Plant Physiol. (1971) 48, 249–254

Growth and Respiratory Response of Fig (*Ficus carica* L. cv. Mission) Fruits to Ethylene[1]

Received for publication February 12, 1971

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ABSTRACT

Growth in diameter of the fig (*Ficus carica* L. cv. Mission) fruit takes place in three distinct periods; two periods (I and III) of rapid growth are separated by a period (II) of slow growth. With respect to exposure to ethylene, the fruit exhibits a two phase response. Ethylene inhibits fruit growth in phase A (period I), the period of cell division, stimulates growth in early phase B (early period II), and stimulates both growth and ripening during the remainder of phase B (late period II and period III). The adverse effect of exogenous ethylene on fruits during phase A is thought to be due to inhibition of cell division. The gradual transition occurring in the response of fruits during phase B was interpreted in terms of carbohydrate level in the fruits.

The onset of period III and a respiratory climacteric rise was preceded by or concomitant with a sudden burst of endogenous ethylene synthesis. This, together with the fact that exogenous ethylene applied at the proper stage of fruit growth triggers both ripening and the climacteric rise, leads to the conclusion that ethylene is the causal agent. In other words, the data support the concept that ethylene is a growth hormone that initiates a chain of metabolic and physiological events leading to fig fruit ripening.

Cumulative growth in diameter of the fig fruit is portrayed by a double sigmoid curve (12)—an intermediate period (period II) of relatively slow growth separates two periods of rapid growth (periods I and III). Treatment of Calimyrna fig fruits with 2,4,5-trichlorophenoxyacetic acid at the beginning of period II resulted in continued rapid growth and maturation several weeks earlier than control fruits (13, 14). Later it was found that 2,4,5-T[3] stimulated ethylene synthesis in fig fruits and leaves, which was accompanied by rapid fruit growth and respiration (36). Maxie and Crane (36) concluded that ethylene rather than auxin *per se* was probably the direct active agent in stimulating growth, maturation and ripening of 2,4,5-T-treated fruits. Indeed, that was the case as they found later that ethylene treatment of figs during the second half of period II or in period III markedly enhanced fruit growth and ripening (37). Furthermore, the stimulation in growth and maturation resulting from the application of a drop of olive oil to the ostiole, a practice predating Christianity, has been shown to be brought about by the degradation of olive oil and the liberation of ethylene (26, 41). Ethrel (2-chloroethylphosphonic acid), which decomposes to form ethylene, also has been shown to enhance fig fruit growth and ripening (17).

Maxie and Crane (37) pointed out that "Before C_2H_4 can be established as a growth regulator in figs, it must be verified that production of the gas is correlated with the onset of renewed growth (Period III)." Evidence indicating the existence of such a correlation is presented here.

MATERIALS AND METHODS

Curves of growth in diameter were developed for both first- and second-crop fruits and were used for reference in timing of ethylene treatment and in fruit sampling. Diameters of 10 basal-most fruits on each of five 10-year-old trees were measured periodically with a vernier caliper. Sampling of treated fruits as well as controls was confined to the basal-most fruits. Average fresh and dry weights were determined by weighing triplicate five-fruit samples before and after drying at 60 C until weights remained constant.

Ethylene (5 μl/l in an air mixture) was applied to fruit-bearing branches in the orchard. For this purpose, a 1900-liter tank was evaculated, a predetermined volume of ethylene gas was injected, and the tank was compressed to the appropriate pressure (about 110 kg/cm^2). Whole branches were enclosed in large polyethylene bags provided with an inlet and an outlet, and ethylene was introduced into them through Tygon tubing at the rate of 100 ml/min, as regulated by a flow meter (8). Other branches that were similarly treated with compressed air served as controls.

Rate of respiration at different stages of fruit development was monitored using triplicate fruit samples, each consisting of 200 to 300 g. The samples were placed in 4-liter glass jars, the lids of which were tight and provided with two glass tubes that served as inlets and outlets. Respiration rate, measured as mg CO_2/kg fruit·hr, was determined by the colorimetric method of Claypool and Keefer (8). The fruits were kept at 20 C, and the first measurement was made 24 hr after harvest, followed by daily measurement for the following 6 days.

Changes were monitored in the concentration of endogenous C_2H_4, CO_2, and O_2 in the internal atmosphere of the fruits during development and following treatment. The gases were extracted from the fruits by the vacuum method described by Maxie *et al.* (38). Their concentrations were determined by gas chromatography (31, 38).

