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Ethylene, a Regulator of Young Fruit Abscission[1,2]

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ABSTRACT

In an earlier study we reported that detached cotton flowers produced sufficient ethylene before the period of natural abscission to suggest that ethylene might be a natural regulator of young fruit abscission. The present report explores this probability further. Intact cotton (*Gossypium hirsutum* L.) fruits produced ethylene at rates as high as 36 μl ethylene/kg fresh wt·hr during the 2 days before they abscised. Direct measurements of ethylene in gas samples withdrawn from fruits indicated that production of 1 μl ethylene/kg fresh wt·hr is equivalent to an internal concentration of approximately 0.1 μl/l. Fumigation of fruiting cotton plants with only 0.5 μl/l caused 100% abscission of young fruits and floral buds within 2 days. This correlated with the estimated endogenous levels of ethylene. Reduced pressure, which reduced the internal levels of ethylene, delayed abscission of young fruits and leaves, a result which supports our conclusion from this study—that ethylene is one of the regulators of young fruit abscission in cotton.

There is considerable evidence that ethylene is produced by flowers and young fruits where it has usually been associated with petal fading and abscission (17). The capacity of exogenous ethylene to stimulate abscission of young fruits and buds is well known (9). However, a possible role of ethylene as a regulator of young fruit abscission has received relatively little attention. Hall *et al.* (9), using rather insensitive methods, noted that intact cotton plants did not produce significant amounts of ethylene until the initiation of the reproductive stage—indicating that squares and young fruits possibly produced significant amounts of ethylene. Teubner and Murneek (19) noted that aborting apple fruits produced ethylene, and they suggested that ethylene may have a part in young fruit abscission. Heilman *et al.* (10) found that cotton flowers produced relatively large amounts of ethylene, and they proposed that a buildup of ethylene under the plant canopy may cause fruit abscission. Recently, Blanpied (2) found that high ethylene levels were associated with flower abscission in apple and cherry.

We have observed that significant amounts of ethylene were produced by developing cotton fruits during the period just preceding young fruit abscission (12). This observation prompted the additional investigations reported here. We have studied in detail the production of ethylene relative to young fruit abscission of cotton and okra, the relationship of ethylene production rates to internal levels in the fruits, the effect of low levels of exogenous ethylene on fruit abscission, and the effect of reduced pressure on fruit and leaf abscission.

MATERIALS AND METHODS

Ethylene production by detached floral buds, flowers, and fruits of okra (*Hibiscus esculentus* L.) was monitored. Buds, flowers, and fruits were sampled from field-grown Louisiana Green Velvet variety plants growing under near optimal fruit set conditions—temperatures near 34 C during the day and 24 C during the night. Other floral buds, flowers, and fruits were sampled from field-grown USDA Plant Introduction No. 65 growing under poor conditions for fruit set—temperatures of 18 to 25 C during the day and 5 to 15 C during the night. Ethylene production was measured from material ranging from buds 3 to 4 days before bloom, to fruits 3 to 4 weeks old. Each group of samples over this age range was collected at the same time. Samples of each age of tissue were replicated three times with three buds, flowers, or fruits per flask.

Ethylene production by intact floral buds, flowers, and fruits of cotton (*Gossypium hirsutum*, L. cv. Stoneville 213) was monitored and observed relative to abscission. Floral buds were enclosed in 400-ml glass chambers described previously (11). In one experiment, where little abscission occurred, ethylene production was monitored at 3-hr intervals during the day and 4.5-hr intervals during the night. A similar experiment was conducted with different plants which had passed the phase of maximum fruit set, and all of the young fruit abscised. Ethylene production was checked at 5-hr intervals during the day and a single 9-hr interval during the night. Chambers were opened and aired out to remove accumulated ethylene after the analysis at the end of each collection period. Collection of gas samples and analysis of ethylene was done as in earlier experiments (11). Growthroom conditions for this portion of the study included a 15-hr photoperiod (2000 ft-c) at 30 C, 9 hr of darkness at 24 C, and constant 70% relative humidity.

