The abscission of maturing fruit is an important process which has not been extensively studied. Earlier reports on fruit abscission in the cherry have stressed premature drop associated with failures in fruit-set (2, 20). With the development of various mechanical harvesting devices and the rapid commercial adoption of machine harvesting (14, 15), attention has now been focused on abscission of mature fruit.

There is a need for a better understanding of the processes involved in abscission of mature fruit and to what extent these processes determine the forces required for fruit removal. Further, a precise understanding of the abscission process may provide a basis for its control, and thus make possible more efficient machine harvesting and a realistic programming of the harvest operation.

Data on abscission of cherry fruit during maturation are reviewed with emphasis on facilitating machine harvest.

Nature of fruit separation during development

The weakest point of fruit attachment varies with fruit development (Fig. 1). If a force is applied to the fruit in the direction of the long axis of the pedicel, the weakest point early in fruit development is the pedicel. During Stage II of fruit growth, separation generally occurs between the pedicel and peduncle, or the peduncle may peel free from the spur or shoot. Beginning in early Stage III and persisting through maturity, separation occurs between the fruit and pedicel.

Fruit which fail to develop (lack of fertilization, embryonic abortion, insect infestation, other physical damage, etc.) generally abscise with the pedicel attached. Fruit abscission can be induced with the pedicel attached in sound fruits if the apical half or more of the fleshy pericarp is excised. Defructification will cause the pedicel to abscise within a few days.

Both sour (Prunus cerasus L.) and sweet (Prunus avium L.) cherry follow the above pattern; however, the force required to remove the sweet cherry fruit at maturity may be several fold greater than for the sour cherry.

Histological characteristics of the abscission zone and layer

There are 2 abscission zones in the sour and sweet cherry, one being between the peduncle and pedicel (upper) and the other between the fruit and pedicel (lower). Since in both fruits no significant change was observed during maturity in the upper abscission zone and since fruit separation at maturity takes place at the lower abscission zone, the following discussion will be limited to the latter zone.

The abscission zone may be viewed as a transition region where the cells of the apical portion of the pedicel are contiguous with the larger cells of the pericarp. The vascular bundles passing through this region are shown when viewed in cross-section. Sclerenchyma tissue which is associated with the vascular tissue in the pedicel is not evident in the abscission zone, but diverges into the recepable and terminates there after the calyx cup is shed. The tissues in the abscission zone appear constricted. Thus, the abscission zone would appear to have inherent structural weakness.

The anatomical development of the abscission layer in mature sour cherry fruit ('Montmorency') has been recently described by Stöesser et al. (24). The cells in the lower abscission zone through which the separation layer develops are generally thin-walled and less rigid than cells of the fruit or pedicel tissue. The development of the abscission layer can be first noted approx 12-15 days before maturity by a lower affinity of the cells for haematoxylin. Abscission layer development starts in the central portion of the abscission zone, generally just above the stony pericarp, and extends toward the periphery to the juncture of the fruit and pedicel tissues. Separation appears to take place, for the most part, by dissolution of the middle lamella followed by a collapse of the cells. There is little or no fracturing of cells and no cell enlargement or divisions have been noted in the layer. No abscission layer is formed across the vascular bundles or in a few rows of cells at the periphery. Thus, when the fruit is mature and the abscission layer completely developed, final separation of the fruit from the pedicel apparently occurs by a mechanical fracturing of the vascular strands and tearing of the ring of tissue at the periphery of the juncture of the fruit and pedicel.

Separation of sweet cherry fruit from its pedicel appears to be less well defined (24, 26). Wittenbach (26) has recently shown that

**THE NATURE AND CHEMICAL PROMOTION OF ABDICATION IN MATURING CHERRY FRUIT**

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2I am grateful to my students and colleagues who have contributed so very much.

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formation of a cavity just above the stony pericarp appears to be the first change in the lower zone during abscission of mature 'Windsor' fruit. As this cavity enlarges, mechanical stress probably causes a shearing and collapse of adjacent tissue and of the tissue in the outer cortex at the juncture of the fruit and pedicel (Fig. 2). Often when cell layer separation is observed in the cortical tissue, it occurs in the distal region of the abscission zone. Separation was not restricted to the middle lamella but considerable fracturing of cells was noted. There was no well-defined abscission layer, as indexed by staining with haematoxylin, in the sweet cherry as observed in the sour cherry.

