Sycomore fig trees (*Ficus sycomorus* L.) originate from the savanas of eastern Central Africa, where they reproduce by seed. There, the flowers of *Ficus sycomorus* are pollinated by a single species of *Ceratosolen* wasp. We don't know how or when *Ficus sycomorus* was introduced to eastern Mediterranean countries, but remains of this species in Egypt date earlier than the predynastic period, ie., before 3000 BC. Since the pollinating *Ceratosolen* wasp is not present in Mediterranean countries, it is not surprising that dried sycomore fruit were seedless in the grave of Ani of the 10th dynasty (about 1100 BC). Probably the earliest written record of human manipulation of fruit is contained in the old testament of the Bible, where it is written that the 8th century BC prophet Amos described himself as either a ''piercer'' or ''gatherer'' of sycomore fruit. Contemporary evidence suggests that ''piercer'' is the correct translation from the ancient Hebrew manuscript. The earliest explanation for piercing figs came from the 3rd century BC Greek philosopher Theophrastus, who recorded the observation that sycomore figs did not ripen unless they were scraped with an iron claw, which caused the fruit to swell and ripen in 4 days (6).

With a dried, seedless, pierced sycomore fig in hand, we must take several brobdingnagian steps through 23 centuries to 1912, the next date in our story of the evolution of human understanding of, and involvement with, ethylene and fruit ripening. In that year, Sievers and True (USDA) reported that it was the gaseous combustion products, not the heat from kerosene stoves, that caused lemon degreening and abscission of lemon buttons in California lemon curing rooms. An interesting addendum at the conclusion of the Sievers and True bulletin noted that when lemon handlers were told of these tests, many switched from the ''rather objectionable'' kerosene stoves to the exhaust products of gasoline burning motors (11). In 1924, Denny (USDA) identified ethylene as the active component in the combustion fumes from the kerosene stoves and described the use of ethylene as a ripening agent (5). Eleven years later, Gane (Low Temperature Research Station, Cambridge, England) proved by chemical methods that ripening apples give off ethylene (7). In that same year, Crocker, Hitchcock, and Zimmerman (Boyce Thompson Institute) proposed that ethylene is an endogenous fruit ripening hormone (4).

In 1950, Williamson, a Cornell plant pathologist, reported that cutting plant tissue increased the rate of ethylene production (12). For many of you, 1959 may not be a significant date. But to us old timers, who waded through ethylene bioassay techniques, wet chemistry, and/or manometric procedures to measure ethylene production rates, this year marked a significant breakthrough in ethylene research. Burg and Stolwijk (3) at Harvard as well as Huelin and Kennett (8) in New South Wales, reported the use of the gas chromatograph for ethylene analyses. Abeles (1) published an interesting graph that showed 1959 as the beginning of a climacteric-like rise in the number of published ethylene papers. Lieberman and Mapson (USDA-Beltsville) reported in 1964 the formation of ethylene from methionine (9). The last 2 entries are from Yang's laboratory at the Univ. of California, Davis. In 1979, Adams and Yang elucidated the methionine→S-adenosylmethionine (SAM)→l-aminocyclopropane-l-carboxylic acid (ACC) ethylene biosynthetic pathway in apple tissue (2). Riov and Yang showed in 1982 that the increase in wound ethylene production by citrus flavedo was paralleled by an increase in ACC content, i.e., wounding increased ACC synthase activity (10).

I will conclude these brief historical notes by observing that if scientific license is taken by future translators of ancient Hebrew manuscripts, Amos 7:14 will quote Amos as saying, ''I was no prophet, neither was I a prophet's son; but I was a herdsman and an activator of ACC synthase in sycomore fig fruits''.

Each of the 5 symposium participants is in the vanguard of his section of the spectrum of ethylene responses. First, there will be a discussion of the regulation of ethylene responses; then a review of studies of the biology and biochemistry of abscission; the 3rd participant will indicate what is known about the mechanisms of fruit ripening; then you will learn of the detrimental effects of ethylene on a wide range of horticultural crops. Finally, methods of applying ethylene to products and methods of protecting products from ethylene will be described.