Ratio of Internal Ethylene Concentration to Ethylene Production. The ratio of internal concentrations of ethylene to production of ethylene by young cotton fruits was determined so that ethylene production rate data could be used to calculate approximate internal ethylene levels. This allowed levels of ethylene used in fumigation studies to be selected that would approximate those which occur naturally. A population of fruits of Stoneville 213 cotton was sampled at times ranging from the day of anthesis to 8 days after anthesis. One group of fruits was sampled during a period of no abscission, while a second group of fruits was sampled during a period of considerable abscission. (When cotton begins to flower, fruit set

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is high initially, but it declines considerably with time as the plant becomes loaded with fruit.) Immediately after detachment, individual fruits were stoppered in 500-ml Erlenmeyer flasks, and ethylene production was measured after 2 to 3 hr. The actual level of ethylene that accumulated in the flasks was so small as to have an insignificant effect on the ethylene levels subsequently observed in the fruits. Internal ethylene was then measured from 0.2 to 0.5 cc air samples withdrawn from each fruit while holding it under water. Air samples were taken by inserting the needle of a gas-tight syringe into the fruit. From the data a ratio of internal ethylene levels (μl/l air) to ethylene production (μl/kg fresh weight·hr) was calculated.

Fumigation with Ethylene. The effect of ethylene on young fruit abscission of cotton was studied in two experiments involving two levels of ethylene. Flowering plants of the Stoneville 213 cultivar were enclosed in 260-liter Plexiglas chambers (1 plant/chamber), and single chambers were fumigated with 0.5 μl of ethylene and 0.1 μl of ethylene per liter air (μl/l). Ethylene levels were verified gas chromatographically and were found to decline from 0.5 to 0.3 and from 0.1 to 0.03 μl/l respectively at the end of each 24-hr period. This decline was assumed to be due to absorption of the ethylene into the peat moss-perlite growing media, since the absence of leakage from the chambers was verified. Treatment with each level of ethylene was replicated twice—once under each of the two sets of conditions. One group of plants was under 100 ft-c light at 32 C for the duration of the experiment. Another group of plants was fumigated under a 15-hr photo-period (2000 ft-c) at 33 C with a night temperature of 24 C. A dish containing saturated potassium permanganate mixed with two parts vermiculite and one part celite was put in the control chamber to absorb any plant-produced ethylene. Beakers of 10% KOH were kept in all chambers to absorb excess CO_2. Young fruit and floral buds were touched lightly each day to test abscission.

Reduced Pressure. The effect of reduced pressure on abscission of leaves, floral buds, and young fruits of cotton was observed. Flowering Stoneville 213 cultivar plants were placed inside 24-liter chambers consisting of two 12-liter bell jars placed end to end. The plants were maintained under a reduced pressure of 200 mm Hg with an air flow of approximately 1000 ml/min to prevent accumulation of ethylene (11). A 1-gallon pot with one or two plants was placed inside each chamber with two chambers per treatment. The plants under reduced pressure were allowed to become water stressed to a leaf water potential of approximately −28 bars (determined with a pressure bomb) and then were rewatered (18). Control plants received the same treatment, but at atmospheric pressure. Severe water stress and rewatering were employed to stimulate maximum abscission (14), thereby creating a large potential difference between the treated (reduced pressure) and control (atmospheric pressure) plants.

At 200 mm pressure, 3 days were usually required for plants to become stressed to −28 bars, whereas plants in the control usually took 5 days to reach this stress level. The data were corrected to report the abscission each day with respect to the time of rewatering for each treatment. Young fruit, floral bud, and leaf abscission was recorded daily until completed—generally within 5 days after rewatering.

RESULTS

Time Sequence of Ethylene Production and Abscission. Results from an earlier, well replicated study (daily samples, 3 fruit/sample, 3 samples/day) revealed that detached cotton fruits produced ethylene at a rate of approximately 3 to 4 μl/kg fresh weight·hr on the day of bloom and the next 3 days (15). Maximum young fruit abscission of approximately 15% occurred 3 days after bloom and was essentially complete 6 days after bloom, with a total of over 40% of the young fruits abscised (11).