Histochemical changes in the lower abscission zone during fruit separation

Only limited data are available on the nature of the chemical changes associated with abscission in the cherry (21, 22, 23). Marked changes have been noted histochemically in cell wall constituents of the abscission layer during separation. The low affinity of the cell walls in the abscission layer, compared to those proximal or distal to the layer, for haematoxylin, and the visual (microscopic) appearance of cell separation suggest that degradation of cell wall constituents is a primary factor. Pectic materials, as indexed by ruthenium red and hydroxyamine-ferri chloride, were lost from the middle lamella of cells in the abscission layer.

The role of Ca in the abscission process has been of longstanding interest (8, 17, 18, 21, 22). Stossel et al. (22) have shown a loss of Ca from the lower abscission zone of the sour cherry during fruit separation at maturity. Ca was apparently lost before visual (microscopic) appearance of the abscission layer (Fig. 3). Subsequent studies designed to relate the loss of Ca and Mg to abscission layer development have not been conclusive (21, 26). Both Ca and Mg were localized in the walls of cells of the abscission zone and those cells proximal to the abscission layer had a higher content than those distal. Ca and Mg may have been lost from walls of cells in the abscission layer during layer development. However, since these walls are generally thinner and partially degraded, it was not possible to establish a conclusive relationship between Ca loss and cell separation. Nevertheless, on a total abscission zone basis there appeared to be a definite loss of Ca and Mg. The question remains—how does the loss of Ca and possibly Mg relate physiologically to abscission layer development?

There is good evidence that walls of cells of the abscission layer have a lower affinity for Ca with progressive development of the abscission layer. $^{45}$Ca injected into the pedicel before the development of the abscission layer was found uniformly distributed throughout the abscission zone. When $^{45}$Ca was injected into the pedicel during development of the separation layer, the walls of cells comprising the layer and a few cells proximal or distal to the layer bound less $^{45}$Ca than the adjacent tissue. The loss of binding sites is probably related to degradation of the cell wall.

With progressive development of the abscission layer, there was less staining of cell walls of the abscission layer with periodic acid-Schiff's reagent, indicating a loss of cell-wall polysaccharides. Hemicellulose and at least some cellulose were also degraded during the formation of the abscission layer in the sour cherry (22, 26). Walls of cells in the abscission layer lost birefringence, suggesting that physical changes had occurred in the walls. There was no evidence of starch accumulation immediately before or during abscission. No lignification was observed on either the pedicel or fruit side of the abscission layer during separation (22, 26).

Inhibition of cherry fruit abscission with inhibitors of protein synthesis suggests that newly synthesized proteins may play an important role (23, 26). Stüsser (23) has recently shown that labelled leucine and uridine were preferentially incorporated into cells of the developing abscission layer. He concluded that those cells making up the abscission layer have a higher rate of protein and RNA synthesis than adjacent cells of the abscission zone.

Cell wall degrading enzymes no doubt play a significant role in fruit abscission, as they do in leaf abscission (1); however, no data have been reported, as yet, for the cherry. Poovalah and Rasmussen (unpublished) have documented the localization of dehydrogenase and peroxidase activity in the abscission zone of cherry. With both enzymes the pedicel tissue had considerably higher activity than the fruit tissue, there being a clear demarcation between the two tissues. Four peroxidase isozymes were present with no apparent qualitative changes during the development of the abscission layer. However, some quantitative changes occurred in two of the isozymes during layer development. The significance of this finding in the fruit abscission process remains to be established.

![Fig. 2. Photomicrograph illustrating the cavity formed above the stony pericarp and localized separation at the juncture of the fruit and pedicel (note arrows) in the lower abscission zone of a mature sweet cherry fruit, 'Windsor'. After Wittenbach (26).](image-url)

![Fig. 3. Ca content of the lower abscission zone of the sour cherry during maturation. Each point represents a mean of the calcium content of 10 abscission zone sections (2.5 x 2.5 x 1.5 mm). The solid and dotted lines represent separate determinations on two collections of fruit. After Stüsser et al. (22).](image-url)

Relationship between abscission layer formation and fruit removal

With progressive development of the abscission layer, the sour cherry fruit can be removed from its pedicel with correspondingly less force. The fruit removal force (FRF) decreases to a min at full maturity when the separation layer is completely developed. At this time a force of 80 to 200 g may still be required to detach the fruit, since no abscission layer develops across the vascular tissue and at the periphery where the pedicel and fruit tissues are contiguous. Final detachment appears to take place as a result of mechanical fracture of these tissues.

