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Relationship between Ethylene and the Growth of *Ficus sycomorus*

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ABSTRACT

The relationship between ethylene and growth was investigated in *Ficus sycomorus* L. A marked increase in ethylene emanation preceeded all the phases of rapid growth and ripening of the syconium.

Gashing of fig during the 16th to 22nd day of syconium development induced a 50-fold increase in the rate of ethylene emanation within the 1st hour, and a 2- to 3-fold increase in diameter and weight, followed by ripening within 3 days. Application of ethylene, Ethephon, and auxins caused the same effects as wounding. Since the auxin and Ethephon induced ethylene emanation, it is concluded that ethylene is mainly responsible for the marked morphological changes caused by gashing. The stage of slow growth of this fruit is characterized by slow emanation of ethylene, low sensitivity to exogenous ethylene, and no morphological responses to gashing.

In the coastal plain of Israel, development of the fruit of the sycamore fig (*Ficus sycomorus* L.) may follow two courses (11):[1] (*a*) The full or regular course, which is undergone only by part of the figs, the so-called "fertile B" (BF) type. The growth of these figs follows a typical double sigmoid curve (Fig. 1), and they ultimately produce large, seedless, stimulative parthenocarpic fruit. (*b*) The abbreviated course, which is followed by the majority of figs in each crop, the so-called "sterile B" or BS type. These figs start swelling spontaneously very early, at the end of phase A. As a result, vegetative parthenocarpic fruit are formed within 3 to 4 days. While somewhat smaller than the former, these figs are sweet and edible.

In the Egyptian varieties of figs, no vegetative parthenocarpic fruit develop, since all figs are of the BF type. Upon inhabitation by sycophilous wasps, the figs undergo the full developmental course, ultimately producing large but heavily infested, inedible fruit. The ancient Egyptians evolved a unique technique for advancing the ripening of the figs before their infestation by wasps. This technique entailed gashing of the figs while at phase B on the tree, which resulted in very rapid growth, and ripening within 3 to 4 days.

Preliminary observations on the effects of various growth substances on figs at phase B have shown that ethylene plays a significant role in the ripening process (10). This led us to believe that the acceleration of ripening in gashed figs might be connected with increased ethylene production due to wounding of the tissues. The present study was set up to investigate the possible correlation between ethylene emanation and the morphological changes which occur in the fig during the full and abbreviated developmental courses. Special attention was given to the effects of gashing on ethylene emanation.

MATERIALS AND METHODS

Experiments were carried out on the figs of *Ficus sycomorus* L. var. Balami, growing on the campus of Tel-Aviv University. Syconia were labeled when the fig emerged from the bud scales; subsequently, a sample of figs was harvested every 2 to 3 days, weighed, and the fruit diameter was measured. Ethylene emanation was determined according to Burg and Burg (5). The figs were enclosed for 1 to 2 hr in jars of varying sizes, having volumes of 50 to 375 cc, according to size of syconia. Gas samples of 1 cc each were withdrawn from the jar with a gas-tight syringe every 15 min or (for phase C) every 5 min. The samples were injected into a Packard gas chromatograph equipped with a column 6 feet × ¼ inch, 80 to 100 mesh alumina and a flame ionization detector. The concentration of ethylene was determined by measuring the area of the peak with a disc integrator. After this measurement, the figs were dried at 80 C for 48 hr and then weighed. Ethylene emanation rate was calculated, considering only the time of linear increase of ethylene concentration in the jar, on the bases of μl/kg fresh weight·hr and μl/fig·hr. The instrument could detect ethylene at a concentration of 10 nl/l in a 1-ml sample.

Ripening stage was determined by color, texture, and taste of the figs, as determined by visual, manual, and individual organoleptic test, respectively. The diameter of the figs was measured with calipers to an accuracy of 0.05 mm.

All measurements were repeated three or four times with 3 to 10 jars per test and 2 to 10 figs in each jar.

Gashing was performed on attached figs, by inserting a scalpel to the fig's cavity, thus producing 11 mm wide cuts on the surface.

