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Nucellar Senescence and Ethylene Production as they Relate to Avocado Fruitlet Abscission[1]

TOM L. DAVENPORT AND MALCOLM M. MANNERS[2]

University of Florida, IFAS Agricultural Research and Education Center, 18905 SW 280 St., Homestead, FL 33031

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ABSTRACT

Events preliminary to avocado (*Persea americana* Mill) fruitlet abscission include senescence of the nucellus and seed coat. The dynamics of nucellar deterioration and ethylene production leading to seed abortion and abscission in avocado was examined. Excised branches bearing clusters of fruit from 1·0–2·5 cm diameter were placed in humid chambers to reduce transpirational water loss. Fruitlets synchronously began nucellar and seed coat deterioration 27–33 h after excision and rapidly progressed through stages of increasing degradation culminating in abscission approximately 2 days later. The nucellus-seed coat produced a temporary burst of ethylene at the first visible sign of nucellar senescence followed by less ethylene production in the mesocarp approximately 12 h later. All fruit underwent nucellar degradation prior to abscission. Exogenously applied ethylene accelerated fruitlet abscission with concentrations as low as 1·0 μl l^{-1} and with maximum response at 100 μl l^{-1} or greater. Maximal response took 2 days. Aminoethoxyvinyl-glycine (AVG) at 30 μM inhibited ethylene production and fruitlet abscission. The senescence process, however, was not affected in any way by ethylene or AVG treatments. Observations of attached fruit suggest that nucellar-seed coat senescence, concomitant ethylene production, and resulting abscission take place in a manner and within a time period similar to that observed on detached branches. It is concluded that nucellar and seed coat senescence is prerequisite to avocado fruitlet abscission, and the time required from the first indication of nucellar breakdown to abscission of that fruitlet appears to be approximately 2 days. The senescence process is responsible for a large, transient rate increase in ethylene production by the nucellus and perhaps seed coat. Ethylene is considered to be the result rather than the cause of nucellar-seed coat senescence. The ethylene thus produced induces fruit abscission.

INTRODUCTION

Many varieties of avocado set a large number of fruitlets at the time of flowering. Along with flower abscission, the fruitlets separate initially at a high rate, gradually decreasing in rate as the fruit load is reduced over time until horticultural maturity is reached (Adato and Gazit, 1977*a*). Blumenfeld and Gazit, 1974, observed that a shrivelled, brown seed coat was often found in abscising 'Fuerte' avocado fruitlets. Adato and Gazit (1977*a*) demonstrated that during the period of decreasing fruitlet abscission there was also a parallelling decrease in the incidence of these defective or aborted seeds. Their results suggested that the high incidence of seed coat deterioration was related to increased ethylene production which in turn correlated with fruitlet abscission (Adato and Gazit, 1977*a*, *b*). They estimated that the time required from peak ethylene production to fruitlet abscission was 3 weeks.

In studies conducted on West Indian varieties grown in South Florida, we too have noted that fruitlet abscission was associated with seed coat senescence. However, when one

[1] Florida Agricultural Experiment Stations Journal Series No. 3279.

[2] Present address: Dept. of Citrus, Florida Southern College, Lakeland, Florida 33802.

compared fruitlets in the active process of abscission with those still firmly attached, rarely was a brown or deteriorated seed coat found in a firmly attached fruitlet. These observations suggested that seed coat senescence was a relatively rapid process measured perhaps in hours, culminating in fruitlet abscission. This paper describes the dynamics of seed abortion, ethylene production and how these events are related to abscission of developing avocado fruit.

MATERIALS AND METHODS

Ethylene production

Terminal branches bearing fruitlet clusters of avocado (*Persea americana* Mill cv. Simmonds) were harvested in April 1980 from a commercial grove. All leaves were removed to reduce transpirational water loss. All fruit were tested for abscission by gently pulling on each, a technique which readily identified those fruit which were in the process of abscission. Fruitlets ranged in diameter from 1·0–2·5 cm and mass from 2·0–17 g. The fruit-bearing branches were recut under water and placed in a 60 l Plexiglass chamber within 3 h after harvest. A flow of humid, ethylene-free air at 1·0 l min^{-1} was maintained in the sealed chamber throughout the course of the experiment to avoid accumulation of ethylene and fruitlet desiccation.