To extend the initial observations on detached cotton fruits, the production of ethylene by detached flower buds and young fruit of okra was observed. Okra that was growing under conditions detrimental to fruit setting, night temperatures of 5 to 15 C and days of 12 to 24 C, produced ethylene in a pattern similar to the young fruit of cotton described previously. All okra fruits that abscised (estimated as 80%) were 1-day-old fruits. More than 5 μl ethylene/kg fresh weight·hr was produced by these 1-day-old okra fruits. No abscission occurred in fruits that had developed beyond this age, and ethylene production correspondingly was well below 1.0 μl/kg fresh weight·hr. Okra that was growing under warm summer conditions optimum for fruit-set produced much less ethylene (Fig. 1). Fruit abscission was less than 1.0%, and maximum ethylene production by detached fruits 1 day after bloom was only 0.27 μl/kg fresh wt·hr. Peak ethylene production of 1.15 μl/kg fresh weight·hr occurred on the day of bloom. Pollination and petal fading possibly contributed to this (1, 5). Note in Figure 1 that these fruits also produced approximately 1.2 μl ethylene/kg fresh weight·hr on the day of bloom. Thus, a survey of the time sequence of ethylene production and abscission in detached fruits of field-grown cotton, floral buds, and fruit of okra indicated that ethylene may influence young fruit shed.

Our next step was continual collection and frequent monitoring of ethylene production by intact young cotton fruits (Figs. 2 and 3). All of the fruits exhibited a very marked diurnal fluctuation in ethylene production with only a trace occurring at night in most cases. Fruits that did not abscise produced as much as 9.3 μl ethylene/kg fresh weight·hr during the day (Fig. 2). Peak ethylene production by these fruits usually occurred on the day of bloom. No fruits were abscising from the plants used in this portion of the study.

The pattern of ethylene production by fruits from a population in which 50% of the young fruits were abscising (Fig. 3) was markedly different from the production pattern for fruits from a nonabscising population (Fig. 2). The fruits which eventually abscised all produced relatively low amounts of

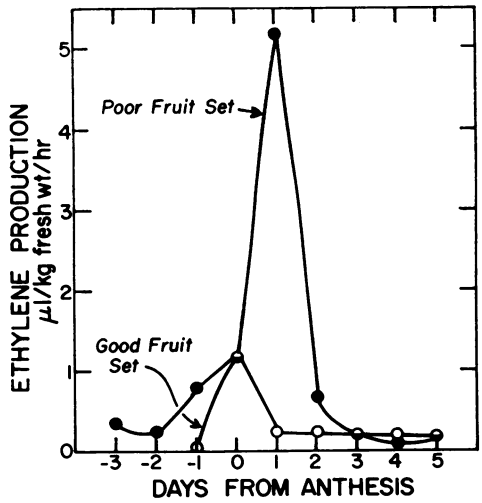

FIG. 1. Ethylene production by detached fruits of field-grown okra (USDA Plant Introduction 65) under conditions detrimental to fruit setting (poor fruit set) and by field-grown Louisiana Green Velvet cultivar okra under conditions favorable to fruit set (good fruit set).

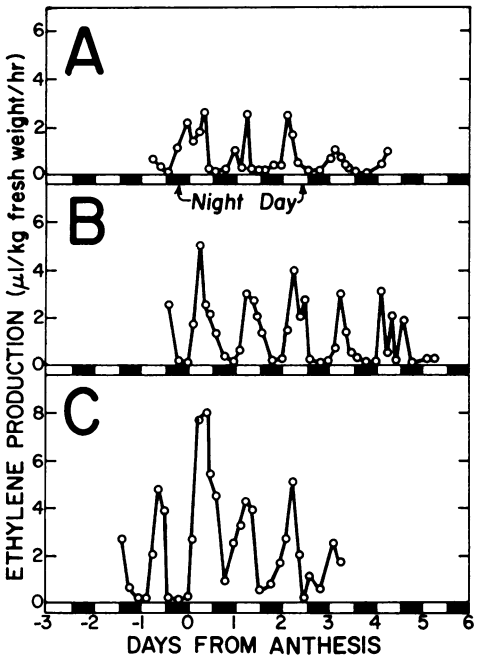

FIG. 2. Diurnal pattern of ethylene production by three intact young fruits of cotton during a period of little young fruit abscission.

