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INTERGENERIC GRAFT COMPATIBILITY  
WITHIN ROSACEAE

Thesis for the Degree of M. S.  
MICHIGAN STATE UNIVERSITY  
George E. Evans

1958

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INTERGENERIC GRAFT COMPATIBILITY WITHIN ROSACEAE

By

GEORGE E. EVANS

AN ABSTRACT

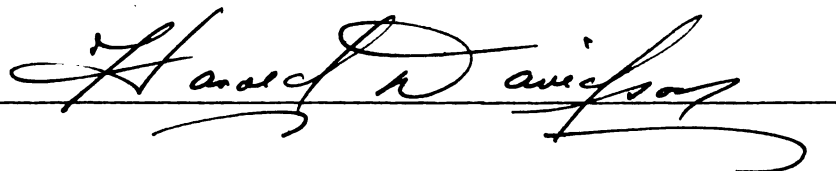
Submitted to the College of Agriculture, Michigan State University  
of Agriculture and Applied Science in partial fulfillment of  
the requirements for the degree of

MASTER OF SCIENCE

Department of Horticulture

1958

Approved

A handwritten signature in cursive script, reading "Harold D. Anderson", is written over a horizontal line.

Five generically different species of Rosaceae were intergrafted in 15 combinations to determine initial success.

Of these combinations, Malus on Sorbus understocks was found best, in terms of anatomical and cultural characteristics. In addition, Malus on Chaenomeles and Chaenomeles on Sorbus appeared worthy of further study. A complete lack of success, attributed to scion quiescence or desiccation of scions, occurred in all combinations involving Pyracantha. Cultural observations showed that the grafts could be separated into the following three distinct categories, as based on degree of success: "Growing", "Living but not growing", and "Dead".

Visual abnormalities, such as "autumn coloration", nutrient deficiency symptoms, defoliation and re-establishment of leaves, and bud breaking followed by scion death, were observed in partial or completely unsuccessful grafts. Other aberrations, such as the formation of thick stubby scions or abnormally great shoot growth, were also noted in successful graft unions.

Anatomical studies revealed the following differences in gross anatomy between the understock species: variation in vessel cross-sectional area, differences in wood-bark ratios, differences in tangential width of rays, and differences in number of vessels per unit area of stem tissue. The following conditions were noted in successful unions: new xylem, in the form of a

smooth arc between stock and scion (cross-sectional view); slightly distorted longitudinal coursing of new xylem relatively undisturbed by undifferentiated parenchyma; isolated patches of fiber or nonfunctional parenchyma, surrounded by phellem in the cortical region; and graft lines often not evident toward the periphery of the graft.

Imperfectly matched cambia, lack of cambial activity of stock or scion, and possible lack of pressure applied to the graft union, were believed to cause many failures.

Grafts classified as "living but not growing" appeared to have made sufficient vascular connection to remain alive, but not grow appreciably. Some apparently completed partial vascular continuity, even though badly mismatched. More dark, necrotic cells were evident between stock and scion than in successful grafts.

Accompanied by two tables and ten figures.

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## TABLE OF CONTENTS

|                                       | Page |
|---------------------------------------|------|
| INTRODUCTION . . . . .                | 1    |
| REVIEW OF LITERATURE . . . . .        | 2    |
| Graftage - General Concepts . . . . . | 2    |
| Compatibility Studies . . . . .       | 5    |
| Morphological . . . . .               | 5    |
| Anatomical . . . . .                  | 8    |
| MATERIALS AND METHODS . . . . .       | 13   |
| General Procedure . . . . .           | 13   |
| Anatomical Procedure . . . . .        | 15   |
| RESULTS . . . . .                     | 17   |
| Cultural . . . . .                    | 17   |
| Anatomical . . . . .                  | 22   |
| DISCUSSION . . . . .                  | 34   |
| SUMMARY . . . . .                     | 44   |
| LITERATURE CITED . . . . .            | 46   |

## LIST OF FIGURES

| Figure                                                                                                                                                                                                                                                                                                                    | Page |
|---------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|------|
| 1. "Autumnal coloration" and deficiency symptoms observed in certain graft combinations . . . . .                                                                                                                                                                                                                         | 21   |
| 2. A diagram of comparative gross anatomy of <u>Pyracantha</u> , <u>Sorbus</u> and <u>Malus</u> . . . . .                                                                                                                                                                                                                 | 23   |
| 3. A diagram of comparative gross anatomy of <u>Rosa</u> and <u>Chaenomeles</u> . . . . .                                                                                                                                                                                                                                 | 24   |
| 4. Photomicrograph of transection stem section showing an unsuccessful graft of <u>Pyracantha</u> on a <u>Pyracantha</u> understock; well matched cambia are inactive. Scion in upper portion of photomicrograph, stock below . . . . .                                                                                   | 26   |
| 5. Photomicrograph of transverse stem section showing an unsuccessful union of <u>Chaenomeles</u> on a <u>Sorbus</u> understock with widely separated cambia, curved graft incision, differences in vessel size, and large amounts of callus tissue. Scion seen in upper portion of photomicrograph, stock below. . . . . | 26   |
| 6. A photomicrograph showing a successful union of <u>Malus</u> on a <u>Sorbus</u> understock . . . . .                                                                                                                                                                                                                   | 29   |
| 7. A photomicrograph showing an unsuccessful union of <u>Pyracantha</u> on a <u>Pyracantha</u> understock . . . . .                                                                                                                                                                                                       | 29   |
| 8. Photomicrograph of a successful union of <u>Sorbus</u> on a <u>Sorbus</u> understock . . . . .                                                                                                                                                                                                                         | 31   |
| 9. Photomicrograph of a successful union of <u>Sorbus</u> on a <u>Sorbus</u> understock . . . . .                                                                                                                                                                                                                         | 31   |
| 10. Photomicrograph of a "living but not growing" union of <u>Chaenomeles</u> on a <u>Sorbus</u> understock . . . . .                                                                                                                                                                                                     | 33   |

## INTRODUCTION

Intergeneric grafting has been the object of considerable study, and of quite extensive use in the field of commercial fruit growing. With ornamental plants, commercial use has been limited to fewer intergeneric combinations.

The present study was designed to determine the compatibility and relative merit of certain species within the family Rosaceae. With more knowledge of compatibility, further investigation may provide added information about winter hardiness, drought and disease resistance, and alterations in growth habits.

## REVIEW OF LITERATURE

### Graftage - General Concepts

Since before the birth of Christ the practice of grafting has been recognized as a horticultural technique to increase the quantity and improve the quality of plants.

Some of the alterations to plants, as a result of graftage are:

(1) alterations of the habit of growth (Tukey and Brase, 1943; Sax 1950), (2) retardations of flowering season (Biffen, 1902), (3) increasing disease resistance (Smith, 1929), (4) development of fruit trees on their own root systems (Kerr, 1935), (5) increase winter hardiness (Filewics and Modlibowska, 1941), (6) alteration of bloom and fruit production (Hatton and Grubb, 1925; Hatton et al., 1928), and (7) alteration of fruit yield (Hatton et al., 1928; Korshunov, 1941; Zebrak, 1937).

Upshall (1941) studied the compatibility of Malus ioensis plena on Malling rootstocks and found that Malling I, although not dwarfing, was the most suitable understock for this crabapple. In similar experiments, using ten varieties and species of ornamental apples on Malling understocks, Shaw (1941) obtained similar results, but found that his observations were, in general, inconclusive. Intermediate stem pieces of Malling IX produced a 10 to 20 percent smaller tree with a more spreading branch habit than did

those using stem pieces of McIntosh (Tukey and Brase, 1943). They observed that single worked trees on Malling IX were smallest in height, spread, and cross sectional area of trunk than those grafted with interstem pieces. Sax (1950) altered the growth of Syringa vulgaris by using Syringa amurensis japonica as a rootstock. This combination produced a non-suckering, tree-like habit of growth. Rootstock varieties have more influence on tree size than does the scion, according to Vyvyan (1955).

Grafting was employed by Kerr (1935) to establish fruit trees on their own root systems. This was accomplished by inverting the root piece when grafting certain fruit species. Results obtained by Sax (1950) also indicated that piece root grafting was effective in establishing Syringa sp. upon its own root system.

The use of grafting to increase disease resistance was exemplified by Smith (1929) who demonstrated that Prunus mume could be used as an apricot understock due to its crown gall resistance. Biffen (1902), in earlier work, cautioned that grafting may, in some cases, increase susceptibility to attacks of animal pests.

Filewicz and Modlibowska (1941) observed that winter hardiness was induced in apples through the use of hardy rootstocks. They found further that the hardiness of the rootstocks was due to inherent resistance as well as to the scion variety.

The results of certain investigations have shown that grafting can alter the time of bloom as well as fruit yield. According to Hatton and Grubb (1925), the rootstocks, to a certain extent, affected the time of blossom in both apples and plums. Experimentally, plums on Pershore stocks increased the crop yield of certain varieties (Hatton et al., 1928). Hatton (1928) reported that earliness and quantity of fruit set was altered in pear varieties budded on certain quince understocks. He observed that Quince C produced the heaviest yield by the seventh year, whereas Korshunov (1941) stated that pear on Sorbus aucuparia rootstocks produced heaviest fruiting by the fourth and fifth years. In work with intergeneric and interspecific grafting of herbaceous plants, Zebrak (1937) found increased yield only for those plants with vigorous root systems or resistance to low temperatures. Tukey and Brase (1943) showed that single working apple varieties upon Malling IX resulted in earlier and heavier fruiting than trees grafted with an intermediate stem piece.