RESULTS

Effect of Ethylene Application on Fruit Development and Ripening. Experiments on first- and second-crop fruits were

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[3] Abbreviation: 2,4,5-T: 2,4,5-trichlorophenoxyacetic acid.

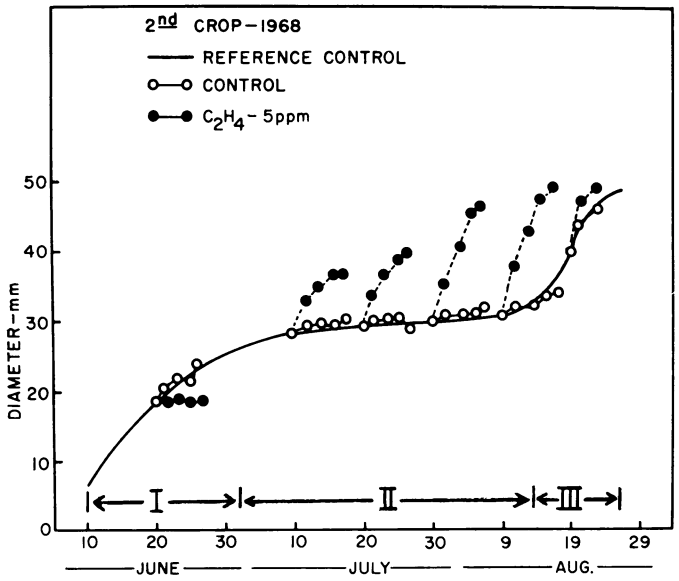

FIG. 1. Effect of ethylene treatment (5 μl/l) on growth of basal fig fruits. Reference control and control fruits were those that were unbagged and bagged, respectively.

carried out in 1968 to determine when ethylene should be applied to produce early maturing fruits of high quality. Since the results obtained with both crops were identical, only those of the second crop are presented in Figure 1. Treatments with 5 μl/l during period I inhibited growth, induced development of an atypical dark reddish color, and abscission in 5 to 6 days. A concentration of 1 μl/l brought about similar effects, but fruit and leaf abscission did not occur until after 9 to 10 days of continuous treatment.

Four ethylene treatments were applied at 10-day intervals during period II (Fig. 1). Treatment on July 10 resulted in a temporary increase in rate of growth for 5 to 6 days, followed by atypical color development and cessation of growth. The fruits were dry, lacked sweetness, and many of them abscised within a week. Treatment on July 20 stimulated growth for 7 days (Fig. 1). Color development in these fruits, as well as size and texture, was somewhat more normal. Although the fruits acquired the appearance of ripe figs, they were smaller in diameter and fresh weight than control fruits. Additionally, they were relatively low in water content, devoid of sweetness, and the floral tissue remained whitish in color. Treatment on July 30, shortly after the drupelets within the fruits had turned pink, resulted in stimulated growth and ripeness on the 6th day (Fig. 1). Although color, texture, and flavor were normal, the ultimate average diameter was slightly smaller than that of control fruits. The fourth ethylene treatment was applied on August 9, when the fruits had about completed period II. The fruits responded exactly as in the preceding treatment, and when ripe, were identical to control fruits in every respect, including diameter. The final ethylene treatment was applied on August 19, about midway in period III (Fig. 1). It imposed a further stimulative effect on the fruits and they ripened within 2 to 3 days, 5 days earlier than untreated fruits.

On July 30 and August 9, several branches bearing fruits were also treated with 0.5 and 1.0 μl/l of ethylene. These concentrations proved to be almost as effective as the 5 μl/l treatment in stimulating fruit growth and ripening. While bagging of fruits had no effect on their growth (Fig. 1), care had to be taken to use fruits in the shade, since direct sunlight caused heat damage. In view of the results obtained in 1968, ethylene treatment during 1969 was restricted to the second half of period II of both first- and second-crop fruits. The first treatment of each crop was applied when pink color had developed within some fruits. The fruit responses were identical to those obtained with the July 30 and August 9, 1968 treatments.

As with the data for growth in diameter, those for fresh and dry weights of untreated fruits also formed double-sigmoid curves (Fig. 2). Similar but more rapid accumulation of fresh and dry weights occurred following ethylene treatment. Slow increases in both were detected 1 to 2 days after treatment, followed by very rapid increases until the fruits were ripe. The later the ethylene treatment, the greater the increase in fresh and dry weight and the more similar they were to ripe control fruits.

