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Whole-fruit Ethylene Evolution and ACC Content of Peach Pericarp and Seeds During Development

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Abstract. **The rate of ethylene evolution of peach fruit (*Prunus persica* L. Batsch) and ACC content of peach pericarp/mesocarp and seeds was determined during development. Ethylene measurements of whole fruit began 18 days after anthesis (DAA), and ACC quantification was started 32 DAA. ACC levels and ethylene evolution followed similar patterns during stages I and II of fruit growth. At 39 DAA, there was an increase in ethylene evolution and extractable ACC concentration of both pericarp and seeds; however, variability was high at this time. Ethylene evolved by nondeveloping fruit of the "second wave" and "June drop" increased after senescence of the ovule was observed. By 49 DAA, ethylene production and ACC concentration reached a minimum that lasted until a 10-fold increase in ethylene evolution was detected in late stage III. This 10-fold increase in ethylene occurred in four different peach cultivars sampled at "firm-ripe" stage. Seeds excised at 67 DAA, which were incubated for 6 hr in ambient O_2 conditions, evolved 400 nl·g^{-1}·hr^{-1} ethylene and ACC concentration averaged 54 nmol·g^{-1} fresh weight. It is suggested that in split-pit fruits, ethylene generated by the seeds may accelerate fruit maturation and ripening. Chemical name used: 1-aminocyclopropane-1-carboxylic acid (ACC).**

Ethylene regulates many stages of plant growth and development (25), and, during fruit development of deciduous trees, ethylene is produced at varying rates (1, 8, 10, 14, 15, 24). Ethylene evolution rates are relatively high in fruits early in the season and decline to low levels after cell division ceases. In climacteric fruits, such as peach, ethylene production increases again during ripening.

High rates of ethylene production during fruit development have also been reported in peach fruit, although the developmental role for early season ethylene production is unknown (10, 14, 15). Jerie and Chalmers (10) researched long-season peaches (not grown in North America) where fresh and dry weight growth curves were displaced in time. They hypothesized that ethylene, which was produced at high rates during rapid stages of dry-weight growth, was responsible for the gain in dry weight. Since freestone peach and nectarine cultivars commercially grown in North America develop in 130 days or less, their data may not be applicable. No evidence exists that dry and fresh weight curves are displaced in time (16).

The availability of the immediate precursor of ethylene, ACC, often determines the rate of ethylene synthesis in plant tissues (9, 25). Most studies on endogenous ACC concentrations and ethylene production during fruit development have been directed toward understanding the differences associated with fruit maturation and the ethylene climacteric. Very limited information is available on the role of ethylene and ACC in early season fruit development. No seasonal studies in stone fruits of endogenous ACC content have been reported previously to the best of our knowledge.

One major objective of this study was to investigate the levels of ACC in peach fruit tissues throughout development while studying the rate of ethylene evolution of whole fruit. While it is difficult to localize ethylene evolution at the tissue level, the discovery of the nonvolatile precursor ACC offers the possibility of testing various tissues for their potential contribution to whole-fruit ethylene. Measuring ACC concentration may enable us to study the onset of ethylene production in peach tissues. To isolate and quantify ACC levels on small tissue samples (100 mg fresh weight), we found it necessary to modify the Lizada and Yang assay (13). In addition, the seasonal changes in ethylene and ACC in peach could suggest critical times when ethylene regulates fruit development throughout the entire season.

Materials and Methods

Development of a modified ACC extraction protocol. The preliminary ACC extraction and purification steps were modified from those of Lizada and Yang (13). Lyophilized pericarp/mesocarp or seed tissue (≈150 mg dry weight) was homogenized in 1 to 3 ml of 80% acetone at 4°C. Acetone was selected to avoid potential problems of spurious ethylene production from ethanol (21). After centrifugation, the supernatant was decanted and its volume raised with distilled water to create a 15% acetone concentration (v/v). The solution pH was adjusted to 3.0 with 1 N HCl.

