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A Study of Ethylene in Apple, Red Raspberry, and Cherry

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ABSTRACT

High ethylene levels were associated with flower abscission in apple (*Malus sylvestris*) and cherry (*Prunus avium* and *Prunus cerasus*), "June drop" of immature cherries, and harvest drop of apple and red raspberry (*Rubus idaeus*). However, an increase in ethylene content was not associated with June drop of apples and harvest drop of cherries. During the period of fruit ripening on the plant, the largest increases in ethylene occurred in apple flesh and red raspberry receptacular tissue. Ethylene remained low throughout the period of sweet and tart cherry ripening. The data obtained indicated marked ethylene gradients between adjacent tissues. Increases of ethylene in some tissues may have resulted from ethylene diffusion from adjacent tissues containing high levels of ethylene.

Ethylene has been associated with the initiation and termination of many physiological processes in plants (16). The purpose of this research was to measure the amount of endogenous ethylene in developing fruits and in tissues adjacent to the fruits to determine if there was a relationship between the amount of ethylene in the tissue and the stage of fruit development. Three types of fruit were selected for study: apple, a climacteric fruit (12); cherry, a nonclimacteric fruit (15, 17); red raspberry, a fruit whose ripening physiology has not been reported.

MATERIALS AND METHODS

At the Cornell Orchard in Ithaca samples were collected from several cultivars of apple (*Malus sylvestris*), several cultivars of red raspberry (*Rubus idaeus*), as well as one cultivar each of sweet cherry (*Prunus avium*) and tart cherry (*Prunus cerasus*). Ethylene extractions were completed in less than 60 min after collection. The method of ethylene extraction has been described (2). Subsequent to that communication ethylene contamination by the extraction apparatus was eliminated by: turning the balloons inside-out and storing them in a vacuum for 24 to 48 hr before use; attaching the balloons directly to the arms of the capillary stopcock; limiting the use of the balloons to a single extraction. Syringe contamination with ethylene was eliminated by using plastic disposable syringes and storing the syringes with the plunger removed from the bore.

Ethylene extractions were made in triplicate. The data represent averages for the three replicates except when, in a few extractions, the value (nl C_2H_4/g) for the highest replicate exceeded by 150% the value for the lowest replicate. When this occurred, the value for the unrepresentative replicate was discarded. Therefore, when comparing ethylene values in the tables and figures, significant differences usually exist when the larger of the two values exceeds the smaller by more than 150%, *e.g.*, a value of 0.160 nl C_2H_4/g is probably significantly higher than a value of 0.100 nl C_2H_4/g.

RESULTS

Apple Bud Development and Bloom. In the vegetative and flower buds of "Golden Delicious," ethylene declined throughout the period of observation. The marked difference in flower bud ethylene and flower ethylene, shown for the tight cluster stage in Table I, was caused by high levels of ethylene in the leaves of the flower buds. Ethylene levels in Golden Delicious flowers were low during early stages of bloom and high in the late stages of bloom. After petal fall the ethylene remained high in the unpollinated flowers, which abscised but declined in pollinated flowers which had started to develop into fruits (Table I). Similar results were obtained in another season for Golden Delicious and "McIntosh" except that in McIntosh flower buds ethylene increased from green tip to tight cluster stage.

Apple Fruits during "June Drop." Unpollinated flowers are the first organs to abscise after petal fall. In mid- to late June fruits with aborted seeds and yellow stems fall to the ground. During this period of June drop abscising and adhering fruits of Golden Delicious, "Delicious," and McIntosh were collected and extracted in two seasons. Fruit pedicel tissues contained 3- to 10-fold more ethylene than fruit flesh tissues, but abscising fruit pedicel and flesh tissues did not consistently contain more ethylene than similar tissue of adhering fruits.

Apple Leaves and Fruits during Growing Season. Monthly averages are presented in Table II for ethylene extracted at weekly intervals from leaves of August ripening (Red Astrachan), September ripening (McIntosh) and October ripening (Golden Delicious) cultivars. Leaf ethylene remained at 0.1 to 0.3 nl/g for most of the growing season. Fruit ethylene was lower than leaf ethylene until the fruits ripened. There was no consistent relationship between the season of fruit ripening and the level or trend in leaf ethylene.