Fruit Respiration and Internal Atmosphere Composition as Influenced by Physiological Age and Ethylene. Respiration rates (Fig. 3) were determined in 1969 throughout development of first- and second-crop fruits. Growth curves of these crops are presented in Figure 4, D and H, respectively. Respiration during growth period I consistently decreased to relatively low and practically constant rates throughout period II. At the initiation of period III, respiration rates abruptly increased and reached climacteric peaks about 5 to 7 days later. These peaks occurred approximately midway in period III and were then followed by rapid declines.

During 6-day postharvest periods of fruits sampled periodically throughout fruit development, rate of respiration declined during period I and the greater part of period II in both crops (Fig. 3). Respiration rates of fruits sampled during the climacteric rise, unlike previous samples, continued to increase and reached climacteric maxima (Fig. 3). On the other hand, respiration rates of fruits harvested at and subsequent to their climacteric maxima declined rapidly.

Respiratory changes induced by ethylene were identical in all four treatments that were made (Fig. 3) and, as exemplified

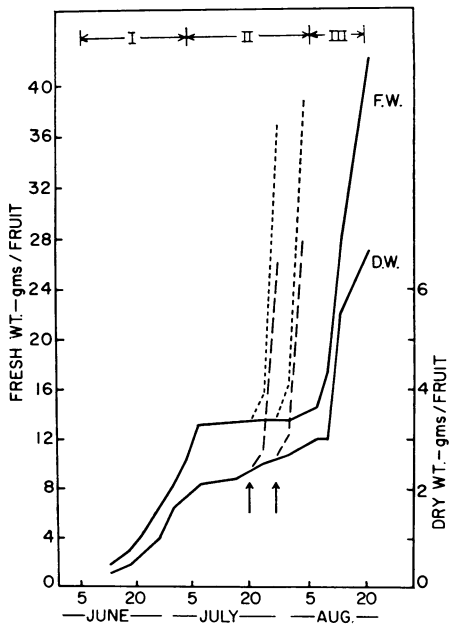

FIG. 2. Increase in fresh and dry weight of ethylene-treated (broken lines) and control (solid lines) second-crop Mission fig fruits (1969). Arrows indicate dates on which the fruits were subjected to 5 μl/l ethylene.

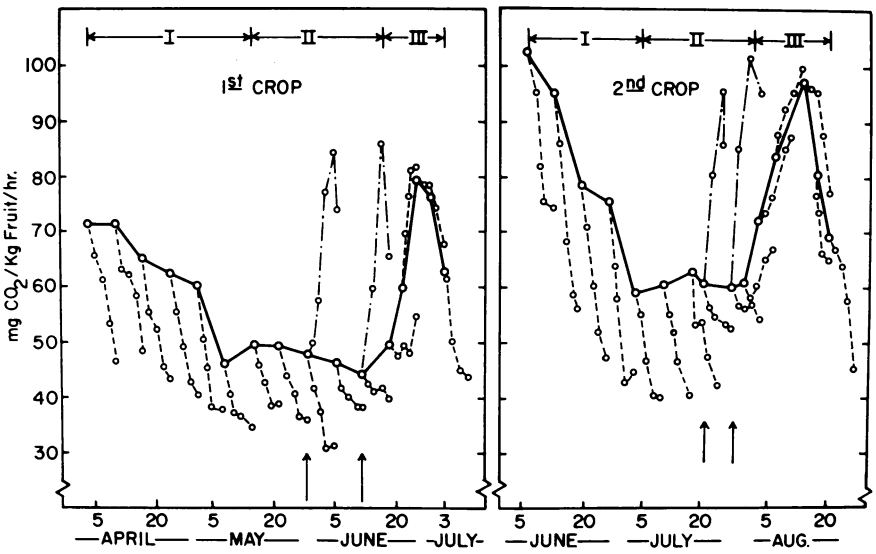

FIG. 3. Respiration rates of Mission first- and second-crop fig fruits (1969); drift in respiration rate of control (O——O) and ethylene-treated fruits (O- · -O) and respiratory drifts during 6-day postharvest periods of control fruits (O- - -O). Arrows indicate dates of ethylene (5 μl/l) treatment.

by treatment of May 27, a rise in respiration rate was detected within 24 hr. Climacteric maxima were attained within 3 to 4 days after the initiation of treatment and were similar to those of normal ripe fruits. Respiration rate began to decline during the 5th day of ethylene treatment, whereas visual ripening occurred 2 to 3 days later.