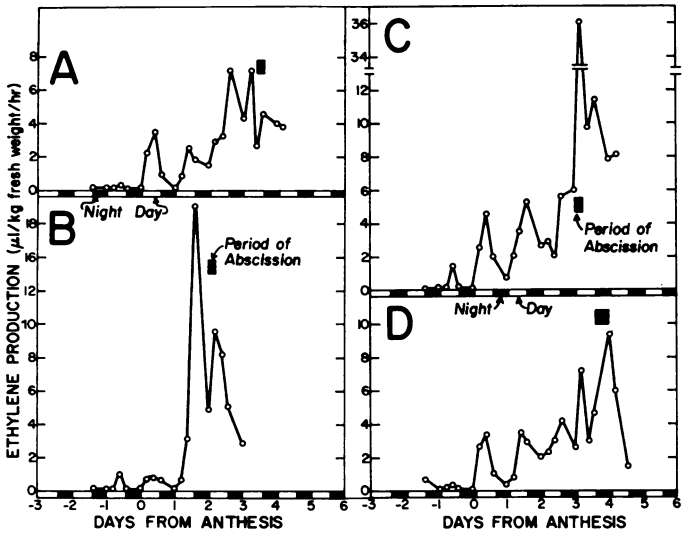

FIG. 3. Diurnal pattern of ethylene production by four intact young fruits of cotton during a period of considerable young fruit abscission. Fruit abscission is represented as the period of time from initial visible formation of the abscission zone until actual abscission.

ethylene prior to bloom (Fig. 3). As the fruits neared abscission, they produced increasingly large daily "waves" of ethylene that sometimes culminated with a large burst of ethylene from 2 or 3 to 12 hr preceding abscission (data shown in Figs. 2 and 3 are representative from about one-half of the fruits that were monitored).

A correlation between the length of time which maximum ethylene production preceded abscission and the magnitude of production is apparent in Figure 3. The closer the peak of ethylene production was to fruit abscission, the higher was the absolute production rate.

Ratio of Internal Ethylene Concentration to Ethylene Production. The ratio of internal ethylene concentration (μl/l) to ethylene production (μl/kg fresh weight·hr) was observed to increase generally as fruits aged, *i.e.*, older fruits contained more internal ethylene relative to emitted ethylene (Table I). Also, fruits that were sampled during a period of considerable young fruit abscission had a noticeably higher ratio than comparable fruits sampled during a period of no abscission. The ratio for fruits from plants that were experiencing no abscission ranged from 0.010 on the day of bloom to 0.076 (μl/l internal/μl·kg hr produced) 6 days after bloom. In fruits from the shedding population, the ratio ranged from 0.014 on the day of bloom to 0.187 six days after bloom. Most young fruits abscised during the first 4 days after anthesis (Fig. 3). Comparison of the average ratio of internal ethylene/ethylene production (0.028) during this period with maximum ethylene production by fruits in Figure 3 indicates that abscising fruits contain between 0.20 and 1.00 μl/l ethylene for periods of 1 to 2 days before they abscised. It should be pointed out that these calculated concentrations of internal ethylene in abscising fruits are admittably rough, but they provided a reference point for selecting concentrations for ethylene fumigation studies. Calculated values of ethylene content are used rather than direct measurements because it was felt that calculated values based on fruits actually in the process of abscising would provide a more accurate index of ethylene in abscising fruits than would direct measurements of ethylene from fruits (Table I) not necessarily in the process of abscising.