The diluted supernatant was loaded onto a Baker-10 SPE aromatic sulfonic acid (1-ml) column. Columns were preconditioned with 3 ml each of HPLC-grade hexane, methanol, 1 N HCl, and distilled water in succession. A Baker-10 SPE vacuum manifold was used to draw the solvent extract through the column at about 20 kPa. Columns were taken to dryness after preconditioning with hexane and methanol, but were not dried after the HCl and water washes.

Since ammonia decreases the conversion efficiency of ACC to ethylene when not evaporated after elution (21), preliminary studies were performed to determine if NaOH could be used to elute ACC from these columns. The use of NaOH also would avoid the tedious evaporation step after elution and allow direct ACC assay of the eluant.

Preliminary experiments were performed eluting 5 nmol of ACC (Calbiochem) with 2 N NH_4OH, or 0.1 N, 1 N, or 2 N NaOH and 2 N NH_4OH plus 1 N NaOH. Five to ten 1-ml fractions were collected individually. Each was assayed for ACC using $HgCl_2$ and freshly purchased household bleach (5.25%

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sodium hypochlorite solution) to release ethylene (13). The elution profiles and amount of ethylene released from these four different base concentrations are shown in Fig. 1. Percentage recovery of ACC was calculated by measurement of the amount of ethylene released divided by the expected molar ethylene release if the conversion of 5 nmol ACC had been complete. The 1 N NaOH elution consistently produced the highest ACC recovery (between 50% and 70%). In our study, direct assays of 5 nmol ACC without any column purification also gave a similar recovery of ethylene from ACC.

Another experiment demonstrated that 5 ml of 2 N NH_4OH elution followed by 5 ml of 1 N NaOH eluted additional ACC. This additional ACC resulted in similar total recoveries as that of 1 N NaOH alone (Fig. 1). When tested using thin-layer chromatography, spots of these column eluants cochromatographed with authentic ACC and developed a similar color with the ninhydrin reagent. Consequently, 1 N NaOH was used throughout the study, and the second and third 1-ml column fractions were pooled and assayed. Controls with no ACC were run to subtract background ethylene obtained from unwashable column contaminants.

Seasonal measurement of ethylene evolution and ACC content in peach fruit. 'Redhaven' peach fruit were harvested twice a week from mature trees at the Univ. of Maryland Research Farm in 1985 for quantification of ethylene evolution and extractable ACC. Sampling for extractable ACC began 32 days after anthesis (DAA), and ended at 88 DAA, when fruits had attained commercial maturity ("firm-ripe"). Two replicates of a minimum of 10 fruit each were frozen in liquid N_2 and stored at −80°C. Just prior to ACC analysis, these fruit were lyophilized, separated into pericarp/mesocarp and seed subsamples, and then powdered.

The rate of ethylene evolution during development was determined beginning at 18 DAA. A minimum of 10 "normal, developing" fruit were collected twice a week. The fruit were incubated in 50-ml syringes for 3 to 5 hr at 20°C for the ethylene measurements. Once these syringes were too small to accommodate the fruits (37 DAA), 500-ml glass jars were used. Fruit were then incubated for ≈16 hr. The incubation times were selected as the minimum times needed to detect measurable (10 nl·liter^{-1}) ethylene at each stage of development. In the longer incubations, ethylene evolution was linear during the sampling period (data not shown). Fruit fresh weights were also measured to determine the major transitions in peach fruit growth. Ethylene was analyzed by a Hewlett-Packard (HP5840A) gas chromatograph equipped with a flame ionization detector and peak integrator.

After ethylene analyses, fruit were dissected and the ovules were observed for signs of senescence. Fruit relatively large, with a green pericarp and cream-colored ovules, were classed as "developing". Two additional classes of fruit were collected based on visible differences in fruit size and color during Stage I. Beginning at 25 DAA, visibly smaller fruit were apparent. These fruit represented the "second wave" of fruit abscission. A second group of smaller-sized fruit were collected beginning 42 DAA. This class eventually abscised during "June drop". In addition, a few insect-damaged fruit were also included in the ethylene measurements.