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Biosynthesis and Action of Ethylene

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Ethylene is a plant hormone which regulates many aspects of growth, development, and senescence (1). Depending upon where and when ethylene occurs, it may be beneficial or harmful to harvested horticultural crops. Efficient postharvest technology therefore requires the ability to control ethylene effects to suit our practical needs. Before ethylene can exert such responses, it has to be biosynthesized by the plants or supplies from external sources. As in the case of other hormones, ethylene is thought to bind to a receptor, forming an activated complex which in turn triggers the primary reaction. The primary reaction then initiates the chain of reactions, including modification of gene expression, and leading to a wide variety of physiological responses (Fig. 1). Thus, there are 4 levels of manipulation we can use to regulate ethylene responses: (a) con-

Chemical names used. ACC: 1-aminocyclopropane-1-carboxylic acid. AOA: (aminooxy)acetic acid. AVG: L-2-amino-4-(2-aminoethoxy)-*trans*-3-butenoic acid. EFE, ethylene-forming enzyme which catalyzes the oxidation of ACC to ethylene. SAM: S-adenosylmethionine.

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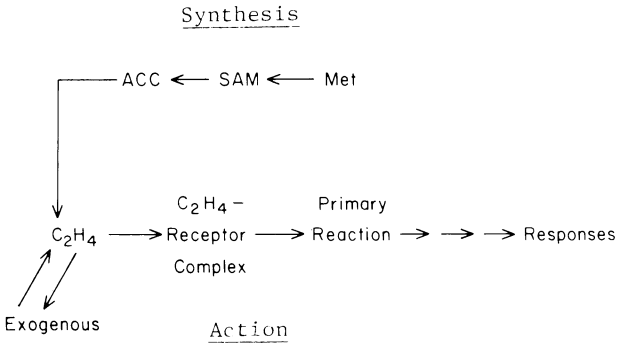

Fig. 1. The chain of events between ethylene and its responses.

trol the level of ethylene in the tissue by addition or removal of ethylene, (b) regulate the level of ethylene in the tissue by stimulating or inhibiting ethylene biosynthesis, (c) modify the binding characteristics of ethylene to the receptor, or modify the amount of the receptor, and (d) manipulate the ethylene-dependent gene expression.

Addition or removal of ethylene

Ethylene can be applied to the horticultural crops directly as ethylene gas in closed chambers, or by application of ethylene-releasing compounds, such as 2-chloroethylphosphonic acid (ETHREL, ethephon), or 2-chloroethyltris-(2′-methoxyethoxy) silane. Ethylene also can be readily generated from ethanol by catalytic dehydration.

(1) $Cl\text{-}CH_2\text{-}CH_2\text{-}PO_3H_2 + 2OH^- \rightarrow Cl^- + CH_2 = CH_2 + H_2PO_4^- + H_2O$

(2) $Cl - CH_2 - CH_2\text{-}Si(O\text{-}CH_2\text{-}CH_2\text{-}O\text{-}CH_3)_3 + 2H_2O \rightarrow Cl^- + CH_2 = CH_2 + SiO_2 + 3HO\text{-}CH_2\text{-}CH_2\text{-}CH_2\text{-}O\text{-}CH_3 + H^+$

(3) $CH_3\text{-}CH_2\text{-}OH \xrightarrow{-H_2O} CH_2 = CH_2$

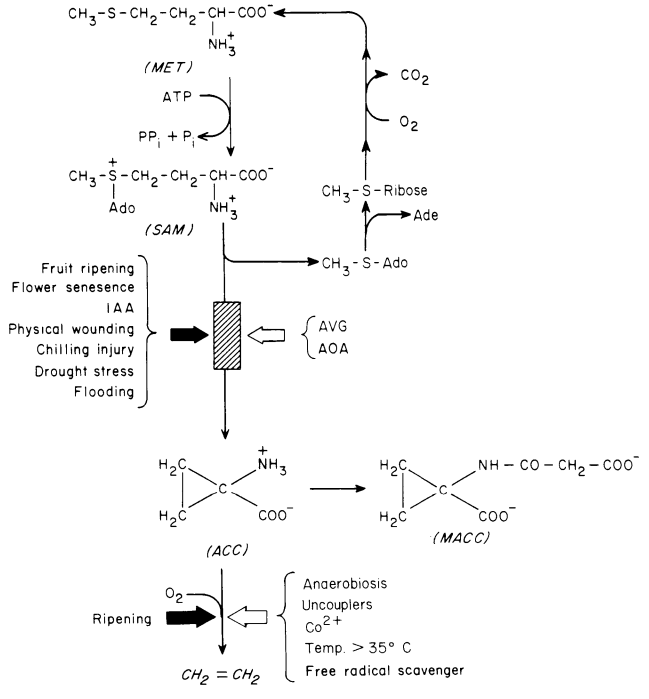

Fig. 2. Regulation of ethylene biosynthesis: ▨, this reaction is normally suppressed and is the rate-limiting step in the pathway; ➡, induction of synthesis of the enzyme; ⇦, inhibition of the reaction. Met, Ado, Ade and MACC stand for methionine, adenosine, adenine, and 1-malonylaminocyclopropane-1-carboxylic acid, respectively. Modified from Yang (33).