Fumigation with Ethylene. Based on the calculated range of 0.20 to 1.00 μl/l ethylene in fruits before they abscised, fumigation of intact fruits with 0.5 and 0.1 μl ethylene/l air was considered to provide levels of ethylene well within the physiological range. Young fruits and floral buds of cotton were readily stimulated to abscise by fumigation with 0.1 and 0.5

Table I. *Internal Concentration of Ethylene Relative to Ethylene Production by Young Fruits of Stoneville 213 Cotton*

The upper group of fruits was sampled during a period of no young fruit abscission. The group designated "abscission" was sampled during a period of considerable young fruit abscission, although none of the fruits samples were abscised. Each sample consisted of 1 fruit.

Days after Bloom	Ethylene Production	Internal Ethylene	Ethylene Ratio (internal/produced)
	μl/kg fresh weight·hr	*μl/l*	
No abscission			
0	5.72	0.062	0.011
0	6.85	0.071	0.010
0	6.77	0.073	0.011
2	2.53	0.061	0.024
2	4.65	0.215	0.046
2	1.34	0.033	0.025
4	1.92	0.051	0.027
4	2.60	0.081	0.031
4	5.40	0.348	0.071
6	1.32	0.100	0.076
6	1.07	0.028	0.026
Abscission			
0	7.24	0.149	0.021
0	8.36	0.117	0.014
2	1.64	0.296	0.180
2	0.58	0.040	0.069
6	0.78	0.146	0.187
6	0.26	0.040	0.154

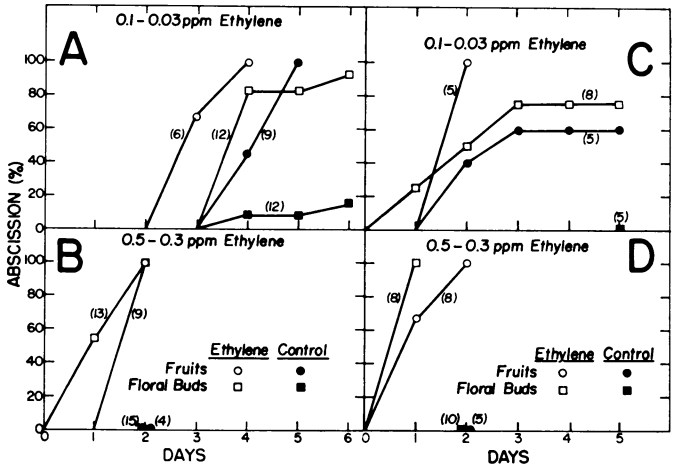

FIG. 4. The effect of physiological levels of ethylene on abscission of floral buds and young fruits of cotton. Fruiting Stoneville 213 plants were fumigated with 0.1 μl/l (A, C) and 0.5 μl/l (B, D) ethylene. Plants in A and B were under continual low intensity light at 32 C. Plants in C and D were under a 15 hr-photoperiod (2000 ft-c) at 34 C and a night temperature of 24 C. Control plants for the 0.5 μl/l ethylene treatment (B, D) were discontinued after 2 days with no abscission. The total number of each organ involved is in parenthesis next to the appropriate abscission curve. Percentage of abscission was recorded daily.

μl/l ethylene (Fig. 4). Fumigation with 0.1 μl/l ethylene speeded abscission of fruits by at least 1 day and caused considerable abscission of floral buds while a total of only 2 or 17 floral buds from the controls abscised (Fig. 4, A and C). The constant temperature of 32 C was optimal for fruit abscission (16) and probably was a factor in the high rate of abscission of control fruits (Fig. 4, A *versus* C).

Abscission of all young fruits and floral buds occurred within 2 days after fumigation with 0.5 μl/l ethylene (Fig. 4, B and D). No fruits or floral buds had abscised from the control plants after 2 days; they were then transferred to a greenhouse where no abscission occurred during the following week. Under both sets of environmental conditions, 0.5 μl/l ethylene caused floral buds to abscise sooner than fruits—a reversal of the abscission pattern caused by 0.1 μl/l ethylene. Leaves were not visibly affected during or after exposure to either of the levels of ethylene.

