like respiratory increase can be induced in nonclimacteric fruit by treating them with ethylene or other unsaturated hydrocarbon. Yet this increased respiration is not accompanied by an increase in endogenous ethylene production, and the respiration rate usually subsides fairly rapidly upon removal of the exogenous ethylene or other unsaturated hydrocarbon. However, ethylene treatment does accelerate senescence in nonclimacteric fruit.

As mentioned by Yang in an earlier paper in this symposium, the distinctive differences in responses to propylene by climacteric and nonclimacteric fruit inspired the hypothesis by McMurchie et al. (27) that the biogenesis of ethylene in climacteric fruit is regulated by 2 systems: System 1, which is involved in the regulation of aging processes and is responsible for the low rate of ethylene production during growth, and System 2, which is responsible for the autocatalytic increase in ethylene production which accompanies ripening. It was further postulated that nonclimacteric fruit have System 1 but not System 2. The present evidence is that ethylene evolved in both systems is produced by the ACC (1-aminocyclopropane-1-carboxylic acid) synthase pathway (43). Many papers have been written describing the physiology of different fruits and probably fruit can be classified clearly as climacteric or nonclimacteric with only a few exceptions. More names are being added, within climacteric species, to the lists of those that show a significant rise in ethylene production before, after or coincident with the onset of the respiratory climacteric. As has been stated on several occasions, however, "the important considerations are not the exact timing of the rise in ethylene production, but rather what alters the sensitivity of fruit tissues to ethylene, how is the production of ethylene regulated and what is its function during ripening" (20). The purpose of this brief review is to assess recent advances in our knowledge of these 3 aspects and to attempt to place them in a practical context.

In practice, postharvest horticulturists focus most of their attention on climacteric fruit. The latter's potential for good taste and quality generally reaches a maximum at about the onset of the respiratory climacteric, hence restricting the period of opt' um harvest; most climacteric fruit become highly perishable once ripening is underway. The lack of synchronization of ripening in a population presents serious logistic and economic problems for commercial growers, despite improvements through plant breeding in annual crops and improved agronomic practices for both annual and perennial fruit crops. The development of a reversible ripening inhibitor would have enormous value. The best inhibitor would be one that does not affect the growth and development of the fruit but simply arrests ripening. Ideally, its effects should be reversed by treatment with ethylene. Some of the possibilities are: 1) a treatment that reduces the sensitivity of the fruit to system 1 ethylene; 2) a treatment that inhibits System 1 ethylene production; and 3) direct inhibition of a key enzyme early in ripening by chemical means or by insertion of a repressor into the part of the genome that controls ripening.

Reduction in sensitivity to System 1 ethylene

Trewavas (42) recently reexamined the conceptual base of research on plant growth substances. He concluded the limiting factor in plant development is the sensitivity of tissues to plant growth substances and not the changes in the concentration of growth substances. This interpretation arose from the general lack of good correlations between concentrations of the plant growth substances and particular stages of development. This conclusion that sensitivity is the limiting factor is well borne out by examination of the responses to exogenous ethylene of a range of climacteric fruit. We find most fruit become increasingly sensitive to ethylene with time after anthesis (25). Examples at opposite ends of the scale are tomatoes and cantaloupes. Immature tomatoes exhibit a climacteric-like increase in respiration when treated continuously with ethylene. The time to the beginning of ripening is reduced by about 50% compared with control fruit held in air (19). We showed by substituting propylene for ethylene there was no change in endogenous ethylene production until other symptoms of ripening appear (22). Processing tomatoes are treated preharvest with ethephon, which accelerates fruit growth and advances the onset of ripening (14). In contrast, treating immature cantaloupes causes the rapid onset of ripening (24). Preharvest sprays of ethephon short circuit the normal accumulation of sugar in this fruit, and, therefore, this treatment has no commercial application (15). Even in cantaloupes, age-related differences in sensitivity to added ethylene can be demonstrated by using a range of low concentrations of ethylene. These apparent changes in sensitivity to ethylene during fruit development were recognized by several investigators working with other species and have led to the deduction of critical or threshold concentrations required for the commencement of ripening (5).