Measurement of ethylene evolution by fruits of three peach cultivars during stage III. Mature 'Jerseyglo' peach fruit were harvested from trees that had been grown in the greenhouse in early and late stage III. The rate of ethylene evolution of mature (firm-ripe) fruit of 'Jersey Queen' (peach) and 'Flavortop' (nectarine) grown in a commercial orchard were measured. Fruit of each cultivar were harvested, transported to the laboratory, and sealed in 500-ml glass jars. Ethylene determinations were first made after about 24 hr at 20°C. During this period, rates of ethylene evolution were linear (data not shown).

Measurement of ethylene evolution and the changes in ACC content of peach seeds during stage III. Seeds were excised from field-grown 'Redhaven' peach fruit 67 and 81 DAA (Stage III) to determine their potential as an ethylene source. On 67 DAA, 32 seeds were removed from the endocarp by splitting on the suture, and then sealed individually in 50-ml syringes with a 20-ml headspace volume. Four replicate seeds were incubated for 0, 0.5, 1, 1.5, 2, 3, 4, or 6 hr. After the designated incubation time, ethylene measurements were made. The seeds were then immediately frozen in liquid N_2 and held at −80°C.

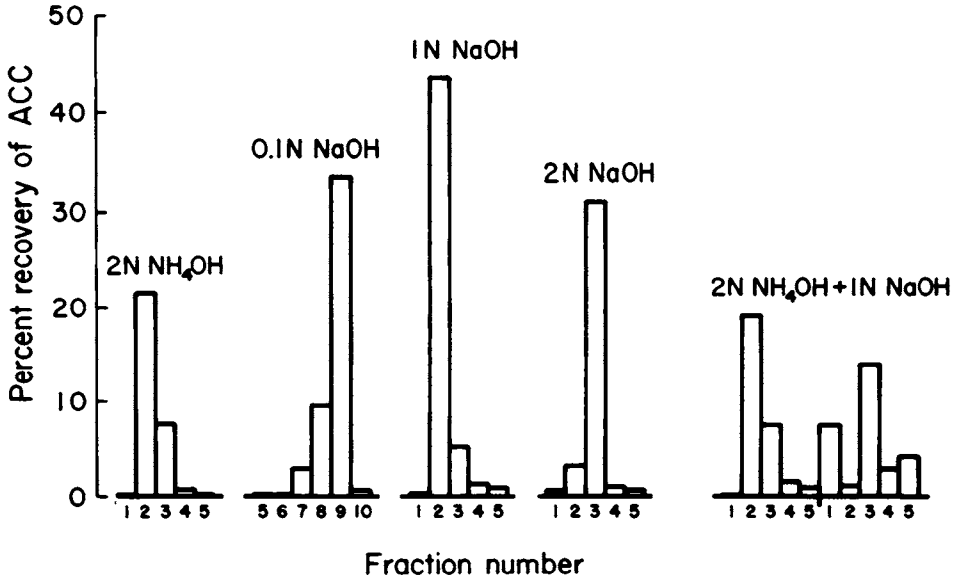

Fig. 1. Elution profiles and percent ACC recovery from Baker-10 SPE sulfonic acid columns using 2 N NH_4OH; 0.1, 1.0, 2.0 N NaOH; and 2 N NH_4OH plus 1.0 N NaOH.

Frozen seeds were extracted directly for ACC. Seeds taken from fruit 81 DAA were incubated for 0.5, 1, 1.5, 2, 3, 4, 6, and 10 hr and ethylene measurements were made; ACC content was not measured on these seeds.