Reduced Pressure. Abscission of young fruits, floral buds, and leaves was markedly delayed on intact cotton plants held at 200 mm pressure (Fig. 5). Organs on plants under reduced pressure did not abscise until after plants were rewatered, whereas abscission often began several days before control plants reached a water stress level of −28 bars. Abscission of almost 90% of the cotyledonary leaves from control plants had occurred by the time of rewatering (Fig. 5A); however, most of the cotyledonary leaves on plants under reduced pressure abscised 2 days after rewatering. Floral buds and leaves from control plants began to abscise 2 days after rewatering and had reached 38 and 36% abscission, respectively, when the experiment was terminated 5 days after rewatering. Only one leaf (3.5%) and no floral buds abscised from plants held at 200 mm pressure.

Data in Figure 5B are from older flowering plants that had lost their cotyledonary leaves. Young fruits, floral buds, and leaves began to abscise from control plants several days before they were rewatered. Abscission of floral buds on plants under reduced pressure was delayed considerably more than abscission of fruits. Only 28% of the floral buds on the treated plants abscised while all floral buds on the corresponding control plants abscised (Fig. 5B). The delay in abscission of fruits under reduced pressure was less striking, as 60% of these friuts had abscised within 5 days after the plants were rewatered (Fig. 5B). However, abscission of fruits on the control plants still occurred much sooner. Abscission of leaves and floral buds from plants under reduced pressure remained well below abscission from the control 5 days after the plants were rewatered. Leaf abscission was 17% from plants under reduced pressure (Fig. 5B), whereas 40% of the leaves on the control plants abscised.

DISCUSSION

In order for ethylene to be one of the regulators of young fruit abscission, it must be produced in adequate amounts, long enough before fruit abscission to cause the response. These criteria are clearly established for cotton fruits by the results of this study.

Individual intact young cotton fruits produced from 4 to 36 μl ethylene/kg fresh weight·hr during the 1 to 2 days before they abscised (Fig. 3B). Detached cotton fruits produced from 2.5 to 4 μl ethylene/kg fresh weight·hr from anthesis until the beginning of young fruit abscission 3 days after anthesis (text and ref. 11). Use of the average ratio of internal ethylene to ethylene production, approximately 0.028 (from fruits sampled within 4 days after bloom, during a period of considerable young fruit abscission, Table 1), indicates that production of

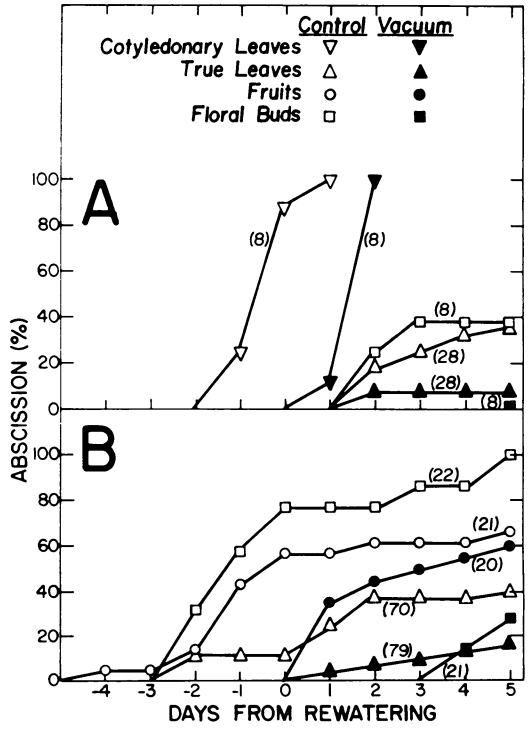

FIG. 5. Effect of reduced pressure on abscission of young fruits, floral buds, and leaves of cotton. Stoneville 213 plants were stressed to a water potential of approximately −28 bars and then rewatered (day 0). Treatment plants were under 200 mm pressure while controls were at atmospheric pressure. Plants in A were used shortly before the initiation of bloom, while plants in B were in full bloom and had already shed their cotyledonary leaves. The total number of each organ involved is in parentheses next to the appropriate abscission curve. Fruits that were more than 10 days from anthesis on day 0 were not included in the data. Percentage of abscission was recorded daily.