Every 6 h (beginning 9 h after harvest) the chamber was opened, and all fruitlets were tested for abscission by a gentle pull. Ten fruitlets were then harvested for observation. Five of these fruitlets were individually weighed, placed in 30 ml beakers, and sealed with heavy duty Saran Wrap® and rubber band. Preliminary tests showed no significant loss of ethylene in the concentrations encountered or production of ethylene by the saran film over this period. The remaining five fruit were longitudinally bisected. The embryonic tissues (cotyledons and endosperm), nucellus-seed coat, and mesocarp were easily separated without damage, individually placed into beakers after being weighed, and sealed with saran. After 2 h incubation at room temperature, several layers of cellophane tape were gently placed on the saran, and a 1·0 ml gas sample was taken into a syringe by piercing the tape thus avoiding tearing the saran with the hypodermic needle. Each gas sample obtained from the whole fruit or fruit parts was injected into a Varian 3700 Series gas chromatograph equipped with 80–100 mesh alumina in a 6 ft × 1/8 in stainless steel column and flame ionization detector. Whole fruitlets were bisected. Each fruitlet was observed for development and extent of nucellar, seed coat, and embryonic deterioration at the time of ethylene assay or dissection. Preliminary studies indicated that the fruit exhibited no wound ethylene in response to any manipulation employed in this study.

Ethylene fumigation

Because of the relatively high respiratory rate exhibited by young avocado fruit (Akamine and Goo, 1973) it was found that results obtained from ethylene fumigated fruit in static chambers, regardless of size, were unreliable. Therefore, a flow-through system was constructed to meter ethylene into a humid air stream (60 l h^{-1}) before entering the enclosed chambers. Branches bearing fruit were excised as described above and placed in the chambers within 1 h after excision. Ethylene concentrations (0, 1, 10, 100, 500 $\mu l\ l^{-1}$) were monitored daily. The progress of nucellus and seed coat senescence as well as abscission of the fruit were checked daily. Each time the chamber was resealed, the proper amount of ethylene was injected into the chamber to reduce any time lag that might exist in returning to the intended ethylene concentration.

Ethylene synthesis inhibition

Aminoethoxyvinylglycine, AVG, a potent inhibitor of ethylene synthesis in many plants (Adams and Yang, 1979; Baker, Lieberman, and Anderson, 1978; Owens, Lieberman, and Kunishi, 1971) was applied to fruitlets borne on detached, defoliated branches. The effective concentration, 30 μM, was found in preliminary tests to be much higher than that required in many plants (Baker *et al.*, 1978; Kende and Hanson, 1976; Owens *et al.*, 1971). Detached, fruit-bearing branches were sprayed to run off with 30 μM AVG and 0·1% Triton X-100 approximately 1 h after harvest of the branches. After drying, they were placed in a 60 l Plexiglass chamber along with control branches sprayed with 0·1% Triton X-100. All fruitlets were checked daily for abscission. Five fruit from each treatment were assayed daily for ethylene production and for indication of tissue senescence.

Ethephon application to attached fruit

Applications of 0·1% Triton X-100 with or without ethephon (500 and 1000 $\mu l\ l^{-1}$ were made to fruit

clusters borne on trees in a commercial grove. Each treatment was applied approximately 1, 2, and 3 weeks after full bloom to 10 inflorescence groups, each on five trees. Observations on the number of remaining fruit were made biweekly for 5 weeks and again at horticultural maturity.

RESULTS

Longitudinal, median slices of sound, firmly-attached avocado fruitlets were characterized by having bright green mesocarp, bright white seed coat, white to slightly green nucellus, and yellow endosperm (Fig. 1A). The cotyledons also had a healthy, white colour. The first visually perceivable changes leading to abscission took place in the nucellus. This tissue took on a grayish cast (Fig. 1B). Nucellar breakdown appeared to initiate uniformly throughout. The intact endosperm of the cut fruit appeared darker than usual as well, but excision of the endosperm revealed that this change was due to the difference in background colour of the nucellus rather than to a change in the endosperm colour. The discoloration increased and spread to the integuments becoming obviously brown in colour (Fig. 1C). The embryonic tissue appeared to be unaffected at this point; however, the darkening lesion in many cases spread to the cotyledons (Fig. 1D). Many affected embryos became water soaked, or most often they appeared to shrink, leaving a cavity between the embryonic tissue and nucellus. Necrosis of the embryonic tissue occurred as well. Deterioration at times advanced to the point where the affected integumental tissue became black before abscission occurred. For convenience, four distinctive phases of fruitlet deterioration represented by Fig. 1 may be classified numerically as described in Table 1.