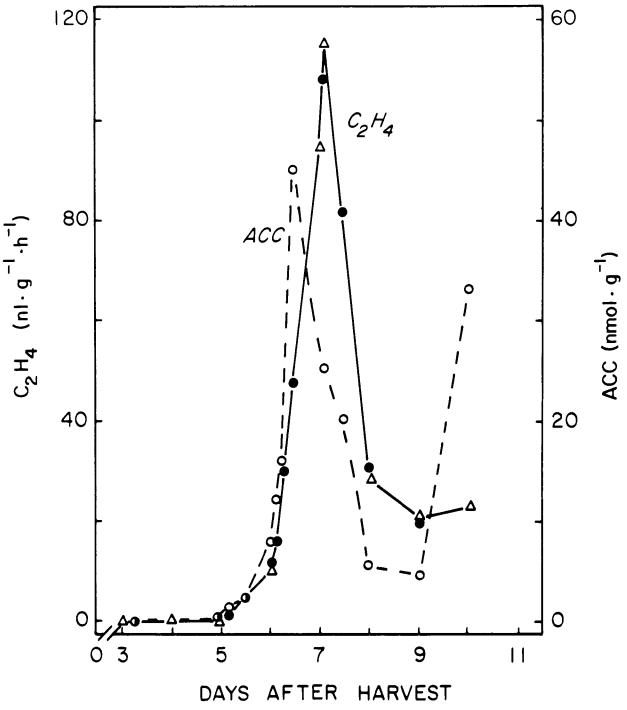

Fig. 3. Changes in ACC content of avocado fruit at various stages of ripeness. Hoffman and Yang (16).

Conversely, ethylene can be removed by ventilation or by scrubbing chemically with $KMnO_4$ or catalytic oxidation. These techniques of controlling the ethylene level in commercial handling and storage situations will be discussed in detail by M. Sherman.

Regulation of ethylene biosynthesis

In 1979, Adams and Yang (2) elucidated the sequence for the pathway of ethylene biosynthesis in ripening apples, and this pathway has since been shown to be operative in all other tested plant tissues. Current understanding of the pathway and regulation of ethylene biosynthesis is summarized in Fig. 2. It has been shown that ACC synthase, which converts SAM to ACC, is the main site of control of ethylene biosynthesis (33). ACC synthase seems to be a pyridoxal enzyme, because the enzyme requires pyridoxal phosphate for maximal activity (34), and is strongly inhibited in vivo (2) as well as in vitro (8, 34) by AOA and AVG, which are well-known inhibitors of pyridoxal phosphate-dependent enzymes. The view that the conversion of SAM to ACC is the rate-limiting reaction in most plant tissues is supported by the observations that application of ACC to various plant organs, including root, stem, leaf, inflorescence, and fruit, resulted in a marked increase in ethylene production (12, 21). This indicates that the enzyme converting ACC to ethylene (EFE) is present in most plant tissues. This enzyme, however, has not yet been identified, but it is known to be very labile and is assumed to be membrane-bound (19).

Ethylene production in vivo is regulated by a variety of developmental and environmental factors. For example, ethylene production is induced during certain stages of development, such as seed germination, fruit ripening, flower and leaf senescence, and abscission; it also is induced by various environmental stresses, such as wounding, chilling and drought, and by treatment with auxins.