Results

Development of a modified ACC extraction protocol. Direct assays of fruit extracts in acetone did not liberate consistent amounts of ethylene. The conversion efficiency of ACC added to peach mesocarp extracts after ion exchange chromatography was similar to that of standards assayed alone (data not shown). This similarity suggested that no inhibitory substances nor any additional ethylene-releasing compounds were present in the plant extract after chromatography. Although conversion efficiencies ranged from 50% to 70% during the modification of the method, once the protocol was standardized we consistently obtained 63% ± 3% conversion of ACC to ethylene on the assay with or without plant extracts. Through the use of the sulfonic acid column, ≥90% recoveries were attained while precision and repeatability were enhanced. These data would suggest that the NaOCl assay is the limiting factor in accurate ACC analysis and thereby only estimates ACC levels. Also, we ruled out potential inhibitor interactions since conversion efficiencies were constant during developmental stages.

ACC content in peach tissues was calculated from a standard curve, which defined the relationship of ACC levels and ethylene production by the assay. There was a highly significant (R^2 = 0.99) linear relationship between ACC and ethylene for the range of ACC concentrations tested (0.25, 0.50, 1.0, 5.0, 10.0, and 20.0 nmol). The calculated equation used was Y = 1.93X (where X = nmol of sample ACC and Y = $\mu l \cdot liter^{-1}$ ethylene released into the headspace gas after adding $HgCl_2$ and bleach to the sample). The use of a standard curve: a) allows the measurement of ACC levels in individual seeds (fresh weight ≥100 mg) and b) removes the time and measurement errors involved in dividing samples for duplicate ("spiked") determinations.

Seasonal measurement of ethylene and ACC in peach fruit. The growth curve of 'Redhaven' peaches is shown in Fig. 2A. Early in development, 'Redhaven' peaches evolved relatively high rates of ethylene (Fig. 2B). Rates declined to their lowest levels during stage II, (0.01 $nl \cdot g^{-1} \cdot hr^{-1}$). The 10-fold increase in ethylene evolution was again detected in the latter part of stage III (Fig. 2B).

Until 35 DAA, fruit dropping during the second wave of abscission evolved ethylene at rates similar to those of developing fruit of similar weight measured at 18 and 21 DAA (Table 1). The pericarp appeared green and healthy in these senescing second-wave fruit, although their seeds appeared abnormal. At 39 to 42 DAA, the pericarp had begun to yellow, and ethylene rates had increased in the smaller second-wave fruit.

An intermediate size category, "June drop" fruit, appeared to have stopped growth at about 32 to 39 DAA. Once these fruit were visibly different, they were evolving higher rates of ethylene than developing fruit. At 52 DAA this class of fruit was not found, as June drop had ended. In some cases, insect-injured fruit were inadvertedly sampled (Table 1). Insect injury increased fruitlet ethylene evolution to ≈1 $nl \cdot g^{-1} \cdot hr^{-1}$.

Pericarp/mesocarp tissues had ACC concentrations of ≈10 $nmol \cdot g^{-1}$ dry weight (DW), whereas ovules had 30 $nmol \cdot g^{-1}$ DW at 32 DAA (Fig. 2C). The levels of ACC in both pericarp and seed peaked at 39 days after anthesis (15 and 40 $nmol \cdot g^{-1}$ DW, respectively). By 54 days after anthesis, ACC concentrations were relatively low in both tissues. Measured ACC concentrations continued to decline in both tissues during stage III. The lowest levels were detected at 88 days after anthesis (1.2 $nmol \cdot g^{-1}$ DW of pericarp/mesocarp and 1.8 $nmol \cdot g^{-1}$ DW of seed).