Various auxins (Sigma Chemical Co.) and Ethephon (as Ethrel, compound No. 68-250, Amchem Products, Inc. Am-

[1] Galil & Eisikowitch (11), divided the full development course of the sycamore fig into five phases, as follows (Fig. 1): Phase A (pre-female): young fig prior to opening of the ostiole. Phase of cell division. Phase B (female): ostiolar scales loosen, female flower matures, the impregnated females of the small wasp *Sycophaga sycomori* (Chalcidoidea, Torymidae) penetrate into the syconia and oviposit in the ovaries of female flowers. Phase C (interfloral): wasp larvae develop within the ovaries thus transforming them into galls. Phase D (male): male flowers mature, wasps reach the imago stage. Fertilized females emerge from their galls and enter the syconial cavity. Later they leave the fig via tunnels bored by the males. Rapid growth and beginning of ripening. Phase E (postfloral): continuation of ripening and rapid growth.

bler, Pa.) were sprayed on intact figs attached to the tree. IAA, 2,4-D, and 2,4,5-T were applied to the figs at concentrations between 0.1 and 200 μg/ml and Ethephon (2-chloroethylphosphonic acid) at concentrations between 25 and 50,000 μl/l.

RESULTS

Growth Pattern of the Syconium. Figure 1 shows the growth of figs as measured by various parameters during the normal and abbreviated developmental courses and after gashing. As can be seen from the data, the fruits show rapid increase in weight and size after gashing and during the abbreviated course of development.

Rates of Ethylene Emanation Throughout the Course of Development. Rates of ethylene emanation rose markedly before and during the phases of rapid growth and ripening (B, D, E, Figs. 2 and 3). The pattern of ethylene emanation expressed on the basis of fresh weight is different from that expressed per fig. The main differences occurred at phases A and C. At phase A the rate of ethylene emanation declined when expressed on the basis of fresh weight but was approximately constant when expressed per fig, except for a 2.7-fold rise on the 5th day. At phase C the rate of ethylene emanation on the basis of fresh weight was constant but rose significantly when expressed per fig. On the last day of phase C the rate of ethylene emanation increased significantly: 5.4- to 5.8-fold. This increase occurred about 20 hr before any increase in diameter could be detected.

Effects of Gashing at Phase BF. Gashing at this phase caused a 50-fold rise in the rate of ethylene emanation within one hr (Figs. 2 and 3). Gashing induced a very rapid increase in diameter as well as in the fresh and dry weights (Fig. 1). By the end of the 2nd day after gashing, the diameter showed a 1.7-fold increase, the fresh weight 2.1-fold increase, and the dry weight 1.8-fold increase. The corresponding increments in untreated control figs during the same period were 1.1-fold in diameter, 1.2-fold in fresh weight, and 1.3-fold in dry weight. No change in diameter or in fresh weight could be detected during the first 3 hours after gashing. During the 4th hr, however, an increase of 0.5 mm in diameter and of 0.2 g in fresh weight was recorded (Fig. 4), the ripening process commencing 1.5 to 2 days after gashing.

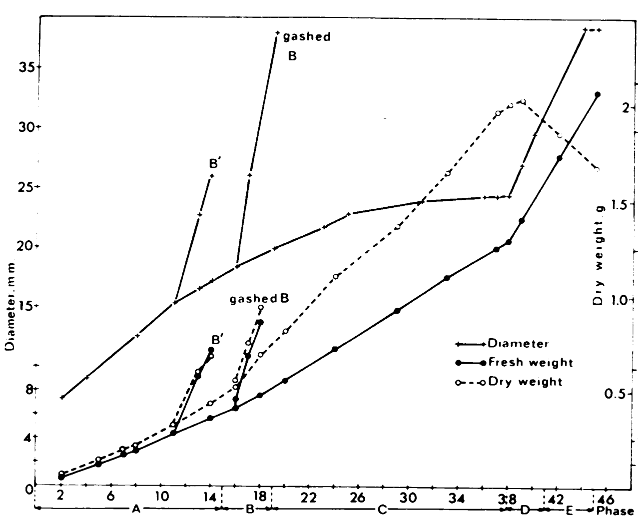

FIG. 1. Growth in diameter, fresh weight, and dry weight of a fig during the regular and abbreviated courses of development.

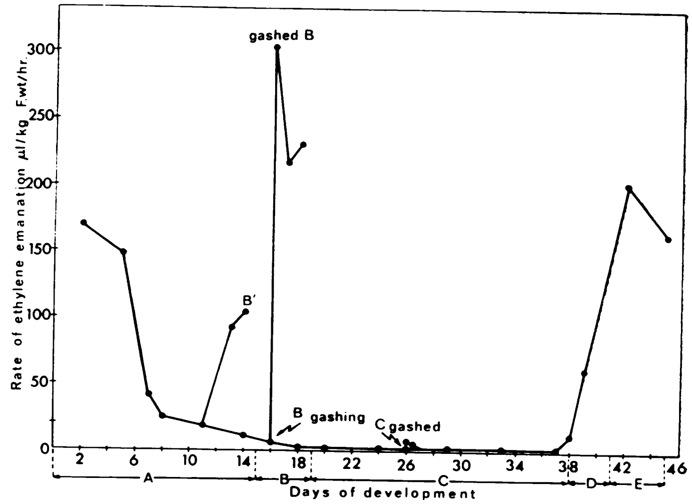

FIG. 2. Rates of ethylene emanation of syconia during the regular and abbreviated courses of development, expressed on a fresh weight basis.