Apple Fruit Maturation and Ripening. Prior to fruit ripening of Golden Delicious apples, the ethylene in fruit flesh was considerably lower than ethylene in the pedicels and cluster bases (Table III). When the fruit started to ripen (157 days past full bloom), fruit flesh ethylene content began to increase. At 162 days past full bloom harvest drop of fruits was well underway, ethylene in fruit flesh tissue was high, but the levels of ethylene in fruit pedicel and cluster base tissue did not increase until 167 days past full bloom. Similar results were obtained in another season.

In McIntosh apple the ethylene started to increase in fruit flesh, pedicel and cluster base tissues at 132, 136, and 143 days respectively past full bloom (Table IV). When an SADH[1] (1 ml/l) tree spray was applied, the increase in ethylene was

[1] Abbreviation: SADH: succinic acid-2,2-dimethyl hydrazide.

Table I. *Extractable Ethylene Content of Golden Delicious Apple Tissue during Various Stages of Flower Bud Development and Bloom in 1970*

Stage of Flower (bud) Development	Date	Vegetative Buds	Flower Buds	Flowers
		nl C_2H_4*/g fresh wt*		
Dormant	Mar. 13	1.09	0.99	
Dormant	Mar. 27	0.86	0.73	
Dormant	Apr. 13	0.75	0.68	
Green tip	Apr. 22		0.41	
Half-inch green	Apr. 27	0.59	0.28	
Tight cluster	May 1	0.53	0.22	0.03
Pink	May 10			0.05
Full pink	May 11	0.14		0.06
Full bloom	May 18			0.05
Petal fall[1]	May 19			0.29
Flower abscission				
abscising flowers	June 1			0.28
developing fruits	June 1			0.11

[1] Flowers without petals.

Table II. *Extractable Ethylene Content of Leaves and Fruits of Several Apple Cultivars during the 1969 Growing Season*

Month	Red Astrachan		McIntosh		Golden Delicious	
	Leaves	Fruits	Leaves	Fruits	Leaves	Fruits
			nl C_2H_4*/g fresh wt*			
June	0.15	0.05	0.19	0.03	0.18	0.03
July	0.13	0.01	0.10	0.01	0.17	0.01
August	0.24	15.00	0.20	0.01	0.26	0.01
September	0.21		0.14	0.80	0.12	0.02
October	0.40		0.22	6.30	0.34	1.11

Table III. *Extractable Ethylene Content of Golden Delicious Tissue during Fruit Maturation and Ripening in 1970*

Days past Full Bloom	Air Temperature (C)	Fruit		Cluster Bases	Cumulative Drop
		Flesh	Pedicels		
			nl C_2H_4*/g*		*fruits/tree*
146	18.3	0.03	0.09	0.15	0
152	17.8	0.02	0.08	0.05	40
157	12.2	0.07	0.11	0.09	96
162	13.3	1.56	0.13	0.04	164
167	6.1	4.90	0.31	0.14	425

delayed (3). More than 10% of the crop had abscised and fallen to the ground soon after (*a*) ethylene in treated and control fruit flesh exceeded 1 nl C_2H_4/g and (*b*) an ethylene gradient was established between pedicels and cluster bases.

Red Raspberry. Blooming flowers of "Early June" red raspberry contained 0.171 nl C_2H_4/g fresh weight on June 5. This high level of ethylene was followed by a rapid decline during berry development and then a several fold increase in ethylene as the berries ripened. Ethylene in the woody receptacular tissues of ripening fruits was higher and increased more rapidly than ethylene in the soft fleshy tissues of the drupelets (Table V). Similar results were obtained for three other red raspberry cultivars.

Forked peduncles, bearing a fruit and a full bloom flower, were collected from "Newburgh" plants in late June. Extractable ethylene was highest in the flowers, intermediate in the peduncles, and lowest in the developing fruits (0.239, 0.140, and 0.025 nl C_2H_4/g respectively).

Sweet and Tart Cherry Bud Development and Bloom. Ethylene declined markedly between half-green calyx and green calyx stages of bloom development, and then declined slightly until petal fall. At the time of flower abscission, ethylene was notably higher in abscising flowers than in fruitlets (Table VI).