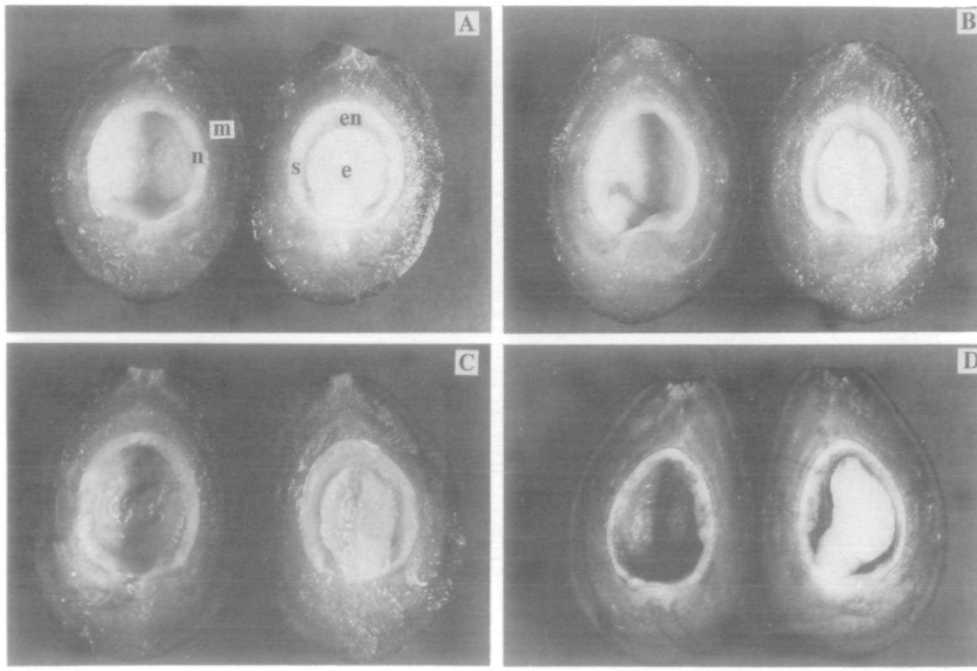

FIG. 1. Median, longitudinal slice of avocado fruitlets in progressive stages of nucellar and seed coat senescence. A. Sound, healthy avocado fruitlet. B. First observable indication of nucellus deterioration. Nucellus acquires grayish cast. Endosperm appears darker as a result. C. Obvious brown discoloration of nucellus. Discoloration spreads to seed coat. D. Dark brown to black nucellus. Shrunken embryonic tissue. Symbols: m, mesocarp; s, seed coat (integuments); n, nucellus; en, endosperm; e, embryo (cotyledons).

TABLE 1. *Description of avocado fruitlets at various stages of seed coat deterioration*

Stage	Remarks
0	White to slightly green nucellus
	Bright white seed coat
	Yellow endosperm
	White cotyledons
1	Nucellar tissue acquires grayish cast
	Seed coat and embryonic tissue unchanged
2	Nucellus and seed coat obviously brown
	Intact endosperm of cut fruitlet perceived to be darker in colour (but only result of darker nucellus)
	Seed coat and embryonic tissue unchanged
3	Seed coat and nucellus darker than above
	Cavity forms between nucellus and embryonic tissue
	Lesion spreads to embryonic tissue

In the experiments described here, events leading to abscission of the fruitlets from excised branches occurred synchronously which revealed the dynamics of nucellar-seed coat senescence. Abscission of fruitlets from excised branches occurred 3–4 d after harvest of those branches. The fruit typically were in Stage 0 when harvested (Fig. 2), but a few were already in some stage of seed coat degeneration at harvest. Some fruitlets began the transition from Stage 0 to Stage 1 by 33 h after harvest. The number of fruitlets in Stage 1 increased while many early Stage 1 fruitlets progressed to Stage 2. The number of Stage 2 fruitlets peaked at about 60 h after harvest. By the time 60% of the fruitlets were in Stage 2, fruitlet abscission began (approx. 70 h after harvest), and by the time 100% abscission of the fruitlets had occurred (approx. 99 h), many fruitlets had proceeded to Stage 3.

This sequence of events, from first appearannce of Stage 1 fruitlets to first abscission took approximately 42 h. Likewise, the time required to pass from maximum number of Stage 1