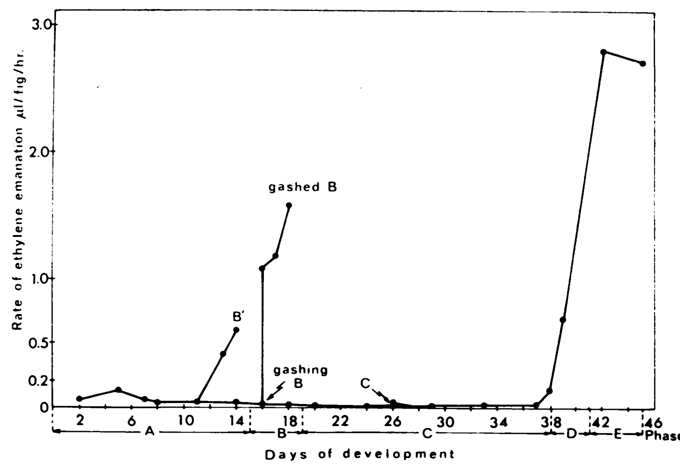

FIG. 3. Rates of ethylene emanation of syconia during the regular and abbreviated courses of development, expressed on a per fig basis.

The marked responses to gashing lasted through all of phase B and at least during the first 3 days of phase C.

Effects of Gashing at Phase C. Gashing of the syconium during most of phase C did not cause an increase in growth rate of the figs (Fig. 4), the gashed syconia following the regular course of development, as did untreated figs. Gashing induced within an hr a 3.5-fold increase in rate of ethylene emanation, as calculated on a fresh weight basis (Figs. 2 and 4). After the 1st hr there was a gradual decline, the level of ethylene emanation dropping to that of untreated fruits by the 27th hr.

Effects of Ethephon and Various Auxins on the Development of Syconia. Ethephon application induced ripening in all phases of syconial development. However, figs at phase **B** responded even to a concentration of 25 μl/l, whereas syconia at phase C reacted only to 500 μl/l or more. Thus, 350 μl/l of Ethephon induced ripening of just about the whole population of figs at phase **B**, whereas 10,000 μl/l was required for the syconia in phase C. Figs at phase A responded to the relatively low concentration of 50 μl/l, but complete ripening was induced only after treatment with 1 ml/l Ethephon (Fig. 5).