Although not shown in Figure 3, the respiration drifts of excised ethylene-treated fruits were identical to those exhibited by fruits sampled during their normal climacteric rise. In other words, respiration rates of fruits sampled during the ethylene-induced climacteric rise continued to increase and reached peaks before they declined. Fruits sampled on or after the 4th day of ethylene treatment showed rapid declines in respiratory rates.

Ethylene concentration in the internal atmosphere of fruits was high during early period I (Fig. 4, C and G). As fruit growth began to decline, ethylene concentration also declined and continued to do so until the low levels in period II were attained. The onset of period III was associated with, or preceded by, a sudden rise in endogenous ethylene level that continued until the fruits were ripe.

Following ethylene treatment, the endogenous ethylene level rose sharply and within 5 to 6 days reached peaks of 4.6 to 5.2 μl/l. Thus, ethylene-ripened fruits contained slightly higher levels of endogenous ethylene than ripe control fruits. As with rate of respiration, the levels of endogenous ethylene during fruit development showed a pattern very similar to that for fruit growth rate (Fig. 4, C, G, D, and H).

The curves for levels of CO_2 (Fig. 4, B and F) in the internal atmosphere of developing first- and second-crop fruits were similar to each other and to the curves for ethylene (Fig. 4, C and G). This gas decreased from maximum levels in early period I to minimum levels that occurred throughout period II. Sharp increases in percentages of CO_2 were detected, however, at the onset of period III, and as expected, maximum percentages coincided with the climacteric peaks that were followed by sharp decreases. When ethylene-induced climacteric peaks were reached, the percentages of CO_2 detected were similar to those found in ripe control fruits. The later ethylene was applied, the closer the CO_2 content when the fruits were ripe to that of ripe control fruits.

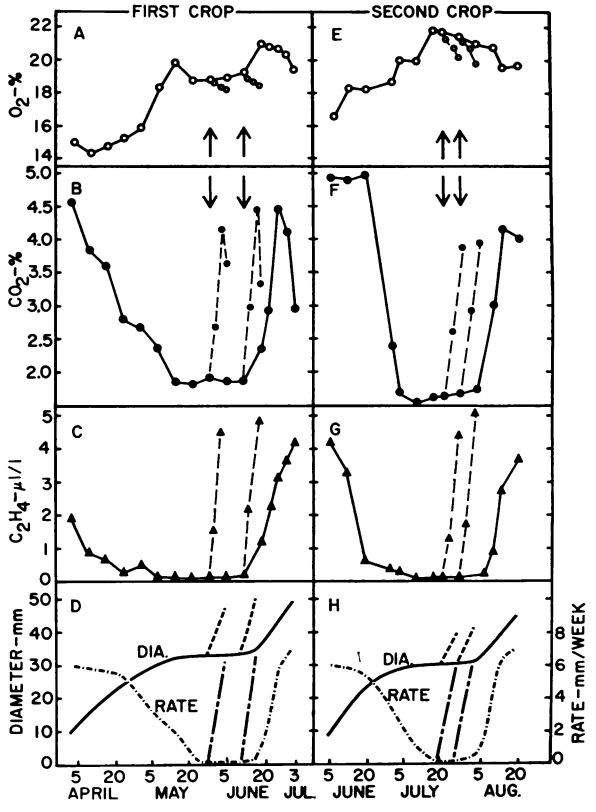

FIG. 4. Concentration of C_2H_4, CO_2 and O_2 in the internal atmosphere of Mission fig fruits in relation to their growth and development and to ethylene treatment. Arrows indicate time of ethylene application.

The lowest levels of O_2 in the internal atmosphere of the fig fruits were recorded during period I (Fig. 4, A and E). At the beginning of period II, the percentages of O_2 increased and reached levels similar to that of the external atmosphere. At the onset of period III and the climacteric rise, O_2 levels

declined slightly. Marked declines in O_2 occurred following ethylene treatment.

DISCUSSION

Effect of Ethylene Application on Fruit Development and Ripening. Fruits treated with ethylene in period I ceased growing and eventually abscised. Treatment during the first half of period II resulted in growth stimulation, but the fruits never ripened from the morphological and edible points of view. Approximately midway in period II and later, however, ethylene treatment stimulated both growth and ripening. Although ethylene-treated fruits ripened as much as 20 days early, they were indistinguishable from ripe, untreated fruits in respect to fresh and dry weight, size, color, flavor, and eating quality. Thus, on the basis of response to ethylene, fig fruit development can be divided into two distinct physiological phases. During phase A, coinciding with growth period I and the first half of period II, exogenous ethylene application results in cessation of fruit growth and abscission. During phase B, coinciding with the last half of growth period II and all of period III, ethylene treatment enhances growth. These results are identical to those obtained with grapes (22), when ethylene promoted ripening only if applied after the midpoint of period II. Ethylene inhibited ripening of grape berries if applied during period I and the first half of period II (22). Looney (30) also showed that apple fruits have two physiologically different stages in response to exogenous ethylene. Apples ripened only if they were ethylene-treated in their second physiological stage. The same concept was also proposed in respect to ethylene and leaf abscission (11, 19). It was maintained that two physiological phases exist and only in the second phase, when explants were aged, was ethylene capable of promoting abscission.