Trewavas (42) summarized the relationship of a plant growth substance with its host tissue in the equation:

$$\text{Growth substance (GS)} + \text{receptor (R)} \rightarrow (\text{GS}\cdot\text{R}) \rightarrow \text{biological response.}$$

In the context of fruit ripening, the change in sensitivity to ethylene can be interpreted as a change in R. Thus, the nature and concentration of R is crucial. Many attempts have been made to isolate specific receptor(s) but with variable success. If a specific receptor(s) can be identified, then the way would be open to devise the means of controlling its concentration or activity. The problem is there are probably several receptors with different functions. It is perhaps significant the best recoveries of cell fractions that appear to bind ethylene specifically have been from non fruit tissues in which ethylene has no known role (3, 11). Sisler (36) found ethylene binds at comparable levels in fruit and leaves of normal, *rin*, and *nor* tomatoes but, nevertheless, it is possible normal fruit produce small amounts of a ripening – specific receptor for ethylene which is not detected by present methods. The concept of a receptor and any cell fractions considered candidates for this role have to

accord with the well-established time × concentration interaction that applies to ethylene responses. Also, the potential receptor should have relative specificities for ethylene homologues in line with known physiological responses to application of these homologues.

A way of viewing the chronometric changes that take place during the preclimacteric phase is to think in terms of the gradual accumulation of a specific ripening receptor. This quantitative aspect is suggested by the length of the preclimacteric development period that is characteristic of each species, and the observations this period can be shortened by treatment with a suitable concentration of ethylene or propylene, or lengthened by storage in modified atmospheres. The latter treatment could provide a useful technique for maximizing the concentration of a specific ripening receptor. We observed that individual bananas could be kept green at 20°C in a flowing stream comprising 5% CO_2, 3% O_2, and 92% N_2 for 182 days, but ripening began immediately as soon as the fruit were returned to air (26). Possibly, the required amount of receptor builds up slowly during long storage in this atmosphere but endogenous ethylene production remains too low to form sufficient of the GS·R complex required for ripening. A similar response in fruit of other species harvested at a preclimacteric stage theoretically should be possible to achieve.

Prospects are good for developing a safe treatment for reducing the sensitivity of fruits to System 1 ethylene. There are indications of the presence of natural inhibitors in attached fruit of some species. The well-known inability of attached fruit of avocado to ripen can be interpreted in terms of anti-ethylene compounds. There are documented changes in sensitivity to ethylene at different stages in the development of figs and grapes, both of which have a double sigmoid growth pattern (25). Silver ion clearly inhibits ethylene action in several plant tissues (4) and is valuable for the commercial storage of flowers (13). According to Saltveit et al. (34), however, applied ethylene does not overcome the inhibitory action of silver ion in mature green tissues of tomato and banana. There also is a report of high concentrations of silver ion accelerating ripening in persimmon fruit, although lower concentrations retarded ripening (38).

Inhibition of System 1 ethylene production

At least 3 kinds of substances of natural origin are known that inhibit ethylene synthesis, but only one of these has been found in fruit tissues. Benzyl glucosinolate plus trace amounts of the hydrolysis product benzyl isothiocyanate occur naturally in papaya fruit (39). There is experimental evidence that the latter compound may be an endogenous regulator of ethylene evolution in papaya (30).

A protein which inhibits auxin-induced ethylene production by mungbean seedlings has been isolated from the hypocotyl of etiolated mungbean seedlings (32). This discovery does not seem to have been pursued further.

The 3rd group of substances include the enol ether amino acid analogues produced by some microorganisms (17). The most commonly used analogue is *N*-[2-(2-amino-ethoxy)-ethenyl]glycine(AVG). It has been shown that AVG and a more recently discovered substance, (aminooxy) acetic acid (AOA), are potent inhibitors of ACC synthase activity preventing the formation of amino-cyclopropane-1-carboxylic acid (ACC), the natural precursor of ethylene (43). Preharvest sprays with AVG delay ripening and ethylene production in apples (8). An outstanding improvement in storage life has been reported in blueberries by postharvest treatment with AVG (10). Complete inhibition of ethylene production by AVG or AOA has not been reported in any fruit tissue (17). The problem with using such inhibitors include: achievement of thorough distribution within the tissue, access of the inhibitor to ACC synthase, and the possibility the treated tissue detoxifies or bypasses the inhibitor. A period of storage at 0° to 2°C which promotes rapid and uniform ripening in 'Bartlett' pears after transfer to 20° counteracted the effects of preharvest applications of AVG (31). However, ethylene production was strongly inhibited in pears removed from storage at 0° and vacuum infiltrated with AVG, and the respiratory climacteric and accompanying ripening changes were delayed. Treatment of inhibited fruit with ethylene overcame the effects of AVG (29).

Other substances implicated in the inhibition of ethylene production include free radical quenching agents, such as n-propyl gallate and sodium benzoate (17), polyamines (2), Vitamin K_5 and menadione (33), and cobalt ion. The polyamines, along with auxins, cytokinins, and calcium ion probably affect the synthesis of ACC, the other substances probably acting on the metabolism of ACC to ethylene (43).