Ethephon applications accelerated also the rate of growth of

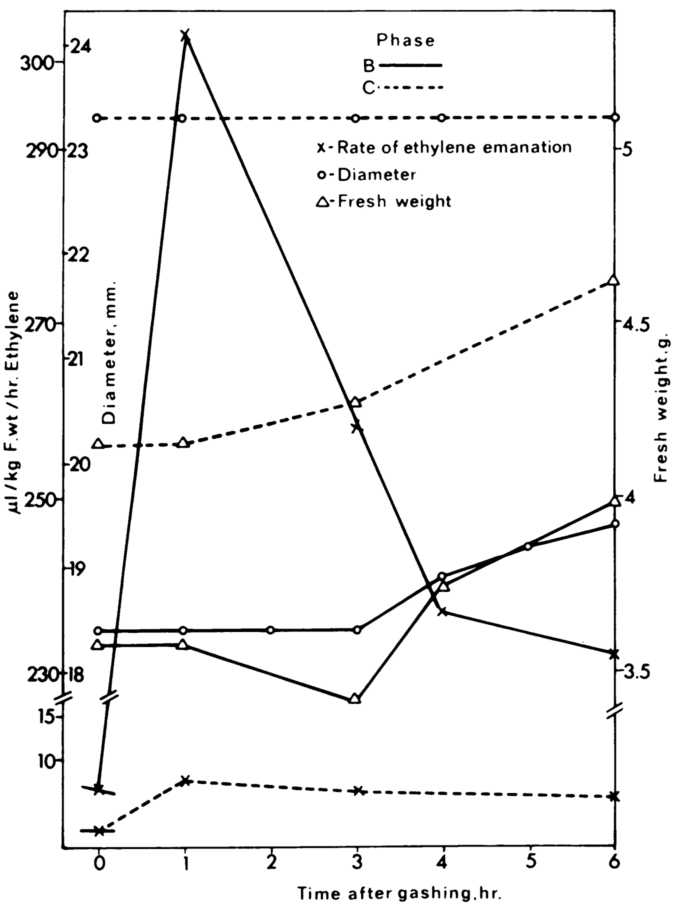

FIG. 4. Effect of gashing at phases B and C on the rate of ethylene emanation, the growth in diameter, and the fresh weight.

the syconia in phases B and C and induced an increase in their final size. The higher the Ethephon concentration, the greater was the diameter of the treated figs (Fig. 6).

Treatment with auxins during phase BF caused effects similar to those of gashing, that is, enhanced ethylene emanation, growth, and ripening. The effective concentrations of the various auxins used were: IAA 1 to 100 μg/ml; 2,4-D 0.5 to 200 μg/ml; and 2,4,5-T 0.5 to 200 μg/ml. Lower concentrations, such as 0.75 μg/ml of IAA or 0.25 μg/ml of either 2,4-D or 2,4,5-T, were not effective.

DISCUSSION

The pattern of ethylene emanation throughout the life of the fruit has been investigated for melons (14), tomatoes (15), and oranges (1, 2). The sycamore fig emanates relatively high amounts of ethylene, particularly in its early phases of development, when other fruits barely evolve any ethylene. At phase A, when the fig is still in the preanthesis stage, its ethylene production is rather high even in comparison with that of flowers. Hall and Forsyth (12) reported that the style and pistil produce 100 times more ethylene than the entire flower. The syconium develops its female organs at phase A and these parts might be responsible for the high rates of ethylene emanation at this phase.

The rate of ethylene emanation per fig showed a constant low pattern during phase A, but a rapid decline per kg fresh weight. This difference indicates that the fresh weight of the individual fig increases rapidly while the ethylene-synthesizing activity remains rather constant.

Similarly to other fruits, the fig shows a marked climacteric-like rise in ethylene production before the ripening in both phases D and E of the normal long course and in phase BS of the abbreviated developmental course of the syconium.

Gashing the sycamore fig or merely piercing it with a needle at phase B evokes the following remarkable results. (*a*) A very rapid rise in ethylene emanation, as much as a 50-fold increase within 1 hr. (*b*) A marked increase in the growth rate of the fig as early as 4 hr after gashing. (*c*) A rapid and uniform ripening of the whole syconium, starting 1.5 to 2 days after gashing. The sycamore fig is unique in this remarkable response to wounding. Although many other fruit have been reported to about double the rate of ethylene production after injury (17), Burg and Burg (6) observed that the slicing of apples reduced their level of ethylene production. Ben-Yehoshua *et al.* (4), McGlasson (17), and Palmer and McGlasson (18) showed that peeling or slicing of the avocado or banana accelerates its ripening by a few days. In comparison, however, the response of the sycamore fig to gashing is much greater and the increase in growth is altogether novel.

The following data strongly suggest that the increase in fig growth upon gashing is due to a rise in ethylene production. (*a*) Previous studies by Galil (10) have shown that the presence

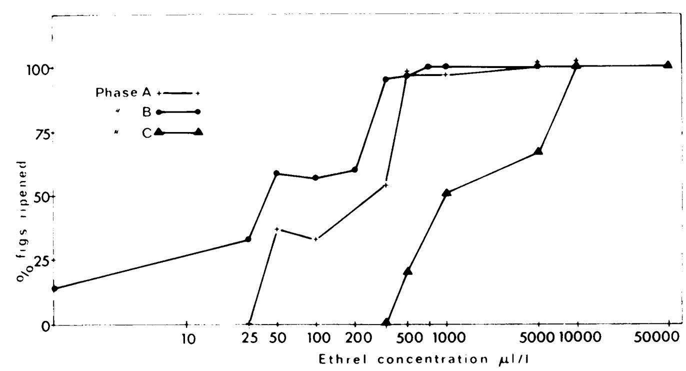

FIG. 5. Effects of various concentrations of Ethephon on the ripening of figs following treatment at phases A, B, and C.

