Table 4. F2 of parental combinations, showing linkage of virescent allele with growth habit allele.

<table>
<thead>
<tr>
<th>Family</th>
<th>Parentage</th>
<th>Green bush</th>
<th>Green bush</th>
<th>Virescent bush</th>
<th>Virescent bush</th>
<th>Total</th>
<th>( \chi^2 ) for 9:3:3:1</th>
<th>( P )</th>
<th>Linkage value %</th>
</tr>
</thead>
<tbody>
<tr>
<td>76</td>
<td>202 virescent-vine x 212 green-bush</td>
<td>224</td>
<td>104</td>
<td>95</td>
<td>5</td>
<td>428</td>
<td>28</td>
<td>0.01</td>
<td>22.4 ± 3.0</td>
</tr>
<tr>
<td>78</td>
<td>205 virescent-vine x 212 green-bush</td>
<td>201</td>
<td>108</td>
<td>92</td>
<td>3</td>
<td>404</td>
<td>39</td>
<td>0.01</td>
<td>16.8 ± 3.1</td>
</tr>
<tr>
<td>81</td>
<td>212 green-bush x 202 virescent bush</td>
<td>146</td>
<td>62</td>
<td>73</td>
<td>3</td>
<td>284</td>
<td>22</td>
<td>0.01</td>
<td>20.7 ± 3.7</td>
</tr>
<tr>
<td>82</td>
<td>212 green-bush x 205 virescent vine</td>
<td>129</td>
<td>70</td>
<td>59</td>
<td>2</td>
<td>260</td>
<td>26</td>
<td>0.01</td>
<td>17.0 ± 4.0</td>
</tr>
<tr>
<td></td>
<td>Total observed</td>
<td>700</td>
<td>344</td>
<td>319</td>
<td>13</td>
<td>1,376</td>
<td>112</td>
<td>0.01</td>
<td>19.4 ± 1.7</td>
</tr>
<tr>
<td></td>
<td>Total expected (9:3:3:1 ratio)</td>
<td>774</td>
<td>258</td>
<td>258</td>
<td>86</td>
<td>1,376</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Flower petals are cream color and fade to a very dull white. The stigmas are orange, and flesh of the mature fruit is yellow, with a few of the fruit developing salmon streaks.

The muskmelon is well suited for genetic studies as it contains a rich reservoir of diversity. However, only 37 genes are recorded, and little linkage information is available (7). Wall (8) reported evidence that the shape of C. melo fruit is determined by a single allele, \( O \) for oval, with incomplete dominance plus minor modifying genes, closely linked in the coupling phase with the allele for determination of sex expression \( a \) for an-dromonoecious.

Bohn and Principe (2) tested 7 simply inherited muskmelon characters for linkage: bush, \( b \); glabrous, \( gl \); male-steriles, \( ms-1, ms-2 \); nectarless, \( n \); powdery mildew resistance, \( pm-2 \); and yellow-green, \( yg \). Freedom from linkage was verified in test crosses of 6 pairs. \( F_2 \) data yielded little indications of linkage among 15 of 21 possible character pairs. The male-steriles \( ms-1 \) and \( ms-2 \) were reported to segregate independently (1).

The changes in ethylene concentration of attached, horticulturally mature 'Lodi', 'McIntosh' and 'Golden Delicious' apples (\( Malus dom estica \)) were estimated by measuring the ethylene present in a tube sealed over the fruit calyx. Measurements of this gas sample (the equilibrium ethylene concentration (EEC)) were directly proportional to the internal ethylene concentration (IEC) of the fruit. In 'Lodi' and 'McIntosh', an increase in the EEC preceded abscission by at least 3 days. The length of time to abscission after increases in EEC were noted was negatively correlated with daily mean temperature in 'McIntosh'. 'Golden Delicious' apples did not show a relationship between the EEC and abscission. The commercial harvest period of 'Lodi' occurred later than the rise in ethylene (2) are correlated with fruit abscission. It has been reported that both these processes (7, 10) may occur over a wide time period among individual fruits on the same tree. The purpose of this study was to describe the variability in the occurrence of high ethylene levels among individual fruits and to relate this to abscission and the commercial harvest period.