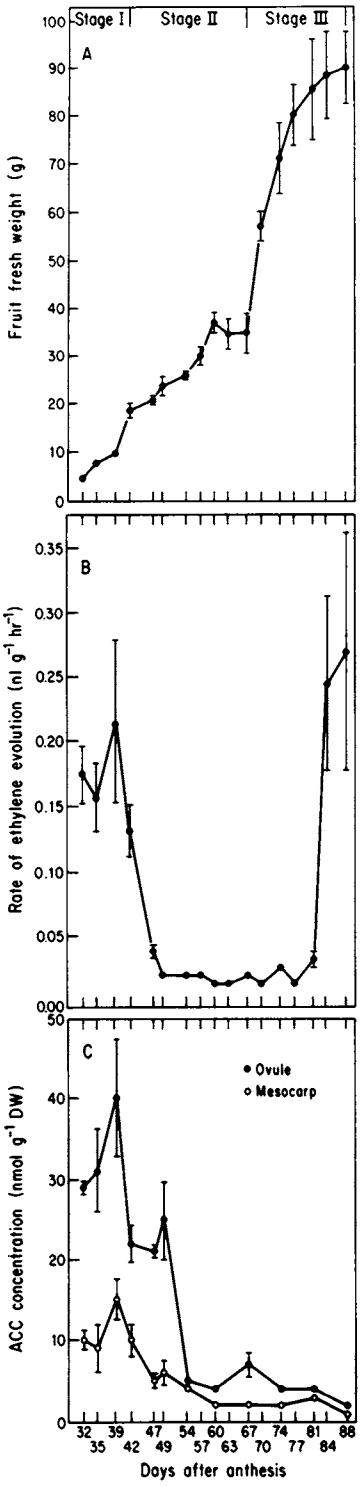

Fig. 2. (**A**) Fresh weight growth curve, (**B**) whole-fruit ethylene evolution, and (**C**) extractable ACC concentration in the pericarp/mesocarp and seeds of developing 'Redhaven' peach fruit. Values presented are means ± SE.

Ethylene evolution by fruits of four peach cultivars during late stage III. Both early and late stage III greenhouse-grown

Table 1. Fresh weight and ethylene evolution of developing and senescing peach fruits during Stage I. SE values are presented in parentheses.

Days after anthesis	Fresh wt (g)		Ethylene ($nl \cdot g^{-1} \cdot hr^{-1}$)	
	Developing fruits			
18	0.40	(0.05)	0.33	(0.06)
21	0.74	(0.09)	0.24	(0.02)
25	1.55	(0.11)	0.12	(0.01)
28	2.71	(0.24)	0.15	(0.02)
32	4.65	(0.44)	0.18	(0.02)
35	7.37	(0.30)	0.15	(0.03)
39	9.65	(0.38)	0.21	(0.07)
42	18.64	(1.65)	0.13	(0.02)
47	20.52	(0.95)	0.04	(0.007)
49	23.55	(1.96)	0.02	(0.003)
	Second wave of abscission			
25	0.23	(0.02)	0.20	(0.05)
28	0.33	(0.03)	0.39	(0.06)
32	0.49	(0.05)	0.38	(0.07)
35	0.80	(0.11)	0.31	(0.09)
39	0.95	(0.16)	1.29	(1.00)
42	1.24	(0.13)	0.55	(0.19)
47	0.84	(0.20)	3.11	(2.56)
	Third wave of abscission (June drop)			
42	4.39	(0.66)	0.41	(0.13)
47	4.34	(0.88)	0.75	(0.26)
49	4.34	(0.86)	0.55	(0.20)
	Insect-injured			
25	2.19		1.14	
42	10.16		1.96	

'Jerseyglo' peach fruit displayed a linear pattern of ethylene evolution when studied in a closed system for < 24 hr. The mean rate of ethylene evolution of late stage III fruit was 0.21 $nl \cdot g^{-1} \cdot hr^{-1}$. The rate of ethylene evolved from three field-grown peach cultivars at harvest was similar to the greenhouse-grown 'Jerseyglo' peaches. 'Redhaven', 'Flavortop', and 'Jersey Queen' fruit evolved 0.27 ± 0.09, 0.19 ± 0.06, and 0.21 ± 0.15 $nl \cdot g^{-1} \cdot hr^{-1}$, respectively.