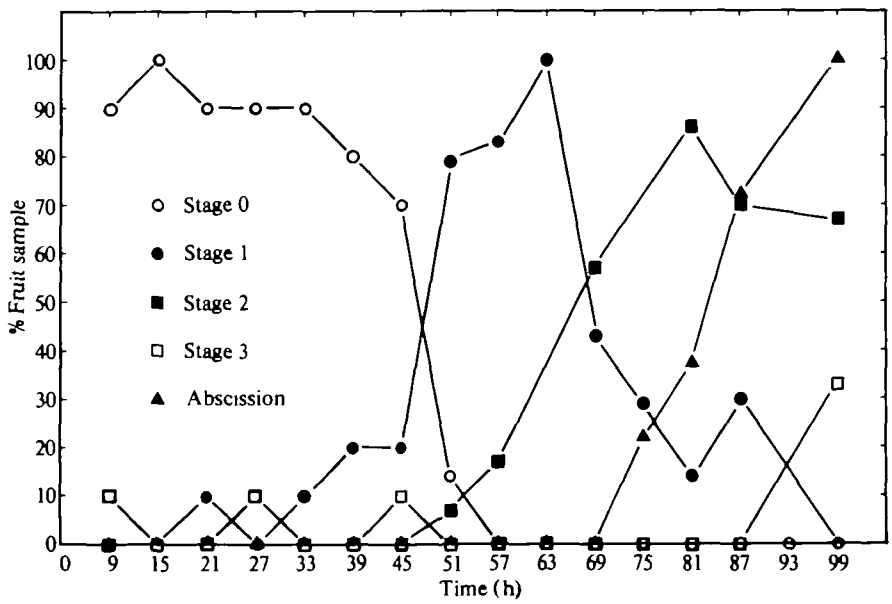

FIG. 2. Development of various stages of nucellar senescence and fruit abscission over time in fruit borne on detached branches. Time represents number of hours from harvest. See Table 1 for detailed description of stages.

fruitlets to maximum abscission ranged from 36–42 h. Similarly, the time required to achieve 50% abscission typically took less than 48 h after 50% of the fruitlets were in Stage 1.

Whole fruitlets and different fruitlet parts, i.e. mesocarp, nucellus-seed coat, and embryo were assayed for ethylene production over time to gain information on the dynamics of these events. There was no measurable ethylene production by the fruitlets sampled from freshly cut branches (Fig. 3). Exception to this statement was found when fruit in advanced stages of senescence were included in the harvest sample. Measurable ethylene production by the fruitlets did not begin until approximately 30 h after harvest of the branches. Production rates of whole fruitlets or fruitlet parts did not correlate with fruitlet size. Therefore, production rates as a function of time are expressed on a $nlg^{-1}\ h^{-1}$ basis (Fig. 3) and without the $mass^{-1}$ term (Fig. 4). Ethylene production by whole fruitlets reached maximum average of about 8·0 $nlg^{-1}\ h^{-1}$ (Fig. 3) or 40 $nl\ h^{-1}$ (Fig. 4) at approximately 48 h after harvest. The average ethylene production rate of whole fruitlets did not change from 48–99 h, the time when all fruitlets had separated.

The average ethylene production rate was followed over time in dissected fruitlet parts (Figs 3 and 4). Embryonic tissue produced virtually no ethylene throughout the experiment, and the mesocarp consistently produced approximately half that of whole fruitlets. The seed