When considering the entire fruit population on a given tree, the FRF required to remove a given portion will also be a function of the no. of fruits in which an abscission layer has developed. This relationship is illustrated in Fig. 4.

Cain (5) has demonstrated, under field conditions, that the % fruit removed from a tree by a harvesting machine was closely related to the FRF. This correlation was surprisingly close when one considers the diverse physical and biological aspects of the tree which may dampen the transfer of the vibrations from the machine to the fruit. Further, those cultural practices which alter the FRF or efficiency of transmitting the shaking force to the fruit will also alter the % of fruit removed with a given force (5).
Although the anatomy of fruit abscission in sweet cherry is quite different from that in sour cherry, nevertheless, changes take place in the abscission zone which are reflected in a reduction of FRF (3, 26). FRF at maturity may be as much as 4-fold greater for the sweet than for the sour cherry. Promotion of tissue separation and, hence, a reduction in FRF would be expected to have the same relationship to fruit removal by machine harvest as in the sour cherry.

Chemical modification of fruit abscission

Much of the early work on the effects of chemicals on fruit abscission has been directed to fruit thinning and control of preharvest drop. Since neither of these are pressing problems in cherry production, little information has been accumulated on chemical modification of cherry fruit abscission. Perhaps the most significant studies have been directed toward minimizing or eliminating failures in fruit-set (20). In recent years, a number of chemicals have been identified which promote abscission of sour cherry fruit, as indexed by a reduction in FRF. These are summarized in Table 1.

Sucinic acid-2,2-dimethylhydrazide (SADH) when applied to sour cherry trees 2 weeks after bloom resulted in a lower FRF for a period of about 1 week just prior to commercial harvest (25). However, no significant differences were apparent at full maturity. The chemical effect on abscission appears to be indirect by advancing the maturity of the treated fruit.

For a broader treatment of chemical modification of abscission in agricultural crops the reader is referred to a recent review by Copper et al. (6). In addition, extensive evaluations of various chemicals for promotion of fruit abscission in olives (9, 10, 11, 13) and citrus (12) have been made for the purpose of facilitating mechanical harvest.

Chemical facilitation of machine harvest

Mechanical shaking has been demonstrated to be an effective method of harvesting cherry fruit (15). When the tree is shaken the fruit is accelerated (a) and a force (F) is created which equals the mass (m) of the fruit times acceleration (F = ma). If this force (F) is greater than the FRF, the fruit will be detached. Therefore, it is self-evident that if we can chemically reduce the FRF, fruit can be removed with a lower force.

Of several chemicals evaluated (Table 1), 2-chloroethylophosphonic acid (ethephon) appears to be one of the most effective in consistently reducing FRF in the cherry (3, 7, 16, 19). Therefore, the following discussion will focus on the effects of ethephon.

Foliar sprays of ethephon at 100 to 1000 ppm 6 to 15 days before maturity may reduce the FRF by 40 to 60% as compared to the control. The effect of the chemical is rapid, in that, a significant decrease in FRF is apparent within 3 days. Fruit separation is promoted between the fruit and pedicel. The chemical is somewhat more active in the sour than in the sweet cherry.

The FRF distribution curves from treated trees have lower mean values and the individual observations are clustered nearer to the mean than for nontreated trees (Fig. 5). By relating the FRF to cumulative % of fruit removed one should theoretically be able to predict % fruit removal based on FRF (Fig. 6), clearly a higher % of the fruit present on a treated tree would be removed with a given force than on a nontreated tree. We have established with the sweet cherry in field

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### Table 1. Some chemicals which have biological activity in modifying sour cherry fruit abscission.