The response of the fig fruit to exogenous ethylene poses the question as to why it varies with physiological age. Period I is characterized by high respiratory rates, active cell division and differentiation, dense protoplasmic material, and rapid synthesis of ribosomes, nucleic acids, and proteins (35). During period II, on the other hand, mitosis in the peduncular tissue of the fruit ceases, respiration, growth, and biosynthetic activities are minimal. Period III is associated with rapid cell enlargement, as well as temporary increases in synthesis of ribosomes, RNA, and enzymes (35) and the occurrence of the different processes associated with normal ripening, such as changes in color, flavor, and texture. Changes in specific constituents of fig fruits as related to periods of growth have been investigated. These include starch and reducing sugars (18, 24–26), malic acid, nitrogen levels, volatiles (23, 24, 26), and growth regulators (15, 24, 26, 28). The data obtained from these studies show marked changes in the various constituents as a function of fruit ontogeny.

The level of one or more of the fig fruit components could be responsible for the differential response of fruits in phases A and B to ethylene. The levels and forms of carbohydrates, for example, may be a key factor in this respect. The slight increase in dry weight that occurs during period II is probably due mainly to carbohydrate accumulation since no significant increase in protein has been detected during that period (35). Crane and Brown (16), Crosby (18), and Hirai (23) found a continuous, although slow, accumulation of carbohydrates (starch and reducing sugars) during period II. It is well known that sufficient sugar is a prerequisite for the climacteric rise and ripening, and that ethylene-stimulated fruit ripening is associated with the conversion of starch into sugars (1, 2, 20, 21). Therefore, it is possible that low levels of carbohydrates during the early part of phase B prevent fruit ripening in response to ethylene. Reaching and surpassing the critical level of carbohydrates, the fruits are stimulated not only to grow but also to ripen when subjected to ethylene. Tentatively it is believed that the attainment of this critical level of carbohydrates coincides with the development of red color in the fruitlets (drupelets). Indeed, a correlation between anthocyanin development and carbohydrate level has been well established (43). Ethylene, as well as olive oil treatment (41), initiated ripening only if applied after red color development. It is not intended to imply, however, that carbohydrate level is the only limiting factor in ethylene-stimulated ripening of fig fruits. Hale *et al.* (22) have indicated, for example, that an auxin-ethylene interaction regulates the ripening responses of grape berries to ethylene treatment.

The data indicate that ethylene (exogenous or endogenous) induces fruits to act as powerful sinks with considerable mobilization capability. Coombe (10) proposed that sugar accumulation is the controlling factor in the initiation of grape berry ripening. Ethylene enhances starch conversion into sugars, and also induces changes in the metabolism of pectic substances in cell walls (1, 2, 20). Several investigators (see Pratt and Goeschl [40] for detail and references) proposed that ethylene alters cellular membrane permeability and uptake of solutes. Based on this evidence, it is hypothesized that ethylene establishes an osmotic gradient in figs by enhancing starch conversion into, and accumulation of, soluble sugars, thus creating an osmotic potential leading to the influx of water. Ethylene also increases cell wall plasticity and alters cell permeability which are two processes that result in cell enlargement and hence increased ability to accommodate water and soluble materials. This concept is substantiated by the following observations: (*a*) fresh and dry weight of fig fruits increase rapidly following ethylene application. The dry matter is composed mostly of sugars (23, 24, 26). Similar increases in dry matter and sugars occur during normal ripening (16, 18). (*b*) Crosby (18) presented evidence that fig fruits, during normal ripening, mobilize sugars and nutrients from wood and leaves. Fruits ripened by treatment with 2,4,5-T, an effect that was later attributed to ethylene by Maxie and Crane (36, 37), exhibited the same phenomenon. (*c*) The ethylene effect is on fig fruits directly rather than via leaves subtending them (37). (*d*) Extensive cell enlargement has been found to occur in fruit tissue (*in situ* or cultured *in vitro*) in response to ethylene (35).