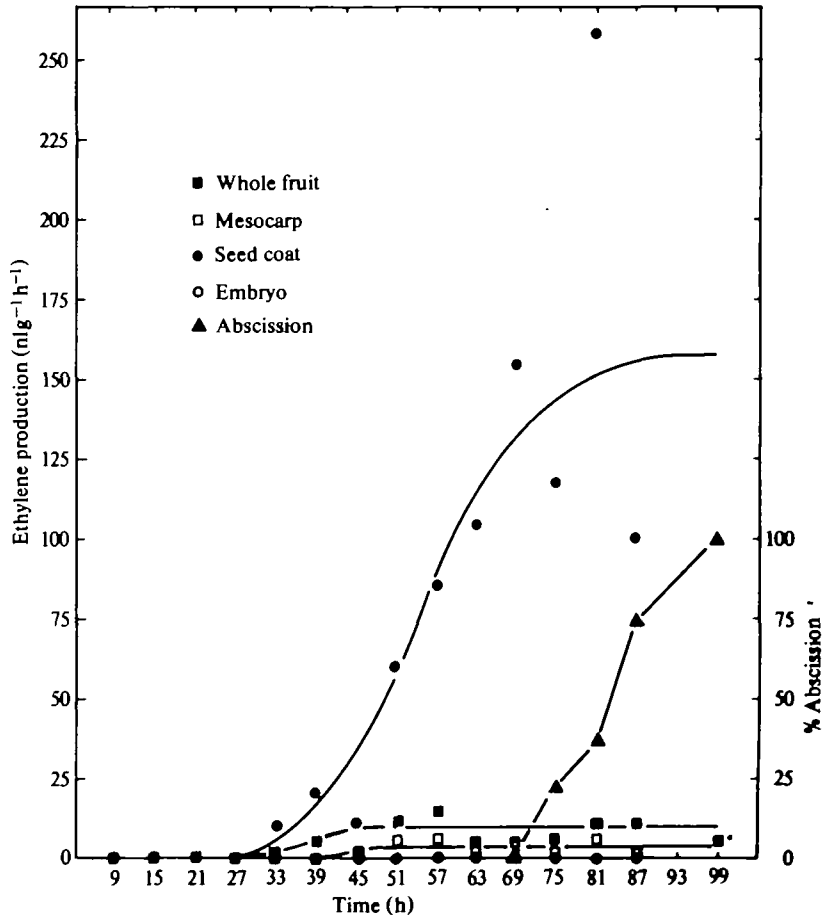

FIG. 3. Ethylene production, based on tissue weight, of avocado fruitlets and excised parts of fruitlets borne on detached branches. Abscissa represents time elapsed after harvest of branches from trees. Each datum represents average of five fruitlets.

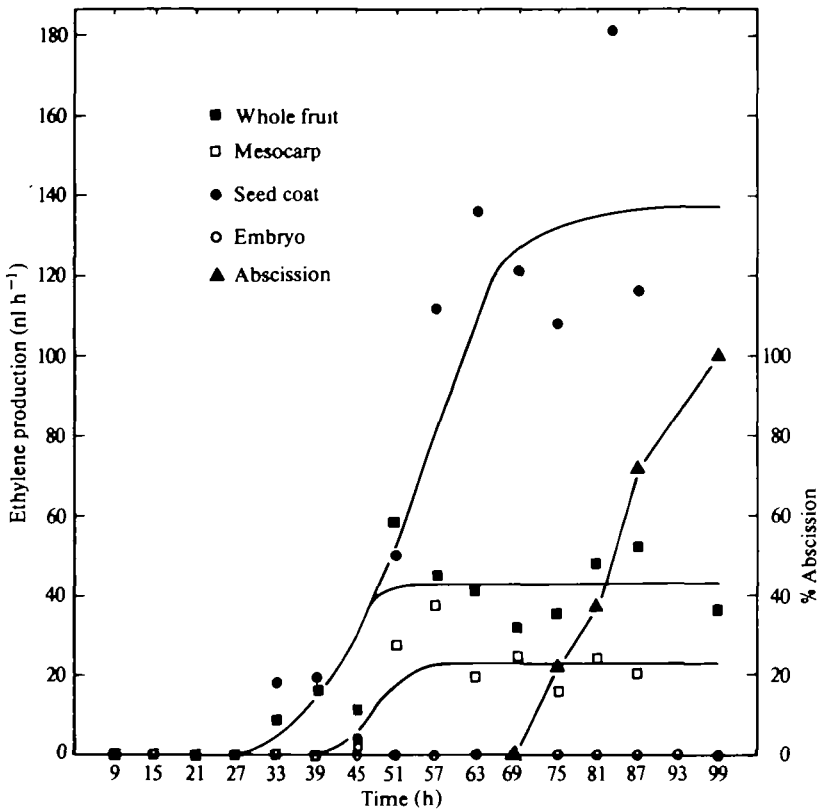

FIG. 4. Ethylene production of avocado fruitlets and excised parts of fruitlets borne on detached branches. Abscissa represents time elapsed after harvest of branches from trees. Each datum represents average of five fruitlets.

TABLE 2. *Ethylene production (nl h^{-1} ± se) of individual fruit at various stages of seed coat deterioration*

Fruit were harvested directly from intact branches of grove trees and percent abscission of fruit noted, or sampled from fruit borne on detached branches used in laboratory experiments. Enclosure time was 2 h. See text for definition of stages.

	Stage			
	0	1	2	3
Intact branches	0·031 ± 0·031	90·27 ± 0·031	28·76 ± 4·44	26·78 ± 2·91
Abscission	0	29%	91%	90%
Detached branches	1·71 ± 0·50	78·18 ± 6·73	66·56 ± 4·0	43·76 ± 15·15

coat produced greater than 20 times the ethylene produced by the whole fruitlets or mesocarp on a per g.h basis (Fig. 3) and greater than seven times on an absolute production rate basis (Fig. 4). There was a 12 h time lag in ethylene production by the mesocarp following the initial production by the nucellus-seed coat tissue.

Determination of ethylene production rates by fruitlets sampled directly from trees clearly indicated that sound, firmly-attached avocado fruitlets produce trace or undetectable amounts of ethylene (Table 2). Fruitlets exhibiting symptoms of initial stages of nucellar senescence, Stage 1, produced the most ethylene with fruitlets sampled from intact branches

averaging approximately 90 nl h^{-1} (Table 2). Fruitlets with brown nucellus and seed coat (Stage 2) or dark brown to black nucellus and seed coats with deformation of the embryo (Stage 3) produced ethylene at approximately one-third the rate of Stage 1 fruit. Interestingly, several Stage 3 fruit produced little or no ethylene. Fruit sampled from detached branches followed similar patterns.