Extensive work was done by Zebrak (1936 and 1937) on intergeneric grafting of herbaceous plants. He demonstrated successful grafts between both annual and perennial species including Pisum sativum, Helianthus tuberosum, Helianthus annuus and Medicago sativa. Hatton (1928) has shown certain quince varieties to be successful understocks for Pyrus sp. Chester (1931) used the commercially popular combination of Syringa sp.

on Ligustrum sp. to describe graft blight. Results of 30 years work by Korshunov (1941) indicated that Sorbus aucuparia was a favorable rootstock for Pyrus sp. Roberts (1949) explained that intergeneric and interspecific grafting has been practiced with pears, apples, peaches, plums, roses, shrubs and other ornamental plants.

### Compatibility Studies

Numerous investigators have been interested in the compatibility of various intergeneric and interspecific grafts (Hatton, 1928; Heppner, 1928; Argles, 1937; Chang, 1937; Shaw, 1944; Mosse and Herrero, 1950). Stock and scion relations were also reviewed recently by Rogers and Beakbane (1957).

### Morphological

The exact cause of incompatibility is not clearly understood, although it has had considerable study. Goodale (1864) reported in experiments with Canada plum as a rootstock for other plum varieties that budded plants produced less than half the root system of unbudded ones. According to Booth (1913, 1914), Proebsting (1926, 1928) and Chang (1937), incompatibility is often accompanied by a physically weak union. However, Waugh (1904) stated that in many cases the graft union was physically stronger than the adjacent stem pieces. Abnormal coloration and early foliage drop was another morphological symptom often exhibited by incompatible graft com-

binations of fruit species (Shaw and Southwick, 1944; Herrero, 1951).

Leaf yellowing was observed by Chester (1931) in graft combinations of Syringa sp. upon Ligustrum sp. There was a reduction in number and size, as well as brittleness and leaf curling. Overgrowth at the point of union has long been considered a symptom of incompatibility. Bradford and Sitton (1929b) reported that an uncongenial combination of pear on apple showed no exterior swelling or other visible sign of incompatibility. They explained that the largest swellings were found in congenial unions. This view was shared by Argles (1937) when he listed the following as unreliable indicators of incompatibility: (1) a low percentage "take" of grafts; (2) differences in growth rate of scion or stock before or after grafting; (3) swellings of the union; and (4) differences in time of growth initiation in the spring or cessation of growth in the fall, between stock and scion.

Booth (1913, 1914) proposed seven conditions as possible barriers to successful grafting: (1) lack of physical strength at the graft union; (2) inability of the leaves to utilize sap produced by the stock; (3) inability of the root system to utilize food materials produced by the scion; (4) interruption of upward sap flow due to poor xylem union; (5) interruption of downward sap flow due to poor phloem continuity; (6) quantity of food materials taken up by the root system being too great or inadequate to support scion growth; and (7) sap produced by the scion being deficient

or in excess for growth of the stock.

Improper procedure has resulted in graft failures. Roberts (1925) demonstrated that the position of the distal scion bud, in relation to the tongue of the union had a profound effect upon the success of the graft. Most successful unions occurred when the top bud was oriented directly above the point of tongue contact on the matched side of the union. At this point, the callus union was best. Often a standard practice has been to tilt scions outward to insure matching of the two cambia. Bradford and Sitton (1929a) observed quite frequently that poor unions were the result of this procedure. They explained that when the scion was tilted, the wood did not tend to reorient itself and pressure exerted by the growth process tended to break the scion from the stock. These workers found defective unions of apple on apple and pear on pear were due to faulty grafting techniques. Chang's (1937) budded plants produced a higher percent "take" than grafted plants.

The physiological condition of propagation wood has been shown to have an effect upon the success of grafting. Cherry stocks grown under irrigation or in areas having a long growing season were more favorable, in terms of vigor, than those grown where maturity was earlier (Tukey and Brase, 1930). They stated that No. 1 or good No. 2 Mahaleb stocks gave best results. In studies of fruit tree grafting, Matubara (1931) considered

that a positive correlation existed between ease of grafting and hardness of the wood used, but this was not true for all varieties of the same species. Korshunov (1941) mentioned that in combinations of pear on Sorbus aucuparia, one-year-old scion wood made good unions and grew very satisfactorily.

Recently, attempts have been made to overcome the failure of graft combinations which are not entirely compatible. Garner (1944) demonstrated the use of double-working and bridge grafting as a solution to the problem of incompatibility of pear varieties grafted on Quince A. Anatomical studies of graft unions by Herrero (1951) employed the use of an interstem piece compatible to the quince and pear scion. Standard, double-working, and ring grafting were used by Mosse and Herrero (1950) to determine the compatibility of pear on quince. They found that ring grafted trees were more incompatible than those in which an interstem piece was employed.

#### Anatomical

In addition to morphological symptoms of incompatibility, certain anatomical characteristics have been found typical of unions which fail. Certain investigators have agreed that wood discontinuity was a common indicator of incompatibility (Waugh, 1904; Proebsting, 1926; Bradford and Sitton, 1929a; Chester, 1931; Chang, 1937). Xylem distortion was found by Proebsting (1928) in many graft unions, and explained the aberration

being uneven growth rates between stock and scion, which did not always cause physically weak unions. His evidence also indicated that isolated parenchymatous masses interrupted vascular elements, resulting in mechanically weak unions. A successful graft union was formed, according to Bradford and Sitton (1929b), by a bridging of vascular elements between stock and scion, across a zone of parenchymatous tissue. Sass (1932) suggested that this "bridging" was accomplished through the differentiation of callus tissue and the formation of cambia.

Incompatibility studies of fruit trees by Proebsting (1926, 1928) and Chang (1937) showed that excessive callus formation caused graft failures. Bradford and Sitton (1929b) considered seasonal regrafts of cambial breaks as causing parenchymatous, or often suberized tissue, which resulted in the ultimate death of the scion. Sass (1932) and Herrero (1951) agreed that wood discontinuity did not occur the first year after grafting. Cambium destruction or impairment was believed by Herrero (1951) as the cause for undifferentiated tissue formation between stock and scion. Bark interruption, in addition to wood discontinuity, was a cause of graft failures (Herrero, 1951). Lack of phloem continuity was a symptom of uncongeniality, according to Bradford and Sitton (1929a), who later (1929b) observed tissue necrosis closely associated with uncongenial unions. They described how, in combinations of Prunus sp., the xylem between medullary rays had degenerated to a gummy mass.

In further work with graft unions, Proebsting (1926, 1928) described unions in which bark tissue was found between stock and scion instead of parenchyma. This three-layered bark was composed of a middle corky layer of unknown origin, and a layer on each side which was characteristic of the adjacent tissue of the union. He explained that the anatomical structure was typical of unions which initially grew well but occasionally did not live through the season. Water transport was studied by reversing the flow of water through excised plant parts, by Harvey (1931), who concluded that certain scions can not utilize the xylem elements previously existing in the stock. He believed that the scion obtained translocated materials only through new conducting tissues produced by the original cambium. This controlling effect was exemplified by a one-year-old graft, in which all basal xylem elements were oriented toward, and connected with, the scion.

Except in the case of Diospyros Kahi, Maturbara (1931) indicated that negative correlations existed between grafting success and the amount of tannin present in the cambium. He stated, however, that a positive correlation was present between the number of vessels in a given shoot area and graft survival. Ring grafts made by Roberts (1934) formed varied new xylem elements beneath the bark ring. Some of these elements resembled the ring variety, some were typical of the stem variety, and others were unlike either of the graft components. Beakbane (1941) noted differ-

ences in vessel number, wood fibers per unit area, vessel and fiber sizes, and wood-bark ratios between Malling stocks and various fruit wood scions.

Anatomical callus studies of Kostoff (1928) showed that callus was primarily of rootstock origin. Kac (1931), however, believed that scions produced the greater amount of callus. He reported large accumulations of food materials at the base of the scion at the graft line caused asymmetrical callus. Occasionally the scion produced various kinds of proliferations which formed leafy shoots and roots at the graft line. Cambial derivatives penetrated the callus first on the lower part of the scion. Abnormal vascular tissue was present both in the pith and proliferated tissue. Sass (1932) stated that callus was formed exclusively by tissues outside the xylem cylinder, and that, except for periderm, any tissue of the bark may proliferate. He believed that excess callus formation occurred wherever vascular obstruction occurred.

Uneven starch balance in grafted plants frequently has been considered as an anatomical indication of incompatibility (Kostoff, 1928; Proebstin, 1928; Chang, 1937; Mosse and Herrero, 1950; Herrero, 1951). Proebsting (1928) explained that obstruction of basipetally translocated food material at the graft union caused swellings. Accumulation of starch and calcium oxylate crystals were observed in graft unions studied by

Kostoff (1928). This accumulation may have caused the slowed water and solute movement described by Chang (1937). Mosse and Herrero (1950) pointed out that a lack of starch below a graft union was not necessarily a sign of a discontinuous vascular system. They observed that in tissues lacking starch a reducing material (possibly sugar) was present, indicating that a certain amount of translocation had occurred. It was noted that pear on quince combinations, which were low in starch content, also showed signs of incompatibility.