Inhibition of a key ripening enzyme

The possibility of inhibition is hypothetical because no key enzyme for ripening has been identified. One recent candidate, at least in the tomato, was endopolygalacturonase (PG), but clearly this enzyme is produced *de novo* after the beginning of autocatalytic production (6, 12). An obvious contemporary contender is ACC synthase. This enzyme increases its activity before PG and at the same time as autocatalytic ethylene production (37). However, although this increase in ethylene production (System 2) is a hallmark of the climacteric class of fruit, ACC synthase may not be a good candidate for the role of a key enzyme in ripening, and clearly there must be an earlier signal which induces the increase in this enzyme. A large body of data show that the ACC synthase system is universal in plant and fruit tissues and that this enzyme is readily "turned on" by many stimuli, including wounding (1). It is possible that different ACC synthases are involved, although it seems clear that preclimacteric (System 1) ethylene is produced via the same biochemical pathway as System 2 or wound ethylene.

Ripening involves a programmed sequence of events according to the genetic model. What is the sequence of enzymes intrinsic to ripening? The tomato fruit is an excellent experimental material for studies on this question. Two of the advantages of the tomato are its low sensitivity to ethylene during growth and the existence of the ripening mutants *rin*, *nor*, *Nr* and alcobaca. Fruit of heterozygotes of *rin* and *nor* are particularly valuable because these genes exert quantitative effects on several processes involved in ripening. Several distinct stages of fruit development can be defined (Fig. 1). The developing fruit is dependent on translocates from the vine until about 35% of the growth period is completed. Some parts of the fruit continue to grow and eventually ripen, and the remaining tissues senesce if very young fruit are detached and held in moist air. The entire fruit from the 35% stage onwards ripens normally after detachment and takes about the same time to ripen in air as do attached fruit maintained at similar temperatures (21). One apparent transition is reached at about 80% of development. Fruit younger than this have the capacity to reutilize soluble N released as a result of γ-irradiation with 2 kilograys and to ripen normally. However, these capabilities progressively are lost in older fruit (23). The mucilaginous tissue (jelly) around the seeds begins to lose its integrity from about the 80% stage onwards. The transformation of chloroplasts to chromoplasts and the synthesis of lycopene can be dectected in the pericarp tissue (35). PG also appears at about the same time, within 1 or 2 days after the commencement of autocatalytic ethylene production (12). There is recruitment of ribosomes to polysomes during the 1st 2 days following the onset of autocatalytic

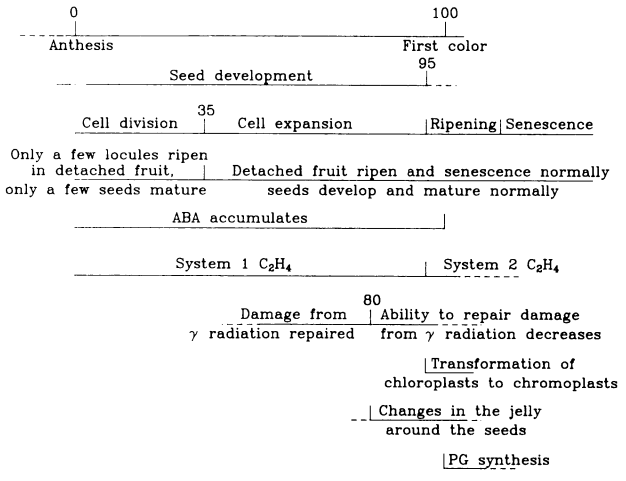

Fig. 1. Fruit development and ripening in the tomato.

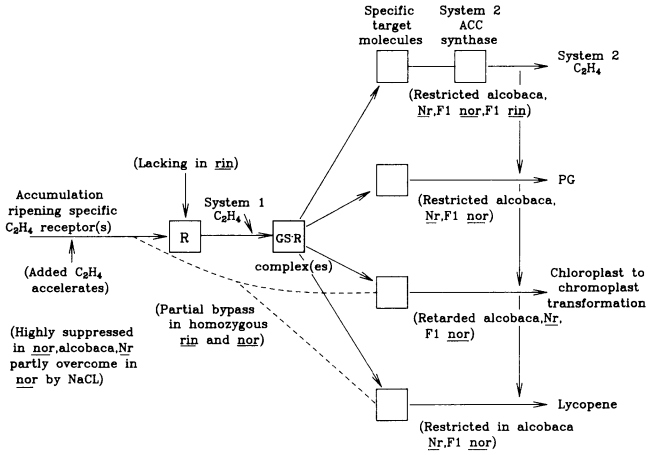

Fig. 2. Genetic control of ripening in the tomato.

ethylene production (Brady, Speirs, and Grierson, personal communication).