Fruit Respiration and Internal Atmosphere Composition as Influenced by Physiological Age and Ethylene. The respiratory pattern of fig fruits was found to be similar to that of many fruits (1, 2, 20). A high respiratory rate during period I coincided with active growth and metabolism. Period II, the quiescent growth phase, was characterized by a low respiration rate. When period III was initiated, growth rate and metabolic activities increased and respiration rose sharply.

The occurrence of the climacteric in figs was confirmed in both first and second crops. Association of the rise with inception of period III further substantiates the existence of a true climacteric. Claypool and Ozbek (9) failed to demonstrate the occurrence of a climacteric in figs. Hirai (23) and Hirai *et al.* (24, 26), however, demonstrated its occurrence under natural conditions and also following oil or ethylene treatment. Therefore, the fig should be removed from the list of "nonclimacteric" fruits (1) and placed in the list of "climacteric" fruits such as apple, pear, banana, and others (1, 5, 40).

Respiratory rates of fruits sampled during periods I and II declined upon removal from the tree and throughout the postharvest period. Fruits harvested while undergoing the climacteric on the tree continued to do so in jars, but those

harvested at or after the climacteric peak showed a decline. The decline in respiratory rate of fruits sampled during periods I and II is probably due to low levels of sugar which serves as the substrate from which energy is liberated by respiration. Approaching period III, however, the sugar level is sufficient and no longer limits respiration.

Ethylene application late in period II initiated a typical climacteric rise in respiration. This was evidenced by a sudden increase in both respiratory rate and CO_2 level (and a concomitant decline in O_2) in the internal atmosphere of the fruit. The ethylene-initiated climacteric pattern was identical to that displayed by fruits that ripened normally: an attainment of a respiratory peak that was followed by a rapid decline. Consequently, a correlation between the level of endogenous ethylene in fruit tissue and the climacteric rise must exist. Indeed, it was found that the onset of period III and the climacteric rise were either slightly preceded or associated with a sudden burst of endogenous ethylene synthesis. Such a correlation is by no means unique to fig fruits and was reported for bananas (3, 4), cantaloupes (32, 33), tomatoes (33), and honey dew melons (39). When accumulation of endogenous ethylene in fruit tissue was prevented by adequate ventilation or by subjection to partial vacuum, ripening was delayed (5, 6, 34). Furthermore, CO_2, a competitive inhibitor of ethylene (7), delayed the climacteric by retarding ethylene production (5, 27).

In this connection, the question may be asked as to why the high endogenous ethylene level during period I does not cause fruit ripening, while a similar concentration triggers ripening in period III. Several possibilities exist: (*a*) a limiting level of carbohydrate, the respiratory substrate in period I, (*b*) the high level of CO_2 during period I may be competitively inhibiting ethylene action (7), and (*c*) the presence of an inhibitor of ripening either native to the fruit or translocated to it from the vegetative organs. The concept of ripening inhibitor(s) in some fruits such as mango and avocado has been developed by others (see Pratt and Goeschl [40] for references). A change from an ethylene-insensitive to a sensitive state has been shown in other fruits (3, 4, 21, 40). This could be a manifestation of a ripening inhibitor(s) that diminishes as fruits age. Further support of the hypothesis is the inhibition of apple ripening by the plant growth suppressor, succinic acid-2,2-dimethylhydrazide which acts by inhibiting ethylene biosynthesis (29, 30). Ethylene application overcomes the inhibitory effect of succinic acid-2,2-dimethylhydrazide. Finally, Simons (42), who found a high level of endogenous ethylene in early stages of tomato fruit growth, presented evidence that the ovules and developing seeds produce an inhibitor of ethylene-induced ripening. The nature of the inhibitor, whether hormonal or otherwise, is as yet unknown.

In conclusion, it appears that a sudden rise in the rate of ethylene synthesis in fig fruit tissue is responsible for the initiation of period III, the respiratory climacteric rise and the various processes accompanying them leading to ripening. Ethylene, although synthesized during period II, does not reach physiologically effective levels until just prior to the onset of period III and the climacteric rise. Evidence shown here and that obtained by Maxie and Crane (37) indicate that ethylene application autocatalytically stimulates tissue to synthesize its own ethylene and thus reaching a physiologically active concentration capable of stimulating growth and enhancing ripening. The data presented support the concept that ethylene is a growth hormone that initiates a chain of metabolic and physiological events leading to increase in size of fig fruits and a ripening hormone in that it leads to acceleration of ripening.

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