Sweet and Tart Cherry Fruit Growth, Development, and Ripening. During the period of early fruit drop, ethylene in abscising cherry fruits was higher than ethylene in adhering fruits (Table VI). Ethylene in the flesh of sweet and tart cherry fruits declined from early season through fruit ripening in 1970 (data not shown) and 1971 (Fig. 1). There was a rise of flesh ethylene in overripe "Montmorency" tart cherries in 1970, but not in 1971. Conversely, there was an increase in flesh ethylene of overripe "Hedelfingen" sweet cherries in 1971, but not in 1970. Respiration of sweet and tart cherry fruits decreased in rate from the end of pit hardening through the overripe stage of fruit development.

Levels of pedicel and leaf ethylene for sweet and tart cherry were variable throughout the periods of observation. Ethyl-

Table IV. *Extractable Ethylene Content of McIntosh Apple Tissues during Fruit Maturation and Ripening on the Tree in 1969*

Days past Full Bloom	Air Temperature (C)	Cumulative Fruit Drop		Ethylene Content					
				Fruit				Cluster Bases	
				Flesh		Pedicles			
		Control	SADH[1]	Control	SADH	Control	SADH	Control	SADH
		% of crop		*nl* C_2H_4*/g fresh wt.*					
128	18.3	0	0	0.04	0.03	0.13	0.08	0.13	0.16
132	20.6	1	0	0.52	0.01	0.11	0.06	0.12	0.10
136	15.6	7	1	1.85	0.02	0.40	0.06	0.18	0.07
139	22.2	24	2		0.05	0.57	0.05	0.14	0.06
143	21.1	40	3	5.05	0.23		0.14	0.25	0.15
146	20.0	58	5	9.24		1.39	0.18	0.22	0.18
149	21.7	86	6	34.20	1.14	2.39	0.24	0.24	0.16
153	8.3		15		6.43		0.35		0.27
156	23.9		20		4.76		0.69		0.35
160	8.9		34		2.02		0.51		0.31
164	5.6		39		4.35		0.66		0.24

[1] Tree spray 1 ml/l July 30, 1968 and 1 ml/l August 15, 1969.

Table V. *Extractable Ethylene Content of Early June Red Raspberry Fruits in 1970*

Date	Stage of Development	Ethylene		
		Whole fruit	Receptacle[1]	Drupelets
			nl C_2H_4*/g*	
June 17	Green fruit	0.090		
24	Green fruit	0.063		
29	Green fruit	0.046		
July 6	Green fruit	0.015		
7	Yellow fruit	0.095	0.187	0.084
7	Pink fruit	0.212	0.784	0.150
7	Light red fruit	0.372	1.453	0.265
7	Dark red fruit	0.687	1.725	0.575

[1] Calyx tissue was not cut from receptacles before extraction.

Table VI. *Extractable Ethylene Content of Sweet (Hedelfingen) and Tart (Montmorency) Cherry during Various Stages of Bloom and Early Fruit Development in 1970*

Stage of Development	Tissue Extracted	Hedelfingen		Montmorency	
		Date	C_2H_4	Date	C_2H_4
			nl/g		*nl/g*
Half-green calyx	Flower buds	Apr. 17	0.83	Apr. 17	0.92
Green calyx	Flower buds	Apr. 27	0.19	Apr. 27	0.13
Tight cluster	Flower buds			Apr. 30	0.16
Open cluster	Flower buds	Apr. 28	0.15	May 1	0.15
Full bloom	Flowers with petals	May 1	0.14	May 7	0.13
Petal fall	Flowers without petals	May 10	0.12	May 11	0.10
Flower abscission	Abscising flowers	May 19	0.11	May 23	0.16
	Set fruitlets	May 19	0.02	May 23	0.03
Fruit growth	Green fruits	May 27	0.03	May 27	0.04
Early fruit drop	Abscising fruits	June 9	0.03	June 9	0.10
	Adhering fruits	June 9	0.01	June 9	0.02

ene did not increase in these tissues at the time of fruit ripening and abscission (data not shown).