## MATERIALS AND METHODS

### General Procedure

In October 1957, the following five species: Rosa multiflora, Sorbus aucuparia, Malus pumila, Pyracantha coccinea la'landi, and Chaenomeles japonica of the family Rosaceae were selected for study. The dormant plants, to be used as understocks, which ranged between 1/8 inch and 3/8 inch caliper, were potted on December 20, using previously steamed sterilized pots and sandy loam soil. The potted plants were pruned to approximately 5 inches above the soil line and placed in a 60° F greenhouse for seven days to become established.

Between December 23 and December 27, 252 whip and tongue grafts were made, using fresh wood 4 to 6 inches long) collected locally. The 12 combinations were:

1. Scion of Sorbus on an understock of Sorbus.
2. Scion of Pyracantha on an understock of Pyracantha.
3. Scion of Rosa on an understock of Rosa.
4. Scion of Chaenomeles on an understock of Chaenomeles.
5. Scion of Rosa on an understock of Sorbus.
6. Scion of Pyracantha on an understock of Sorbus.
7. Scion of Chaenomeles on an understock of Sorbus.
8. Scion of Malus on an understock of Sorbus.

9. Scion of Rosa on an understock of Chaenomeles.
10. Scion of Pyracantha on an understock of Chaenomeles.
11. Scion of Malus on an understock of Chaenomeles.
12. Scion of Pyracantha on an understock of Rosa.

Additional combinations of a scion of Malus on an understock of Malus, and a scion of Pyracantha on an understock of Malus, totalling 63 grafts, were made approximately two months later. All graft unions were 2 to 4 inches above the crown, tied with 4-inch rubber grafting strips and waxed with a standard resin grafting compound. Twenty-one grafts of each combination were made, and the components labelled for identification. Immediately after grafting, the plants were stored for 30 days at 40 to 42° F and 60 percent relative humidity, to provide environment for callus formation. After storage the grafts were moved into a 60° F night temperature greenhouse, where they remained for further growth and observation. The plants were placed on the bench in three replications of seven plants each. The replications were randomized in such a way that each combination was spaced equidistant apart.

Growth measurements, in terms of total elongation (cm), and number of shoots measured, were recorded at 30-day intervals. After three months graft unions were collected for anatomical studies. One month later, graft survival was recorded on the basis of the following three categories:

(a) plants with scions dead, (b) plants which initiated growth but did not continue, and (c) grafts which made successful growth. Photographs of plants showing typical incompatibility symptoms were taken.

#### Anatomical Procedure

Half inch samples of one-year-old ungrafted stems from the five understock species were collected. Two half-inch stem segments, including the graft union, were cut from each of a selected group of graft combinations. Both collections were placed in glass vials containing formalin alcohol killing and fixing solution. All samples were dehydrated, using the tertiary butyl alcohol series and infiltration was accomplished using the colloidin procedure described by Johansen (1940). Samples were then placed in securely stoppered bottles containing colloidin and placed in a 50° Centigrade oven to hasten the infiltration process.

The infiltrated samples were placed on wooden blocks using colloidin and hardened in chloroform for 12 hours. Following a softening period of 24 hours in a 1:1 solution of glycerin and 70 percent ethyl alcohol, the samples were sectioned, using a sliding microtome. Both longitudinal and transverse sections were microtomed approximately 20 micra in thickness and placed in 70 percent ethyl alcohol. After staining with safranin and fast green, sections were dehydrated and cleared in xylol and absolute ethyl alcohol, and mounted permanently for observation in piccolyte. To prevent

non-living unions from becoming separated during staining and clearing, a substitution was made of benzene and chloroform as clearing solutions (Johansen, 1940) to prevent dissolving of the celloidin matrix.

Diagrams of transverse sections of one-year-old understocks and photomicrographs of longitudinal and transverse sections of growing and non-growing graft unions were prepared.

## RESULTS

### Cultural

Total linear growth and survival of grafts were variable, but indicated certain trends. Observations showed that the entire group of grafted plants could be separated, in terms of degree of survival or failure, into the three categories summarized in Table I. The plants within seven graft combinations grew in excess of 50 percent, whereas those within five other combinations were dead in excess of 50 percent. The majority of the plants within the other combinations were included in the category of "living but not growing". This group included grafts which had grown but became dormant, at the time data was taken, as well as scions which were alive but had not grown.

A tabulation of survival percentages, listed under the heading of "growing" in Table I, is based on the number of plants of each combination which grew successfully. All the control combinations, such as Sorbus on Sorbus, exhibited a high degree of success, with the exception of Pyracantha on Pyracantha (Table I). Pyracantha grafted on Pyracantha failed to grow and exhibited leaf drop beginning 10 days following removal from storage. It was observed that Pyracantha scions failed when grafted on all other understocks.

Sorbus grafted on Sorbus understocks and Rosa grafted on Rosa

TABLE I

Percent Survival of Graft Combinations (21 Plants per Combination)

| Graft Combinations |                    | Growing | Living but<br>not Growing <sup>1</sup> | Dead   |
|--------------------|--------------------|---------|----------------------------------------|--------|
| Scion              | Stock              |         |                                        |        |
| <u>Sorbus</u>      | <u>Sorbus</u>      | 100.00  | 0.00                                   | 0.00   |
| <u>Malus</u>       | <u>Sorbus</u>      | 100.00  | 0.00                                   | 0.00   |
| <u>Chaenomeles</u> | <u>Sorbus</u>      | 52.38   | 42.85                                  | 4.76   |
| <u>Rosa</u>        | <u>Sorbus</u>      | 0.00    | 52.38                                  | 47.61  |
| <u>Pyracantha</u>  | <u>Sorbus</u>      | 0.00    | 0.00                                   | 100.00 |
| <u>Chaenomeles</u> | <u>Chaenomeles</u> | 85.71   | 0.00                                   | 14.29  |
| <u>Malus</u>       | <u>Chaenomeles</u> | 95.23   | 0.00                                   | 4.76   |
| <u>Rosa</u>        | <u>Chaenomeles</u> | 0.00    | 52.38                                  | 47.61  |
| <u>Pyracantha</u>  | <u>Chaenomeles</u> | 0.00    | 9.52                                   | 90.47  |
| <u>Malus</u>       | <u>Malus</u>       | 80.95   | 0.00                                   | 19.05  |
| <u>Rosa</u>        | <u>Malus</u>       | 0.00    | 52.38                                  | 47.61  |
| <u>Pyracantha</u>  | <u>Malus</u>       | 0.00    | 19.05                                  | 80.95  |
| <u>Rosa</u>        | <u>Rosa</u>        | 76.19   | 0.00                                   | 23.81  |
| <u>Pyracantha</u>  | <u>Rosa</u>        | 0.00    | 0.00                                   | 100.00 |
| <u>Pyracantha</u>  | <u>Pyracantha</u>  | 0.00    | 0.00                                   | 100.00 |

<sup>1</sup>Plants of this category included scions which had grown but became dormant, as well as those which were alive but had not grown.

understocks produced the greatest growth of those grafted on their own understocks (Table II). A scion of Sorbus on a Sorbus understock was observed to have made nearly twice the total growth of other plants of this combination. One Rosa developed spotting of its leaves, thought to be a nutrient deficiency, and complete defoliation within 45 days following removal from storage. Twenty-one days later, this plant produced new leaves from axillary buds and grew normally. In certain graft combinations of Malus on Sorbus understocks purple "autumn colorations" developed in the leaves. Figure 1 illustrates the extent to which this color developed. An abnormal leaf coloration (Figure 1) was present, to a lesser degree, in several Chaenomeles on Chaenomeles grafts.

Of the grafts studies, a combination of Malus grafted on Sorbus understocks was the most successful. No graft failures occurred and total linear growth (Table II) surpassed that of all other combinations, as well as that of many grafts on their own stocks, including Sorbus grafted on Sorbus, which is approximately equalled.

Shoot diameter was slightly greater in this combination than that of many other grafts of comparable size. A shoot arising from the scion of one plant was observed to have a greater caliper size than that of Malus grafted on other understocks. It was noted that the scion and distal bud developed to nearly double the size of other scion shoots of this combination,

TABLE II  
Average Shoot Elongation of 4 Month Old Grafts

| Species            |                           | Replications |       |       | Average |
|--------------------|---------------------------|--------------|-------|-------|---------|
| Scion              | Stock                     | 1            | 2     | 3     |         |
| <u>Sorbus</u>      | <u>Sorbus</u>             | 38.61        | 46.43 | 41.71 | 42.27   |
| <u>Rosa</u>        | <u>Sorbus</u>             | 0.64         | 0.43  | 0.36  | 0.47    |
| <u>Chaenomeles</u> | <u>Sorbus</u>             | 32.36        | 14.00 | 13.43 | 19.93   |
| <u>Malus</u>       | <u>Sorbus</u>             | 37.64        | 30.21 | 50.00 | 39.28   |
| <u>Chaenomeles</u> | <u>Chaenomeles</u>        | 46.43        | 41.93 | 28.79 | 39.05   |
| <u>Rosa</u>        | <u>Chaenomeles</u>        | 0.57         | 0.57  | 0.86  | 0.667   |
| <u>Malus</u>       | <u>Chaenomeles</u>        | 24.00        | 25.43 | 28.00 | 25.81   |
| <u>Rosa</u>        | <u>Rosa</u>               | 99.71        | 90.43 | 73.79 | 87.98   |
| <u>Malus</u>       | <u>Malus</u> <sup>1</sup> | 16.36        | 34.64 | 13.57 | 21.52   |

<sup>1</sup>Two months old. Not included in analysis of variance.