Measurement of ethylene evolution and changes in ACC content concentration in stage III peach seeds. The initial ACC concentration of 'Redhaven' peach seeds at 67 DAA was 3.4 $nmol \cdot g^{-1}$ fresh weight. After 1.5 hr, ACC concentration and ethylene evolution increased exponentially (Fig. 3). By 6 hr of incubation, levels of ACC concentration and ethylene evolution rates had increased 16 and 400 times, respectively. Similar ethylene evolution data were obtained for seeds excised 81 DAA.

Discussion

This modified method for extractable ACC quantification provides certain advantages for peach tissues over the original method. The acetone extraction prevents potential spurious production of ethylene obtained when incompletely evaporated ethanol is reacted with NaOCl and ammonia/amines (21). The evaporation step, which is normally required after NH_4OH elution to avoid destruction of ethylene (21), is not needed since elution of extractable ACC from the sulfonic acid column is with NaOH. This procedure saves time and eliminates a step where losses of ACC could occur.

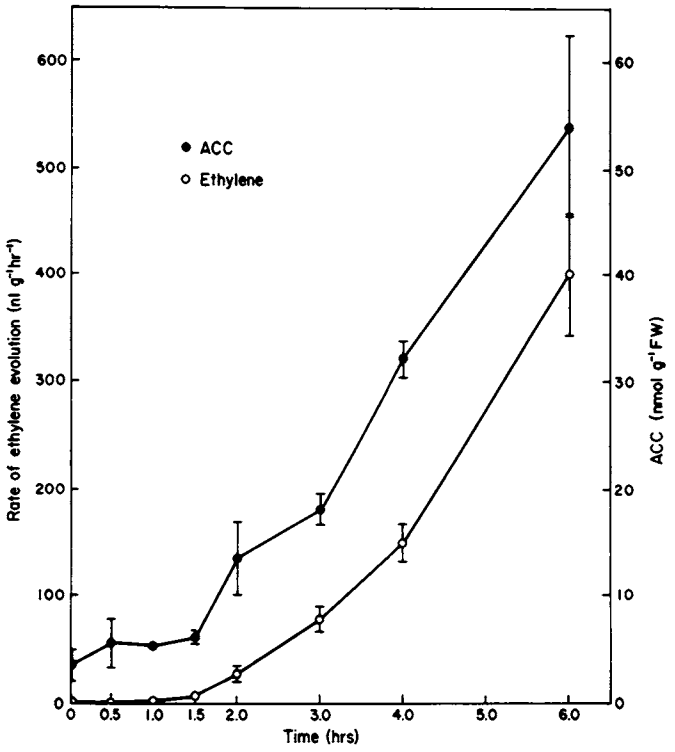

Fig. 3. Ethylene evolution and ACC concentration in mature peach seeds after removal from the endocarp at 67 DAA. Values presented are means of four individual seeds ± SE.

Rates of ethylene evolution by developing peach fruit (Fig. 2B) are similar to seasonal rates for ethylene evolution reported previously (2, 3, 10, 14, 15). At 39 DAA, we noticed an increased variability and a trend towards a rise in the rate of ethylene evolved. Previous researchers have also reported a slight increase of ethylene at this time (10).

At 39 DAA, an apparent peak of ACC in both the seed and mesocarp also were observed (Fig. 2C). The coordinated increase of ACC and ethylene may be evidence of increased ACC synthase. Yoshii and Imaseki (26) reported that a number of growth-promoting hormones can stimulate ACC levels and ethylene evolution. During early season peach development, high levels of auxin are measurable in both peach pericarp and the seed (19, 20). It is not known, however, if levels of growth promoters, ACC, and ethylene are correlated. In addition, the data suggest that our measurements of ethylene during stage I were probably not wound-induced, as ACC determinations were carried out too rapidly to be influenced by tissue wounding (22).