<table>
<thead>
<tr>
<th>Compound</th>
<th>Conc</th>
<th>% change</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>Abscisic acid</td>
<td>5 x 10^-5 M</td>
<td>-40</td>
<td>(28)</td>
</tr>
<tr>
<td>Ascorbic acid</td>
<td>2%</td>
<td>-15</td>
<td>(4)</td>
</tr>
<tr>
<td>2-Chloroethylophosphonic acid</td>
<td>1000 ppm</td>
<td>-48</td>
<td>(4)</td>
</tr>
<tr>
<td>Cyclheximide</td>
<td>25 ppm</td>
<td>+41</td>
<td>z</td>
</tr>
<tr>
<td>Iodosacetic acid</td>
<td>300 ppm</td>
<td>-15</td>
<td>(4)</td>
</tr>
<tr>
<td>Olive water extract</td>
<td>0.5%</td>
<td>-35</td>
<td>(27)</td>
</tr>
<tr>
<td>Salicylic acid</td>
<td>500 ppm</td>
<td>-21</td>
<td>(4)</td>
</tr>
<tr>
<td>1,5,5-tetramethyl-3, - dimethylaminodithiobiuret</td>
<td>500 ppm</td>
<td>-33</td>
<td>z</td>
</tr>
</tbody>
</table>

*6A negative or positive sign preceding a value signifies a lower or higher fruit removal force, respectively, in comparison to the control. Data were collected 6 days after treatment except for abscisic acid which was determined after 5 days.

7One component tentatively identified as abscisic acid.

Bukovac, M. J., unpublished data.

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**Fig. 4.** Relationship between abscission layer development and the force required to separate the sour cherry fruit from its pedicel. After Stösser et al. (24).

**Fig. 5.** Frequency polygon of FRF of control and ethephon-treated fruit populations of sour cherry. After Bukovac et al. (4).

**Fig. 6.** Relationship between FRF and total fruit removed in the sour cherry as influenced by ethephon. After Bukovac et al. (4).
trials under commercial conditions that a significantly greater percentage of the fruit can, in fact, be removed with a comparable shaking procedure with the use of ethephon.

Certain undesirable features are also apparent with ethephon, mainly on weak trees and at higher concentrations (1000 ppm and greater): (a) excessive leaf abscission, (b) terminal dieback and (c) gummosis. To what extent excessive gummosis will influence long term productivity remains to be documented.

There are other advantages, in addition to improved fruit removal, to be realized if we can effectively reduce the FRF. They are: (a) higher quality of the harvested fruit, (b) less force required to shake the tree, (c) use of smaller shaking units, (d) longer tree life, (e) uniform maturity and (f) perhaps programmed harvesting.

Summary

Anatomical and histochemical changes occurring in the fruit pedicel abscission zone during maturation of sour and sweet cherry are described. Less force was required to remove the fruit as it approached maturity. Several chemicals when applied as foliar sprays promote fruit abscission; ethephon being one of the more effective compounds. Chemical reduction of the fruit removal force resulted in increased fruit removal. The implications of chemical modification of fruit removal force are discussed in relation to facilitation of machine harvest.

Literature Cited


CITRUS ABDISSIO

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During the last decade intensive research has been conducted on the phenomenon of organ abscission in plants, as evidenced by several reviews (5, 9, 10, 40) and this symposium. Abscission is of interest because, among other things, a knowledge of the processes involved gives insight into the metabolism of cell walls, the ramifications of which are well known. Horticulturists have an additional interest, for a basic knowledge of this process has application in fruit production programs.

One of the most obvious advantages of controlling abscission of plant organs is that of choosing the time and no. of organs to abscise, which in turn affects the size and quality of a particular crop. In most tree crops, including citrus, there is a definite need for a method of controlling the number of flowers which set fruit (22). Also, there is a need for a method of Preventing the abscission of flowers and young fruit. In the season (25), and later in the season, a need for promoting abscission of mature fruits at a desired time to aid harvest (45). In connection with the latter, a citrus production man would like to have a chemical that would reduce the bonding force of fruit to stem to approx 1 to 2 kg (not to fruit drop), is predictable in its action, and is relatively non-toxic. If he is interested in the fresh fruit market, he will add 2 other conditions; that is, fruit free of injury and more desirable colored.

My comments will be slanted toward abscission of citrus fruits, particularly mature fruits, and to whether a chemotherapeutic approach to fruit loosening is feasible.

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1Florida Agricultural Experiment Station Journal Series No. 3972.
2Professor of Biochemistry, Department of Fruit Crops. Grateful acknowledgement is made to my students and colleagues who have contributed much.