Ethylene plays an essential role in the ripening of climacteric fruit. Hoffman and Yang (16) have examined the changes in internal ACC content during ripening. In preclimacteric (unripe) avocado, banana, and tomato fruit, the ACC content was very low (less than 0.1 nmol/g), but a massive increase occurred at the time vigorous ethylene production commenced, which accompanied the ripening process. The relationship between the change in ACC content and the change in the ethylene production rate in ripening avocado is illustrated in Fig. 3. Application of ACC to preclimacteric apple and cantaloupe tissues, however, resulted in only a slight (less than 5-time) increase in ethylene production, whereas the increase in ethylene production at their climateric peaks was several hundred

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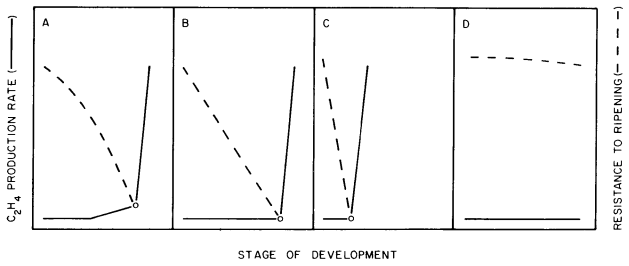

Fig. 4. Changes in ethylene production rates and changes in resistance to ripening during fruit maturation and ripening. It is thought that resistnace of fruit tissue to ripening decreases with time as the fruit matures, and this decrease is regulated by the low level of endogenous ethylene: when the resistance to ripening decreases to a point (o) at which the fruit tissues become responsive to their endogenous ethylene levels, the autocatalytic burst of ethylene production and ripening occur. Some fruit increase their ethylene rates prior to the onset of ripening (**A**), whereas others remain unchanged (**B**), although both types of fruit exhibit accelerated rates of ethylene production resulting from the ripening process. Application of exogenous ethylene (**C**) results in an accelerated decreases in resistance to ripening and, consequently, the ripening process is promoted. Conversely, decrease in resistance to ripening is retarded by the application of an antagonist of ethylene action (**D**) resulting in little changes in resistance to ripening and, consequently, the ripening process is not initiated.

times. Thus, in addition to lacking ACC, preclimacteric fruit tissues also lack the ability to convert ACC to ethylene. It should be noted, however, that application of ACC to intact preclimacteric tomato fruit significantly enhanced the ripening process (20), suggesting that the slight increase in ethylene production caused by the application of ACC may be enough to trigger the ripening process. Autocatalysis of ethylene production is a common feature of ripening fruit and some senescing tissues (1, 24) in which an increased synthesis of ethylene is triggered by exposure to ethylene. Recently, Y. Liu, L. Su, and N.E. Hoffman (unpublished data) treated intact immature tomato or cantaloupe fruit with ethylene for a short period (6-12 hr), and observed that such a short ethylene treatment markedly increased the capability to convert ACC to ethylene but failed to cause a significant increase in ACC content. Thus, application of exogenous ethylene induced the synthesis of EFE enzyme before the synthesis of ACC synthase.

Senescence of carnation flowers is accompanied by a marked increase in the synthesis of ethylene and a concomitant climacteric rise in respiration similar to that in ripening fruit. Changes in ACC content in excised petals of tradescantia and cut carnation flowers in relation to their senescence were studied by Suttle and Kende (29) and Bufler et al. (10), respectively. In freshly harvested carnation flowers, ACC content and ethylene production rates were very low. There was a rapid increase in ACC content which accompanied the onset of senescence and the autocatalytic rise in ethylene production. Ethylene production fell as senescence progressed, but the ACC content of the tissue remained high, perhaps the result of a more rapid fall in the rate of ACC conversion to ethylene than in the rate of ACC synthesis. This would be expected if EFE and not ACC synthase is associated with a membrane which is disintegrated during the later stage of senescence. Thus, the characteristics of carnation flower senescence are similar to those of ripening fruit.

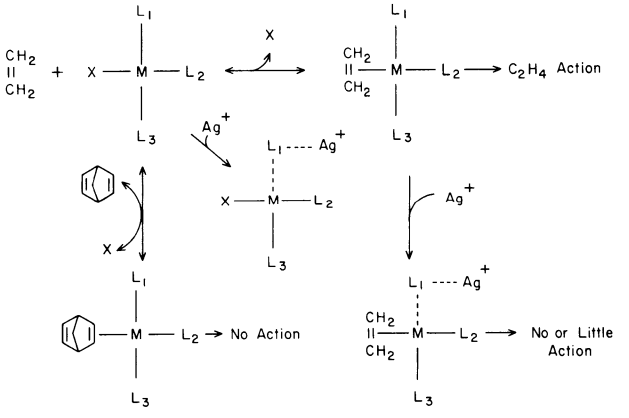

Fig. 5. Possible mode of action of ethylene and its antagonists, Ag^+ and norbornadiene (⬡). M is a metal ion in the ethylene receptor; L_1, L_2, L_3 and X represent ligands interacting with M.