Ethylene did not appear to be the cause of seed senescence, since developing fruit of the same size evolved similar rates. However, the climacteric-like increase observed at 39 to 47 DAA in ethylene may trigger the final stages of the abscission process. The behavior of stage I peaches is quite different from that observed during early season apple development. In apple, a high fruitlet variability in ethylene production exists throughout the first 4 to 6 weeks after anthesis. In addition, June drop apple fruit do not differ in ethylene evolution from developing fruit (1, 24). Developing peaches evolved relatively low uniform levels of ethylene, but, after insect injury or prior to natural drop, higher levels were measured.

When ethylene evolution decreased, measured ACC levels were also low in stages I and II. There was a rise in ethylene production at 81 DAA, signaling the onset of fruit maturation

and ripening. No concomitant rise in ACC was noted. These data are similar to those reported for peach and other fruit (4, 9, 12, 23). Sitrit et al. (23) showed that the ethylene-forming enzyme (EFE) is active in preclimacteric avocado fruit. Although EFE activity is low in preclimacteric avocado, it may stimulate additional ethylene synthesis, whereas ACC concentrations do not increase. In nectarines, Brecht and Kader (3) also demonstrated that EFE activity increases prior to ACC synthase activity. Ethylene production began to increase, whereas ACC levels appeared to remain constant. Since commercially harvested peach fruit are just beginning to increase ethylene evolution at that time, ethylene produced at harvest may result from constitutive EFE activity.

Most studies of changes in ethylene synthesis have concentrated on the behavior of fruit after harvest. In our studies, we have concentrated on fruit development during attachment to the tree. During stages I and II of peach fruit development, ethylene and ACC levels are closely correlated, suggesting that ethylene production arises primarily through system I (18). In previous studies in our laboratory, ethylene levels were also reported to correlate closely with endogenous levels of 1*H*-indole-3-acetic acid (IAA) (19, 20).

During stage III of peach fruit development, a 10-fold increase in the level of ethylene evolution was noted. This increase appears to be typical of a wide number of peach and nectarine cultivars (3, 10, 14, 15). However, ACC levels do not increase at this time (Fig. 2). It appears that a stable, transitional pathway for ethylene production, preceding system II ethylene production, occurs on the tree at this time. It is likely that the increased ethylene production occurs through increased EFE activity (25). This rise in fruit ethylene in late stage III does not appear to promote growth as it does in fig (17). In addition, in preliminary trial applications of silverthiosulfate and [*S*-(*E*)]-2-amino-4-(2-aminoethoxy)-3-butyric acid (AVG) to early stage III 'Redhaven' fruit, no effect on "final swell" was noted (data not shown).

This observation is interesting from both a biological and horticultural viewpoint. The 10-fold increase in ethylene evolution by attached fruit occurs at a time when endogenous auxin levels are again increasing (19, 20). This increase in ethylene during late stage III may signal a final stage in the maturation process, prior to the full development of system II ethylene production during the climacteric.

Gauging peach fruit maturity is a difficult process that currently relies on the use of color chips to determine commercial maturity (6). In pome fruits, measurements of ethylene have been recommended to assess fruit maturity and storagability despite a relatively constant rate of ethylene production during fruit maturation of 0.1 $nl \cdot g^{-1} \cdot hr^{-1}$ (7). This observed 10-fold rise in peach fruit ethylene that occurs during late Stage III may be useful in assessing peach maturity and the capacity of harvested fruit to ripen after shipment, and should be investigated further.

The ethylene evolution data for 'Redhaven' peach seeds (Fig. 3) are similar to those reported by Jerie and Chalmers (11) for 'Golden Queen' seeds. They also noted a large phase of $\approx$ 1 to 1.5 hr before an exponential increase in ethylene occurred and suggested that the site of this rapid ethylene evolution was the seed coat. Since the role of ACC, ACC synthase, and EFE had not been elucidated, Jerie and Chalmers could not test their hypothesis.