No fruitlets sampled in Stage 0 have been found abscising. Less than one-third of those found in Stage 1 and approximately 90% of the fruitlets sampled from the field in Stages 2 and 3 were in the process of abscission (Table 2).

Results of trials measuring abscission response of fruit from detached branches subjected to various levels of ethylene or AVG are shown in Fig. 5. Typically, 100% of the original number of control fruit separated between days 3 and 4 following harvest of branches (see also Figs 2 and 3). Branches in an environment of 1·0–10 $\mu l\ l^{-1}$ ethylene lost all their fruit 1 day earlier. All fruit exposed to 100 $\mu l\ l^{-1}$ or greater ethylene separated within 2 d after harvest of the branches. Those fruit sprayed with 30 μM AVG required more than twice as long as controls to reach 100% abscission. The average ethylene production rate in the AVG treated fruit never rose above 2·1 nl h^{-1} in the initial 4 d. The events taking place in the nucellus and seed coat, i.e. tissue senescence, were unaffected by ethylene at any concentration of AVG. Senescence began in all treatments at the same time, proceeded at the same rate, and developed with the same intensity as controls.

Ethephon at rates of 500 and 1000 parts 10^{-6} was applied to fruit in the field. Rates of abscission were significantly greater than control in both ethephon treatments (Fig. 6).

DISCUSSION

Tomer, Gazit, and Eisenstein (1980) examined seedless fruitlets 5·0–20 mm long and found breakdown of the integuments to be a primary event in the production of seedless avocado fruits. They observed nucellar degeneration beginning at the chalazal end and spreading to the micropylar end. In the present study, breakdown appeared to initiate uniformly throughout

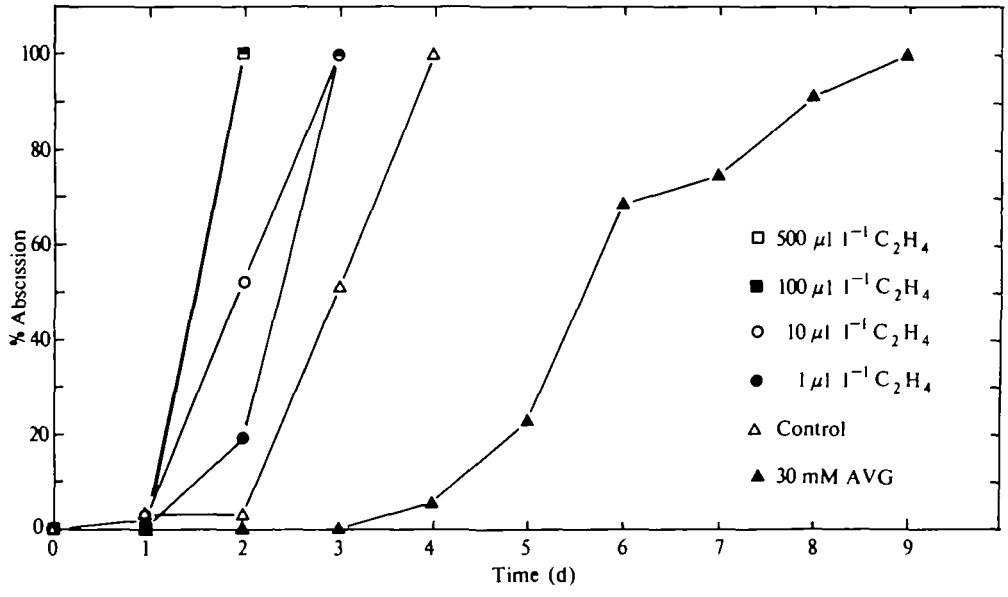

FIG. 5. Effect of ethylene and 30 μM AVG on avocado fruitlet abscission from detached branches. Abscissa represents time elapsed after harvest of branches from trees.