Inhibition of ethylene production by AVG and AOA, inhibitors of ACC synthase, has been tested for practical application in a number of plant organs or whole plants. AVG or AOA significantly inhibited ethylene production and prolonged the longevity of cut carnation flowers (3, 14). Spraying apple trees with AVG before harvest delayed fruit ripening, reduced preharvest drop, and increased fruit-removal force (4, 9, 32). Elimination of "June drop" of apples by AVG also was reported (32). Similarly, retardation of ripening in pears by AVG treatments also was reported (25, 31). AVG induced staminate flowers when applied to gynoecious lines of cucumber (22). Thus, the use of AVG or AOA in selected horticultural crops seems promising and warrants further investigation. It should be noted that the conversion of SAM to ACC, but not the conversion of ACC to ethylene, is sensitive to AVG and AOA inhibition (Fig. 1). Response to these inhibitors requires their application prior to the onset of rapid ACC synthesis. When an ethylene-producing tissue contains low levels of ACC and produces ethylene at high rates, the turnover rate of ACC is high, and the tissue is, consequently, sensitive to AVG or AOA inhibition. For example, apple tissue, known to be very sensitive to AVG inhibition, contains only 2–10 nmol/g of ACC but produces ethylene at a high rate of 5 nmol/g-hr.

Other inhibitors include those which are capable of interfering with the conversion of ACC to ethylene. In detached oat or rice leaves, Co^{2+} and Ni^{2+} were shown to inhibit ethylene evolution and correspondingly retard chlorophyll loss (15, 17). Development of highly specific EFE inhibitors may be possible, when the biochemical mechanism of EFE is better understood.

Ethylene action model

In a detailed analysis of the structural requirements for ethylene-like action of a series of unsaturated compounds in the pea stem bioassay, Burg and Burg (11) observed that the structural requirements for biological activity were very similar to the stability constants of olefin-silver complexes. These observations led them to propose that ethylene initiates its effects in plants by binding reversibly to a metal-containing receptor site. Copper has been suggested as a likely candidate but direct evidence is lacking. Today, this idea generally is accepted and seems highly plausible based on well established principles of organometallic chemistry.

Ethylene binding in plants has been determined in vivo as well as in vitro (5, 26). Kinetic data revealed that the concentration of ethylene needed to occupy one-half the total binding sites was similar to the concentration inducing the half-maximal ethylene responses. Also, there was a reasonably good correlation between the ability of ethylene analogs to compete with ethylene for the binding sites and to mimic ethylene responses. Thus, binding of ethylene seems reversible and specific, and exhibits saturation kinetics. As in the case of other studies of hormone binding, however, it has not been possible to determine if the observed ethylene binding is a requisite for the action of ethylene.

Modification of the binding characteristics of ethylene to the receptor

The dose-response relationships observed for many ethylene-mediated processes in vegetative tissues are similar; concentrations of 0.01, 0.1 and 10 μ liter · liter^{-1} represent threshold, half-maximal, and saturating doses, respectively (1). In other tissues, however, such as preclimacteric fruit, these relationships could be quite different. It has been well documented that the concentrations of ethylene required to induce ripening of preclimacteric fruit vary with different species (for example, banana may require as low as 0.1 μ liter · liter^{-1} whereas honeydew melon requires 3 μ liter · liter^{-1}) with different maturity stages of the same species (many fruit become more sensitive to ethylene as the fruit matures) and with whether they are attached to the tree or not (e. g., avocado fruit do

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not ripen while attached to the tree). An increase in the binding affinity of ethylene to the receptors and/or an increase in the number of receptors in these fruit organs during development would account for the changes in this model for ethylene action. Since the metal-containing receptor also must interact with other ligands, it is reasonable to assume that the quantity and quality of these ligands could influence greatly the binding affinity between ethylene and the receptor. In parallel with this view is the action model of Burg and Burg (11), who have interpreted from their kinetic studies that the binding affinity of ethylene to the receptor depends upon O_2 and CO_2; i.e., O_2 increases the affinity, whereas CO_2 reduces it. The responsiveness of fruit tissues to ethylene also is known to be affected by the other plant hormones.