If the seeds were hypothesized to be the source of ethylene production in peach fruit, the rate of fruit ethylene evolution could be estimated on a whole-fruit basis. Ethylene evolution at 6 hr after splitting the endocarp would be ≈ 10 $nl \cdot g^{-1} \cdot hr^{-1}$ at 67 DAA and 4 $nl \cdot g^{-1} \cdot hr^{-1}$ at 81 DAA, when expressed on a whole-fruit basis. However, measured rates of ethylene evolution were 0.03 $nl \cdot g^{-1} \cdot hr^{-1}$ and 0.26 $nl \cdot g^{-1} \cdot hr^{-1}$ on these dates. Since the calculated rates are one to two orders of magnitude higher than those measured, seed ethylene probably does not serve as the source of whole-fruit ethylene.

The intact endocarp probably serves as a diffusion barrier to both oxygen and ethylene, implying that the seed and flesh function independently during the latter stages of peach fruit development. The conversion of ACC to ethylene requires molecular O_2 (25). If low levels of O_2 are maintained within the endocarp, ethylene production also would be inhibited. Once the ovule is excised, O_2 would become available for conversion of ACC to ethylene by EFE.

A serious commercial problem in many early season peach cultivars is split-pits. During stage II of growth, the endocarp may fracture along its dorsal and ventral sides (5). Fruit with split-pits generally ripen earlier than do normal fruit. Also, the embryos of these fruit are aborted at harvest.

The potentially high rates of ethylene production of these excised seeds suggests a possible hypothesis for the early ripening of split-pit fruit. Once the endocarp splits, the diffusion barrier is broken, O_2 becomes available, and the seed synthesizes high levels of ethylene. Perhaps this autocatalytically produced ethylene of the seed serves as an internal source of ethylene to lessen the resistance to ripening and enhance the maturation of split-pit fruit. 'Redhaven' fruit with split-pits were observed to evolve ethylene at late stage III rates, 1 to 2 weeks earlier than nonsplit-pit fruit with undamaged pits.

Autocatalysis of ethylene production by system II is traditionally associated with ripening fruits and other senescing tissues (18). Ethylene has been shown to enhance the further formation of ACC by stimulating ACC synthase activity, and the formation of ethylene from ACC by EFE (4, 25). These peach seeds appeared to respond to ethylene like climacteric fruits, and may be an ideal model system for future research in ethylene biosynthesis.

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Yield Component Analysis of Strawberry Genotypes Differing in Productivity

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Abstract. **Strawberry genotypes (*Fragaria ×ananassa* Duchesne) varying in yield per plant were studied. In 1985, genotypes were grown in matted rows and in 1986 as individual plants. Yield per plant within genotypes was mainly dependent on the number of berries per plant, regardless of cultural system. Other variables were correlated with yield, including crown dry weight and leaf area after harvest, and number of inflorescences, which indirectly affected berry number. Potential differences in yield within genotypes apparently were established prior to flower bud differentiation. Variables associated with yield among genotypes differed with cultural conditions. When genotypes were grown in matted rows, vegetative variables were highly correlated with yield. With less interplant competition, reproductive variables were correlated with yield among genotypes. Data suggested that, in some genotypes, runnering and fruiting may have competed for assimilates. Genotypic variability in yield components suggests that genotypes with similar yield can have different routes to yield.**

A yield component analysis can be used to identify which components are most associated with yield within a particular genotype. Yield per hectare in strawberry plantings was found most correlated with the number of crowns per hectare (5, 6, 8). Various components have been found correlated with yield per plant, including number of crowns (7, 12), number of leaves per crown (9), number of leaves per plant (7), plant size (4, 10), number of inflorescences (4, 10, 12), number of berries per inflorescence (3, 4, 10, 12), number of berries per plant (7), fruit set, and total number of achenes per berry (9).

The objectives of this study were to determine which variables account for yield variation within genotypes and whether strawberry genotypes that differ in average yield per plant have a different balance of yield components. Also, genotypes were grown in matted rows and ribbon rows to determine whether cultural practices and/or the environment affected the contribution of various components to yield variation. Understanding which variables are most responsible for yield variation among

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