The abscission of mature apple fruits is a process of considerable commercial interest, as preharvest drop decreases crop value. Repeated observations have shown that chemicals that alter fruit ethylene levels affect fruit drop (3, 4). Studies of bulk samples of apples suggest that the occurrence of the respiratory climacteric (12) and high levels of endogenous ethylene (2) are correlated with fruit abscission. It has been noted that both these processes (7, 10) may occur over a wide time period among individual fruits on the same tree. The purpose of this study was to describe the variability in the occurrence of high ethylene levels among individual fruits and to relate this to abscission and the commercial harvest period.


The Relationship Between Endogenous Ethylene and Abscission of Mature Apple Fruits

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Additional index words. Malus domestica

Abstract. The changes in ethylene concentration of attached, horticulturally mature 'Lodi', 'McIntosh' and 'Golden Delicious' apples (Malus domestica Borkh.) were estimated by measuring the ethylene present in a tube sealed over the fruit calyx. Measurements of this gas sample (the equilibrium ethylene concentration (EEC)) were directly proportional to the internal ethylene concentration (IEC) of the fruit. In 'Lodi' and 'McIntosh', an increase in the EEC preceded abscission by at least 3 days. The length of time to abscission after increases in EEC were noted was negatively correlated with daily mean temperature in 'McIntosh'. 'Golden Delicious' fruits did not show a relationship between the EEC and abscission. The commercial harvest period of 'Lodi' preceded the rise in EEC. In 'McIntosh', ethylene accumulation occurred both during and after the commercial harvest.

The changes in ethylene concentration of attached, horticulturally mature 'Lodi', 'McIntosh' and 'Golden Delicious' apples (Malus domestica Borkh.) were estimated by measuring the ethylene present in a tube sealed over the fruit calyx. Measurements of this gas sample (the equilibrium ethylene concentration (EEC)) were directly proportional to the internal ethylene concentration (IEC) of the fruit. In 'Lodi' and 'McIntosh', an increase in the EEC preceded abscission by at least 3 days. The length of time to abscission after increases in EEC were noted was negatively correlated with daily mean temperature in 'McIntosh'. 'Golden Delicious' fruits did not show a relationship between the EEC and abscission. The commercial harvest period of 'Lodi' preceded the rise in EEC. In 'McIntosh', ethylene accumulation occurred both during and after the commercial harvest.

The relationship between endogenous ethylene and abscission of mature apple fruits was studied. The changes in ethylene concentration of attached, horticulturally mature 'Lodi', 'McIntosh' and 'Golden Delicious' apples (Malus domestica Borkh.) were estimated by measuring the ethylene present in a tube sealed over the fruit calyx. Measurements of this gas sample (the equilibrium ethylene concentration (EEC)) were directly proportional to the internal ethylene concentration (IEC) of the fruit. In 'Lodi' and 'McIntosh', an increase in the EEC preceded abscission by at least 3 days. The length of time to abscission after increases in EEC were noted was negatively correlated with daily mean temperature in 'McIntosh'. 'Golden Delicious' fruits did not show a relationship between the EEC and abscission. The commercial harvest period of 'Lodi' preceded the rise in EEC. In 'McIntosh', ethylene accumulation occurred both during and after the commercial harvest.

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2Present address: Department of Pomology, Cornell University, Ithaca, NY 14853.

Literature Cited


Materials and Methods

Fruit samples used in this study were taken from 10-year-old trees growing at the Cornell Univ. orchard, Ithaca, N.Y. ('Lodi') or the Univ. of Massachusetts orchard in Belchertown, Mass., ('McIntosh' and 'Golden Delicious'). For each cultivar, ethylene levels were followed in 24 randomly selected apples growing on a single tree. These experimental fruits represented about 15% of each tree's crop.

Ethylene samples were collected using a method described by Blanpied (1) for measuring fruit oxygen content. A 2 cm length of 7 mm glass tubing was sealed over the calyx using asphaltum. The outer end of the glass tube was sealed with a serum cap, leaving a volume of about 1.5 ml in equilibrium with the fruit. These tubes were placed on the fruits prior to the occurrence of fruit drop in each cultivar. To test the accuracy of this method, the equilibrium ethylene concn (EEC) was compared with the internal ethylene concn (IEC) extracted from the same fruits by a method described by Sfakiotakis and Diley (10).