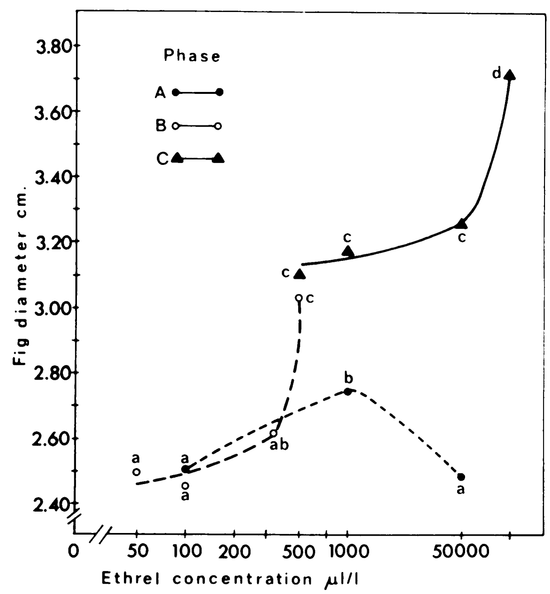

FIG. 6. Effects of various concentrations of Ethephon on the final size of the ripened syconia, following treatment at phases A, B, and C.

of a detached and gashed sycamore fig within a cellophane bag was sufficient to induce growth and ripening of attached intact figs enclosed in the same bag. (*b*) Ethephon application (which is now accepted as a practical way to apply ethylene; 19) also induced growth and ripening in rather low concentrations. Similar results were obtained by enclosing the fig panicle in a tightly sealed polyethylene bag containing 1 or 10 μl/l ethylene. (*c*) IAA, 2,4-D, and 2,4,5-T accelerate both ethylene production and fig growth, much as gashing did. The growth cannot be attributed to the direct action of auxins because Ethephon duplicated this effect, and ethylene is known to reduce the level of auxins in plant tissues (7). (*d*) The rise in ethylene production precedes the growth of the syconium regardless of the developmental course of the fig (Figs. 1–4).

The role of ethylene as an inducer of growth in fig fruit has been demonstrated also by Maxie and Crane with the common fig (16). Ben-Yehoshua *et al.* (3) and subsequently Crane *et al.* (9) showed that ethylene or Ethephon induced a marked mobilization of nutrients into the fig, thus accelerating considerably the accumulation of dry weight by the fruit. However, Iwahori *et al.* (13) have shown that Ethephon accelerates the maturation of the tomato fruit but not its growth. The patterns of development of the syconia of both the common fig and the sycamore fig differ from those of most fruit in that the ripening is accompanied by increase in diameter and weight of the fruit. Possibly ethylene accelerates growth of the syconia by hastening the ripening process. Byers *et al.* (8) have shown that Ethephon accelerates slightly the growth in diameter of peach fruit which like the common fig and sycamore fig but unlike the tomato exhibits a double sigmoid growth pattern. Evidently more extensive studies with a greater variety of fruits are necessary in order to clarify the exact role of ethylene in fruit development.

Gashing or Ethephon application of up to 500 μl/l did not induce grow and ripening of figs at phase C. The gashed figs did produce about 3.4 times more ethylene than the control figs, thus attaining the level reached by intact phase B figs, but parthenocarpy was not induced. The lack of response to gashing or Ethephon application at phase C, may be due to a reduced sensitivity to ethylene or else to the presence in the figs of an inhibitor of growth and ripening.

Phase A syconia apparently are also less sensitive to ethylene since these figs do not ripen although their rate of ethylene production is much higher than that at phase B. Few figs, particularly injured ones, might turn pink during phase A, but they drop before the syconium sweetens. Thus, a high rate of ethylene production is not *per se* sufficient to induce ripening at this early phase. Similar changes in sensitivity of fruit to ethylene during their development were reported by Burg and Burg (6).

The growth curve of the syconia as expressed by the increase in diameter differed from the curves expressed by the increase in fresh and dry weight. The difference was particularly conspicuous at phase C, when the fresh and even more markedly the dry weight kept rising at a more rapid rate than the diameter, and at phase D-E, when the dry weight declined significantly, while the diameter and fresh weight increased. These differences are due to the development within the syconium of the parasitic wasp *Sycophaga sycomori*. During phase C the larvae of the wasp and the nucellus of the figs' ovules keep growing rapidly. This growth contributes to an increase in fresh and dry weight but not to an increase in the syconium's diameter. The decline in dry weight during phases D and E might be attributable to the emergence of the mature wasps which contain a higher percentage of dry matter than the syconium.

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