Two systems of ethylene production during fruit maturation and ripening have been distinguished (18): System 1 is the low level of ethylene present in fruit before the onset of ripening, while System 2 represents the autocatalytic burst of ethylene production accompanying the ripening process. In preclimacteric fruit, the resistance to ripening or resistance to ethylene action is so high that the ripening process is not initiated. As fruit undergo maturation, there is a progressive decrease in resistance to ethylene action (or an increase in sensitivity to ethylene action) and this process is thought to be controlled by endogenous ethylene (23). The decrease in resistance to ethylene action is accelerated by the external application of ethylene and is retarded by storage in a low O_2/high CO_2 atmosphere and by removal of ethylene. When the resistance to ethylene action decreases to a point at which the fruit tissues become responsive to their endogenous ethylene levels, the ripening process is initiated, resulting in the autocatalytic burst of ethylene production (System 2). Hence, the important factor that triggers the onset of ripening is the decrease in the resistance (or an increase in the sensitivity) to ethylene action. According to this concept, an increase in System 1 ethylene production prior to the onset of ripening is not a prerequisite for ripening. Indeed, measurements of internal ethylene concentrations in climacteric fruit have revealed 2 types: type 1 fruit (Fig. 4A) in which ethylene concentration clearly rises before the onset of ripening as shown by the respiratory increase (such as banana, tomato, and muskmelon), and type 2 fruit (Fig. 4B) in which a rise in ethylene production does not occur prior to the onset of ripening (such as apple, avocado, and cherimoya) (7).

Antagonists of ethylene action

In addition to the natural inhibitors of ethylene action which have been postualted, there are 3 known types of ethylene antagonists which may be applied exogenously to inhibit ethylene action.

Carbon dioxide. CO_2 prevents or delays many ethylene responses, and has often been used as a diagnostic test for ethylene action. The inhibitory action is effective under conditions of low ethylene concentrations, but is lost when the ethylene concentration exceeds 1 μ liter $\cdot$ liter^{-1}. In certain fruit, CO_2 accumulates in the intercellular space and functions as a natural ethylene antagonist. CO_2 is used commercially in controlled atmosphere storage of fruit where high CO_2 levels help to delay the ripening action of ethylene. The mode of action of CO_2 inhibition is not known, but Burg and Burg (11) have suggested that CO_2 competes with ethylene for the binding site with a Ki of 15 ml liter^{-1}.

Silver. Ag^+ inhibits ethylene action in a wide variety of plant responses including growth inhibition, abscission, and change in sex expression of cucurbit flowers (6). Ag^+ has been used commercially in cut carnations to extend their vase-life (30). Ag^+ reacts with ethylene to form a complex, but such a simple scavenging effect of Ag^+ has been ruled out as a possible mechanism of action. The exact mechanism by which Ag^+ blocks or reduces ethylene action is unknown. The effectiveness of Ag^+ in reducing ethylene action declines as the ethylene concentration is increased. However, the anti-ethylene effect of Ag^+ is more pronounced than that of CO_2 at the high ethylene concentrations, suggesting that the inhibiting action of Ag^+ is not simply competitive with ethylene. A simple model accounting for the anti-ethylene effect of Ag^+ is presented in Fig. 5. It is assumed that one or more of the coordination ligands (L) in the receptor site facilitates the binding of ethylene to the receptor, resulting in a biologically active complex; Ag^+ interacts with these ligands when it is applied, resulting in a receptor having little capability to bind ethylene, or in an ethylene-receptor complex which is biologically inactive or less active.

Norbornadiene. Sisler and Pian (27) reported that some cyclic olefins counteracted ethylene-induced increases in the respiratory rate of tobacco leaves. Sisler and Yang (28) have since compared the structure-activity relationship of a number of olefins which possess anti-ethylene activity in the pea seedling bioassay. Among those tested, 2,5-norbornadiene was the most active compound, and it inhibited ethylene action in a competitive fashion with a Ki of 170 μ liter $\cdot$ liter^{-1}. This conclusion was based on the kinetic results obtained from double reciprocal plots of inhibition of pea stem elongation vs. ethylene concentration in the presence and absence of norbornadiene. The competitive inhibition of norbornadiene on ethylene action is depicted in Fig. 5. It is assumed that norbonadiene, which resembles ethylene structurally, competes with ethylene for the same binding site, and the resulting norbornadiene-receptor complex is biologically inactive. When norbornadiene (1000 μ liter $\cdot$ liter^{-1}) was applied to green tomatoes, all fruit remained green during the 2-week experimental period, whereas those fruit which received no norbornadiene ripened within 5 days (L. Su, E.C. Sisler, and S.F. Yang, unpublished data). These results support the view of Peacock (23) that the low endogenous levels of ethylene existing in green fruit exert their ripening influence by shortening the green life of the fruit. When the effect of low endogenous levels of ethylene existing in green fruit was counteracted by norbornadiene, the onset of ripening was inhibited. When ethylene was applied to those norbornadiene-treated green fruit, the ripening processes were accelerated, indicating that ethylene was capable of counteracting the norbornadiene action, as expected for competitive inhibition. Norbornadine also is effective in retarding the senescence of cut carnation flowers and in inhibiting abscission of citrus leaves (E.C. Sisler, unpublished data). Norbornadiene is a gas and can be applied and removed reversibly; thus, it has proved to be a useful tool to study ethylene action.