Gas samples were taken from each apple at about 8 AM. Sampling of the 'Lodi' apples was done daily, while the other cultivars were sampled 3 times a week. The samples were taken in disposable syringes. The needles of the syringes were plugged immediately with rubber stoppers. Within 3 hr of sampling the ethylene measurements were made by a gas chromatograph. Less than 1% of the ethylene in the syringes was lost between sampling and analysis. No measurable ethylene was generated by the syringes during that 3 hr period.

The EEC of each apple was determined until fruit abscission occurred. Using these determinations it was possible to develop summary curves for the changes in the EEC during the period of rapid ethylene accumulation. The initiation of the increase in EEC of each apple was judged to have occurred when 2 criteria were met. Firstly, an individual apple showed a significantly higher (P = 2.5%) EEC than the mean of the day's sample using z values for each individual fruit. Secondly, on the following 2 sampling dates the EEC of that fruit continued to rise.

Once the date of the increase in EEC had been calculated, the date of the previous sample was called day 0. All ethylene measurements after day 0 were used to generate the summary curves. Equations for these curves were derived using a stepwise polynomial regression after log transformation of the EEC values.

Results and Discussion

Evaluation of the sampling procedure. EEC measurements were compared to the IEC of the same fruits (Fig. 1). The EEC had a linear relationship (slope = 1.03) to the IEC. Throughout the range of ethylene levels observed, the average EEC was 15% of the IEC.

Ethylene and fruit abscission of 'Lodi' and 'McIntosh'. Apples of these cultivars showed 100- to 1000-fold changes in their EEC (Fig. 2 and 3) while attached to the tree. Similar results have been reported for 'Delicious' fruits (10). A wide range was also seen in the time of occurrence of this logarithmic

Fig. 1. Comparison of internal ethylene concn vs. equilibrium ethylene concn in 'McIntosh' fruits. Each point represents a single apple that was sampled using both methods (F linear = 83.73**).

Fig. 2. Changes in the EEC of 3 mature 'Lodi' fruits representative of the range observed. Apple A was the first of 24 fruits to drop, B the median and C the final fruit to drop.

Fig. 3. Changes in the EEC of 3 mature 'McIntosh' fruits representative of the range observed. Apple A was the first of 24 fruits to drop, B the median and C the final fruit to drop.
increase among individual fruits of each cultivar. In ‘Lodi’ the range was 11 days while in ‘McIntosh’ the range spanned 33 days.

Little fruit drop occurred prior to the logarithmic increase in EEC. Of the 24 apples studied in each of these cultivars, only 1 fruit of ‘McIntosh’ dropped prior to the occurrence of an increase in its EEC. In ‘Lodi’ the fruits dropped between 4 and 10 days after increased levels of ethylene had first been detected (Fig. 4). The EEC varied from 0.2 to 75 ppm on the date of abscission. Most ‘Lodi’ fruits had maximal or declining EEC levels when they dropped. It has been previously reported (2, 10) that increasing levels of internal ethylene are associated with fruit drop. The great range in EEC on the date of abscission suggests that the ethylene level is not as important as the length of time when increased levels of ethylene are present.

In ‘McIntosh’ abscission occurred between 3 and 25 days after EEC levels began to increase (Fig. 5). The EEC varied from 0.9 to 71 ppm on the date of abscission. Ethylene levels in most fruits were still increasing when fruit abscission occurred. Similar results were noted in the previous year for ‘McIntosh’ (data not shown). It was thought that this wide disparity in the time between EEC increase to abscission was attributable to weather differences during the period of increasing EEC. While temp are reasonably uniform during the period of ‘Lodi’ abscission in late July and early August, there was a great variability in temp during the period of ‘McIntosh’ abscission in Sept. and Oct. The time of high EEC prior to abscission showed the highest correlation with daily mean temp. A less significant correlation was also found between growing degree hours accumulated during high EEC and the time to abscission (data not shown). An Arrhenius plot (Fig. 6) of the daily mean temp and the days of increased EEC prior to abscission was linear. The Q10 for this plot is 1.86. The effect of temp on abscission is a widely observed process (9, 11), though no similar published Q10 values could be found for comparison. The time of high EEC prior to abscission was not significantly correlated with the date when high EEC was first detected. (data not shown).