#### Analysis of Variance

|              | D. F. | S. S.    | M. S.   | F.      |
|--------------|-------|----------|---------|---------|
| Total        | 23    | 17486.08 |         |         |
| Treatments   | 7     | 16501.98 | 2357.42 | 38.30** |
| Replications | 2     | 122.43   | 61.21   | 0.99    |
| Error        | 14    | 861.67   | 61.54   |         |

\*\*F value significant at the .01 level of probability.



Figure 1. "Autumn coloration" and deficiency symptoms observed in certain graft combinations.

Left to right: Malus on Chaenomeles, Malus on Sorbus, and Chaenomeles on Chaenomeles.

and its leaves were abnormally leathery in texture. This extreme thickness originated at the upper portion of the graft union and progressed, essentially unchanged, to the tip of the new growth, which was limited to approximately five inches.

Intergeneric grafts of Malus on a Chaenomeles understock were successful to nearly the degree found for Malus on Sorbus stocks. The former, however, showed a tendency to develop more "autumn coloration" and considerably less vigorous growth (Figure 1).

Many grafts which eventually failed were found to have grown approximately 0.5 to 1 centimeter in length before death of shoots occurred. It was noted frequently that death and re-initiation of new buds occurred before final death of the scion.

#### Anatomical

The understocks studied were compared in the transverse sections shown in Figures 2 and 3. It was apparent that the following distinct differences exist among species: vessel cross-sectional area; number of vessels and rays per unit area of stem; amount of pith; wood to bark ratio; and number of radial rows of ray parenchyma. The preparations showed that the rays, vessels and pith of Rosa were substantially greater in volume than those of the other understocks (Figures 2 and 3).

Successful graft unions, as characterized by plants grafted on their

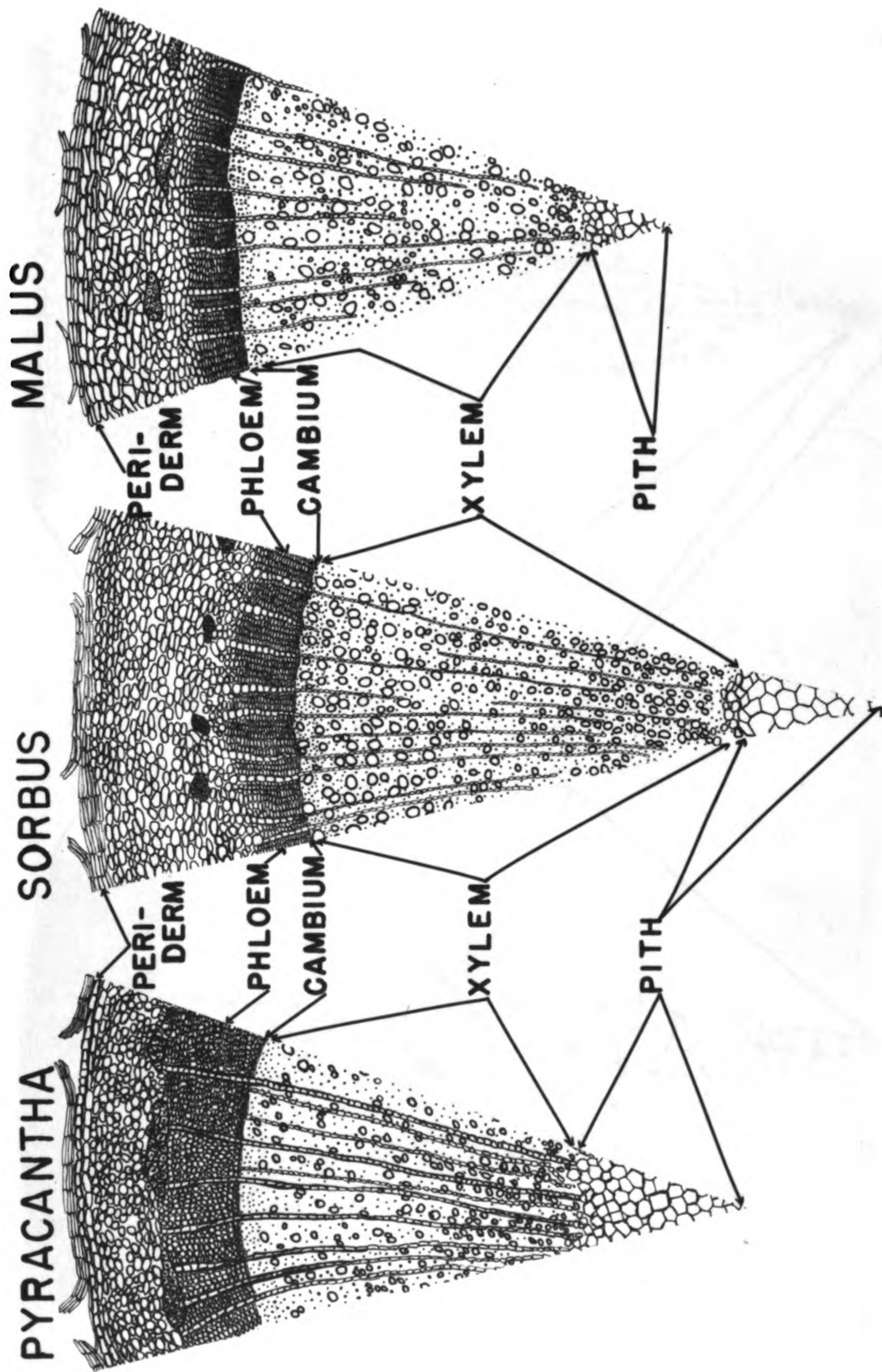


Figure 2. Diagram to show comparative gross anatomy of transverse stem segments of Pyracantha, Sorbus and Malus (X 130).

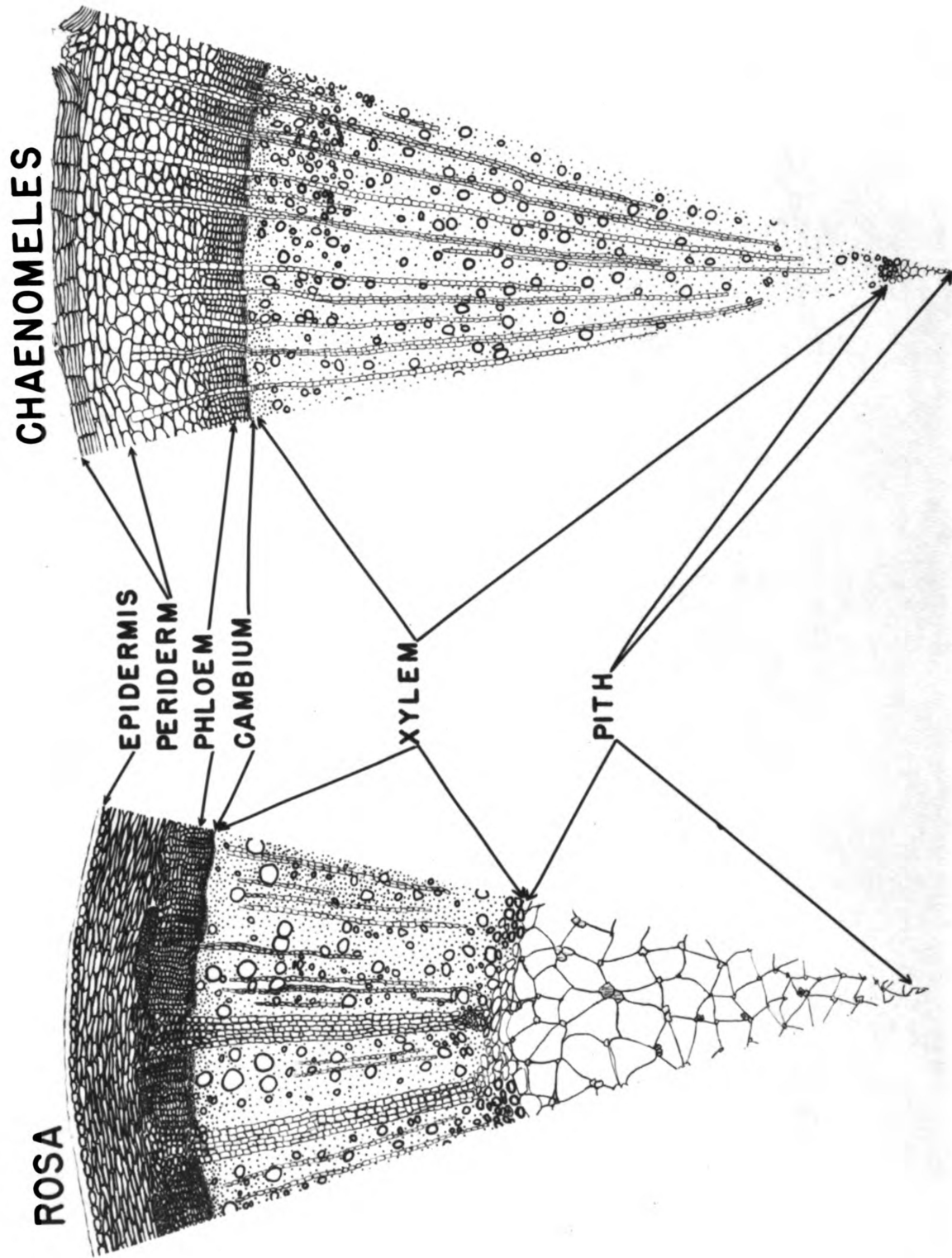


Figure 3. Diagrams to show comparative gross anatomy of transverse stem segments of *Rosa* and *Chaenomeles* (X 130).