DISCUSSION

Abscission. Production of ethylene by flowers of a number of plant species has been reported (1, 5, 7, 8, 10, 14). Hall and Forsyth (10) reported pollination increased ethylene production by blueberry and strawberry flowers. An increase in ethylene production has been observed in senescing orchid (1) and carnation (14) flowers. Flower abscission has been induced by ethylene accumulation (7, 11).

In the studies reported here, at the time of flower abscission, there was considerably more ethylene in abscising cherry and apple flowers than in developing fruitlets. In Montmorency tart cherry and McIntosh apple these differences in ethylene content were caused by an increase in abscising flower ethylene and a concomitant decrease in the ethylene content of developing fruitlets. However, in Hedelfingen sweet cherry and Golden Delicious apple the differences in ethylene levels were caused by only a decline in fruitlet ethylene content—the ethylene content of abscising flowers did not increase.

No literature was found on the relationship between ethylene and abscission of young developing fruits with aborted seeds. At the time of early fruit drop (June), when apple and cherry fruits with aborted seeds were abscising, there was markedly more ethylene in the pedicels than in the flesh of these fruits. In sweet and tart cherry there was more ethylene in abscising fruit flesh and pedicles than in comparable tissue of adhering fruits. With apple, however, there was certainly no clear cut relationship between the levels of ethylene and abscission of fruits with aborted seeds. These observations indicated ethylene may play a role in the abscission of early fruit drop in cherry, but not in apple.

Although it has been common knowledge for centuries that ripening apples fall from the tree to the ground and it has been known for 3 decades that ripening apples evolve ethylene (13), the literature appears to be devoid of any direct observations of the relationship between endogenous ethylene and harvest drop of apples. Our data, which establish this relationship, appear to indicate that the presence of high levels of ethylene in the tissues immediately adjacent to the fruit abscission zone may have diffused to these tissues from the flesh of the ripening fruits, where ethylene was very high. In contrast, the red raspberry data suggest that ethylene may have

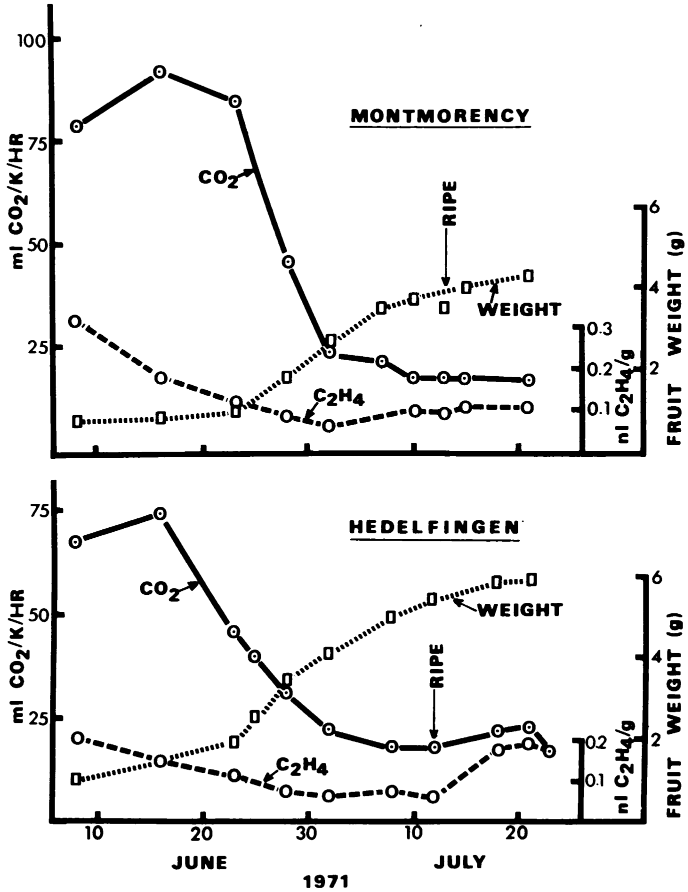

FIG. 1. Average weight, ethylene content at harvest, and respiration 24 hr after harvest for Montmorency and Hedelfingen cherry fruits.

Table VII. *Harvest Dates at Which Exogenous Ethylene Induced Various Ripeness Criteria to Reach Ripeness Levels*[1] *in Delicious Apples Held for 14 Days and Bartlett Pears Held for 7 Days at 70 F after Harvest*

Fruits were harvested each week beginning July 24, 1967.