Fruit of *rin* and *nor* have the following characteristics: they are non-climacteric; they senesce slowly; the transformation of chloroplasts to chromoplasts is protracted; pericarp tissue from developing fruit of the mutants yield similar amounts of wound ethylene as compared to normal fruit, even when fully colored (yellow and yellow-orange respectively); mutant fruit lack the characteristic aroma of normal ripe tomatoes; and the mutants do not produce PG (40). However, attached *nor* fruit had a small increase in ethylene production and produced small amounts of PG and some lycopene when the plants were stressed by the addition of 3 g/liter of NaCl to the nutrient solution (28). Fruit of *rin* and *nor* hybrids, *Nr*, and alcobaca show quantitative effects of the mutant genes. The time from anthesis to the attainment of maximum size is the same, but the onset of ripening is significantly delayed in F_1 *nor*, F_1 *rin* × *nor*, and *Nr* fruit. The rate of ripening is slightly reduced in F_1 *rin* and much slower in F1 *rin* × *nor*, F1 *nor*, *Nr* and alcobaca. Coloring is normal in F_1 *rin* but lycopene production is deficient in F_1 *rin* × *nor*, F_1 *nor*, *Nr* and alcobaca. Maximum rates of ethylene production in all of these strains are considerably reduced. So, also, are the rates of softening and increase in PG activity (7, 16). The fact that these genes which are located on different chromosomes, *Nr* on 9, *rin* on 5, *nor* and alcobaca on 10, produce several similar responses as well as some different responses highlights the complexity of fruit ripening; at the same time, however, these observations offer considerable encouragement.

The following are suggested early actions of these genes at the molecular level (Fig. 2). Homozygous *rin* and *nor* fruit lack the ability to produce ripening-specific ethylene receptor(s) as evidenced by the failure of added ethylene to induce normal ripening. They both fail to produce System 2 ACC synthase for autocatalytic ethylene production. Salt stress in *nor* but not *rin*, may partly restore some of the changes associated with normal ripening (28). The effect of *rin* may, therefore, be due to a mutation in a gene coding for the production of ethylene receptor but *nor* may exert its action through a regulatory gene. Alcobaca, which is situated close to the *nor* locus (18), shows quantitative effects on ripening similar to those apparent in F_1 hybrids of *nor*. Ripening is delayed; thus, presumably the build-up of ethylene receptor is slowed and the ACC synthase system is partly suppressed because the rate of ethylene production is much reduced. The alcobaca locus may involve another regulatory gene or part of a complex of genes which includes the *nor* locus. *Nr* also seems to have quantitative effects on the production of ethylene receptor and ACC synthase, but since it is located on a different chromosome, there must be at least 2 genes in the tomato for regulating these 2 functions. Ripening of F_1 *rin* fruit is not delayed significantly, thus *rin* is acting in this case as a simple recessive gene which may further support the suggestion that *rin* is due to a mutation in a gene for the production of ethylene receptor. The ACC synthase system in F_1 *rin* is partly suppressed, however, because the rate of ethylene production during ripening is half normal. Some regulatory effects on the early events of ripening may still be ascribed to *rin* because ripening of F_1 *rin* × *nor* fruit is delayed compared to F_1 *nor* fruit (41).

The hypothetical key event in normal tomatoes that emerges from this examination of the deficiencies in the mutants is the production of ripening-specific ethylene receptor(s). The evident suppression of the ACC synthase system in mutant fruit is not itself critical, because adding ethylene does not overcome the inhibition of ripening in homozygous *rin* and *nor* and does not alter the rates of the ripening events that follow the onset of system 2 autocatalytic ethylene production in hybrid fruit.

How can we detect ripening specific receptor(s)? Our best hope is to exploit the techniques of the genetic engineers. Evidence has been presented for the avocado that at least 3 mRNAs increase with the climacteric rise in respiration and ethylene production (9). In the tomato, the *de novo* synthesis of PG and the increase in ACC synthase serve as good starting points. Already, work is progressing towards isolating the mRNAs for these 2 enzymes. The structural genes for the enzymes can be located using cloned DNA copies of these mRNAs as probes. Gene dosage and location can be determined, and the hypothetical System 1 and System 2 ACC synthase question can be resolved. Probably more importantly, the mode of regulation of the genes can be examined by searching in adjacent regions of DNA for common regulating sequences, or for clusters of ripening-specific genes in one DNA domain regulated by a single regulatory molecule (perhaps the complexed ethylene and ethylene receptor)!

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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).