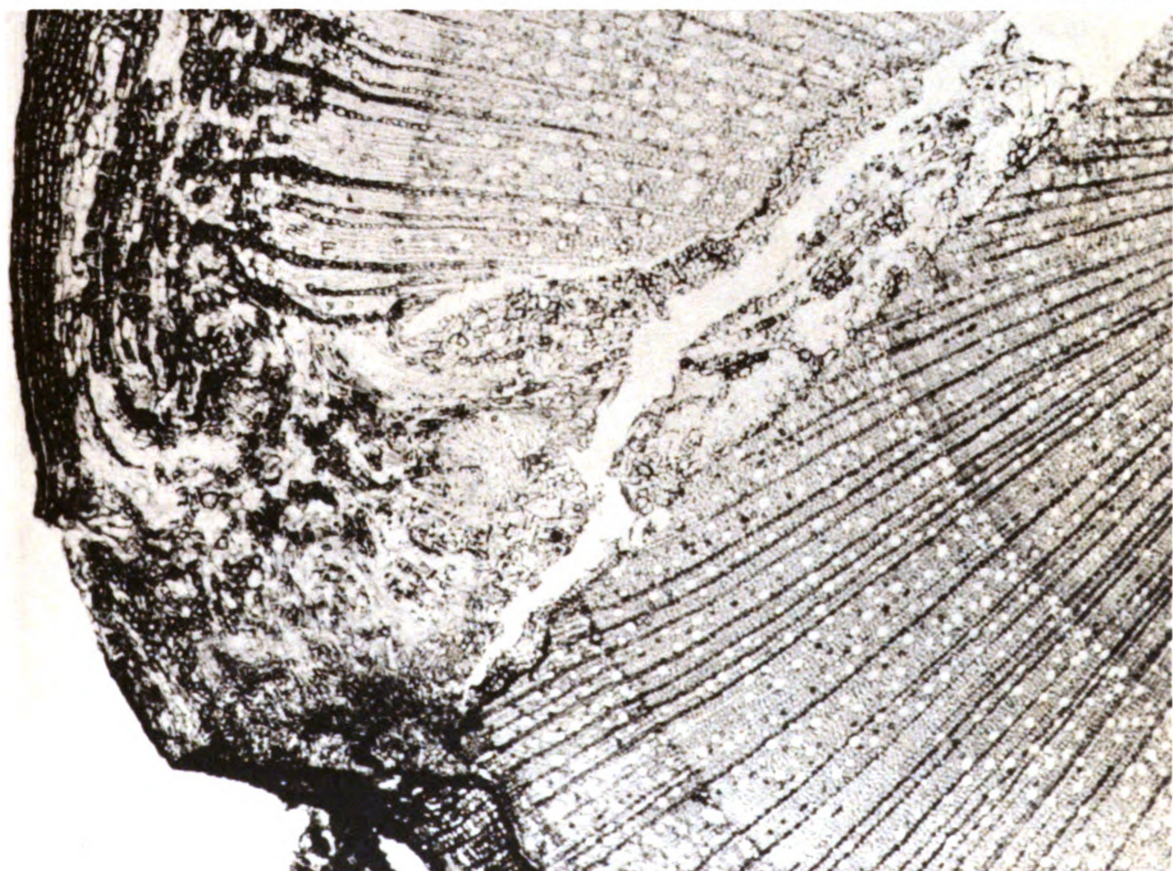
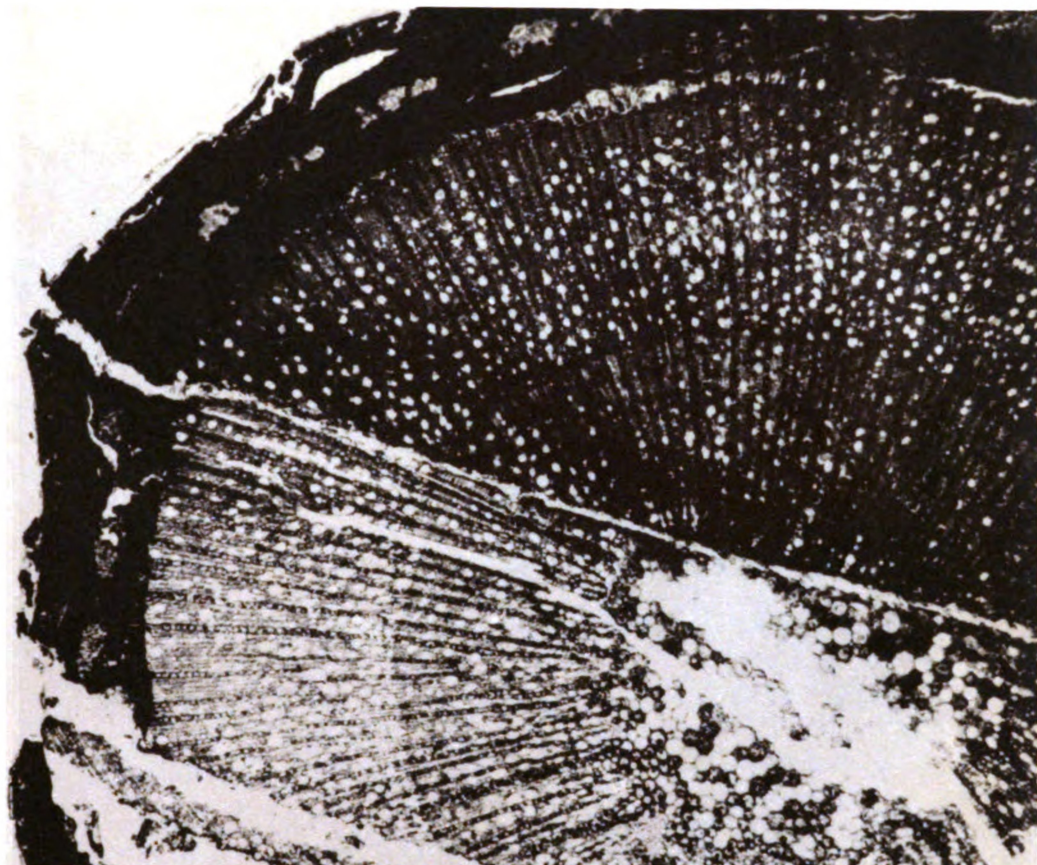
own understocks, were found, in cross-sections, to have produced vascular connections in the form of an arc oriented almost parallel to the plane of cutting. This arc of vascular tissue was evident in the vicinity of the original cambial matching, but became less conspicuous in a centrifugal direction. The gross anatomical appearance of a successful union is illustrated in Figure 4. The original incision was visible toward the center of the stem below or above the presence of the graft "tongue". Darkly stained parenchyma cells appeared to have grown centripetally from the original point of cambial contact. This tissue seemed to have been derived jointly from both cambia. In the phloem and cortical region no separation was visible between stock and scion, but isolated, darkly stained, disorganized patches were often observed. Isolated tissue of this description was occasionally found between stock and scion along lines of original xylem contact. This tissue was bounded by rows of cells resembling the phellem of the periderm. These surrounding rows of cells were equal in number to that of the cork at the periphery of the stem and were frequently found to be centered around patches of phloem or cortical fibers.

The isolated patches of parenchyma found in the cortex and bordered by phellem produced by the phellogen appeared to be formed at the original point of graft contact.

The isolated patches of parenchyma appeared to be formed at the

Figure 4. Photomicrograph of transection stem section showing an unsuccessful graft of Pyracantha on a Pyracantha understock; well matched cambia are inactive. Scion in upper portion of photomicrograph, stock below (X 30).

Figure 5. Photomicrograph of transverse stem section showing an unsuccessful union of Chaenomeles on a Sorbus understock with widely separated cambia, curved graft incision, differences in vessel size, and large amounts of callus tissue. Scion seen in upper portion of photomicrograph, stock below (X 30).



original point of graft contact. Longitudinal coursing of vascular elements across the graft union in newly formed xylem, although somewhat two-dimensionally distorted, was relatively undisturbed. A longitudinal section of Sorbus on Sorbus (Figures 8 and 9) showed that some vessels were distorted, from the vertical, so that they were observed in cross section. In the region of original cambial contact, vascular continuity was intermittently located along the graft line with intervening undifferentiated, darkly stained parenchyma. Similar to that noted in transverse sections, the vascular arcing became less evident toward the periphery of the newly formed xylem tissue (Figure 9).

Imperfectly matched cambia, apparent lack of pressure between graft components, and lack of cambial activity of stock and scion appeared to explain some of the unsuccessful graft unions in the samples studied. Figure 7 illustrates gross anatomy of an unsuccessful Pyracantha on Pyracantha graft.