4 to 36 μl ethylene/kg fresh weight·hr represents an internal ethylene concentration of about 0.11 to 1.00 μl/l. Young fruits and floral buds were stimulated to abscise when fumigated with 0.1 μl/l and 0.5 μl/l ethylene. Thus, abscising fruits appeared to contain appreciably more ethylene than was necessary to stimulate abscission.

The data on ethylene production by young okra fruits lend qualitative support to the hypothesis that ethylene is a regulator of young fruit abscission. Fruits from okra plants that were experiencing considerable young fruit abscission produced an average of 5 μl ethylene/kg fresh weight·hr, whereas fruits from plants with no young fruit abscission produced only 0.25 μl ethylene/kg fresh weight·hr during a comparable stage of development (Fig. 1).

Cotton fruits that did not abscise (Fig. 2) generally produced more ethylene during the days before and 1 day after anthesis than was produced by fruits that abscised (Fig. 3). However, the pattern of ethylene production by fruits from the two populations was entirely different. After anthesis ethylene production by the nonabscising flowers dropped to a very low level in 4 days, while production reached a maximum 2 to 4 days after anthesis in those fruits that abscised. The peak production rates were higher in the latter case (Fig. 3), than in the former (Fig. 2). The difference in the pattern of ethylene production plus the association of the highest levels of production with time intervals near the time of abscission may explain the different behavior of the two populations.

The high ethylene production in the days near anthesis of the nonabscising fruits probably includes some auxin-induced ethylene production associated with pollination (1, 8). High levels of auxin and other juvenile hormones in these fruits may have helped prevent abscission (6, 7, 20). The static system of ethylene collection undoubtedly affected abscission of the fruits, since all of the fruits in Figure 4 abscised while only about 50% of the total population was abscising. However, in a substantial number of cases the buildup of ethylene around enclosed fruits was inadequate to cause abscission (Fig. 2).

The rhythmic pattern of ethylene production by intact cotton fruits (Figs. 2 and 3) is possibly a combined response to daily light and temperature changes. Light is necessary for ethylene synthesis by model systems and these systems are enzymatically activated (21). Thus, the low production during the night may result from a depletion of light synthesized substrate and slowed enzyme activity.

The ratio of internal ethylene to ethylene production was more than 3-fold greater for the fruits sampled during the period of young fruit abscission (Table I); however, the number of replications was small. Therefore, this aspect of the problem deserves further attention. The obvious differences in ratios of ethylene in abscising and nonabscising populations of fruits may be related to the presence or absence of abscission in the two populations observed. Possibly more of the ethylene from abscising fruits was produced internally or the fruits differed in their resistance to diffusion. The fruit walls of several fruits appear to be formidable barriers to gas exchange (3).

The effects of reduced pressure were observed to aid in determining whether or not ethylene acts as a regulator of young fruit abscission. Reduced pressure was quite successful in delaying abscission of fruits, floral buds, cotyledonary leaves, and true leaves (Fig. 5), apparently by removing ethylene from the tissue. This contention is supported by the data of Burg and Burg (4) and our observations that reduced pressure and 13% CO_2 delay fruit dehiscence (12), which also appears to be under ethylene control.

McMichael *et al.* (13, 14) have shown that water-stressing cotton plants causes accelerated ethylene production with subsequent abscission of leaves and young fruits upon rewatering. Severe water stress and rewatering were employed here as a tool to cause a major increase in ethylene production and abscission, thereby creating a situation where a delay or reduction of fruit and leaf abscission would be very apparent.

There was a differential response to reduced pressure by fruits and floral buds. Very little abscission of floral buds occurred, whereas young fruits were delayed only a few days under reduced pressure.

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