In both cultivars it appeared that abscission did not occur until a minimum of 3 to 4 days after increases in the EEC were observed. Robitaille and Emerson (9) recently reported a similar lag between the time of enhanced ethylene production in apple fruitlets and thinning. A comprehensive study of the time required for induction and action of the enzymes which dissolve the tissue of the abscission zone in apple has not been published. While endogenous levels of ethylene in the abscission zone were not measured in this study, Blanpied (2) reported that they were about 10% of the IEC. Wang and Mellenthin (13) found that a 4-day lag occurred between an increase in endogenous ethylene and softening in pears at 20°C. Like abscission, this process is also known to require the synthesis of new protein and the maceration of tissue (5).

Ethylene and fruit abscission of ‘Golden Delicious’. The pattern of ethylene accumulation followed by abscission did not occur in ‘Golden Delicious’. Prior to the beginning of the study the apples were frozen on the tree for 2 consecutive nights (min orchard temp, −4°C). While the fruits did not show any breakdown, it appears that some freezing damage did occur. Two response patterns were found (Fig. 7). Two of the 24 apples showed a 10-fold increase in their EEC prior to abscission. These fruits dropped by separation at the abscission zone and had turgid, undamaged pedicels. The other fruits showed little change in their EEC prior to abscission. These fruits had shriveled pedicels and did not drop by separating the pedicel from the cluster base. Fig. 8 shows the breaking points observed in these fruits with shriveled pedicels. The predominant breaking point was between the pedicel and the fruit. Harley et al. (6) noted a similar occurrence in ‘Stayman Winesap’ which had been sprayed with 2, 4, 5-TP to prevent drop. They noted that injured fruits dropped, but their pedicels remained firmly attached to the tree. In some cases, drop also occurred when the pedicel cracked about 4 mm below the abscission zone. This left part of the pedicel attached to the
cluster base, while the distal segment of the pedicel was attached to the fruit.

Preharvest drop of 'Golden Delicious' in Massachusetts is not normally a problem. Usually these fruits are harvested regardless of maturity in mid-Oct. to avoid freezing damage. Ethylene production is usually thought to increase with damage to plant tissue. However, in mature apples, it has been shown that bruising can decrease fruit ethylene production (8). It is conceivable that freezing may have raised the basal EEC (Fig. 6) but damaged the mechanism required for the logarithmic increase in the EEC.

Ethylene and the commercial harvest period. In the cultivars studied the commercial harvest period and increasing EEC were not related. Table 1 shows the commercial harvest period for each cultivar and the range in time when increases in the EEC of individual fruits were first detected. 'Lodi' apples were harvested prior to any fruits showing increased EEC. In 'McIntosh' the range in the first observed increase in EEC of individual fruits started almost immediately after harvest began and stretched for 2 weeks after picking had finished. This cultivar is prone to severe preharvest drop (4), and it is possible that the increase in fruit ethylene before the end of harvest causes the problem.

Table 1. Commercial harvest period and the range in the initiation of ethylene production by individual fruits of 2 apple cultivars.

<table>
<thead>
<tr>
<th>Cultivar</th>
<th>Commercial harvest period</th>
<th>Date of initiation of ethylene production</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>Total % of sample</td>
</tr>
<tr>
<td></td>
<td></td>
<td>5</td>
</tr>
<tr>
<td>Lodi</td>
<td>July 15-18</td>
<td>July 21</td>
</tr>
</tbody>
</table>

Fig. 6. Arrhenius plot of the reciprocal of the mean Kelvin temp during the period of high EEC vs. the reciprocal of the natural logarithm of the time in days between EEC rise and abscission in each 'McIntosh' apple (F linear = 13.24**).