Imperfectly matched unions appeared to have been caused by uneven graft incision as well as by mis-alignment during the grafting procedure. It was noted, in certain combinations of Chaenomeles grafted on Sorbus (Figure 5) that the incision was not straight and its irregularity caused wide separations between cambia. Differences in vessel size were also noted in this photomicrograph. It was observed in Rosa grafted on Sorbus

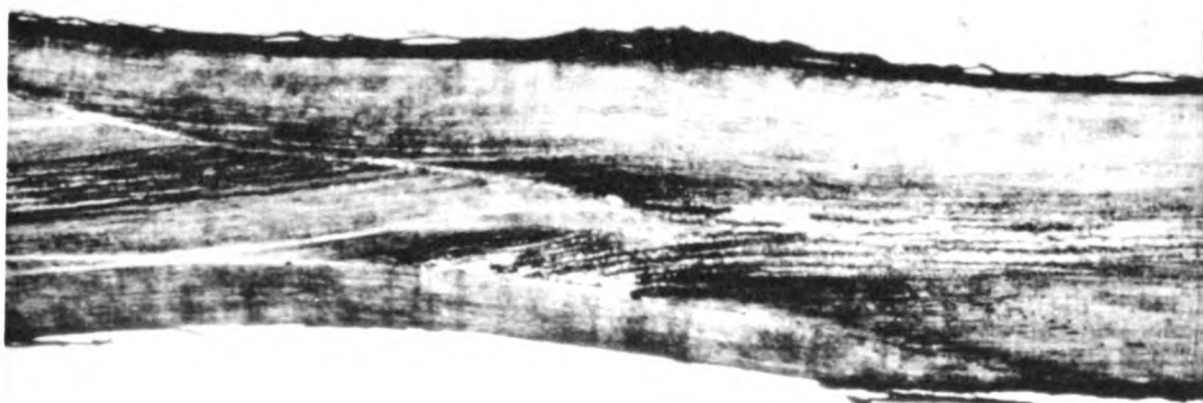
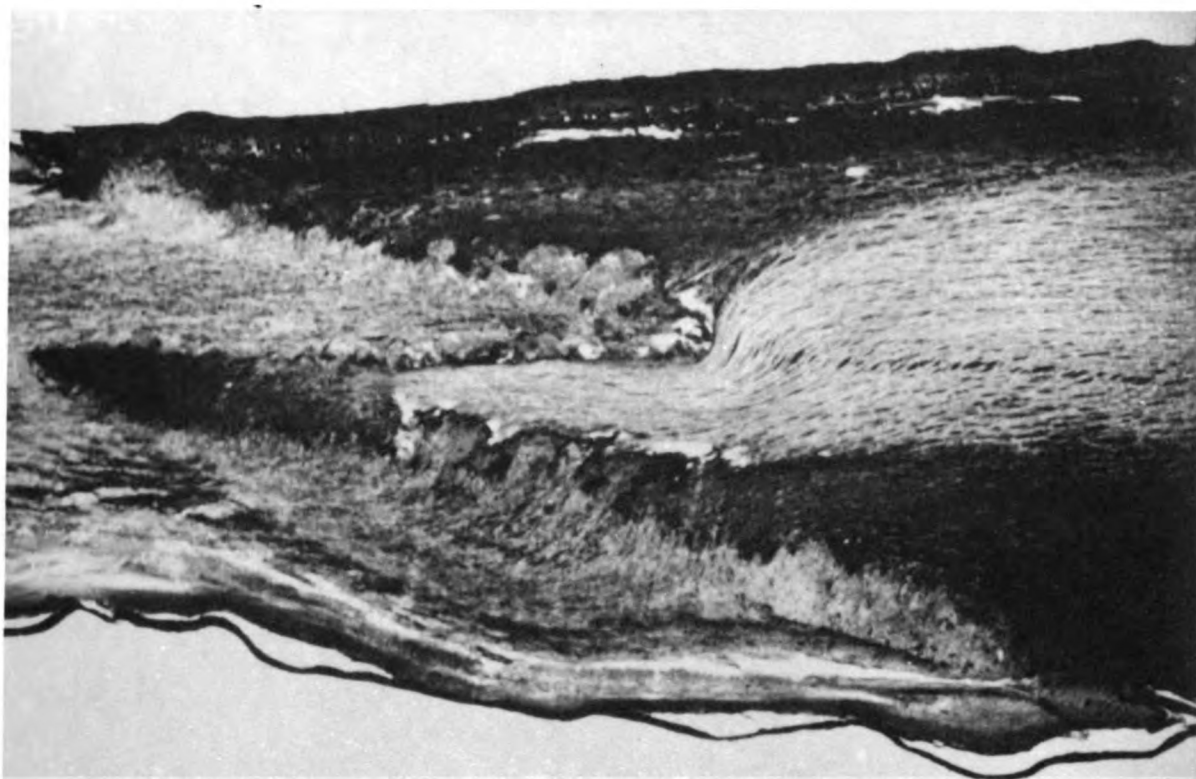
that the scion had been inserted too deeply into the stock, causing an overlapping and a mismatching of the tissues.

Certain unsuccessful grafts, although well matched, appeared to be loosely fitted together. Some of this was caused by disruption during processing of sections, but in general, failure of grafts, in which incisions were irregular, was believed to be caused by lack of pressure applied at the union.

In many graft unions a partial or complete lack of cambial activity was observed. This inactivity appeared limited to the scions in all combinations involving Pyracantha with some other species. In all grafts of Pyracantha on its own understock, and in certain grafts of Rosa on Sorbus, cambial inactivity of both stock and scion was observed in apparently well executed grafts. Figures 4 and 7 illustrates this lack of stock and scion activity in a well matched union of Pyracantha on Pyracantha understocks. Nearly complete lack of stock cambium activity was observed in certain poorly formed graft combinations. The transverse section of Figure 5 showed that the Chaenomeles scion had produced the majority of the proliferated tissue present. The lack of activity of this scion cambium, and other quiescent cambia studied, seemed to be accompanied by necrotic or tannin-filled cells along the boundary of the inactive component. This condition appeared to block vascular "bridging" across the union.

Figure 6. A photomicrograph showing a successful union of Malus on a Sorbus understock. Illustrates well established vascular continuity across the graft union (X 15).

Figure 7. A photomicrograph showing an unsuccessful union of Pyracantha on a Pyracantha understock. Illustrates a complete lack of cambial activity and the presence of necrotic tissue (X 15).