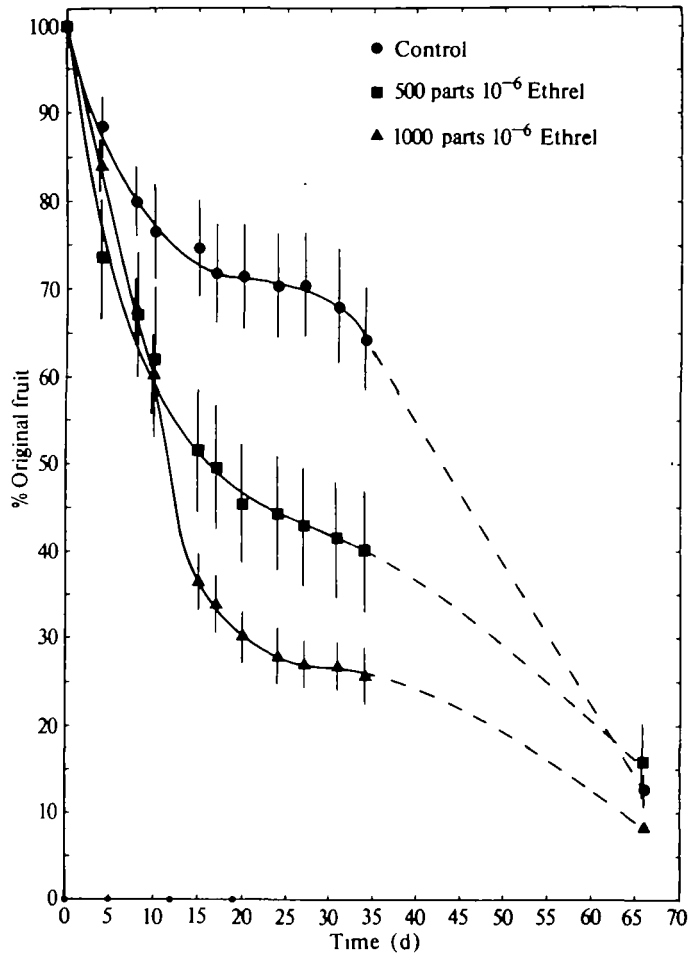

FIG. 6. Effect of ethephon on avocado fruitlet abscission from intact branches. Fruit, ranging 0·5–1·0 cm in size, and adjacent leaves were sprayed to dripping at 0, 7, and 14 d.

the nucellus before rapidly spreading to the seed coat (Fig. 1). This discrepancy may be explained by varietal differences or perhaps by different mechanisms of degeneration. For example, the events described by Tomer *et al.* (1980) result in seedless fruit, i.e. the seed aborts but fruitlet abscission does not occur. Virtually no seedless fruit are produced by the varieties used in the present study. Every fruit examined during the course of the various experiments had normally developed embryos, and the events described resulted in fruit abscission.

Previous work (Adato and Gazit, 1977*a*; Blumenfeld and Gazit, 1970, 1974), suggested that a high incidence of seed coat damage was associated with similarly high levels of fruitlet abscission. Observations made during the course of the present study clearly indicate that seed coat abortion is prerequisite to fruitlet abscission. This appears to be true for immature fruit up to a point prior to onset of horticultural maturation when the seed coat shrivels (Blumenfeld and Gazit, 1970, 1974). This shrivelling occurs perhaps as a result of a different controlling mechanism since the process is not associated with fruit abscission. We have noted seed coat abortion prior to abscission in fruit as large as 6·0 cm diameter. Adato and Gazit (1977*a*) have demonstrated that seed abortion and abscission occur at the greatest rate

when the fruit are smallest and gradually decreased in rate as the fruit enlarges. In general, this is true; however, because flowering occurs over a period of 2–3 weeks one may find fruit in a range of sizes on a branch. Tagging experiments in the field revealed that large fruit in a cluster were just as likely to drop as small ones (data not shown). Thus, competition between fruit within a cluster is apparently not dictated by fruit size.

The time frame of events beginning with seed coat senescence and ending with fruitlet abscission has been independently estimated to be from 1 week (Sedgley, 1980) to 3 weeks (Adato and Gazit, 1977*a*). The latter estimate was based on peak ethylene production which correlated with the number of fruitlets with degenerating seed coats. If we assume that the varieties used in these and the present study are comparable (similar results in the three varieties examined in the present study would suggest that they are) then both estimates appear to be high. If the process were as slow as suggested, then one might expect to find relatively large numbers of firmly attached fruitlets in various stages of seed coat deterioration. We found none.

Abscission data obtained from excised branches perhaps more accurately reflects the dynamics of seed abortion and fruitlet separation (Fig. 2). The time required from the first detectable sign of nucellar-seed coat deterioration to fruitlet abscission was approximately 42 h. If these data accurately reflect the time frame of events taking place *in vivo*, then the rate is much faster than previously suggested (Adato and Gazit, 1977*a*; Sedgley, 1980). Field observations suggest that this sequence of events appears to occur on the tree over a similarly short period of time. Major evidence includes: (1) Abscising fruitlets are most often in Stages 2 or 3. A small percentage of fruitlets in Stage 1 were found to be abscising. Fruitlets in Stage 0 have never been found to be abscising (Table 2). (2) Non-abscising fruitlets are virtually never found in any stage of deterioration. Exceptions are those varieties which typically produce seedless avocados (Blumenfeld and Gazit, 1974; Tomer *et al.*, 1980). Considering these observations, it is reasonable to suggest that the time frame of events from initiation of seed coat abortion to abscission is approximately 2 d.