Ripeness Criteria	Delicious Apple		Bartlett Pear	
	Air	Air + 0.5 ml/l C_2H_4	Air	Air + 0.5 ml/l C_2H_4
CO_2 climacteric	Sept. 11	Sept. 11	Sept. 4	July 31
Protein N	Oct. 2	Oct. 2	Sept. 4	July 24
Varietal flavor	Oct. 9	Oct. 9	Sept. 11	Aug. 21
Starch	Oct. 16	Oct. 9	Sept. 4	July 24
Flesh firmness	Oct. 16	Oct. 16	Sept. 4	Aug. 21
Skin chlorophyll	Oct. 16	Oct. 16	Sept. 11	Sept. 4

[1] Ripeness levels: CO_2 climacteric a pronounced increase in CO_2 production; starch: no reaction to IKI solution; all other criteria; the levels attained by "air" fruit on the harvest dates indicated in the "air" columns.

diffused from the receptacle to the ripening abscising drupelets. It is not surprising that endogenous ethylene did not markedly increase in the flesh of ripe abscising cherry fruits, because both sweet (17) and tart (15) cherry fruits are nonclimacteric. However, since exogenous ethylene does promote the abscission of sweet and tart cherries (6), and inasmuch as differences may exist in rates of ethylene production by adjacent plant organs or organ parts (9, 10), one might have anticipated an ethylene increase in sweet and tart cherry pedicels at the time of fruit abscission. This did not occur.

Fruit Ripening. In their review of ethylene as a fruit ripening hormone, Pratt and Goeschl (16) categorized fruits by their ripening responses to ethylene: fruits, such as "Honey Dew" melons, which have an absolute requirement for a minimum concentration of ethylene in the tissue to induce ripening, whose sensitivity to ethylene does not change as the fruit matures, and whose ripening is not controlled by attachment to the parent plant; fruits, such as avocado and mango, which have a stimulatory concentration of ethylene present in the fruit tissue, but will not respond to the ethylene until the fruit is removed from the parent plant; and finally, fruits such as banana, which have a stimulatory level of ethylene present in the tissue but will not ripen until the decreasing sensitivity to ethylene reaches the endogenous ethylene content of the tissue.

Ethylene in red raspberry fruits declined until the onset of ripening, which coincided with a marked increase in ethylene content in the fruits, indicating red raspberry would probably be classified by Pratt and Goeschl with banana (16), which has a changing sensitivity to ethylene (4). Although respiration measurements were not obtained, the ethylene data for red raspberry indicated it is a climacteric fruit.

Apple, which ripens on the parent plant, maintained a low level of ethylene until ripening commenced. The data presented do not indicate whether the ethylene ripening response in apple is caused by a reduction in the level of sensitivity to ethylene or by an increase in ethylene to a level required for response. Although ethylene treatment of harvested Bartlett pears stimulated various ripening responses long before the fruits ripened without exogenous ethylene treatment, ethylene treatment did not produce an earlier-than-normal ripening of Delicious apples (Table VII). This observation indicated that ripening of Delicious apple was not dependent upon an increase in ethylene content of the flesh. Either Delicious apple had a changing sensitivity to ethylene or its ripening mechanism was ethylene insensitive until maturity.

There was an increase in flesh ethylene of overripe sweet and tart cherry fruits in one season, but there was no increase in flesh ethylene during fruit senescence in the other season of observation. During the entire period of cherry ripening (from the beginning of growth phase 3 to fully ripe), the ethylene content of the fruit flesh was very low. It seems likely that either the ethylene sensitivity of cherry fruits dropped to a very low level at the beginning of growth phase 3 (final swell in fruit size/fruit ripening) or the fruits responded to ethylene during growth phase 1 or growth phase 2 or, perhaps more likely, cherry fruit ripening is not normally ethylene dependent.

Worthy of particular note is the contrast, during fruit ripening, between apple, which develops very high ethylene levels in the fruit flesh, and red raspberry, which develops very high ethylene levels in the woody tissues of the receptacle, and cherry, which maintains a very low level of ethylene throughout the period of ripening.

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