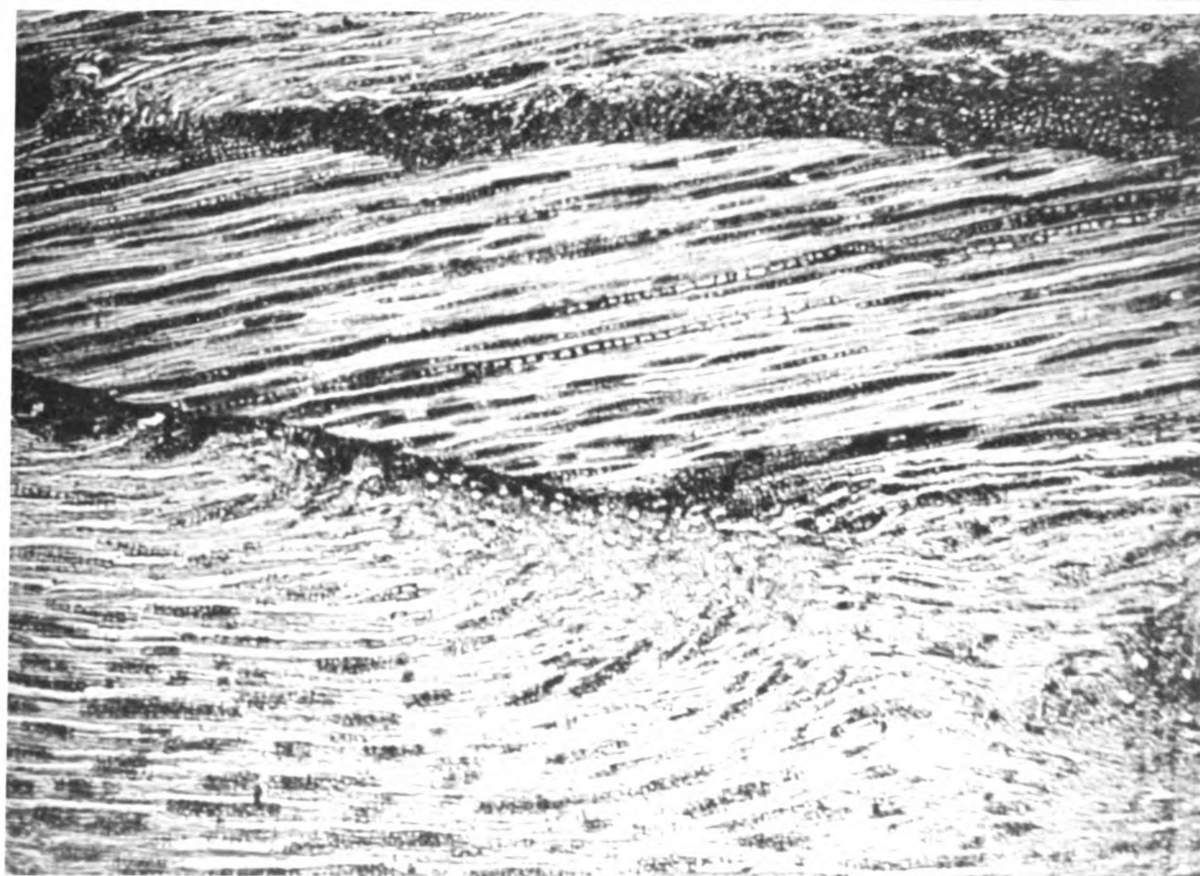
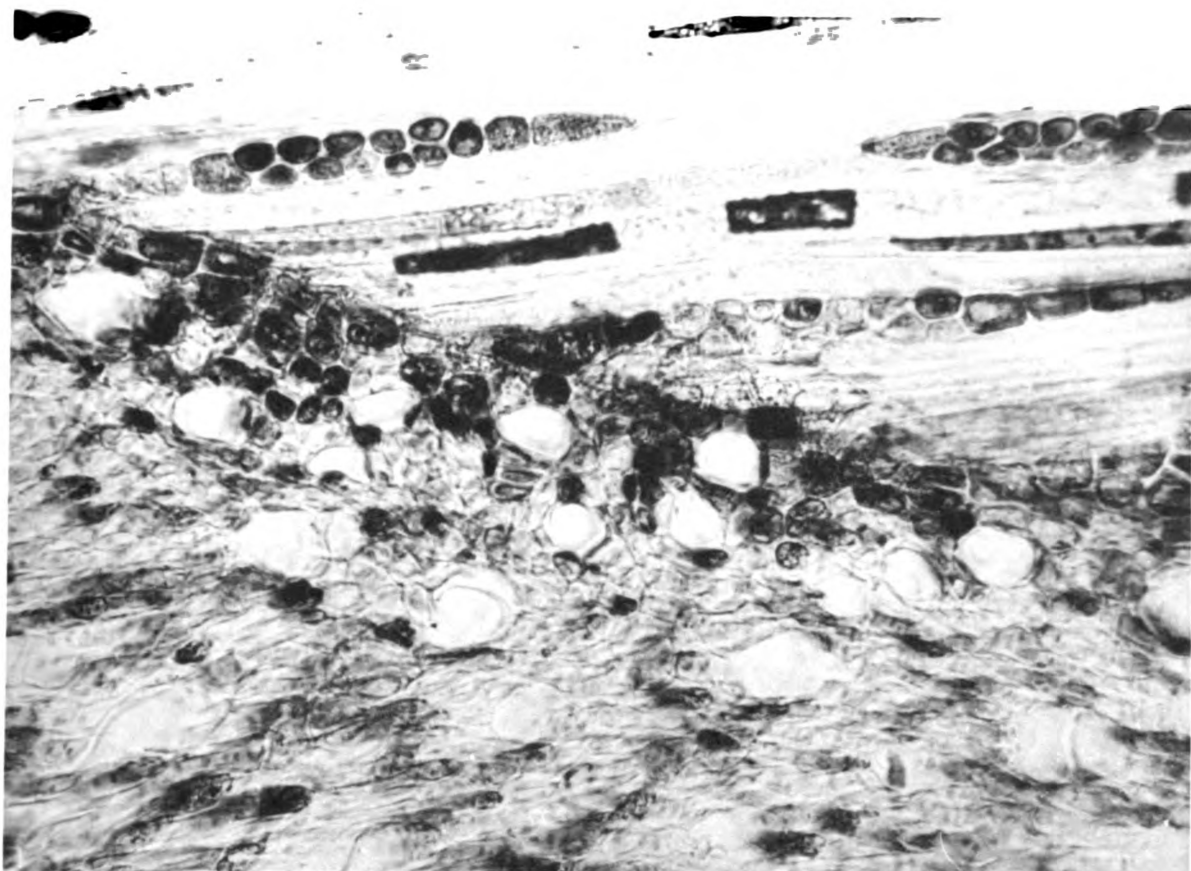
Grafts classified as "living but not growing" showed many characteristics of both living and non-living unions previously described, but, in general, seemed to lack the qualities necessary for sustaining growth.

Figure 10 illustrates a grossly mis-matched union where vascular elements were being differentiated in a "S" shaped pattern between the widely separated stock and scion. Observations of Rosa on Sorbus understocks revealed that the scion had been inserted too deeply into the stock causing the mis-matching previously noted in unsuccessful grafts of this combination. In "living but not growing" unions, however, occasional points of vascular uniting were observed.

Lack of scion activity was observed in "living but not growing" unions to a somewhat lesser degree than if they were not living. In a sample of Rosa on a Sorbus understock, which was living but not growing, dark non-functional cells similar to those found in non-living unions, appeared to be formed ahead of proliferating tissue, which had advanced into the cortical region of the quiescent scion. The advance of only partially differentiated parenchyma into scion tissue was evidenced by the distortion of cells in its path. It was further observed that connecting parenchyma developed between stock tissues on the un-matched side of the graft, had caused an "imbedding" of the scion in the stock at this point. Essentially all "bridging" tissue appeared to be produced by the scion.

Figure 8. Photomicrograph of a successful union of Sorbus on a Sorbus understock showing a highly magnified view of distorted vessels in cross-section (X 400).

Figure 9. Photomicrograph of a successful union of Sorbus on a Sorbus understock showing distorted vessels in cross-section and little evidence of isolated parenchyma masses along graft lines. "Bridging" becomes less evident in successively newer xylem (X 60).



Dead unions as well as ones which were alive, but not growing, were often found to contain large amounts of tissue between stock and scion which had not differentiated into vascular elements of time of collection. In certain unions with widely separated cambia the direction of differentiation of parenchyma cells was occasionally toward the center (Figure 5) or toward the periphery of the stem, rather than in a direct line between the cambia of each stem piece.

Grafts of Malus on Sorbus understocks appeared to have made equally as good vascular connection as those of Sorbus on its own understock. Little evidence of the graft incisions was visible in the cambial and bark regions and connecting vascular strands were more numerous than in combinations of Sorbus on Sorbus stocks. This appeared to be due to more complete differentiation of parenchyma tissue between stock and scion.



Figure 10. Photomicrograph of a "living but not growing" union of Chaenomeles on a Sorbus understock, illustrating a grossly mis-matched union, in which an "S" shaped coursing of partially differentiated parenchyma has formed between stock and scion (X 85).

## DISCUSSION

Of the grafts studied, certain combinations including Malus on Sorbus understocks, Chaenomeles on Sorbus understocks, and Malus on Chaenomeles understocks, were sufficiently successful to justify additional long-range compatibility tests. Analysis of variance indicated that differences in shoot elongation between graft combinations (treatments) was highly significant but that variations between replications was insignificant (Table II). Malus on Sorbus understocks was the best intergeneric graft studied, in terms of percent survival (Table I) and total growth (Table II). No graft failures occurred in this combination, and average total growth was nearly equal to that of Sorbus grafted on Sorbus understocks. A limited amount of "autumn coloration", which was considered by certain workers (Shaw and Southwick, 1944; Herrero, 1951) as a symptom of incompatibility, was observed. The high degree of success attained by this graft combination paralleled the results of Korshunov (1941), in which he reported success using Sorbus as an understock for the apple's close relative, Pyrus sp.

Grafts of Malus on Chaenomeles understocks resulted in few failures, but total average growth was considerably less than that of Malus on other stocks. With the exception of a few plants showing a moderate amount of leaf necrosis, resembling potassium deficiency, growth appeared normal. Since this malady was not observed in all plants of the combination, it may

have been the result of a mis-matched union, which subsequently contributed to a nutritional unbalance. Incompatibility symptoms, in the form of purple coloration of leaves, were intense in some plants of this combination than that observed in Malus on Sorbus understocks.

Since intergeneric combinations of Chaenomeles grafted on Sorbus resulted in 52 percent successful "growing" unions, and all but 5 percent of the remaining were classified as "dead", they should not be disregarded for further study. Its total average growth, however, was somewhat lower than that of other combinations.

With the exception of Pyracantha on Pyracantha, all plants grafted on their own stocks, as control plants, had successfully grown in excess of 75 percent of the species tested. Since these grafts were executed by severing and regrafting a portion of the understock into position, the error due to faulty technique was reduced to a minimum. The observation that Pyracantha, a broad-leaved evergreen, on its own understock had failed entirely was baffling, but may have been caused by disrupted water relations. Since scion drying and leaf drop did not occur until removal from storage, it is believed that the rapid increase in transpirational rate may have resulted in death of the graft. Failure may also have been caused because plants used for Pyracantha on Pyracantha graft wood were not in a quiescent condition at the time of grafting. Since results of anatomical

studies indicated that no cambial activity had occurred between stock and scion, the repeated failures may have been caused by a wound substance which inhibited callus formation.

The extreme dwarfing observed in one union of Malus on Sorbus was attributed to a distortion or a lack of vascular continuity at the graft union, a view which was somewhat supported by the observation that the extremely "stubby" growth did not occur below the graft union. It was possibly the result of blocked downward translocation of food material. Although Proebsting (1928) reported the swellings at graft unions due to obstruction of basipetally translocation of food materials, the swelling noted in this graft was unique, since it extended from graft union to the tip of the short scion shoot. The abnormally leathery leaves and mature appearance of the wood resembled a normal "hardened off" twig seen in the autumn.