Fig. 7. Changes in EEC of 2 representative 'Golden Delicious' fruits. Two of the 24 apples studied had turgid pedicels and showed an increase in their EEC prior to separation of the abscission zone. The rest of the apples had shriveled pedicels and did not show a change in their EEC prior to drop. These fruits did not separate at the abscission zone.

Fig. 8. Abscission zone (A) and breaking point (B) observed in 'Golden Delicious' apples. Abscission occurred by either breaking the pedicel (upper) or separation of the pedicel from the fruit (lower).
Branching Habit and Apical Dominance of Compact and Normal Apple Seedlings as Influenced by TIBA and GA$_3$

Jung M. Lee$^2$ and N. E. Looney$^3$

Additional index words. Malus domestica, phyllotaxy, dwarfing, abscisic acid, gibberellins, 2,3,5-triiodobenzoic acid

Abstract. Regrowth of decapitated seedlings of apple (Malus domestica Borkh.) of a compact phenotype revealed stronger apical dominance and narrower branching angle than normal seedlings. Normal and compact seedlings were also found to differ in their phyllotaxy at lower nodes. Spraying with 2,3,5-triiodobenzoic acid (TIBA) before and/or after decapitation increased apparent apical dominance in compact seedlings; reduced shoot thickness in normal seedlings; and reduced shoot length and increased branching angle of both phenotypes. Gibberellic acid (GA$_3$) increased shoot length and reversed the TIBA effect on branch angle in the compact seedlings. These differing growth regulator effects are thought to relate to differences in endogenous growth substance levels. Shoot tips of normal seedlings were higher in abscisic acid (ABA) but the dwarf pea bioassay indicated the presence of another acidic inhibitor present only in the compact seedlings. Normal seedlings exhibited higher levels of gibberellin-like growth promoters.

'McIntosh Wijcik', a very compact natural mutant of 'McIntosh', crossed with non-spur cultivars, produces progeny with nearly 50% of the seedlings exhibiting the compact or spur-type habit (5, 6). This compact growth type is characterized by strong upright growth, shorter, fewer, and thicker shoots and a tendency to form spurs at almost every node on 2-year-old wood. The pattern of heritability suggests that a single gene with pleiotropic effects determines this growth type (5).

Earlier work with apple seedlings arising from 'McIntosh Wijcik' crosses concluded that ABA levels were higher in shoot tips of normal seedlings and that it is unlikely that differing ABA levels explain the compact phenotype (7). The objective of the present study was to gain a clearer understanding of the genetics and physiology of the compact habit by observing the response to applied growth regulators.

Materials and Methods

Apple seeds arising from the cross 'McIntosh Wijcik' × 'Golden Delicious' were stratified at 2 to 4°C for 90 days and planted in sand in a greenhouse on Feb. 14, 1976. Shortly after germination, 500 seedlings were transplanted into 10-cm Jiffy pots (and into 15-cm pots 50 days later) and grown with supplemental light (16-hr days) in a temp-controlled greenhouse. At about 4 months after germination all 500 seedlings were sorted into normal and compact phenotypes using criteria previously described (5, 7).

An interesting observation made in the course of the present study was that the compact seedlings strongly tended toward a 3/8 phyllotaxy at the lower nodes whereas the normal seedlings favored a 2/5 arrangement (Table 1). Counterclockwise phyllotaxy predominated in both populations. This new information was useful in segregating the compact and normal seedlings. From each group 96 very uniform seedlings were selected for the following experiments using a randomized block design with 12 plants per treatment.

On June 18, 1976, the shoot tip of each of the 48 seedlings of each phenotype used for expt. I was excised and instantly frozen. These shoot tips, containing no expanded leaves, were later extracted for acidic plant growth substances. The subtending section of each shoot, containing 3 expanded leaves, was sampled in an identical manner. On the day after decapitation, 12 compact and 12 normal seedlings were sprayed to drip with 250 ppm GA$_3$ and equal numbers were sprayed with 250 ppm TIBA or a combination of 250 ppm GA$_3$ plus 250 ppm TIBA. These treatments were repeated 17 days later. Growth observations and measurements were made 21, 42 and 63 days after decapitation. At the end of the experiment all new shoots were...