High levels of ethylene production prior to abscission have been shown to be correlated with abscising avocado fruitlets (Adato and Gazit, 1977*a*). It has further been suggested that the incidence of defective seed coats is responsible for high ethylene production levels by the fruit (Adato and Gazit, 1977*a*, *b*). The present study shows that the dynamic changes in ethylene production by fruitlets correlate precisely with the visual events described above. Samples taken from both excised and intact branches clearly indicate that ethylene production by sound fruitlets was undetectable or near-undetectable under the conditions tested (Figs 3 and 4, Table 2). Those fruit harvested in Stage 1 produced maximum levels of ethylene. Tissue in subsequent stages of senescence produced less. Some fruitlets harvested in Stage 3 produced near undetectable levels of ethylene. Thus, there is a burst of ethylene which was produced initially upon the first visible sign of nucellar senescence (cf. Figs 2, 3, and 4) that tapers off as the fruitlets progress through subsequent stages of senescence. This decline in ethylene production is not apparent in Figs 3 and 4 because the ethylene production rate at any point in time was an average of fruit sampled in various stages of deterioration.

The burst of ethylene begins to occur at the time that nucellar senescence begins, suggesting that it is a consequence of the senescence process and not involved in the inductive mechanism of that process. Several additional lines of evidence support this view. The nucellus which shows the first signs of senescence and deterioration is the tissue which is responsible for the initial and highest level of ethylene production (Figs 3 and 4) (Adato and Gazit, 1977*a*, *b*),. Fruit maintained in an atmosphere of 100 μl l^{-1} or more ethylene separated from branches in less than 2 d (Fig. 5); yet no acceleration in the senescence process was observed. Fruit treated with AVG produced much less ethylene than controls, and

abscission rates were reduced as a result (Fig. 5); however, senescence of the nucellus-seed coat progressed at the same rate in treated fruit as controls.

Measurable ethylene production by the mesocarp follows that of the nucellus and seed coat by approximately 12 h (Figs 3 and 4). It is not completely clear at this time whether the ethylene assayed in this tissue was autocatalytically produced by the mesocarp or was simply diffusing from it as a result of production by the integuments. It is also possible that 1-aminocyclopropane-1-carboxylic acid, the metabolic precursor to ethylene (Adams and Yang, 1979) may be diffusing from the integuments into the mesocarp to facilitate ethylene production. It is interesting to note that ethylene production by the whole fruit was substantially less than that of the nucellus-seed coat. This may be explained by the auto-inhibitory nature of ethylene found in some plants (Riov and Yang, 1982; Zeroni, Galil, and Ben-Yehashua, 1976). The ethylene producing nucellus-seed coat tissue is enclosed within the mesocarp of whole fruit which could partially trap the ethylene giving rise to levels which may inhibit its production by the enclosed tissue.

Clearly, ethylene is the triggering hormone in the abscission process. Figure 5 demonstrates the accelerating effect of ethylene on fruit abscission. At concentrations of 100 $\mu l\ l^{-1}$ or greater, abscission occurred in all fruitlets within 2 d (Fig. 5). This is the same period of time required from first production of fruitlet ethylene to fruitlet abscission (Figs 3 and 4). Increased abscission was also observed with spray applications of ethephon on intact branches (Fig. 6). Furthermore, AVG not only inhibited ethylene production by fruitlets borne on excised branches but also delayed abscission of those fruitlets.

In conclusion, young avocado fruit abscission appears to be a randomly selected process among individual fruitlets and apparently is not related to fruitlet size within a cluster; however, the more fruit there are in a cluster the greater the number are abscised (Adato and Gazit, 1977*a*). The young avocado fruit elimination process begins with senescence and deterioration of the nucellus and rapidly spreads to the seed coat and embryo. This senescence is prerequisite to fruit abscission. A powerful but temporary burst of ethylene accompanies the initial stage of nucellar senescence. The mesocarp later evolves ethylene. The resulting ethylene, either from diffusion through or production by mesocarp tissue adjacent to the abscission zone, thus induces formation of the separation layer and subsequent abscission. The entire process from initial nucellar senescence to separation appears to take approximately 2 d.

ACKNOWLEDGEMENT

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