The previous discusison implies that ethylene action can be manipulated by modifying the binding characteristics of ethylene to receptor. This can be achieved by exchange, addition, or removal of ligands involved in the ethylene receptor. Further studies may lead to the development of more powerful and useful effectors of ethylene action.

Regulation of ethylene-dependent gene expression

What is ethylene turning on or initiating, and how is this being translated into biochemical and physiological events? Some ethylene responses, such as inhibition of growth in pea seedlings, can be observed within as little as several minutes; however, many of the responses require several hours or days. Protein synthesis may not be involved in the initial action of ethylene, but observations are consistent with the idea that RNA and protein synthesis are involved in most ethylene-mediated responses. Ethylene causes polysomes to proliferate and new mRNAs to appear in carrots. It was proposed that ethylene acts directly or indirectly on 2 levels of genetic regulation: the translational machinery, and the expression of specific messages (13).

At present, we know very little about the mechanisms by which these events are controlled. Ethylene action can be regulated at the level of gene expression; however, our current knowledge is too limited to allow discussion of this option.

Summation

Ethylene has profound effects on harvested horticultural crops. It is apparent that the capability to manipulate ethylene responses to suit our practical needs is essential for efficient postharvest technology. The state of current knowledge concerning ethylene biosynthesis and ethylene action is reviewed in this paper. Some practical means of regulating ethylene effects by modification of the level of ethylene in the tissue, such as by addition or removal of ethylene, regulating the rate of ethylene biosynthesis, and modulation of ethylene binding to the receptor site, are discussed. Another form of manipulation that can be exploited is the genetic selection of genotypes which have either varied ability to synthesize ethylene or varied sensitivity or responsiveness to ethylene action. Undoubt-

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edly, our capability to manipulate ethylene effects in postharvest systems will be enhanced as the understanding of ethylene biosynthesis and ethylene action advances in the future. The prospects are promising.

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Ethylene and Abscission

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Abscission (Latin: *ab*–from, *scindere*–to cut or sunder), is the process by which plants shed lateral organs. The fundamental event in all abscission is the secretion of enzymes which hydrolyze the cellulose "exoskeleton" and the pectin "cement" of the cells in the abscission zone. This hydrolysis often is accompanied by ingenious mechanisms to assist removal of the abscising organ. The early appearance of these processes in the fossil record (6) is evidence of the strong evolutionary advantage to plants of shedding organs, whether it be the removal of leaves to avoid snow load or drought stress, or the shedding of fruit or seeds to ensure their dispersal and continuation of the species.

Researchers have studied the biology of the processes leading to abscission for more than 130 years (51). It is not the purpose of this article to replicate the several recent and excellent reviews (2, 6, 9, 54, 60, 80, 99) of this extensive literature, but rather to present a consensus of the role of ethylene in abscission, and to describe the horticultural implications of that role. It seems appropriate, however, to commence with a brief summary of our present understanding of the anatomy, biochemistry, and regulation of abscission.

Anatomy

In most plants, the processes of abscission occur in a rather specific part of the abscising organ called the abscission zone (Fig. 1). The zone may be apparent throughout the life of the plant, or may become much more obvious as the time of abscission approaches (6, 84), frequently as a lighter-colored, slightly swollen area. Typically, the zone comprises a plate of thin-walled, narrow cells which are differentiated clearly from the isodiametric cells of the cortex of the axis, and from the columnar cells of the petiole or pedicel. Cells of the abscission zone, sometimes now referred to as "target" cells (83), commence a phase of intense activity immediately prior to the start of physical separation of the abscising plant parts.

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