Nearly the opposite of this autumnal effect was observed in a graft of Sorbus on its own understock, in which the scion growth was more vigorous and approximately double that of all other similar grafts. The possibility that this graft was more perfectly matched than others of this group may explain its added growth vigor. Sorbus appeared to have the inherent capacity to grow intermittently, rather than at a constant rate, and to form a soft terminal bud after each growth segment is terminated. The majority of the extreme growth observed in this Sorbus graft occurred following a "rest period" and reopening of this bud.

In many scions which eventually failed, it was often noted that buds grew approximately one centimeter before death of the scion occurred. In others, a second set of buds developed and grew approximately the same amount before complete death of the scion occurred. This growth was undoubtedly supported by stored food materials in the scion at time of grafting. Certain grafts, both living and dead, appeared due to accidental derangement of scions in handling and while under greenhouse observation. This physical weakness was believed due, in general, to the immaturity of grafts.

Successful graft unions were, in general, characterized by the following anatomical conditions: (a) cavities between stock and scion were partially or completely filled with light or darkly stained parenchyma; (b) newly formed vascular elements, differentiated from parenchyma of cambial origin, in the form of a smooth arc; (c) the presence of isolated patches of callus parenchyma surrounded by phellem tissue of periderm origin.

Contrary to the results of Sass (1932), gaps between stock and scions of certain successful unions were completely filled with callus tissues after four months of growth. In others, however, scattered areas along graft lines lacked callus formation.

In cross sections of successful unions vascular "bridging" appeared

as a smooth arc becoming less evident in successively newer xylem. In longitudinal sections, however, this "bridging" in the region of cambial contact, was separated, intermittently, by masses of undifferentiated parenchyma, which often appeared necrotic or tannin filled. In the new xylem beyond the original point of cambial contact, these parenchyma masses were not evident (Figure 9). A longitudinal section of Sorbus on Sorbus (Figures 7 and 9) showed that some vessels were distorted from the verticle so that they were observed in cross section. Distortion noted in Malus on Sorbus grafts may have been the result of differences in species growth rates, as proposed by Proebsting (1928). Harvey (1931) also reported an orientation toward, and connection with the scion of a one-year-old graft.

Isolated masses of disorganized cells were often observed in the cortical region along the graft line between stock and scion. Some of these masses were observed to be fibers, while others appeared as cortical tissue or non-functional, darkly stained parenchyma. These isolated tissues were surrounded by corky, suberized cells. These surrounding cells were believed to be phellem, since the number of rows of cells were equal to, and content and size seemed identical to the cork of the stock and scion species. The isolated patches of tissue were believed to have resulted from periderm formation around fibers or cortical tissue, which were torn free at

time of grafting, and later segregated during wound healing.

Graft failures appeared to be the result of imperfectly matched cambia, lack of pressure between graft components, lack of cambial activity of either, or both graft components, or differences in gross anatomy between understock species.

Imperfectly matched unions were apparently due to uneven graft incisions or faulty manipulation at the time of grafting. Bradford and Sitton (1929a) also believed that many graft failures were due to faulty grafting technique, rather than to incompatibility. In cross section of certain Chaenomeles on Sorbus grafts, the incision of the scion was convex causing a separation of cambia when placed in contact with the straight incision of the stock (Figure 5). In other grafts, the cambia were misaligned at time of grafting or disturbed in handling. In general, mismatched unions were observed to have produced large amounts of parenchyma which did not differentiate into new vascular elements. In one graft of Chaenomeles on Sorbus understocks, however, a long "S" shaped coursing of partially differentiated xylem was visible between the widely separated cambia (Figure 10). This indicated that it was possible for poorly matched unions to become, at least partially, established. Irregular oblique cuts of certain grafts appeared to have been the reason for

failure due to lack of cambial contact. The scions of Rosa on Sorbus grafts were too deeply inserted into the stock incisions and caused an overlapping at one side of the graft union. This resulted in poorly matched cambia on two sides of the graft. The deep insertion of the scion was undoubtedly due, in part to the excessively large volume of pith of Rosa (Figure 3), which did not lend enough physical strength to support the scion.

In several combinations, certain apparently well matched but unsuccessful grafts appeared to be loosely fitted together. Although this was probably largely the result of derangement during collection and processing of anatomical samples, it may also be due to a lack of pressure applied at the graft union. Since this lack of pressure could result in widely separated cambia, it may help to explain certain graft failures. Graft failures of unions in which the oblique graft incisions were irregular may have been prevented by added pressure applied with the grafting strips.

Lack of cambial activity appeared to be associated with many unsuccessful graft combinations. This inactivity was limited, in certain cases to the stock or to the scion, but in certain grafts of Pyracantha on Pyracantha understocks (Figures 4 and 7) and Rosa on Sorbus understocks the inactivity of the cambia was present in both graft partners. Somewhat

contrary to the results of Kostoff (1928), cambial activity of a graft of Chaenomeles on Sorbus, was limited almost entirely to the scion (Figure 5). Quiescence of scions was particularly evident in grafts involving Pyracantha as a scion. This may be the result of propagation wood which was still in a rest period or it may be due to desiccation after removal from storage. Scion inactivity was often accompanied by the presence of non-functional tissue between stock and scion in the cambial and cortical region. This necrotic tissue seemed to block vascular "bridging", produced by the active cambium. In cross sections of Rosa on Sorbus, in which the scion cambium appeared inactive, this tissue proceeded the advance of callus produced by the stock. The proliferated callus appeared to crush cortical tissue on its path and may be a partial cause of this necrotic tissue.

Differences in gross anatomy, which include wood to bark ratio, number of vessels per unit area, size of pith, and size of vessels, were observed between the five understock species. These differences are much the same as those observed by Beakbane (1941) between Malling stocks and various fruit tree scions. The wood-bark ratio is considerably larger in Sorbus and Chaenomeles than in the other species. Mis-matching of cambia would be predisposed by differences in wood-bark ratios between the two graft species. Number and cross-sectional area of vessels may

have an effect on conduction of food materials across the graft unions. This would be especially true if a species with large vessels or many vessels per unit area was grafted upon one which was possessed the opposite condition. Extremely large pith, such as found in Rosa may cause graft failures, since its lack of strength could allow shifting of in relation to the other graft partner.

Graft unions classified as "living but not growing" were noted to have made limited vascular connections, but also possessed many of the aberrations observed in unsuccessful graft combinations. In these grafts, acropetal translocation of solutes may be obstructed or limited sufficiently that sustained growth cannot occur and the grafted plant remains dormant or in a stunted condition.

In many partially, or totally unsuccessful unions, large amounts of undifferentiated parenchyma was present between stock and scion. This condition was described by Proebsting (1926, 1928) and Chang (1937) as a cause of graft failures. Herrero (1951) explained that this undifferentiated parenchyma formation was the result of cambial destruction or impairment. The results of these workers may help to explain graft failures in which this condition was observed.

Between widely separated cambia of certain grafts, vascular "bridging" tissue produced by the cambium was noted to have coursed

toward the center of the stem or toward the epidermis, rather than in a direct line between cambia of the graft components. This differentiating tissue may have at a later date, changed course to form a somewhat distorted vascular uniting of the cambia.

Grafts of Malus on Sorbus understocks appeared to have made as good, if not better, vascular connection than that of Sorbus on its own understock. More complete differentiation of intervening parenchyma seemed to result in a greater number of connecting vascular bridges between stock and scion.

## SUMMARY

Five generically different species of Rosaceae were intergrafted in a total of 15 combinations to determine initial graft success.

Of the combinations studied, Malus on Sorbus understocks was found to be the best, in terms of both anatomical and cultural characteristics. In addition, grafts of Malus on Chaenomeles and Chaenomeles on Sorbus appeared to be worthy of further, long range study. A complete lack of success, attributed to scion quiescence or desiccation of scions, occurred in all combinations involving Pyracantha. Cultural observations showed that the grafts could be separated into the following three distinct categories, as based on degree of success: "Growing", "Living but not Growing", and "Dead".

Visual abnormalities, such as "autumn coloration", nutrient deficiency symptoms, defoliation and re-establishment of leaves, and bud breaking followed by scion death, were observed in partial or completely unsuccessful grafts. Other aberrations, such as the formation of thick stubby scions and abnormally great shoot growth, were also noted in successful graft unions.

Anatomical studies revealed the following differences in gross anatomy between the understock species: variation in vessel cross-sectional area, differences in wood-bark ratios, differences in tangential

width of rays, and differences in number of vessels per unit area of stem tissue. The following conditions were noted in successful unions: new xylem, in the form of a smooth arc, between stock and scion (cross-sectional view), slightly distorted longitudinal coursing of new xylem relatively undisturbed by undifferentiated parenchyma, isolated patches of fiber or non-functional parenchyma, surrounded by phellem, in the cortical region, and graft lines often not evident toward the periphery of the graft.

Imperfectly matched cambia, lack of cambial activity of stock or scion, and possible lack of pressure applied to the graft union were believed to cause many failures. Poorly matched cambia often were due to curved or irregular graft incisions or too deeply inserted scions. In grafts of Pyracantha on its own understock, inactivity was observed in both stock and scion, while in others it was limited to either stock or scion.

Grafts classified as "living but not growing", appeared, in general, to have made sufficient vascular connection to remain alive, but not grow appreciably. Some apparently completed partial vascular continuity, even though badly mismatched. More dark, necrotic cells were evident between stock and scion than in grafts which were successful.

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